Predictors of white shark *Carcharodon carcharias* presence at two recreational beaches in a major metropole

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Declaration

I, Kristina Loosen, confirm hereby that the research and work presented in this dissertation is my own. Where knowledge and information has been derived from other people's work, I confirm that this has been cited and referenced in the thesis.

I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work.

Signed by candidate Signature Removed

Kristina Loosen

Acknowledgement

One does never really know where to start, when it comes to thanking people who helped you achieving your goals. I am grateful for everyone along the way.

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Last but not least I want to thank you, Milan. You believed in me from the beginning. When I was still doubting that I will be accepted to UCT and accepted as student by Alison, you were absolutely sure that it'll work out. You supported my plan even though that meant that we'll be 10 000km apart. You didn't hesitate and just followed me down south. I'm forever thankful for the time that we spent in our new home. You were by my side during the ups and downs. You always knew how to motivate me, cheer me up when I was feeling down or calm me down when I was stressing out (which is not an easy task). I love that you share my thirst for adventure and that you don’t think I’m entirely crazy for working with white sharks. Thank you for all that and I can’t wait for our next adventure to start.

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1. Abstract

The presence of white sharks *Carcharodon carcharias* in False Bay, South Africa follows a clear seasonal cycle. In the austral winter months, white sharks aggregate around Seal Island with female sharks in particular moving to the inshore areas in summer. What triggers these fine scale migrations at one of the largest white shark aggregation sites in the world remains a subject of debate. Previous research identified the environmental variables, water temperature and lunar phase, as significant influences on white shark presence inshore. In this study, I attempt to investigate the influence of prey fish availability on the presence of white sharks at two inshore areas of False Bay, namely Muizenberg and Fish Hoek. In addition, I explored the influence of sea surface temperature (SST), El Niño/Southern Oscillation (ENSO), dolphin presence, diatom patch presence and the occurrence of purse-seine fishing (treknetting) on shark presence. A total of 1209 shark sightings were recorded from 1 January 2006 – 31 December 2015 with 742 sightings at Muizenberg and 467 at Fish Hoek. I used randomization tests to determine whether the occurrence of shark sightings was randomly distributed across the environmental and biological variables and determined the dependencies between the predictor variables. I confirmed that shark sightings were clearly seasonal and sightings peaked between 17.49 - 18.57°C. Fish presence revealed a similar peak at 17.94°C. Randomization tests indicate that a spotter is 66% more likely to detect a shark when fish are present, which supports my prediction of a prey mediated cue. The occurrence of treknetting was also found to be non-randomly linked to white shark presence, increasing the probability to spot a shark to 38% instead of 20% at random. The presence of diatom patches was found to be negatively correlated with SST; with numbers increasing in colder waters. The presence of dolphins, as other predators in False Bay, didn’t show a significant pattern with any of the analysed variables. The influence of ENSO on the presence of white sharks was also hypothesized and the data revealed that there was a significant influence of weak negative ENSO values on their inshore occurrence. In addition to providing a better understanding of the ecology of white sharks in False Bay, my results can also be used in shark safety and education programs to reduce the risk of shark human conflict.

2. Introduction

An elusive male great white shark swimming calmly in clear, blue water (Morne Hardenberg)

2.1 Study species *Carcharodon carcharias*

2.1.1 Taxonomy, biology and life history

The white shark, *Carcharodon carcharias* (Linnaeus 1758), is a member of the Class *Chondrichthyes*, which incorporates 1200 species of sharks, skates, rays and chimeras (Fowler *et al.* 2005). White sharks belong to the Order Lamniformes, and the Family Lamnidae (Bruce 2008; Fergusson *et al.* 2009). Lamnid sharks are characterised by a large, spindle-shaped body, large teeth and crescent-shaped caudal fins with a strong caudal keel. They are also characterised by having a counter current heat exchange system (*retia mirabilia)* that allows them to maintain a body temperature up to 14.3 °C higher than ambient water (Goldman *et al.* 1999). This adaptation allows white sharks to actively hunt in cooler temperate waters where most other large predatory shark species are not foraging (e.g. tiger shark *Galeocerdo cuvier* and bull shark *Carcharhinus leucas*) (Best *et al.* 2013; Daly *et al.* 2014).

Over the last decade significant strides have been made in understanding the biology and ecology of white sharks. Male white sharks are thought to reach sexual maturity at a length of 360 - 380 cm and between 7 - 9 years of age. Females reach maturity at a length of 450 - 500 cm and at an age of 12 -17 years (Bruce 2008). There is currently a lack of consensus on white shark longevity, with estimates ranging from 22 years (Anderson *et al.* 2011) to 70 years (Hamady *et al.* 2014). White sharks are clearly long-lived which when combined with a slow specific growth rate, low fecundity and late maturity results in a low intrinsic potential for recovery from exploitation (Cortés 1999; Dudley *et al.* 2006; Bruce 2008).

2.1.2 White shark distribution, migration and site fidelity

White sharks have a circumpolar distribution and are typically found in temperate and subtropical regions with occasional observations in tropical waters (Fergusson *et al.* 2009). Early research on white sharks assumed that they primarily inhabit shelf regions (Compagno 2001), but more research by Boustany *et al.* (2002) revealed that they were also abundant in offshore pelagic waters. The broad movement patterns seem to be directed predominantly to pelagic and coastal aggregation areas (Jorgensen *et al.* 2009) in Australia (Pardini *et al.* 2001; Bruce *et al.* 2006), the north-eastern Pacific (Boustany *et al.* 2008; Domeier *et al.* 2008) and South Africa (Bonfil *et al.* 2005).

The white shark's coastal and island aggregation sites are often linked to the presence of pinniped colonies (Goldman *et al.* 1999; Domeier *et al.* 2007), a preferred prey species (Pyle *et al.* 1996). The timing of arrival at these aggregation sites corresponds to the peak of pinniped abundance and juveniles in particular (Klimley *et al.* 1996; Pyle *et al.* 1996). Johnson *et al.* (2009) documented residency for white sharks at inshore beaches of Mossel Bay, South Africa, which they ascribed to socializing and resting behaviour. Inshore residency of female white sharks has also been shown in False Bay (Kock *et al.* 2013), but the driver(s) of this behaviour remains uncertain. The movements and behaviour of white sharks seem to differ between regions and habitats which emphasizes the need for site-specific studies (Domeier *et al.* 2008).

2.1.3 Composition of diet and ontogenetic shift

Over 500 shark species are classified as top predators in marine food webs (Cortés 1999; Hussey *et al.* 2012). As such they exert an important top-down effect on the composition and functioning of marine ecosystems (Stevens *et al.* 2000; Heithaus *et al.* 2008). Sharks exhibit considerable dietary diversity in both prey composition and feeding behaviour. Some of the largest species such as the basking shark (*Cetorhinus maximus*) feed on zooplankton while several other species are entirely piscivorous, such as the striped smooth-hound shark (*Mustelus fasciatus*) (Cortés 1999). White sharks are the largest of the predatory sharks (over 6.1m, (Castro 2012)) and eat mainly teleosts, chondrichthyans and mammals (Cortés 1999; Heithaus 2001b; Hussey *et al.* 2012) with cephalopods, molluscs, crustaceans, birds and marine reptiles being consumed less frequently (Cortés 1999) (Table 2.1). There is evidence of an ontogenetic shift in the diet, with juvenile white sharks (Tricas 1985; Heithaus 2001b; Estrada *et al.* 2006) being predominantly piscivorous (Estrada *et al.* 2006; Bruce 2008) while sub-adults and adults supplement their diet with marine mammals, especially pinnipeds (Long *et al.* 1996; Cortés 1999). Both stomach content and stable isotope analyses suggest a dietary shift when sharks reach a total length of 341 cm (Klimley 1985; Estrada *et al.* 2006; Kim *et al.* 2012) corresponding with the change in the teeth composition of the shark species, known as ontogenetic heterodonty (Estrada *et al.* 2006).

Bruce *et al.* (2006) noted that stomach content samples of large white sharks (>5 m TL) off the Australian coast were found to just contain finfish and chondrichthyans. Differences between individuals may reflect both individual dietary preferences and the availability of prey species at differing locations and seasons (Kim *et al.* 2012). Seasonality of prey is hypothesized to be a major factor influencing white shark distribution (Cliff *et al.* 1989; Heithaus 2001b; Domeier 2009). At the Farallon Islands, California, the occurrence of white sharks is more closely linked to the availability of prey (pinnipeds) than to sea surface temperature (Ainley *et al.* 1985). Similarly, the peak of white shark numbers coincided with the annual peak of harbour seals on the west coast of North America (Long *et al.* 1996). Together these results suggest that white sharks are opportunistic generalist feeders whose diet broadens with age and the morphological attributes needed to catch more mobile and elusive prey, such as seals.

Table 2.1: White shark (in precaudal length (PCL)) diet composition in percentages from three different studies using stomach content analysis. FISH (teleosts), CEPH (cephalopods), MOL (molluscs, excluding CEPH), CR (crustaceans), INV (invertebrates, excluding CEPH, MOL and CR), ZOO (zooplankton), BIR (birds), REP (reptiles), MAM (mammals) and CHON (chondrichthyan).

	Cortes	**Hussey**				**Heithaus**	
Years of study	Review	1978-2009				1983-1988	1989-1993
No of stomachs	259	225				58	33
Maturity	combination	juvenile	juvenile	juvenile	adult	juvenile	mostly juvenile
Data type	combination	% mass	% mass	% mass	% mass	% mass	% mass
Length (PCL in cm)		<185	185-234.9	235-284.9	≥285		
FISH	35.5	21.25	29	25.98	5.55	12.8	39
CEPH	3.6	0.43	0.15	<0.01	0.08	0.2	0.1
MOL	0.4	0.02	<0.01	0	0		
CR	1.8					0	0
INV	0.4						
ZOO	0						
BIR	1.1						
REP	0.4						
MAM	21.1	6.49	24.54	29.14	70.19	40.8	23.4
CHON	35.7	71.81	46.31	44.88	24.18	31.2	25.2

2.1.4 White shark population and conservation status

The highly migratory and elusive nature of white sharks complicates the estimation of the global population number. Even regional abundances from aggregation sites are debatable because of the difficulties associated with observing and identifying individuals (Chapple *et al.* 2011). Despite these limitations, abundance estimates are available from some of the major white shark aggregation sites, with estimates of 142 individuals at Guadalupe Island, Mexico (Domeier *et al.* 2007), 191.7 individuals at Neptune Islands, Australia (Strong *et al.* 1992) and 1279 individuals off the south and east coast of South Africa (Cliff *et al.* 1996). The regional South African abundance estimates include Seal Island, False Bay with 723 sharks (Hewitt 2014) and Gansbaai with 908 estimated individuals (Towner *et al.* 2013b). A recent study suggested that there were only ~500 white sharks in South Africa (Andreotti *et al.* 2016), however the methods and conclusions of the study are contested by Irion *et al.* (in press). They argue that the mark-recapture data just originates from a single aggregation site, which flaws the conclusions based on the model assumptions.

How these local populations are linked globally is still poorly understood (Bruce 2008). Two genetically distinct clades have been identified by analysing the mitochondrial DNA (Jorgensen *et al.* 2009). These data suggest distinct South African (SA) and Australian-New Zealand (ANZ) populations (Jorgensen *et al.* 2009). These populations are not discrete, with mixing confirmed by satellite tagged individuals (Bonfil *et al.* 2005; Jorgensen *et al.* 2009). It has been hypothesised by Bonfil *et al.* (2005) that the SA and ANZ populations exchange mates within one generation, with individuals travelling between these areas.

It is clear that further work is needed to provide better estimates of local and global populations and to use these estimates and long-term trends to inform conservation activities and fisheries management to prevent their demise. South Africa was the first country to implement protection laws for white sharks in April 1991 (Compagno 1991). These laws prohibit the selling of any white shark products and their intentional catching or killing. Since 1996 white sharks have been categorized as Vulnerable (A2cd+3cd) on the International Union for the Conservation of Nature (IUCN) Red List (Fergusson *et al.* 2009). The white shark has also been included in Appendix II of the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES) since 2004 (Fergusson *et al.* 2009) , which necessitates all countries to monitor and govern the trade of white sharks and their body parts, to ensure the population is not negatively influenced (Bruce 2008). However illegal trade of white shark fins and exploitation due to bycatch persists and threatens the population of these apex predators (Dulvy *et al.* 2004; Shivji *et al.* 2005). The intrinsic population growth rate of the species is slow to begin with (4.0 - 11.9%) and there has been no evidence of a recovery of the South African white shark population since the implementation of the protective legislation in 1991 (Dudley *et al.* 2006). The biology of the white shark makes it vulnerable to lethal control methods and consequently there is a limited intrinsic capacity to respond to rapid population declines (Bruce 2008).

2.2 Ecological role and importance of sharks

Both the abundance and health of marine apex predators, such as white sharks, have been hypothesized to act as indicators of the general health and productivity of the ecosystems they inhabit (Sekiguchi *et al.* 1992; Cortés 1999). Despite their ecological importance there is still a lack of foundational knowledge on the behaviour and ecology of most shark species, including research on habitat use, movement patterns and trophic interactions. Such data are essential to realising a better understanding of poorly studied marine ecosystem networks and represents an essential first step in improving the management of conflict between humans and sharks and ultimately the conservation of increasingly threatened marine apex predators (Caro *et al.* 2011).

Apex predators have been shown to have an effect on biodiversity and stability at lower levels of the food web, in terrestrial and marine systems (Sergio *et al.* 2008). With reduced or enhanced predatory behaviour, tertiary consumers can alter prey dynamics, density and resource use (Ruppert *et al.* 2013). With a trophic level of 4.5 the white shark has the second highest trophic position amongst sharks, coming second only to the broadnose sevengill shark (*Notorynchus cepedianus*) (Cortés 1999). The removal or reduction of marine apex predators, such as white sharks, is thus predicted to result in ecosystem degradation and a change of abundance in prey species (Heithaus *et al.* 2008; Ruppert *et al.* 2013). A study by Ruppert *et al.* (2013) found empirical evidence for a 'top-down' relationship between the reduction in coral shark abundance and the release of mesopredators, which concludes in an altered trophic ecosystem with negative impact on coral reefs.

Predatory pressure does not have to be sustained at high rates in order for large predators to influence the behaviour of lower trophic level species (Lima 1998), for example through changes in group composition, group size and habitat use (Heithaus 2001b). The mere presence of a predator can lead to measurable differences in behaviour, abundance and movements of prey species (Heithaus 2001b). With the global decline in apex predators (Ripple *et al.* 2014) and the subsequent reduction in predatory pressure on lower trophic levels, marine ecosystems are being altered rapidly and in unpredictable ways (Heithaus *et al.* 2008). It is thus important for research to focus on understanding the ecological connectivity between marine apex predators, such as the white shark, and their prey and how this manifests in movement patterns and habitat use and ultimately brings top predators into close proximity with humans at inshore beaches.

2.3 False Bay as an aggregation site

False Bay is a well-established aggregation site for white sharks throughout the year (Kock *et al.* 2013). White sharks aggregate around Seal Island, which has a resident population of approximately 70 000 Cape fur seals (*Arctocephalus pusillus pusillus*) (De Vos *et al.* 2015) during austral winter. Research at Seal Island suggests that it is the inexperienced young-of-the-year seals that are the primary prey of white sharks (Martin *et al.* 2005; Laroche *et al.* 2008; Kock *et al.* 2013; De Vos *et al.* 2015). Young seals are fat from nursing and naïve to the unique shark foraging tactics (breach attacks from the depths) and consequently offer a high density, spatially predictable and catchable prey item which explains the aggregation of white sharks (Martin *et al.* 2005; Kock *et al.* 2013). Importantly as these pups learn the risks around the island so their behaviour conforms to the adults and they avoid commuting to and from the island in the early mornings when environmental conditions are optimal for ambush attacks by white sharks from the depths (Hammerschlag *et al.* 2006; De Vos *et al.* 2015).

Conversely, during the austral summer, when the Cape fur seals give birth the naïve seal pups are unavailable to the sharks in their first few months as they don't leave the rookery during this time, unless they wash off and drown (De Vos *et al.* 2015). It was shown by Kock *et al.*

(2013), that during this time few white shark are present at the seal colony. Instead, sharks (predominantly females) are found closer to shore and in particular in the northern areas of False Bay (Kock 2014). Furthermore, white shark presence at two popular recreational beaches in False Bay was shown to peak during summer periods with warmer water and during dark moon phases (i.e. new moon) (Weltz *et al.* 2013). Weltz *et al.* (2013) went on to suggest that shark presence may be positively related to an increase in prey fish availability, which in turn might be influenced by warmer water temperatures and lunar phase. As there are many other environmental and biological variables influencing the marine animals in False Bay further analysis of the linkages between shark presence and these variables is important to understand the drivers of shark presence.

2.4 What could influence the inshore presence of white sharks in False Bay?

2.4.1 Influence of environmental variables on the presence of white sharks

The characteristics of a specific marine environment such as sea surface temperature (SST), lunar cycle, wind or cloud cover have all been shown to have measurable effects on ecosystem processes (Pörtner *et al.* 2014). Changes in physiology, phenology (Largier *et al.* 2009), behaviour and population dynamics have all been shown in response to changes in various abiotic variables. These changes in turn can lead to alterations in the spatial distribution and seasonal abundance of entire populations (Doney *et al.* 2012).

Understanding how abiotic variables influence all ecosystem processes is seldom possible (Doney *et al.* 2012) and consequently researchers often focus their attention on key species, such as apex predators which serve as sentinels for ecosystem health and functioning. Site specific behaviour and distribution of white sharks has been associated with select environmental variables including water temperature and clarity, water current patterns and lunar phase (Bass *et al.* 1975; Strong *et al.* 1992; Jorgensen *et al.* 2009; Weltz *et al.* 2013). Application of these data to mitigating adverse shark-human interactions was first proposed by Pyle *et al.* (1996) and supported by Weltz *et al*. (2013) who stated that a detailed understanding of the influence that physical oceanography parameters have on white shark presence and their movements, in coastal areas could reduce shark human encounters.

2.4.2 Sea surface temperature (SST)

SST is one of the most important variables affecting global climatology (Kaplan *et al.* 1998). From polar regions to the low latitudes of the tropics the surface temperature fluctuates by more than 30°C. In the temperate regions with marked seasonality the annual temperature fluctuation can also vary over 10°C (Reynolds *et al.* 1994). Interannual temperature phenomena such as ENSO complicate and intensify the influence of temperature on the global and local climate (Tourre *et al.* 1995). The climate and temperature distribution of False Bay, South Africa is globally unique (Dufois *et al.* 2012). It is influenced by the cold eastern boundary current, the Benguela, as well as the warm western boundary current, the Agulhas. The Benguela on the west coast of the Cape Peninsula can be seen clearly in Figure 2.1, and is characterised by cold, nutrient rich upwelling water which supports high fish biomass (Shannon 1985).

