THE INFLUENCE OF ENVIRONMENTAL VARIABLES ON WHITE SHARK (*CARCHARODON CARCHARIAS*) SIGHTINGS AT FALSE BAY BEACHES

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Chapter 1: Literature review & Aims

The importance of animal movement in relation to environmental conditions

The relationship between environmental variables and animal distribution has been investigated for terrestrial species, including mammals (Svendsen 2011; Real *et al.,* 2003), birds (Seoane *et al.,* 2005), amphibians (Muths *et al.,* 2008) and reptiles (Guerrero *et al.,* 2005). Although more challenging, this relationship has also been investigated for a variety of marine animals, including marine invertebrates (Olive 1995), fish (O'Donoghue *et al.,* 2010), mammals (Littaye *et al.,* 2004) and birds (Abrahams and Kattenfeld 1997; Durant *et al.,* 2004). Researching the movement of marine animals in relation to environmental conditions dates as far back as 1920 (Orton 1920).

Monitoring habitat use and movement of top predators in relation to environmental conditions is particularly important, since they have a major influence on lower food chains and the functioning of ecosystems (Chapin 2000; Brauman *et al.,* 2007; Baum and Worm 2009; Jorgensen *et al.,* 2010). White sharks *(Carcharodon carcharias)* are apex predators and changes in their distribution can affect community compositions (Myers *et al.,* 2007; Ferretti *et al.,* 2008; Heithaus *et al.,* 2008; Baum and Worm 2009), ultimately affecting ecosystem functioning (Chapin *et al.,* 2000; Brauman *et al.,* 2007).

Furthermore, the relationship between animals and environmental conditions can be used as a tool for minimizing human-animal conflict. This study aims to understand white shark habitat use in False Bay in relation to environmental conditions. The results from this study could potentially be used to inform water-users of conditions of higher risk of encounters with the aim of minimizing encounters between sharks and waters-users.

White sharks of False Bay

The white shark is globally distributed and most abundant in the waters of Australia, US, Mexico and South Africa (Compagno 2001; Klimley *et al.,* 2001; Dewar *et al.,* 2004; Bonfil *et al.,* 2005; Bruce *et al.,* 2006). Despite completing transoceanic migrations, linking the populations of South Africa and Australia (Bonfil *et al.,* 2005), white sharks are known to aggregate seasonally in specific coastal areas (Martin *et al.* 2005; Bruce *et al.,* 2006; Jorgensen *et al.,* 2010). The Western Cape, in particular False Bay, is an area where white sharks are attracted by high abundances of prey species including marine mammals, teleosts and elasmobranchs (Ferreira and Ferreira 1996; Martin *et al.,* 2005; Hammerschlag *et al.,* 2006; Johnson and Kock 2006; Laroche *et al.,* 2008). Despite maintaining a wide range of diet throughout their lifecycle, white sharks undergo ontogenetic dietary shifts (Tricas and McCosker 1984; Klimley 1985; Estrada *et al.,* 2006). Juvenile (<2m) white sharks shift from diets consisting of invertebrates (Squid), demersal teleosts and elasmobranchs, to diets dominated by marine mammals and larger fish at maturity (>3m) (Tricas and McCosker 1984; Klimley 1985; Estrada *et al.,* 2006). Moreover, seasonal shifts in diet and corresponding distribution are suspected for white sharks in False Bay, shifting from feeding on weaned seal pups at Seal Island during winter to feeding on fish species occurring in high abundances inshore in summer. Furthermore, white sharks are an ovoviviparous species, giving birth to live young (~1.5m in length) (Dulvy and Reynolds 1997; Compagno *et al.,* 1989). They attain a maximum size of 6 m (Dulvy and Reynolds 1997; Compagno *et al.,* 1989). Since larger sharks are more likely to bite a human, it is not surprising that the Western Cape has the highest percentage of white shark bites (67%) in comparison to other locations in SA (KZN, EC) (Cliff 2006; Curtis *et al.,* 2012).

In order to minimize human encounters with white sharks in False Bay, it is important to increase our knowledge on white shark biology, behaviour and movement within the bay so that particular areas and times of high risk can be avoided. Research conducted on white sharks in the Western Cape has focused on white shark attacks (Levine 1996; Cliff 2006), cage diving and white shark ecotourism (Johnson and Kock 2006; Laroche *et al.,* 2007), commercial trade of white shark products (Barnette and Marshall 1997; Gallagher and Hammerschlag 2011), interaction with local fisheries (Lamberth 2006), hunting and predation strategies (Martin *et al.,* 2005; Hammerschlag *et al.,* 2006; Laroche *et al.,* 2008; Martin *et al.,* 2009) and population distribution (Gubili *et al.,* 2009). However, few studies have focused on the driving forces behind such behavioural trends, namely the changes in environmental conditions.

Shark distribution and habitat preference in relation to environmental conditions have been investigated for species including leopard shark (Triakis semifasciata), brown smoothhound shark (Mustelis henlei) (Hopkins and Cech 2003), lemon shark (Negaprion brevirostris) (Wetherbee *et al.,* 2007), bull shark (Carcharhinus leucas (Ortega 2008), blue shark (Prionace glauca) (Lessa 1994; Damalas and Megalofonou 2010), hammerhead shark (Sphyrna lewini) (Holland *et al.,* 2011), porbeagle shark (Lamna nasus) (Saunders *et al.,* 2011) and shortfin mako shark (Isurus oxyrinchus) (Velez-Martin and Marquez-Farias 2009; Abascal *et al.,* 2011). Less work has specifically focused on coastal and nearshore shark distributions in relation to environmental conditions (Carlson *et al.,* 2008; Knip *et al.,* 2010) and even less so in sheltered bays such as False Bay (Hopkins and Cech 2003; White and Potter 2004). There has been little focus on the distribution of white sharks in shallow coastal locations (Bonfil *et al.,* 2005; Raye 2005; Jorgensen *et al.,* 2010), with some work conducted in the western North Atlantic (Casey and Pratt 1985) and between Hawaii and the Line Islands (Raye 2005). In False Bay, the only study investigating the relationship between shark behaviour and environmental conditions was conducted by Hammerschlag *et al.,* (2006), suggesting that white shark predation rate and success is affected by environmental conditions.

Shark attacks and the shark spotting programme

Shark attacks are defined as any unprovoked physical interaction between a shark and its victim or the victim's equipment or non-motorised personal craft (e.g. scuba tanks, surfboards, kiteboards, kayaks etc.) (Burgess and Callahan 1996; Cliff 2006). Shark attacks attract large amounts of media attention, often resulting in negative public perceptions impacting the economical livelihoods of tourism and local businesses of the surrounding areas (Curtis *et al.,* 2012; Hazin *et al.,* 2008). The frequency of shark attacks have increased steadily over the past few decades, and are generally attributed to an increase in the human population in the coastal zone (Burgess and Callahan 1996; Burgess *et al.,* 2010; Hazin *et al.,* 2008; Klimley and Curtis 2006). Due to the impact on tourism and the potential loss of confidence in the coast as a safe recreational asset, authorities have had to mitigate shark encounters (Nel and Peschak 2006).

Prevention approaches vary according to time and region, and are split into removal and non-removal methods (Curtis *et al.,* 2012). Historically, removal methods involved the hunting and killing of sharks by authorities or the public in search of the responsible shark (Curtis *et al.,* 2012). Yet the likelihood of finding and killing the responsible shark is small, and even if successful, only provides a temporary solution. Alternatively, regular organized, governmental culling methods such as shark nets and drumlines which reduce local shark populations provide a long term solution for minimizing the risk of shark encounters (Cliff 2006; Curtis *et al.,* 2012). Despite its proven success in reducing the number of shark attacks at specific locations, including Durban (up to 90% since implementation), culling is economically and ecologically costly with high gear maintenance and large fauna by-catches respectively (Dudley *et al.,* 2005; Curtis *et al.,* 2012).

Non-removal methods are preventative methods without the aim of killing and removing sharks. Robust shark barriers constructed of smaller meshed gillnets or pylons constructed of concrete, steel or wooden pylons have proven successful, yet are vulnerable to erosion and limited in use to sheltered, calm waters (Curtis *et al.,* 2012). Moreover, aerial helicopter surveys, although effective, are very costly and can't be done regularly enough without large amounts of funding (Curtis *et al.,* 2012). In contrast, visual land-based surveys are less costly and a more ecologically friendly method of minimizing the risk of shark encounters (Curtis *et al.,* 2012).

The first permanent land-based surveying programme was implemented in 2004 in Cape Town, South Africa. This programme is called the Shark Spotters and was implemented in response to an increase in shark attacks in the Western Cape over the last decade *(Kock et al.,* 2012). Kock et al., 2012 explains the aim and the functioning of the spotting programme in the following way: The aim of the spotting programme is to warn bathers and surfers of the presence of white sharks and minimize human-shark encounters. This programme appoints 14-28 community based spotters at 5-10 popular beaches along the Cape Peninsula 365 days a year. Two spotters are assigned to each beach, one positioned at an elevated mountain-side position, the other on the beach. Both are equipped with polarized sunglasses, binoculars and a two-way radio, allowing for direct communication with one another. The spotter at the elevated position scans the surf-zone and shallow waters for the dark silhouettes of sharks contrasted against the sandy bottom or shallow reefs. When a shark is spotted, the elevated spotter informs the spotter on the beach of the shark's presence, who then raises the appropriate flag and sets off a siren (Green flag= good visibility, no sharks spotted; black flag= poor visibility, no sharks spotted; red flag=shark spotted earlier, no longer visible; white flag= shark in sight, exit water immediately) (Fig 1). Information boards posted on each beach educate the public on the flag protocol and provide numbers to call in case of an emergency (Fig 1).

Figure 1. Example of signage used along spotting beaches to provide information to the public on the protocol of the Shark Spotters flag warning system, daily shark activity and emergency numbers.

Possible influences of environmental variables on the presence of white sharks nearshore: White shark biology vs. spotting ability of shark spotters

To understand the influence of environmental variables on the presence of white sharks in the surf-zones of False Bay, it is important to distinguish between the ability of shark spotters to sight a shark (termed the "spottability") and the actual presence of sharks within the surf-zone. No sharks sighted could be as a result of the spotter not being able to detect any sharks present, or that the sharks are not there. In order to distinguish between these two scenarios, the environmental variables are reviewed in terms of their influence on biology and "spottability". Environmental variables can have an impact on shark biology or "spottability" or both.

Cloud cover

Cloud cover influences the amount of light which is scattered by the surface waters, affecting light availability underwater in the marine environment (Bowmaker 1995) (McFarland 1990; Sims *et al.,* 2003). The extent to which marine fauna can tolerate limitations in light availability underwater depends on their sensory system and their ability to perceive light (Bozzanao *et al.,* 2001).

Elasmobranchs rely to a great extent on their specialized sensory systems to enable them to be successful predators (Moss 1977; Bozzanao *et al.,* 2001). Research on shark vision dates back as far as 1890, when it was thought that sharks had poor vision (Gruber 1977; McFarland 1990; Hart *et al.,* 2004; Lisney and Collin 2007; McComb and Kajiura 2008). It is now understood that sharks have well developed visual sensory systems, which depend greatly on the retina morphology (Moss 1977; Bozzanao *et al.,* 2001; Lisney and Collin 2007). The location, shape and structure of the photoreceptors in the retina, including rods and cones forms, connect environmental perceptions and behavioural responses (Bozzanao *et al.,* 2001; Litherland *et al.,* 2009). Cone photoreceptors control vision under bright light conditions, where rod photoreceptors control vision under dim light conditions (Cohen 1991; Hart *et al.,* 2004). The ratio of cone-rod photoreceptors is dependent on the depth in the water column in which the elasmobranchs spend most of their time, and determines the vision ability (Bozannao *et al.,* 2001).

The white shark resides mainly within the photic zone and has a duplex retina with a cone-rod ratio of 1:4, allowing for good vision over a wide range of light spectra, but specifically in poor light conditions (Cohen 1999; Bozzanao *et al.,* 2001; Hart *et al.,* 2004). Moreover, with an enhanced ability to perceive and process visual information (14% of its brain mass) as well as to warm its eye tissue, white sharks have a heightening ability to see in cold, turbid waters (Block and Finnerty 1994; Fritsches *et al.,* 2005; Bozzanao *et al.,* 2001; Yopak *et al.,* 2007). Furthermore a recent study demonstrated an increased predation success at low light intensities in early morning hours (Hammerschlag *et al.,* 2006; Martin *et al.,* 2005; McComb *et al.,* 2010). It is therefore be unlikely that cloud cover could affect shark biology and behaviour.

