Environmental predictors of *Carcharodon carcharias* presence at two popular beaches in False Bay, South Africa using acoustic telemetry

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Abstract

By understanding when white sharks (*Carcharodon carcharias*) are likely to be at certain popular beaches, it is possible to predict when the risk of overlap between water users and white sharks is highest, and to convey this information to the public so they can make informed decisions about using these areas. Previous studies have shown that white shark presence near popular recreational beaches in False Bay, South Africa, is influenced by a range of environmental variables. These studies have relied on land-based observers (shark observers), whose ability to detect sharks is subject to the depth at which the sharks swim and a suite of environmental conditions that influence water visibility, including cloud cover, wind speed and ambient light levels. In this study, I use passive acoustic telemetry on 56 tagged white sharks to determine whether the same or other environmental variables explain variation in white shark presence at the same beaches. A total of 13 803 and 1 481 white shark detections were recorded between April 2005 and December 2007 at Muizenberg and Fish Hoek beaches, respectively. This represented 32 and 16 individual white sharks with a median number of 32.5 (range 5.5 – 57.8) and 7 (range 4 – 14.8) detections per shark at Muizenberg and Fish Hoek beach, respectively. The low number of detections at Fish Hoek resulted in the data being highly zero-inflated with the result that the subsequent modelling of the data with environmental covariates did not converge, and hence I focused solely on Muizenberg beach. The probability of detecting a white shark at Muizenberg beach was modelled using binomial generalised additive mixed models (GAMMs) with water temperature, wind speed, wind direction, cloud cover, lunar phase, tide height, barometric pressure, year, season and time of day as predictor variables. Water temperature was a significant predictor of white sharks at Muizenberg beach during summer, autumn and winter while wind speed, time of day and barometric pressure were significant predictors of shark presence during the summer and autumn months. There was significant inter-annual variability in white shark detections and a strong seasonal relationship, with presence being highest during spring and lowest during winter. Encouragingly, the findings from this study support some of the key findings of previous studies using observational data, including the significant positive effects of increasing temperature, year, season and time of day.

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Thank-you to my parents for always supporting me and my decision to pursue my studies and career in conservation. To my grandmother, Grootje, for providing me with the gift of a tertiary education, I will be forever grateful! To my supervisors Justin and Alison, thank-you so much for all the comments and support with this project. To Dylan, Tate, Matt Lewis and Marion, thanks for all the help with the stats, I wouldn’t have been able to progress without your patience and help. Thank-you to the South African Weather Service for providing much of the environmental data and to the South African Coastal Temperature Network for water temperature data. I am very grateful to the University of Cape Town for providing me with funding which contributed towards my studies. To the conservation biology class of 2017, it’s been an intense and crazy year, I’m so glad to have met you all and to have been on this journey together, thanks for all the good times and all the rough times – we made it! And finally thank-you to Colleen, we’ve been on this journey together and have made it through! You’ve been an immense support this year, thank-you for everything.

Plagiarism Declaration

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Date: 19 February 2018

Dave van Beuningen

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Introduction

Distribution and movement patterns of white sharks

White sharks have a global distribution, with major concentrations in South Africa, Australia/New Zealand, the north-eastern Pacific and north-western Atlantic (Pardini et al. 2001; Domeier and Nasby-Lucas 2008; Skomal et al. 2017). They are capable of transoceanic migrations, with individuals recorded swimming 3 550 km from Australia to New Zealand (Bruce et al. 2006), 3 800 km from California to Hawaii (Boustany et al. 2002; Weng et al. 2007; Block et al. 2011) and 20 000 km from South Africa to Australia and back (Bonfil et al. 2005). In spite of these vast distances travelled, white sharks are normally encountered along continental shelves, often exhibiting fine-scale patterns of site fidelity and seasonal aggregation in coastal areas where prey availability is high (Martin et al. 2005; Bruce et al. 2006; Domeier and Nasby-Lucas 2008; Jorgensen et al. 2010; Skomal et al. 2017). White sharks in South Africa mostly occur in the southern and western Cape in close proximity to resident Cape fur seal (*Arctocephalus pusillus pusillus*) colonies (Jewell et al. 2012; Kock et al. 2013; Towner et al. 2013). However they also frequent the inshore regions (Figure 1) of Algoa Bay (Dudley 2012), Mossel Bay (Johnson et al. 2009; Jewell et al. 2012), Gansbaai (Towner et al. 2013) and False Bay (Kock et al. 2012) when not feeding on seals (Kock et al. 2013).

False Bay attracts considerable numbers of white sharks which is thought to be due to an abundance of prey species, including elasmobranchs, teleosts and marine mammals (Ferreira & Ferreira 1996; Martin et al. 2005; Hammerschlag et al. 2006; Laroche et al. 2008; Weltz et al. 2013; Hewitt et al. 2017). Similar to the aggregation sites of Gansbaai (Towner et al. 2013; Wicsel et al. 2015) and Mossel Bay (Johnson et al. 2009; Jewell et al. 2012), white sharks in False Bay exhibit site fidelity to Seal Island (Figure 1) in winter, and to the inshore region in summer (Kock et al. 2013). Both male and female white sharks prey on Cape fur seals (mostly pups) at the island (De Vos et al. 2015a; De Vos et al. 2015b), and are hypothesised to switch to a primarily teleost-based diet during spring and summer, when migratory prey species abundance peaks inshore (Clark et al. 1996a; Lamberth 2006; Kock et al. 2013; Loosen 2017). It is well established that white sharks undergo ontogenetic dietary shifts, with the diet of smaller white sharks (<2 m) consisting primarily of squid, teleosts and elasmobranchs, while larger individuals (>3 m) consume larger fish species and marine mammals and (Tricas and McCosker 1984; Klimley 1985; Estrada et al. 2006; Hussey et al. 2012).

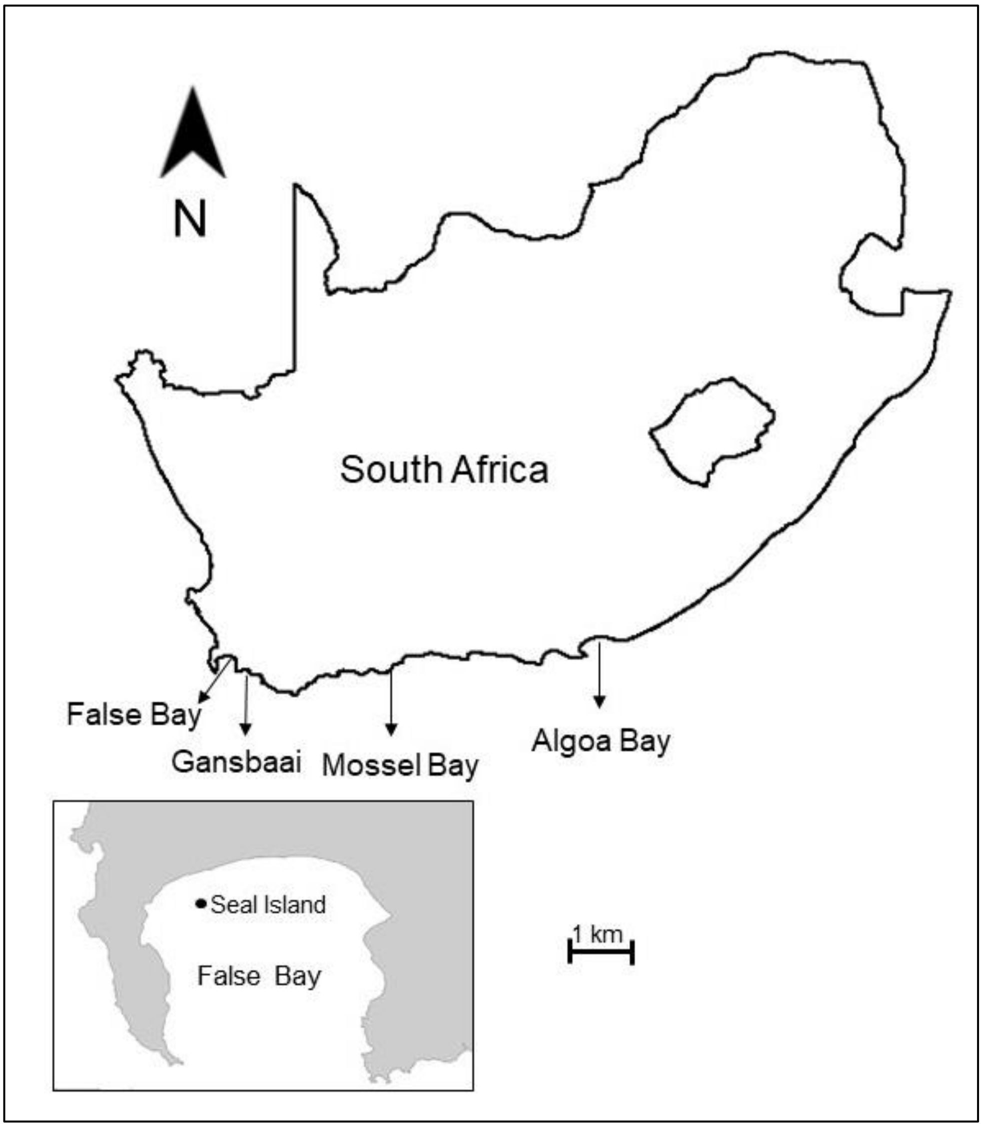

Figure 1: Map of South Africa indicating positions of Algoa Bay, Mossel Bay, Gansbaai and False Bay mentioned in the text. Inset shows the location of Seal Island in False Bay.

Influence of environmental variables on shark movement and distribution

Environmental variables provide species with cues for reproduction (Olive 1995; Pankhurst and Porter 2003; Frederiksen et al. 2004), feeding (Kestemont and Baras 2001; Kasumyan and Doving 2003; Trippel and Neil 2003; Stoner 2004) and migration (Kamykowski 1981; Jetz et al. 2008; Warner 2011), and hence have a critical influence on the temporal and spatial distribution of plant and animal species (Orton 1920; Jackson et al. 2001). Within marine ecosystems environmental variables have been shown to influence diverse taxa, including invasive polychaete density and occurrence (Garaffo et al. 2016), sardine presence (O'Donoghue et al. 2010), seabird distribution (Durant et al. 2004) and the occurrence of fin whales (Littaye et al. 2004).

Marine predators are often predictable in how they use their environment, with movement driven by oceanic mechanisms, spatial and temporal fluctuations in prey abundance and species-specific thermal tolerances (Block et al. 2011). Thus, changing environmental conditions can prompt changes in habitat use of marine apex predators (such as sharks) (Schlaff et al. 2014). Understanding variation in the presence of highly mobile marine apex animals in coastal and continental shelf ecosystems and how this varies with environmental variables has only recently been achieved through the combined use of modern telemetry (Klimley and Butler 1988; Ropert-Coudert and Wilson 2005; Hays et al. 2006; Heupel et al. 2006) and remote instrumentation.

Using environmental conditions to predict shark behaviour and distribution is useful, as abiotic variables are generally easier to measure than biotic variables, including sharks themselves (Schlaff et al. 2014). Shark movement may be influenced by environmental variables either indirectly (e.g. by affecting prey abundance and distribution) or directly (e.g. affecting the sharks physiological processes) (Schlaff et al. 2014). Numerous studies have provided a clear link between environmental variables and both the distribution and habitat preference of sharks (Holland et al*.* 1993; Hazin et al*.* 1994; Hopkins and Cech 2003; Wetherbee et al. 2007; Ortega et al. 2009; Vélez-Marín and Márquez-Farías 2009; Damalas and Megalofonou 2010; Abascal et al. 2011; Saunders et al. 2011; Weltz et al. 2013; Schlaff et al. 2014). These studies are important for several reasons: 1) they enable authorities to put catch restrictions in place during times when presence is highest and during crucial life-history stages (Agardy 2000; Speed et al*.* 2010); 2) they present a baseline for the possible impacts of anthropogenic activities (Block et al. 2011) and 3) for species of shark which pose a threat to human safety, such as the white shark (*Carcharodon carcharias*), they provide authorities with the information necessary to minimise shark-human conflict (Weltz et al. 2013; Engelbrecht et al. 2017).

This paper seeks to improve on our understanding of how environmental variables influence white shark presence at two popular recreational beaches in

Cape Town, South Africa, namely Muizenberg and Fish Hoek beach. These two beaches have seen the highest levels of shark-human conflict in Cape Town (Kock 2014) and hence there is a need to understand what variables best explain high shark presence at these beaches. Two previous papers have used long-term data of white shark sightings collected by trained shark observers to explore the relationship between white shark presence and a range of environmental and biological variables, including water temperature, lunar phase, tide state, wind speed and direction, prey presence, diatom (phytoplankton) presence and dolphin presence (Weltz et al. 2013; Loosen 2017). To understand how environmental variables may influence white shark presence, one first needs to consider how these variables might influence aspects of their life history and biology.