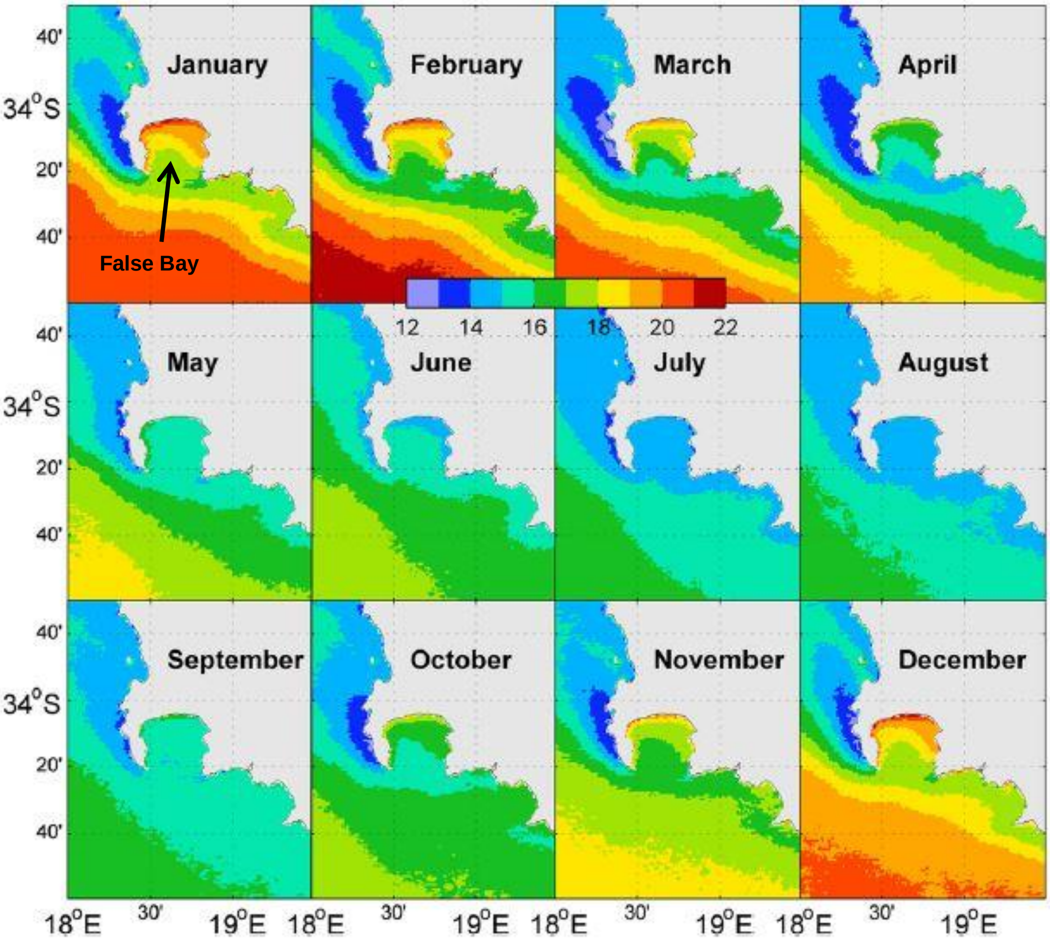


Figure 2.1: Monthly sea surface temperature distribution in the Southern Benguela around the southwestern tip of South Africa and including False Bay (Dufois *et al*. 2012).

In the summer months with a prevailing south-easterly wind, warmer water from the Agulhas bank are pushed into the bay and causes a rise in SST (Atkins 1970; Shannon 1985;

Armstrong *et al.* 1987). The northern half of the bay experiences temperatures of 14 - 22°C during the year, with the north-western shore having the highest mean temperature throughout the bay with 16.9°C and Cape Point, the coldest mean of 16.1°C. During the winter months the sea surface temperature over the bay is more homogenous, with mean temperatures ranging from 14.6 – 15.0°C. The marked seasonal variation in the northern part of False Bay has led to the suggestion that temperature is best described by seasonality, whereas the rest of the bay seems to be controlled by inter-annual sources of variability such as the El Niño/ Southern oscillation (ENSO) (Dufois *et al.* 2012).

SST not only exerts a major influence of global climate, but is also one of the major environmental influences on marine ecosystems (Hoegh-Guldberg *et al.* 2010). An increase in temperature stimulates primary production of the world's oceans with an estimated 10% increase in the photosynthetic rate of phytoplankton for every one degree Celsius increase in water temperature (between the range of 4 - 20°C) (Colijn *et al.* 1975). Zooplankton also responds positively to increased water temperature with 90% of the variance in the growth rate of 33 copepod species being best explained by temperature differences (Huntley *et al.* 1992). Higher trophic levels are also positively affected by increasing water temperature with the growth rate in early life stages of fish increasing with temperature while mortality decreases (Pepin 1991). Given the well-established effect of increased water temperature (within an acceptable temperature range) it is understandable that both fish abundance and diversity has been hypothesized to be stimulated by a higher water temperature in False Bay (Clark *et al.* 1996b).

Furthermore, both the distribution and movements of marine animals have been linked to changes in SST (Humston *et al.* 2000; Malcolm *et al.* 2001; Weltz *et al.* 2013). Schools of large pelagic fish, such as swordfish *Xiphias gladius* (Podestá *et al.* 1993), bluefin tuna *Thunnus thynnus* (Roffer 1987) and albacore *Thunnus alalunga* (Laurs *et al.* 1984; Kimura *et al.* 1997) were found to accumulate in areas characterised by ocean fronts with strong SST gradients (Humston *et al.* 2000). Rather than suggesting that predators have a preference for these temperature regimes it has been suggested that these are clear thermal indicators for the occurrence of prey and subsequently for the occurrence of predators (Humston *et al.* 2000).

Lamnid sharks are endothermic (Carey *et al.* 1982) and can keep their body temperature relatively stable and independent from the ambient water temperature (Goldman *et al.* 1996). This trait has been used to suggest that white shark movements are not strongly dependent on water temperature. In support of this white sharks have been recorded in both the cold waters (0.5°C) off Alaska (Martin 2004) and warm waters (26°C) off South Africa (Cliff *et al.* 1989). Despite their broad thermal tolerance Cliff *et al.* (1989) suggested that white sharks prefer temperate waters with 63% of the catches in the nets off the KwaZulu-Natal coast being recorded in water 19 - 22°C. However, recent evidence suggests that smaller white sharks may not be as temperature tolerant as larger white sharks (Bernvi 2016). Many other studies have found an influence of SST on sharks in general (Malcolm *et al.* 2001; Hopkins *et al.* 2003; Dewar *et al.* 2004) and white sharks in particular (Pyle *et al.* 1996). In False Bay, the presence of white sharks along the inshore was significantly influenced by SST (Weltz *et al.* 2013). However, while a direct relationship between white shark presence and water temperature was not rejected outright (especially as the average white shark size is 3.5 m in False Bay, Hewitt 2014), it was suggested that the increase in shark sightings is more likely as a consequence of how water temperature influences the movements of their prey rather than the white sharks directly. As with the aggregation of Atlantic tuna along ocean fronts (Humston *et al.* 2000), the SST could be used as a proxy for prey availability which in turn could lead to a rise in white shark presence.

2.4.3 El Niño/Southern Oscillation

ENSO is one of the most important phenomena generating global climate variability (Collins *et al.* 2010; Wolter *et al.* 2011). In warm events, or El Niño years, the atmospheric pressure rises in the western part of the Pacific and decreases in the eastern part, along the west coast of South America (Enfield *et al.* 1980). This pressure change is associated with a change in south east trade winds which either lose strength or reverse direction. This in turn leads to a suppression of the thermocline, which allows warmer water from the east coast of Australia to surge eastwards along the equator and results in a reduction in the sea level in the western Pacific (Enfield *et al.* 1980). This in turn is linked to a reduced primary productivity (Miller *et al.* 1992). The reverse happens in cold events, the so called La Niña years (Enfield *et al.* 1980).

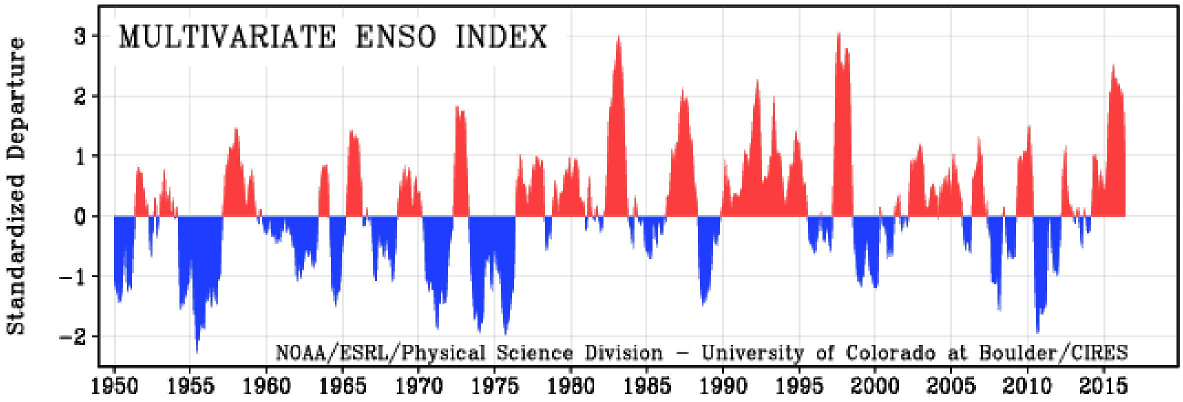


Figure 2.2: Multivariate El Niño/ Southern Oscillation index time series since 1950 - 2016. Blue phases indicate the negative cold MEI events (La Niña) and red the positive warm MEI values (El Niño) (Wolter, 2016).

The multivariate ENSO index (MEI; Figure 2.2), which quantifies the strength of the Southern Oscillation, is the first seasonally varying index to describe the multivariate nature of the phenomenon and includes six atmosphere-ocean variable fields in the tropical Pacific basin (Mazzarella *et al.* 2010; Wolter *et al.* 2011). The MEI includes data on sea level pressure, zonal and meridional surface wind components, SST, near-surface air temperature and total cloudiness (Mazzarella *et al.* 2010; Wolter *et al.* 2011). The lowest or negative MEI values indicate a La Niña event or the cold ENSO phase. Whereas the warm ENSO phase or El Niño is indicated by the highest positive MEI values (Wolter *et al.* 2011).

It has been hypothesised that the ENSO in the tropical Pacific impacts the climate of Southern Africa including the seasonal rainfall along the north-eastern coast (Reason *et al.* 2002; Fauchereau *et al.* 2003; Rouault *et al.* 2010; Philippon *et al.* 2012). Since March - April 2015, southern Africa has been experiencing the most severe El Niño event in the last 50 years, with a peak of + 2.53 on the MEI index in August - September 2015 (Wolter 2016). Besides the climate, ENSO has been shown to influence the distribution and abundance of animals within marine ecosystems (Long *et al.* 1996; Neumann 2001; Hoegh-Guldberg *et al.* 2010). Unusual offshore movement of short-beaked common dolphins (*Delphinus delphis*) off the coast of New Zealand was recorded during a La Niña event, which local fishermen attributed to offshore drift of their prey (Neumann 2001). Seal abundance off the Californian coast was found to increase during moderate to strong ENSO events (Long *et al.* 1996). The influence of ENSO on fish was found to be variable (Miller *et al.* 1992; Roessig *et al.* 2004). Jordan (1991) found a relationship between ENSO and the temporary displacement of fish populations. A shift in salmon populations off the US west coast, caused by the 1983 - 1984 ENSO event, led to a poor harvest on the west coast and an increase on the Alaskan coast (Miller *et al.* 1992). Traditional migration pathways of large pelagic fish can be altered by ENSO and thereby cause effects on higher trophic levels (Roessig *et al.* 2004).

Robbins *et al.* (2012) suggested that the white shark distribution at the Neptune Islands, Australia may be influenced by water temperature and ENSO. White sharks in South Africa have been found to respond to large scale meteorological processes such as the ENSO (Towner *et al.* 2013a). Cliff *et al.* (1996) reported cyclical peaks in catch rates of white sharks along the KZN coast every 4–6 y between 1966 and 1993 and suggested that the cyclical peaks might reflect shifts in large-scale meteorological phenomenon that influence shark distribution. Furthermore, evidence of an influence is provided by Towner *et al.* (2013a) that showed that in the summer of 2010/2011, when the water was found to be colder than average (La Niña) more male sharks were found in the waters off Gansbaai. By comparison in warmer years (El Niño) with positive MEI values more female sharks were detected along the coast of Gansbaai. These results support the findings of Kock *et al.* (2013) who observed that female white sharks in False Bay moved to the warmer inshore waters during the spring and summer months while males left the bay.

2.4.4 Seasonality of prey availability in False Bay

The strong seasonality of fish abundance in False Bay is mirrored by most near-shore ichthyofaunal studies across the globe (Lamberth *et al.* 1995) and is largely attributed to the increased occurrence of diatom patches in summer (Clark *et al.* 1996a). Clark *et al.* (1996a) found a difference in prey fish numbers across various areas in False Bay with a strong positive relationship between turbidity and high fish abundance. For example, Muizenberg beach with an intermediate water turbidity had both high abundance and also high diversity in prey species (Clark *et al.* 1996a). During the summer months Muizenberg experiences the highest number of white shark sightings along the False Bay coastline which has been hypothesised to be related to the increased presence of prey (Kock *et al.* 2013; Weltz *et al.* 2013; De Vos *et al.* 2015).

By austral spring the young of the year seals have lost their fat and are wiser to the predatory behaviour of white sharks at Seal Island (De Vos *et al.* 2015) which reduces the catch per unit effort for predators such as the white shark. Spring thus corresponds with a decrease in the number of white sharks at the island and an increase along inshore areas of False Bay (Kock *et al.* 2013). Importantly 93% of the total catch of fish along the inshore region of False Bay is taken in over spring, summer and autumn months (Lamberth *et al.* 1995) suggesting that white shark presence along the inshore may reflect a shift in their diet from seals to fish. 86% of over 311 beach-seine hauls is comprised of a harder species (*Liza richardsonii*). Large predatory fish, such as yellowtail *Seriola lalandi* and small predatory fish such as horse mackerel (*Trachurus capensis)*, which are commonly included in white shark diet, contributed only 1.1% and 1.9% to the catches (Lamberth *et al.* 1994).

2.4.5 Interactions between dolphins and sharks

Various large shark species, such as, tiger sharks (*Galeocerdo cuvier)*, oceanic whitetip sharks (*Carcharhinus longimanus)* and dusky sharks (*Carcharhinus obscurus)*, have been recorded to prey on odontocetes (Heithaus 2001b; Heithaus *et al.* 2002). A study done by Heithaus *et al.* (2002) found that the predation risk from tiger sharks influenced the spatial and temporal habitat use of bottlenose dolphins. During warm months, the dolphins avoid the shallow waters where prey fish are more abundant presumably because the risk of predation by abundant tiger sharks exceeds the benefits of foraging in this area. There is thus a clear trade-off between food availability and the predation risk for the dolphins, the final result of which is a shift in the latter's spatial distribution (Heithaus *et al.* 2002). White sharks also predate on several dolphin species and in some areas they form the bulk of their diet (Cliff *et al.* 1989) with a study in South Australia reporting dolphin remains in 44% of white shark stomachs (Bruce 1992).

White sharks in False Bay are predicted to pose a predation risk to odontocetes and this might result in limited spatial overlap. However, dolphins and white sharks in False Bay have been observed in close proximity, occurring in the same area in False Bay on the same day (Shark Spotters 2016). Furthermore white sharks and dolphins have a high degree of dietary overlap (teleost fish and cephalopods) and this is predicted to lead to high spatial overlap (Leatherwood 1977). Thus, one of the objectives of this study was to record the temporal and spatial overlap between white sharks and dolphins along the inshore areas to determine whether common prey drives spatial overlap despite the risk of predation to dolphins.

2.5 Local shark safety program 'Shark Spotters'

In over 115 years a total of 35 fatal white shark attacks have been recorded across the globe (ISAF International Shark Attack File 2012). Although the number mirrors a relatively low risk to humans, it led to the implementation of several lethal methods throughout the years to reduce the risk of a shark attack. The South African 'Natal Sharks Board' was established in 1952 to increase bathers' safety by setting protective gill nets and drumlines to catch and kill sharks at South African beaches. It was a standard measure to kill living sharks found tangled in the nets until 1989. With the prohibition of 1991 the 'Natal Sharks Board' was asked to reduce the environmental impact of the gill nets on and accordingly shark mortality was reduced by 64% (Cliff *et al.* 2011). After seven fatal attacks from 2010 to 2013 in Australian waters the Australian government implemented, in oppose to the protection law signed by Australia, the culling of big sharks by baited drum lines. The plans to set the lines were abandoned in September 2014 after many parties, organisations and common people protested against these actions. However, drum lines can still be deployed after fatal shark human encounters occur (Sprivulis 2014). After a series of fatal bites in 2016/2017, the Australian government reconsidered using drumlines or other lethal methods to ensure bather safety along their beaches (Hennessy 2017).

In contrast to these measures stands the South African non-governmental organisation 'Shark Spotters'. The organisation was introduced to the beaches of False Bay in 2004 and adopted by the City of Cape Town in 2006 (Kock *et al.* 2012; Weltz *et al.* 2013). 'Shark Spotters' implemented an innovative shark awareness and safety system to reduce harmful shark-human encounters. With the highest number of near-shore shark sightings (also highest recording effort) in the world and a high number of recreational water users, Cape Town has been in the international spotlight as the leader in the non-lethal mitigation of shark-human interactions (Kock *et al.* 2012).

Trained Shark Spotters are tasked with detecting sharks along the inshore of popular beaches by observing with binoculars from elevated spots. With two-way communication between spotters and people operating a flag system and siren on the beach, both beach and water users are informed about the current spotting conditions and whether a shark has been sighted. The green flag is flown when the spotting conditions are good and no sharks are visible. The black flag, which is the most commonly flown, is raised when the spotting conditions are poor, because of turbid water, glare, cloudy conditions or any other environmental condition that limits the ability of the spotters to detect a shark on the inshore. The red flag is flown to warn of the high potential of sharks, such as when smaller fish species that sharks prey on are moving near the beach. The white flag is flown when a shark has been spotted moving in the direction of the inshore and is accompanied by a siren and active attempts to signal to everyone to get out of the water (Kock *et al.* 2012; Engelbrecht 2013). The response of bathers to the siren is encouraging, whereas there seems to no significant reaction of water users to the specific flags being flown (Engelbrecht 2013). However, since the implementation of the program there have been just three shark attacks at False Bay beaches monitored by Shark Spotters; only one of which was fatal. Two of the incidents occurred when the black flag was flying and the other while the white flag was up, where the person chose to ignore the warning (Kock 2016).

The program is broadly hailed as a success and generates useful consistent data on the temporally and spatial presence of white sharks. Additionally, sightings of dolphins and whales, smaller fish and fishing activity at popular beaches in False Bay are recorded, which provides crucial information to researchers that study the False Bay ecosystem. The non-lethal nature of the program is unique and promotes shark conservation in concordance with bather safety. The spatial overlap of recreational water users with the white sharks in the inshore beaches of Cape Town would, in other areas, have led to lethal shark mitigation measures. The Shark Spotters program prohibited such measures and promotes a non-harmful way of coexistence between sharks and humans on the west coast of South Africa.

2.6 Objectives

This study seeks to extend the work by Weltz *et al.* (2013) who revealed that white shark presence (2006 - 2011) at two False Bay beaches, namely, Fish Hoek and Muizenberg beaches were influenced by the abiotic variables of SST and lunar phase. Weltz *et al.* (2013) argued that, while the lower light levels at new moon could improve the foraging success of white sharks at night (the effects of which persisted in daylight hours), the warmer SST may in fact be a driver for increased prey abundance, which in turn could attract white sharks to the inshore. As a result, it was recommended that the Shark Spotters collect additional information on fish presence (shoaling fish), as well as the presence of other predators (e.g. dolphins), the presence of diatom patches and shore based purse-seine fishing activity (treknetting) events, as indirect indicators for prey availability.

The specific aims of this study were to:

(1) test these alternative variables as potential predictors for daily occurrence of white sharks along bathing beaches.
(2) further explore the effect of SST as an environmental predictor using an expanded dataset (2006 - 2015).
(3) investigate if white shark sightings are related to ENSO at a broader temporal scale, given its effect on both SST and the distribution of a variety of marine organisms.

To do this, a non-parametric hierarchical permutation (randomization) test was developed, which is designed to account for the nested data structure of days within month, year and beach. Ultimately the results from this dissertation will be used to improve our understanding of the biological and abiotic variables that influence fine-scale temporal patterns of white shark presence along coastal regions. These data can then be used to better manage the risk to recreational users of an encounter with a threatened marine apex predator.

3. Material & Methods

A shark has been sighted by a Shark Spotter at the shores of Muizenberg in False Bay (Rowlands 2013)

3.1 Study sites

The study included two beaches, Muizenberg and Fish Hook, located along the north-western shore of False Bay (Figure 3.1). False Bay is situated on the south-west coast of South Africa (34°04` - 34°23`S, 18°26` - 18°51`E) with Cape Point forming its western edge. With a total area of 1082 km^2 it is Southern Africa's biggest natural bay (Dufois *et al.* 2012). The bay is situated between the cold Benguela Current to the west and the warm Agulhas current to the south and east of the bay (Shannon 1985; Dufois *et al.* 2012). In contrast to the rest of Southern Africa the Cape Peninsula and False Bay experience a Mediterranean climate, with warm, dry and windy summer months and cold, wet winter months (Clark *et al.* 1996b; Philippon *et al.* 2012).