Conversely, cloud cover may affect the ability of shark spotters to spot the dark silhouettes of white sharks contrasted against the sandy bottom. Low light levels decrease this contrast and make the spotting of white sharks more difficult

Wind and current patterns of False Bay

By way of upwelling, wind speed and direction are the main drivers controlling nutrient input in False Bay (Atkins 1970). An increase in fish abundance and diversity observed within the surf-zones of False Bay in response to increased available nutrients (Clark *et al.,* 1996; Lamberth *et al.,* 1995) have been suspected to coincide with the seasonal increase in white shark presence close to shore (Kock *et al.,* 2012).

Winds also influence surface water circulation which determines water temperatures of the bay (Atkins 1970). In summer months (September - May) False Bay is dominated by strong south-easterly (SE) winds, which cause cool water to upwell outside the bay and drives warmer water onto the northern beaches (Atkins 1970). Furthermore, being situated between the Agulhas bank and the Cape Peninsula, False Bay receives occasional inputs from the warm Agulhas and cold Benguela currents from the outer shelf (Lutjeharms *et al.,* 2001). This gives False Bay a relatively large seasonal range of water temperatures compared to the surrounding coastline (an average of 11^{o}C in July - 22^{o}C in December) (Edwyn and Isaac 1937).

Temperature is thought to be one of the most important environmental variables determining the distribution of sharks in coastal environments (White and Potter 2004; Harley *et al.,* 2006; Carlson *et al.,* 2008; Vogler *et al.,* 2008; Knip *et al.,* 2010; Hopkins and Cech 2003; Dewar *et al.,* 2004; Abascal *et al.,* 2011). However, differences in evolutionary histories and physiological adaptations to temperature play a major role in determining geographic distribution and habitat choice (Martin 2001).

White sharks belong to the family Lamnidae, along with salmon sharks (*Lamna diptrosis*), probeagle sharks (*Lamna nasus*), shortfin mako sharks (*Isurus oxyrinchus*) and longfin mako sharks (*Isurus paucus*) (Compagno 1999). They are distinguished from other species by large gill slits and a prominent caudal keel, these species have large *rete mirabili*, allowing them to raise their body temperature up to 15^{o}C above that of the surrounding ambient water (Klimley *et al.,* 2001; Goldman 1997; Carey *et al.,* 1982; Carey *et al.,* 1971; Abascal *et al.,* 2011). The elevated temperatures of the brain, eyes, stomach and muscle tissues, increases their ability to control physiological processes and hunt successfully in cooler waters (Klimley *et al.,* 2001; Block and Finnerty 1994; Goldman 1997; Dewar *et al.,* 2004). Despite having a wide range of tolerance, inhabiting waters at from 0.5^{o}C in Alaska to 22^{o}C in California (Martin 2004; Dewar *et al.,* 2004), previous work has suggested a preferred optimal average seas surface temperature (SST) of 13.3 to 22^{o}C (Goldman 1997).

Previous work supporting the importance of SST in determining the movement of large sharks and predatory fish is based in fisheries data for targeted or by-caught sharks (Bigelow *et al.,* 1999; Begg and Marteinsdottir 2002). Studies conducted on cod, swordfish, striped marlin, blue marlin and tuna catches, show that SST is highly important in determining the distributions of these species (Gonzalez-Ania *et al.,* 2001; Begg and Marteinsdottir 2002; Walsh *et al.,* 2005; Damalas *et al.,* 2007; Hazin and Erzini 2008; Ortega-Garcia *et al.,* 2008). For some species a preferred temperature range existed, whereas a negative relationship was found for others (Begg and Marteinsdottir 2002; Bigelow *et al.,* 1999; Walsh and Kleiber 2001).

By affecting the physiology of white sharks, SST can influence the actual presence of white sharks within the surf-zone. SST is not expected to influence the spotting ability of shark spotters, since it has no direct affect on the chance of spotters to sight a shark.

Wind speed and direction affect both shark biology and "spottability". Wind patterns determine nutrient upwelling and play a role in controlling SST within the bay, which can influence shark behaviour and determine the actual presence of white sharks within the surf-zone. Strong winds affect the turbulence of surface-waters and can make the sighting of sharks difficult for shark spotters.

Lunar phase and tidal states

Lunar phase has no effect on "spottability" during daytime hours, but is rather known to play an important role in the biology of many marine organisms (Naylor 2001). The lunar cycle provides predictable environmental patterns to which many marine organisms structure a variety of behavioural functions affecting habitat use, including reproduction and settlement of larvae, predation, group living, locomotion, daily and seasonal migrations and physiological changes (Barlow *et al.,* 1986; Robertson *et al.,* 1990; Sponaugle and Cowen 1994; Horning and Trillmich 1999; DeBruyn and Meeuwig 2001; Pittman and McAlpine 2003; Yamahira 2004; Naylor 2005; Katselis *et al.,* 2007; Benoit-Bird *et al.,* 2009; Guttridge 2009). This cycle is determined by the orbit of the moon around the earth (27.95 days one cycle), and with the combination of the relative positioning of the sun to the moon, controls the moon phase and tides of the ocean (McDowall 1969). Previous work focused on the effect of moonlight on large fish and shark catches in fisheries, with the certain fish species enhancing their predator avoidance by remaining closer to the surface on new moon than during full moon (Horning and Trillmich 1999; Damalas and Megalofonou 2010). Sharks also exhibit changes in swimming depth, altering their position in the water-column in relation to moon cycles e.g. the porbeagle shark, a relative of the white shark (Cartamil *et al.,* 2011; Saunders *et al.,* 2011; West and Stevens 2001; Poisson *et al.,* 2010; Damalas and Megalofonou 2010). Other work found no relationship between lunar phase and predatory fish distributions and behaviour (Ortega-Garcia *et al.,* 2008).

Although this study is limited to shark presence during daylight hours, previous work has suggested that the effect of the lunar cycle may still persist into day time hours (Trillmich *et al.,* 1981, 1985). For example, seals vary in their numbers ashore during the day in the Galapagos in correlation to different stages of the lunar cycle (Trillmich *et al.,* 1981; Trillmich *et al.,* 1985). Furthermore, predator-prey interactions may also be influenced by the lunar cycle (Horning and Trillmich 1999; Bestley *et al.,* 2008; Benoit-Bird *et al.,* 2009).

Related to the lunar cycle is the tidal cycle, known to significantly affect marine species behaviour and habitat utilization (McDowall 1969; Naylor 2001), particularly of coastal species (Butner and Brattstrom 1960; Wetherbee *et al.,* 2007). Despite recent work showing an increased predation rate of white sharks at high tides around Seal Island (Hammerschlag *et al.,* 2006), no studies have been conducted to investigate the relationship between tidal state and white shark presence nearshore. Since tides alter the size of the surf-zone, it has been shown that some shark species might come closer inshore on the incoming tide to exploit available resources (Knip *et al.,* 2010).

Since tidal states can determine shark movement nearshore, it can have a direct effect on shark biology. Additionally, since sharks swimming at a closer proximity to the shore are more likely to be sighted by spotters, tidal states can also affect the "spottability". However, the effect of tidal state is unique to each beach, depending on the bottom topography and the size of its surf- zone.

Aims & Objectives

This study makes use of the recorded shark spotting data to investigate the relationship between environmental variables and shark sightings at three of False Bay's popular beaches, namely Fish Hoek, St. James and Muizenberg. Environmental variables tested in ecological models were SST, wind speed and direction, cloud cover, lunar phase and tidal state. The additional independent variables, spotter and year, were considered to incorporate the effect of "spottability" and annual variance respectively. Incorporating the variable spotter into the analysis, allows for the correction of the effect of the abilities of different spotters to detect sharks on the number of shark sightings recorded. The aim of this study was to determine whether there are any correlations between the number of shark sightings nearshore and certain environmental conditions, with the objective of using this information for minimizing shark encounters by water-users.

Hypothesis

The number of white shark sightings at the beaches Fish Hoek, St. James and Muizenberg in False Bay are influenced by SST, wind speed, wind direction, cloud cover, lunar phase and tidal state.

The environmental variables act differently, with SST and lunar phase influencing the biology and movement of white sharks, where cloud cover determines spotting ability of shark spotters. Wind speed, wind direction and tidal state play a role in both the biology and spotting frequency of white sharks at the beaches Fish Hoek, St. James and Muizenberg in False Bay by affecting the spotting abilities of shark spotters.

Review of ecological modelling of fish distribution patterns and processes

Recent investigations of relationships between environmental variables and species distributions generally follow a modelling approach (Johnson and Omland 2004). Modelling is a tool used in ecology as a way of testing and comparing multiple hypotheses simultaneously to determine the best possible explanation for the variation observed in the data (Johnson and Omland 2004). The modelling process consists of basic model selection steps, including understanding and articulating clear hypotheses; translating these hypotheses to the data by identifying variables and selecting mathematical functions relating to them; devising a candidate set of models by adding and removing variables; and selecting the 'best fitting model' by using standard selection criteria, e.g. Akaike's information criterion (AIC), to determine which variables best explain the variation in observed data (Bozodogan 1987; Johnson and Omland 2004). The 'best fitting model' is then used to estimate and predict certain parameters and observed responses (Johnson and Omland, 2004). There are a variety of underlying linear mathematical model functions to choose from, all ascending in complexity, including linear regression models, generalized linear regression models (GLM's), generalized additive models (GAM's) and linear mixed models (GLMM's or GAMM's) (Zuur *et al.,* 2009). Generally the modelling process is conducted through all of these linear model options in ascending complexity, until the linear modelling function which best explains the research question is found, without becoming overly complex (For more information on available modelling functions including GLM's, GAM's, GLMM's, GAMM's, see Hastie and Tibshirani 1990; Zuur *et al.,* 2007; and Zuur *et al.,* 2009). For any chosen model function, variable parameters are estimated and predicted using the final model (Johnson and Omland 2004). Along with the basic model function one has a choice to assume an underlying distribution of the data's residuals (e.g. Gaussian, Gamma, Poisson, negative binomial etc.) (Zuur *et al.,* 2007).

The response variable focused on in this study is the number of shark sightings per shift (count data). Modelling the abundance (count data) of rare or large species has various problems, in particular that the observed response variable usually contains many zero observations (Welsh 1996; Podlich *et al.,* 2002; Cunningham and Lindenmayer 2005; Fletcher *et al.,* 2005). Data of such nature are commonly referred to as zero-inflated data, and are subjected to various modelling techniques to correct for this including binomial or zero-inflated approaches (Cunninghman and Lindenmeyer 2005).

Most studies investigating the relationship between environmental variables and marine fauna abundance and distribution, are based on fisheries catch data. Some studies used GLM's (Hoey *et al.,* 2002; Andrade 2005; Ortega 2008) where as others used GAM's (Bigelow *et al.,* 1999; Emmett *et al.,* 2005; Tserpes *et al.,* 2008; Poisson *et al.,* 2010), GLMM's (Bestley *et al.,* 2008) or a combination thereof (Damalas and Megalofonou 2010) as their final underlying model functions. In terms of dealing with excess zeros, work conducted on counts of shark depredation rates and shark by-catch in fisheries used underlying zero-inflated Poisson (ZIP) or zero-inflated negative Poisson (ZINP) distributions, which work to include the excess amount of zero's in the response variable (Minami *et al.,* 2007; Watson *et al.,* 2008; MacNeil *et al.,* 2009). However, where fitting, regular Poisson distributions in conjunction with GAM's were preferred in modelling environmental and catch abundance relationships (Bigelow *et al.,* 1999, Damalas *et al.,* 2007; Hazin and Erzini 2008; Ortega-Garcia *et al.,* 2008). Examples of the preferred use of GAM's exist for catches of sharks (Bigelow *et al.,* 2008; Watson *et al.,* 2008), swordfish (Bigelow *et al.,* 2008; Damalas *et al.,* 2007), tuna (González-Ania et al., 2001; Zagaglia et al., 2004) and marlin species (Walsh *et al.,* 2005; Walsh *et al.,* 2006; Ortega-Garcia *et al.,* 2008).