Barometric pressure

Fish can sense changes in barometric pressure and alter their behaviour accordingly (Guy et al. 1992; Mallekh et al. 1998; Jeffrey and Edds 1999; Heupel et al. 2003). Although several correlative studies in freshwater environments have suggested that fish can react to fluctuations in barometric pressure (Stoner 2004), the only direct study of barometric pressure on changes in fish catch (northern pike) found no relationship (Kuparinen et al. 2010; Lennox et al. 2017). It is thought that for fish which possess swim bladders, changes in barometric pressure are slow and small relative to changes in hydrostatic pressure experienced by fish during vertical movements (Lennox et al. 2017). In the marine environment, however, barometric pressure has been shown to influence shark movement.

Heupel et al. (2003) reported that a sharp decrease in barometric pressure caused juvenile blacktip sharks (*Carcharhinus limbatus*) to leave a nursery area in Terra Ceia Bay, USA, while Udyawer et al. (2013) found that five species of coastal shark (*Carcharhinus tilstoni, C. limbatus, C. amboinensis, C. sorrah and C. melanopterus*) responded to changes in barometric pressure associated with storm events in Terra Ceia Bay and Cleveland Bay, Australia, where all species but *C. melanopterus* exhibited a short-term flight response. Contrastingly, barometric pressure had no influence on grey reef shark (*Carcharhinus amblyrhynchos*) movement on an Australian coral reef (Heupel and Simpfendorfer 2014). These findings suggest that shark movement in response to a drop in barometric pressure may be species- and context-specific (Udyawer et al. 2013).

In False Bay, preliminary data from Hammerschlag et al. (2006) indicate that just prior to an approaching storm, white shark predation frequency on Cape fur seals increases around Seal Island. This could however be an indirect consequence of changes in seal presence, as the seals are more likely to haul-out during bad weather (Hammerschlag et al. 2006). In Algoa Bay, South Africa, aerial sightings of white sharks increased at higher barometric pressure (Dicken and Booth 2013), although it was unclear whether this was a direct effect or indirect effect, as changes in pressure may influence other environmental variables or patterns of prey availability (Cabanellas-reboredo et al. 2014; Lennox et al. 2017). Furthermore, a confounding factor in this research (Dicken and Booth 2013) was that there were more flights on good weather days which are typically associated with higher (or increasing) barometric pressures.

Water temperature

Spatial and temporal variation in water temperature is one of the most ubiquitous and ecologically pertinent parameters in marine systems (Stoner 2004), and has a notable influence on the abundance and distribution of temperate bay and estuarine fishes (Hopkins and Cech 2003). In ectothermic fishes, water temperature is the most important factor which governs metabolism (Fry 1971), and can significantly affect swim speed, activity, feeding and reproductive behaviour (Gonzalez-Ania et al. 2001; Stoner 2004). Shark distribution in coastal environments is also known to be heavily influenced by water temperature (Hopkins and Cech 2003; Dewar et al. 2004; White and Potter 2004; Harley et al. 2006; Carlson et al. 2008; Vögler et al. 2008; Knip et al. 2010; Abascal et al. 2011, Weltz et al. 2013). In the KwaZulu-Natal shark (gill) nets, temperature was a significant predictor of catch for several species of shark, including white sharks (Wintner and Kerwath 2017). Water temperature may either influence predator behaviour indirectly, by affecting prey distribution and abundance, or directly, by affecting thermoregulation (Campana and Joyce 2004; Higham et al. 2015; Wintner and Kerwath 2017).

The hydrodynamic processes within False Bay are influenced by two major ocean currents – the warm Agulhas current in the east and the cold Benguela current in the west (Dufois and Rouault 2012). During the austral spring and summer months (September-May), the south-easterly wind dominates, causing cold water to upwell along the eastern headland (Cape Hangklip), while at the same time pushing warm surface water to the northern shores of False Bay (Atkins 1970; Dufois and Rouault 2012). Therefore wind speed and direction are the main forces which drive water circulation, temperature and nutrient levels in False Bay (Atkins 1970).

Fluctuations of catches in the beach-seine fishery along the northern reaches of False Bay mirror seasonal variations in sea temperature and nutrient input, with more fish being caught during the summer months when sea temperatures are warmer (Lamberth et al. 1995; Clark et al. 1996b). White shark presence at Muizenberg and Fish Hoek beach during the summer months has also been shown to be significantly influenced by water temperature, whereby the probability of spotting a white shark increases at temperatures above 14°C, peaking at 18°C, after which the probability of presence remained high (Weltz et al. 2013). In addition, Loosen (2017) determined that white shark sightings at these two beaches peaked between 17.4°C and 18.6°C.

Although white sharks possess vascular counter-current heat exchangers (Carey et al. 1982; Bone and Chubb 1983) which enables them to elevate their body temperature as much as 15°C above the surrounding ambient water (Carey et al. 1971; Carey et al. 1982; Goldman 1997; Klimley et al. 2001; Dewar et al. 2004), previous work suggests that white sharks prefer inhabiting waters between 13°C and 22°C (Goldman 1997). However, it is likely that water temperature affects white shark presence inshore of False Bay indirectly through prey distribution and abundance (Kock et al. 2013; Weltz et al. 2013) rather than directly through thermoregulation, as the average size of white sharks in False Bay is roughly 3.25 m (Hewitt et al. 2018), and larger white sharks are known to have greater endothermic ability (Bernvi 2016). This idea is supported by Loosen (2017) who determined that white sharks were 66% more likely to be seen at Muizenberg and Fish Hoek beach when prey fish were present, indicating that prey is a major factor determining white shark presence inshore of False Bay. Interestingly, although wind strength and direction influences water temperature in False Bay (Atkins 1970), Weltz et al. (2013) found no relationship between shark sightings and wind speed and direction, with the authors proposing that the lack of an effect could be explained by the lag effects of wind, which would have been too complex for the model to interpret .

Cloud cover

Cloud cover affects the amount of light which is absorbed in the atmosphere and which is scattered by surface waters, decreasing underwater light availability in the marine environment (McFarland 1990; Bowmaker 1995). Cloud cover could therefore influence the ability of white sharks to detect their prey, and the ability of their prey to detect them. However, white sharks are known to successfully hunt Cape fur seals at dawn at Seal Island in False Bay, with lower light levels significantly increasing attack frequency and success rate (Martin et al. 2005; Hammerschlag et al. 2006; McComb et al. 2010; Kock 2014), suggesting that white sharks exploit low light levels to avoid detection by their prey (Martin et al. 2005). Due to their endothermic nature, white sharks are able to warm their eyes and brain, which significantly improves their temporal resolution and their ability to see in cold, turbid waters, as well as their ability to detect fast moving prey (Block and Carey 1985; Fritsches et al. 2005; Lisney and Collin 2007). Together these findings strongly suggest that vision is an extremely important sense for this species, and that white sharks could make use of cloudy days, and the concomitant decreased light availability in the water column, to better ambush prey.

Lunar phase and tidal state

The biology of various marine animals across different taxa are affected either directly by the lunar cycle or indirectly by associated tidal states (Horning and Trillmich 1999; Naylor 2001; Benoit-Bird et al. 2009). Behaviours such as reproduction (Masterson et al. 1997), predation (Benoit-Bird et al. 2009), migration (Last et al. 2016), aggregation (Cowley et al. 2001) and habitat use (Miller and Skilleter 2006) are all known to be influenced by lunar phase and associated tidal state. In the case of white sharks, predator behaviour and distribution may be affected by lunar phase either directly through abiotic factors such as tide (Hammerschlag et al. 2006; Afonso et al. 2014) and lunar illumination (Poisson et al. 2010), or indirectly through impacts on prey distribution (Weltz et al. 2013; Wintner and Kerwath 2017).

Although some studies have shown no effect of lunar phase on predatory fish distributions and behaviour (Ortega-Garcia et al. 2008), other studies have shown that porbeagle sharks (*Lamna nasus*), a close relative of the white shark, alter their depth in the water column in relation to lunar cycles (Damalas and Megalofonou 2010; Poisson et al. 2010; Cartamil et al. 2011; Saunders et al. 2011). Lunar phase has also been shown to affect catchability of certain shark species in various fisheries. Wintner and Kerwath (2017) discovered that lunar phase was a significant predictor of catch for six species of shark in the KwaZulu-Natal shark nets, although no relationship was found between lunar phase and white shark catch. It is thought that increased prey availability, together with increased hunting success due to low lunar illumination, may affect the inshore abundance and therefore catchability of certain shark species (Wintner and Kerwath 2017). In addition, white shark catches in shark nets in Australia increased at new moon, with the authors proposing that the low light conditions at new moon either enabled white sharks to hunt more successfully or that they were unable to visually detect the nets (Werry et al. 2012). In False Bay, Weltz et al. (2013) determined that lunar phase was a significant predictor of white shark presence at Muizenberg and Fish Hoek beach, with the probability of spotting a shark being highest at new moon and lowest at full moon. The authors proposed that the new moon may provide a hunting advantage or an improved feeding opportunity for white sharks by providing camouflage due to the decreased light availability in the water column.

Lunar cycle is closely related to tidal cycle, which is also known to affect the behaviour and distribution of many marine species, particularly those that inhabit coastal areas (Butner and Brattstrom 1960; McDowall 1969; Naylor 2001; Wetherbee et al. 2007). Tides alter the size of the surf zone, and some shark species, for example the leopard shark (*Triakis semifasciata*), have been documented moving with the incoming tide to exploit food resources which are unavailable at low tide (Ackerman et al. 2000). However, Weltz (2012) found no relationship between white shark sightings inshore and tidal state, and suggested that the amount of available habitat as a result of tidal fluctuations may not be sufficient to influence the movement of white sharks in these areas. In comparison, white shark predatory frequency on elephant seals (*Mirounga angustirostris*) at the Farallon Islands off the coast of California, United States increased with tidal height (Anderson et al. 1996; Pyle et al. 1996). It is thought that increased tidal height forces elephant seals into the water by reducing the size of their haul-out area and hence forcing them into the water with white sharks (Pyle et al. 1996). In False Bay, predation rates on Cape fur seals by white sharks around Seal Island have also been shown to increase at high tides, as the sharks are able to approach closer to the island without being detected (Hammerschlag et al. 2006). Therefore it is possible that lunar phase and tidal state can influence white shark presence by having a direct effect on their ability to ambush prey and an indirect effect on the behaviour of potential prey species.

Shark-human conflict and mitigation

Shark-human interactions occur worldwide and represent a major challenge for coastal management authorities who are mandated to keep recreational water users safe (Conover 2001; Woodroffe et al. 2005; Nel and Peschak 2006; Dickman 2010; Neff 2012; Redpath et al. 2015). Managing the risk to water users is particularly difficult when the shark species is globally protected by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Fergusson et al. 2009), as the use of lethal control becomes even more controversial. The white shark is one of three species of shark most commonly associated with unprovoked[1] shark-human interactions (Curtis et al. 2012), and worldwide, the incidence of unprovoked shark-human interactions has been increasing (McPhee 2014).

Engelbrecht et al. (2017) showed that water user activity decreased significantly (up to 3 months) at Muizenberg and Fish Hoek beach following fatal shark-human interactions. Although infrequent, shark-human interactions often attract substantial and exaggerated media attention which influences public opinion, resulting in pressure being placed on local authorities to prevent future shark-human interactions and so restore public confidence in beach safety (Curtis et al. 2012; Neff 2012; McPhee et al. 2015). Most attempts at prevention around the world have adopted lethal control (Lemahieu et al. 2017) with the goal of reducing shark numbers and hence the probability of an interaction with water users.

Lethal control varies from targeted culls and shark hunts in the short-term to the deployment of static fishing gear such as baited drum lines and/or shark nets at

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[1] "Unprovoked" shark-human interactions refer to when humans are bitten by sharks in their natural environment despite no prior harassment of the shark taking place; "provoked" shark-human interactions refer to when humans try to touch or handle sharks (e.g. to remove fishing hooks or whilst scuba diving) and are subsequently bitten (Curtis et al. 2012).

popular beaches in the long-term (Curtis et al. 2012). Despite its widespread use, lethal control remains controversial with short-term culling typically being ineffective, as catching the “culprit” shark is extremely unlikely for a wide-ranging species like the white shark (Wetherbee et al. 1994; Holland et al. 1999; Curtis et al. 2012). Long-term culling, while effective at reducing the total number of large sharks and hence the number of shark-human interactions (Paterson 1990; Dudley 1997; Green et al. 2009), is extremely costly to both sharks, non-target species and hence the broader ecosystem within which they function (Paterson 1990; Krogh and Reid 1996; Cliff and Dudley 2011).

Various non-lethal control methods are being developed which aim to improve human safety without negatively impacting on sharks or the marine environment. Examples of non-lethal shark control measures include aerial detection and warning systems (Robbins et al. 2014), shark exclusion barriers (Curtis et al. 2012) and various other deterrents including electric and magnetic devices (for a review see McPhee et al. 2015).

In response to an increase in shark-human interactions in False Bay over the previous decade, a permanent land-based shark detection and warning system called Shark Spotters was implemented in 2004 (Kock et al. 2012). The goal of the programme is to change the behaviour of water users (rather than that of the sharks) by alerting them to the presence of a white shark close to shore (Kock et al. 2012). Detecting sharks is enhanced by popular beaches being in close proximity to mountains, which provide an elevated vantage point from which trained shark observers can scan the waters below. If a large shark is detected moving in the direction of water users then beach-based shark observers will alert them via auditory (a siren) and visual (flags) warnings (Kock et al. 2012; Engelbrecht et al. 2017).