Figure 3.1: (A) South Africa with the location of Cape Town in the Western Cape (Cheal), (B) Location of Muizenberg and Fish Hoek in relation to False Bay (AfriGIS (Pty) Ltd 2017a), (C) Fish Hoek and the position of the Shark Spotter on the mountain and (AfriGIS (Pty) Ltd 2017b) (D) Muizenberg with the relative position of the Shark Spotter (AfriGIS (Pty) Ltd 2017c).

False Bay is characterised by two rocky headlands on the eastern and western arms of the bay (Hangklip and Cape Point, respectively). The northern portion of the bay is characterised by extensive dissipative beaches with the two study site beaches at Muizenberg and Fish Hoek on the western shores being heavily used for a variety of recreational activities (e.g. surfing and swimming). Both beaches are monitored during daylight for 365 days a year by Shark Spotters (Kock *et al.* 2012; Engelbrecht 2013).

3.1.1 Muizenberg

Muizenberg (34°06.3′S, 18°28.3′E) is a predominantly residential suburb of the City of Cape Town on the seaward side of the Cape flats. The gently sloping Muizenberg beach stretches over 2 km in a west-east direction along the northern coast of False Bay (Clark *et al.* 1996a). It is very popular with diverse water users and is said to be the site where surfing originated in South Africa. The surfers exploit the large surf zone (~300 m wide) of the sandy-bottomed beach (Clark *et al.* 1996a; Weltz 2012). Accumulations of surf plankton (diatom) are frequently observed within the surf zone. Bordering the shore of Muizenberg is the Zandvlei estuary, a nature reserve, which acts as nursery area for a variety of fish species. The estuary is manually opened and closed to the ocean at Muizenberg beach in attempt to mimic natural cycles that have been interrupted by hard development at the mouth of the estuary (Clark *et al.* 1994).

The Muizenberg Mountain is on the western side of the town and the foothills are used as a vantage point for the local Shark Spotters (Figure 3.1). The Shark Spotter site is 98 m above sea level and allows the spotter to examine the beach as well as a broad area of the northern part of the bay. Since 2006 - 2011, there have been a total of 336 shark sightings by spotters (Weltz 2012).

3.1.2 Fish Hoek

Fish Hoek (34°13.6’S, 18°43.0’E) is approximately 10 km west of Muizenberg. In contrast to Muizenberg, Fish Hoek beach has a smaller, more sheltered bay with a substantially smaller surf zone (~50 m wide) owing to a steeper sloping beach. Fish Hoek has a high diversity of fish species that attracts a lot of fishing activity in the form of beach purse-seine netting (Bennett 1989). Whereas overall there have been fewer white shark sightings than Muizenberg (121 sightings 2006 - 2011; Weltz (2012)), there have been more shark incidents (50% of bites, 75% of fatalities in False Bay) (Kock 2014). This combined with less wave action than Muizenberg led to the deployment of a small-meshed shark exclusion net in 2013 (Pollack 2015). This net is designed to be non-lethal to sharks and minimises the risk of encountering white sharks by swimmers (Cliff *et al.* 2011). Shark Spotters make use of the Elsie’s Peak Mountain (Figure 3.1) at an elevation of 110 m to monitor for sharks (Kock *et al.* 2012).

3.2 Shark spotter data

The primary dataset for this study was provided by the Shark Spotters program. Shark Spotters have a morning shift from 7:00 - 13:00 and an afternoon shift from 13:00 - 19:00 during the austral summer (Kock *et al.* 2012; Engelbrecht 2013; Weltz *et al.* 2013). During each shift, spotters perform hourly scans of the water to estimate the number of each type of water user (i.e., swimmer, surfer, surf skier) in the water. The spotter records all occurrences (time and position relative to the bay) of white sharks. Sharks are not individually recognisable to spotters and thus it is not possible to determine if multiple sightings represent the same or different sharks. In addition, it is not possible to determine the number of times a shark is present, but not detected by spotters. Thus, the data on shark sightings provide relative abundance estimates with spotters being careful not to count the same shark twice when it has not left the spotters field of view. White sharks are not the only species recorded by the Shark Spotters and other shark species observed are bronze whaler sharks (*Carcharhinus brachyurus*), smooth hammerhead sharks (*Sphyrna zygaena*), thresher shark spp. and various ray spp. Where noted, records of other species were discarded and only those records believed to be white shark sightings were analysed. In addition, spotters record all occurrences (time and position relative to the bay) of other predators such as dolphins and prey fish (e.g. yellow tail (*Seriola lalandi*) and harders (*Liza richardsonii*)).

3.2.1 Environmental variables

SST for the period January 2006 - April 2015 was provided by 'The South African Coastal Temperature Network v4.1' (Schlegel *et al.* 2016). The network includes temperature data from several South African institutions, including the South African Weather Service (SAWS), who recorded the data used here for both Muizenberg and Fish Hoek. SST was measured to a precision of 0.5ºC using hand-held mercury thermometers at both beaches (Fish Hoek: 34° 13.525212' S, 18° 43.59169' E; Muizenberg: 34° 10.398726' S, 18° 48.363876' E) (Schlegel *et al.* 2016). SST data was also collected by the Shark Spotters. However, the manual data collection protocol was less standardized than the SAWS data collection and therefore deemed less reliable and subsequently dropped from this analysis.

ENSO data was obtained online from the National Oceanic and Atmospheric Administration (NOAA) (www.esri.noaa.gov/psd/mei/table/html). NOAA monitors ENSO in the form of the MEI, which describes the strength of the multivariate Southern Oscillation phenomenon. The index is calculated for each of twelve sliding bi-monthly seasons (Dec/Jan, Jan/Feb, etc.). The six variables included in the calculation are sea-level pressure (P), zonal (U) and meridional (V) components of the surface wind, SST (S), surface air temperature (A), and total cloudiness fraction of the sky (C) (Wolter 1987). The individual fields are spatially filtered and clustered after which the MEI is calculated. This is carried out by the normalization of the individual total variances, which is then extracted from the covariance matrix of the combined variables (Wolter *et al.* 1993). The seasonal values are standardized towards each season and to the reference in 1950 - 93, which enables comparison within the MEI (Wolter 1987).

3.2.2 Predictor for prey availability

Data on daily presence/absence information for prey fish, dolphins, diatoms and treknetting were obtained from the Shark Spotters data sheets for the period 2013 - 2015. Prey fish is defined by the presence of bait balls and fish shoals and was considered as the most direct predictor for prey availability. Common shoaling fish along False Bay beach include yellowtail (*Seriola lalandi*) and southern mullet (*Liza richardsonii*), but species names are not further specified by the spotters. Depending on the sea conditions and shoaling behaviour, the presence of prey may not always be detected. Therefore, the presence of other predators (dolphins), diatoms and treknetting events were considered as indirect predictors for prey availability. Although dolphin sightings and treknetting events have been collected since 2006, the analysis of all predictors for prey availability was limited to the period 2013 - 2015 to allow for a more direct comparison with prey fish sightings.

3.2.3 Statistical analysis

Parametric tests make assumptions of normality, homogeneity of variances and independence of errors (Prager *et al.* 1989; Zuur *et al.* 2009), which are violated in many ecological datasets (Adams *et al.* 1996; Peres-Neto *et al.* 2001). The white shark sighting dataset is particularly challenging for statistical analyses because the distinct monthly pattern of shark sightings is likely to pose a confounding effect with predictor variables, such as SST (Weltz *et al.* 2013). If not accounted for, such confounding effects can either lead to falsely identifying a significant effect when there is none (type I error) or failing to identify significant effects by falsely accepting the null hypothesis (type II error) (Zuur *et al.* 2010).

Hierarchical permutation (randomization) tests provide a statistically robust alternative for nested datasets and minimise the risk of type I and II errors (Anderson 2001). The basic idea of any permutation test is to test the null hypothesis that the observed pattern in the response variable is independent of the predictor variable of interest. One way to test this is by reshuffling ("randomizing") the observations while keeping the predictor variable at a fixed position and then assessing the expected distribution of the test statistic based on a sufficiently large number of randomizations (D_{rand}) against observed test statistic (D_{obs}) calculated from the original dataset (Ladah *et al.* 2005). In a hierarchical permutation test, the reshuffling can be nested (blocked) at different levels. Here, month was chosen as the smallest resampling unit, which was nested within beach and year to implicitly account for higher level spatial (beach) and temporal (Month/Year) effects that can otherwise confound the variable of interest. The null hypothesis is therefore that the day-to-day variation in shark sightings is independent of the investigated environmental or biological variable within any month *m*, year *y* and beach *b*. The corresponding test statistic used here is:

$$D_x = \frac{\sum_i^N \left(Y_{i,b,y.m} X_{i,b,y,m}\right)}{\sum_i^N Y_{i,b,y,m}},$$

where $Y_{i,b,y,m}$ is either the presence/absence (0/1) or the number of sightings of white sharks during day i at beach b, in year y and month m, N is the total number of observer days and $X_{i,b,y,m}$ is the predictor variable of interest (SST, fish etc.).

If the null hypothesis is supported, the test statistic D_{obs} would fall within the distribution of randomly generated D_{rand} values. Accordingly, if the calculated value for D_{obs} is outside the D_{rand} distribution above the (1-α)th percentile, the null hypothesis is rejected and the shark sightings are not independent of the variable of interest (Ladah *et al.* 2005). The *p*-value for D was approximated after Edgington (1986),

$$p - value = \frac{(x+1)}{(I+1)},$$

where x is the number of D_{rand} values from that were greater than D_{obs} and I the number of permutations. The number of times the data is shuffled was set to 10000 for all conducted tests as the *p*-value was found to stabilize around at least 5000 replications (Adams *et al.* 1996).

Randomization tests for all variables, except ENSO (MEI), were run on the complete dataset from 2013 - 2015. The environmental influence of SST and ENSO was further investigated for the entire time series over the period 2006 - 2015. The bi-monthly nature of the MEI used to monitor ENSO and the year specific La Niña and El Niño events in the analysed years made it necessary to drop year level and perform the randomization test by only reshuffling daily sighting within month and beach. All statistical analyses were conducted within the statistical platform R 3.2.2 (R Development Core Team 2008).

3.2.4 Dependencies among predictors

The variables for treknetting and dolphins were recorded for the full dataset from 2006 - 2015. To test if treknetting or dolphins could be used as proxy for fish presence Pearson contingency tables (Table 3.1) were produced (Fisher 1922) and a χ^2-test was executed.

Table 3.1: Contingency table for the independence testing of the treknetting and dolphin variable against the presence of fish for combined beaches.

	Treknetting			**Dolphins**		
Fish	present	absent	total	present	absent	total
present	177	2056	2233	44	327	371
absent	225	373	598	121	1684	1805
total	402	2429	2831	165	2011	2176

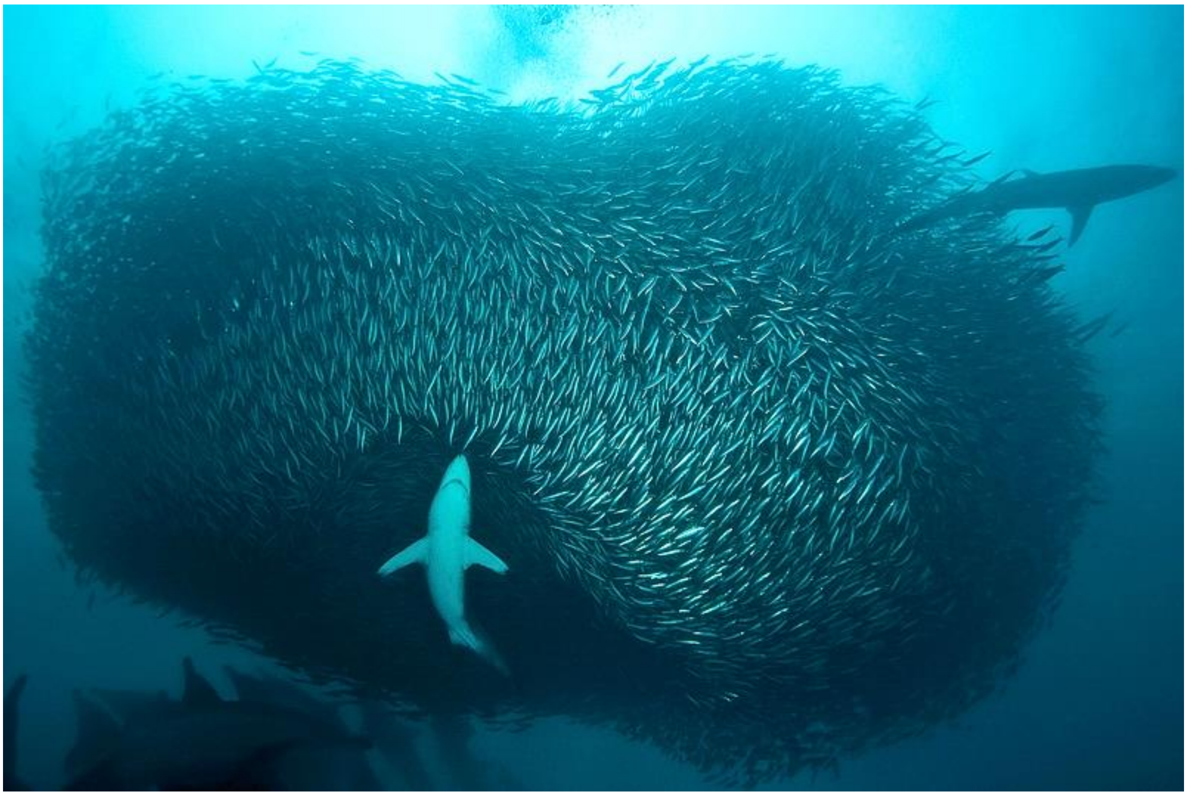
To calculate the similarity coefficient the following equation was used after Jaccard (1912):

$$S_{Jac} = \frac{a}{p_1 + p_2 - a}$$

where, a is the proportion of presence of the variables that the two variables share at the same position, p_1 the proportion of presence in the first variable (fish) and p_2 the proportion of presence in the second variable (treknetting) (Warrens 2008). The closer the dissimilarity coefficient is to 1 the less similar the variables are (Warrens 2008).

To further explore the dependencies among predictor variables, the hierarchical permutation (randomization) tests were applied by implementing each predictor variable as a response variable. First the number of shark sightings and presence/absence of sharks are used as a response variable, with all of the predictors (SST, fish, treknetting, dolphins and diatom patches). Thereafter fish, treknetting, dolphins and diatom patches were separately used as response variables with the remaining predictors. Thus, the interactions between each variable is determined which allows for a better understanding of their interconnectivity and the ecosystem.

4. Results



The Sardine run off the South African coast is one of the largest animal migrations in the world; a festival of marine predator-prey relations (Rochat 2015)

4.1 Shark sightings

A total of 742 and 467 shark sightings were made by spotters at Muizenberg and Fish Hoek respectively, over the 10-year study period. Shark sightings vary with both year and beach, peaking at both beaches in 2010 and 2011. The number of shark sightings does not differ significantly between the two beaches as judged by a Mann-Whitney-U test (W = 79714, p = 0.2732). Fish Hoek, however, has the highest recorded number of shark sightings (n = 10) within one day (18/02/2015) with the maximum recorded at Muizenberg being six (10/02/2014).

The trend in shark sightings over the period analysed does reflect a significant inter-annual difference for Fish Hoek (K = 27.358, df = 9, p < 0.01; Kruskal-Wallis test) whereas for Muizenberg there was no significant difference between the number of shark sightings over the years (K = 9.721, df = 9, p = 0.3735) (Figure 4.1).

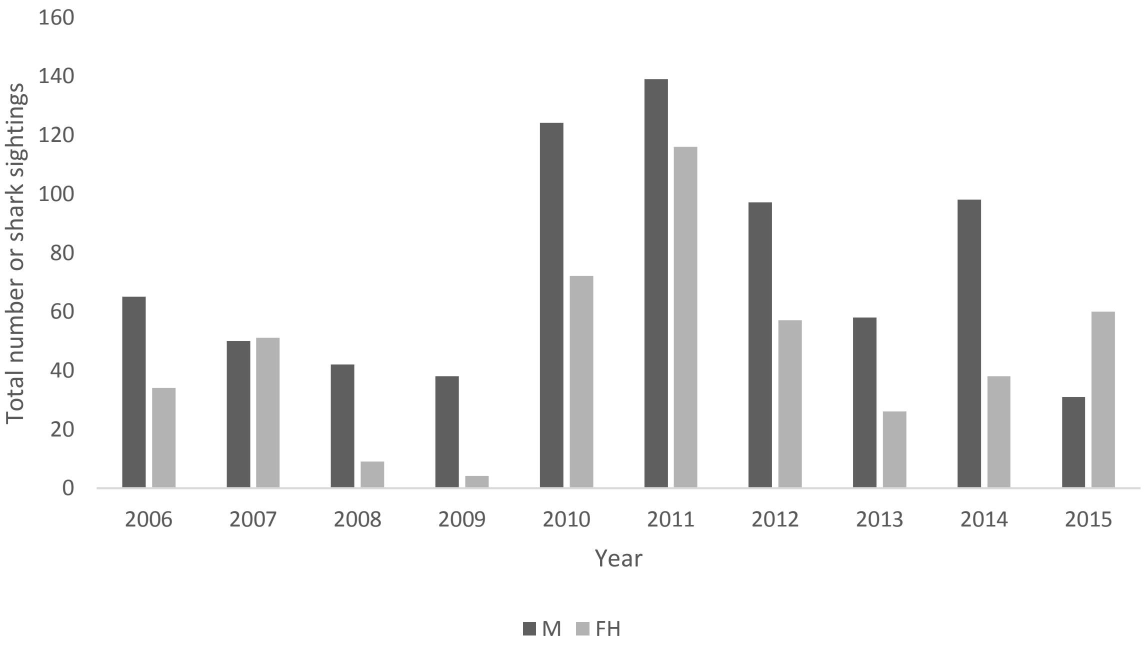


Figure 4.1: Total number of shark sightings per year (2006 - 2015) at Muizenberg (M) and Fish Hoek (FH) beaches.

Shark sightings at both beaches showed a symmetric unimodal distribution in relation to SST, ranging from 11 - 23°C and with modes at 17 and 18°C for Fish Hoek and Muizenberg, respectively (Figure 4.2). The frequency distribution of recorded temperatures at both sites differs from the shark sightings distribution, with modes at 12 and 18°C (bimodal) for Muizenberg and a multimodal distribution (13 - 17°C) for Fish Hoek.

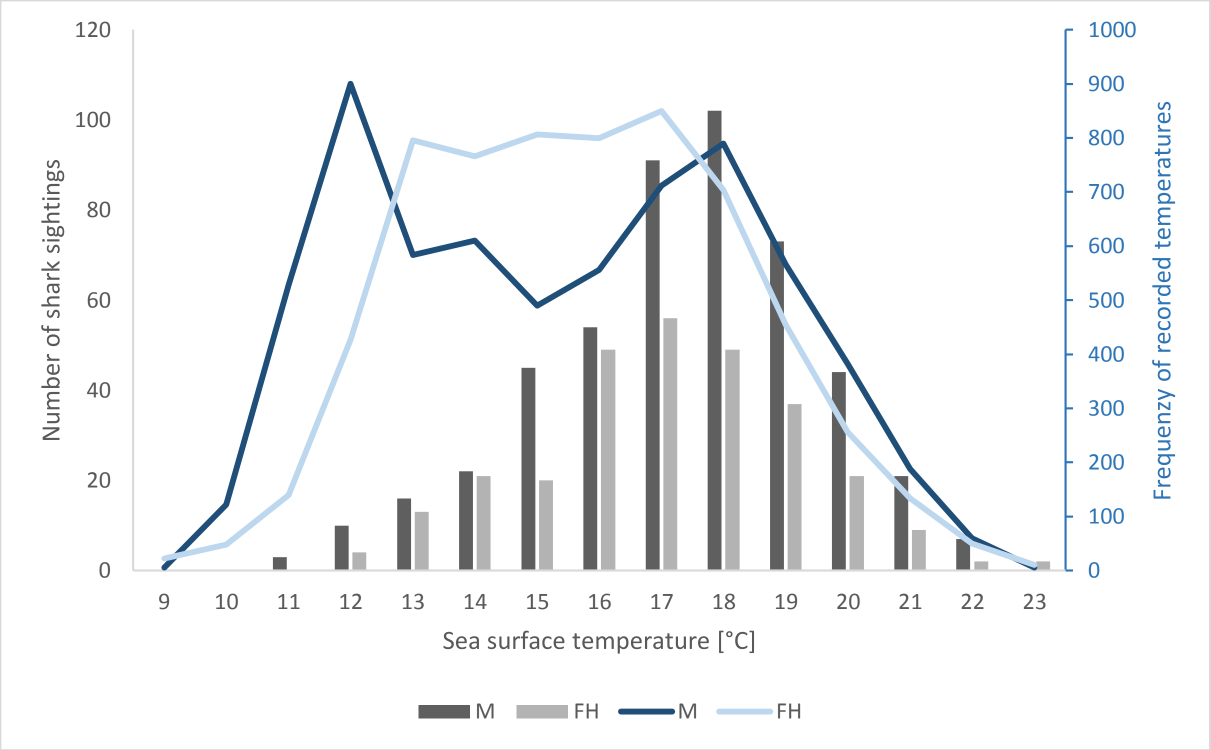


Figure 4.2: The frequency distribution of shark sightings with sea surface temperature (SST) and the frequency of recorded temperatures at Muizenberg (M) and Fish Hoek (FH).

