Spatiotemporal ecology and potential displacement of white sharks in southern Africa

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By

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STATEMENT OF CONTRIBUTION BY OTHERS

Chapter 1

The introduction was my own work. My supervisors, Tony Booth and Malcolm Smale read and commented on earlier versions of the chapter.

Chapter 2

This chapter was published in *Functional Ecology* in 2016. I am the primary author and Vianey Leos-Barajas, Roland Langrock, Robert Schick, Malcolm Smale, Tami Kaschke, Oliver Jewell and Yannis Papastamatiou are co-authors. I was responsible for conception of the project, field work, data analysis, interpretation of results and writing the manuscript. Oliver Jewell and Tami Kaschke assisted in the field with tagging and tracking. Malcolm Smale and Yannis Papastamtiou assisted with interpretation, Vianey Leos-Barajas, Roland Langrock, Robert Schick provided statistical assistance, and all co-authors proofread the manuscript which was then improved upon by three anonymous reviewers for *Functional Ecology*.

Chapter 3

This chapter was published in *African Journal of Marine Science* in 2022. I am the primary author and Ralph Watson, Alison Kock, Yannis Papastamatiou, Marlene Sturup, Enrico Gennari, Kelly Baker, Tony Booth, Matt Dicken, Wilfred Chivell, Simon Elwen, Tami Kaschke, David Edwards and Malcolm Smale are co-authors. I was responsible for conception of the project, field work, data analysis, interpretation of results and writing the manuscript. Enrico Gennari provided additional shark data from Mossel Bay and manuscript edits. Malcolm Smale and Tony Booth provided edits with the manuscript and the chapter. Ralph Watson provided statistical assistance and edits. Tami Kaschke helped with killer whale necropsies, data collection and proof reading. Yannis Papastamatiou and Alison Kock helped with interpretation of results and edits. Simon Elwen provided Killer whale information and proofreading. Wilfred Chivell and Kelly Baker facilitated the data collection from both boat-based data and necropsies but did not contribute to the writing or provide edits. David Edwards helped with some earlier figure editing and some promotional material for the paper but did not contribute to the writing or provide edits. The manuscript was further improved by two anonymous reviewers at *African Journal of Marine Science* and its editor.

Chapter 4

This chapter was published in *Ecology: The Scientific Naturalist* in 2022. I am the primary author and Alison Kock, Christiaan Stopforth, David Hurwitz and Simon Elwen are co-authors. I was responsible for conception of the project, field work, data analysis, interpretation of results and writing the manuscript. Christiaan Stopforth provided drone footage. Alison Kock provided interpretation of results and edits, Simon Elwen provided edits and assistance with the final figures. David Hurwitz helped with stabilising and analysing the raw helicopter video footage. The manuscript was improved on by two anonymous reviewers for *The Scientific Naturalist* along with its editor.

Chapter 5

I was responsible for conception of the Chapter, conducted the field work data analysis, interpretation of results and writing. Victoria Goodall, Kim Whorskey and Rob Lennox provided some statistical assistance with network analysis. Tony Booth and Malcolm Smale provided edits and guidance with the chapter.

Chapter 6

The discussion was my own work. My supervisors, Tony Booth and Malcolm Smale

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ABSTRACT

The white shark *Carcharodon carcharias* (Linnaeus, 1758) is one of the largest predatory sharks, with a cosmopolitan global distribution. The objective of this thesis was to explore the spatiotemporal ecology of this species in coastal South Africa, from both a fine and large-scale perspective (a bay versus the entire coastline). Furthermore, this study aimed to identify and quantify the impacts of a novel biological driver on white shark movement in the region.

This study revealed that two hunting modes were employed by white sharks to hunt seals. Mixed Hidden Markov models (HMMs) were applied to acoustic tracking data of 14 white sharks in the aggregation area, to quantify changing movement states (area-restricted searching vs. patrolling) and the factors that influenced them. White sharks demonstrated individual preferences for fine-scale movement patterns, which may be related to their use of different hunting modes. As such, individual variability should be considered when modelling the behavioural effects of predators on prey species.

Risk-induced fear effects exerted by top predators are pervasive in terrestrial and marine systems, with lasting impacts on ecosystem structure and function. The loss of top predators can disrupt ecosystems and trigger trophic cascades, but the introduction of novel apex predators to ecosystems is not well understood. In 2017, during the middle of the data collection period of this study, a rare shark-eating morphotype of killer whale *Orcinus orca* appeared along the Western Cape coast. This highly distinctive pair of killer whales preyed on at least eight white sharks, seven at Gansbaai. Sightings per unit effort and telemetry data revealed that white sharks emigrated from the site, following these attacks, in response to further sightings of the killer whales. White sharks responded rapidly to risk from a novel predator, and their absence triggered the emergence of another meso-predator, the bronze whaler shark

Carcharhinus brachyurus, demonstrating trophic changes in mesopredator composition at the site, determined by sightings data from shark dive operators.

Unique aerial footage was analysed on the same killer whales hunting white sharks at another aggregations site, 300 km east, Mossel Bay. This footage substantiated the hypothesis that killer whales are hunting white sharks in South Africa and it revealed the hunting behaviour of the killer whales in additional to the evasive strategies utilised by the white sharks. Cage diving vessel and drone survey data confirmed that white sharks exhibited flight responses for at least 45 days from Mossel Bay and were similar to the behavioural patterns observed in Gansbaai. Furthermore, cultural transmission was documented, with other adult killer whales hunting white sharks in Mossel Bay, together with the known pair.

Large-scale movement data from 118 individual white sharks fitted with with V16 R-coded acoustic tags between 2012 and 2022 were examined. Spatial network analysis was applied to note if any differences occurred in coastal space use between white sharks pre- and post-killer whale presence. Declines in white shark acoustic detections were noted after 2018, along the coast, and the complete disappearance of detections in the Western Cape hotspots of False Bay (Cape Town) and Gansbaai between 2015 and 2018. There are broader ecological, economic, and bather safety impacts of white sharks being displaced by killer whales in South Africa, and while there are no clear solutions, suggestions for management are proposed as these interactions are likely to continue.

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Moving to South Africa from the UK, at the age of 21, was the most exciting chapter of my life. I arrived in the country to study white sharks and never anticipated how much I would fall in love with the place and its people. Fifteen years later, South Africa is still home. Tony and Malcolm, this thesis would not have been possible without your unwavering support, as my academic supervisors. Both of you stood by me when I needed help the most. I found myself unemployed, in the middle of a global pandemic and pregnant, yet you were both gracious. You believed in me and guided me to the end and for that I am endlessly grateful. This work is only possible because of your patience, encouragement and support, but mostly for being kind humans.

I would like to thank Wilfred Chivell for hiring me as a newly graduated marine biologist to guide for his shark dive company, Marine Dynamics, and later as a senior biologist for his non-profit organisation the Dyer Island Conservation Trust. Thanks for supporting me through my Masters degree and through most of my PhD. We all worked so hard to make your dive business grow into the thriving empire it is today, even post the pandemic. I am grateful as working for you taught me so much about life, my own character, as well as conservation. To all the staff, many volunteers and Susan, thanks to you too. A further thanks to the Save Our Sea Foundation for the financial support you gave me, which was integral to setting up the acoustic tracking array for my PhD research in Gansbaai and later, the Southern tip of Africa.

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1.1.2 Ecological role of apex predators

Apex predators are typically the largest-bodied extant carnivores in an ecosystem. Their presence may shape the structure of communities they inhabit from the highest trophic level downwards, in two ways. Either directly, through predation pressure, limiting lower trophic species numbers or indirectly, by influencing species' behavior through risk effects, triggering anti-predatory behavioural responses (Heithaus et al. 2008; Wallach et al. 2015). Risk effects may be larger than direct effects on communities (Creel & Christianson 2008; Ripple et al. 2014). Some ecosystems contain a diverse guild of large predators, making it challenging to draw the line between apex- and mesopredators (Prugh et al. 2009). Some of the world's most iconic apex predators coexist with larger and fiercer predators (Palomares & Caro, 1999), and a number of the world's largest predators, such as hyper-carnivore species from the Pleistocene, are now extinct (Myers & Worm, 2005; Wallach et al., 2015, Galetti et al. 2017).

Predators of all sizes kill or intimidate predators smaller than themselves (Wallach et al., 2015): Humans displace wolves (Paquet et al., 1996), Grey wolves *Canis lupus* exclude coyotes *Canis latrans* (Ripple et al. 2014), coyotes control foxes *Vulpes macrotis* (Crooks and Soulé 1999), foxes kill rats *Rattus fuscipes* (Banks 2001) and rats prey on seabird chicks (Towns et al. 2009). The trophic implications of apex predator loss from ecosystems have been widely studied and can be profound, causing top-down trophic cascades (Prugh et al. 2009; Estes et al. 2011, Ripple et al. 2014). In the absence of apex predators, 'mesopredator release' occurs whereby smaller predators become over-abundant, diminishing diversity and increasing predation pressure (Estes et al. 2011).

The ecological roles of top predators in both marine and terrestrial ecosystems may be more similar than previously thought, and studies that fail to account for multiple modes of antipredator behavior are likely to underestimate these roles and the consequences of eliminating predators from ecosystems (Heithaus et al. 2008, Wirsing and Ripple 2011). By comparing the interactions between tiger sharks (*Galeocerdo cuvier)* and dugongs (*Dugong dugon*) and between gray wolves (*Canis lupus*) and elk (*Cervus elaphus*), it was concluded that top predators in marine and terrestrial ecosystems trigger three similar types of anti-predator behaviour; (1) encounter avoidance, (2) escape facilitation, and (3) increased vigilance. The close match between dugong and elk defensive behaviours suggested that predator risk effects are transmitted through marine and terrestrial communities in a strikingly similar manner (Wirsing and Ripple 2011).

1.1.3 When predators become prey

Sympatric carnivorous apex predators may compete for similar resources, which can lead to dominant species influencing the ecology of subordinate ones (du Preez et al. 2015, Muller et al. 2022). However, apex predators often use coevolutionary strategies, which enable them to minimise competition with dominant competitors and thus facilitate coexistence (Muller et al. 2022). One of the most common antipredator strategies is to spatially avoid areas with high densities of predators (Caro 2005), which can be achieved at several scales (Lima and Zollner 1996). Leopards *Panthera pardus* and caracals *Caracal caracal* in South Africa showed high overlap in their diets and habitats. As a result, caracals showed temporal fine-scale adjusted behavioural responses to the presence of leopards to limit direct competition for resources and minimise predation on themselves (Muller et al. 2020). In North America, with the introduction of wolves *Canis lupus* into the Yellowstone National Park, coyotes *C. latrans* completely switched their diet from elk *Cervus canadensis* to deer *Odocoileus virginianus*, as the wolves dominated the access to elk and drove coyotes out of prime hunting sites (Merkel et al. 2009).

The re-introduction of predators has acute impacts on ecosystems, and such interactions have been studied widely in terrestrial environments such as national parks, nature reserves and game farms. In the African Serengeti, while increased lion presence caused leopards to change their daily behavior, they caused another top predator, wild dog *Lycaon pictus*, to alter their entire home range, so as not to overlap with lions *Panthera leo* in both time and space (Swanson et al. 2014).

Human beings are arguably the most impactful apex predators in marine and terrestrial environments (Surachi et al. 2019, Madin et al. 2016). Fewer examples exist of top predator displacement in marine environments due to the complexities of studying such behavior in the ocean. Just as the building of human roads caused wolves and lions to entirely re-route their natural hunting corridors, industrial fishing activities have caused top predators such as sharks to forage in different locations due to direct competition for resources, habitat damage, or risk of being caught themselves (Surachi et al. 2019, Madin et al. 2016).

Killer whales *Orcinus orca*, often called the 'wolves of the sea', hunt all marine mammal families, except river dolphins *Inia geoffrensis* and manatees *Trichechus manatus*. They have been observed to hunt twenty species of cetaceans, fourteen species of pinnipeds, dugong *Dugong dugon* and sea otters *Enhydra lutris* (Jefferson et al. 1991). Many marine predators change their behavior and distribution in response to the risk of killer whale predation (Cure et al. 2006, Pitman and Durban 2010, Breed et al. 2017). The decision of 'fight or flight' is usually dependent on the trade-off between the risk of death and access to, or lack of, prey (Ripple et al. 2014).

1.1.4 Displacement

Displacements have occurred at various spatial scales from localised habitats to large geographic areas. Given the environmental, ecological, and evolutionary impacts, there is an urgent need to understand competitive interactions leading to displacement and their effects (Reitz and Trumble, 2002). Displacement among actively hunting predators typically involves intraguild predation and occurs among species within the same trophic level. The majority of displacements cause negative impacts such as the loss of biodiversity, for example, when a native species is displaced by an invasive species. Displacement of keystone species (species with critical influence on community structure) has had adverse impacts on other native species (Reitz and Trumble, 2002). Interactions leading to displacement are complex and often involve multiple mechanisms; and many documented cases of displacements have occurred in anthropogenically disturbed habitats. Furthermore, high-human disturbance can displace large carnivore predators then indirectly benefitting prey species by reducing predation risk, a trait-mediated indirect effect of humans, that spatially decouples predators from prey (Muhly et al. 2011).

1.1.5 Tracking marine predators

The first radio collars to study terrestrial wildlife were deployed in the 1960s on elk and grizzly bears in Yellowstone National Park (Craighead 1982; Craighead et al.1995). Since then, ecologists have adapted their technology worldwide to study the distribution of terrestrial and aquatic species (Hebbelwhite and Hayden, 2010). Today, scientists can follow the movements of their subject animals from the comfort of their desktops. They are unlimited by even the most difficult-to-study species, such as GPS radio-collared African wildebeest *Connochaetes taurinus* to Argos-tagged Pacific bluefin tuna *Thunnus thynnus.* Even wandering Albatross *Diomedea exulans,* a species that circumnavigates the globe, can be tracked with relative ease.