Observational data recorded by shark observers has been used to investigate the drivers of white shark presence at Muizenberg and Fish Hoek beach as detailed above and by Weltz et al. (2013) and Loosen (2017). Although these studies have reported significant environmental predictors of white shark presence at both beaches, these studies were limited by the difficulties associated with detecting a marine animal from land, as discussed below.

Benefits and limitations of previous studies in relation to current study

The main advantage of using data collected by shark observers at the Shark Spotters organisation is that these data have been recorded daily for over a decade and thus include a large range of environmental variables which can be used to determine the predictors of shark presence. These data are, however, biased to environmental conditions that allow for the visual detection of sharks, e.g. good water visibility with cloudless and calm weather conditions. Furthermore, the detection of sharks is influenced by both the depth that the shark is swimming at and the levels of vigilance of the human observers, with the potential of misidentification of shark species, particularly when large (>2 m) bronze whalers (*Carcharhinus brachyurus*) are present inshore of False Bay. An additional limitation of shark observer data is that it is restricted to daylight hours, while sharks are active along the inshore at all times (Kock et al. 2013). In this study I use passive acoustic telemetry of tagged white sharks to address the challenges of limited visual detection, temporally constrained sampling and potential misidentification of shark species.

Acoustic receivers can detect sharks at any time provided they come within the detection range of the receiver. Furthermore, receivers are not impacted by either water visibility or cloud cover, although there is evidence that temperature, salinity, wind speed, suspended particles and wave action can influence the overall range at which tagged sharks are detected (Heupel et al. 2006; Kessel et al. 2014). This issue will be discussed for each environmental predictor variable where applicable.

An additional limitation of passive acoustic telemetry is that one is limited to detecting only those sharks that are tagged and consequently there may be instances when untagged sharks are present on the inshore and detected by observers only. It is thus essential to ensure that a significant proportion of the resident population is tagged in order to make broader generalisations about factors influencing the species presence in particular areas.

Aims and Objectives

The primary aim of this study is to investigate whether white shark presence can be explained by environmental predictors at Muizenberg and Fish Hoek beach, using acoustic telemetry. The secondary aim is to determine whether the results from this study differ from two previous studies that relied on shark observer data at the same beaches. Environmental variables that are hypothesised to influence marine life presence and abundance along the inshore include water temperature, barometric pressure, wind speed, wind direction, cloud cover, lunar phase, tidal state and time of day. As the results from Weltz et al. (2013) have subsequently been used by the Shark Spotters organisation and the City of Cape Town for shark-safety awareness campaigns, the results of this study have important management ramifications – they can either validate the findings of Weltz et al. (2013) and support the current shark safety warnings used to inform water users in False Bay, or refute their findings and provide new insights into how white sharks make use of the inshore environment at Muizenberg and Fish Hoek beach. Unfortunately, data for prey availability is not available for this study, therefore any influence of environmental variables on prey species may indirectly explain white shark presence at inshore beach sites.

Methods

Ethics statement

“All research methods were approved and conducted under the South African Department of Environmental Affairs: Oceans and Coasts permitting authority. Permit # V1/1/5/1, V1/8/5/1.” (Kock et al. 2013).

Study site

This study was conducted at two popular recreational beaches – Muizenberg and Fish Hoek beach – located on the north-western coastline of False Bay, South Africa (Figure 2). This region of South Africa experiences a Mediterranean climate with cool, wet winters and hot, dry and windy summers (Clark et al. 1996b). Muizenberg and Fish Hoek beach were selected for this study as they consistently have both the highest number of shark sightings (based on shark observer data) in False Bay (Kock et al. 2012) and incidences of shark-human interactions (Kock 2014).

Despite their close proximity, Muizenberg and Fish Hoek beach differ in terms of their orientation and bathymetry and therefore experience different environmental conditions and attract a different subset of water users (Engelbrecht et al. 2017). Muizenberg beach has a sandy substrate which slopes gently with depth creating an extensive surf zone (>300 m from the beach) that is popular with surfers (Kock et al. 2012). Fish Hoek also has a largely sandy substrate but with a steeper slope and hence a narrower surf zone (<100 m from beach) and is more popular with swimmers and kayakers (Kock et al. 2012; Engelbrecht et al. 2017).

Detecting white sharks

White shark detections were obtained from two underwater acoustic receivers (VR2, Vemco Ltd. Nova Scotia, Canada). These receivers are omni-directional, and record the presence of acoustic transmitters affixed to free-swimming white sharks using one channel (69 kHz) (Voegeli et al. 2001). One receiver was positioned near Fish Hoek beach (Figure 2B) and the other near Muizenberg beach (Figure 2C).

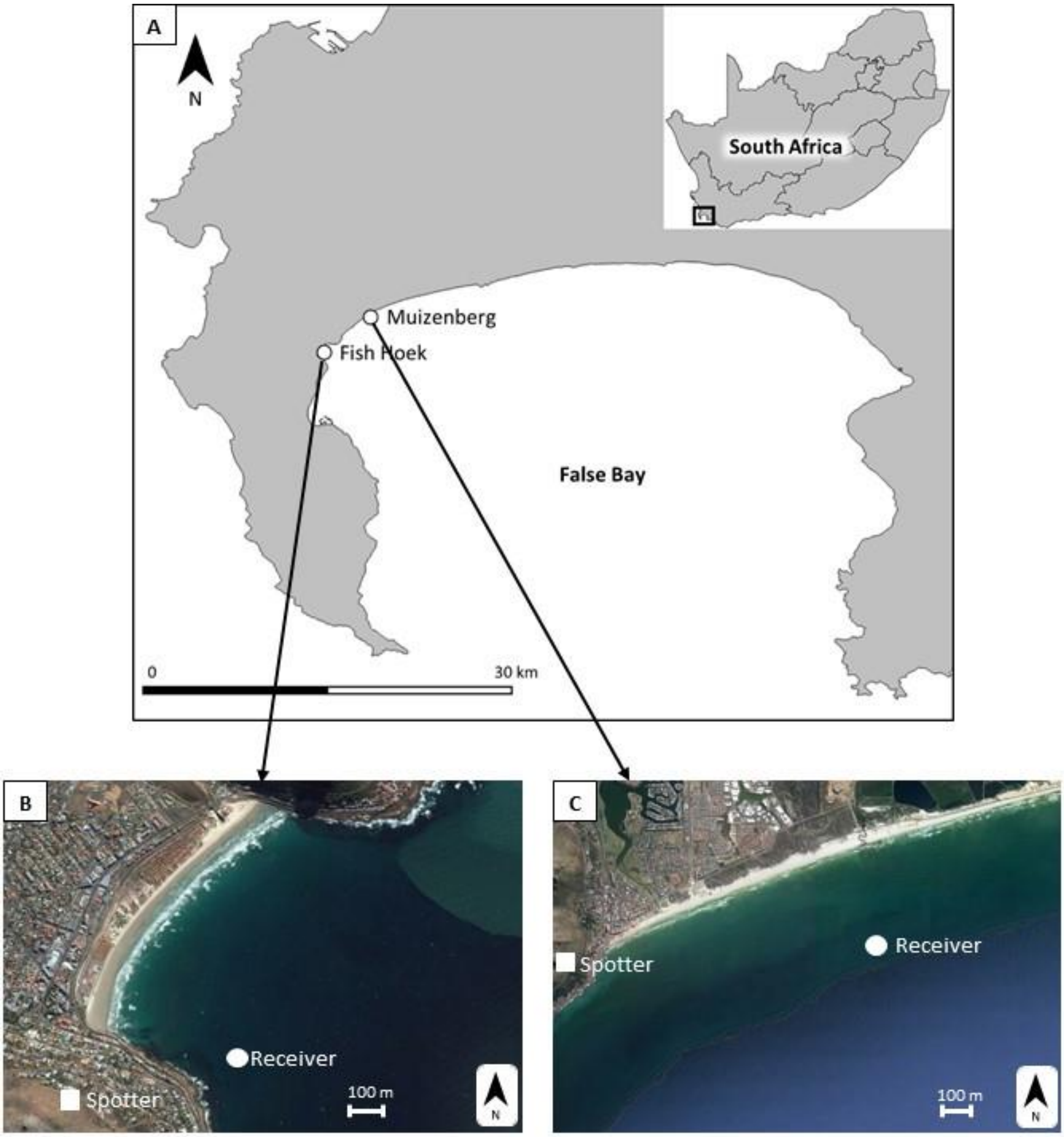

Figure 2: (A) South Africa with location of False Bay and Muizenberg and Fish Hoek beaches (Adapted from Engelbrecht et al. 2017), (B) Fish Hoek beach with approximate position of shark observer (Spotter) and position of Vemco underwater acoustic receiver (Receiver) used in this study (Google Earth image, 2018), (C) Muizenberg beach showing approximate position of shark observer (Spotter) and position of Vemco underwater acoustic receiver (Receiver) used in this study (Google Earth image, 2018).

Shark tagging

White sharks were tagged both along the inshore region of False Bay and at Seal Island (Kock et al. 2013). White sharks had to be attracted to the research vessel to be tagged. At Seal Island, they were attracted using a standardised baiting and chumming method (Laroche et al. 2007). In the inshore region, however, white sharks which were swimming at or near the water surface were approached by the research vessel and a tuna head and/or foam seal decoy tied to a rope was used to lure them closer to the boat for tagging. The width of the research vessel (2.6 m) was used as a reference to estimate shark length (to the nearest 0.5 m). The sex of the shark was determined by visual inspection for the presence or absence of claspers, and only tagged once sex was confirmed.

A total of 56 white sharks were tagged with acoustic transmitters (Vemco Ltd. V16, Nova Scotia, Canada) from 25th April 2005 until 14th September 2007. A modified spear gun was used to deploy the acoustic transmitters into the base of the first dorsal fin. Sharks were tagged with V16-5H-R04K transmitters (battery life approx. 36 months, 17 x 95 mm, code intervals: 150-300 s) (Kock 2014). To improve protection from physical damage, transmitters were encased in the manufacturers “shark case” (Kock et al. 2013). Shark cases had previously been painted with two layers of anti-fouling paint to reduce bio-fouling, which can reduce signal transmission and through increased frictional drag compromise the welfare of the shark (Heupel et al. 2008).

Each white shark is uniquely identifiable by its transmitter, which periodically emits 69 kHz pings in a closely-spaced pulse train. If the pulse train is successfully decoded by the VR2 receiver, it is recorded and stored in the receiver memory as a single detection with the date, time of detection and unique transmitter number (Lacroix and Voegeli 2000). Acoustic mooring design and range testing was conducted as described by Kock et al. (2013) and included in the appendix.

Data collection

All white shark detections on the Muizenberg and Fish Hoek receiver (Figure 2) between the 28th April 2005 and the 31st December 2007 were used in this study. To determine the duration of tags at liberty, I used detections from all receivers located in Algoa Bay, Mossel Bay, Gansbaai and False Bay (Kock et al. 2013). This was important in verifying that times of no detection were not necessarily due to tag failure, but of shark movement outside of the study area (Kock et al*.* 2013).

A range of environmental variables were recorded for the study period. Water temperature data were measured using a hand-held mercury/alcohol thermometer at waist depth at each beach, and were obtained from the South African Coastal Temperature Network (SACTN) (Schlegel and Smit 2016). Wind speed (m/s) and direction (degrees from north), barometric pressure (hPa) and total cloud cover (in octas) measurements were obtained from the South African Weather Service (SAWS) which recorded these variables at Cape Town International Airport (17 km from the study site). Lunar phase (full, first quarter, new and last quarter) and tide data (time of low and high tide) were obtained from the South African Naval Hydrographic Office (South African Navy Hydrographic Office 2005, 2006, 2007). Low and high tide times were obtained for the entire study period.

Statistical analyses

The relationship between white shark presence and environmental variables was modelled for each beach separately.

Models

Generalised Additive Mixed Models (GAMMs) (Wood 2006) were used to investigate the relationship between the probability of detecting a white shark and the predictor variables. GAMMs are commonly used to explore relationships which are likely non-linear and not normally distributed and are able to incorporate parametric, non-parametric smooth- and random model components within a binomial error model (Wood 2006). GAMMs are different to Generalized Linear Mixed Models (GLMMs) in that they are not based on an assumed relationship between the predictor and response variables that are specified *a priori* (Zuur et al. 2009). Instead, GAMMs fit ‘smooth’ functions to continuous predictor variables and then establish relationships between these functions and the response variable via link functions (Wood 2006; Zuur et al. 2009). Therefore GAMMs are able to model relationships which are highly non-monotonic and non-linear (Guisan et al. 2002; Zuur et al*.* 2009), which are typical of tidal, lunar and temporal patterns.