4.2 SST and ENSO

The SST varied by 14.5°C annually with the highest temperature (23.5°C) recorded during the austral summer and the lowest (9°C) during austral winter. The mean SST at Muizenberg was 15.8°C (± 3.0), which showed no significant difference (W = 19897000, p = 0.01596; Mann-Whitney U test) from the mean SST of 15.8°C (± 2.4) at Fish Hoek using a Mann-Whitney U test (Table 4.1).

Table 4.1: Mean (±S.D.) annual sea surface temperatures (SST) for Muizenberg and Fish Hoek beaches from 2006 to 2015.

	Muizenberg		**Fish Hoek**	
Year	Mean [°C]	S.D.	Mean [°C]	S.D.
2006	15.5	±3.1	16.3	±1.8
2007	17.7	±2.6	16.6	±2.0
2008	15.3	±3.0	16.0	±2.4
2009	16.1	±2.4	15.2	±2.1
2010	15.1	±3.1	15.7	±2.5
2011	15.4	±3.0	15.2	±2.1
2012	15.8	±3.4	16.1	±3.2
2013	15.7	±2.8	14.9	±3.1
2014	15.9	±3.0	15.7	±2.6
2015	15.1	±3.3	16.1	±2.6
Mean	15.8	±3.0	15.8	±2.4

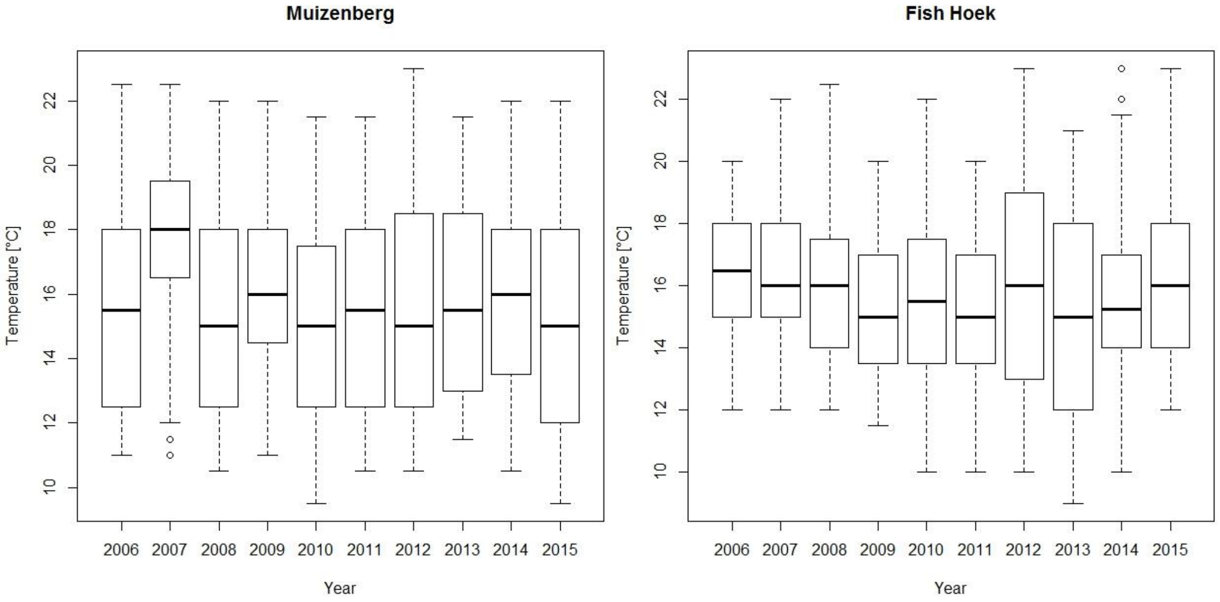


Figure 4.3: Boxplots of annual mean temperatures for Muizenberg and Fish Hoek (2006 – 2015).

The ENSO index varied markedly during the study period (Figure 4.4) with strong negative values (La Niña) in 2007/2008 and 2010/2011. Strong El Niño events were apparent in 2006/7, 2009/10 and 2015/16 with 2012/13 and 2014/15 being characterised by relatively weak El Niño events. In August/September 2015 an MEI value of + 2.53 was recorded which is one of the strongest ENSO events on record worldwide and corresponds with a severe drought in the interior of South Africa.

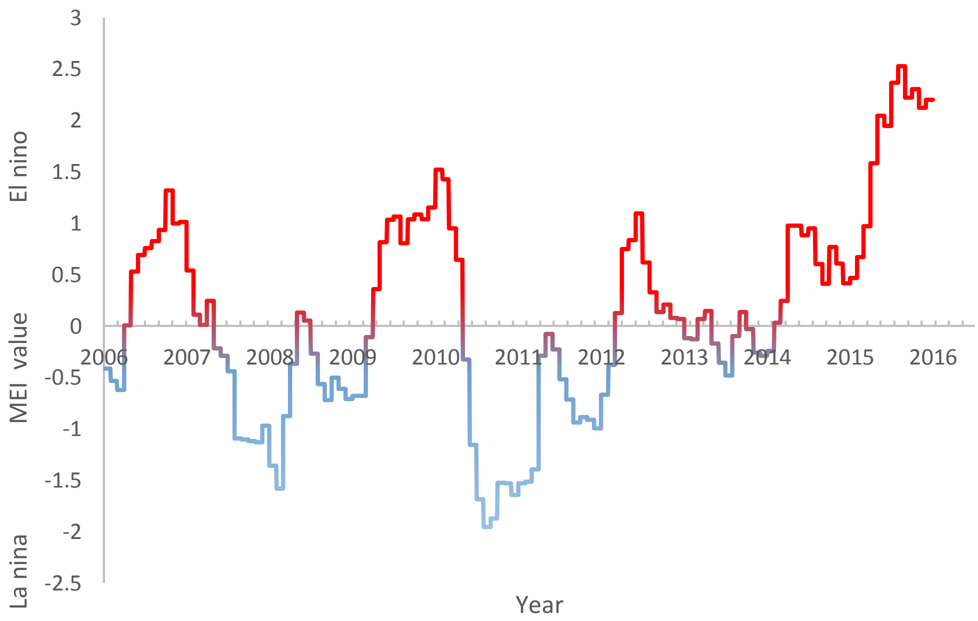


Figure 4.4: The mean bi-monthly El Niño/Southern Oscillation (ENSO) value from the Pacific Ocean from 2006 - 2015 with El Niño (red, warm-water) and La Niña (blue, cold-water) events.

There was no visibly discernible pattern between shark presence and ENSO at either beach (Figure 4.5). However, the two outliers are true outliers, reflecting months where shark presence was very high at both beaches. At extreme events, either cold or warm, there were few shark sightings.

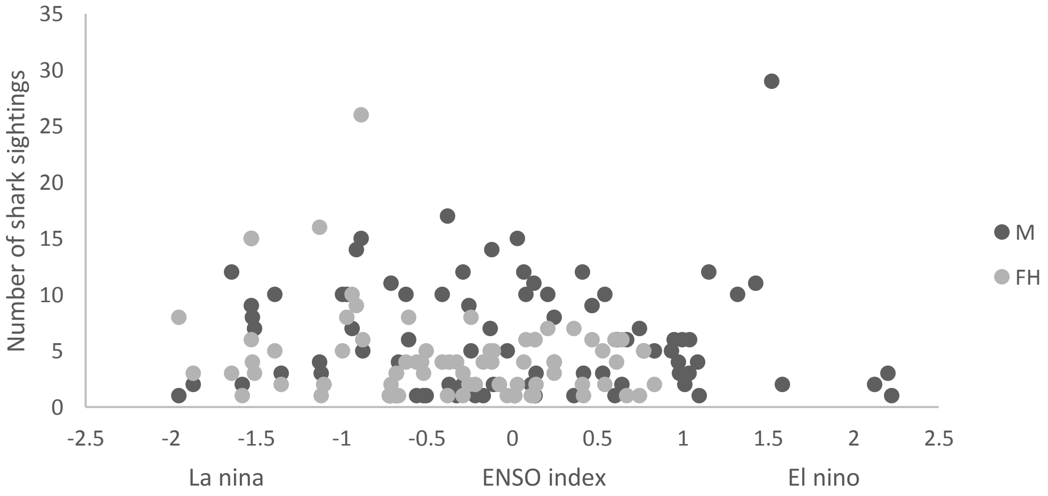


Figure 4.5: The total number of shark sightings relative to the El Niño/Southern Oscillation (ENSO) index from 2006 - 2015 for the beaches Muizenberg (M) and Fish Hoek (FH).

4.3 Monthly distribution of variables

Sightings of sharks, prey fish and dolphin were all higher in spring, summer and autumn months when SST is higher. Shark sightings peak in October (spring) at Fish Hoek and January (summer) at Muizenberg (Figure 4.6).

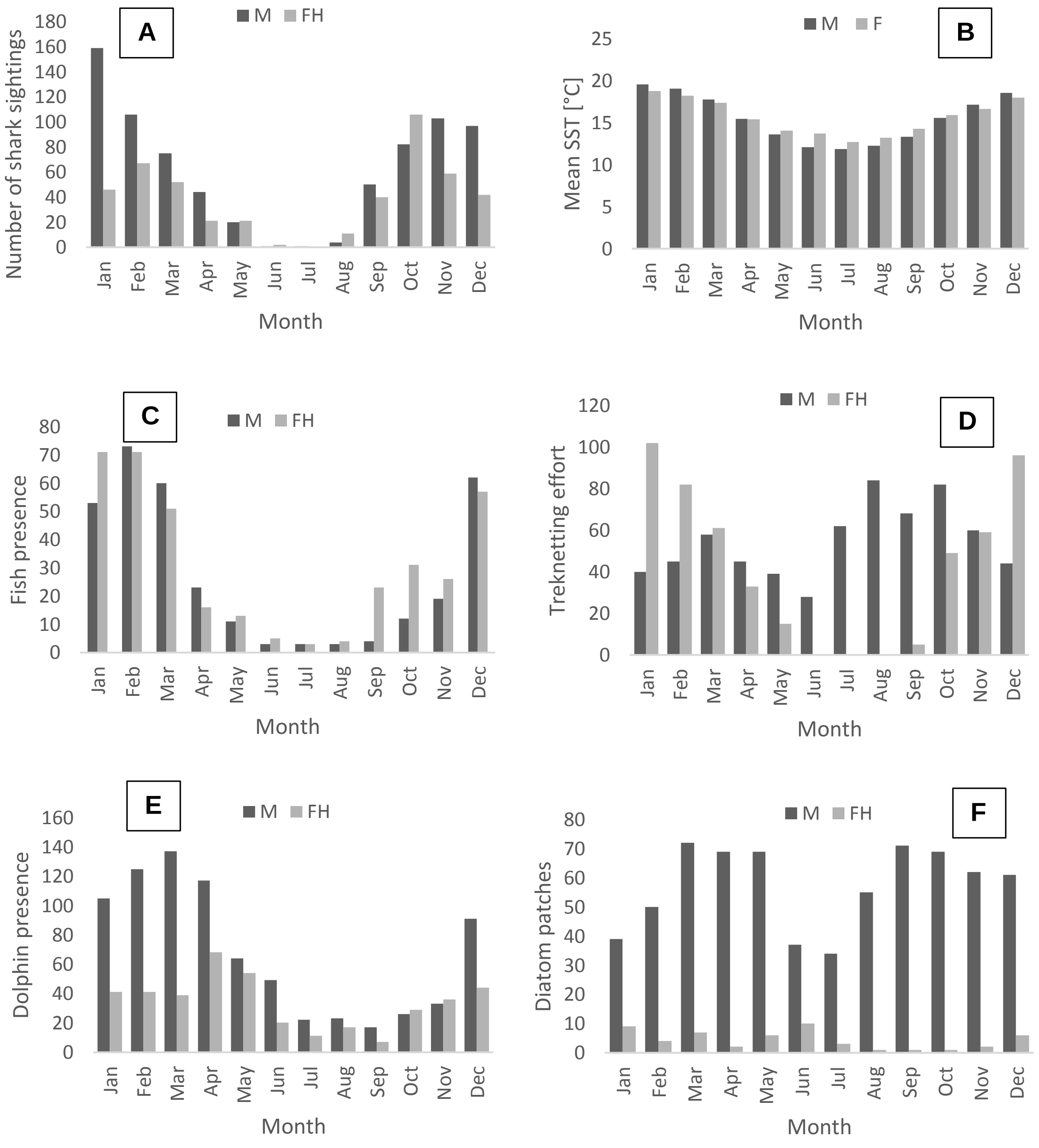


Figure 4.6: Monthly distribution of (A) white sharks, (B) mean SST, (C) prey fish, (D) treknetting (E) dolphins and (F) diatom patches, at Muizenberg (M) and Fish Hoek (FH) beaches. Fish and diatom patch sightings includes data from 2013 – 2015; other variables 2006 – 2015.

Prey fish sightings showed a distinct increase during the summer months, peaking in February at both beaches. Similar to sharks, both dolphin and fish sightings are lowest during the winter months (June - August) when SST is low, with dolphin sightings remaining low into spring (September) when both fish and shark sighting begin to increase sharply.

The occurrence of treknetting and diatom patches showed different trends between both beaches, with Fish Hoek following the austral summer-winter trend as displayed by the other variables. In Muizenberg, however the treknetting effort peaked during the winter months (July - October). Diatom patches were seen more often at Muizenberg than Fish Hoek and barring slight dips in June/July and January, varied little across the year.

4.3.1 Predictor variables and SST

By overlaying the biotic variables with SST across years the marked seasonal patterns in sightings of sharks, prey fish and to a lesser extent dolphins was once again apparent with clear peaks in sightings in warmer water, whereas neither treknetting nor diatoms show a discernible trend with SST across time (Figure 4.7).

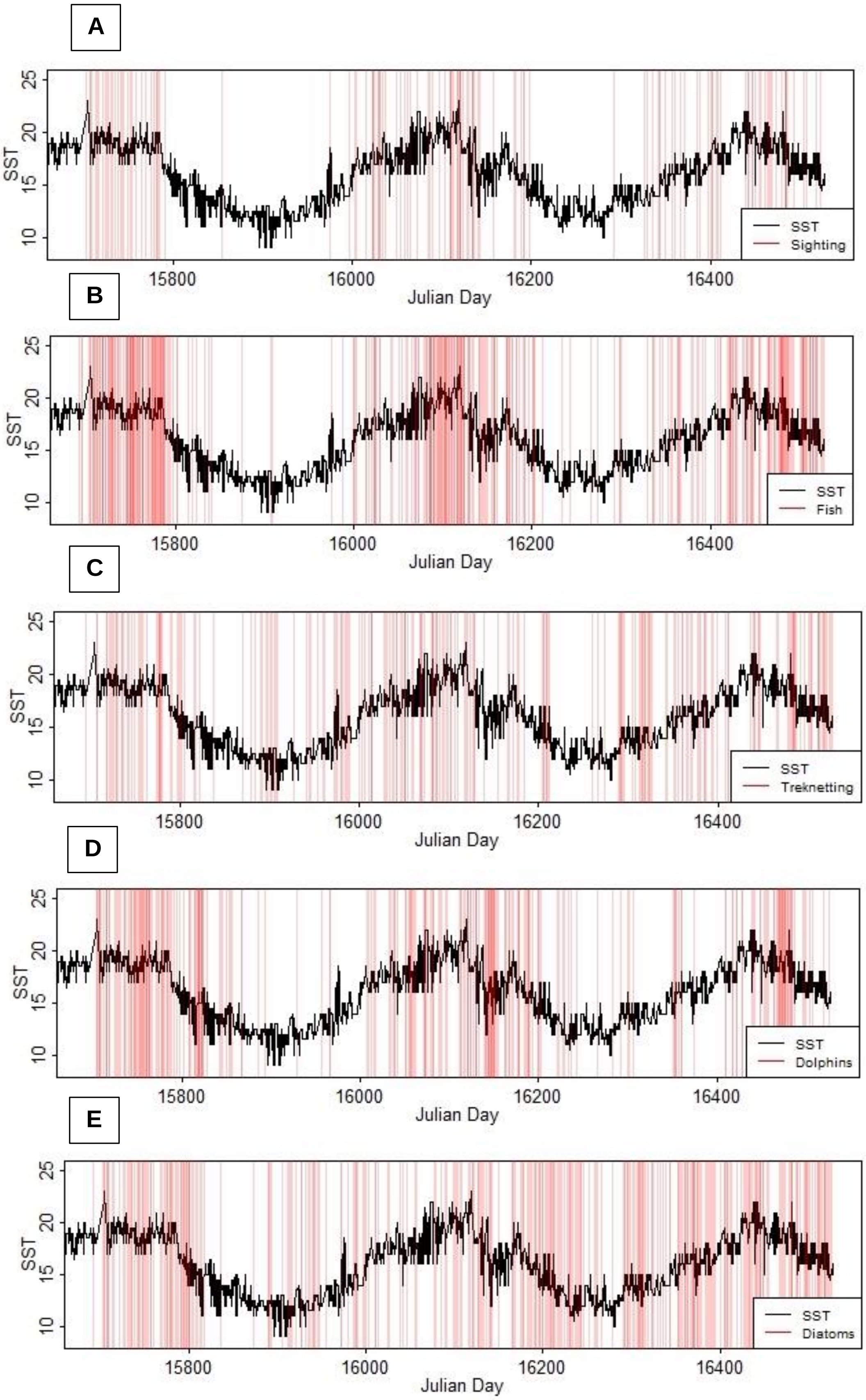


Figure 4.7: Daily sea surface temperature (SST) trend from 2013 - 2015 (in Julian day) with the daily occurrence of (A) white shark sightings, (B) prey fish, (C) treknetting, (D) dolphins and (E) diatom patches.

4.4 Randomization tests

4.4.1 Randomization tests using counts and presence/absence of shark sightings

For the period 2013 - 2015, the observed means (D_{obs}) of shark sightings with SST, fish presence and treknetting (Figure 4.8) all differed significantly from the expected distributions ($p < 0.001$) and were higher at warmer SST (18.56°C) and when both prey fish and treknetting were more frequently sighted. The graph for fish presence (see Figure 4.8) showed a significant difference between the observed probability of fish occurrence (0.66) when sharks were present which lies outside of the expected probability (0.42) if the occurrence of fish were to be randomly distributed. There was no difference between the expected and observed frequency distributions for either dolphin ($p = 0.362$) or diatom ($p = 0.196$) sightings.