Chapter 2: Patterns in white shark sightings on False Bay beaches in relation to environmental variables

Abstract

In response to an increase in shark attacks in the Western Cape over the last decade, a shark warning system called Shark Spotters that records white sharks (*Carcharodon carcharias*) in the surf zone was implemented in 2004 in Cape Town, South Africa. A total of 563 shark sightings were recorded during 6730 sharks spotting shifts conducted at three popular beaches in False Bay, namely Fish Hoek, St. James and Muizenberg, over summer months (September – May) from 2006 to 2011. The frequency of shark sightings at each beach were modelled using Poisson GAM's with sea surface temperature (SST), wind speed and direction, cloud cover, spotter and lunar phase as independent variables. SST and lunar phase were most influential, with other factors being significant, but of a lesser importance. SST was significant for all three study beaches, with an average of a 78% greater chance of sighting a shark at a SST of 20^{0}C than at 14^{0}C. Lunar phase was significant for Fish Hoek and Muizenberg, with most sharks sightings recorded during last quarter moon. Beach management can incorporate this information into shark safety programs by issuing additional warnings of high sharks activity through daily surf-reports or radio and T.V. weather broadcasts.

Introduction

White sharks (*Carcharodon carcharias*) are responsible for the majority of shark encounters with humans in Cape Town (Cliff 2006). Shark attacks in the Western Cape have been increasing over the last decade, with 13 of the 26 recorded shark bites since 1960 having occurred since January 2000, three of which were fatal and took place between September 2003 and December 2009 (Kock *et al.,* 2012). In response to the increase in shark attacks, the shark safety programme called Shark Spotters was implemented in 2004 in Cape Town, South Africa (Kock *et al.,* 2012). This programme assigns two trained spotters per morning (7:00 - 13:00) and afternoon (13:00 – 19:00) shift at a popular Cape Peninsula beach

(365days/year), with one spotter situated at an elevated mountain-side position overlooking the surf-zone, the other spotter placed directly on the beach. Equipped with polarized sunglasses, binoculars and two-way radios, the spotters manage a flag warning system and a siren alarm to inform beach users of nearshore shark activity and to evacuate water-users in the immediate presence of a shark (Kock *et al.,* 2012). Additional to being a successful, cost effective and non-intrusive way of reducing human-shark encounters (Curtis *et al.,* 2012; Kock *et al.,* 2012), the shark spotting programme can help increase our understanding of white shark activity and biology in nearshore environments.

To date, research on understanding the population biology and activity of white sharks in False Bay has focused on shark encounters (Levine 1996; Cliff 2006), hunting and predation strategies (Klimley *et al.,* 2001; Martin *et al.,* 2005; Hammerschlag *et al.,* 2006; Laroche *et al.,* 2008; Martin *et al.,* 2009) and distributions associated with predation (Gubili *et al.,* 2009). One study focused on the correlation between environmental conditions and white shark activity in False Bay, with particular focus on the predation rate and success around Seal Island (Hammerschlag *et al.,* 2006).

The aim of this study was to investigate the relationship between environmental variables and the number of shark sightings recorded during spotting shifts by shark spotters at popular beaches Fish Hoek, St. James and Muizenberg in False Bay over the peak summer seasons (September- May) for years 2006 (January) to 2011 (May). Environmental variables of interest are sea surface temperature (SST), wind speed and direction, cloud cover, lunar phase and tidal state.

In order to achieve this aim, it is important to distinguish between the ability of shark spotters to sight a shark (termed the "spottability") and the actual presence of sharks within the surf-zone. A 'No shark sighting' recorded can either imply that the shark spotter was unable to sight the shark present in the surf-zone or that no shark was present. To incorporate the effect of "spottability", the additional independent variable 'spotter' was considered and all results will be discussed in terms of the possible roles each variable plays in shark biology and "spottability". The objective of this study was to add to an understanding of nearshore activity of white sharks in False Bay over the peak summer season, and to minimize human-shark encounters.

Materials and Methods

Study site

Investigations were conducted using shark sightings recorded at three popular beaches on the western side of False Bay, South Africa. This south orientated, 35x30km wide embayment has a Mediterranean climate and is dominated in summer months by strong south-easterly (SE) winds, causing upwelling and warming nutrient rich waters(up to 24°C) in the shallow banks (Schumann *et al.*, 1982; Waldron *et al.*, 2008; Edwyn and Isaac 1937; Atkins 1968). The beaches chosen for this study, namely Fish Hoek, St. James and Muizenberg, have the highest number of white shark sightings as well as the highest number of white shark encounters (Kock *et al.*, 2012). They provide the best quality and quantity of spotting data available over the study period.

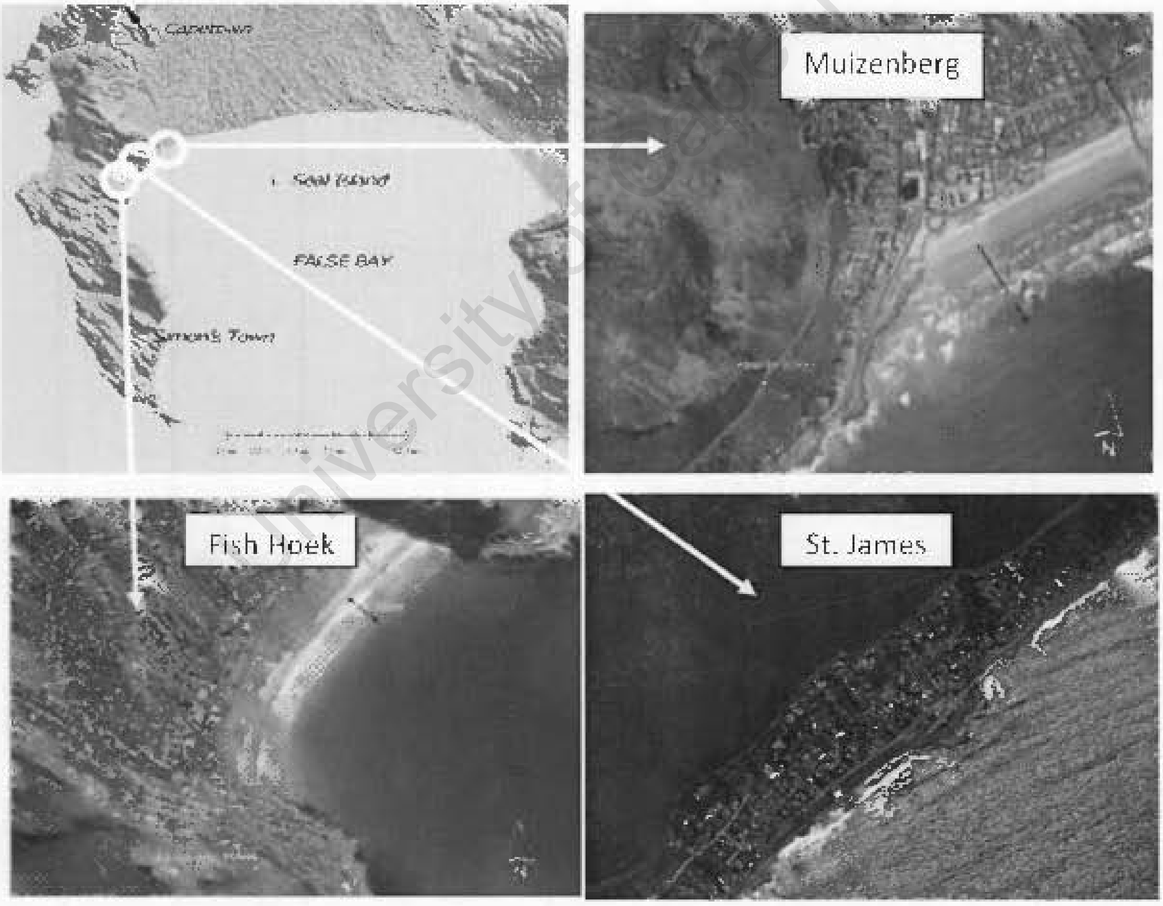

Figure2. Map of False Bay and the three beaches where sharks were monitored by Shark Spotters. Each beach has distinct characteristics like a large surf-zone (>300m) at Muizenberg in comparison to smaller surf-zones at Fish Hoek (<100m) or ST. James (<50m) (modified from Kock *et al.*, 2012).

Despite being adjacent to one another and sharing similar seasonal environmental trends, the exact positioning of each beach within the bay allows them to be unique in terms of their exposure to environmental conditions, size of surf-zone, type of water-users and spotting ability (Kock *et al.,* 2012). Fish Hoek is sandy bottomed with a small surf-zone, many swimmers and exposed to SE winds (Fig 2). In contrast, St. James is a rocky shore and protected from strong winds by the nearness of the mountainside (Fig 2). Muizenberg beach is again sandy bottomed with a large surf-zone and is exposed to strong onshore and offshore winds (Fig 2).

Data recording

White shark sightings data were recorded by shark spotters assigned randomly to morning (7:00 - 13:00) and afternoon (13:00 - 19:00) shifts, called spotting shifts, at the three study beaches over the study years (2006 - 2011). The information recorded on data sheets included the site, date, spotter name, number of sharks sighted and the exact timing of sighting.

Environmental data were externally sourced for January 2006 to June 2011. SST (^{0}C), wind speed (ms^{-1}) and direction and cloud cover (total portion of the sky in eighths covered by all types of cloud) were sourced from the South African Weather Services (SAWS). Measurements for wind and cloud data were used from records taken at the Cape Town International Airport, as this was the best representative wind and cloud cover data available for False Bay. Wind data were provided in hourly measurements, whereas cloud data were available for 08:00, 14:00 and 20:00 o'clock daily. SST data were physically measured by SAWS by using a SST bucket and provided the average daily measurements for Fish Hoek, Kalk Bay (including St. James area) and Muizenberg separately.

Lunar phase and tide data were sourced from the SA Naval Hydrographic Office. The date at which each phase, including full, first quarter, new and last quarter, were in their fullest was provided throughout all study years. Tide data were in the form of the times of high and low tides in the 7 hourly tidal cycles for the whole of False Bay over the study years.

Statistical analysis

The relationship between environmental conditions and the number of white shark sightings was statistically modelled for each study beach. Prior to modelling, the data had to be prepared for inclusion in GLM and GAM modelling environments. These procedures are described below.

<u>*Dependent variable*</u>

Preparation

Shark sightings data were sorted into morning and afternoon shifts according to the time at which they were first sighted. Since most shark sightings data were recorded during summer months very few were recorded during winter months, only shark sightings over the periods September – May over years 2006 - 2011 were included and months June – August were excluded.

Data exploration and distribution

A histogram was created for the number of shark sightings per shift. Shark spotting data indicated a high number of zero sightings (Fig 3). Given the many zero's present within this data, the underlying distributions of binomial and Poisson were considered.

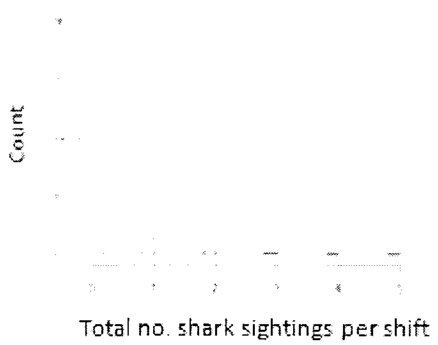

Figure 3. Histogram of the number of shark sightings in spotting shifts indicating a non-normal distribution with high excess amounts of zeros.

The binomial distribution is applied to presence/absence data (O'Neill and Faddy 2003). For this distribution, data were transformed into binomial values of 0 and 1, representing the presence and absence of shark sightings respectively. The Poisson distribution is particularly useful for analysing count data for which no transformation was required (Zagaglia *et al.,* 2004; Zuur *et al.,* 2007). Analyses were run using both the binomial and Poisson distribution models, determining which distribution best predicted the excess amount of zero's within the data. Should neither of these adequately represent the excess amount of zero's, alternatives including a over-dispersed Poisson or zero-inflated Poisson distributions have been used in previous work on shark count data (Minami *et al.,* 2007; MacNeil *et al.,* 2009).

<u>Independent variables</u>

Preparation

The sample unit in this study was one spotting shift. All environmental data was therefore prepared in order to be allocated to daily spotting shifts over the study period. The spotting year was allocated to blocks according to the individual summer spotting periods as year 1 (Sep 2006 - May 2007), year 2 (Sep 2007 - May 2008), year 3 (Sep 2008 - May 2009), year 4 (Sep 2009 - May 2010) and year 5 (Sep 2010 - May 2011). Data for SST was provided in the form of daily averages and were applied in that form to both daily spotting shifts. Wind speed (ms^{-1}) and direction (given in degrees) data were averaged for each shift. Wind direction was categorised into on-shore, off-shore, cross-shore and long-shore winds depending on the given degrees relative to each beach independently. Cloud data were averaged from 08:00 - 14:00 and 14:00 - 20:00 for the morning and afternoon spotting shifts respectively.