If a shark was tagged before the start of the study period (i.e. 28th April 2005), then that shark's time at liberty commenced on the 28th April 2005 until 31st December 2007 – the end of the study period. If a shark was tagged after 28th April 2005, then that shark's time at liberty started on the date that it was tagged until the end of the study period. The presence/absence of each shark's time at liberty was apportioned into 24, 1 hr time bins for each receiver, as per methods of Lindholm et al. (2007). For example, Bin 1 started every day at 00h00 and ended at 00h59, while Bin 24 started at 23h00 and ended at 23h59. To prevent the inclusion of "phantom" detections, solitary detections for a particular shark that were not followed nor preceded by another detection within 59 min were not included in the final data set, as per the methods of Lindholm et al. (2007). Therefore only sharks with two or more consecutive detections within the hour were considered to have been present for that hourly bin (*sensu* Bond et al. 2012). Analyses were run using binomial distribution models, whereby the binomial values of 1 and 0 were used to represent the presence or absence of each shark at the receiver, respectively.

The sample unit in this study was an hourly bin, therefore each predictor variable was selected to match this temporal scale as closely as possible. Thus wind speed was obtained for each hour of each day. Wind direction (degrees from north) was also obtained hourly, and was categorised as either offshore, onshore, cross-shore from left or cross-shore from right (with cross shore defined as a vector 45 degrees from the perpendicular). Barometric pressure data was also obtained for each hour of each day. Variables that were not available in hourly format include water temperature, cloud cover, lunar phase and tide. Water temperature data were provided in the form of daily averages. Cloud cover data were provided at 08h00, 14h00 and 20h00. Data for 08h00 and 14h00 periods were averaged and assigned to all hourly bins between 0h00 and 11h00. Data for 14h00 and 20h00 were averaged and assigned to the hourly bins between 12h00 and 23h00. Lunar phase was determined for each of the eight standard moon phases, i.e. (1) new moon (2) waning crescent (3) last quarter (4) waning gibbous (5) full moon (6) waxing gibbous (7) first quarter and (8) waxing crescent, and then allocated to corresponding hourly bins over the 24 hour time period. For tidal state, high tide and low tide were assigned to the hourly bin in which they occurred as well as the previous and subsequent hourly bins. The hours between low and high tide were categorised as “flood”, and the hours between high and low tide were categorised as “ebb”. These categories were assigned to all hourly bins outside of low and high tide time bins.

Once all data were allocated to their respective hourly bins, any bins which contained missing values were removed before starting the modelling process, as recommended by Zuur et al. (2009). As model approximation and subsequent prediction can be severely distorted by collinearity (Dormann et al. 2013), multi-panel scatterplots were used to test for collinearity between environmental variables (Zuur et al. 2009). If the Pearson correlation coefficient (|r|) exceeded 0.7, then two variables were considered to be collinear. No variables were found to be collinear and hence all were retained for the modelling. In addition to each environmental variable tested against shark presence/absence in each hour, the variables year, season, Julian day and hour were also included as predictor variables to explore the effects of temporal variation on white shark presence. Each season was categorised as follows: summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November).

Initially a GAMM was used to model the probability of a shark detection against the various predictor variables using the ‘mgcv’ package (Wood 2013) available in the R statistical platform (R Core Team 2016). However, due to the large data sets for Muizenberg and Fish Hoek beach (~314 000 and ~179 000 lines of data, respectively) the models were not able to converge. I therefore used the ‘bam’ function (Wood et al. 2015) which is also available in the ‘mgcv’ package (Wood 2006). The bam function is able to fit GAMMs to very large data sets containing upwards of several tens of thousands of data (Wood et al. 2015). The advantage of using the bam function is that it has a much lower memory footprint than a GAMM, leading to faster model computation. The full bam model, evaluated independently for Muizenberg and Fish Hoek beach, included the categorical variable ‘Year’; smoothing functions for the variables ‘Julian day’, ‘Cloud cover’, ‘Tide height’ and ‘Lunar phase’; interaction terms between ‘Hour’ and ‘Season’, ‘Water temperature’ and ‘Season’, ‘Wind speed’ and ‘Season’, ‘Wind direction’ and ‘Season’, and ‘Barometric pressure’ and ‘Season’; and random effects for ‘Shark ID’ and ‘Date’, such that:

$$\text{logit}(p) = \beta_0 + \text{Year} + f_1(\text{Julian day}) + f_2(\text{Hour x Season}) + f_3(\text{Tide height}) + f_4(\text{Lunar phase}) + f_5(\text{Cloud cover}) + f_6(\text{Water temperature x Season}) + f_7(\text{Wind speed x Season}) + f_8(\text{Wind direction x Season}) + f_9(\text{Barometric pressure x Season}) + \alpha_i + \alpha_{ii},$$

where logit represents the binomial link function, p is the probability of detecting a shark in a given hour (i.e. response = 1), $f_{1\text{-}4}$ denotes the smooth functions realised by cyclic cubic regression splines, $f_{5\text{-}9}$ represents smoothing functions realised by thin plate regression splines (Wood 2006), α_i is the random effect for Shark ID and α_{ii} is the random effect for Date (Zuur et al. 2009). The error structure of GAMMs corrects for non-independence of statistical units and allows for the 'random effects' variance to be decomposed at different levels of clustering (Wood 2006). I therefore treated Shark ID as a random effect to manage the issue of pseudo-replication, as this enabled me to account for lack of independence between detections for each identified shark. The issue of temporal autocorrelation was managed by treating Date as a random effect to account for the possible lack of independence between predictor variables (Zuur et al. 2009).

Model Building

The Fish Hoek receiver recorded far fewer total white shark detections than the Muizenberg receiver (1 481 total detections vs. 13 803 detections respectively). Once false detections and detections that did not meet the detection criteria were removed, these detections were reduced to 160 vs. 1 364 hourly detections for Fish Hoek beach and Muizenberg beach respectively. This resulted in the Fish Hoek data being highly zero-inflated with the result that the models did not converge. I consequently excluded Fish Hoek beach from further model analyses. The variables included in the final models for Muizenberg beach were determined using the top-down approach as described by Zuur et al. (2009). For each set of models, I first started with a model containing all the predictor variables with as many interactions as possible, including random effects which were thought to contribute towards the optimal model – this model is termed the 'beyond optimal model' (Zuur et al. 2009). The optimal structure of random effects were determined and I then began a backwards stepwise variable selection to determine the best combination of predictor variables which gave me the most parsimonious model. The Akaike's Information Criterion (AIC) was used to determine the optimal combination of predictor variables (Zuur et al. 2009). Each predictor variable in the final model was determined using ANOVA tables with Chi-squared tests.

As the p-values produced by GAMMs are approximate, values close to 0.05 may not indicate true significance (Zuur et al. 2009). As such, predictor variables with $p < 0.01$ were immediately included in the model and predictor variables which did not contribute significantly ($p > 0.05$) were dropped from the model. If a variable showed some level of significance, but not low enough for immediate inclusion into the model (i.e. $0.01 < p < 0.05$), the most parsimonious model (i.e. lower AIC value) was selected by running two models (one that incorporated the variable in question and one that did not). AIC values of the full and final models were then compared to ensure that the final model was indeed a better fit than the full model (AIC_{final} = 13 145.9, AIC_{full} = 13 164.2). The final model was used to predict the probability of detecting a white shark at Muizenberg beach for all significant predictor variables using the 'predict.gam' function in the 'mgcv' package (Wood 2013). The predict.gam function simulates experimental conditions for the variable to be predicted whilst all other variables are held constant (Table 1).

Table 1: Reference set of variables for each predictor variable used to model white shark detection probability at Muizenberg beach. 'Corresponding' refers to the corresponding season that was being predicted (i.e. summer, autumn or winter). Mean refers to the mean observed value for that variable, 'x season' refers to that variable interacting with a specific season.

Variable	Value
Year	2005
Day	280
Hour x season	Mean x corresponding
Water temperature x season	Mean x corresponding
Wind speed x season	Mean x corresponding
Barometric pressure x season	Mean x corresponding

Results

At total of 16 individual white sharks (29% of tagged white sharks at liberty) were detected at Fish Hoek beach over 955 days from 20th May 2005 to 31st December 2007 (Table 2), totalling 1 418 detections, which were binned into 160 hourly detections (Figure 5). The range tests determined that the range of the Fish Hoek receiver was ≤500 m (Kock 2014).

Table 2: Summary of tagged white sharks detected on the Fish Hoek receiver between 20th May 2005 and 31st December 2007. Data include the unique Shark ID number, the date the shark was tagged and monitoring start date for each shark, last date the tag was recorded on the Fish Hoek receiver, detection period, total number of days detected at Fish Hoek beach and total number of hours detected at Fish Hoek beach.

Shark ID	Date tagged and monitoring start date	Date of last acoustic detection at Fish Hoek beach	Detection period (days)	No. days detected at Fish Hoek beach	No. hours detected at Fish Hoek beach
603	20-05-2005	07-11-2005	171	9	11
621	06-06-2005	10-11-2005	157	4	5
620	17-06-2005	07-04-2007	659	27	38
601	25-08-2005	14-09-2005	20	8	14
611	02-09-2005	06-11-2005	65	2	2
546	28-04-2006	07-11-2006	193	4	5
630	25-05-2006	28-09-2006	126	3	5
547	30-06-2006	07-11-2006	130	13	26
556	09-08-2006	21-10-2006	73	8	10
560	13-11-2006	19-03-2007	126	9	15
545	14-11-2006	24-10-2007	344	6	6
551	14-11-2006	03-10-2007	323	3	4
634	14-11-2006	25-11-2006	11	1	2
633	26-01-2007	22-10-2007	269	3	4
638	10-03-2007	24-10-2007	228	9	11
639	12-06-2007	24-10-2007	134	2	2

White shark detections at Fish Hoek beach occurred across a range of barometric pressures, wind speeds and lunar phases, however they were confined to water temperatures ranging primary between 13°C and 18°C (Figure 3). The highest number of white shark detections at Fish Hoek beach occurred during September, October and November (Figure 5), with the majority of detections (47, representing 29% of detections at Fish Hoek) occurring in October. Fish Hoek beach had very few detections in all other months, with February exhibiting the fewest detections (0). The maximum number of detections at Fish Hoek beach in one day was five, occurring on the 6th November 2006 and representing two different white sharks. The number of individual white sharks detected per month also varied, with the spring months exhibiting the most numbers of individuals (Figure 6).

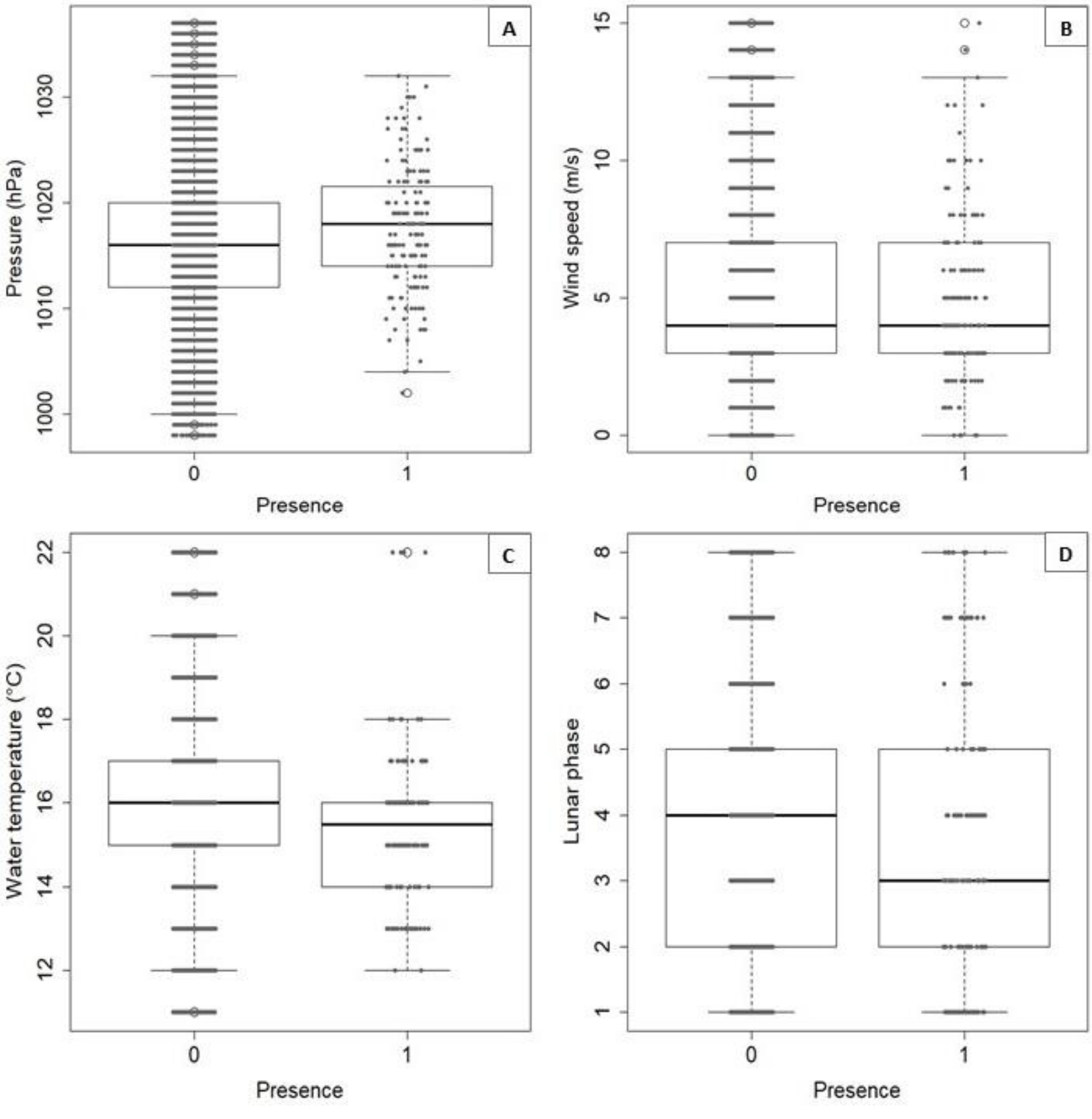

Figure 3: Boxplots indicating white shark absence (0) and presence (1) at Fish Hoek beach corresponding to environmental variables (A) Barometric pressure, (B) Wind speed, (C) Water temperature and (D) Lunar phase. Grey dots represent jittering of data points to prevent overplotting.