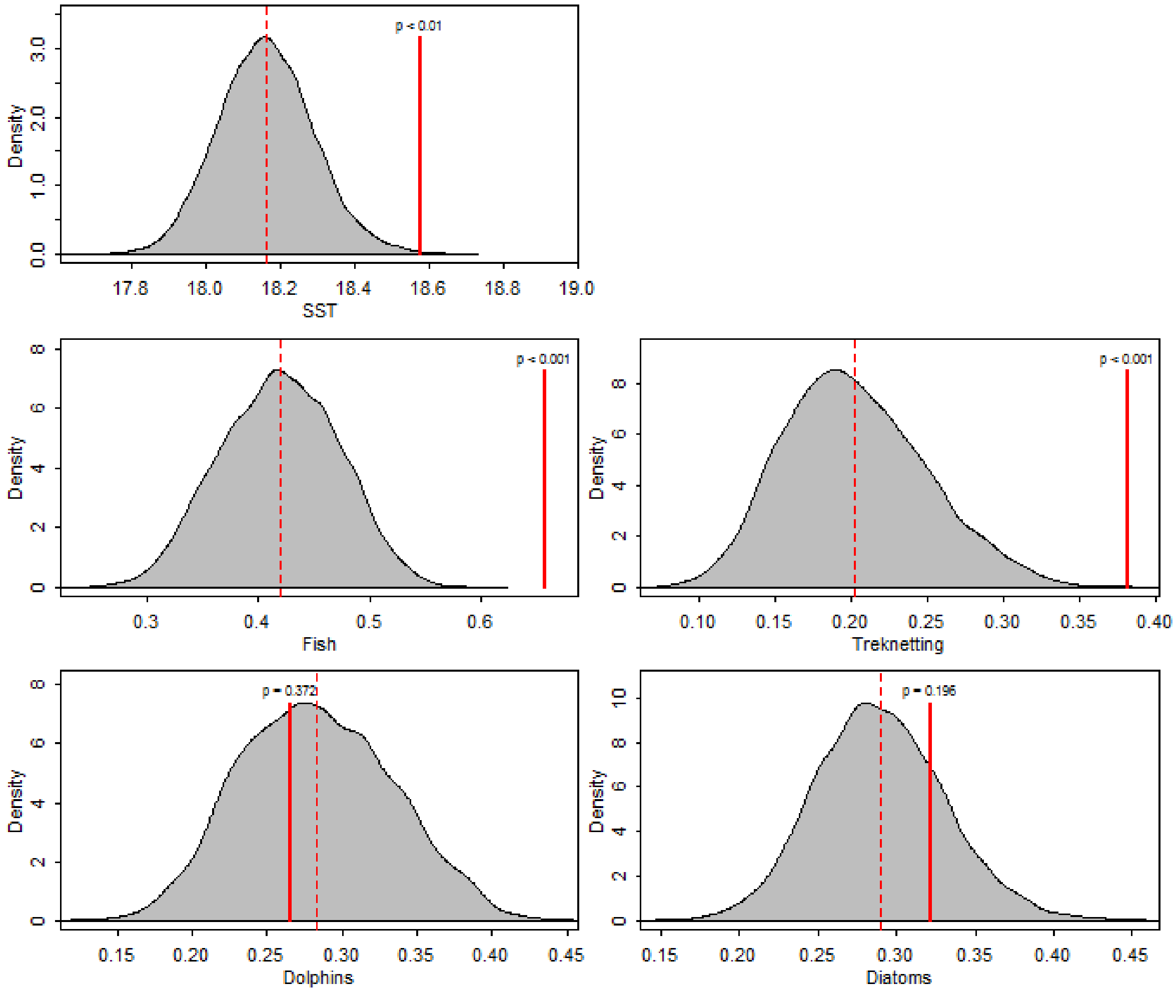


Figure 4.8: Randomization test results using daily counts of shark sightings as a response variable, showing the observed and random distribution for the years 2013 - 2015 for (1) SST, (2) fish, (3) dolphins, (4) treknetting and (5) diatoms.

Similar to the results for the frequency of shark sightings (counts) the presence-absence distribution of white sharks at both beaches was significantly different from random for SST, prey fish and treknetting ($p < 0.001$), but not different from random for either dolphin ($p = 0.431$) or diatom ($p = 0.063$) presence (Figure 4.9). The highly significant non-random variables fish ($p < 0.001$) and treknetting ($p < 0.001$) thus show the same trend as was observed for the frequency of shark sightings. SST was also significantly non-random with the peak of shark presence at 18.23°C which was significantly different from the randomized peak at 17.95°C. Overall, the range of the random distributions became narrower when using shark presence data.

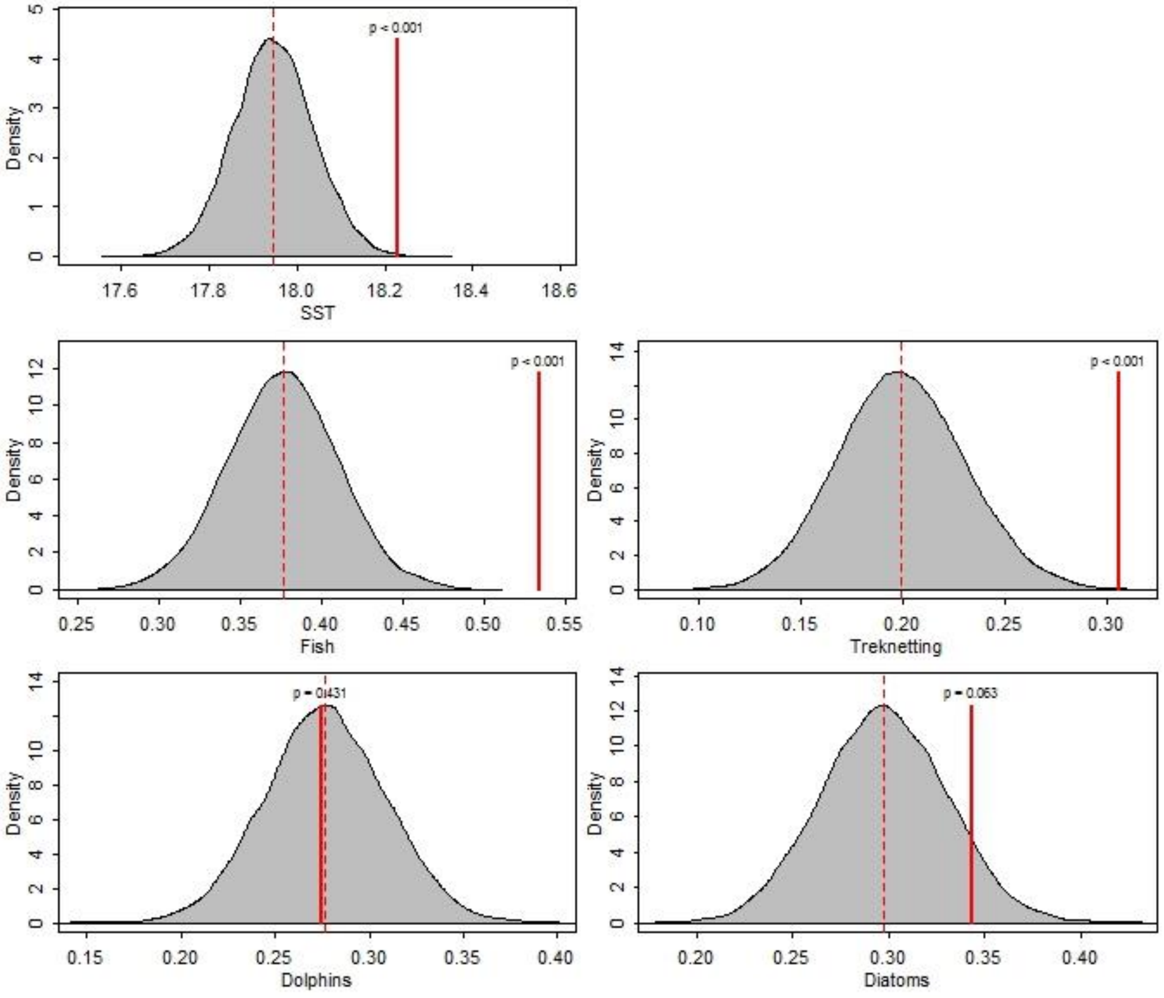


Figure 4.9: Randomization test results using shark presence-absence data as response variable, showing observed and random distribution for the years 2013 - 2015 for (1) SST, (2) fish, (3) dolphins, (4) treknetting and (5) diatoms.

4.4.2 Dependencies among predictor variables

To determine if treknetting or dolphin presence could be used as a proxy for fish presence, the dependencies amongst the predictor variables were tested. The result shows that the variables, treknetting and fish, are not independent ($\chi^2 = 339.04$, *df* = 1, $p < 0.001$). Dolphins and fish presence were also found to be dependent on each other ($\chi^2 = 10.951$, *df* = 1, $p < 0.001$). From the calculated similarity coefficient of 7.20% for treknetting and 8.94% for dolphins the respective dissimilarity coefficients can be drawn ($D_{Jac} = 1 - S_{Jac}$), resulting in a D_{jac} of 0.93 (treknetting) and 0.91 (dolphins). This means that fish presence and treknetting activity are not correlated and thus treknetting cannot be used as a proxy for fish availability. The same is found for the relationship between dolphin and fish presence.

The dependencies between predictor variables were further analysed by using fish, treknetting, dolphins and diatom patches as response variables in the permutation tests. The relationship between SST and fish presence (Figure 4.10) was found to be highly significant ($p < 0.001$) with the observed temperature peak (17.94°C) outside the upper percentile of the random distribution (*CI95%* = 17.86°C). The occurrence of treknetting in concordance with fish presence was also found to be highly significantly non-random ($p < 0.001$), supporting the findings of the χ^2-test. The only non-significant variable was dolphin presence, where the observed peak fell within the randomized distribution ($p = 0.114$) (Figure 4.10).

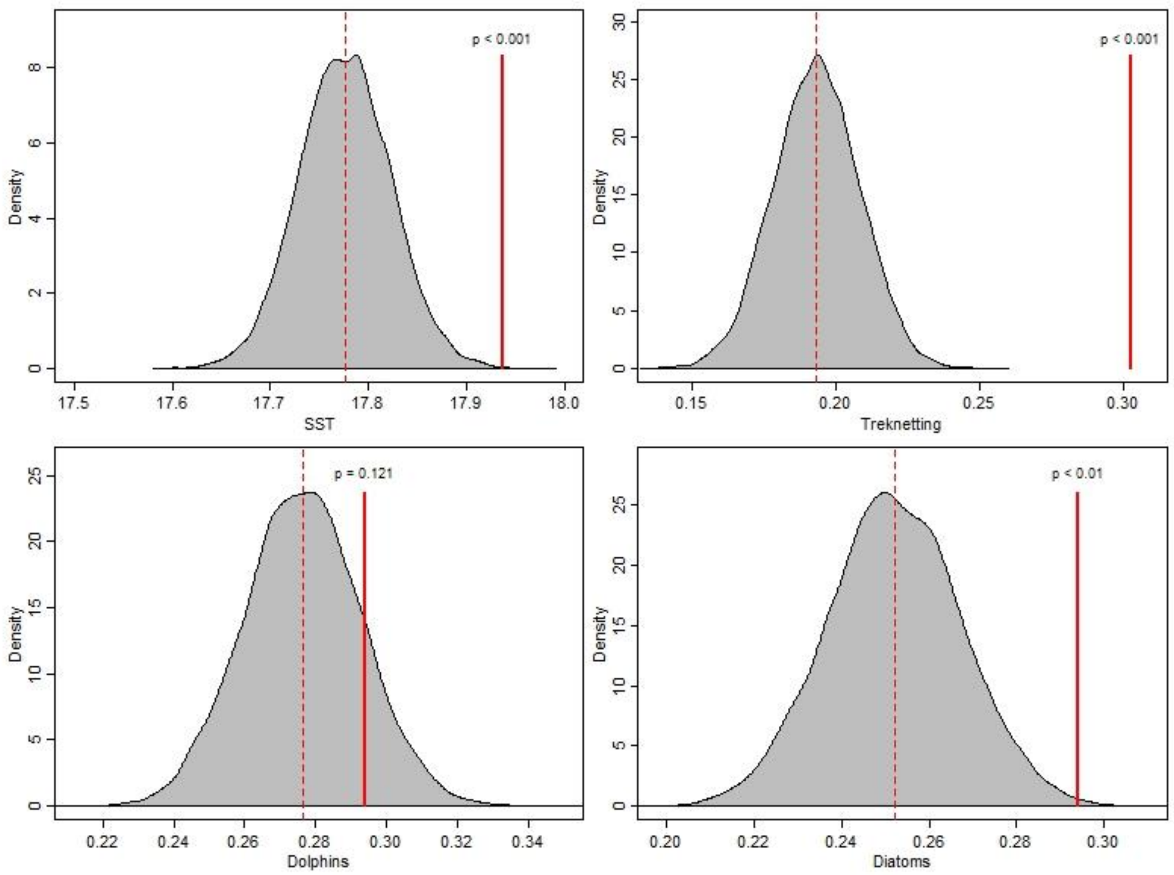


Figure 4.10: Randomization test results using fish presence as response variable, showing observed and random distribution for the years 2013 - 2015 for (1) SST, (2) treknetting, (3) dolphins and (4) diatoms.

The data show that SST is randomly distributed (*p* = 0.482) with the peak of the random distribution and the observed data both at 16.53°C (Figure 4.11). The observed dolphin presence also did not show a significant difference from the random distribution (*p* = 0.069). The occurrence of diatom patches was the only variable that had a non-random distribution with treknetting as the response variable (*p* < 0.001).

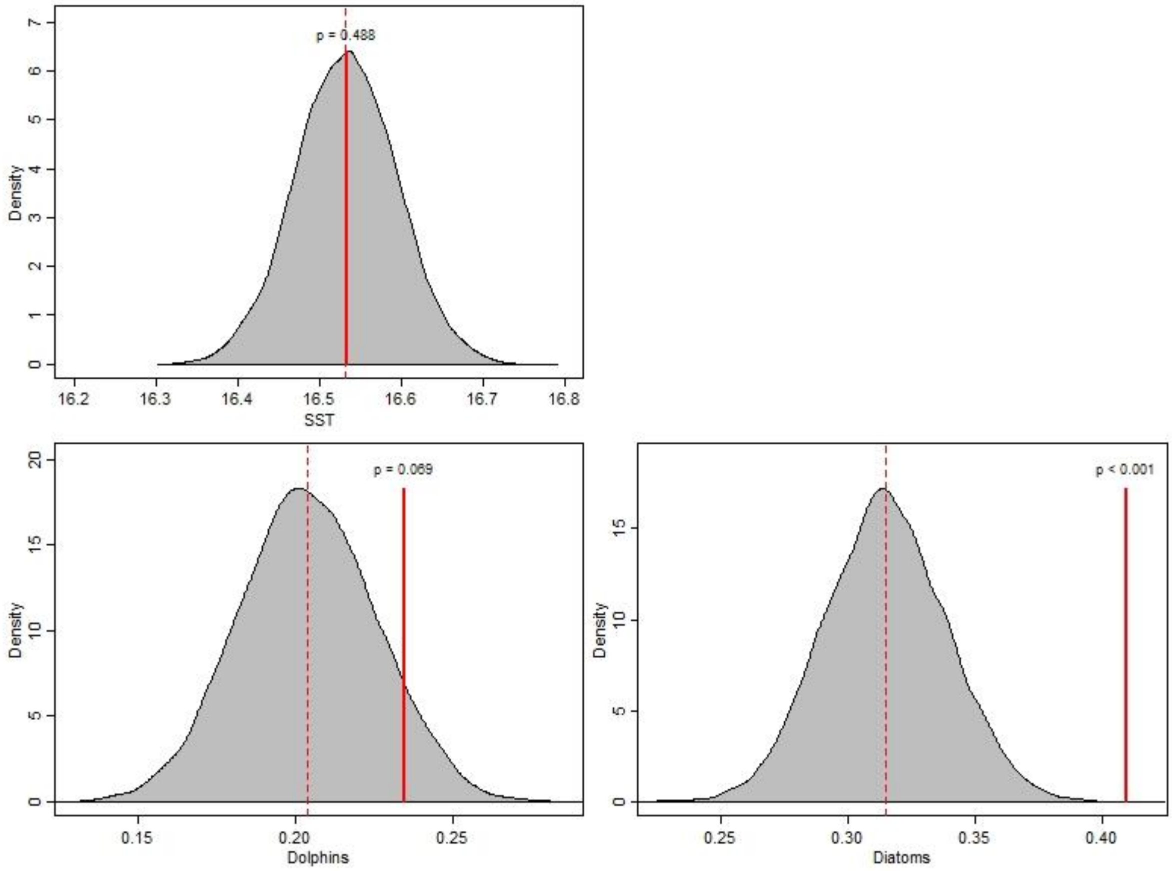


Figure 4.11: Randomization test results using treknetting as response variable, showing observed and random distribution for the years 2013 - 2015 for (1) SST, (2) fish, (3) dolphins and (4) diatoms.

When dolphin presence is incorporated into the randomization test as the response variable (Figure 4.12) the results show that there is no clear pattern with either SST (*p* = 0.225) or diatom patches (*p* = 0.349).

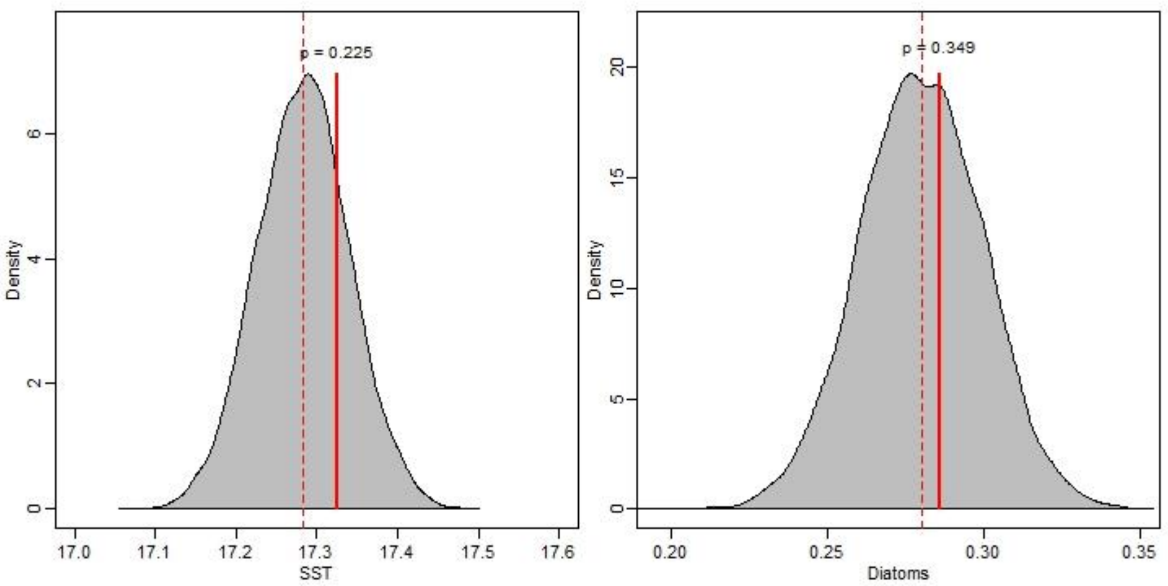


Figure 4.12: Randomization test results using dolphin presence as response variable, showing observed and random distribution for the years 2013 - 2015 for (1) SST and (2) diatoms.

The randomization test results using diatom patches as response variable (Figure 4.13) show that SST is significantly non-randomly distributed ($p < 0.01$) with the observed peak of 16.15°C below the expected peak of 16.25°C.

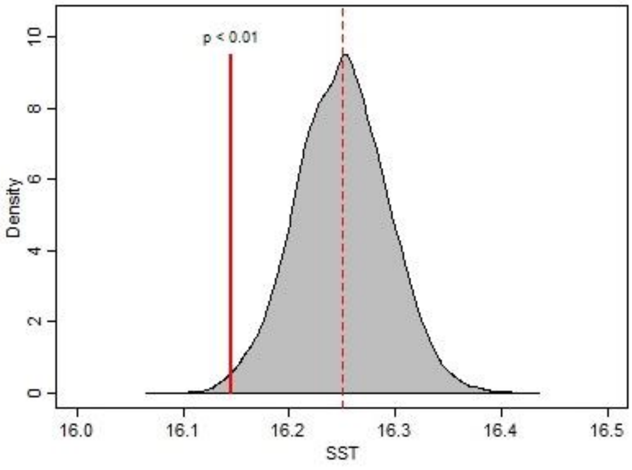


Figure 4.13: Randomization test results using diatoms as response variable, showing observed and random distribution for the years 2013 - 2015 for SST.