The spotter on duty during each shift was identified and assigned to the corresponding shift. Since employment of spotters has varied in length over the study years, only data for spotters which had worked over 100 spotting shifts, namely spent over 50 working days (roughly just over one month) as a shark spotter at a particular beach, were included. The numbers of shark spotters included in the analysis was 7, 13 and 10 for Fish Hoek, St. James and Muizenberg beaches respectively. Since shark spotters having worked over a 100 spotting shifts were responsible for the largest percentage of shark sightings, therefore only a minimal amount of shifts with sightings were excluded from the analysis. After excluding the winter months and only including shifts with certain observers, the same data set for spotters was used throughout each model selection for a particular beach,.

Lunar phase was assigned to each shift according to date. Lunar phase data was used as a categorical variable representing the four lunar phases of full (1), first quarter (2), new moon (3) and last quarter (4). After allocating the lunar phases to each spotting shift, only those shifts which occurred within two days before and two days after the given date of each phase were included in the analysis (Fig 4). Due to the large data set (<6000 shifts), any possible trends within these periods will be expected to be clear.

Since tidal state and the exact timing of a shark sighting do not correspond to shifts, a separate spreadsheet was constructed. As with lunar phase, tide data were transformed into a categorical variable by including an hour and a half on either side of the given tide times and creating four categories of tidal state, namely 1) high, 2) ebb, 3) low and 4) flood. For each tidal state, the number of shark sightings per study year was calculated according to the date of sighting for each study beach.

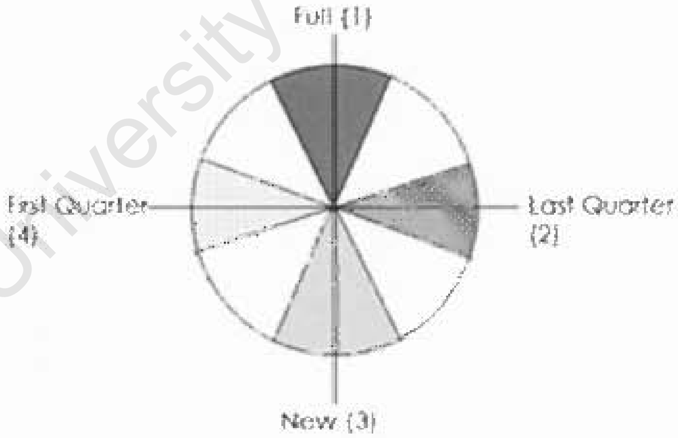

Figure 4. Pie chart used to show the categories used to divide the lunar phase cycle into full (1), last quarter (2), new (3) and first quarter (4), including two days on either side of actual date.

Data exploration

Once all shifts were assigned corresponding environmental variables, the relationship between environmental variables was explored using the guidelines provided by Zuur *et al.,*

(2009) on data exploration in R (12.3.0). Since winter months were excluded from this study, all environmental variables needed to show an adequate spread over the remaining summer months. This was investigated using box-plots and cleveland dot-plots for continuous variables (SST and wind speed) and pivot tables for categorical variables (cloud cover, wind direction, moon phase and spotter). To enhance apparent seasonal patterns within pivot tables, September – May months were further divided into autumn, spring and summer.

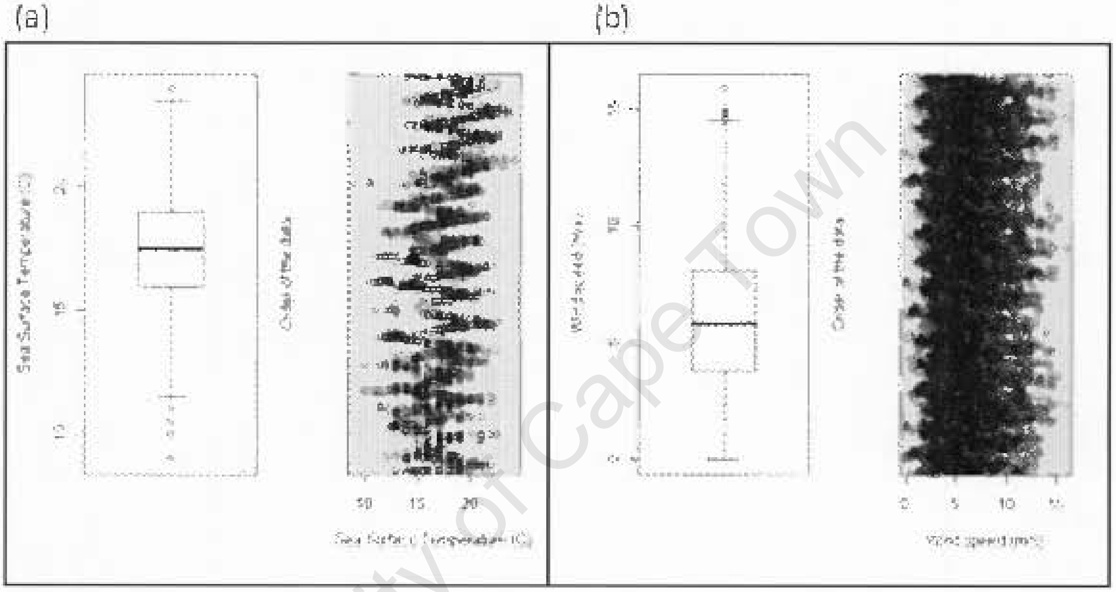

Figure 5. Example of box-plot and cleveland dot-plot for SST (a) and wind speed (b) for Muizenberg beach excluding the data for winter months.

For all sites, SST and wind speed showed an even spread over the summer months when winter was excluded. An example of this can be seen for Muizenberg in Figure 5. Simultaneously no true outliers where present for SST and wind speed at the beaches Fish Hoek, St. James and Muizenberg. Pivot tables also showed a relatively even spread for all categorical variables, including cloud cover, wind direction, moon phase and spotter, for all three beaches. An example of this is shown for cloud cover at Muizenberg in Table 1. Since all variables showed an even spread over September – May months, data for winter months June - August were excluded.

Table 1. The example of a pivot table showing an even spread of degrees of cloud cover for Muizenberg over remaining seasons (autumn, spring and summer) when excluding winter months.

Season	Cloud cover (1/8 portion covering sky)									
	0	1	2	3	4	5	6	7	8	Total
Autumn	926	496	230	116	128	116	188	180	102	2518
Spring	348	418	258	170	190	178	384	510	162	2618
Summer	1224	440	184	114	72	56	144	242	54	2550

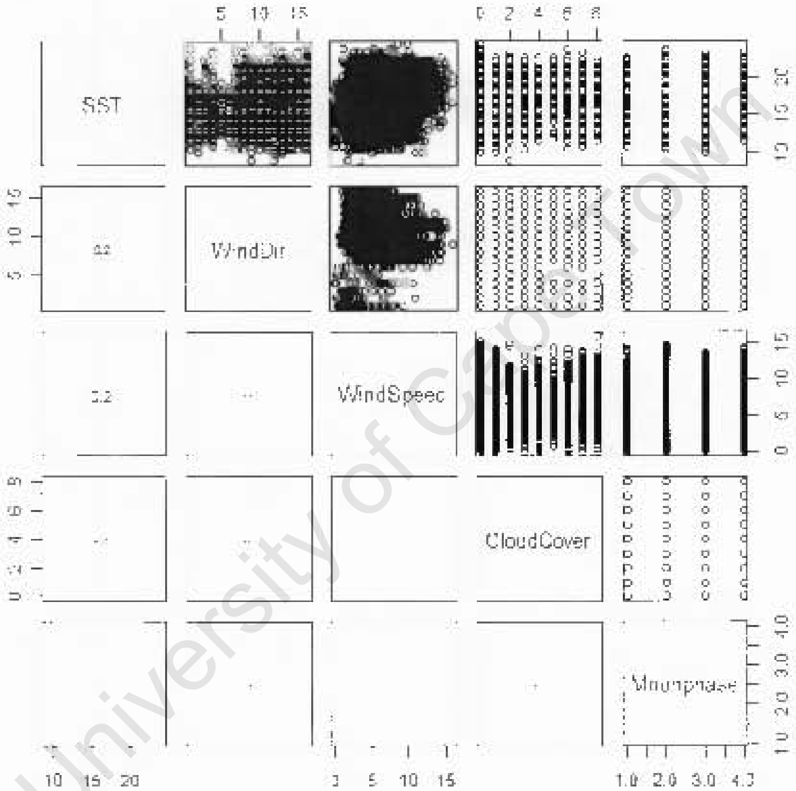

Figure 6. Multi-panel scatterplot showing the correlation between environmental variables SST, wind speed, wind direction, cloud cover and lunar phase.

Multi-panel scatterplots were used to identify any possible co-linearity between environmental variables. Upon visual inspection, no clear correlation existed between any pair of environmental variables. This was confirmed by low correlation coefficients between continuous variables (Fig 6). The strongest correlation was shown between SST and wind speed (correlation coefficient of 0.2) and between SST and wind direction (correlation coefficient of 0.2). All variables were kept in for the analyses and the final variables tested were SST, wind speed, wind direction, cloud cover and lunar phase.

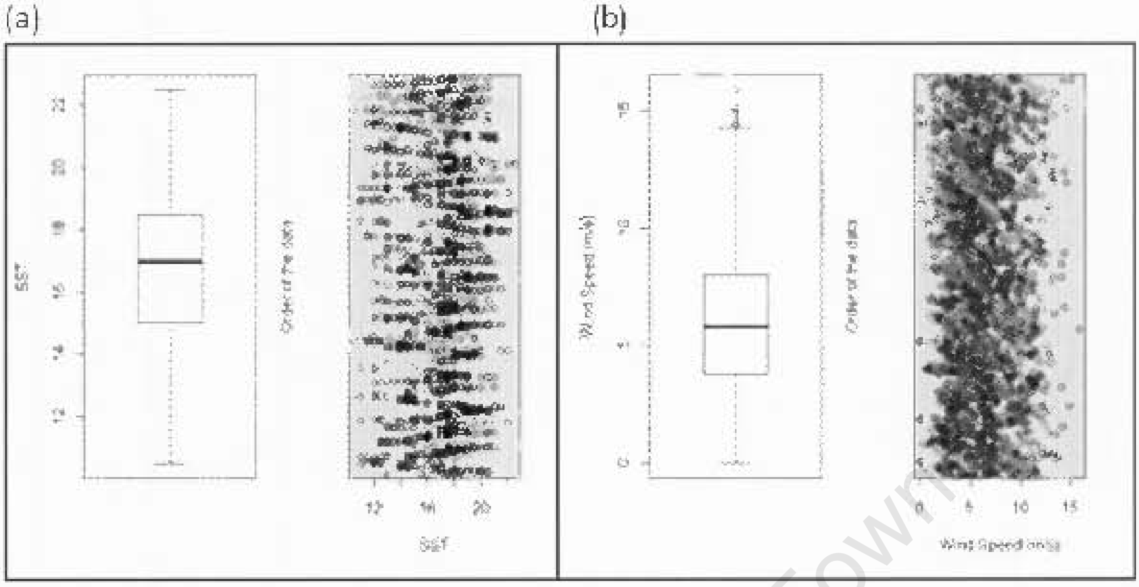

Figure 7. Example of box-plot and cleveland dot-plot for SST (a) and wind speed (b) for summer months at Muizenberg beach after filtering data for the variable spotter.

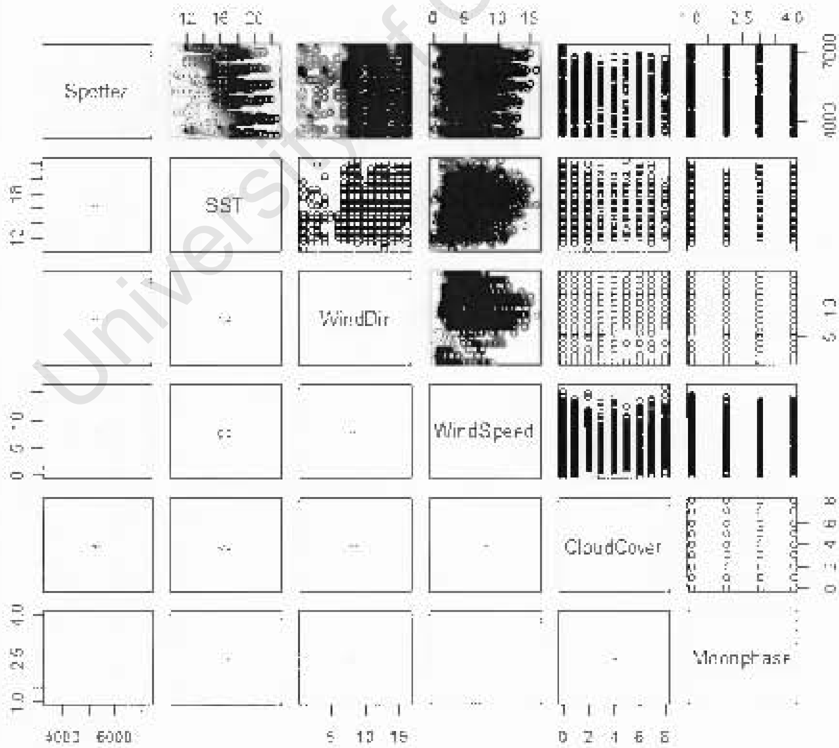

Figure 8. Multi-panel scatterplot showing the correlation between spotter and environmental variables including SST, wind speed, wind direction, cloud cover and lunar phase.