A total of 32 individual white sharks (57% of tagged white sharks at liberty) were detected at the Muizenberg receiver over 981 days from 28th April 2005 to 31st December 2007 (Table 3), with a total of 13 803 detections which were then binned into 1 168 hourly detections (Figure 5). The range tests determined that the range of the Muizenberg receiver was >500 m, but <1000 m (Kock, 2014).

Table 3: Summary of tagged white sharks detected on the Muizenberg receiver between 24th April 2005 and 31st December 2007. Included is the unique Shark ID number, the date the shark was tagged and monitoring start date for each shark, date of last detection on the Muizenberg receiver, detection period, total number of days detected at Muizenberg beach and total number of hours detected at Muizenberg beach. * Shark 521 was tagged prior to the study period on the 25-04-2004.

Shark ID	Date tagged and monitoring start date	Date of last detection at Muizenberg beach	Detection period (days)	No. days detected at Muizenberg beach	No. hours detected at Muizenberg beach
521*	28-04-2005	10-06-2005	43	1	2
603	20-05-2005	29-12-2005	223	50	174
608	04-06-2005	27-09-2005	115	7	9
614	06-06-2005	20-06-2005	14	1	1
621	06-06-2005	16-11-2005	163	24	53
624	06-06-2005	10-06-2005	4	1	1
623	10-06-2005	08-01-2006	212	2	3
626	10-06-2005	30-12-2005	203	15	34
620	17-06-2005	27-12-2005	193	76	184
607	17-06-2005	13-01-2006	210	37	81
601	25-08-2005	14-09-2005	20	4	8
611	02-09-2005	07-05-2006	247	24	71
546	28-04-2006	16-12-2006	232	16	21
548	28-04-2006	20-03-2007	326	16	21
630	25-05-2006	29-09-2006	127	5	6
547	30-06-2006	21-04-2007	295	54	103
556	09-08-2006	25-10-2006	77	18	25
549	17-08-2006	02-02-2007	169	25	44
558	06-10-2006	27-02-2007	144	28	50
560	13-11-2006	07-04-2007	145	26	55
632	13-11-2006	25-11-2006	12	1	1
545	14-11-2006	08-11-2007	359	27	35
551	14-11-2006	29-12-2006	45	10	15
562	14-11-2006	12-04-2007	149	12	19
634	14-11-2006	15-04-2007	152	44	70
635	14-11-2006	23-12-2006	39	3	4
636	14-11-2006	23-11-2006	9	2	3
637	17-01-2007	08-08-2007	203	29	42
633	26-01-2007	25-04-2007	89	17	18
638	10-03-2007	26-09-2007	200	11	15
639	12-06-2007	21-10-2007	131	6	9
642	14-09-2007	25-09-2007	11	1	1

In comparison to Fish Hoek beach, white shark detections at Muizenberg beach occurred over a greater range of barometric pressures and water temperatures, but over the same range of wind speeds and lunar phases (Figure 4).

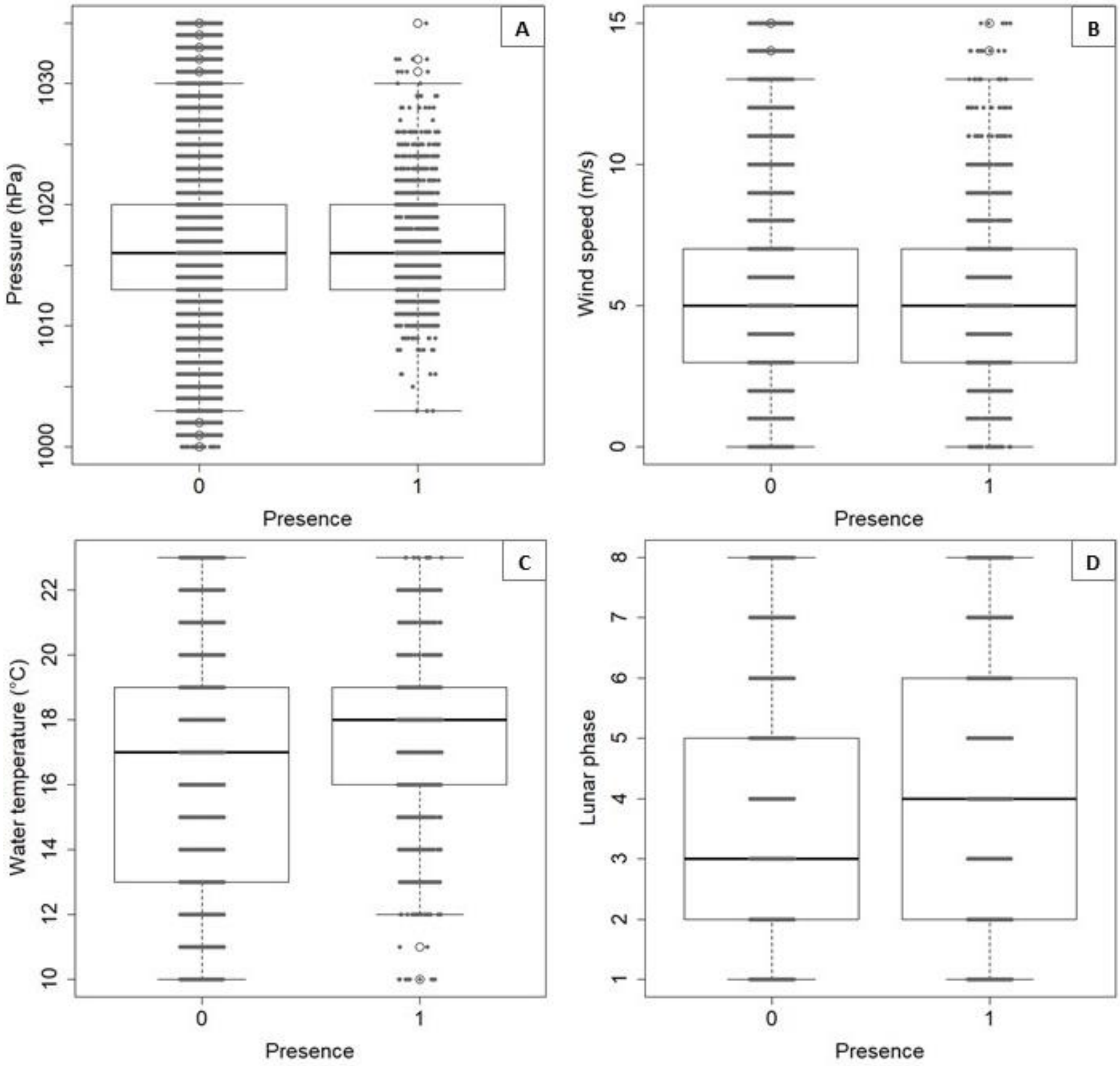

Figure 4: Boxplots indicating white shark absence (0) and presence (1) at Muizenberg beach corresponding to environmental variables (A) Barometric pressure, (B) Wind speed, (C) Water temperature and (D) Lunar phase. Grey dots represent jittering of data points to prevent overplotting.

Results from the model revealed that year, day, hour, water temperature, wind speed and barometric pressure were significant predictors of white shark presence at Muizenberg beach (Table 4), but wind direction, cloud cover, tide height and lunar phase were not ($p > 0.05$) and were therefore excluded from the model. Although there were several significant predictors of white shark presence at Muizenberg beach, the GAMM model only explained a minimal percentage of the variation in shark detections (19%).

Table 4: Results of ANOVA tables with Chi-squared tests for significance of each predictor variable towards the final model. For smooth terms, edf = estimated degrees of freedom and Chi.sq = Chi squared value; for parametric terms $^{+}$ refers to Estimate value and $^{\#}$ refers to z value. * represents variables significant at the 5% level of significance.

Predictor variable	**edf**	**Chi.sq**	**p-value**
Year:2005	-2.790^{+}	-5.225$^{\#}$	**<0.001**
Year:2006	-1.501^{+}	-9.822$^{\#}$	**<0.001**
Year:2007	-1.390^{+}	-6.930$^{\#}$	**<0.001**
Water temperature:Summer	1.0003	5.298	**0.021***
Water temperature:Autumn	1.0007	6.538	**0.011***
Water temperature:Winter	1.0009	4.583	**0.032***
Water temperature:Spring	2.3598	4.167	0.168
Julian day	6.2996	640.227	**<0.001**
Wind speed:Summer	3.5377	14.137	**0.01***
Wind speed:Autumn	2.1594	21.653	**<0.001**
Wind speed:Winter	1.0238	0.2	0.689
Wind speed:Spring	1.001	0.004	0.952
Hour:Summer	1.8556	7.099	**0.018***
Hour:Autumn	2.5249	14.952	**0.002**
Hour:Winter	1.5454	3.407	0.089
Hour:Spring	1.0858	1.755	0.202
Barometric pressure:Summer	1.0106	19.816	**<0.001**
Barometric pressure:Autumn	3.7022	14.985	**<0.01**
Barometric pressure:Winter	1.0008	2.207	0.138
Barometric pressure:Spring	2.3854	5.373	0.155
Shark ID	0.9633	26.531	**<0.001**
Date	286.865	1051.13	**<0.001**

Temporal variation – Year/Season/Time of day

White shark presence varied with year, season and time of day at Muizenberg beach. Throughout the study period, the highest numbers of shark detections occurred during spring (Figure 5), with October being the month with the highest number of detections overall (263, representing 23% of total white shark detections at Muizenberg beach). In comparison, the months of June, July and August (corresponding to the winter season) had the fewest numbers of shark detections at Muizenberg beach (Figure 5), with July exhibiting the fewest detections (3 in total).

The number of individual sharks detected also varied by month for Muizenberg beach, with the spring months exhibiting the highest number of individuals detected per month, and the winter months having the fewest numbers of individuals detected (Figure 6). The maximum number of detections in one day at Muizenberg beach was 25, on the 30th October 2005 and representing five different white sharks.

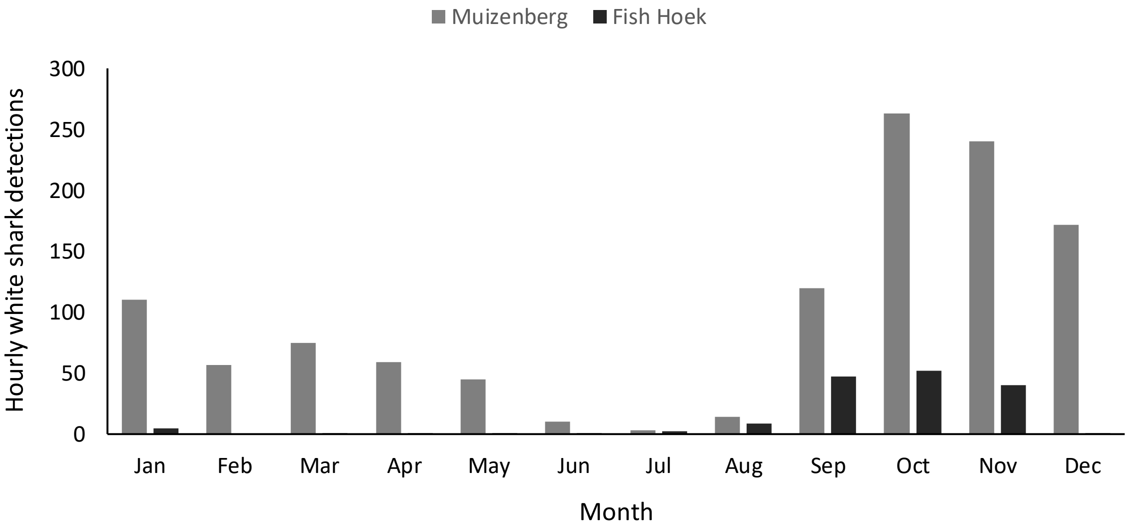

Figure 5: Combined frequency of white shark hourly detections per month at Muizenberg and Fish Hoek beaches from April 2005 to December 2007.