Global Positioning System (GPS) telemetry provides the most precise spatial and temporal location data about animal movements at small time intervals to a degree never before possible with VHF telemetry or other methods such as camera trapping. Within a few decades this technology advanced to allow for the collection of movement data in challenging environments such as low light, night time hours, in environments as harsh as the freezing poles or scorching deserts. The ability to collect data in a manner that is not biased by the ability of human observers in the collection process has further enhanced the capabilities of GPS tracking. Together with the ability to withstand the corrosive and intense pressures of aquatic environments, this method has paved the way in terms of our knowledge of how a plethora of different animals use space and move through their habitats (Hebbelwhite and Hayden 2010, Hussey et al. 2019).

Understanding marine predator movement still remains more challenging than that of land predators, as radio signals do not transmit well through saltwater (Lennox et al. 2017, Hussey et al. 2019). Two types of satellite transmitters have been widely used to track marine predator movement, the archival tag, which stores data to transmit once it detaches from the animal, and the ARGOS-based satellite-linked radio transmitters (Satellite Linked Radio Transmitters), which transmit data once the animal surfaces, thus they are usually attached to the fin or a body part that will break the surface (Weng et al. 2005, Spaet et al. 2020). Limitations of these satellite devices are their low spatial resolution, and logistical difficulties to retrieve them if they detach in remote areas (Jewell 2022). Furthermore, satellite tags are expensive; the average price for a simple Smart Position Only Tag/SPOT (surface locations only) is

USD$1,700, while depth and temperature capable tags (SPLASH tags) are approximately USD$3,300 (wildlifecomputers.com). When combined with satellite fees of USD$1,700 per year, per tag (www.argos-system.org), such expense has significantly restricted the sample size of most studies, hindering the power of findings and limiting their influence on management decisions (Elliot 2021). The strengths of satellite telemetry methods are the ability to record large scale migratory behaviour and collect information showing space use overlap with marine protected regions or heavily threatened areas (Block et al. 2011, Quieroz et al. 2019).

Acoustic telemetry is an alternative method for tracking marine predator movement; these devices are ultrasonic. Once deployed on the animal, they transmit a signal which can be collected either by a boat-based hydrophone, a moored acoustic receiver array or a sail drone (Hussey et al.2015). Each transmitter has a unique set of 'pings' that are associated with a specific identification number, allowing for the detection of the individual, along with time and date. Acoustic tags are more accessible and cost-effective for researchers; a simple radio or acoustic tag costs $200 or $300, respectively. The cost of simple receivers for tracking ranges from $500 to $2000, however, the maintenance of arrays and datasets can be costly on long-term projects due to the investment in divers or releases to recover and re-deploy the receivers, equipment loss in storm conditions and the general housing of large datasets. Acoustic tags allow for the collection of high-resolution fine-scale movement data and can be equipped with accelerometers to track activity levels (Hussey et al. 2015, Jewell 2022). Foraging, localised movements and routines can be recorded by acoustic telemetry, yet data collection is limited to the animal passing within range of the receiver, or hydrophone, which has a restricted detection range, dependent on environmental and physical conditions, this can range from 100-1000 m (Voegeli et al. 2001, Hussey et al. 2015). Intensity and frequency of ambient noise can further limit detection range (Hussey et al. 2015).

1.2 Study species

1.2.1 White sharks

The white shark is one of the largest enigmatic ocean carnivores and member of the order Lamniformes and family Lamnidae (Compagno 2001). The species was first described by Carl Linneaus in 1758 as *Squalus carcharhinus*. During the nineteenth century, eleven different synonyms of the species were published; including a colour illustrated South African holotype by Andrew Smith (1850), from the Western Cape waters, *Carcharodon capensis* (Figure 1.1). Many regional synonyms were described in the early 20th century, including an Australian variant, *C. albimors*, but most of these accounts lacked characterisation; thus, the genus and species name *C. carcharias* (Linneaus) was officially allocated by the International Commission on Zoological Nomenclature in 1965 (Compagno 1999).

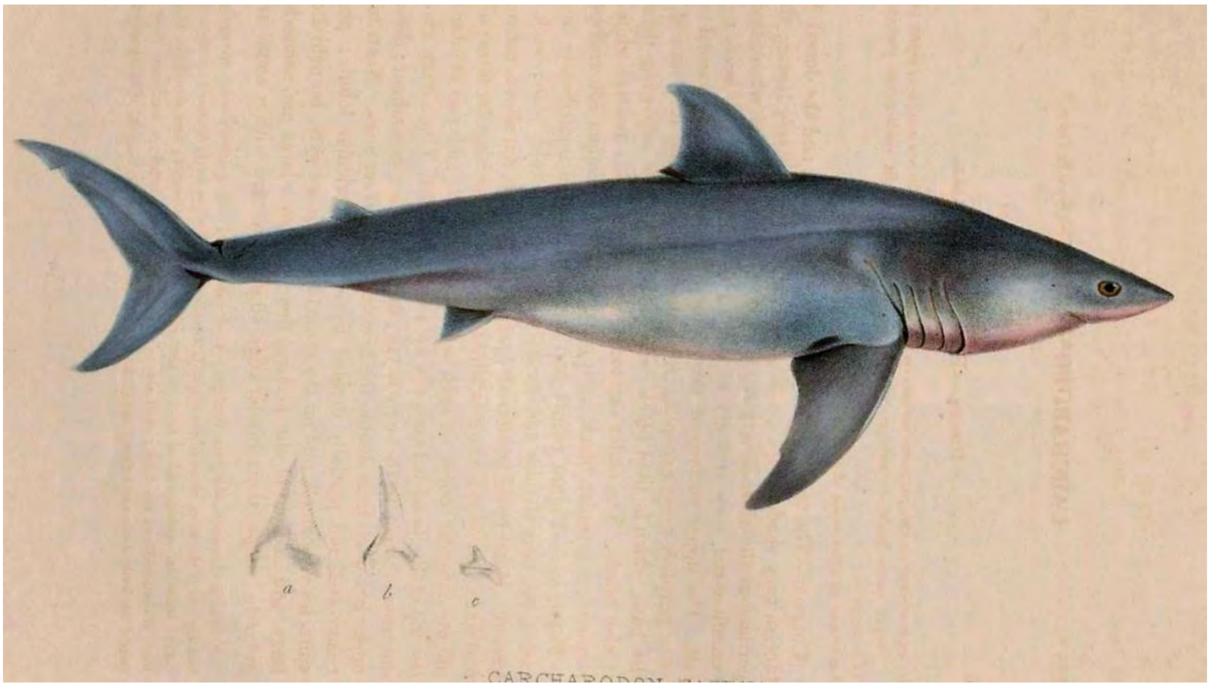

Figure 1.1: The original illustration of *C. capensis* (*C. carcharias* holotype) by Andrew Smith, 1849. This specimen is housed at the Natural History Museum of London (Compagno 1999).

White sharks are characterised by their heavy torpedo-shaped body, large eyes, flat, jagged teeth, grey-black countershading, muscular caudal peduncle with pronounced keels, conical-shaped snout, and five long gill slits (Compagno 2001, Ebert and Fowler 2014). The species is a regional endotherm, capable of maintaining an internal body temperature up to 17°C above ambient seawater (Gennari 2015). White sharks are considered key apex predators with a highly important ecological role, throughout the world's oceans, as a top-down mediator of ecosystem balance, as well as various additional ecosystem functions (Huveneers et al. 2018).

1.2.2 Distribution and habitat

White sharks have a cosmopolitan distribution range, inhabiting temperate and tropical seas from shallow coastal regions to pelagic environments, diving to maximum depths of 1,200m (Bonfil et al. 2005; Francis et al. 2012). However the species likely exceeds the depth limits that satellite tags can record to thus the species true maximum dive limit is unknown. They exhibit periodic latitudinal (or longitudinal in southern Australia) movements, broadly occupying sea surface temperatures ranging from -1 °C to 30 °C during their coastal distribution (Bruce et al. 2006; Weng et al. 2007a; Francis et al. 2012; Dicken and Booth 2013; Domeier and Nasby-Lucas 2013, Curtis et al. 2014, Franks et al. 2022). Principal aggregation sites for the species are in North America and Canada (Domeier 2012, Skomal et al. 2017, Lowe et al. 2020, Franks et al. 2021), Mexico (Domeier 2012, Papastamatiou et al. 2022), Australia (Bruce et al. 2012, Huveneers et al. 2018a) New Zealand (Francis, Duffy and Lyon 2015) and southern Africa (Bonfil et al. 2005, Smale and Cliff 2012, Kock et al. 2022). Historical regions with more cryptic records of white shark presence include some parts of Asia (Chang et al. 2014, Christiansen et al. 2014), the Northeast Atlantic (Fergusson 1996), the

Mediterranean (Kabaskal et al. 2017, Boldrocchi et al. 2017) and the South East Pacific (Gubili et al. 2012)

1.2.3 Overview of white shark acoustic tagging studies

The first white shark tagged and tracked was by Francis Carey and his research team off the coast of the USA, in 1979. They adapted research gear consisting of animal-borne thermistors and acoustic transmitters and monitored the shark by a boat-based directional hydrophone previously used to track swordfish (Carey & Robinson 1981). The shark was monitored for three and a half days as it moved 190 km from the tagging location. As ultrasonic acoustic transmitters and receivers became more readily accessible, biotelemetry studies expanded rapidly on white sharks (Voegeli et al. 2001). A literature review revealed that to date, approximately 40 publications describe white sharks as the primary species and acoustic telemetry as the primary or secondary telemetry technique. These two techniques have been used together and separately in a variety of studies, such as; to determine coastal movements and residency times (i.e., Johnson & Kock 2006, Bruce & Bradford 2013, Kock et al. 2013, McAuley et al. 2017, Tanaka et al. 2021), activity areas (Goldman & Anderson 1999, Jewell et al. 2013, Winton et al. 2021), rates of movement (Strong et al. 1992, Johnson et al. 2009), predatory activity (Laroche et al. 2008, Jewell 2013, Jewell et al. 2014, Towner et al. 2016), population connectivity and structure (Chapple et al. 2016, Braccini et al. 2017a, Braccini et al. 2017b, Bowlby et al. 2022, Franks et al. 2022), bather safety (Winton et al. 2020, Spaet et al. 2021) the effect of cage-diving techniques on natural behaviours (Laroche et al. 2007, Huveneers et al. 2013, Towner et al. 2016) and movement relative to environmental parameters (Tanaka et al. 2021, Spaet et al. 2021). Collaborations between national, continental, and worldwide research groups have been developed to form 'Ocean Tracking Networks' (OTNs)

(Cooke et al. 2011) and have the potential to further applications of receivers by ecosystem-wide approaches to aid in identifying linkages between populations and aggregation sites. In South Africa, the national Acoustic Tracking Array Platform (ATAP) consists of over 250 receivers and currently monitors over 800 individual acoustic-tagged fish, of various species (Murray et al. 2022).

1.2.4 *Conservation status*

A recent review on large carnivore population recoveries revealed that less than 10% of global large carnivore populations are increasing, and only twelve species (3.3%) have exhibited any real improvement in extinction risk (Ingeman et al 2022). Marine mammals showed the lowest proportion of threatened species in the review, at 27%, whereas sharks and rays were at a significantly higher risk, ranking at 61% threatened. While almost half of all large carnivore species are categorised as Least Concern, only 17% of shark species occupy this lowest extinction risk category (Ingeman et al. 2022, Figure 1.2).

The first global assessment of chondrichthyans concluded that one-quarter (24%) of species were threatened (Dulvy et al 2014). Based on new information, the most recent update of this work currently puts this percentage up to 32.6%, this is an increase of 8.6% in only seven years, which is striking (Dulvy et al. 2021). When this threat percentage is applied to species that are Data Deficient, over one-third (37.5%) of chondrichthyans are estimated to be threatened. A large amount of this is due to overfishing, which is considered the biggest global threat, accounting for 63.7% of all threats. Three other threats for the remaining third are loss and degradation of habitat (31.2% of threatened species), climate change (10.2%), and pollution (6.9%) (Dulvy et al. 2021).

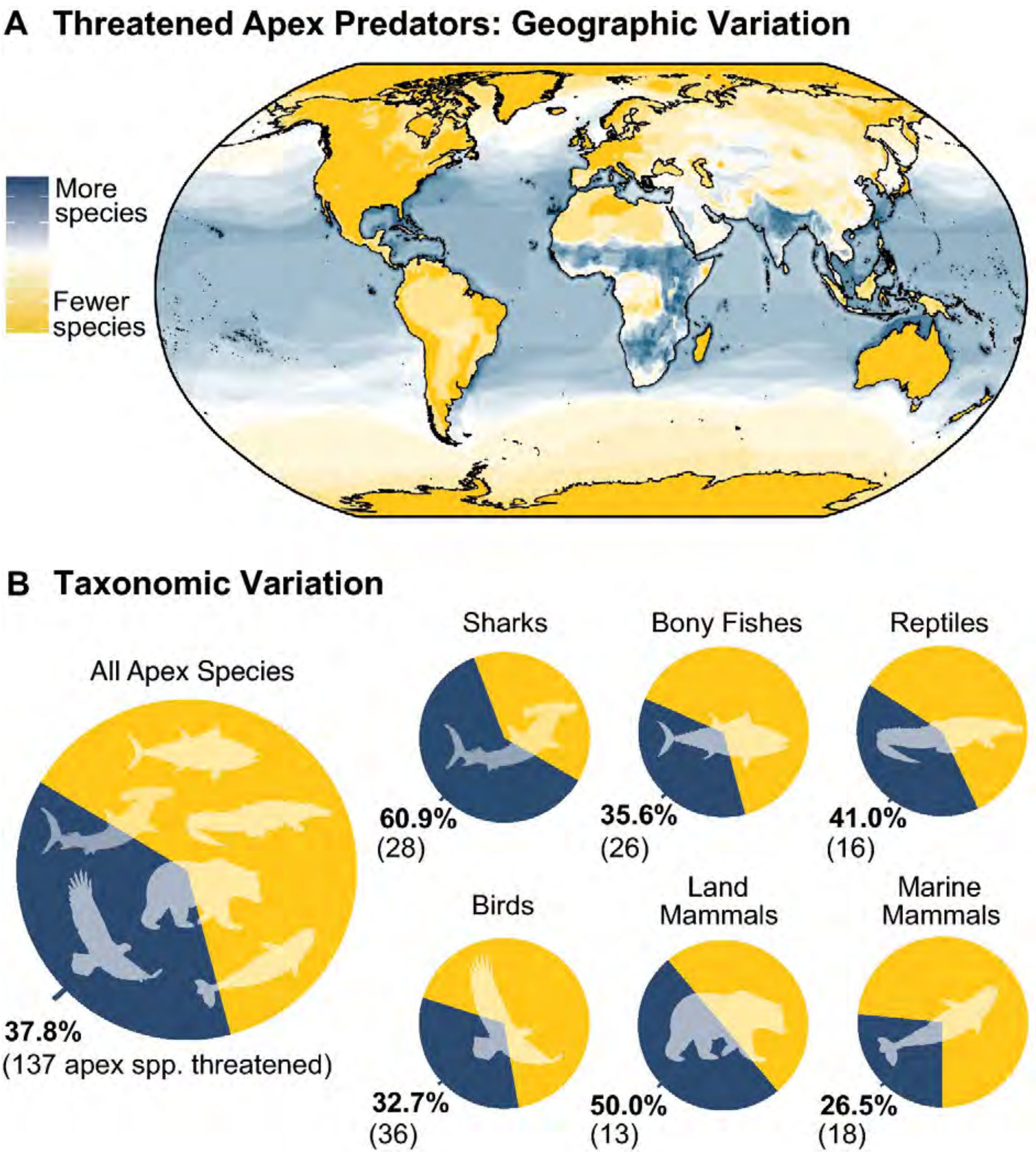

Figure 1.2: Variation in current large carnivore extinction risk (status). Large carnivores are divided taxonomically into sharks and rays, bony fishes, reptiles and amphibians, birds, terrestrial mammals, and marine mammals. Bold values are the percent threatened in each taxon; values in parentheses are the number of threatened species (From Ingelman et al. 2022).