The relationship between the environmental variables and shark spotters was also investigated using pivot tables to determine whether equal spotting shifts of spotters existed for all environmental conditions. Once the data had been edited to include only the chosen spotters for each site, the above exploratory analyses were re-run. Box-plots and cleveland dot-plots for continuous variables (SST and wind speed) and pivot tables for categorical variables (wind direction, cloud cover, lunar phase) for all sites continued to suggest no outliers and showed an even spread over the summer months. An example for box-plots and Cleveland dot-plots are shown for SST and wind speed at Muizenberg in Figure 7. Furthermore, a second multi-panel scatter-plot was created including the spotter as another variable. No correlation was found between spotter and environmental variables (Fig 8). Also, only including the environmental data corresponding to the chosen spotters for the study did not change correlations between any pair of environmental variables (Fig 8). The variable spotter was therefore included as an independent variable in the models. Furthermore, in order to get an understanding of the annual variance in the number of shark sightings over the study years, the variable year was considered as an additional variable to the models.

Modelling process

Initially generalized linear models (GLM's) were considered (Zuur *et al.,* 2009). However, GLM's assume parametric relationships and do not allow for the possibility of non-parametric relationships. Since the relationship investigated in this study is more likely to be non-parametric, I therefore applied a generalized additive model (GAM) which, despite its tendency to overfit relationships, is less restrictive with regards to the underlying distribution of the data (Hastie and Tibshirani 1986; Wood 2006). GAM's are non-parametric generalizations of multiple linear regression which replace the least square estimates of GLM's by maximum likelihood estimates using smoothing functions (Hastie and Tibshirani 1986; Wood 2006). Hence GAM's are commonly used to examine relationships which are likely non-linear and not normally distributed.

The modelling process for the Poisson GAM's was based on techniques described by Johnson and Omland (2004) and extended into R (version 2.13.0) by help of Zuur *et al.,* (2007), Zuur *et al.,* (2009) and Wood (2006) in understanding the R programming language and how to apply it to ecological data using a GAM. The variables included in the final models for each site were determined using a forwards and backwards stepwise variable selection procedure, selecting the best fitting model based on the lowest Akaike's information criteria (AIC) value (Bozodogan 1987). The contribution of each variable in the final model was determined using ANOVA tables with Chi-squared tests, selecting only variables significant at a p< 0.001 significance level.

Full model Poisson GAM

SS ~ s(SST) + Spotter + s(LunarPhase) + te(WindSpeed, WindDir) + s(Year) + s(Cloudcover)

Where **s** indicates the use of a smoothing spline, **te** the use of a thin plate regression spline used for interaction terms.

Additionally, the predict.gam function, provided by a programming package in R called mgcv, was used to predict the isolated effects of significant independent variables on the number of shark sightings. The predict.gam function simulates experimental conditions in which other variables are kept constant for optimal shark sighting conditions. The optimal shark sighting conditions were chosen based on the maximum number of sightings recorded for each environmental variable included in the analysis. Predictions were conducted with regards to an average reference year for the number of shark sightings over the study period.

Making use of a separate spreadsheet containing the exact date and timing of sighting and its corresponding state of tide, the influence of tidal state on the number of shark sightings at each study site was related using a linear regression model. The number of shark sightings was compared among the four tidal states within each year separately (according to months from Sep to May) for all beaches combined, assuming equal number of shifts per tidal state per year. The significance of each tidal state was determined using a one-way ANOVA with Chi-squared tests.

Full linear regression model for tidal state

Shark sightings per year ~ Tidal State

Where SS Time is the time when each shark was first sighted.

Results

A total number of 6730 spotting shifts were included in this study, with a total of 563 white shark sightings. Of these, 2050 shifts with 121 sightings were recorded at Fish Hoek, 2243 shifts with 106 sightings at St. James, and 2437 shifts with 336 sightings at Muizenberg (Fig 9).

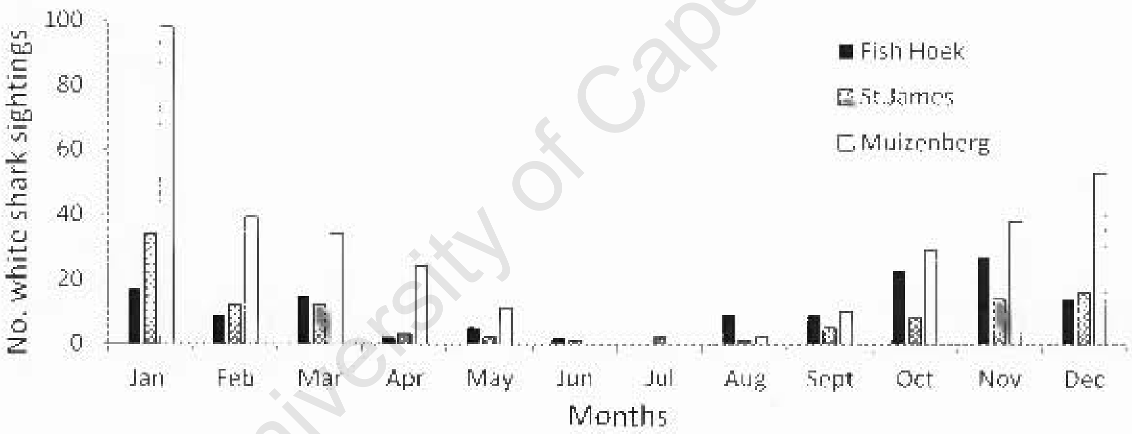

Figure 9. The combined frequency of white shark sightings per month at the three study beaches Fish Hoek (total=132, summer months=121), St. James (total=110, summer months=106) and Muizenberg (total=338, summer months= 336) from January 2006 to June 2011.

The final models for Fish Hoek (1) St. James (2) Muizenberg (3) contained the following variables:

(1) Num SS ~ s(SST) + Spotter + s(LunarPhase) + te(WindSpeed, WindDir) + s(Year)

(2) Num SS ~ s(SST) + te(WindSpeed, WindDir) + s(Year)

(3) Num SS ~ s(SST) + s(WindSpeed) + s(CloudCover)+ s(LunarPhase) + s(Year)

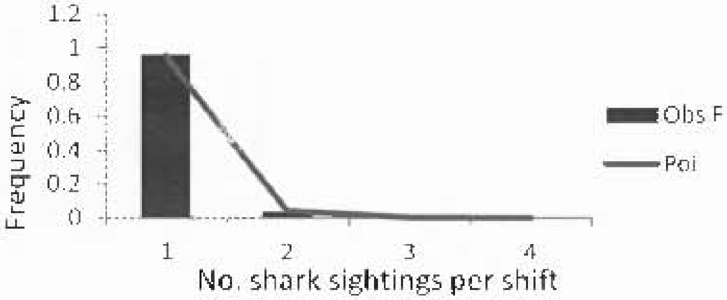

Figure 10. The frequency of observed vs. expected number of white shark sightings at St. James, successfully estimated by Poisson distribution.

Binomial GLM and GAM models were only capable of explaining very minimal variation within the data (5-9% deviance). Furthermore, with low maximum counts of shark sightings (maximum 5 sightings per shift), the Poisson GLM and GAM adequately predicted the excess amount of zero's within the data (Fig 10, example for St. James). However, GLM only explained minimal percentage of the variation in shark sightings for Fish Hoek (15.8%), St. James (10%) and Muizenberg (12.1%). In contrast, the Poisson GAM explained 24.4 %, 16.6 % and 16.5 % of the total variation in the number of shark sightings for the beaches Fish Hoek, St. James and Muizenberg respectively (Table 2).

Table 2. Poisson GAM results for Fish Hoek, St. James and Muizenberg showing the variables included, the percentage each variable contributed to the explained variance, including the level of significance (p-value).

	Fish Hoek			**St James**			**Muizenberg**		
Model	POI GAM	% contributed	p value	POI GAM	% contributed	p value	POI GAM	% contributed	p value
SST	√	11.2	*	√	40.4	***	√	43.5	***
WDI/WSP	√	30.0	.	√	36.4				
WIND SPEED							√	13.0	***
CLOUD COVER							√	18.0	***
MOON PHASE	√	23.8	***				√	9.2	**
SPOTTER	√	17.7							
YEAR	√	17.2	***	√	23.3	***	√	16.3	***
Total % Dev explained	**24.3**			**16.6**			**16.5**		

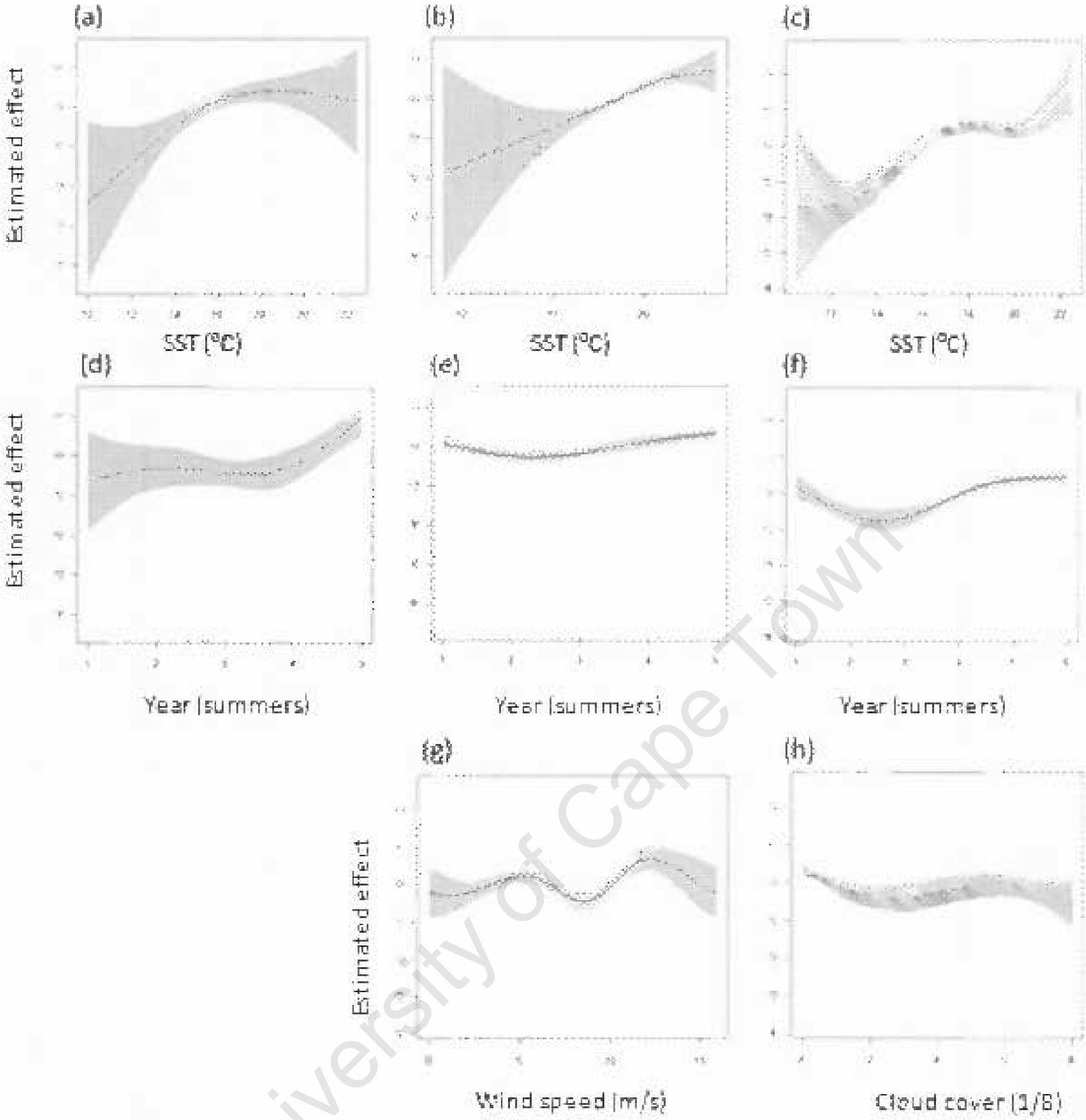

Figure 11. Significant effects of environmental conditions on the number of shark sightings recorded at the beaches Fish Hoek [(a)= SST, (d)= Year], St. James [(b)= SST, (e)=Year] and Muizenberg [(c)= SST,(f)=Year,(g)=Wind speed,(h)=Cloud cover] over the summer period of the study years.