4.4.3 SST and ENSO using the long-term data set from 2006 - 2015

A time series plot of the frequency of shark sightings and SST over 10 years revealed a clear seasonal pattern with fewer sighting during the cooler winter months (Figure 4.14). The distribution of the number of shark sightings with SST was non-random ($p < 0.01$) with the mean SST for all shark sightings at a higher temperature (17.49°C) than expected (17.32°C) for a random sample. The presence-absence frequency distribution of sharks with respect to SST is also significantly different from random ($p < 0.05$).

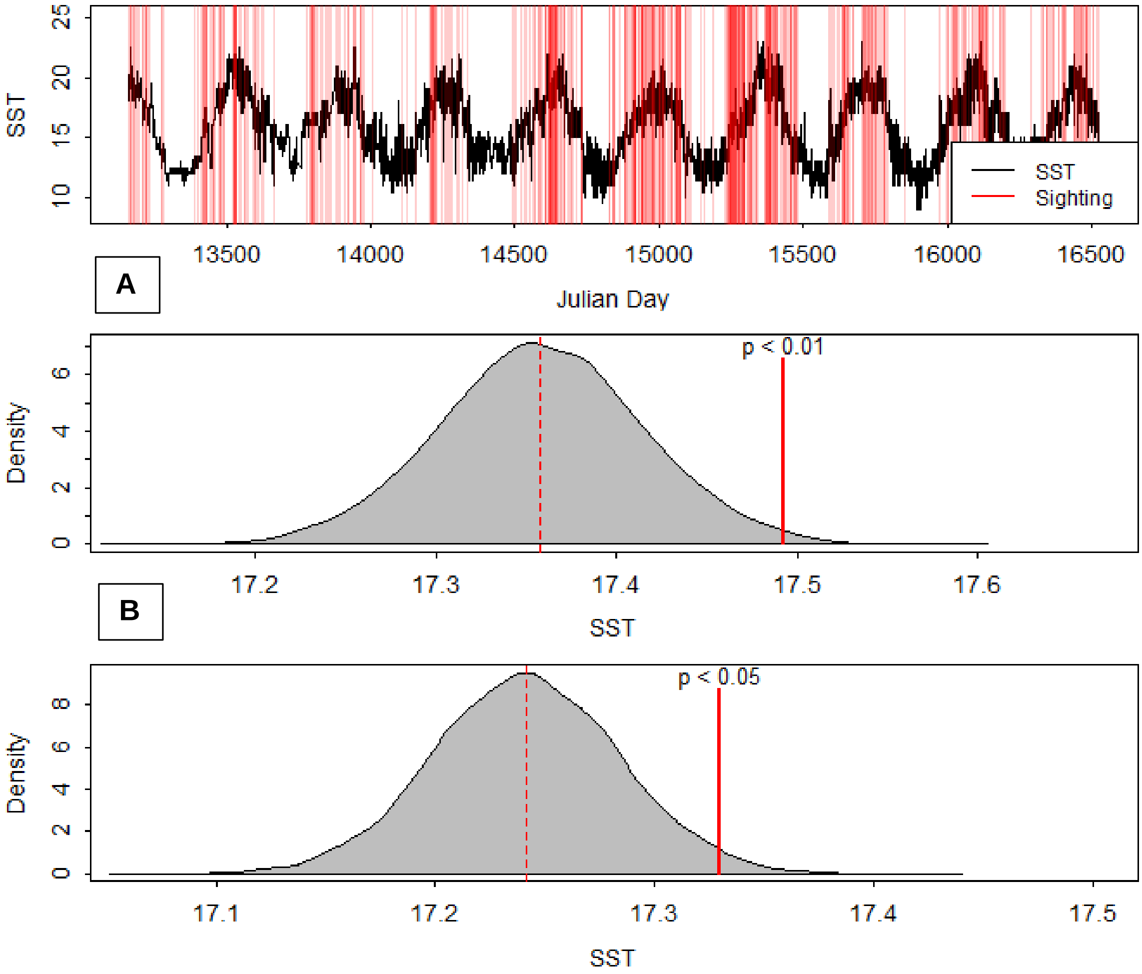


Figure 4.14: SST trend from 2006 - 2015 (in Julian days), with (A) the number of shark sightings per day and the observed and random distribution of the shark sightings and (B) the presence of sharks.

The frequency of shark sightings with ENSO does not provide a clear pattern, with peaks in sightings apparent during both positive (El Niño) as well as negative (La Niña) ENSO values (Figure 4.15). However, randomization tests reveal an effect of ENSO with both the frequency of sightings (D_{obs} = - 0.012; $p < 0.05$) and presence-absence (D_{obs} = - 0.147, $p < 0.001$) of white sharks on the inshore regions of False Bay being significantly different from the randomized distribution.

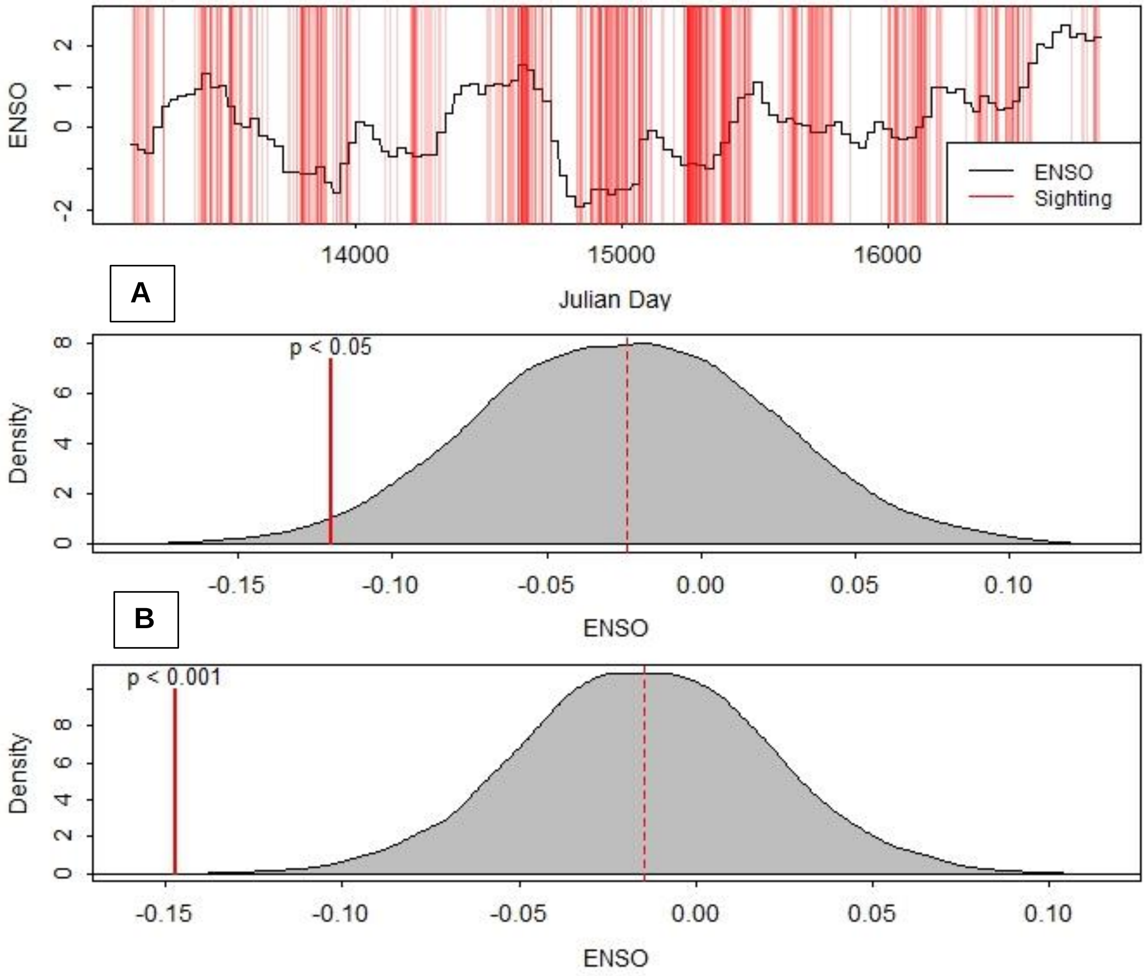


Figure 4.15: ENSO trend from 2006 - 2015 (in Julian days), with (A) the number of shark sightings per day and the observed and random distribution of the shark sightings with the ENSO value and (B) the presence of sharks.

Table 4.2: Summary table of the randomization tests using different response and predictor variables, calculated mean of the random distribution (Mean(xrand)) plus standard deviation (S.D.), the observed mean (Mean(xobs)), p-value, lower quantile, median and upper quantile (CI95%).

	Number of sightings					
	Mean(xrand)± S.D.	Mean (xobs)	p-value	lower quantile	median	upper quantile (CI95%)
Temperature	18.16 ± 0.1270	18.57	0.00120	17.91	18.16	18.37
Fish	0.418 ± 0.0520	0.66	0.00010	0.32	0.42	0.50
Treknetting	0.204 ± 0.0465	0.38	0.00010	0.12	0.20	0.29
Dolphins	0.283 ± 0.0505	0.27	0.37266	0.19	0.28	0.37
Diatoms	0.289 ± 0.0413	0.32	0.20268	0.21	0.29	0.36
	Shark presence					
	Mean(xrand) ± S.D.	Mean (xobs)	p-value	lower quantile	median	upper quantile (CI95%)
Temperature	17.95 ± 0.0913	18.23	0.00140	17.77	17.95	18.10
Fish	0.376 ± 0.0336	0.53	0.00010	0.31	0.37	0.43
Treknetting	0.199 ± 0.0308	0.31	0.00040	0.14	0.20	0.25
Dolphins	0.277 ± 0.0321	0.27	0.43866	0.21	0.27	0.33
Diatoms	0.298 ± 0.0328	0.34	0.06389	0.24	0.30	0.35
	Fish presence					
	Mean(xrand) ± S.D.	Mean (xobs)	p-value	lower quantile	median	upper quantile (CI95%)
Temperature	17.78 ± 0.0466	17.94	0.00030	17.69	17.78	17.85
Treknetting	0.193 ± 0.0150	0.30	0.00010	0.16	0.19	0.22
Dolphins	0.276 ± 0.0160	0.29	0.11389	0.24	0.28	0.30
Diatoms	0.252 ± 0.0152	0.29	0.00180	0.22	0.25	0.28
	Treknetting presence					
	Mean(xrand) ± S.D.	Mean (xobs)	p-value	lower quantile	median	upper quantile (CI95%)
Temperature	16.53 ± 0.0608	16.53	0.48145	16.41	16.53	16.63
Dolphins	0.203 ± 0.0214	0.23	0.06199	0.16	0.20	0.24
Diatoms	0.315 ± 0.0239	0.41	0.00010	0.27	0.32	0.36
	Dolphin presence					
	Mean(xrand) ± S.D.	Mean (xobs)	p-value	lower quantile	median	upper quantile (CI95%)
Temperature	17.28 ± 0.0575	17.33	0.23318	17.17	17.28	17.38
Diatoms	0.279 ± 0.0196	0.29	0.33357	0.24	0.28	0.31
	Diatom presence					
	Mean(xrand) ± S.D.	Mean (xobs)	p-value	lower quantile	median	upper quantile (CI95%)
Temperature	16.25 ± 0.0429	16.15	0.00740	16.17	16.25	16.32
	SST 2006-2015					
	Mean(xrand) ± S.D.	Mean (xobs)	p-value	lower quantile	median	upper quantile (CI95%)
Number of sightings	17.36 ± 0.0571	17.50	0.00790	17.25	17.36	17.45
Shark presence	17.24 ± 0.0424	17.33	0.01790	17.16	17.24	17.31
	ENSO 2006-2015					
	Mean(xrand) ± S.D.	Mean (xobs)	p-value	lower quantile	median	upper quantile (CI95%)
Number of sightings	- 0.023 ± 0.0477	- 0.012	0.01920	- 0.1154	- 0.0233	0.0558
Shark presence	- 0.014 ± 0.0356	- 0.147	0.00030	- 0.0850	- 0.0142	0.0443

5. Discussion

A great white shark surrounded by fish at Seal Island, South Africa (Morne Hardenberg)

The previous decade has seen an improvement in our understanding of white shark ecology and behaviour at various aggregation sites around the world, including in False Bay (Bruce *et al.* 2006; Bruce 2008; Hussey *et al.* 2012; Jorgensen *et al.* 2012; Kock *et al.* 2013). In False Bay, research initially focussed on the extraordinary predatory-prey behaviour at Seal Island (Martin *et al.* 2005; Hammerschlag *et al.* 2006; Kock *et al.* 2013), but more recently attention has focussed on the inshore region of False Bay with suggestions by both Kock *et al.* (2013) and Weltz *et al.* (2013) that white sharks (females in particular) aggregate along the inshore region in summer to forage on a variety of teleost and chondrichthyan prey species. In this study, I provide evidence in support of this prediction using randomization tests. These tests suggest that both the occurrence and frequency of white shark sightings at two inshore beaches, Muizenberg and Fish Hoek, are non-random with respect to both the presence and frequency of fish sightings. Furthermore, I found that the probability of white shark sightings was influenced by SST, ENSO and treknetting, which together suggests a complex interaction between abiotic and biotic variables influencing white shark presence and frequency of visits to these inshore areas of False Bay.

5.1 Detection of white sharks along the inshore region

The data collected by the shark spotting program is valuable in that it monitors the presence of white sharks at select beaches in False Bay for 365 days of the year. However, given that the data collection is dependent on the observers' ability to visually detect sharks swimming close to shore, it is important to consider what implications detectability has on the observed patterns. It is likely that some fish or sharks were not detected, which would mean that the numbers presented here are lower than actual presence, and thus represent an index of abundance, rather than the actual number of sharks present at both beaches.

In poor spotting conditions, it is more likely to spot sharks compared to fish because of the differences between their colour, shape and size (personal observation, Monwabisi Sikweyiya). Thus, if detectability was driving the observed relationship between fish and sharks, one would expect more shark sightings than fish sightings which is not the case. Even though sharks are more detectable than fish we still found a pattern between shark presence and prey fish availability. At Muizenberg and Fish Hoek, the predominant summer (southerly) winds are onshore which typically results in high wave action and poor water clarity. In contrast, the predominant winter (northerly) winds are offshore and result in very clean, but colder upwelling waters close to shore. Given that most shark sightings are recorded during summer when spotting conditions are on average more difficult I would argue that the observed trends of more sharks being sighted in summer are a real behavioural trend.

Due to the large size of white sharks (2 – 5 m range and 3.5 m average in False Bay, Hewitt (2014)), spotters can invariably distinguish between them and smaller species. However, misidentification may occur when large >2 m bronze whaler (*Carcharhinus brachyurus*) are on the inshore. Consequently, shark sighting estimates presented here may be over-estimated and the future use of drones to confirm the identity of the shark species in the 2 – 3 m range will be an important step in addressing this source of error.

5.2 White shark sightings

The annual number of white shark sightings varied markedly across the 10-year study periods from 2006 - 2016. The number of sightings initially decreased from 2006 - 2009, but this was followed by a significant increase in sightings in 2010 and 2011 (Weltz *et al.* 2013). Further analysis of the data (this study) showed another decrease from 2012 - 2016. However, the overall trend from 2006 - 2016 is of a slight increase in the number of white shark sightings. It is not currently known whether the South African white shark population is stable, increasing or decreasing, and datasets like these will be valuable in the longer term to better understand the population status. However, given the k-selected characteristics of white sharks, the annual variability is unlikely to be driven at the population level, but rather due to changes in distribution. Malcolm *et al.* (2001) suggested that inter-annual variations in white shark sightings are largely independent of the actual size of the white shark population and are more likely to mirror changes in the distribution of the population associated with variation in environmental factors and the influence these have on both prey distribution and predators. This statement is supported by the results of this study which found evidence for an influence of biological (fish and treknetting presence) and environmental (SST and ENSO) variables on the inshore presence of white sharks.

5.2.1 Dependencies among predictor variables

Globally most white shark aggregations occur in cold and temperate waters with sharks being capable of maintaining a warmer body temperature than the ambient water temperature (Goldman 1997; Klimley *et al.* 2001) and hence being characterised by a high temperature tolerance (Carey *et al.* 1982). Shark sightings occurred across a broad range of SST within this study (11 - 23°C), but the possibility of a shark being sighted increased with SST between 17.49 - 18.57°C. This supports the previous findings of Weltz (2012) and Goldman (1997) who recorded shark sightings at SST ranging from 13 - 22°C, but with peak sightings between 18 - 20°C (Weltz *et al.* 2013). Similarly in the warmer waters of the KwaZulu-Natal coastline, 63% of all white shark captures in gill nets occurred when SST was between 19 - 22°C (Cliff *et al.*

1989) while off the coast of California white sharks are detected in water temperatures ranging from 16 - 22°C (Dewar *et al.* 2004). Together these results suggest that white shark presence is affected by SST with more sharks detected when SST's are 17 - 22°C. Whether this is a direct (thermoregulatory) or indirect (prey availability) effect remains debateable.

Given the wide temperature tolerance and endothermic abilities of white sharks it is unlikely that increased presence at this narrow temperature range reflects a thermoregulatory constraint. Although, some studies suggest that females prefer warmer waters to promote the growth and development of young *in utero* (Jorgensen *et al.* 2012; Towner *et al.* 2013a). However this explanation is unlikely to define the apparent preference for warmer temperatures at the inshore sites sampled here, because most sharks sampled in False Bay are sexually immature (Kock *et al.* 2013).

Alternatively, as argued by Weltz *et al.* (2013) warmer waters are known to influence the presence of various prey species and may thus act as a cue for white sharks to adjust their distribution to increase their overlap with potential food (Ferreira *et al.* 1996; Robbins *et al.* 2012). Fish presence at both beaches showed a clear seasonal pattern with warmer SST, peaking in the warmer months of the year at 17.94°C. Warmer temperatures have been shown to boost the productivity, biomass and biodiversity of the inshore ecosystem within False Bay (Lamberth *et al.* 1995; Clark *et al.* 1996b).

In spring, many fish species in False Bay spawn, which is timed for recruitment into the surf-zone during summer where both food and oxygen levels are high and provide favourable conditions for the growth and survival of the juvenile fish (Clark *et al.* 1996b). The primary food source along the inshore region of False Bay during spring and summer for smaller fish are the surf-diatoms e.g. *Anaulus birostratus/australis* (Talbot *et al.* 1990) which is corroborated by the finding that 80% of the fish catches made by treknetters along the northern shore of False Bay occurred in the presence of diatom patches of *A. birostratus* (Clark *et al.* 1996a). Given the clear seasonal pattern of fish at both beaches it is perhaps not surprising that treknetting increased during the warmer months with a higher probability of occurrence when both prey fish and white sharks were present. Thus, the probability of a white shark sighting was 38% higher when treknetting was in progress on a given day. Treknetting was also 41% more likely when diatoms were present.

Diatoms are promoted by intermediate energy surf zones combined with longshore or rip currents and strong onshore winds, all of which are common features along the north shore of False Bay (Talbot *et al.* 1990; Clark *et al.* 1996a). Peaks of diatom patches have been recorded in Muizenberg during spring, summer and autumn with the lowest occurrence of diatom patches recorded in July (Clark *et al.* 1996b). Although diatom patches were rarely sighted at Fish Hoek beach they were common at Muizenberg and peaked in spring and autumn with the warmer months have marginally higher sightings compared to winter months. The lack of a marked seasonal pattern for diatoms is similar to the findings of Campbell *et al.* (1988) who showed that patches of *A. birostratus* recorded over a year revealed no seasonal trends, a finding they concluded related to the lack of an effect of temperature on the yearly bioaccumulation of diatom patches (Talbot *et al.* 1990). It is therefore possible that diatom presence along the north shore of False Bay is driven more by the combination of accumulating wind and wave action (Clark *et al.* 1996a) confounding any clear relationship with seasonality and SST in this study, but perhaps explaining the overall higher presence during the windier summer season when south-easterly winds dominate the weather and increase wave action.