The wide disparity in status between marine megafauna groups, mammals and sharks, corroborates evidence that while the reduction of industrial exploitation of marine mammals has initiated successful recoveries within this group, many shark species remain intensely and unsustainably exploited (Ingeman et al.2022).

White sharks have been given some of the highest levels of protection of any elasmobranch species (Curtis et al. 2014, Rigby et al. 2019). They have been listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), on the appendices of The United Nations Convention on Law of the Sea (UNCLOS), and the Convention for the Conservation of Migratory Species (CMS). The World Conservation Union (IUCN) currently lists the white shark globally as vulnerable (Rigby et al. 2019). The species has a circumglobal distribution, yet populations structures are complex and vary geographically.(Bruce and Bradford 2012; O'Leary et al. 2015). While in some regions populations are showing signs of recovery following decades of protection (Burgess et al. 2014; Curtis et al. 2014), others are not (Towner et al. 2013; Andreotti et al. 2016). The southern African population is a local metapopulation with low genetic diversity and needs directed conservation measures to avoid extinction (Gubili et al. 2012; O'Leary et al. 2015). White shark populations are inherently vulnerable to anthropogenic mortality due to their low fecundity and slow growth (Bruce and Bradford 2012; Hamady et al. 2014; Braccini et al. 2017; Bowlby and Gibson 2020). They are protected from all consumptive activities and have formal protective legislation in various countries, including Mozambique, South Africa and Namibia (Rigby et al. 2019, Kock et al. 2022).

In light of an accelerating extinction crisis, scientists should draw insights from successful conservation interventions to uncover promising strategies for reversing broader declines (Ingeman et al. 2022). Recovery is associated with species legislation enacted at national and international levels and with the management of direct exploitation (Ingeman et al. 2022). While management plans are often put into place on paper in South Africa, physically enforcing such laws is often the problem, with government resources constantly lacking (NPOA 2 report). Furthermore, the KwaZulu-Natal Sharks Board removes between 20-30 white sharks a year in South Africa; it is the largest targeted source of mortality to the species in the region (Kock et al. 2022). While this lethal gillnet and drumline program has been in operation since the 1960s to provide bather safety, alternative options such as electrical cables are being trialed. However, these alternative options should be prioritised in light of its life history traits that include a low fecundity and late maturity. Therefore, killing >10 white sharks annually may have the potential to cause population declines over time (Bowlby et al. 2022).

1.3 Study site

1.3.1 Overview of South African Oceanography

Off the southern coast of Africa, the Indian and Atlantic oceans mix, creating habitat for a unique and diverse array of marine fauna, ranging from cold temperate to sub-tropical marine species. From Cape Agulhas eastwards, coastal habitats become less characterised by kelp forest reefs (Pfaff et al. 2019). The warm Agulhas current flows down the east coast and folds back on itself roughly midway along the south-central coast. Seasonality dictates the wind direction and water temperatures are driven by wind direction. South-easterly winds are typically strongest during the month of January and February (austral summer) with monthly mean speeds of 2 to 3 $m.sec^{-1}$ and daily averages showing a high frequency of wind speeds in the 8-10 $m.sec^{-1}$ range (Towner et al. 2012b). The strongest winds in winter occur in June and are associated with north-westerly winds with monthly averages in the 3 to 4 $m.sec^{-1}$ range and peak daily averages often greater than 10 $m.sec^{-1}$. April (September) is a transition month from north-westerly (south-easterly) winds to become more prominent and south-easterlies (north-westerlies) to weaken (Figure 1.3).

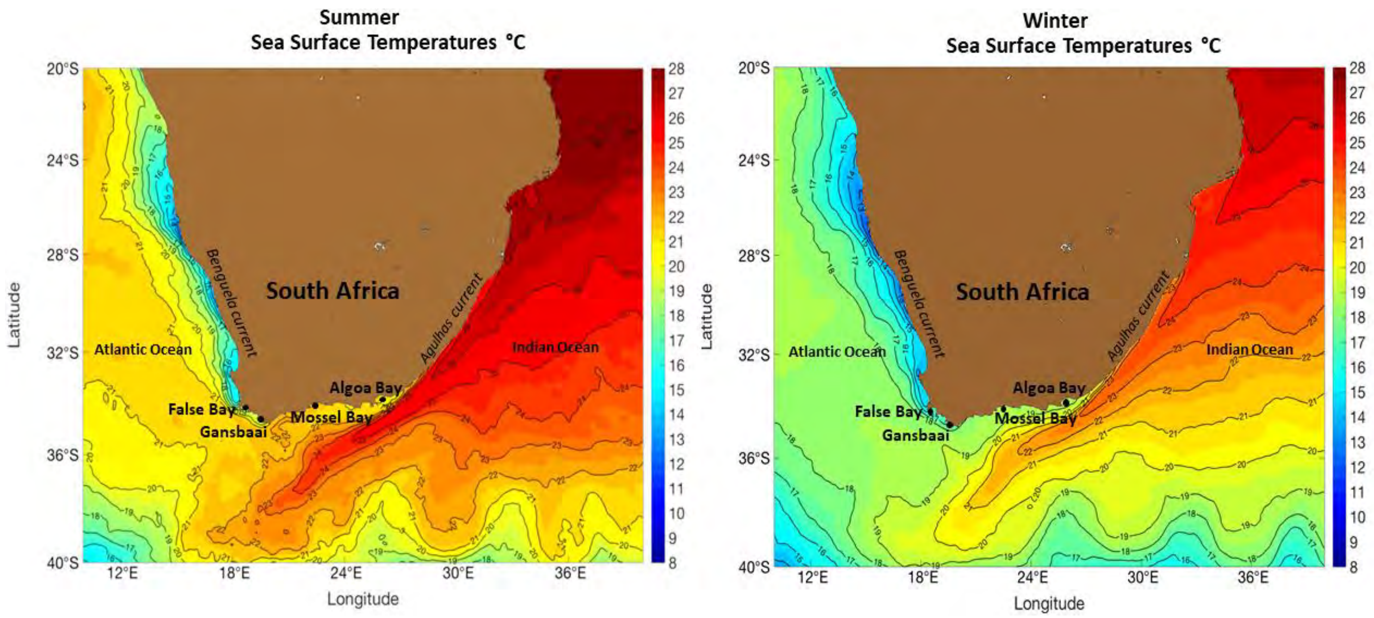

Figure 1.3: Maps of South Africa showing typical summer and winter oceanographic conditions (Data from Marine Copernicus).

Dubois and Rouault (2012) used two monthly SST products (MODIS and Pathfinder) to investigate the annual cycle and inter-annual variability of SST in South Africa. They showed that during summer (January-March), upwelling at Cape Hangklip leads to an intrusion of cold water as a result, a strong temperature gradient develops in Western Cape coastal bays, by contrast, when upwelling subsides during winter (June-August), SST tends to be homogeneous. Sea surface temperature in the Western Cape varies from about 13-22 °C during the year, while in the southern half, there is less amplitude, with SST varying from 14-20 °C. Variability is higher during summer than in winter. The inter-annual variability is associated with the variability in upwelling along the west coast from Cape Agulhas to Cape Columbine (Dufois & Rouault, 2012). Upwelling favorable south-easterly winds, which predominate during summer, perpetuate phytoplankton blooms through nutrient input to the photic surface layer (Grindley & Taylor, 1970; Largier et al., 1992).

Previous research on white sharks in South Africa has analysed the impact of environmental conditions on their numbers and has shown increased white shark abundance in both False Bay and Gansbaai in warmer water Winter conditions (>15°C) and positive El Nino Southern Oscillation (ENSO) phases (Weltz et al. 2013, Towner et al. 2013b).

1.3.2 Gansbaai and the Greater Dyer Island System

Gansbaai is a semi-closed embayment situated on the south coast of the Western Cape in South Africa. Dyer Island lies 4 km from the nearest shore within Gansbaai (Figure 1.4). Geyser Rock lies directly southwest of Dyer Island and contains a breeding colony of Cape fur seals *Arctocephalus pusillus pusillus* with an estimated total population of ~55,000 seals (Cape Nature unpubl. data). The two islands – Dyer Island and Geyser Rock – are separated by a shallow channel known as Shark Alley, which measures approximately 160 m at its widest point, with a maximum depth of 7 m. The Dyer Island system is surrounded by dense kelp forests (predominantly *Ecklonia maxima*) and rocky reefs, outcrops, and shallow reef pinnacles. Directly inshore of Dyer Island, an extensive reef system, Joubertsdam, runs parallel to a 4 km stretch of sandy beach. The reef is characterised by rocky patch reefs interspersed with gullies and patches of sandy bottom. Eight cage-diving operators are permitted to anchor around the reefs at Dyer Island and Joubertsdam (Towner et al. 2013). Several other rocky reefs and kelp forest structures exist within the bay.

Figure 1.4: Map of the study site Gansbaai, 200km East of Cape Town, in the Western Cape of South Africa. Dyer Island, the Cape Fur Seal colony of Geyser Rock, Shark Alley, and Joubertsdam are the designated Cage dive boat anchor sites and prime white shark aggregation sites within the region.

1.4 Objectives of thesis

This thesis aims to understand how white sharks use their coastal environments in South Africa and the impact of a novel biological driving factor on their movement. Two approaches were employed at different temporal and spatial scales, examining fine and large-scale movement, describing and analysing predation pressure and its direct impact on white shark movement. Information on interactions between killer whales and white sharks is considered sparse in South Africa therefore the research questions were:

1. How do white sharks hunt and use their habitats on a fine scale, within a key coastal aggregation site?
2. What are the impacts of killer whale predation and how do they hunt white sharks in coastal aggregation sites?
3. Are southern African white sharks showing displacement behaviour subsequent to predation pressure from killer whales, and could their predominantly western Cape epicenter of distribution be shifting east or offshore?

CHAPTER 2: FINE-SCALE BEHAVIOUR OF WHITE SHARKS IN SOUTH AFRICAS LARGEST CAGE DIVING SITE, GANSBAAI.

2.1 Introduction

Animals may use various movement strategies to locate prey, including systematic searching and different types of random walk (Papastamatiou et al. 2011; Sims et al. 2012). The type of strategy used will also depend on the hunting mode of the predator with two general modes: 'active search/patrolling' and 'sit and wait' (Huey & Pianka 1981; O'Brien, Browman & Evans 1990). 'Patrolling' or 'roving' behaviour is defined by a predator moving through its environment looking for prey (although the movement strategy may vary, e.g., random walks vs. directed); whereas 'sit and wait' or area-restricted searching behaviour (ARS, especially if the predator must move continuously) sees the forager waiting for prey to cross the boundary of its strike space, over long time periods (O'Brien et al. 1990; Alpern et al. 2011). Experimental work in terrestrial systems has suggested that predators' patrolling/roving or sit-and-wait hunting modes may cause trophic cascades that act in opposing fashion and on different trophic levels (Schmitz 2008). Although predator hunting mode may cause variations in predator-induced trophic cascades, it is rarely considered in studies of top-level predators (Heithaus et al. 2009; Martin & Hammerschlag 2012, Higginson & Ruxton 2015).

Predator movements are commonly found to differ between the time of day, sex, season, and in response to prey distribution. Predator movements will not only be concerned with finding prey but also relate to other needs, such as finding mates or optimal environmental conditions. Movement path structure will vary in time and space in response to the environment and as the goals of movement change (Papastamatiou et al. 2011; Langrock et al. 2012). There may also be considerable variability in individual movements within a population, potentially due to individual specialisation.

Individual specialisation in animal behaviour is increasingly recognised as prevalent in animal populations and may manifest itself in an animal's diet, patterns of movement, or other specific behaviours (Bolnick et al. 2003; Estes et al. 2003; Matich, Heithaus & Layman 2011). The presence and degree of individual specialisation can have large-scale implications from both an ecological and conservation standpoint and may even affect a population's stability (Bolnick et al. 2003). Individual specialisation may be driven by intra and inter-specific competition levels and/or be related to size, sex, habitat, and available prey (Matich et al. 2011; Nifong et al. 2015; Rosenblatt et al. 2015).