SST was significant ($p<0.05$) at all three study beaches. SST was particularly highly significant at St. James and Muizenberg, where it accounted for the majority of the explained variance (40.4 % and 43.5% respectively). White sharks were sighted in SST's ranging from 10-22.5 °C at Fish Hoek, from 9-24 °C at St. James and from 10.5-22.5 °C at Muizenberg over the study period. For all three beaches, white shark sightings were most abundant between the ranges of 13-23°C. The graphical GAM output for SST for Fish Hoek (Fig 11 a) and Muizenberg (Fig 11 c), suggests a similar trend with the number of shark sightings peaking around an optimal range of 18-20 °C. For St. James the relationship is more linear with shark sightings increasing with increasing SST, with a minor peak evident at 20°C (Fig 11 b).

Wind speeds for all three beaches ranged from zero to 15.1 ms^{-1} for Fish Hoek and from zero to 15.9 ms^{-1} for both St. James and Muizenberg. However, wind speed was only significant for Muizenberg (13%). The graphical GAM output for Muizenberg indicates two peaks of increased shark sightings at wind speeds of 6 ms^{-1} and 12 ms^{-1} (Fig 11 g).

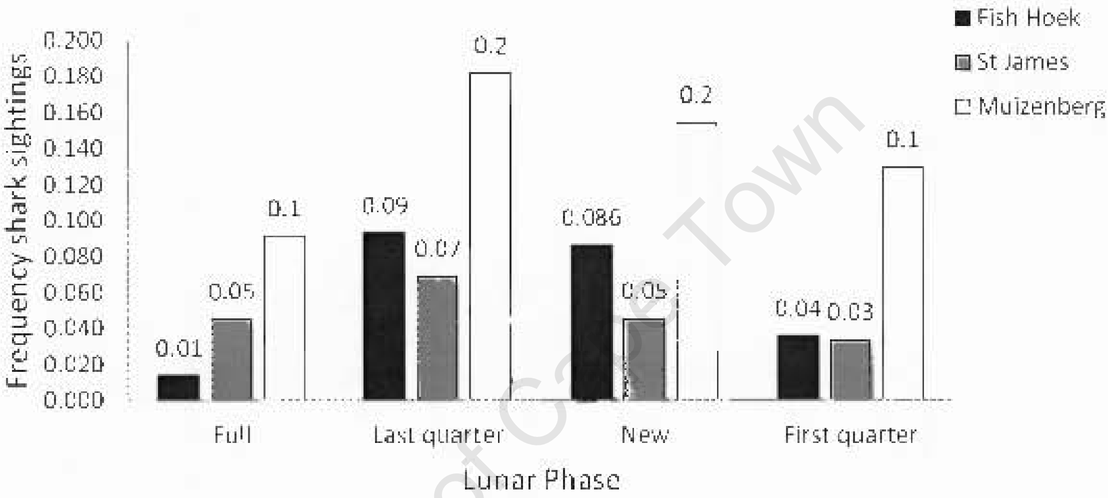

Figure 13. The frequency of white shark sightings during different lunar phases (standardized per shifts) at the beaches Muizenberg, Fish Hoek and St. James.

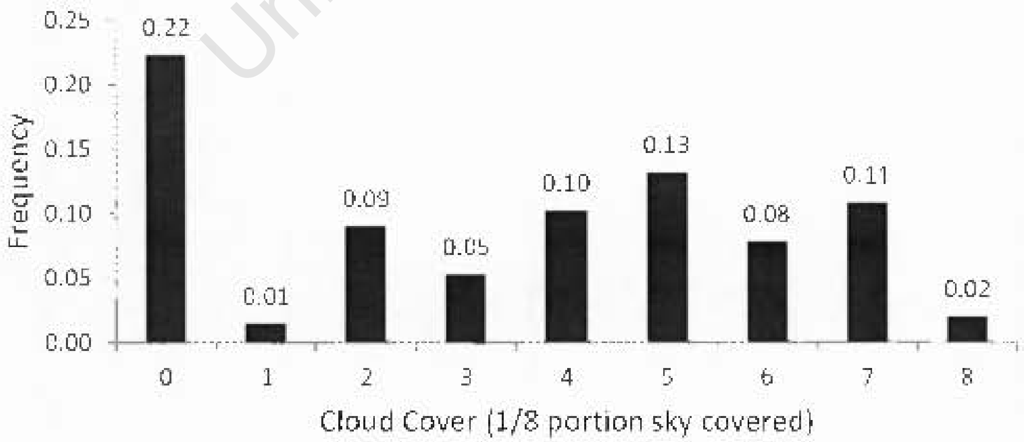

Figure 14. The frequency of white shark sightings during different degrees of cloud cover at the beaches Fish Hoek, St. James and Muizenberg.

The lunar cycle was significant in contributing to the explained variance at Fish Hoek (23.2%) and at Muizenberg (9.2%). At both beaches, the lowest number of shark sightings was recorded during full moon and the highest number of sightings was recorded during last quarter moon (Fig 13).

Cloud cover could not explain the variance in shark sightings, with the highest number of shark sightings were recorded when cloud cover was zero and the lowest number of shark sightings was recorded when cloud cover was 1/8 (Fig 14). Furthermore, cloud cover was only significant at Muizenberg (18%) and showed no clear relationship to shark sightings in the GAM output (Fig 11 h).

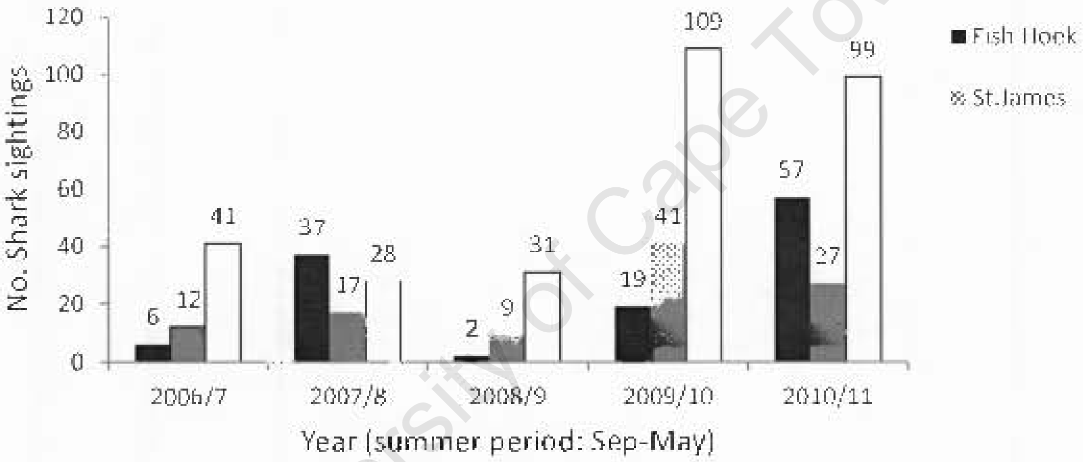

Figure 15. The frequency of white shark sightings over sequential summers at the three study beaches.

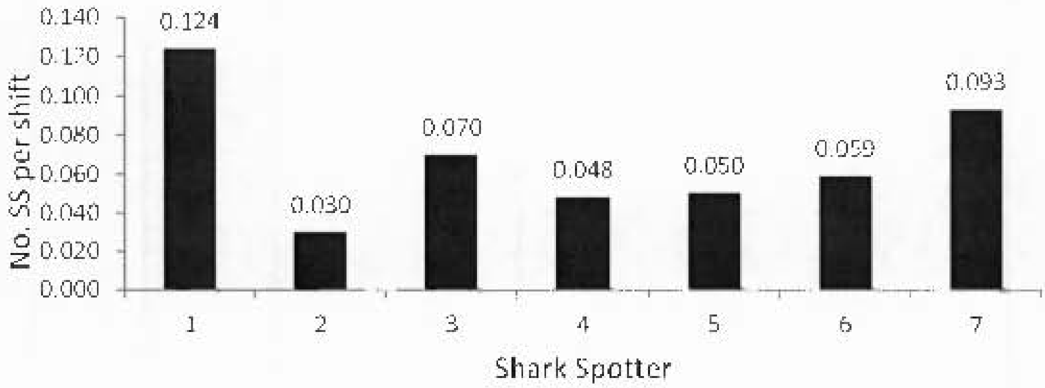

Figure 16. The frequency of white shark sightings by individual shark spotters at Fish Hoek beach over the summer months of years 2006 to 2011. Only spotters 1 and 2 were significantly different from the rest.

For all beaches, the year (yearly summer spotting period) was highly significant (p>0.05) with relatively high explanatory power for Fish Hoek (17.2%), St. James (23.3%) and Muizenberg (16.3%). The graphical GAM output shows the variability in shark sightings over the sequential summer periods for Fish Hoek (Fig 11 d), St. James (Fig 11 e) and Muizenberg (Fig 11 f). Although the number of shark sightings varies in time, the number of shark sightings has significantly increased over the last two summers (2009/10- 2010/11) at all three beaches (Fig 15).

The spotter was only included as a variable in the GAM for Fish Hoek, yet was not significant in explaining variance in shark sightings. Only two spotters were significantly different from the selected seven (Fig 16). Spotter 1 had sighted the highest number of shark sightings per spotting shift, while Spotter 2 had sighted the lowest number of sharks per spotting shift (Fig 16).

Tidal state did not significantly affect the number of shark sightings (p>0.05) (Table 3). There was no significant difference between the number of shark sightings per year during high, low, ebb or flood tides at beaches Fish Hoek (Fig 17), St. James (Fig 18) and Muizenberg (Fig 19).

Table 3. The results for one-way ANOVA conducted for all study sites indicating no significant difference in the number of white shark sightings per study year at different tidal states of high, ebb, low and flood.

One-way ANOVA: Shark sightings per year vs. Tidal state

Site	Df	Sum Sq	Mean Sq	F value	p value
Fish Hoek	3	1.35	0.45	0.0181	0.9965
Muizenberg	3	4.95	1.65	0.0754	0.9723
St. James	3	130.95	43.65	0.6086	0.6191

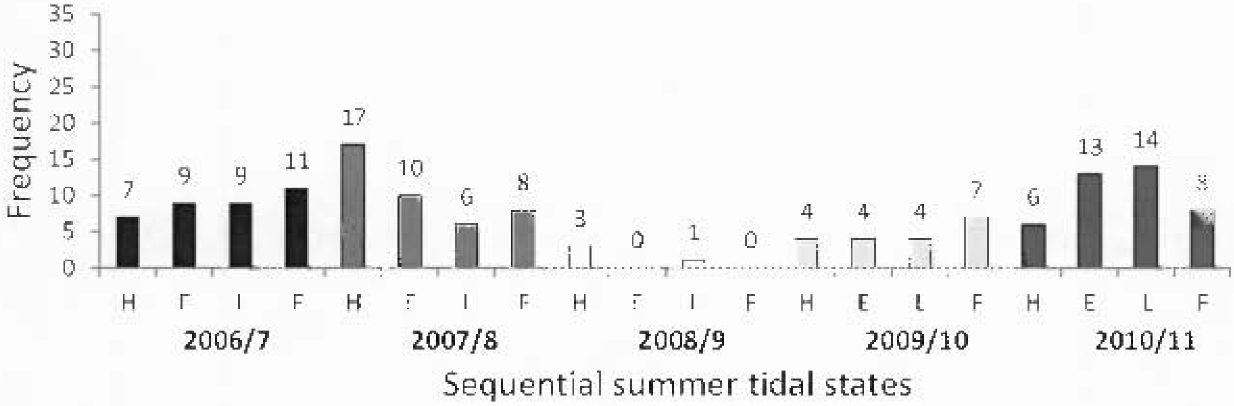

Figure 17. Frequency distribution of the number of white sharks sighted during different tidal states, including high (H), ebb (E), low (L) and flood (F) at Fish Hoek over sequential summer periods. No significant influence of tidal state on the number of shark sightings (p>0.05).