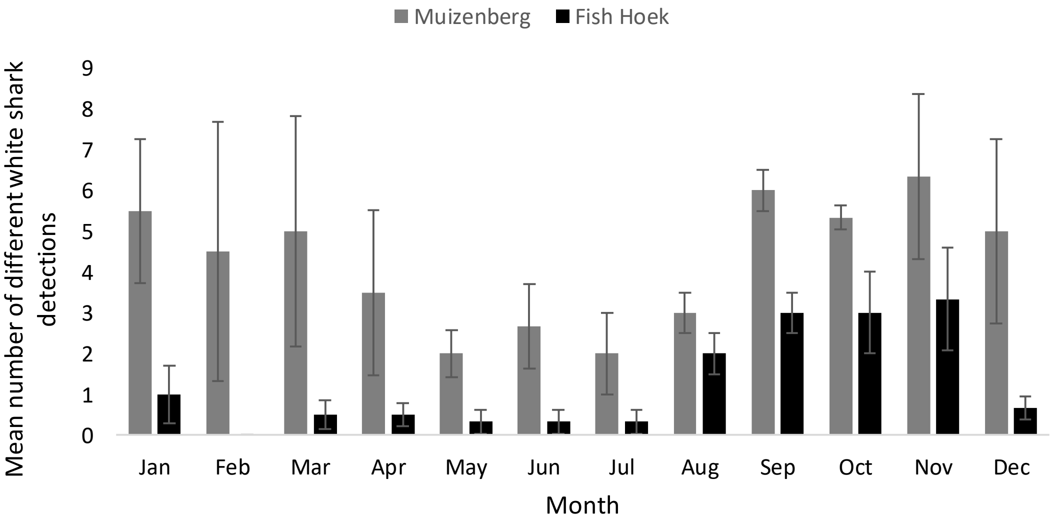

Figure 6: Mean number of different white sharks detected per month for Muizenberg and Fish Hoek beaches. Error bars indicate standard deviation.

The probability of detecting a white shark at Muizenberg beach was 3 times higher in 2005 than 2006 and 2007 (Figure 7A). Detection was 2.7 times higher in spring than summer, 3 times higher than in autumn and 23 times higher than in winter (Figure 7B). In addition, during the summer and autumn months, the probability of detecting a white shark increased between the hours of 10h00 and 15h00 (Figure 8A and B).

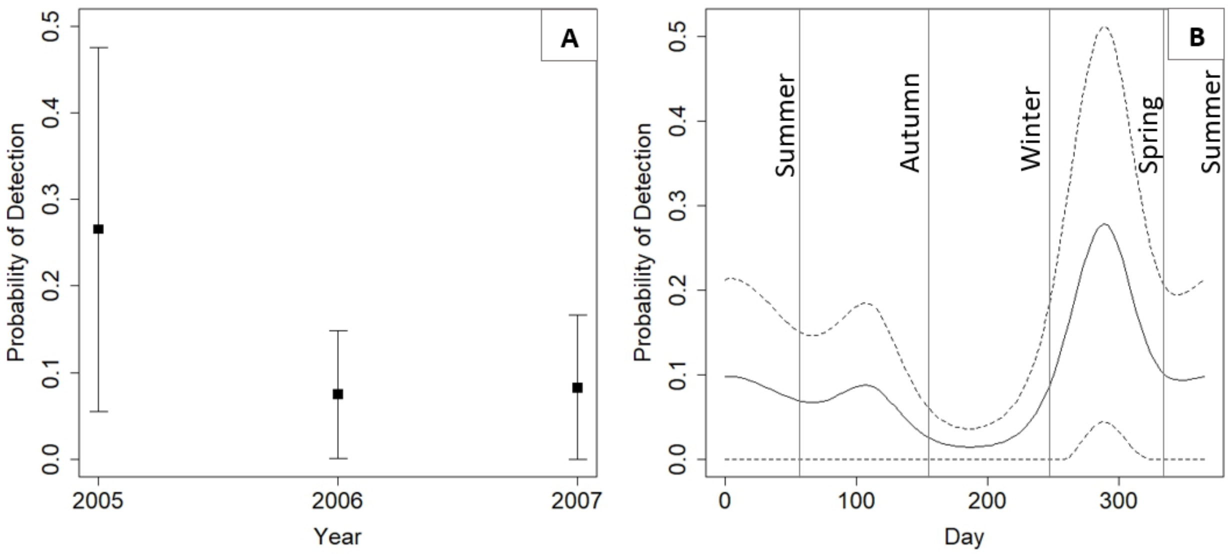

Figure 7: Probability of detecting a white shark at Muizenberg beach with (A) year and (B) for each day and corresponding season for 2005, 2006 and 2007 combined. Error bars (A) and dashed lines (B) represent 95% confidence intervals.

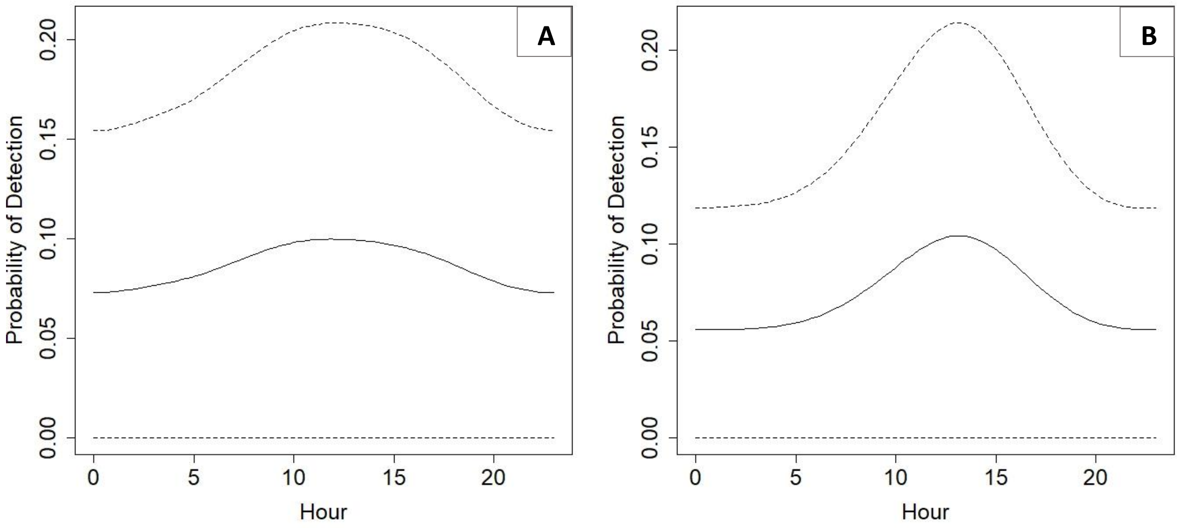

Figure 8: Probability of detecting a white shark at Muizenberg beach per hour during (A) summer and (B) autumn. Dashed lines represent 95% confidence intervals.

Barometric pressure

The probability of detecting a white shark in summer increased as barometric pressure increased (Figure 9A), with the probability of detecting a shark being 7 times higher at 1030 hPa compared to 1010 hPa. This trend is also evident during autumn (Figure 9B), with the probability of detecting a white shark being 6 times higher at 1030 hPa compared to 1010 hPa. In both instances, the 95% confidence intervals started to grow larger as barometric pressure increased above 1020 hPa.

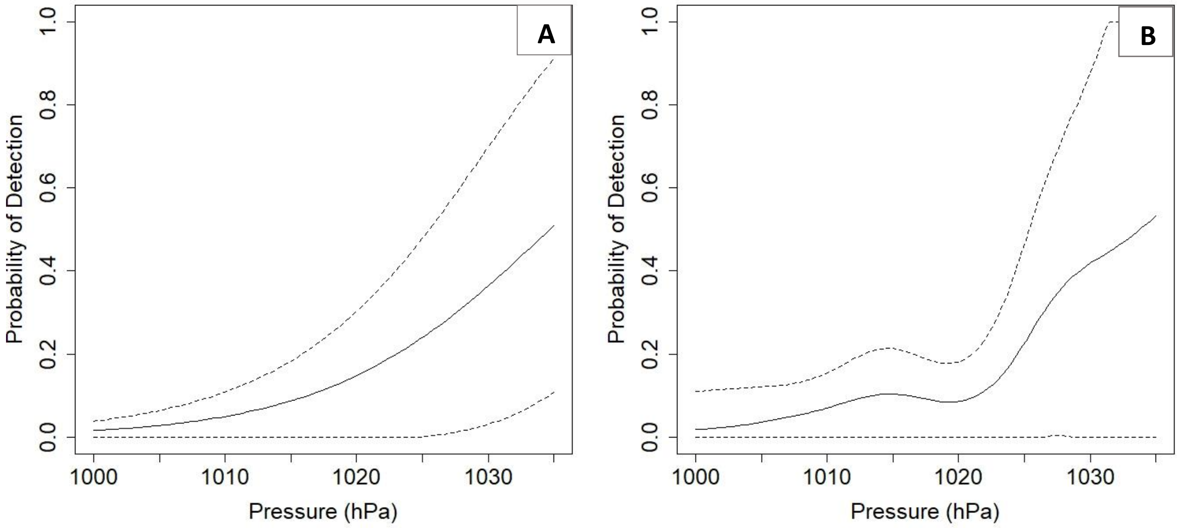

Figure 9: Probability of detecting a white shark at Muizenberg beach by barometric pressure during (A) summer and (B) autumn. Dashed lines represent 95% confidence intervals.

Wind speed

Wind speed was also a significant predictor of white shark presence during summer and autumn (Figure 10A and B), however the effects of wind speed differed for each season. During summer, the probability of detecting a white shark increased when wind speed reached 10m/s or higher, with the probability of detecting a white shark being 3 times higher at 15 m/s compared to 10 m/s. However, the 95% confidence intervals at 15 m/s were much larger than at 10 m/s. In comparison, the probability of detecting a white shark decreased as wind speed increased during the autumn season, where the probability of detecting a white shark was 26 times higher when wind speed was 0 m/s compared to 15 m/s. During autumn, the 95% confidence intervals were large below 8 m/s, with little difference from 8 to 15 m/s.

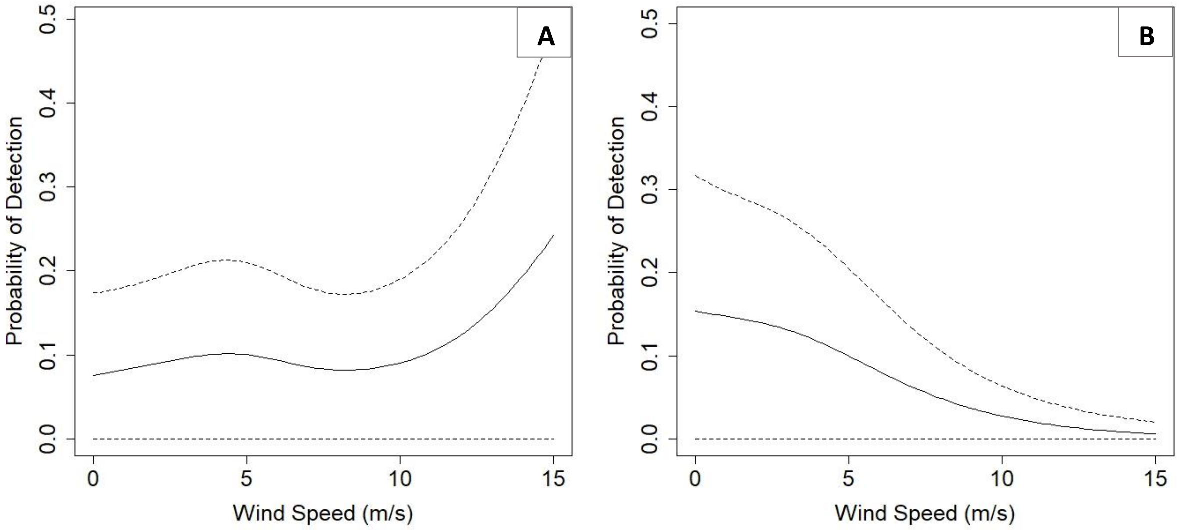

Figure 10: Probability of detecting a white shark at Muizenberg beach with wind speed during (A) summer and (B) autumn. Dashed lines represent 95% confidence intervals.

Water temperature

Water temperature was a significant predictor of white shark presence at Muizenberg beach with an increase in detection probability as temperature increases during the summer, autumn and winter seasons, although the 95% confidence intervals also increased as water temperature increased for all seasons (Figure 11A, B and C). White sharks were detected over a range of temperatures (from 10°C to 23°C) during the study period. The most pronounced differences in detection probability occurred during the autumn season, with the probability of detection being 8 times higher at 22°C compared to 12°C.