Generally, individual variability in movement is measured by comparing some aspect of the movement process to model predictions (e.g., correlated random walks) or the degree or even presence of cyclical behaviour (e.g., diel habitat shifts, Austin, Bowen & McMillan 2004; Papastamatiou et al. 2010, 2011; Matich & Heithaus 2015). Such an approach may miss movement processes at fine spatial scales, which is ultimately the scale at which foraging occurs. Furthermore, these studies identified intra-specific variability, not specifically if individuals prefer a particular movement strategy or routinely reuse the same strategy.

An analytical framework is required to detect fine-scale differences in movements between individuals while accounting for other factors such as size and sex. Movement data from marine predators also suffers from significant positional errors or being collected at irregular intervals, making it difficult to select suitable metrics.

However, some movement data can still be collected regularly with relatively low spatial errors (e.g., active tracking), making movement analysis easier. In these cases, hidden Markov models (HMMs) offer a robust and readily applicable set of analytical tools. In particular, HMMs can be applied to movement data to identify behavioural switches and how these are driven by environmental conditions (Patterson et al. 2009; Langrock et al. 2012). HMMs are time series models where an observation model (e.g., step lengths and turning angles between movement steps) is driven by an underlying hidden process model (e.g., ARS or transient behaviour, Patterson et al. 2009; Langrock et al. 2012). HMMs directly account for the serial dependence prevalent in electronic tagging data and allow for decoding latent behavioural states, or at least proxies thereof (Patterson et al. 2009). Often these states are assumed to be associated with foraging (ARS) and non-foraging (transient) behaviour, although designating foraging activity based purely on movement paths is problematic (e.g., Bestley et al. 2008). If foraging can be verified, ARS movements before foraging would be considered a 'sit-and-wait' strategy while patrolling and foraging would be a more active searching mechanism and considered 'patrolling or roving.'

White sharks are the world's largest carnivorous fish and are widely distributed in temperate and tropical waters. The species has received considerable telemetric focus, largely due to its charismatic profile, important ecological role, and conservation status. White sharks often show seasonal residency to pinniped pupping areas, as juvenile seals or sea lions may present a suitable prey source (Klimley et al. 1992; Klimley et al. 2001; Laroche et al. 2008). While associated with pinniped colonies, sharks are thought to patrol parallel to the shoreline or target specific locations where prey may be vulnerable (e.g., entry or haul-out sites, Goldman & Anderson 1999; Klimley et al. 2001; Martin, Rossmo & Hammerschlag 2009; Jewell et al. 2014). Pinnipeds are primarily ambushed at the surface, although previous studies have not quantified if the sharks were performing ARS or patrolling behaviour before the attack (e.g., Martin et al. 2005). There may be spatial segregation and differences in long-term movements or migration cycles between the sexes (Kock et al. 2013; Domeier & Nasby-Lucas 2013).

Further complicating the study of white shark behaviour, is that shark cage diving ecotourism occurs at several aggregation sites, where bait and/or chum is used to attract individuals to boats for tourist viewing. Available evidence suggests that cage diving operations will alter the short-term movements of white sharks but are unlikely to influence long-term migrations (Strong et al. 1992; Laroche et al. 2007; Huveneers et al. 2013; Gallagher et al. 2015, Huveneers et al. 2018). However, a statistical framework is required which can detect changes in behaviour while being able to account for the presence of ecotourism activities, shark size and sex,

Mixed HMMs were developed and fitted to fine-scale acoustic tracking data to identify the drivers of switching movement states (ARS or patrolling) in individual white sharks within a heterogenous seascape environment in South Africa. By definition, all white shark strikes of seals at the surface are ambush strikes, but individuals are faced with a choice regarding how to hunt; remain residential in a chosen location by performing ARS to wait for prey; or actively patrol to locate seals swimming on the surface (Klimley et al. 2001; Martin et al. 2009). While these terms are associated with foraging, they are broader in scope. They do not define the resource (e.g., shark movements may be non-foraging and associated with other functions such as digestion). By simultaneously recording predation attempts on seals at the surface by tracked sharks, movement processes could be specifically linked to a hunting mode. The study aims were to a) determine the role of shark size, sex, and individual preference on movement state dynamics and b) evaluate if sharks use both ARS and patrolling to catch prey and if individuals switch between them.

2.2 Materials and Methods

2.2.1 Active Tracking

Fourteen individual white sharks were attracted to a research vessel using a bait line and mixture of teleost-based chum and water (Jewell et al. 2014). Vemco (Now Innovasea, Halifax, Canada) V16 continuous acoustic transmitters (size 16 x 54 mm, frequency 50-85 kHz) with umbrella dart heads Domeier et al. 2005) were inserted externally at the base of the shark's dorsal fin, using a modified tagging pole. Animal ethics clearance was obtained from the Department of Environmental Affairs (Figure 2.1, permit number RES2011/54).

Figure 2.1: Deploying a continuous acoustic tag at the base of the dorsal fin of a white shark in Gansbaai.

Figure 2.2: Active tracking and data collection of an acoustic tagged white shark inshore in Gansbaai, with a Vemco (Now Innovasea) VR100 receiver and directional hydrophone. Along with receiver logs, manual GPS positions were recorded every five minutes. Inset left: an acoustic tag, attached to the base of a white sharks dorsal fin. Initially tags were anti-foul painted red, then white (photo credit: Harry Stone).

Shark size was estimated (total length, TL cm) as the shark swam past measured sections of the vessel. Active tracking commenced immediately after tagging, using a Vemco VR100 receiver and hydrophone mounted to the side of the tracking vessel (Figure 2.2). To avoid impeding shark movements, a distance of 20 m minimum was maintained from the animal, determined by tag detections of approximately 80 dB (Johnson et al. 2009; Jewell et al. 2014, Figure 2.3).

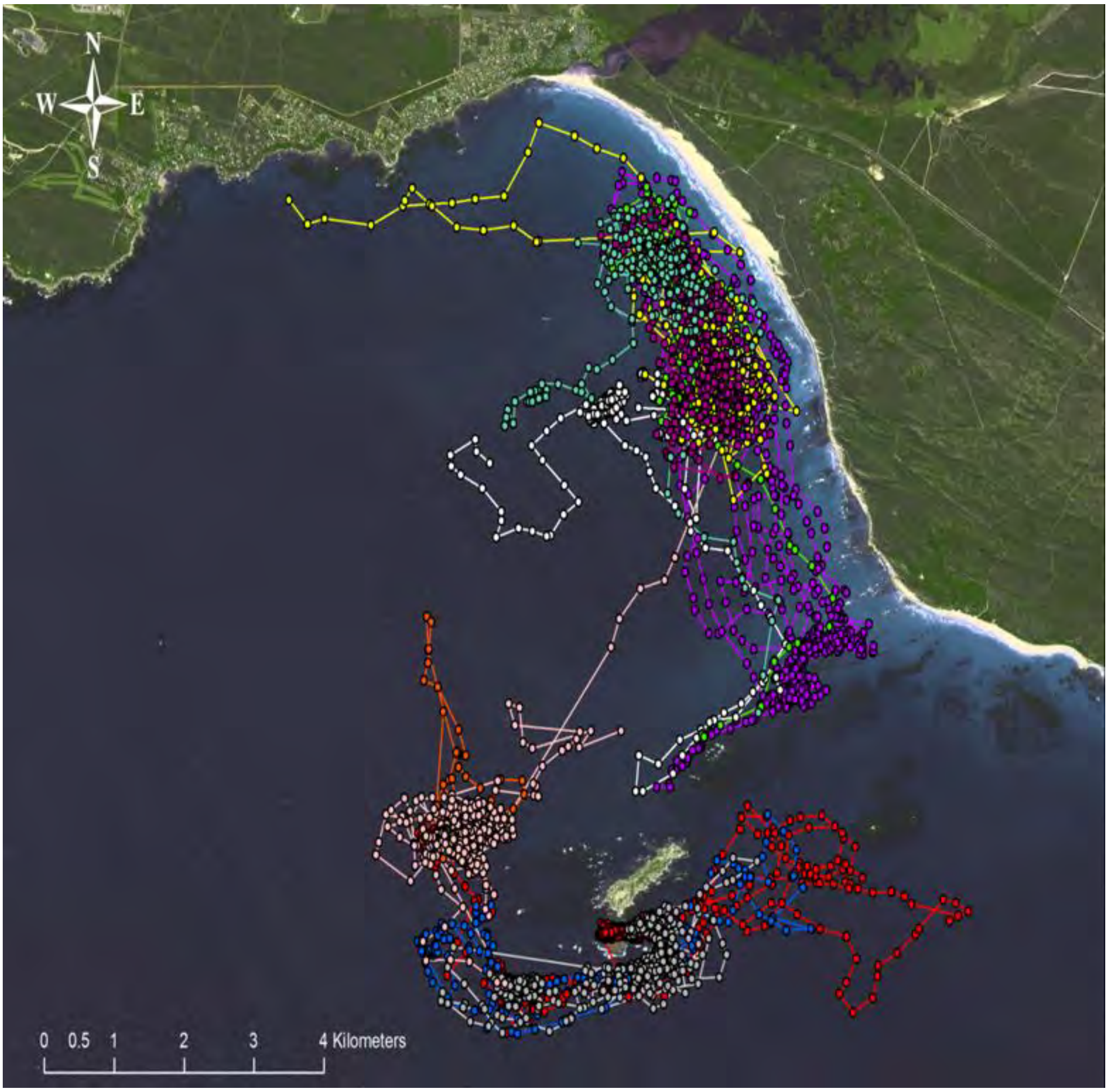

Figure 2.3: Colour differentiated active tracks of 14 white sharks in Gansbaai showing habitat use of both the Dyer Island system and inshore reef system (Image: Oliver Jewell).

Geographic locations were recorded every 5 minutes and surface predation events or attempts were noted during the track. Externally applied transmitters were bright red making it easy to visually recognise the tracked individual when it was attacking a pinniped. Due to frequent changes in weather, tracking was broken up into multiple smaller segments. Tracking at night was particularly difficult so most data were from daylight hours. When tracks were cut short due to weather or nightfall, tracking would resume the next day or at the start of the next possible weather window. Sharks were located by conducting transect searchers with the VEMCO omni directional hydrophone and VR100, deploying it from the vessel every 500m from the last GPS position the shark was in.

2.2.2 Mixed Effects Hidden Markov Models

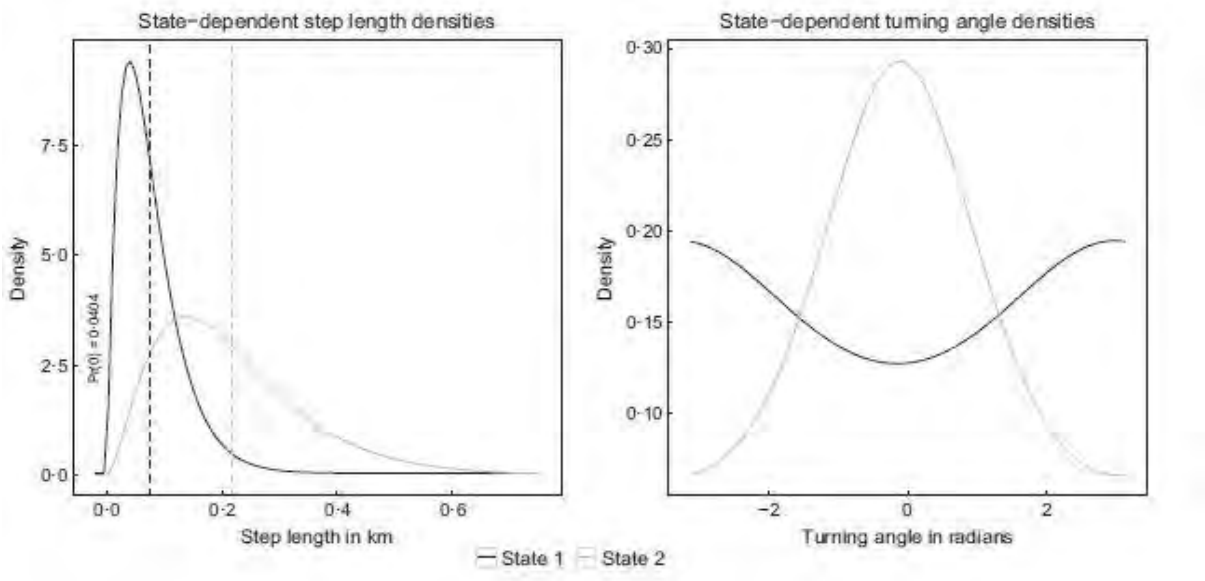

Figure 2.4: State-dependent conditional densities of step length and turning angles for tracked white sharks. For the state 1 step length density, Pr (0) corresponds to the point mass at zero of the zero-inflated gamma distribution. The dashed lines correspond to the mean of the step length distributions.

Two measures of movement were considered from the white shark tracks: step length (distance shark moved between 5 minute sampling intervals) and turning angles between movement steps in successive sampling intervals. A 2-state HMM was developed to analyse the 76 observed bivariate time series of step lengths and turning angles. These did not represent 76 individuals, but rather multiple tracking segments of the 14 individuals tagged. Each time series was assumed to behave according to a (multi-state) correlated random walk, with turning angles and step lengths generated by (state-dependent) von Mises and gamma distributions, respectively. For each track, it was assumed that an underlying, non-observable Markov chain determines the time-varying (behavioural) states. Each state was associated with a distinct set of parameters for both the von Mises turning angle distribution and the gamma step length distribution. State 1 Area Restricted Searching (ARS) behaviour consisted of relatively small step lengths with frequent turnings, while state 2 patrolling behaviour consisted of longer movement steps and fewer turnings (Figure. 2.4).

A point mass was included on zero in the step length distribution in state 1 to accommodate the observed zero step lengths (cf. McKellar et al. 2015; here ~2% of the data points). White sharks necessarily never stop moving so a zero-step length was an artefact of the sampling process, corresponding to sharks moving distances smaller than error measurements of tracking (20 m).