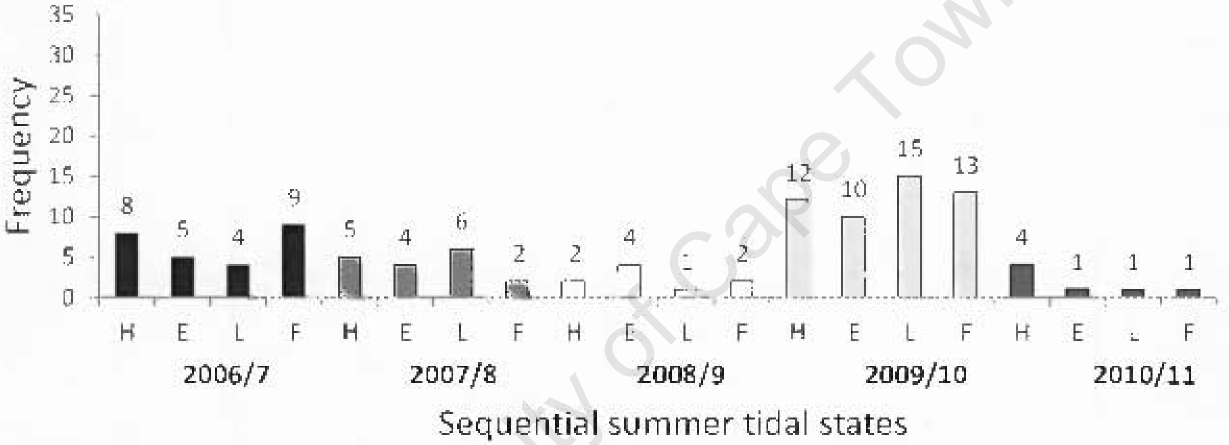

Figure 18. Frequency distribution of the number of white sharks sighted during different tidal states, including high (H), ebb (E), low (L) and flood (F) at St. James over sequential summer periods. No significant influence of tidal state on the number of shark sightings (p>0.05).

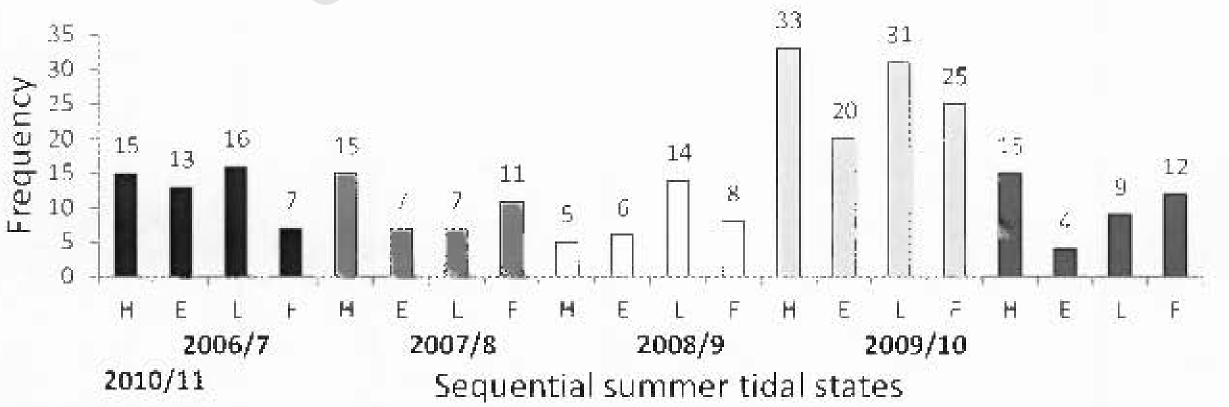

Figure 19. Frequency distribution of the number of white sharks sighted during different tidal states, including high (H), ebb (E), low (L) and flood (F) at Muizenberg over sequential summer periods. No significant influence of tidal state on the number of shark sightings (p>0.05).

Table 4.The reference set of variables for each factor used for model predictions. As far as possible, reference set values corresponded to optimal shark sighting conditions.

Site	Year	Wind speed	Lunar phase	Wind dir	Cloud cover	Spotter
Fish Hoek	4	8 ms^{-1}	Last quarter	offshore	0	Ashley
St. James	2	4 ms^{-1}	-	onshore	-	-
Muizenberg	4	4 ms^{-1}	Last quarter	-	0	-

Model predictions against a reference set of environmental conditions and years (Table 4) clearly illustrate the influence of SST in terms of sighting probability (Fig 20). The magnitude of the influence of SST on the probability of sightings shark is an average of 78% higher at 20°C than at 14 °C along False Bay's surf-zone in summer months. To illustrate this, the predicted sightings rate at 20°C is 62.5% greater at Fish Hoek, 100% greater at St. James and 73.3% greater at Muizenberg than the sightings rate at 14°C (Fig20).

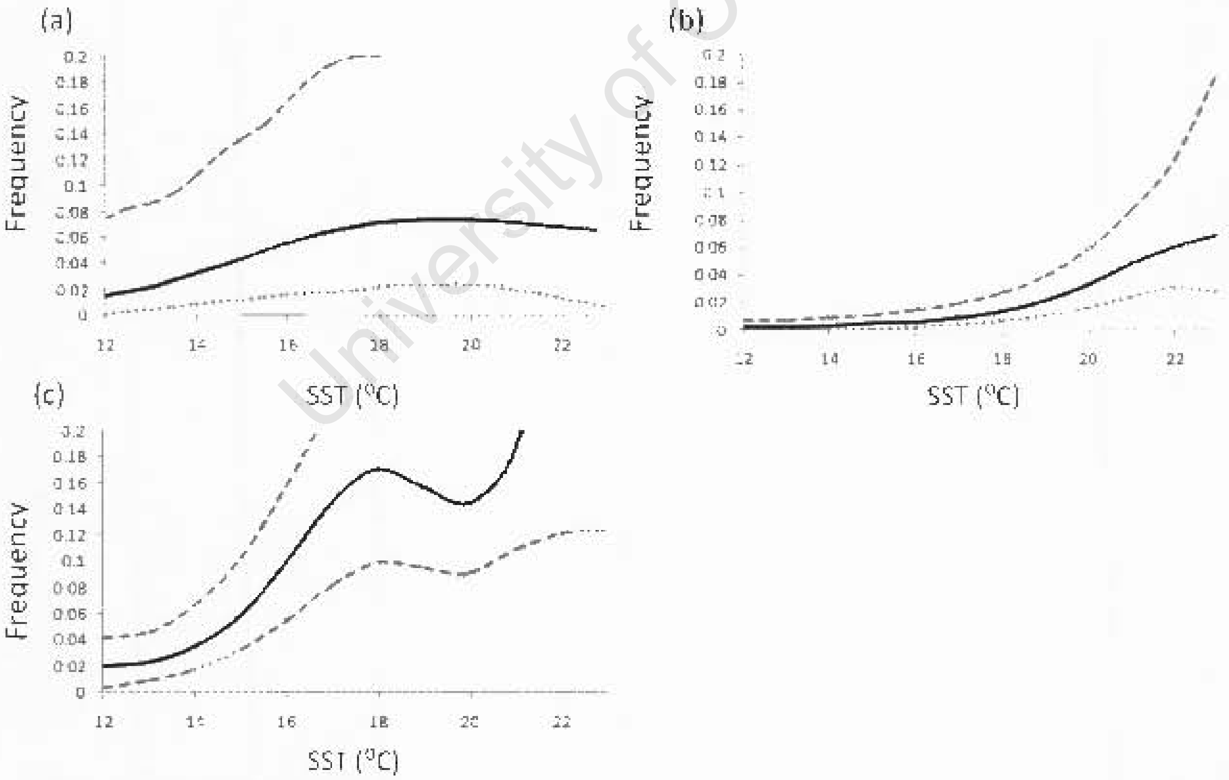

Figure 20. Predictions of the frequency of the number of white shark sightings per shift at different SST values at the beaches Fish Hoek (a), St. James (b) and (c) Muizenberg.

Discussion

Identifying significant relationships between local environmental conditions and the frequency of white shark sightings nearshore at popular False Bay beaches is the first step towards incorporating environmental information into shark safety programs in the Cape Peninsula. Using daily predictable weather conditions, incorporating environmental aspects can help determine times and areas of increased risk of shark encounters within False Bay's surf-zones during peak summer season, minimizing the risk of shark encounters by water-users.

Sea surface temperature (SST)

SST was significant for all three beaches and showed most white sharks sightings were recorded over a SST range of 13-23^{0}C at popular beaches in False Bay. This is in agreement with previous findings by Goldman (1997) which suggests a preferred SST range of 13.3-22^{0}C for white sharks. Additionally, results from this study narrow the preferred temperature range, showing consistent peaks in shark sightings between 18-20^{0}C at Fish Hoek and Muizenberg beaches. Model predictions for the isolated effect of SST suggest a 62.5% - 100% greater chance of spotting a shark during 20^{0}C than at 14^{0}C along False Bay's surf-zones over months September – May.

Since SST has no effect on "spottability", it is accepted here that the findings for SST are due to its impact on shark biology and behaviour. However, since white sharks are capable of regulating their internal body temperature (Klimley *et al.,* 2001; Abascal *et al.,* 2011) and tolerating a wide range of water temperatures (Martin 2004; Dewar *et al.,* 2004), physiological aspects seem unlikely to be limiting white sharks to such optimal temperature ranges (18-20 °C). Alternatively, the observed optimal trends could be explained by investigating the relationship between the distribution of its prey species and water temperature. White sharks are apex predators with a wide range of diet including marine mammals, teleosts, elasmobranchs, invertebrates and occasional marine birds or reptiles (Compagno 1984; Fergussen 1999). Stomach content analysis of white sharks, caught in gill nets off the southern African Kwazulu-Natal (KZN) coastline, suggest smaller elasmobranchs to be the most common prey for white sharks, followed by teleosts (Fergusson *et al.,* 2000;

Tricas and McCosker 1984; Cliff *et al.,* 1989). Such elasmobranchs include the juveniles of dusky sharks (*Carcharhinus obscurus),* copper sharks (*Carcharhinus brachyurus*), milk shark (*Rhizoprionodon acutus*), hammerhead sharks (*Sphyrna lewini*), and several dogfish (family Squalidae) and ray species (family Dasyatidae and Myliobatidae) (Cliff *et al.,* 1989). The most commonly found teleosts in the stomachs of white sharks in KZN included various species of tuna (family Scombridae), kob (*Argyrosomus hololepidotus*) and pilchards (*Sardinops ocellatus*) (Cliff *et al.,* 1989). In False Bay there are a variety of potential teleost prey for white sharks which include white steenbrass (*Lithognathus lithognathus*), yellowtail (*Seriola lalandi*), Elf (*Pomatomus saltatrix),* horse mackerel (*Trachurus trachurus capensis*) harders (*Liza richardsonii*) and very rarely yellowfin tuna *(Thunnus albacares),* which are all frequently caught by commercial fisheries over the summer months (Clark *et al.,* 1994; Lamberth *et al.,* 1995; Hutchings and Lamberth 2002). Moreover, it's suspected that white sharks have a seasonal shifts in diet, by shifting from a diet dominated by inexperienced seal pups at Seal Island during winter months (end of May- beginning of September) to a diet consisting primarily of fish species occurring in high abundances nearshore in summer months (Martin *et al.,* 2005).

The seasonal increase in abundance, species diversity and richness of juvenile fish (highest in months Jan-May) coincides with warmer waters, which provide favourable environmental condition for fish species and their prey within False Bay's surf-zones (Atkins 1970; Lamberth 2006; Lamberth *et al.,* 1995; Clark *et al.,* 1996). For example, *L. richardsonii* feeds on increased blooms of the surf-zone diatom *Anaulus birostratus*, triggered by summer upwelling and warmer waters around 21-23°C (Talbot and Bate 1986; Webb *et al.,* 1988; Lamberth *et al.,* 1995). Moreover, spawning of fish species in False Bay is timed in accordance with spring months in order to directly recruit into the surf-zones in summer, maximising juvenile growth and survival (Clark *et al.,* 1996; Sheaves 2006). In fact, water temperatures are suggested to be the most important physiological factor in determining seasonal fish assemblages in False Bay's surf-zones (Clark *et al.,* 1996).