The increase in diatoms during warmer months is hypothesised to promote the inshore movement of teleost prey such as harders (e.g. southern mullet, *Liza richardsonii*), yellowtail (*Seriola lalandi*) and white steenbras (*Lithognathus lithognathus*) (Lamberth *et al.* 1994; Clark *et al.* 1996b) with anecdotal observations by both fishermen and Shark Spotters of white sharks following and feeding on these species along the inshore region (Kock 2014). White sharks were 66% more likely to be detected at both beaches when fish was present, which would decrease to 42% if the relationship was purely random. Teleosts together with marine mammals and other chondrichthyans comprise the majority of the white sharks' diet (Cliff *et al.* 1989; Cortés 1999; Heithaus 2001b; Hussey *et al.* 2012) with teleosts considered to be more important in the diet of sub-adult than adult sharks (Estrada *et al.* 2006; Kim *et al.* 2012). While shark size is not a variable that can be reliably estimated by Shark Spotters, Kock *et al.* (2013) report that most of the sharks in False Bay are juveniles and sub-adults.

Similar to white sharks, dolphins are predicted to actively track the presence and movement of migratory teleosts (Heithaus 2001b,a). A variety of dolphins including bottlenose (*Tursiops truncates aduncus*), common (*Delphinus delphis*), heavyside's (*Cephalorhynchus heavisidii*) and dusky (*Lagenorhynchus obscurus*) occur within False Bay (Findlay *et al.* 1992). Despite this and the similar seasonal peak (Dec - Mar) in sightings during the summer months there was no difference in the probability of detecting a white shark when dolphins were present or not. The lack of overlap may be a consequence of the different fish targeted by white sharks and dolphins. Unfortunately, the data does not always specify which species of fish are present, but it is likely that sharks and dolphins probably target different species e.g. dolphins may target schools of baitfish, with southern mullet making up 26.5% of the diet of bottlenose dolphins along the southern African coast (Sekiguchi *et al.* 1992). White sharks on the other hand target schools of larger predatory fish like yellowtail. Furthermore it has been shown that various shark species, including white sharks, predate on dolphins (Heithaus 2001b; Heithaus *et al.* 2002). In South Australia dolphin remains were found in 44% of analysed white shark stomachs (Bruce 1992) and in False Bay Shark Spotters have observed a large white shark chasing a pod of common dolphins off Muizenberg beach (Shark Spotters, unpublished data).

Thus, it might also be possible that dolphins avoid sharks at a finer scale because they are vulnerable to being predated on themselves.

Together with previous works my findings suggest a shift in the white sharks' diet from young-of-the-year seals in winter to inshore fish during summer in False Bay, which conforms to the predictions of the 'optimal diet theory' (ODT) (Heithaus 2001b; Carrier *et al.* 2012), where predators rank their potential prey items concordant to their net energy gain (energy content of the prey minus the energy used in capture and handling of the prey) (Stephens *et al.* 1986). Achieving this shift in diet requires selection of the habitat with the highest energetic return (Weimerskirch *et al.* 2007; Carrier *et al.* 2012), which invariably means a move to areas with the highest spatial density of available prey (Weimerskirch *et al.* 2007). White sharks in Australia are locally abundant when snapper (*Chrysophrys auratus*) availability peaks, leaving the area rapidly once this food source is depleted or has moved on (Bruce *et al.* 2006). Similarly the occurrence of white sharks at the South Farallon Islands, California increases after the arrival of young northern elephant seals (*Mirounga angustirostris*), which are the preferred prey (Klimley *et al.* 1996). This dynamic between prey and predators is evident in other shark species too, with scalloped hammerhead sharks, *Sphyrna lewini* in Florida Bay spatially overlapping with their teleost prey (Torres-Rojas *et al.* 2006). Thus, predators can improve their chances of encountering and successfully feeding on their preferred prey by aligning their movements and effort with the availability of their prey (Hammerschlag *et al.* 2006), which might explain the spatio-temporal distribution of white shark on the inshore of False Bay.

5.2.2 ENSO

The ENSO has been described as a major global climate phenomenon which has an impact on marine ecosystems and the distribution and abundance of marine animals (Radovich 1961; Karinen *et al.* 1985). My results suggest that white shark presence at two beaches in False Bay may also be influenced by ENSO, with a higher probability of detecting sharks during weak La Niña years. These events are defined by colder (< 0.5°C anomalies) than average SST and an increase in strong south easterly winds (Rouault *et al.* 2010; Dufois *et al.* 2012; Wolter 2016) which favour the accumulation of diatom patches (Clark *et al.* 1996a) and consequently higher primary production (Towner *et al.* 2013a). It is thus possible that very weak La Niña events, although associated with cooler waters, have higher white shark presence because they support or attract more prey fish species. White shark catches off KwaZulu-Natal were also higher during La Niña conditions (Cliff *et al.* 1996). However, in strong La Niña events, there is a decline in shark sightings suggesting a negative impact on the inshore movements of white sharks in False Bay, during extreme conditions.

By contrast El Niño events are defined by warmer (> 0.5°C anomalies) than average water temperatures, a decrease in south easterly winds and a concomitant decrease in upwelling and thus primary production in False Bay (Rouault *et al.* 2010; Dufois *et al.* 2012). If white sharks are using the inshore region of False Bay to feed, then reduced primary productivity would result in less prey, which in turn could result in fewer sharks using the bay during these periods. The latest El Niño event of 2015/2016 is one of the strongest ever recorded and is associated with a severe drought in South African (FAO 2016). This event was also associated with very low shark sightings at Muizenberg and Fish Hoek (this study) as well as at Seal Island (Kock, unpublished data). Our data also suggests that white shark sightings decline during very strong events, either cold or warm, with only a few sharks visiting the bay during these extreme conditions.

5.3 Application of results to shark safety programs

The Shark Spotting program in Cape Town uses a red flag to alert water users of the increased risk of encountering a shark. This flag is flown for one hour following a shark sighting, during whale strandings, when there are schools of fish sighted, particularly yellowtail (*Seriola lalandi*), and when treknetting taking place. In addition to supporting the findings of Weltz *et al.* (2013) that the probability of sighting a shark is higher when the water temperature is >18°C, this study confirms that there is an increased probability of sighting a shark when schools of fish are present. This provides scientific support for the spotter's deployment of the red (high risk) flag when schools of fish are present at both beaches. This result in addition to increased sightings of sharks during treknetting can be used to improve the education and awareness of the key drivers of shark presence at popular beaches. For example, following the findings of Weltz *et al.* (2013) the City of Cape Town included information on both SST and lunar phase in their press releases on shark safety and tips to avoid encountering shark, and the Shark Spotters provide this information on shark signage and their mobile app.

5.4 Future research

False Bay is the biggest natural bay in South Africa and supports a complex ecosystem and many livelihoods (Shannon 1985). As one of the apex predators within this system, the status and ecological role of white sharks can be used to assess its health and productivity (Sekiguchi *et al.* 1992; Cortés 1999) and thus long term monitoring of the population is essential.

To improve the confidence in the shark sighting data I strongly support the use of drones to confirm the identity of sharks along the inshore and strongly recommend that telemetry data is compared with the observational dataset from the Shark Spotters to provide an estimate of detectability which can then be used to improve estimates.

Wind speed and direction emerged as potentially important variables, driving diatom patches and hence fish and predator presence along the inshore in this study. Weltz (2012) did include wind speed and direction within a generalized additive mixed model and concluded that the effect was not significant. I thus omitted wind from my analyses, but suggest that future work should include such data with incorporation of a possible lag effect of the wind direction and speed on the False Bay ecosystem and ultimately on white shark inshore movement into statistical models or randomization tests.

The significant effect of ENSO on shark sightings from 2006 – 2015 is an important finding and I would recommend that this analysis is extended to include data from 2016, which was associated with exceptionally low number of shark sightings at both Seal Island and along the inshore.

Lastly, I would recommend that the composition of the treknetting catches should be monitored to provide information on the type of fish present and whether different prey species can be shown to influence the probability of shark sightings. These data could be supported by acoustic telemetry data of large pelagic fish (such as white steenbras and yellowtail) on the inshore areas, to confirm the importance of these species to the white sharks' diet in the False Bay ecosystem.

6. Conclusions

As I predicted, the presence of fish had a significant influence on white shark presence and the frequency of sightings at both Muizenberg and Fish Hoek. My results also confirmed that both white shark presence and fish presence are influenced by SST with a higher probability of spotting a shark at temperatures between 17.49 and 18.57°C and at 17.94°C for fish. The SST influence on white sharks could reflect behavioural thermoregulation of white sharks or as I argue reflects an increase in teleost prey availability which in turn attracts the sharks to the inshore area in summer. Other studies have previously suggested that the temperature effect on white sharks is secondary (Pyle *et al.* 1996; Robbins *et al.* 2012; Weltz *et al.* 2013) which we support with these findings.

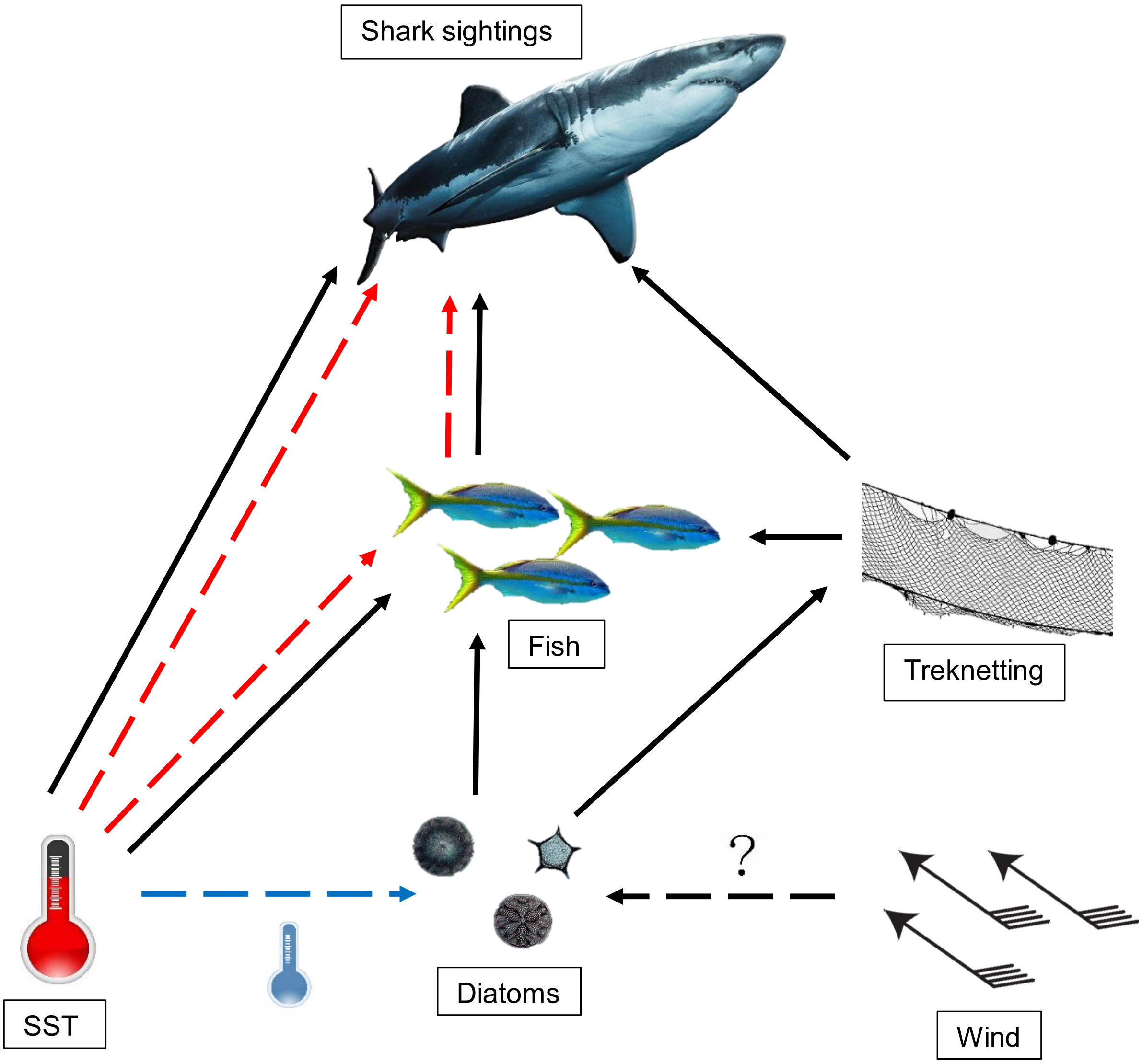


Figure 6.1: A mental map of the possible drivers of the presence of diatoms, treknetting, prey fish and white sharks along the inshore region of two popular recreational beaches in False Bay. Hypothesized

connection of environmental and biological variables analysed in this study on the inshore of False Bay, with the black solid arrows giving the found influence of one variable on the other one. The red dashed arrows describe the hypothesized direct or indirect warm water influence on white sharks and the blue dashed arrow the cold-water influence on the diatom. The potential influence of strong south-easterly wind in summer rather than SST is here displayed by the black dotted arrow.

Inshore movement of dolphins were also shown to follow a seasonal pattern, but seem to be statistically independent from SST, fish or white shark presence. The relationship between dolphins and white sharks with the competition and the predatory risk is referred to as asymmetrical intraguild predation (IGP), which generates a special trade-off for the dolphins (Carrier *et al.* 2012). It was stated to have an extreme effect onto the concurrence and habitat usage of both intraguild predator (here white sharks) and prey (here dolphins) (Heithaus 2001a; Carrier *et al.* 2012). It could be the reason for the possible predator avoidance of dolphins at the inshore of False Bay. Since there is a global lack of data on this relationship (Heithaus 2001b) my study provides valuable information on the habitat usage of white sharks and odontocetes, promoting either co-occurrence or avoidance.

My findings support previous studies (Kock *et al.* 2013; Weltz *et al.* 2013) showing the marked seasonal presence of white sharks along the inshore region of False Bay. But my study provides the first evidence to suggest that this may be a function of increased fish presence in spring and summer. The effect of fish migration on the movement patterns of white sharks have been previously described by Bruce *et al.* (2006), where white sharks followed fish shoals along the Australian coast. When our data are overlaid with the increased presence of naïve seals at Seal Island in winter, it would appear that white sharks in False Bay are moving in response to the availability of preferred foods.

I found a highly variable inter-annual trend in shark sightings at two of False Bay’s most popular beaches, with an overall increase in shark sightings since 2006. The variability is likely to be caused by variations in environmental and biological variables rather than reflecting changes at the population level (Malcolm *et al.* 2001). However, ongoing data collection is essential to better understand what the long-term trend continues to do.

We now know that there is a high spatial overlap between people and sharks in summer along the inshore areas of False Bay, and furthermore that there are greater probabilities of encountering a shark during SST of 18°C and during new moon. My results also show an increased risk of encounters when fish are present, during treknetting and during La Niña years. I therefore strongly recommend that this information also be incorporated into shark education and safety programmes in Cape Town to improve people’s ability to asses risk and make informed decisions when using the ocean.

References

Adams DC, Anthony CD. 1996. Using randomization techniques to analyse behavioural data. *Animal Behaviour*, 51: 733-738.

AfriGIS (Pty) Ltd. 2017a. False Bay. *Google Maps.* ['Retrieved from' https://www.google.de/maps/@-34.1123223,18.4273218,13z/data=!3m1!4b1!4m2!6m1!1s1-cD2znNz4twdRFkH01XUaWpjkqo?hl=en]. ['accessed' 08/03/2017]

AfriGIS (Pty) Ltd. 2017b. Fish Hoek. *Google Maps.* ['Retrieved from' https://www.google.de/maps/@-34.1452286,18.4311104,17z/data=!3m1!4b1!4m2!6m1!1s1F5_dyLEnljD4-AEMymq8x9pqXcI?hl=en]. ['accessed' 08/03/2017]

AfriGIS (Pty) Ltd. 2017c. Muizenberg. *Google Maps.* ['Retrieved from' https://www.google.de/maps/@-34.1125462,18.4610653,17z/data=!3m1!4b1!4m2!6m1!1s1UxKRGUtLwXfPsss5hsytdF8icBQ?hl=en]. ['accessed' 08/03/2017]

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

Anderson MJ. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 626-639.

Anderson SD, Chapple TK, Jorgensen SJ, Klimley AP, Block BA. 2011. Long-term individual identification and site fidelity of white sharks, Carcharodon carcharias, off California using dorsal fins. *Marine Biology*, 158: 1233-1237.

Andreotti S, Rutzen M, van der Walt S, Von der Heyden S, Henriques R, Meÿer M, Oosthuizen H, Matthee CA. 2016. An integrated mark-recapture and genetic approach to estimate the population size of white sharks in South Africa. *Marine Ecology Progress Series*, 552: 241-253.

Armstrong M, Berruti A, Colclough J. 1987. Pilchard distribution in South African waters, 1983–1985. *South African Journal of Marine Science*, 5: 871-886.

Atkins G. 1970. Thermal structure and salinity of False Bay. *Transactions of the Royal Society of South Africa*, 39: 117-128.

Bass A, D'aubrey J, Kistnasamy N. 1975. Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding Mustelus and Carcharhinus) and Sphyrnidae. *S. Afr. Ass. Mar. Biol. Res., Oceanogr. Res. Inst., Invest. Rep*, 39: 1-100.

Bernvi D. 2016. Ontogenetic influences on endothermy in the great white shark (Carcharodon carcharias). Master thesis, Stockholm University.

Best LN, Attwood CG, Da Silva C, Lamberth SJ. 2013. Chondrichthyan occurrence and abundance trends in False Bay, South Africa, spanning a century of catch and survey records. *African Zoology*, 48: 201-227.

Bonfil R, Meÿer M, Scholl MC, Johnson R, O'Brien S, Oosthuizen H, Swanson S, Kotze D, Paterson M. 2005. Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science*, 310: 100-103.

Boustany AM, Davis SF, Pyle P, Anderson SD, Le Boeuf BJ, Block BA. 2002. Satellite tagging: expanded niche for white sharks. *Nature*, 415: 35.

Boustany AM, Weng KC, Anderson SD, Pyle P, Block BA. 2008. Case study: White shark movements in the North Pacific pelagic ecosystem. *Sharks of the open ocean: Biology, fisheries and conservation*: 82-86.

Bruce B, Stevens J, Malcolm H. 2006. Movements and swimming behaviour of white sharks (Carcharodon carcharias) in Australian waters. *Marine Biology*, 150: 161-172.

Bruce BD. 1992. Preliminary observations on the biology of the white shark, Carcharodon carcharias, in south Australian waters. *Marine and Freshwater Research*, 43: 1-11.

Bruce BD. 2008. The biology and ecology of the white shark, Carcharodon carcharias. *Sharks of the open ocean: Biology, fisheries and conservation*: 69-81.

Campbell E, Bate G. 1988. The photosynthetic response of surf phytoplankton to temperature. *Botanica marina*, 31: 251-256.

Carey FG, Kanwisher JW, Brazier O, Gabrielson G, Casey JG, Pratt Jr HL. 1982. Temperature and activities of a white shark, Carcharodon carcharias. *Copeia*: 254-260.

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

Carrier JC, Musick JA, Heithaus MR. 2012. *Biology of sharks and their relatives*. CRC press.

Castro JI. 2012. A Summary of Observations on the Maximum Size Attained by the White. *Global perspectives on the biology and life history of the white shark*: 85.

Chapple TK, Jorgensen SJ, Anderson SD, Kanive PE, Klimley AP, Botsford LW, Block BA. 2011. A first estimate of white shark, Carcharodon carcharias, abundance off Central California. *Biology Letters*: rsbl20110124.

Cheal DB. 2016. South Africa map with capital Pretoria. [accessed 01/03 2017].

Clark B, Bennett B, Lamberth S. 1994. A comparison of the ichthyofauna of two estuaries and their adjacent surf zones, with an assessment of the effects of beach-seining on the nursery function of estuaries for fish. *South African Journal of Marine Science*, 14: 121-131.

Clark B, Bennett B, Lamberth S. 1996a. Factors affecting spatial variability in seine net catches of fish in the surf zone of False Bay, South Africa. *Marine Ecology Progress Series*, 131: 17-34.

Clark B, Bennett B, Lamberth S. 1996b. Temporal variations in surf zone fish assemblages from False Bay, South Africa. *Marine Ecology Progress Series*, 131: 35-47.

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

Cliff G, Dudley SF. 2011. Reducing the environmental impact of shark-control programs: a case study from KwaZulu-Natal, South Africa. *Marine and Freshwater Research*, 62: 700-709.