For each track k, $k = 1, \dots, 76$ the Markov chain generating the state sequence was assumed to be non-homogeneous, with time-dependent transition probability matrix given by

$$\mathbf{\Gamma}^k(t) = \begin{pmatrix} \gamma_{11}^k(t) & \gamma_{12}^k(t) \\ \gamma_{21}^k(t) & \gamma_{22}^k(t) \end{pmatrix}$$

where $\gamma_{ij}^k(t)$ is the conditional probability of the shark being in state *j* in the time interval (*t*, *t*+1), given it is in state *i* during the interval (*t*-1, *t*). For a single bivariate time series of step lengths and turning angles, observed for an individual track k, the likelihood of such a basic model was calculated in the standard way, i.e.

$$L_k = \boldsymbol{\delta}^k \mathbf{P}(\boldsymbol{z}_{1k}) \left(\prod_{t=2}^{n_k} \mathbf{\Gamma}^k(t) \mathbf{P}(\boldsymbol{z}_{tk}) \right) \mathbf{1}, \qquad (1)$$

where n_k is the number of data points for track k, the row vector $\boldsymbol{\delta}^k$ is the Markov chain initial state distribution, $\mathbf{1}$=$(1,1)^t$ and

$$\mathbf{P}(z_{tk}) = \begin{pmatrix} f_1(\boldsymbol{z}_{tk}) & 0 \\ 0 & f_2(\boldsymbol{z}_{tk}) \end{pmatrix},$$

with $f_i(\boldsymbol{z}_{tk})$ denoting the conditional density of the observation $\boldsymbol{z}_{tk}$, made at time t, given that the current behavioural state is i. The conditional density was simply the product of the state-dependent densities of the von Mises and the gamma/zero-inflated gamma distribution, respectively. Thus, it was assumed that step lengths and turning angles were conditionally independent, given the states. The above matrix product expression for the likelihood was a consequence of applying a recursive scheme called the forward algorithm; a powerful HMM tool and one of the main reasons for the popularity of these models (Zucchini & MacDonald 2009). Even for fairly large n_k, the evaluation of the likelihood usually requires only a fraction of a second, rendering parameter estimation via numerical maximum likelihood feasible in most cases.

The state transition probabilities were allowed to be functions of up to three covariates: presence/absence of chum, shark total length (in meters) and time of day (hours). More specifically, an indicator variable was used x_{1kt} to denote the presence/absence of chum at occasion t of track k, a variable x_{2k} to denote the total length (m) of the shark associated with track k, and two trigonometric functions with period 24 hours, $\sin(2\pi t/288)$ and $\cos(2\pi t/288)$, to account for the diel pattern. As modelled data were collected at regular time intervals, with observations every five minutes, the 24-hour periodicity was represented by 288 time points.

To account for heterogeneity across tracks caused by individuals being observed in different environmental and general behavioural contexts, random effects were additionally incorporated in the state transition probabilities. The full model is as follows:

$$\text{logit}\left(\gamma_{ii}^{k}(t)\right) = \epsilon_{i,k} + \beta_{1,i}x_{1kt} + \beta_{2,i}x_{2k} + \beta_{3,i}\sin\left(\frac{2\pi t}{288}\right) + \beta_{4,i}\cos\left(\frac{2\pi t}{288}\right) \qquad (2)$$

for i =1,2 and k =1,2,…,76. Here $\boldsymbol{\epsilon_k} = \left(\epsilon_{1,k}, \epsilon_{2,k}\right)$ are bivariate random variables, with one realization for each shark track (track lengths varied from 2-9 h). Such random effects are often assumed to be Gaussian. However, such an assumption was restrictive, the resulting models can be difficult to interpret, and computational problems arise in the estimation because each continuous-valued random effect adds an integral to the likelihood (cf. Altman 2007). Therefore, a discrete random effects model was implemented within the HMM (Maruotti & Rydén 2009). It was assumed that $\boldsymbol{\epsilon_k} = \left(u_{m,1}, u_{m,2}\right)$ with probability π_m^k for $m = 1, \dots, M$, with $\sum_{m=1}^{M} \pi_m^k$=1. Each possible outcome of the bivariate random effects distribution and associated transition probability matrix corresponds to one particular movement pattern exhibited during a track. The probabilities π_m^k, also referred to as the mixture proportions, denote the expected proportion of tracks that correspond to the m-th movement pattern. To assess how the covariates affected the state-switching dynamics of the M random effects groups, the stationary distribution was computed at each time t for given values of the covariates, as described by Patterson et al. (2009). In this manner, the marginal probability of each state was obtained throughout the day for the M groups under different values of the random effects and covariates.

To examine differences in observed movement patterns by sexes, mixture proportions were allowed to depend on sex in the following manner,

$$\text{logit}(\pi_m^k) = \alpha_m + \eta_k x_{sk}, \qquad (3)$$

for $m = 1, \dots, M$, where $x_{sk} = 1$ if the shark associated with track k was male, and $x_{sk} = 0$ for female. In other words, it was assumed that some of the M possible state-switching dynamics may be exhibited more often by females than males, and vice versa. The state transition probabilities were also considered as a function of sex but it was not selected for inclusion by the Akaike Information Criterion (AIC). The value of M, giving the number of possible values of $\boldsymbol{\epsilon_k}$, was chosen based on the AIC. Assuming independence of the individual tracks, the log-likelihood of the model has the following form:

$$l = \log L = \sum_{k=1}^{K} \log\left(\sum_{m=1}^{M} L_{k,m}\, \pi_m^k\right),$$

where $L_{k,m}$ is calculated exactly as in Eq. (1), but with the values $u_{m,1}$ and $u_{m,2}$ plugged in for $\epsilon_{1,k}$ and $\epsilon_{2,k}$, respectively, in the state transition probabilities, as defined by Eq. (2). That is, $L_{k,m}$ is the likelihood for track k assuming that it was generated by the m-th of M possible state-switching processes, corresponding to the different values for the discrete random effects.

Further, values of $L_{k,m}$ and π_m^k can be used to classify each track into one of the M random effects groups. Using Bayes' theorem, the probabilities p_m^k of the m were computed with the state-switching process having given rise to each track k, in the following manner:

$$p_m^k = \Pr\left(\boldsymbol{\epsilon}_k = \left(u_{m,1}, u_{m,2}\right) \middle| z_{1k}, \dots, z_{n_k k}\right) = \frac{L_{k,m}\, \pi_m^k}{\sum_{m=1}^{M} L_{k,m}\, \pi_m^k}$$

For each track k, classification was conducted by selecting the value of m that provides the maximal probability among $\{p_1^k, \dots, p_M^k\}$.

The model formulation allowed for a numerical optimization of the likelihood, i.e. a simultaneous estimation of all model parameters via maximum likelihood, which was conducted within R (R Core Team 2014). For each model, several sets of initial values were considered in the numerical maximization to ensure the global maxima of the respective likelihoods. A forward selection approach was implemented and covariates included according to the AIC of the corresponding models. Fixed effects were assumed for the covariates across the M values of the random effects. All plots were generated using the *ggplot2* and *ggmap* packages in R.

2.3 Results

2.3.1 Tracking Criteria

Between September 2010 and April 2014, 14 individual white sharks, 5 males and 9 females, were tracked for a total of 468 hours (Table 2.1). Individuals ranged in size from 290-450cm TL and were tracked on multiple days over periods of 2-9 h for a total of 76 tracking bouts.

Males and females differed in their habitat use, with females using habitat closer to the bay in addition to Dyer Island and Geyser Rock, while males spent more time directly off Dyer Island (Figure 2.5). Model results showed clear geographic patterns of sharks being in state 1 (Area Restricted Searching (ARS)) in certain habitats (Figure 2.4). These habitats include the channel between Dyer Island and Geyser Rock, the edge of the kelp forest NW of Geyser Rock, and areas adjacent to the beach where fish abundance is high. However, overlaying location of chumming by dive boats identified clear overlap between the presence of chum and sharks being in state 1 (Figure 2.5). While tracking, surface predation attempts on seals were observed 9 times, five of which were for an individual in state 1, and four for individuals in state 2.

Table 2.1: Tracking criteria from 14 white sharks tagged and tracked at Dyer Island and Joubertsdam in Gansbaai, from 03 September 2010 until 11 April 2014. Shark sex was confirmed from both surface and underwater photographs showing presence/absence of claspers.

Shark.ID	Sex	TL (cm)	Start Date	End Date	Tracking Segments	Tracking Hours	Mean (+/- SD) in Hours
WSF1	F	420	2010/09/03	2010/10/17	12	60.75	5.06 +/- 2.02
WSF2	F	400	2010/09/05	2010/09/29	6	25.08	4.19 +/- 2.36
WFS3	F	350	2010/11/22	2010/12/13	7	33.83	4.85 +/- 2.27
WFS4	F	290	2022/01/26	2011/03/03	11	55.00	4.91 +/- 2.16
WSM1	M	420	2011/04/11	2011/05/12	9	75.20	8.37 +/- 2.84
WSM2	M	350	2011/05/15	2011/05/12	3	18.50	6.17 +/- 0.12
WSF5	F	350	2011/07/11	2011/07/20	8	32.50	4.06 +/- 2.24
WSM3	M	300	2011/11/15	2011/11/16	2	13.00	6.50 +/- 4.50
WSM4	M	450	2012/02/16	2012/03/12	7	57.05	6.44 +/- 2.17
WSF6	F	340	2012/09/07	2012/10/12	7	27.50	3.93 +/- 1.81
WSF7	F	440	2012/11/03	2012/11/19	5	20.00	4.00 +/- 0.95
WSM5	M	430	2013/05/12	2013/06/03	9	33.30	3.73 +/- 1.48
WSF8	F	430	2013/10/09	2013/10/10	2	7.00	3.50 +/- 1.10
WSF9	F	380	2014/04/11	2014/04/18	4	8.88	2.22 +/- 1.36
Total						**468.04**	

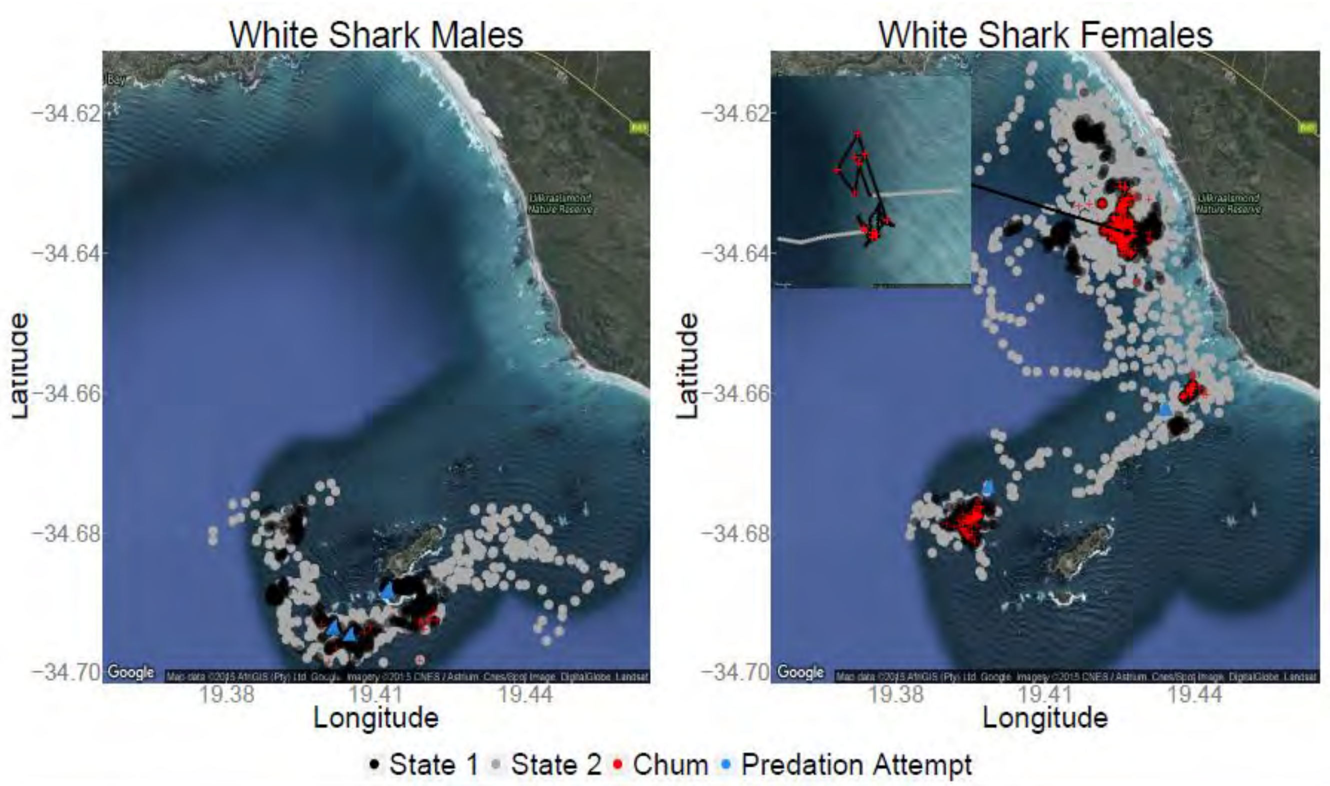

Figure 2.5: Active tracks of white sharks (n = 14, comprised of 5 males and 9 females) within Gansbaai, South Africa. Locations have been colour coded based on whether the HMM allocated the individual to state 1 or 2 behaviour at that time. The location of shark ecotourism operations (crosses) and observed predation attempts on seals by tracked sharks (dorsal fins) are also shown. Tracks have been split by sex.