Certain elasmobranchs even migrate southward from KZN to take refuge from too warm waters present there summer period (Compagno *et al.,* 1989; Dudley *et al.,* 2005). Examples of such include dusky (*C. obscurus)* (Compagno 1989; Dudely *et al.,* 2005) and copper sharks (*C. brachyurus*) (Cliff *et al.,* 1989), both identified as important prey of white sharks (Cliff *et* *al.,* 1989). In particular, juvenile *C. obscurus*, feeding on juvenile fish species, have been shown to have an optimal range of 19-23°C (Dudley *et al.,* 2005). This corresponds to the same optimal temperatures discovered in this study for white sharks at Fish Hoek and Muizenberg beaches (18-20°C). This temperature range has also been observed for white sharks in Californian waters, ranging from 16-20°C (Cartamil *et al.,* 2011). A similar optimal temperature range is evident for some of the above mentioned teleost prey items in False Bay, including *S. lalandi* with 17-27°C (Nakada 2002), *L. lithognathus* 16-20°C (Bennett 1993a) and prey of *Thunnus albacares*, namely saury (*Scomberesox saurus scombroides*) with optimal temperatures of 18-22°C (Olson and Boggs 1986; Dudley *et al.,* 1985).

Furthermore, since white shark distribution is probably related to its feeding behaviour and preferences of prey species, it should be expected that environmental conditions can only explain a small percentage (16.5-24.5%) of shark occurrences along False Bay's surf-zones. A better understanding of the effect of environmental variables on white shark sightings nearshore will come about by incorporating variables on prey availability and distribution in different environmental conditions (Lamberth *et al.,* 1995).

Lunar phase

Lunar phase was significant for Fish Hoek and Muizenberg, with the most shark sightings recorded during last quarter moon and the lowest number of sharks sightings recorded during full moon. At both beaches, the number of shark sightings decreased consistently from last quarter moon to full quarter moon, with the lowest amount of shark sightings recorded during full moon and the highest amount of shark sightings recorded during last quarter moon. As with SST, lunar phase has no effect on the "spottability" during daytime hours and findings here can be explained by the effect of the lunar cycle on shark biology and behaviour. The lunar cycle provides predictable environmental patterns to which many marine organisms structure a variety of behavioural functions affecting habitat use, including, predation, group living, locomotion, daily and seasonal migrations, physiological changes reproduction and settlement of larvae (Naylor 2005; Katselis *et al.,* 2007; Benoit-Bird *et al.,* 2009; Guttridge 2009). Reproduction of marine invertebrates and fish in particular, is significantly affected by full moon (Fox 1924; Johannes and Hviding 2000). In areas with strong tidal currents, full moon has been correlated with 'full' gonads and ovaries during the reproductive cycle of marine species including echinoderms, molluscs and fish such as snappers and groupers, which are released into the water column either during or shortly after the period of full moon (Fox 1924; Johannes and Hviding 2000). Similarly, a peak in swarming of oyster larvae has been shown to occur ten days after full moon (Laroche *et al.,* 1997).

The lunar phase is also believed to control hunting timing, strategy and behaviour of marine predators and play a role in predator-prey interactions (Horning and Trillmich 1999, Bestley *et al.,* 2008). The prey species of white sharks over the summer period, including teleosts and juvenile elasmobranchs species, feed primarily on an array of fish and invertebrate larvae and juveniles, including demersal and pelagic fish species, cephalopods, molluscs and crustaceans (Natanson and Kohler 1996; Compagno *et al.,* 1989; Bennett 1993a). This might be related to an increased abundance of teleosts and elasmobranchs in the nearshore environment of Fish Hoek and Muizenberg beaches shortly after full moon, responding to an increased availability of invertebrate and fish juveniles and larvae in the water column. This might explain why the highest amount of white shark sightings was observed over the corresponding lunar phase. Furthermore, other predatory fish such as tuna show similar trends by increasing their feeding events directly after full moon (Bestley *et al.,* 2008).

Furthermore, a gradual decline in white shark sightings after the last quarter phase could be correlated with decreasing invertebrate and fish resources, which are being depleted towards the next reproductive bout occurring around full moon. Additionally, migrations of fish species into estuaries around full moon, observed for species such as breams or mullets (harders) (Johannes and Hviding 2000), could further reduce available prey for white sharks nearshore around full moon.

Cloud cover

Cloud cover was only significant at Muizenberg beach, where model results showed the highest number of sightings recorded during zero cloud cover. However, the second highest number of shark sightings was recorded during a degree of cloud cover of 5. Moreover, a similar amount of shark sightings was recorded during low degrees of cloud cover of one as during a high degree of cloud cover of 8. This would suggest that spotters are able to detect white sharks relatively well in clear as well as cloudy weather. This implies that although cloud cover was significant at Muizenberg, the significant effect can not be explained by its influence on "spottability" or the number of shark sightings recorded. However, since white sharks have excellent vision and a high predation success rate in dim light conditions, it is unlikely that shark behaviour can explaining the trends found here for cloud cover (Bozzanao *et al.,* 2001; Hart *et al.,* 2004; Hammerschlag *et al.,* 2006). Further work needs to be conducted into the relationship between cloud cover and shark sightings nearshore in order to explain the findings in this study. Perhaps time of day (e.g. sunrise, daytime, sunset) might be more capable of explaining the effect of light availabilities on shark biology and "spottability".

Wind patterns

Wind speed was significant in affecting the number of shark sightings recorded at Muizenberg beach. However, results show that the highest number of shark sightings was recorded at medium (6 ms-^{1}) and relatively high (12 ms^{-1}) wind speeds. This suggests that wind speed has no apparent effect on "spottability", since similar amounts of sharks were sighted during medium and strong winds.

The fact that wind can not explain the variation in shark sightings for any of the study beaches might be attributed to a suggested lag effect of wind speed and direction on the marine environment, with effects of wind only becoming apparent after a continuous period of a particular wind direction at certain wind speeds (Rose and Leggett 1988). A study conducted on Atlantic cod observed winds to be lagged two days prior to catch day on the north shore of the Gulf of St. Lawrence (Rose and Leggett 1988). Several days of strong SE are followed by several days of warmer murky waters in False Bay (Atkins 1970). Therefore, instead of the direct effect of wind at the recorded timing of shark sighting, it may rather be the after effect of wind speed and direction which influences the number of shark sightings nearshore. Additional to a possible lag effect, wind might truly not be significant for individual beaches based on their geographic positioning. St. James is known to be relatively wind sheltered by being situated in close proximity to the mountain side and results for St. James could be indicating the correct trends. This is why Muizenberg, which is more exposed, is more vulnerable to the influence of wind speed.

However, perhaps instead of the interactions between wind speed and wind direction as well as the geographic positioning of the study beaches, the effect of wind on shark presence nearshore is expressed through its ability to control upwelling of nutrients and the SST of the bay. Over summer periods, strong SE winds cause upwelling along the outer shelf of the bay, driving and trapping trap warmer waters in shallow western banks of False Bay (Atkins 1970; Lamberth *et al.,* 1995). Since we determined that prey availability and SST largely determine white shark distribution, wind could play an indirect role in determining shark behaviour and the actual presence of sharks within the surf-zone. However, although Muizenberg and St. James beaches showed similar interactions between SST and wind speed, no strong relationship was evident.

Tidal state

Tidal state was not significant for explaining the number of shark sightings recorded for any of the study beaches, with minimal variation in the number of shark sightings at different tides between years throughout the study period. This results is unexpected, since tidal states may potentially effect shark behaviour or "spottability" or both. Some shark species, e.g. juvenile lemon shark (*Negaprion brevirostris*), have been observed to move further inshore with incoming tides to exploit previously unattainable resources (Guttridge 2009; Knip *et al.,* 2010). Furthermore, should incoming tidal states allow for sharks to move closer inshore, this would increase "spottability". However, the effect of tidal state depends particularly on the bottom topography of a beach. All study sites have a gradually declining bottom topography and lack any sudden drop-off of the coastal shelf (Atkins 1970). Therefore, the amount of available habitat which increases or decreases with incoming (flood) or outgoing (ebb) tide respectively, is not substantial enough to significantly affect the movement of white sharks in these areas. Perhaps it is for this reason that tidal state played no significant role in determining the number of shark sightings recorded nearshore at Fish Hoek, St. James and Muizenberg.

Year

Year was significant for all three study sites, with a variation in the number of shark sightings at each beach over the individual summer spotting periods (September – May). Results show that the number of shark sightings has significantly increased over the last two years. This suggests that white sharks are currently spending more time inshore at False Bay beaches in summer months than in previous years. Whether this is attributed to changes in prey distribution inshore in summer months, changes in environmental conditions or simply a behavioural preference by white sharks in False Bay, is not certain. However, according to our environmental data, the significant environmental variables affecting shark sightings nearshore, such as SST, wind speed or cloud cover, have on average remained the same over the summer study years for each study beach individually. This would suggest that an increase in shark sightings nearshore in summer months at these beaches is more likely attributed to changes in prey distribution than shark behaviour related to environmental conditions. Future investigations should therefore relate continuous monitoring of annual shark sighting numbers nearshore at popular False Bay beaches to prey distribution and numbers at such beaches.

Spotter

Spotter was only included in the model for Fish |Hoek, but was not significant in determining the number of shark sightings recorded over the study period in relation to environmental conditions. My results show that each shark spotter has different capabilities of spotting sharks, with spotter 1 having a very high number of sharks sighted per spotting shift and spotter 2 a very low number of sharks sighted per spotting shift in relation to the remaining spotters. This is attributed to the natural ability and different concentration rates of each spotter. Nonetheless, the variable spotter played no significant role in affecting the relationship between the number of shark sightings recorded and measured environmental conditions.

Conclusion

Environmental factors play an important role in determining marine predator distributions. My study showed a significant relationship between white shark distribution nearshore and SST and lunar phase, with an increase in shark activity in surf-zones when SST was higher than of 18^{0}C and during the last quarter moon phase. With an increase in shark sightings over recent years at all three study beaches, the risk of shark encounters could potentially be decreased through knowledge of the results of this study by acting as a valuable tool for increasing water-user safety. Future research should continue to monitor the frequency of shark sightings in relation to environmental conditions and can be combined with information on shark behaviour and the biology of their preferred prey species.

Chapter 3: Practical application and future recommendations

The main findings and their practical implementation into shark safety programs in the Cape Peninsula

It is evident from the results of this study that a link exists between the number of shark sightings in False Bay and environmental conditions. SST and lunar phase are the most significant variables influencing the presence of white sharks in the surf-zone of False Bay. The highest number of shark sightings was recorded at SST's between 18-20°C, with on average a 78% greater chance of sighting a shark at 20°C than at 14°C. The most shark sightings were also recorded during the lunar phase of last quarter moon, while the lowest amount of shark sightings took place during full moon. This information can be used as a tool for providing beach management with an increased knowledge on days of higher risk of human-shark encounters.

Of the summer days included in this study, a SST higher than 18°C was measured at the beaches of Fish Hoek, St. James and Muizenberg 28.4%, 61.4% and 55% of the time respectively. On average (48.3%), half of the days in summer have a SST above 18°C. Since the results of this study show that the most shark sightings were recorded above a SST of 18°C, half of the days over the summer period have a higher chance of water-users encountering a shark in the surf-zone along False Bay.

Beach management could incorporate the findings here into shark-safety warning systems by distinguishing between 'high shark-alert days' from 'lower risk days' and issuing increased spotting awareness on higher risk days, such as when SST are above 18°C or lunar phase is in last quarter phase, in which shark sightings were at their highest. Increase the public caution could also be urged such high risk periods. Furthermore, it is important to understand that these recommendations will be updated as additional data become available in the future. Nonetheless, the overall conclusion from this study confirms that not only does a relationship exist between white shark distribution nearshore and environmental conditions in False Bay, but that including such relationships in shark safety programs is a possibility for further managing human-shark conflict.

Future updates and research

To ensure that future shark spotting data is recorded correctly, I recommend that Shark Spotters transfer the data from recording sheets into a database which uses the spotting shift as its unit. This format will allow Shark Spotters to enter the name of the individual spotter on duty for each shift. On this note, I would like to suggest that shark spotters with relatively low numbers of shark sightings per spotting shift are better positioned on the beach instead of at elevated spotting positions. Moreover, data sheets should be collected daily and entered weekly in order to ensure information is up to date.

The models used in this study will be updated annually, which will allow for the further monitoring of the influences of environmental conditions on the number of shark sightings recorded in False Bay's surf-zones in the future. New variables which can be added to future models include the lag effect of wind on white shark movement, time of day (e.g. sunrise, daytime, sunset) and the response of prey abundance and distribution to changes in SST and lunar phase.

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