Cliff G, Van Der Elst R, Govender A, Witthuhn T, Bullen E. 1996. First estimates of mortality and population size of white sharks on the South African coast. *Great white sharks: the biology of Carcharodon carcharias*: 393-400.

Colijn F, Van Buurt G. 1975. Influence of light and temperature on the photosynthetic rate of marine benthic diatoms. *Marine Biology*, 31: 209-214.

Collins M, An S-I, Cai W, Ganachaud A, Guilyardi E, Jin F-F, Jochum M, Lengaigne M, Power S, Timmermann A. 2010. The impact of global warming on the tropical Pacific Ocean and El Niño. *Nature Geoscience*, 3: 391-397.

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

Compagno LJ. 2001. *Sharks of the world: an annotated and illustrated catalogue of shark species known to date*, vol. 2. Food & Agriculture Org.

Cortés E. 1999. Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science: Journal du Conseil*, 56: 707-717.

Daly R, Smale MJ, Cowley PD, Froneman PW. 2014. Residency patterns and migration dynamics of adult bull sharks (Carcharhinus leucas) on the east coast of southern Africa. *Plos One*, 9: e109357.

De Vos A, O'Riain JM, Meÿer MA, Kotze PG, Kock AA. 2015. Behavior of Cape fur seals (Arctocephalus pusillus pusillus) in response to spatial variation in white shark (Carcharodon carcharias) predation risk. *Marine Mammal Science*, 31: 1234-1251.

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

Domeier ML. 2009. Experimental scavenging preference for the adult white shark, Carcharodon carcharias. *California Fish and Game*, 95: 140-145.

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

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

Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, English CA, Galindo HM, Grebmeier JM, Hollowed AB, Knowlton N. 2012. Climate change impacts on marine ecosystems. *Marine Science*, 4.

Dudley SF, Simpfendorfer CA. 2006. Population status of 14 shark species caught in the protective gillnets off KwaZulu–Natal beaches, South Africa, 1978–2003. *Marine and Freshwater Research*, 57: 225-240.

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

Dulvy NK, Freckleton RP, Polunin NV. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology letters*, 7: 410-416.

Edgington E. 1986. Randomization tests. In: Kotz S JN editor. *Encyclopedia of statistical sciences*. New York: Wiley. p. p 530–583.

Enfield DB, Allen J. 1980. On the structure and dynamics of monthly mean sea level anomalies along the Pacific coast of North and South America. *Journal of Physical Oceanography*, 10: 557-578.

Engelbrecht T. 2013. The impact of White Shark (Carcharodon carcharias) sightings and attacks on recreational water use patterns in False Bay, University of Cape Town.

Estrada JA, Rice AN, Natanson LJ, Skomal GB. 2006. Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology*, 87: 829-834.

FAO. 2016. El Niño set to have a devastating impact on southern Africa's harvests and food security. [accessed 15/07/2016 2016].

Fauchereau N, Trzaska S, Rouault M, Richard Y. 2003. Rainfall variability and changes in southern Africa during the 20th century in the global warming context. *Natural Hazards*, 29: 139-154.

Fergusson I, Compagno LJV, & Marks M. 2009. Carcharodon carcharias. In: Species IRLoT editor. *IUCN 2013*.

Ferreira C, Ferreira T. 1996. Population dynamics of white sharks in South Africa. *Great white sharks: the biology of Carcharodon carcharias. Academic, San Diego*: 381-391.

Findlay K, Best P, Ross G, Cockcroft V. 1992. The distribution of small odontocete cetaceans off the coasts of South Africa and Namibia. *South African Journal of Marine Science*, 12: 237-270.

Fisher RA. 1922. On the interpretation of χ 2 from contingency tables, and the calculation of P. *Journal of the Royal Statistical Society*, 85: 87-94.

Fowler SL, Cavanagh RD, Camhi M, Burgess GH, Cailliet GM, Fordham SV, Simpfendorfer CA, Musick JA. 2005. *Sharks, rays and chimaeras: the status of the Chondrichthyan fishes: Status Survey*, vol. 63. Switzerland and Cambridge, UK: IUCN/SSC Shark Specialist Group.

Goldman K, Anderson S, McCosker J, Klimley A. 1996. Temperature, swimming depth, and movements of a white shark at the South Farallon Islands, California. *Great White Sharks: The Biology of Carcharodon carcharias, Academic Press, San Diego*: 111-120.

Goldman KJ. 1997. Regulation of body temperature in the white shark, Carcharodon carcharias. *Journal of Comparative Physiology B*, 167: 423-429.

Goldman KJ, Anderson SD. 1999. Space utilization and swimming depth of white sharks, Carcharodon carcharias, at the South Farallon Islands, central California. *Environmental Biology of Fishes*, 56: 351-364.

Hamady LL, Natanson LJ, Skomal GB, Thorrold SR. 2014. Vertebral bomb radiocarbon suggests extreme longevity in white sharks. *Plos One*, 9: e84006.

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

Hardenberg M 2015. Cover picture: White Shark at Guadalupe.

Heithaus MR. 2001a. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos*, 92: 542-554.

Heithaus MR. 2001b. Predator–prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *Journal of Zoology*, 253: 53-68.

Heithaus MR, Dill LM. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83: 480-491.

Heithaus MR, Frid A, Wirsing AJ, Worm B. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, 23: 202-210.

Hennessy M. 2017, 19/04/2017. Australian government to consider shark cull after death of 17-year-old. *The Journal*.

Hewitt AM. 2014. Demographics of a seasonal aggregation of white sharks at Seal Island, False Bay, South Africa, University of Cape Town.

Hoegh-Guldberg O, Bruno JF. 2010. The impact of climate change on the world’s marine ecosystems. *Science*, 328: 1523-1528.

Hopkins TE, Cech Jr JJ. 2003. The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. *Environmental Biology of Fishes*, 66: 279-291.

Humston R, Ault JS, Lutcavage M, Olson DB. 2000. Schooling and migration of large pelagic fishes relative to environmental cues. *Fisheries Oceanography*, 9: 136-146.

Huntley ME, Lopez MD. 1992. Temperature-dependent production of marine copepods: a global synthesis. *American Naturalist*: 201-242.

Hussey NE, McCann HM, Cliff G, Dudley SF, Wintner SP, Fisk AT. 2012. Size-based analysis of diet and trophic position of the white shark (Carcharodon carcharias) in South African waters. *Global Perspectives on the Biology and Life History of the White Shark'.(Ed. ML Domeier.) pp*: 27-49.

Irion D, Noble L, Kock A, Gennari E, Dicken M, Hewitt A, Towner A, Booth A, Smale M, Cliff G. in press. Pessimistic assessment of white shark population status in South Africa: Comment on Andreotti et al. (2016).

ISAF International Shark Attack File. 2012. World's Confirmed Unprovoked Attacks by White Sharks. Florida Museum of Natural History, University of Florida. http://www.flmnh.ufl.edu/fish/sharks/White/World.htm. [accessed 17/08/2017.

Jaccard P. 1912. The distribution of the flora in the alpine zone. *New phytologist*, 11: 37-50.

Johnson R, Bester MN, Dudley SF, Oosthuizen WH, Meÿer M, Hancke L, Gennari E. 2009. Coastal swimming patterns of white sharks (Carcharodon carcharias) at Mossel Bay, South Africa. *Environmental Biology of Fishes*, 85: 189-200.

Jordan R. 1991. Impact of ENSO events on the southeastern Pacific region with special reference to the interaction of fishing and climatic variability. *ENSO Teleconnections Linking Worldwide Climate Anomalies: scientific basis and societal impacts*: 401-430.

Jorgensen SJ, Chapple TK, Anderson S, Hoyos M, Reeb C, Block BA, Domeier M. 2012. Connectivity among white shark coastal aggregation areas in the Northeastern Pacific. *Global perspectives on the biology and life history of the white shark*: 159-168.

Jorgensen SJ, Reeb CA, Chapple TK, Anderson S, Perle C, Van Sommeran SR, Fritz-Cope C, Brown AC, Klimley AP, Block BA. 2009. Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society of London B: Biological Sciences*: rspb20091155.

Kaplan A, Cane MA, Kushnir Y, Clement AC, Blumenthal MB, Rajagopalan B. 1998. Analyses of global sea surface temperature 1856–1991. *Journal of Geophysical Research: Oceans*, 103: 18567-18589.

Karinen J, Wing B, Straty R. 1985. Records and sightings of fish and invertebrates in the eastern Gulf of Alaska and oceanic phenomena related to the 1983 El Niño event. *El Nino North: Nino effects in the Eastern Subarctic Pacific Ocean. Edited by WS Wooster and DL Fluharty. Washington Sea Grant Publication WSG-WO*: 85-83.

Kim SL, Tinker MT, Estes JA, Koch PL. 2012. Ontogenetic and among-individual variation in foraging strategies of northeast Pacific white sharks based on stable isotope analysis. *Plos One*, 7: e45068.

Kimura S, Sugimoto MN. 1997. Migration of albacore, Thunnus alalunga, in the North Pacific Ocean in relation to large oceanic phenomena. *Fisheries Oceanography*, 6: 51-57.

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

Klimley A, Pyle P, Anderson S. 1996. The behavior of white sharks and their pinniped prey during predatory attacks. *Great white sharks: the biology of Carcharodon carcharias (ed. AP Klimley and DG Ainley)*: 175-191.

Klimley AP, Le Boeuf BJ, Cantara KM, Richert JE, Davis SF, Van Sommeran S, Kelly JT. 2001. The hunting strategy of white sharks (Carcharodon carcharias) near a seal colony. *Marine Biology*, 138: 617-636.

Kock A. 2014. Behavioral ecology of white sharks (Carcharodon carcharias) in False Bay, South Africa: Towards improved management of a threatened apex predator, Ph. D. thesis, University of Cape Town, Cape Town, South Africa.

Kock A. (2016). White Shark activity in False Bay in 2016. [pers. comm.]. alison.kock@gmail.com.

Kock A, O'Riain MJ, Mauff K, Meÿer M, Kotze D, Griffiths C. 2013. Residency, habitat use and sexual segregation of white sharks, Carcharodon carcharias in False Bay, South Africa. *Plos One*, 8: e55048.

Kock A, Titley S, Petersen W, Sikweyiya M, Tsotsobe S, Colenbrander D, Gold H, Oelofse G. 2012. Shark spotters: A pioneering shark safety program in Cape Town, South Africa. *Global perspectives on the biology and life history of the great white shark*: 447-467.

Ladah LB, Tapia FJ, Pineda J, López M. 2005. Spatially heterogeneous, synchronous settlement of Chthamalus spp. larvae in northern Baja California.

Lamberth S, Bennett B, Clark B. 1994. Catch composition of the commercial beach-seine fishery in False Bay, South Africa. *South African Journal of Marine Science*, 14: 69-78.

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

Largier EJ, Cheng B, Higgason K. 2009. Draft Climate Change Site Scenario.

Laroche RK, Kock AA, Dill LM, Oosthuizen WH. 2008. Running the gauntlet: a predator–prey game between sharks and two age classes of seals. *Animal Behaviour*, 76: 1901-1917.

Laurs RM, Fiedler PC, Montgomery DR. 1984. Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep Sea Research Part A. Oceanographic Research Papers*, 31: 1085-1099.

Leatherwood S. 1977. Some preliminary impressions on the numbers and social behavior of free-swimming, bottlenosed dolphin calves (Tursiops truncatus) in the northern Gulf of Mexico. *Breeding dolphins: present status, suggestions for the future*: 143-167.

Lima SL. 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, 48: 25-34.

Long DJ, Hanni KD, Pyle P, Roletto J, Jones RE, Bandar R. 1996. White shark predation on four pinniped species in central California waters: geographic and temporal patterns inferred from wounded carcasses. *Great White Sharks: The Biology of Carcharodon carcharias, Academic Press, San Diego*: 263-274.

Malcolm H, Bruce BD, Stevens JD. 2001. *A review of the biology and status of white sharks in Australian waters*. CSIRO Marine Research Hobart.

Martin RA. 2004. Northerly distribution of white sharks, Carcharodon carcharias, in the eastern Pacific and relation to ENSO events. *Marine Fisheries Review*, 66: 16-26.

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

Mazzarella A, Giuliacci A, Liritzis I. 2010. On the 60-month cycle of multivariate ENSO index. *Theoretical and applied climatology*, 100: 23-27.

Miller KA, Fluharty DL. 1992. El Niño and variability in the northeastern Pacific salmon fishery: implications for coping with climate change. *Climate variability, climate change and fisheries. Cambridge University Press, Cambridge*: 49-88.

Neumann DR. 2001. Seasonal movements of short-beaked common dolphins (Delphinus delphis) in the north-western Bay of Plenty, New Zealand: Influence of sea surface temperature and El Niño/La Niña.

Pardini AT, Jones CS, Noble LR, Kreiser B, Malcolm H, Bruce BD, Stevens JD, Cliff G, Scholl MC, Francis M. 2001. Sex-biased dispersal of great white sharks. *Nature*, 412: 139-140.

Pepin P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 503-518.

Peres-Neto PR, Olden JD. 2001. Assessing the robustness of randomization tests: examples from behavioural studies. *Animal Behaviour*, 61: 79-86.

Philippon N, Rouault M, Richard Y, Favre A. 2012. The influence of ENSO on winter rainfall in South Africa. *International Journal of Climatology*, 32: 2333-2347.

Podestá GP, Browder JA, Hoey JJ. 1993. Exploring the association between swordfish catch rates and thermal fronts on US longline grounds in the western North Atlantic. *Continental Shelf Research*, 13: 253-277.

Pollack M. 2015. City to consider a proposed trial installation of a shark exclusion net for Fish Hoek Beach. [accessed 01/03 2017].

Pörtner H-O, Karl DM, Boyd PW, Cheung W, Lluch-Cota SE, Nojiri Y, Schmidt DN, Zavialov PO, Alheit J, Aristegui J. 2014. Ocean systems. *Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change*: Cambridge University Press. p. 411-484.

Prager MH, Hoenig JM. 1989. Superposed epoch analysis: a randomization test of environmental effects on recruitment with application to chub mackerel. *Transactions of the American Fisheries Society*, 118: 608-618.

Pyle P, Anderson S, Klimley A, Henderson R. 1996. Environmental factors affecting the occurrence and behavior of white sharks at the Farallon Islands, California. *Great white sharks: the biology of Carcharodon carcharias. Academic, San Diego*: 281-291.

R Development Core Team 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Radovich J. 1961. *Relationships of some marine organisms of the northeast Pacific to water temperatures: particularly during 1957 through 1959*. California Department of Fish and Game.

Reason C, Rouault M, Melice J-L, Jagadheesha D. 2002. Interannual winter rainfall variability in SW South Africa and large scale ocean–atmosphere interactions. *Meteorology and Atmospheric Physics*, 80: 19-29.

Reynolds RW, Smith TM. 1994. Improved global sea surface temperature analyses using optimum interpolation. *Journal of Climate*, 7: 929-948.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP. 2014. Status and ecological effects of the world’s largest carnivores. *Science*, 343: 1241484.

Robbins RL, Booth DJ. 2012. Seasonal sexual and size segregation of white sharks, Carcharodon carcharias, at the Neptune Islands, South Australia. *Global Perspectives on the Biology and Life History of the White Shark'.(Ed. ML Domeier.) pp*: 287-299.

Rochat L 2015. The ultimate experience is the bait ball. African Dive Adventures.

Roessig JM, Woodley CM, Cech JJ, Hansen LJ. 2004. Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries*, 14: 251-275.

Roffer MA. 1987. Influence of the environment on the distribution and relative apparent abundance of juvenile Atlantic bluefin tuna along the United States east coast.

Rouault M, Pohl B, Penven P. 2010. Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. *African Journal of Marine Science*, 32: 237-246.

Ruppert JL, Travers MJ, Smith LL, Fortin M-J, Meekan MG. 2013. Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. *Plos One*, 8: e74648.

Schlegel RW, Smit AJ. 2016. Climate Change in Coastal Waters: Time Series Properties Affecting Trend Estimation. *Journal of Climate*, 29: 9113-9124.

Sekiguchi K, Klages N, Best P. 1992. Comparative analysis of the diets of smaller odontocete cetaceans along the coast of southern Africa. *South African Journal of Marine Science*, 12: 843-861.

Sergio F, Caro T, Brown D, Clucas B, Hunter J, Ketchum J, McHugh K, Hiraldo F. 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annual review of ecology, evolution, and systematics*, 39: 1-19.

Shannon LV. 1985. The Benguela ecosystem. I: Evolution of the Benguela physical features and processes. *Oceanography and Marine Biology*, 23: 105-182.

Shark Spotters. (2016). Dolphin and white shark occurrence. [pers. comm.].

Shivji MS, Chapman DD, Pikitch EK, Raymond PW. 2005. Genetic profiling reveals illegal international trade in fins of the great white shark, Carcharodon carcharias. *Conservation Genetics*, 6: 1035-1039.

Sprivulis P. 2014. Western Australia coastal shark bites: a risk assessment. *The Australasian medical journal*, 7: 137.

Stephens DW, Krebs JR. 1986. *Foraging theory*. Princeton University Press.

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

Strong W, Murphy RC, Bruce BD, Nelson DR. 1992. Movements and associated observations of bait-attracted white sharks, Carcharodon carcharias: a preliminary report. *Marine and Freshwater Research*, 43: 13-20.

Talbot M, Bate G, Campbell E. 1990. A review of the ecology of surf-zone diatoms, with special reference to Anaulus australis. *Oceanogr Mar Biol Annu Rev*, 28: 155-175.

Torres-Rojas Y, Hernandez-Herrera A, Galvan-Magaña F. 2006. Feeding habits of the scalloped hammerhead shark, Sphyrna lewini, in Mazatlán waters, southern Gulf of California, Mexico. *Cybium*, 30: 85-90.

Tourre YM, White WB. 1995. ENSO signals in global upper-ocean temperature. *Journal of Physical Oceanography*, 25: 1317-1332.

Towner AV, Underhill LG, Jewell OJ, Smale MJ. 2013a. Environmental influences on the abundance and sexual composition of white sharks Carcharodon carcharias in Gansbaai, South Africa. *Plos One*, 8: e71197.

Towner AV, Wcisel MA, Reisinger RR, Edwards D, Jewell OJ. 2013b. Gauging the threat: the first population estimate for white sharks in South Africa using photo identification and automated software. *Plos One*, 8: e66035.

Tricas TC. 1985. Feeding ethology of the white shark, Carcharodon carcharias. *Memoirs of the Southern California Academy of Sciences*, 9: 81-91.

Warrens MJ. 2008. *Similarity coefficients for binary data: properties of coefficients, coefficient matrices, multi-way metrics and multivariate coefficients*. Psychometrics and Research Methodology Group, Leiden University Institute for Psychological Research, Faculty of Social Sciences, Leiden University.

Weimerskirch H, Pinaud D, Pawlowski F, Bost C-A. 2007. Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *The American Naturalist*, 170: 734-743.

Weltz K. 2012. The Influence of environmental variables on White Shark (Carcharodon Carcharias) sightings at False Bay beaches. M.Sc. Master, University of Cape Town Cape Town.

Weltz K, Kock AA, Winker H, Attwood C, Sikweyiya M. 2013. The Influence of Environmental Variables on the Presence of White Sharks, C archarodon carcharias at Two Popular Cape Town Bathing Beaches: A Generalized Additive Mixed Model. *Plos One*, 8: e68554.

Wolter K. 1987. The Southern Oscillation in surface circulation and climate over the tropical Atlantic, Eastern Pacific, and Indian Oceans as captured by cluster analysis. *Journal of Climate and Applied Meteorology*, 26: 540-558.

Wolter K. 2016. Discussion and comparison of recent conditions with historic El Niño conditions [accessed 15/07/2016 2016].

Wolter K, Timlin MS. Monitoring ENSO in COADS with a seasonally adjusted principal component index*1993*.

Wolter K, Timlin MS. 2011. El Niño/Southern Oscillation behaviour since 1871 as diagnosed in an extended multivariate ENSO index (MEI. ext). *International Journal of Climatology*, 31: 1074-1087.

Zuur A, Ieno E, Walker N, Saveliev A, Smith G. 2009. Mixed effects models and extensions in ecology with R. Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, editors. *New York, NY: Spring Science and Business Media*.

Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1: 3-14.