2.3.2 Model output behavioural states

Using AIC, a model with $M = 3$ was selected with pairs of random effects, i.e. three different state-switching patterns (Figure 2.6). This mode was expanded to test the influence of covariates on the state-switching dynamics. The initial state distributions were estimated to account for the fact that immediately after tagging animals might have a higher (or lower) likelihood of occupying the patrolling state than would be implicitly assumed if the stationary/steady-state distribution had been used. By doing so, it is acknowledged that at least to some extent, the behaviour following the tagging event might differ from the average behaviour. According to the fitted model, if chum was present, there was an increase in probability of remaining in state 1 (ARS) when in state 1, and an increase in probability of switching from state 2 to state 1 when in state 2, which overall results in a substantial increase in state 1 occupancy. Regarding the diel pattern, only the results for the time period from about 7:00 to 19:00 were meaningful outside of these hours there were not enough individual tracks and observations to infer the state-switching behaviour. The results indicate that, for each of the three random effects groups, the marginal probability of individuals occupying state 1 was highest during the early morning and decreases throughout the day, reaching a minimum at about 18:00-19:00. In contrast, the marginal probability of individuals occupying state 2 (patrolling) was highest in the evening.

The three random effects groups accounted for the heterogeneity in tracks observed, in part due to sample size and duration of the tracks. In particular, the estimated random effects groups presented here reflected that of the observed behaviour and state-switching patterns of the data used for the analysis. On some occasions, sharks were only observed in state 1 or state 2 throughout the track (i.e. no switching), although most were observed to occupy both states with different degrees of state-switching and dwell time in each state. As such, the random effects groups account for the possibility that shorter or longer lengths could exhibit different state-switching patterns and any biases in covariate effect that could be attributed to the pooling of tracks of varying durations. In the absence of chum, the first random effects group (RE1) is characterized by a higher probability of inhabiting state 2 than state 1 across all times of day (i.e. corresponding tracks comprise a substantial amount of patrolling-type movement, Figure. 3). Random effects group 2 (RE2) represents the other extreme, where the marginal probability of inhabiting state 1 is higher than state 2 throughout most of the day (i.e. corresponding tracks involve mostly ARS behaviour). Random effects group 3 (RE3) lies in-between these extremes, with a lower degree of state-switching through most of the day, higher probability of state 1 through the morning, and higher probability of state 2 in the evening (Figure 2.6). A period of time corresponding to a higher marginal probability of state 1 than state 2 (or vice versa) does not indicate that the tracks in that period will only correspond to state 1, but more generally reflects a higher occurrence of state 1 behaviour. Tracks assigned to RE1 or RE2 may contain multiple state switches, while tracks assigned to RE3 switched states sparingly, if at all. In the presence of chum, the relative roles of the three random effects groups remain the same, but the probabilities of being in state 1 are generally much higher (Figure 2.6).

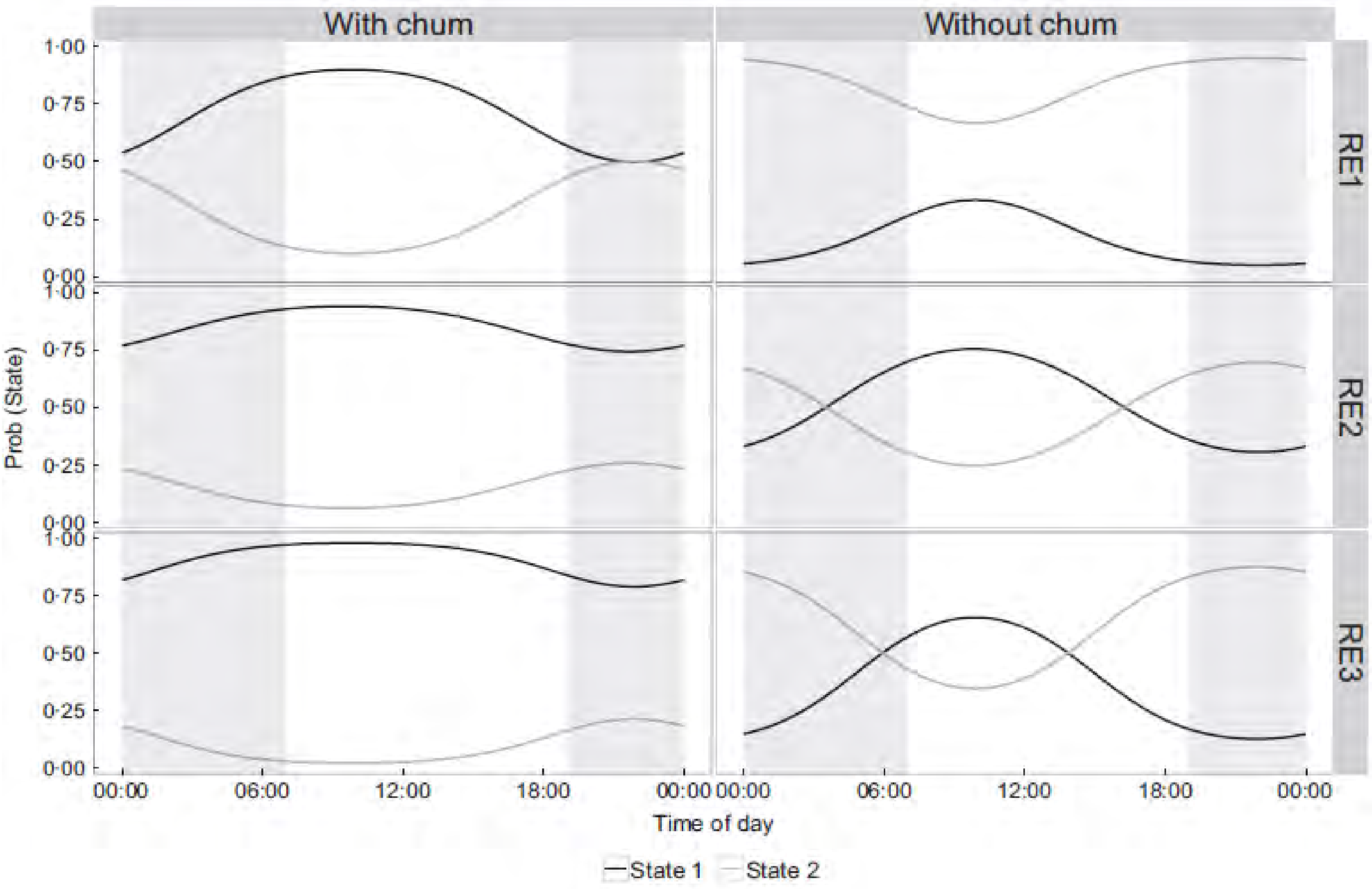

Figure 2.6: Probability of being in state 1 or state 2 throughout the day for each random effects group given values with or without the presence of chum.

2.3.3Random Effects

The mixture proportions for the random effects groups for females were 0.67 (RE1), 0.11 (RE2), and 0.22 (RE3), and for males 0.17 (RE1), 0.18 (RE2), and 0.65 (RE3). The large difference in mixture proportions between sexes for RE1 indicated that females generally spent more time in state 2 than males. The difference in mixture proportions for RE3 indicated that males remained more often in either of the two different movement strategies than females (Figure 2.7).

Table 2.2: Log-likelihood and AIC values obtained for the mixed hidden Markov models with different possible numbers (M) of random effect outcomes and forward selection of covariates and mixture proportions dependent on sex. The best-fit model is in bold.

M	Log Likelihood	AIC	ΔAIC
1 (no covariates)	-2301.671	-4625.342	14.13
2 (no covariates)	-2292.043	-4612.086	0.874
3 (no covariates)	**-2282.606**	**-4611.212**	**0**
4 (no covariates)	-2286.537	-4613.074	1.862
3 (chum)	-2275.309	-4588.618	4.144
3 (Chum, time of day)	-2270.302	-4586.604	2.130
3 (Chum, time of day, size)	-2268.885	-4587.770	3.296
3 (chum, time of day, π m ((sex))	-2267.237	-4584.474	0

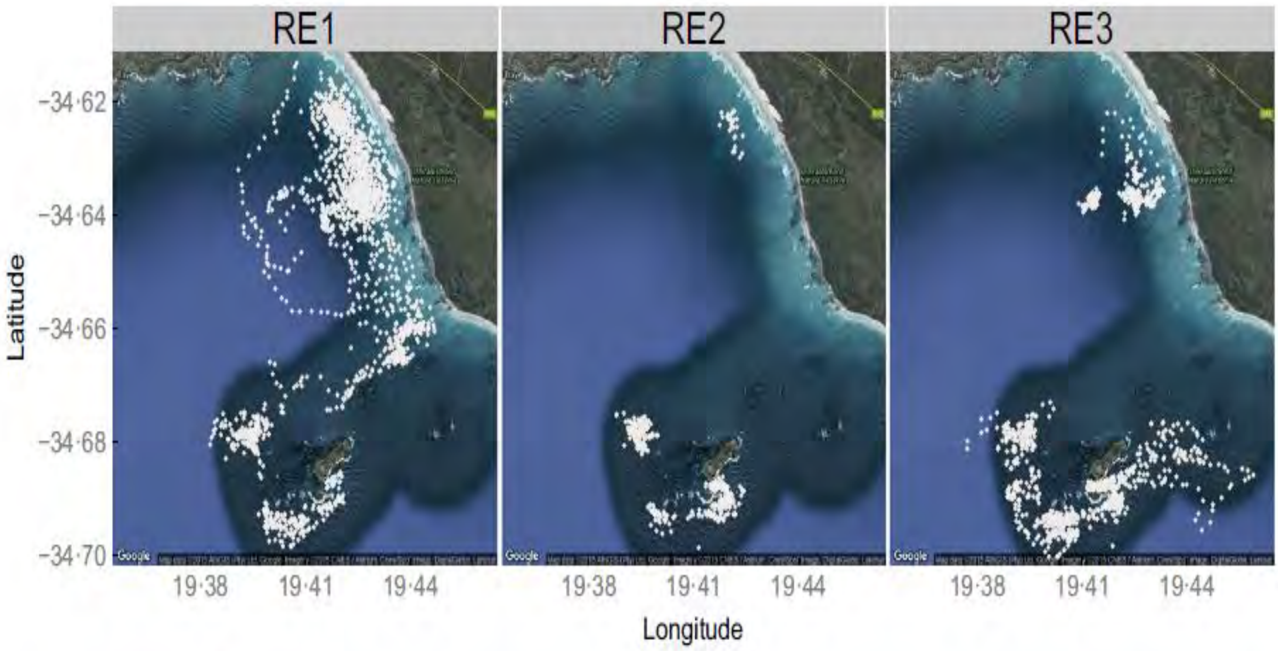

Figure 2.7: Spatial distribution of random effects groupings among white sharks tracked in Gansbaai.

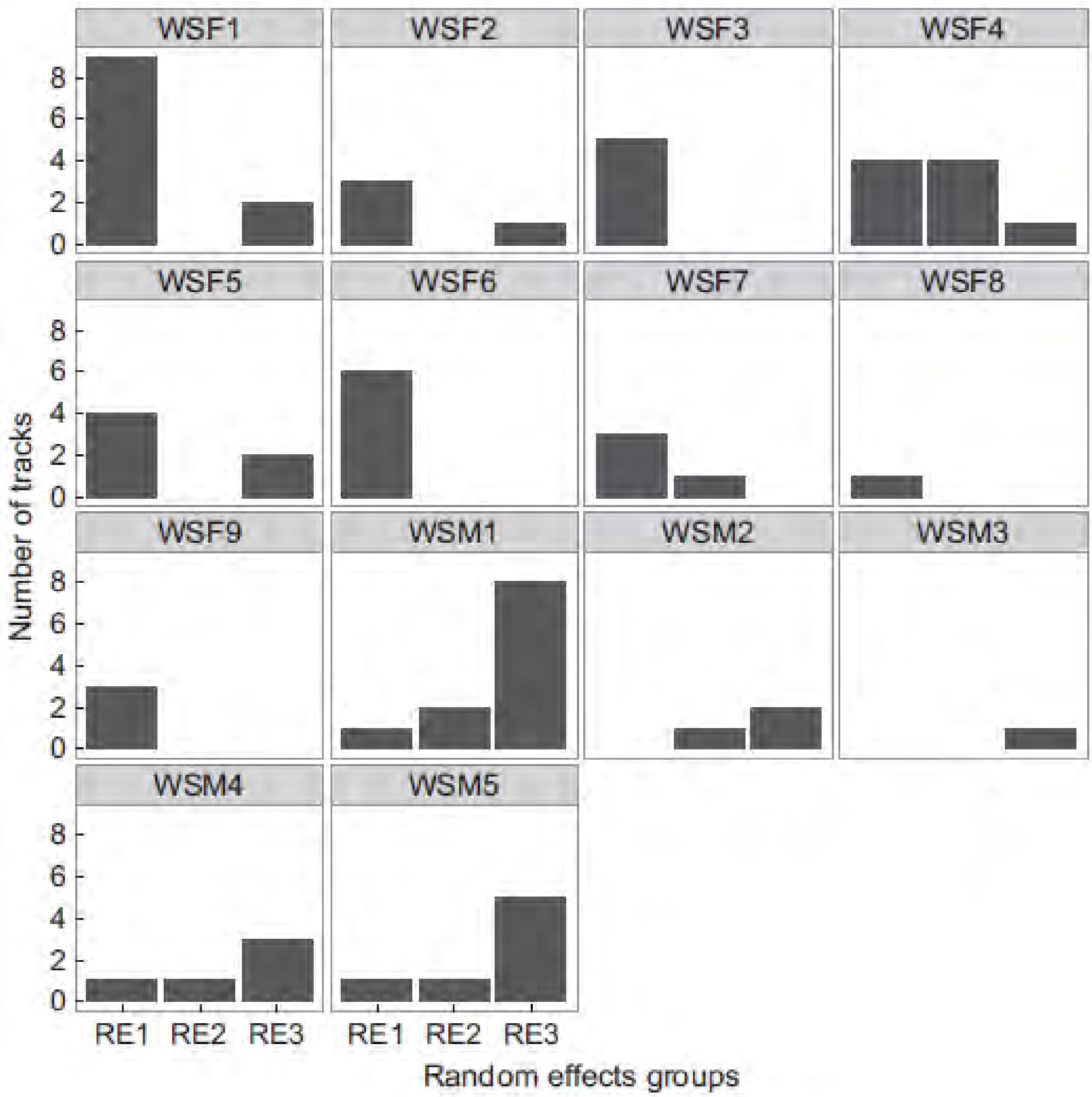

Figure 2.8: Bar charts showing which random effects group individual white sharks fit into and how often they were within these groups. WSF are females and WSM are males.