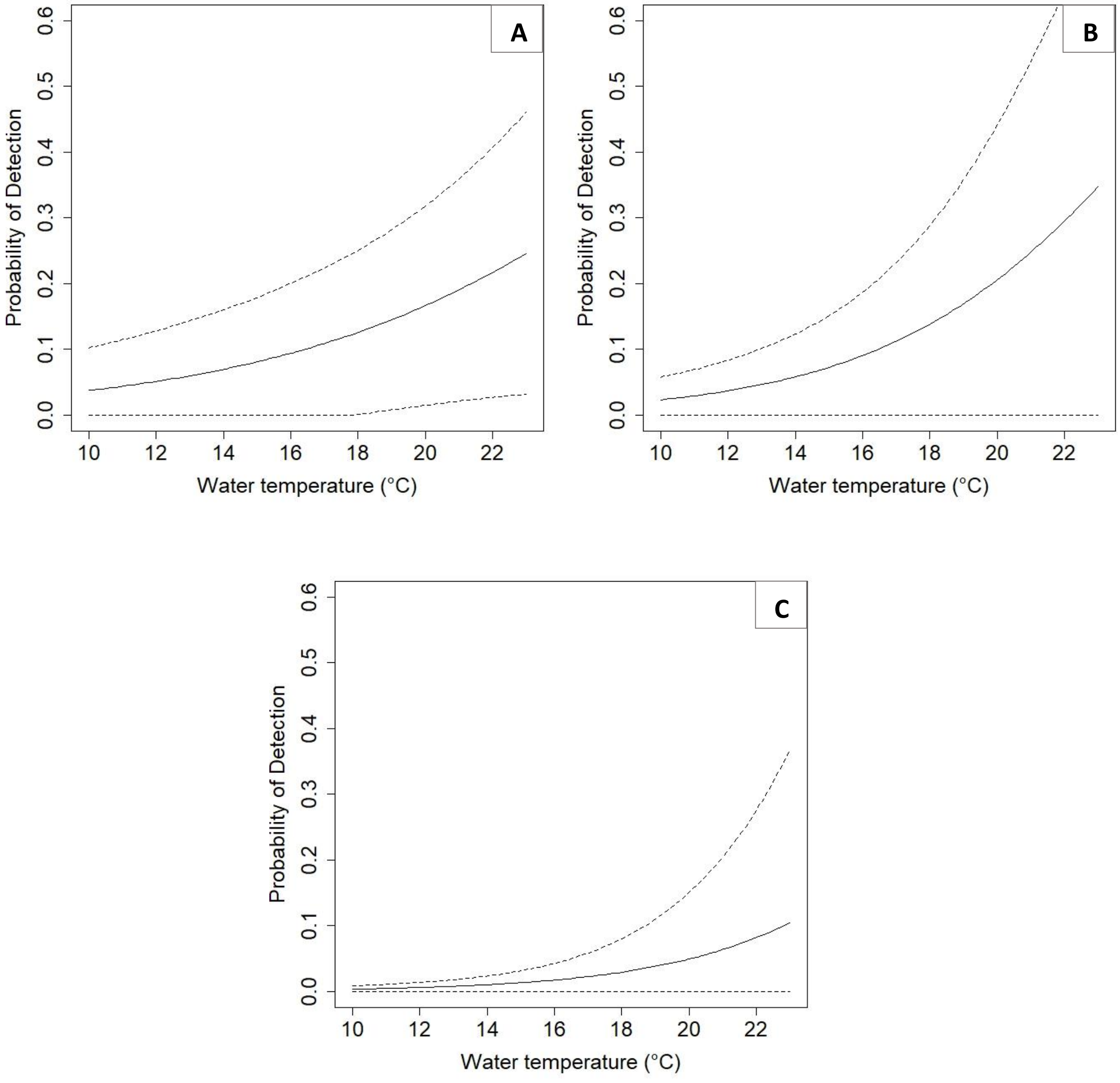

Figure 11: Probability of detecting a white shark at Muizenberg beach with water temperature during the (A) summer, (B) autumn and (C) winter season. Dashed lines represent 95% confidence intervals.

Discussion

Similar to previous studies on the patterns of white shark presence at popular recreational beaches in False Bay (Weltz et al*.* 2013; Loosen 2017), the results of this study suggest that the probability of detecting white sharks at Muizenberg beach is influenced by a suite of environmental variables. Importantly, the findings from this study, which used acoustic telemetry to detect tagged white sharks, support some of the key findings from observation studies including the significant positive effects of year, season, time of day and increasing water temperature (Table 5). Interestingly, this study found no effect of lunar phase on the probability of white shark detection at Muizenberg beach, in comparison to Weltz et al. (2013). A novel finding of this study is the influence of barometric pressure on white shark detection probability at Muizenberg beach (Table 5).

Table 5: Predictor variables of white shark presence at Muizenberg beach for three different studies (Loosen 2017, Weltz et al. 2013 and van Beuningen 2018). "Yes" indicates variables which significantly predicted the probability of white shark presence, "No" indicates variables which had no effect on influencing white shark presence and "NA" refers to those variables which were not tested in the respective study.

	Study		
Variable	Loosen 2017	Weltz et al. 2013	van Beuningen 2018
Year	Yes	Yes	Yes
Season	Yes	Yes	Yes
Time of day	NA	No	Yes
Water temperature	Yes	Yes	Yes
Wind direction	NA	No	No
Wind speed	NA	No	No
Tide state	NA	NA	No
Lunar phase	NA	Yes	No
Prey presence	Yes	NA	NA
Barometric pressure	NA	NA	Yes

Temporal variation – Year/Season/Time of day

There were significant temporal variations in the probability of white shark detections across year, season and time of day. The probability of detecting a white shark at Muizenberg beach was highest in the year 2005. Weltz et al. (2013) and Loosen (2017) also found inter-annual variability in white shark sightings at Muizenberg beach, with sightings decreasing from 2006-2008 (Weltz et al. 2013; Loosen 2017), increasing between 2009 and 2011 (Weltz et al. 2013; Loosen 2017) and decreasing again from 2012-2016 (Loosen 2017). However from 2006-2016 the overall trend was a slight increase in the number of shark sightings (Loosen 2017). In comparison, the sighting rate of white sharks at Seal Island in False Bay decreased over an eight year period from 2004–2012 (Hewitt et al. 2017).

Inter-annual variability was also seen in the catch rate of white sharks in the KwaZulu-Natal and Australian shark nets (Cliff et al. 1996; Malcolm et al. 2001), with Malcolm et al. (2001) suggesting that seasonal and inter-annual variations in catch rates of white sharks are likely a result of changes in the distribution of prey species and are independent of population size. The status of the South African white shark population is currently being debated (Andreotti et al. 2016; Irion et al. 2017), however it is likely that inter-annual variations in white shark detections at Muizenberg beach are also linked to variations in prey availability, not just in False Bay, but along the entire South African coastline. Furthermore, orcas (*Orcinus orca*) are known to predate on white sharks (Pyle et al. 1999), and since 2009 they have been seen increasingly in False Bay (Kock *pers. comm.*). In recent years, white sharks have been absent from False Bay for a period of several months following an orca sighting (Kock *pers. comm.*). It is possible that orcas have been present in False Bay before 2009, but have gone undetected. Therefore the presence of orcas could also influence inter-annual variability in white shark detections in False Bay.

Season was also a significant predictor of white shark presence at Muizenberg beach, with the probability of detecting a shark being highest in spring, then summer and autumn. Very few white sharks were detected in winter. Seasonal variation in white shark presence inshore in False Bay is already well established (Kock et al. 2013; Weltz et al. 2013), with white sharks aggregating at Seal Island during the autumn and winter months where they feed on Cape fur seals (mostly pups) (De Vos et al. 2015a; De Vos et al. 2015b), and moving inshore during the spring and summer, when migratory teleost and elasmobranch abundance peaks in this habitat (Clark et al. 1996a; Lamberth 2006; Loosen 2017). Interestingly, none of the environmental predictors included in the model for white shark presence at Muizenberg beach were significant during spring, the season where the probability of detecting white sharks is highest. This is an unexpected result and suggests that cues other than environmental variables measured in this study and those of Weltz et al. (2013) and Loosen (2017) may be driving white shark presence along the inshore in spring. Ross et al. (1987) suggest that the factors that control temporal variations in surf zone fish assemblages can be viewed as a hierarchy, with annual variations influenced by climatic events, to seasonal patterns of occurrence driven by reproductive and feeding movements, and finally to changes in environmental variables such as salinity, temperature and wave height that influence site-specific abundance. Clark et al. (1996b) support this idea, as they concluded that even when seasonal variations in environmental variables such as water temperature were not pronounced, spawning periods of certain resident and transient fish species were still timed seasonally to allow the juveniles of these species to make optimum use of this habitat in later months. Therefore it is possible that during spring certain prey fish are present, but their presence is not closely linked with ambient environmental variables. This would explain the lack of environmental predictors of white sharks in spring, as they are following prey fish species which are present in high numbers (Clark et al. 1996a), but are not necessarily influenced by ambient environmental conditions.

The probability of detecting a white shark increased during the daylight hours and peaked between 12h00 and 15h00 during summer and autumn, indicating that time of day was also a significant predictor of white shark presence at Muizenberg beach during these months. Contrastingly, time of day was not found to be a significant predictor of white shark presence at Muizenberg beach in a previous study (Weltz et al. 2013), however this could be due to the fact that time of day in their study was broadly categorised into two variables - morning shift (7h00 – 13h00) or afternoon shift (13h00 – 19h00). Engelbrecht et al. (2017) also found that white shark sightings peaked at Muizenberg beach between 11h00 – 15h00, and Kock et al. (2018) discovered that white shark presence inshore of False Bay was higher around midday. The reasons for this temporal variation in time of day remain unclear (Weltz et al. 2013; Kock 2014), but could either be related to thermal regulation, as sun-warming raises the water temperature in the northern shallow waters of False Bay (Dufois and Rouault 2012), where white sharks have been observed swimming at very slow speeds (Kock, *pers. comm.*), or it is possibly related to increased prey availability during these times. Another reason for this temporal variation could be due to diel variations in acoustic detectability of tagged animals, which has been shown to be influenced by biotic and abiotic noise in the marine environment (Payne et al. 2010). Yet, as other studies have also shown that white shark presence at Muizenberg beach (Engelbrecht et al. 2013) and inshore of False Bay (Kock et al. 2018) peaks around midday, it suggests that white shark presence at Muizenberg beach is significantly affected by time of day, rather than being due to diel fluctuations in range detection.

Although the reasons for this temporal peak between 12h00 and 15h00 remain unclear, it is noteworthy that water user activity (bathers, paddlers and surfers) at Muizenberg beach peaks between 11h00 and 16h00 during both the spring and summer months (Engelbrecht et al. 2017). Yet despite this temporal overlap between a large number of water users and white sharks at Muizenberg beach there have only been five recorded shark-human interactions since 1960, none of which were fatal (Cliff 2006; City of Cape Town 2014). This equates to one shark-human interaction every 11.6 years, which strongly supports scientist's assertions that white sharks do not consider humans as a prey source.

Barometric pressure, wind patterns and water temperature

A novel finding of this study is that the probability of detecting a white shark increased with increasing barometric pressure during both the summer and autumn months. A similar result was obtained for white sharks in Algoa Bay, South Africa, where aerial sightings close to shore were significantly higher as barometric pressure was increasing. However the authors of this study were unclear as to the role barometric pressure had on influencing the abundance of white sharks close inshore, but that it could have been confounded by more flights occurring on good weather days, and that the ability to detect sharks on those days was higher (Dicken and Booth 2013).

Barometric pressure has been shown to influence shark behaviour in other parts of the world, with blacktip sharks (*Carcharhinus limbatus*) in Florida, USA leaving a nursery area as barometric pressure dropped ahead of an approaching tropical storm (Heupel et al. 2003). In Cleveland Bay, Australia, some species exhibited a short-term flight response under similar conditions, whilst others were unaffected (Udyawer et al. 2013; Heupel and Simpfendorfer 2014). It is unlikely that white sharks inshore of False Bay are responding directly to barometric pressure, but rather indirectly through its influence on wind patterns, water temperature and primary productivity in the northern reaches of the bay. In addition, barometric pressure is not known to affect acoustic transmission in water bodies (Gjelland and Hedger 2013; Kessel et al. 2013), and therefore changes in barometric pressure would have little influence on acoustic detection range. The 95% confidence intervals for summer and autumn increased substantially above 1020 hPa, indicating that although the probability of detection significantly increased with increasing barometric pressure, so did the variability due to fewer days where barometric pressure was above 1020 hPa (5.6% of days in summer and 28.0% of days in autumn). This demonstrates the need for longer-term data collection to more accurately infer these findings.

During the austral summer months, the South Atlantic High pressure cell off the coast of South Africa intensifies and, combined with the transient coastal low pressure cells and interior low pressure cell over the sub-continent, results in a steep pressure gradient along the coast (Kruger et al. 2010). This pressure gradient results in the development of extreme south-easterly winds in the south-western Cape, known locally as the "Cape Doctor" (Goliger and Retief 2002; Kruger et al. 2010). Consequently wind speed typically increased during the summer months and was associated with an increased probability of detecting a white shark at Muizenberg beach. South-easterly winds push warm surface water to the northern shores of False Bay (Atkins 1970; Dufois and Rouault 2012) and cause an increase in surf action along the inshore. Together these abiotic factors promote blooms of surf-zone diatoms (*Anaulus birostratus*). These blooms are a valuable food source for a variety of smaller fish species which in turn serve as prey for large migratory fish that are targeted by the beach seine fishery, primarily in the spring and summer months (Lamberth et al. 1995; Clark et al. 1996a). Loosen (2017) revealed that white sharks were 66% more likely to be seen at Muizenberg beach when prey fish were present, suggesting that prey is a major factor determining white shark presence inshore of False Bay.