As mentioned previously, female and male sharks differed in their use of habitats. While incorporating an effect of habitat into the model would have been preferable, there were insufficient data in some habitats to make appropriate inferential statements. Although there were some differences in the geographic distribution of RE groupings, there were also considerable overlap making it unlikely that habitat was driving the results (Figure 2.7). There was no difference in track duration for the track segments classified as RE1, RE2 or RE3 (Kruskal-Wallis, χ^2=2.91, df=2, p=0.23). $L_{k,m}$ for $k = 1, \ldots, 76$ and $m = 1,2,3$ was computed along with the mixture proportions for female and male sharks, and used the values to assign each of the 76 tracks to a random effects group. Individual sharks were tracked on multiple days and could be assigned to different random effects groups on different days (Figure 2.8). Individuals appeared to consistently use the same RE grouping despite being tracked over multiple days throughout a month period. Furthermore, predations on seals were observed while sharks were in either of the groups. In other words, foraging could occur during any of the states or random effects groups as both 'ARS' and 'patrolling hunting modes' were observed. The decoded states confirm that females, overall, spent more time in state 2 than males (≈ 56% vs. 46%). In general, about 53% of observations were classified as state 2 and 47% classified as state 1. According to the decoded states, there were 109 state switches out of 2887 possible ones (≈ 3.78%) for females, and 50 state switches out of 1621 (≈3.08%) for males.

2.4 Discussion

The unique combination of being able to follow the same individuals over multiple different tracking periods, along with simultaneous observations of surface foraging attempts on marine mammals allowed the identification of fine-scale individual behaviour and two hunting modes that white sharks may use; area restricted search and patrolling. This analysis quantitatively identified changing behavioural states without user subjectivity within individual animals, and identified some of the factors that cause variability in movements. Furthermore, mixed HMMs allowed for quantification of changing behaviour in white sharks that would not have been apparent using traditional movement analysis methods. For example, movement analysis of a smaller number of acoustically tracked white sharks in Gansbaai identified core areas of habitat use but was not able to detect switching behaviours or differences in movements between the sexes (Jewell et al. 2014). Of course, movements by marine predators will also include a vertical component and swimming depths were not measured. Sharks can switch between diving strategies that include prey-specific strategies (e.g. swimming along the bottom to visually locate prey on the surface) or different forms of random walks (e.g. lévy vs. Brownian movements), based on the abundance and distribution of resources in the habitat (Sims et al. 2012). White sharks in Australia switch their diving behaviour, likely due to changes in potential prey density (Sims et al. 2012).

Movement states and transitions appeared to be a factor of chumming, time of day, sex, individual preferences, and potentially habitat. No effects of shark lengths on movement patterns were observed although there may well be spatial segregation between smaller and larger individuals (e.g. Jewell et al. 2013). Chumming by ecotourism dive vessels generated a high probability of sharks either remaining in or switching to ARS behaviour. This is not an unexpected result as white sharks tracked off Australia responded to chumming by spending more time at the surface and reducing their core use areas (Huveneers et al. 2013, Huveneers et al. 2018). There is mounting evidence that shark ecotourism can cause changes in behaviour over short time frames (hours), but are unlikely to have an impact at longer time scales based on previous studies and on-going satellite tracking (A. Towner unpublished data; Gallagher et al. 2015). However, less clear is how the change in behaviour may influence foraging success or even daily energy expenditure of white sharks, as sharks may spend more time turning and incur additional costs. Huveneers et al. (2018) deployed three axial acceleration loggers on ten white sharks at the Neptune Islands, South Australia. Over nine days the sharks increased their overall dynamic body acceleration OBDA (a good proxy for metabolism) by 61% when they were in the same areas as cage-dive vessels. Even though white sharks interact infrequently with such vessels (Kock and Johnson 2006, Laroche et al. 2007, Huveneers et al. 2018), the net impact on the sharks fitness needs to be better understood, especially if interactions with cage dive vessels increase with tourism demand.

Acknowledging the lack of night time observations in this study, sharks were also more likely to be performing ARS in the morning through early afternoon. At Seal Island, another South African seal rookery, highest rates of foraging success by sharks occur in the hours following dawn (e.g. Martin et al. 2005; Laroche et al. 2008). Seals enter and exit the island from predictable sites and the dawn peak is likely due to a combination of juvenile seals (the primary prey item) being present in the water during this period and optimal ambient light conditions for attacking at the surface (e.g. Laroche et al. 2008; Martin et al. 2009; Martin & Hammerschlag 2012). These conditions lead to white sharks using specific (and presumably optimal) locations to attack, although the behaviour of the sharks prior to surface strikes was not recorded (Martin et al. 2009). Foraging attempts and success by sharks on seals is considerably lower at Geyser Rock than at nearby Seal Island, likely due to the extra kelp refuge provided at Geyser Rock (Wcisel et al. 2015). The added protection provided by kelp causes seal departure locations at Geyser Rock to be more diffuse (i.e. no specific entry/exit point), but there will still be preferable general areas of departure (Wcisel et al. 2015). Hence, it may still be advantageous for sharks to display ARS movements within key areas during the morning period, but with less emphasis specifically at dawn. The uniquely shaped channel between the islands (Shark Alley) may also offer extended predation opportunities on seals throughout daylight hours, here both predation risk and shark habitat-use are notably high (Jewell et al. 2014; Wcisel et al. 2015). As in other areas, selection of ARS sites or predation hotspots are going to be related to a number of factors including prey behaviour, habitat and intra-specific competition (Martin et al. 2009).

By assigning tracks to random effects groups, two additional factors that influence white shark movement patterns were detected: sex and individual preference. Sexual segregation in sharks is well known, although less is known about differences in fine-scale behaviours (e.g. Heithaus et al. 2006). For example, female tiger sharks in a sub-tropical embayment show different microhabitat selection than males, even though they overlap in their overall spatial distribution (Heithaus et al. 2006). In South African bays, white sharks display sexual segregation seasonally, but will overlap at other times of the year (Kock et al. 2013). In Gansbaai there was also some spatial segregation between the sexes, with females more likely to use shoreline habitat (similar to False Bay, Kock et al. 2013), although individuals will also vary their behaviour within those habitats. This study shows subtle differences between the sexes with females more likely to perform ARS behaviour throughout the day. Such fine-scale differences in movements and even hunting tactics between the sexes are seen in other taxa. Male chub would perform sit-and-wait foraging more frequently than females (Katano 1996). Female mantids were more likely to switch hunting modes, especially in relation to prey density, while males tended to remain in one hunting mode (Inoue & Matsura 1983). However, it is difficult to separate the effects of sex and habitat on movement patterns. Were movements different because of the use of different habitats or specific to the sexes (e.g. if females used the same habitats would their movements be similar?) There was some overlap in habitat use so it is believed that the differences are driven by sex, but habitat cannot be ruled out as an important driver.

The repeated tracking of individuals over many days showed that patterns of movement will vary between individuals even within each sex. Individual sharks showed a preference for a particular pattern of movement (defined by a random effect group), which they repeatedly used over short time periods (over a month). Individuals may learn a variety of different movement tactics for encountering and catching prey and they may develop a preference for a particular tactic based on their experiences. Sharks were not tracked for long enough periods to determine if these behaviours are fixed thus cannot define them as true specialisation. Variability in short term strategies should be considered as these may translate to differences in foraging success and potentially even how the predator contributes to changes in prey behaviour (e.g. Heithaus et al. 2009). Additional tools (e.g. accelerometers) will be needed to determine the specific function and success (e.g. foraging rates) of different patterns of movement, and if individual preferences of movement remain fixed over long time periods.

As previously stated, movements by themselves cannot be directly correlated with hunting as there are going to be many times when sharks are not foraging. White sharks have shown residency to coastal areas that do not harbour pinnipeds suggesting times of foraging on other prey, or some other function of ARS behaviour (Johnson et al. 2009; Bruce & Bradford 2012). This research observed actual predation attempts by tracked sharks and these occurred for sharks in either of the three random effects groupings and either movement state (ARS or patrolling). Therefore, sharks will target seals by either remaining in one location (i.e. essentially sit-and-wait) or by actively patrolling for swimming seals. However, while it is highly likely that individuals will switch between these two hunting modes, an individual using both ARS and patrolling hunting modes was not observed. Of course, predations on pinnipeds were only observed at the surface even though other fishes (teleosts and sharks) are likely to also be an important component of the diet, so predation rates are going to be higher than recorded. Furthermore, there may have been sub surface foraging attempts that were missed.

Hunting mode switching is often explained by different levels of hunger, habitat characteristics, prey density and distribution (Inoue and Matsura 1983; Kobler et al. 2009; Michel & Adams 2009; Higginson & Ruxton 2015). Changes in prey density (seal numbers) and habitat complexity (kelp density) may explain seasonal changes in fine scale behaviour (although sample size was lacking to test for seasonal effects). Recent theoretical models predict that active searching becomes more advantageous as prey move slower and/or the energetic cost of predator movements decrease (Higginson & Ruxton 2015, Ross & Winterhalder 2015). Individuals switching hunting modes may be a strategy in itself, and match the predictions of the game theoretic Ambush Search strategy, where a predator alternates ambush with active searching which is predicted to increase the success of systematic searching (Alpern et al. 2011). These results suggest that individual variability in hunting mode, even within the sexes should also be considered in future predator-prey models. Ambush sites at Dyer Island may be more variable due to kelp refuge at the island, and it would be interesting to compare movement behaviours and/or hunting modes with Seal Island where prey (seal pups) use more predictable entry/exit locations (Martin et al. 2009; Wcisel et al. 2015; De Vos et al. 2015). Different hunting modes have also been identified in terrestrial predators although the function of the switching has not been examined (Williams et al. 2014, Higginson & Ruxton 2015). Pumas will use both active stalking and sit and ambush to catch prey with the energetic costs of these different strategies varying widely (Williams et al. 2014).

Different hunting modes may cause trophic cascades that operate in opposite directions and at different trophic levels (Schmitz 2008). While the importance of hunting mode in marine predators has been raised, it is generally assumed that all individuals will use the same mode (i.e. white sharks ambush all prey, Heithaus et al. 2009; Martin & Hammerschlag 2012). However, there are few studies examining the repercussions of top predators that may switch between hunting modes or where individuals prefer a particular strategy. White sharks in South Africa are likely to exert ecosystem level impacts. Pinnipeds at the rookeries almost certainly adjust aspects of their behaviour to account for the threat of predation from sharks (LaRoche et al. 2008; Wcisel et al. 2015; De Vos et al. 2015). How the threat of predation actually alters pinniped population dynamics are unclear, but the changes are likely to cascade through the food web as the mammals themselves are upper level predators (e.g. Johnson et al. 2006).

This work highlights that sharks have essentially two foraging strategies they can use and show individual preference for particular short-term movement strategies. If individuals have preferences for different strategies, and those strategies alter the behaviour of prey in different ways, then not all individuals in the white shark population will be equal in terms of their ecological roles even if they are similar sized. Furthermore, future predictive models will need to consider that top marine predators may still use two modes of hunting, especially those that consider how predators change prey behaviour (e.g. Frid et al. 2008, Heithaus et al. 2009, Higginson & Ruxton 2015). Theoretical models may be expanded to include the situations where sit-and-wait could be more energetically costly if the animals are having to make frequent turns to remain in one location (Wilson et al. 2013; Higginson & Ruxton 2015). While animals are often described as using one form of hunting mode or the other (often at the population level), increasing numbers of studies are showing that in many cases a continuum of modes is likely to exist in wild predators (Cooper 2005).

CHAPTER 3: KILLER WHALES DRIVE WHITE SHARK ABSENCE AT SOUTH AFRICAS LARGEST AGGREGATION SITE

3.1 Introduction

Top predators may substantially impact ecosystem structure and function by controlling prey populations directly through consumption or non-consumptive risk effects (Preisser et al. 2005; Suraci et al. 2016; Estes and Palmisano 1974; Steele et al. 2015). In both terrestrial and marine ecosystems, the threat of predation can influence the foraging behaviour of prey, altering prey habitat selection and potentially foraging and reproductive success (Stier et al. 2014; Schmitt et al. 2015; Catano et al. 2016). The risk of predation can even drive species emigration from specific habitats (Carpenter et al. 2010; Suraci et al. 2016, Jorgensen et al. 2019). Although fear effects appear to be widespread in aquatic ecosystems (Preisser et al. 2005; Heithaus et al. 2008), quantifying these effects for larger marine animals is challenging in the wild (Jorgensen et al. 2019, Hammerschlag et al. 2022).

White sharks and killer whales are both top-order predators, which often overlap across their cosmopolitan distribution. White sharks are one of the largest predatory fishes, reaching 602 cm total length (TL) and weighing ~2530 kg (Christiansen et al. 2014). They feed on a wide variety of prey, including marine mammals, elasmobranchs, teleosts, and invertebrates (Klimley and Anderson 1996; Hussey et al. 2012; de Vos et al. 2015a; French et al. 2017). White sharks have been shown to induce risk effects on other species like Cape fur seals (*Arctocephalus pusillus pusillus*), impacting their spatial and temporal behaviour around seal colonies while also inducing physiological stress (Pyle et al. 1996; de Vos et al. 2015a, b, Hammerschlag et al. 2022). White sharks are found in South Africa within several aggregation sites, including False bay, Gansbaai, Struisbaai, Mossel Bay, and Algoa Bay (Ferreira and

Ferreira, 1996). With the exception of Struisbaai, all aggregation sites can be characterised by the presence of Cape fur seal colonies, a common prey item for white sharks (Hussey et al. 2010).