By contrast, during autumn increased wind speed resulted in a decreased probability of detection. The predominant winds in autumn/winter are a northerly offshore wind which results in cold water upwelling close to shore (Atkins 1970). Therefore when the wind is not blowing during the autumn months, the water temperature is warmer and more favourable for diatom blooms and associated prey which attracts white sharks. In comparison, Weltz et al. (2013) found that wind speed was not a significant predictor of white shark sightings at Muizenberg beach, and suggested that this was possibly due to the lag effects of wind not being incorporated into their model. Another possible explanation is that at higher wind speeds it becomes more difficult for shark observers to spot sharks, leading to a decreased perceived versus actual presence.

Wind speed is known to be a major factor in decreasing detection range (Medwin and Clay 1997). Strong winds can mix air bubbles into the water column which can attenuate sound through scattering and absorption (Gjelland and Hedger 2013). Windy conditions can also stir up the substrate, particularly if the substrate is sandy, such as at Muizenberg beach, resulting in suspended solids in the water column which can also scatter sound and reduce acoustic range (Kessel et al. 2014). Despite the negative effect of wind speed on acoustic detection range the Muizenberg receiver still detected more white sharks as wind velocity increased in summer, suggesting a strong positive relationship between white shark detection probability and increased wind speed at this site. The large confidence intervals above 10 m/s during summer can be explained by the fact that less data is available for those periods (only 7.4% of days). However in autumn, 75.1% of days experienced wind speeds below 7 m/s, when confidence intervals are larger. Therefore the large confidence intervals in autumn can likely be explained by shark presence decreasing at Muizenberg beach, therefore detections are more sporadic during these months. Again these findings demonstrate the need for longer term data collection to more accurately infer these findings.

The distribution of sharks in coastal environments is also considered to be heavily influenced by water temperature (Hopkins and Cech 2003; Dewar et al. 2004; White and Potter 2004; Harley et al. 2006; Carlson et al. 2008; Vögler et al. 2008; Knip et al. 2010; Abascal et al. 2011; Weltz et al. 2013), and was a significant predictor of white shark presence at Muizenberg beach during the summer, autumn and winter months, with an increasing probability of detection as water temperature increased. These results are similar to those obtained by both Weltz et al. (2013) and Loosen (2017) using shark observer data and confirm that white shark presence inshore of False Bay tends to increase as sea temperatures increase. The influence of water temperature on predator behaviour and abundance is complex, as it may act either indirectly, by affecting prey distribution and abundance, or directly, by affecting thermoregulation (Campana and Joyce 2004; Higham et al. 2015; Wintner and Kerwath 2017). However, as the average size of white sharks in False Bay is roughly 3.25 m (Hewitt et al. 2018), and larger white sharks have greater endothermic ability (Bernvi 2016), it appears that any effect of water temperature on white shark presence inshore of False Bay is likely due to an indirect effect on prey distribution and abundance rather than a physiological preference for warmer water (Weltz et al. 2013; Kock 2014).

Sound propagation in water is influenced by temperature gradients, therefore thermoclines have the potential to influence detection probability by deflecting sound waves away from the receiver (Huveneers et al. 2016). As the water column is isothermal during the winter months throughout most of False Bay (Atkins 1970), it is unlikely that water temperature would negatively affect shark detection during these months. In comparison, the water column in False Bay is highly stratified during the summer months (Atkins 1970), therefore during summer there is a higher possibility of water temperature influencing shark detection. Despite the potential negative effect of water temperature on acoustic detection range, the Muizenberg receiver still detected more white sharks as temperature increased in summer suggesting a strong positive relationship between white shark detection probability and increased water temperature at this site.

The larger confidence internals at water temperatures above 16°C in autumn and 14°C winter can also be explained by fewer data available for these days (38.3% of days in autumn and 0.5% of days in winter). It could also be explained by shark presence increasing towards the end of winter and decreasing towards the end of autumn. Importantly, although the large confidence intervals make interpreting these results more challenging, the above variables all follow a certain trend and were found to be significant predictors of white shark presence, indicating that these variables have some degree of influence on white shark presence at Muizenberg beach.

Cloud cover

Cloud cover was not a significant predictor of white shark presence in this study which is in contrast to the findings of Weltz (2012). Cloud cover reduces the visibility of sharks to shark observers positioned on land and thus the reduced detection of sharks by observers may well reflect this, rather than a genuine absence of sharks associated with increased cloud cover. In comparison, cloud cover has no effect on acoustic detection range and was therefore not a limitation in this study.

Robbins (2007) also found that cloud cover was not a significant predictor of white shark sightings at the Neptune Islands, Australia. However, white shark predation success on elephant seals at the Farallon Islands, USA, was found to increase with cloud cover, with the authors proposing that the decreased light availability in the water column provides better camouflage, increasing white shark hunting success (Pyle et al. 1996).

Lunar phase and tidal state

Lunar phase and tidal state were found to have no significant impact on white shark presence at Muizenberg beach. This finding is unexpected because the biology of various marine animals across different taxa has been shown to be affected either directly by the lunar cycle or indirectly by associated tidal states (Horning and Trillmich 1999; Naylor 2001; Benoit-Bird et al. 2009) and Weltz et al. (2013) revealed that lunar phase was a significant predictor of white shark sightings at Muizenberg beach. Weltz et al. (2013) suggested that this trend could be explained by the improved opportunities for feeding provided by the new moon. However a caveat of their study was that data on shark presence was not recorded at night time as they relied solely on diurnal shark observers for shark presence data. Similar to the findings of Weltz et al. (2013), white shark presence increased at a seal colony in California and white shark catches increased in shark nets along the Australian east coast in response to new moon (Pyle et al. 1996; Werry et al. 2012). The authors suggested that the low light levels provided sharks with better conditions for hunting seals as they were concealed from their prey and that the increase in sharks caught in shark nets was attributed to the difficulties of detecting the nets in low light conditions associated with the new moon (Pyle et al. 1996; Werry et al. 2012). However, similar to the findings in this study, lunar phase was not a significant predictor of white shark catches in the KwaZulu-Natal shark nets, with the authors concluding that that the visibility of fishing gear in relation to lunar illumination is unlikely to affect capture.

Lunar cycle is closely related to tidal cycle, which is also known to affect the behaviour and distribution of many marine species, particularly those that inhabit coastal areas (Butner and Brattstrom 1960; McDowall 1969; Naylor 2001; Wetherbee et al. 2007). However, tidal state did not have a significant influence on white shark detection at Muizenberg beach, which supports the findings of Weltz (2012). The effect of tidal state largely depends on the bathymetry of each beach, with a sharply declining bathymetry giving way to more land area being exposed at low tide. The bathymetry of Muizenberg beach is gently sloping, and the mean tidal range in False Bay is a modest 1.48 m (Spargo 1991). Therefore although it is possible that prey species in False Bay may take advantage of higher tides to exploit food resources, the available habitat that changes between the pushing and pulling tides is likely not sufficient to affect white shark movement in this area (Weltz 2012). This may also explain why lunar phase and associated tidal state had no influence on white shark detections at Muizenberg beach.

Management considerations

By understanding when white sharks are likely to be present at certain popular beaches, it is possible to predict when the risk of overlap between water users and white sharks is highest, and to convey this information to the public so that they can make informed decisions about using these areas (Engelbrecht et al. 2017). The findings from Weltz et al. (2013) were used by the City of Cape Town and the Shark Spotters organisation to inform water users as to peak times of risk of encountering white sharks. The findings from this study support the findings of Weltz et al. (2013) that there is an increased probability of encountering a white shark when sea temperatures are higher, and that there is significant inter-annual variability in white shark presence at Muizenberg beach. However, Weltz et al. (2013) found that lunar phase was a significant predictor of white shark sightings and that there was no diel effect at Muizenberg beach, in contrast to the findings of this study. The longer-term dataset of Weltz et al. (2013) provides for a more robust analysis, thus I would not recommend changing the information disseminated by Shark Spotters and the City of Cape Town at this time. I propose that the advice remains the same, but that more research on the topic is performed using a longer-term dataset.

Despite the previous awareness initiatives of Shark Spotters and the City of Cape Town, it does not appear that water users have changed their behaviour to limit their time in the water during peak times of risk (Engelbrecht et al. 2017). Although this information may not change water user behaviour, it appears that it helps foster an acceptance of white sharks and our ability to share the ocean, rather than using lethal control of predators for our recreational benefit. In future, it would be interesting to conduct a public perceptions survey to better understand how the public views their risk of encountering white sharks, and to quantify how well the information available to them has been processed.

Limitations

Ideally the effect of environmental variables on range detection should be tested at Muizenberg and Fish Hoek beach over a longer time frame and under varying conditions to assess how environmental variables influence each specific receiver. This will allow for a greater level of confidence in these results. In addition it would be better to record environmental variables at or near the receivers, particularly those that appear to be significant such as water temperature, wind speed and barometric pressure. This study was also limited in that it only spanned a period of three years, in comparison to five years for Weltz et al. (2013) and nine years for Loosen (2017). A longer dataset would allow for more reliable interpretations of the results. A major limitation was the lack of white shark detections on the Fish Hoek receiver which prohibited a comparison between Muizenberg and Fish Hoek beach, thereby preventing me from comparing the results of Fish Hoek beach to the previous findings of Weltz et al. (2013) and Loosen (2017). Lastly, Loosen (2017) has demonstrated the importance of prey species in influencing white shark presence inshore of False Bay, therefore a study that aims to assess how prey species are using the inshore environment of False Bay both seasonally and daily is important if we are to model what appears to be the most significant driver of white shark presence along the inshore and close to popular recreational beaches.

Conclusion

To date, the Shark Spotters programme has been effective at reducing the spatial overlap between people and sharks by alerting water users when a shark is in the vicinity, forcing them to exit the water (Engelbrecht et al. 2017). Although the City of Cape Town has adopted the use of a non-lethal policy at this stage (Nel and Peschak 2006), more frequent shark-human interactions (as has been seen in countries like Australia and Reunion) could see politicians recommending the addition of lethal control methods which, despite not being supported by science, are driven by popular opinion (Neff 2012; Kock 2014). It is therefore important to conduct research which can aid in mitigating shark-human conflict, and add to the already existing information about when white sharks make use of inshore environments, particularly in the vicinity of popular recreational beaches. The detection of white sharks using passive acoustic telemetry is less influenced by environmental variables compared to observational data from shark observers, and therefore provides a reliable data collection tool to infer white shark presence at Muizenberg beach. This study supports previous findings of the marked seasonal variations of white shark presence in False Bay (Kock et al. 2013; Weltz et al. 2013; Loosen 2017). It also provides the first evidence that barometric pressure is a significant predictor of white shark presence at Muizenberg beach, at least during the summer and autumn months. In addition, the other predictors of white shark presence at Muizenberg beach in this study, other than lunar phase, are consistent with the findings of Weltz et al. (2013). This finding suggests that the Shark Spotters programme is not only an effective shark safety strategy (Engelbrecht et al. 2017), but that it is also a reliable data collection tool which can be used to infer patterns of white shark behaviour, at least in False Bay.

Appendix

A concrete mooring was positioned on the sea floor and was connected to a metal pole to which the acoustic receivers were attached. To construct the mooring, truck tyres were cut in half, creating two equal sized circles. Each half tyre was then filled with concrete and a galvanised steel pole was positioned vertically in its centre before the concrete hardened. Stainless steel nuts and bolts were then used to attach each receiver to its own galvanised pole. Receivers stood approximately 1.75 m off the sea bed. In order to prevent biofouling which again could lead to poor signal detection (Heupel et al. 2008), all moorings and receivers were painted with anti-fouling paint. Receivers were retrieved every 6-12 months and downloaded to secure data. However to ensure continuous monitoring, replacement receivers were prepared beforehand and deployed immediately after retrieval.

Acoustic receiver performance can be affected by environmental conditions, resulting in variability in detection rates, particularly in marine environments (Heupel et al. 2008). A necessary prerequisite to any acoustic telemetry study is to monitor and assess the variability in detection range for a given receiver in the study area in order to make reliable inferences about the study animals behaviour (Kessel et al. 2014). Therefore, an *in situ* range test was performed on each receiver in this study by Kock (2014) to determine its detection range. This was done by placing a V16 transmitter (the same transmitter used in the study) at a depth of 2 m over the side of the research vessel. Using the on-board GPS system, the vessel was then moved away from the receiver in 50 m increments to a maximum distance of 1 200 m away from the receiver. At each 50 m increment, the engines were turned off and for five minutes the vessel was allowed to drift, with the tag overboard. The distances from the transmitter were matched to the timing of the detections to generate a detection profile for each receiver. Range testing was done only once for each receiver, and was performed on relatively calm days when swell was < 3 m and wind < 20 km/h (Kock 2014).

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