Killer whales, the largest delphinid, are much larger than white sharks, reaching 9.0 m TL and weighing >6600 kg (Ford 2009). In the lower latitudes, killer whales are more opportunistic and generalised in their diets, either due to the unpredictability of any specific prey groups or limited research on their diet in this region (Alava and Merlen 2009; de Bruyn et al. 2012). In the higher latitudes, sympatric, non-interbreeding killer whale populations, called ecotypes, feed exclusively on certain prey groups (Bigg et al. 1987; Pitman and Ensor 2003; Baird et al. 2006; Morin et al. 2010; Ford 2019). While ecotypes usually classify the species due to diet and habitat type, morphotypes group the species by differing physical features such as size, fin, and tooth shape (de Bruyn et al. 2012). Some killer whales specialise in hunting sharks, and large elasmobranchs, including mako (*Isurus oxyrinchus*), hammerhead (*Sphyrna* spp.), thresher (*Alopia* spp.), and white sharks, may be prey (Visser et al. 2000; Visser 2005; Ford et al. 2011, Jorgensen et al. 2019). A rare flat-toothed morphotype was identified in South Africa, attaining a smaller length and specialising in a shark-based diet (Best et al. 2014). This morphotype, in several respects, resembles the offshore form in the North Pacific and the Type 1 form in the North Atlantic and does not seem to have been recorded previously from the southern Hemisphere (Best et al. 2014). Killer whales can influence prey abundance and behaviour and have caused shifts in species distributions (Estes and Palmisano 1974; Breed et al. 2017; Jorgensen et al. 2019). They also occasionally prey on white sharks, with long-lasting ecosystem effects (Pyle et al. 1999; Jorgensen et al. 2019). At the Southeast Farallon Islands, North America, brief and occasional visits by killer whales and at least one observed predation resulted in white sharks fleeing the immediate area (Jorgensen et al. 2019). During the time period when killer whales were present at the Farallon Islands, there was a dramatic reduction in pinniped predation rates by white sharks (Pyle et al. 1999; Jorgensen et al. 2019). Hence killer whales may induce rapid trophic cascades by causing changes in the behaviour and habitat use of another top predator, white sharks.

This Chapter documents a series of predations on white sharks by killer whales at Gansbaai, South Africa. This aggregation is a popular ecotourism destination for cage diving viewing operations. Necropsy, boat-based surveys, and telemetry data were combined to document changes in white shark relative abundance at the site before and after the predation events, which induced an increase in a mesopredator prey species for white sharks, the bronze whaler shark, *Carcharhinus brachyurus*.

3.2 Materials and Methods

Gansbaai is located 120 km and 100 km east of Cape Town and False Bay, respectively, in the Western Cape, South Africa (Figure 3.1). Due to the year-round presence of white sharks and its accessibility for tourists, it is a popular location for white shark viewing and cage diving. Eight cage diving operators and two research vessels are permitted to use chum, bait and seal decoys to attract white sharks for tourist viewing and research purposes (Figure 3.1c; Johnson and Kock 2006; Towner et al. 2016). As a result of its locality close inshore, this is one of the few white shark aggregation sites in the world that can be accessed as a day trip.

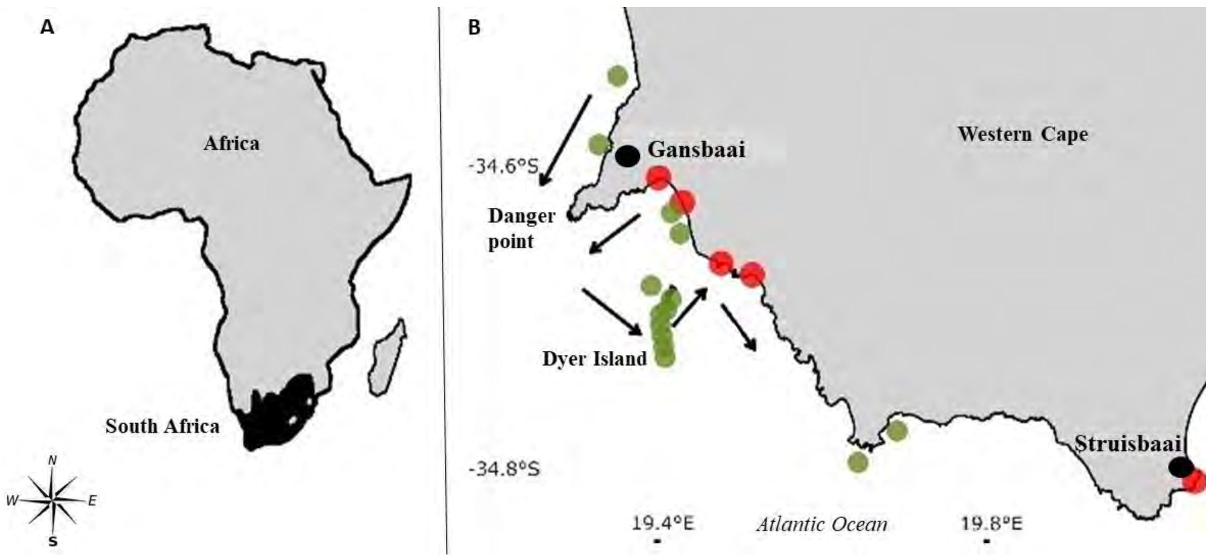

Figure 3.1: (A) Map of Africa with South Africa shaded. (B) Map of Gansbaai and Struisbaai in the Western Cape. Green circles are acoustic receiver locations and red circles are locations of shark carcass standings.

3.2.1 Boat surveys

In Gansbaai, shark tour operators take tourists out daily to observe white sharks. Dive vessels anchor and chum with fish-based products mixed with seawater until sharks are observed, typically operating between 07:00 and 16:00, with a maximum of three trips per day, each up to three hours in length. For each trip, location data and SST were collected from an onboard computer and a handheld YSI Prodo unit. Sightings data were collected on individual white and bronze whaler sharks as part of a long-term monitoring project in Gansbaai (Towner et al. 2013a, b). Shark size was estimated visually, and where possible, sex (confirmed via the presence of claspers in males) and individual identification (from unique marking patterns or externally attached dart tags). Data were collected from 2008-2019, and for each day, the number of white sharks and bronze whalers sightings were normalised by the number of trips performed that day. Long-term boat-based observations of white sharks were plotted before and after killer whale presence (see below) and compared monthly means of white shark numbers using an ANOVA, followed by a posthoc Tukey HSD test. Finally, a change-point analysis was used (Hinkley 1970) to identify a change in the time series of daily sightings and a Box-Ljung test (Ljung and Box, 1978) to determine whether there is significant evidence of non-zero correlations. The absences of white sharks were calculated every week to avoid daily variation in sightings. All analyses were performed in *R* (R Core Team 2019).

3.2.2 Necropsies

Killer whale predations on white sharks occurred within the Gansbaai region between February and July 2017, and five white shark carcasses washed up on sandy beaches between Danger Point (34°37'S, 19°18'E) and Struisbaai (34°49'S, 20°02'E; Figure 3.1; Table 3.1). Four of the five carcasses were dissected within 12 hours of retrieval. One carcass was frozen intact and stored at the Department of Environmental Affairs (DEA) in Cape Town. External examinations on all the shark carcasses were conducted, documenting wounds, markings, any visible signs of hooking or netting, predation, and scavenging indicators. Internal examinations were performed per the methods described in Wintner and Cliff (1999) and included standard measurements, photographs, and organ weights.

Table 3.1: Chronological records of *Carcharodon carcharias* carcasses with locations in Gansbaai, South Africa, and tracking data on the *Orcinus orca* pair with additional notes, between 2017 and 2019.

Date	Time	Location	Sex	Size (TL)	Cause of Death	Liver Missing?	Orca Tracked?
2017/02/09	08.00	Pearly Beach	F	2.6 m	*Orcinus orca* (suspected)	No	Yes
2017/05/03	07.30	Franskraal	F	4.9 m	*Orcinus orca* (confirmed)	Yes	Yes
201705/04	17.15	Franskraal	M	3.6 m	*Orcinus orca* (confirmed)	Yes	Yes
2017/05/07	17.15	Struisbaai	M	4.5 m	*Orcinus orca* (confirmed)	Yes	Yes
2017/06/24	07.45	Pearly Beach	M	4.1 m	*Orcinus orca* (confirmed)	Yes	Yes

*On the 27-06-2021 and the 20-06-2022, a 2.8m male and 2.9m female white shark carcass washed out in Die Dam, 20km East of Gansbaai, respectively. Both times the killer whale pair were sighted in the region, and a year of no white shark sightings was recorded between these events.

Table 3.2: Chronological records of *Orcinus orca* pair between 2017 and 2019.

Date	Time	Location	Track Duration (min)	Heading	Mean Dive Time (min)	Footage	Comments
2011/04/09	11:00	Danger Point	N/A	N/A	N/A	N	Pod of 2 *Orcinus orca*: 1 Male, 1 Female
2012/08/24	11:50	S of Dyer Island	N/A	N/A	N/A	N	Pod of 6 *Orcinus orca*
2015/10/30	14:30	Dyer Island	255	W	04:57	Y	Port & Starboard; Back of seal colony
2015/10/31	08:55	Kleinbaai	62	NW	03:29	Y	Port & Starboard; Away from Dyer, towards shore
2016/04/10	16:00	Danger Point	N/A	N/A	N/A	N	Pod of 6 *Orcinus orca*: 3 Male, 2 Female, 1 Juvenile
2017/02/08	07:30	Franskraal	53	W	N/A	Y	Port & Starboard; In cage diving area, relaxed
2017/04/19	11:00	Dyer Island	40	SE	N/A	Y	Port & Starboard; Moving fast, transient
2017/06/24	13:25	Pearly Beach	58	W	N/A	Y	Port & Starboard; Moved to Dyer Island
2017/10/02	15:15	Danger Point	126	SE	04:40	Y	Port & Starboard
2018/05/15	16:35	Danger Point	45	W	N/A	Y	Port only, evasive
2018/11/02	PM	Walker Bay	N/A	N/A	N/A	N	Port & Starboard
2019/04/03	17:50	Danger Point	45	W	N/A	Y	Pod of 8 *Orcinus orca*: 2 Male, 3 Female, 3 Juvenile
2019/09/23	PM	Walker Bay	N/A	N/A	N/A	N	Pod of 4 *Orcinus orca*: 4 adults plus newborn

3.2.3 Killer whales

Using photographs of their dorsal fins and saddle patches, a pair of killer whales were identified from boat-based observations (Figure 3.2). These matched the description of a pair of male killer whales that were recorded preying on sevengill sharks, (*Notorynchus cepedianus*, in 2015 (Engelbrecht et al. 2019). The pair were first observed around Cape Point in South Africa in 2012 but then not seen again for three years (S. Elwen et al., SeaSearch, unpublished data); they were then observed by several commercial boats in False Bay on 14 January 2015. Subsequently, they have been seen in the area for all years since the end of 2020, with a relatively even spread of sightings across the seasons. They have been seen as far east as Algoa Bay in 2018 (roughly 800 km east of False Bay). However, most sightings have occurred between Table Bay and Gansbaai in the southwestern Cape area (S Elwen et al., SeaSearch, unpublished data). Both whales have collapsed dorsal fins, making them easily recognisable. The killer whales were followed through the use of a small catamaran vessel and commercial whale-watching vessels before or after each white shark predation event in the Gansbaai area and in 2015 before predations were recorded. Data was collected on the killer whales' dive time, swimming direction, GPS position, and noted general behaviour (Table 3.1).

Figure 3.2: The pair of killer whales responsible for the predations on white sharks in Gansbaai. Researchers in South Africa have named them "Port" and "Starboard" due to their highly distinctive flaccid fin causing their dorsal fins to droop in opposite directions. Photo credit Sandra Hoerbst.

3.2.4 Shark movements

Acoustically tagged white sharks were tracked in Gansbaai on an array of fifteen underwater acoustic receivers (VR2W, Vemco- now called InnovaSea, Ltd, Nova Scotia) as part of a long-term study on their movements (Figure 3.1). The VR2Ws were moored at depths ranging from 12 - 20 meters throughout Gansbaai, Walker Bay (34°32'S, 19°22'E), and Quoin Point (34°48'S, 19°42'E). White sharks were dart tagged externally with V16 acoustic transmitters (69 kHz, Vemco Ltd/InnovaSea, Nova Scotia) using a pole spear from a research vessel. VR2Ws record the date and time when acoustically tagged sharks pass within range (400 – 1200 m, dependent on environmental conditions, depth, and habitat type; Kock et al. 2018; Gennari et al. 2018). The receiver array at Gansbaai is part of a national network of 262 private and shared receivers (ATAP: Acoustic Tracking Array Platform; Cowley et al. 2017), spanning from Cape Town to Mozambique. Acoustic telemetry data was collected between 2012 and 2020 as part of a more extensive movement behaviour study on white sharks (Chapter 5) and filtered to remove any singular detections on receivers within 24 hours (to avoid false detections) and concurrent detections on two neighbouring receivers to clarify movement. The daily number of unique tags detected within Gansbaai were determined, and whether there was a significant change in concurrent numbers of sharks detected through a change-point analysis (Hinkley 1970) and a Box-Ljung test (Ljung and Box, 1978).

3.3 Results

3.3.1 Killer whales

A pair of identifiable killer whales, recognisable by their collapsed dorsal fins (known as "Port" and "Starboard" due to the direction the dorsal fins are collapsed) (Figure 3.2), were sporadically seen between 2010-2015 but then frequently observed in Gansbaai starting in late 2015 through to 2019. The first white shark mortality corresponded with the first sighting of the killer whale pair, and then in 2016-2017, five white shark mortalities were observed as the number of killer whale observations increased. The increase in sightings of the killer whale pair has been explored in detail in an updated review on South African killer whales (S. Elwen et al., SeaSearch, unpublished data) These authors have verified that the pair's presence has increased significantly between False bay and Gansbaai and they are now considered 'semi resident' in this region where they are known to hunt multiple elasmobranch species post-2017. (Engelbrecht et al. 2019, Hammerschalg et al. 20199, S.Elwen et al., SeaSearch, unpublished data).

3.3.2 Boat surveys

Between 2008 to 2011 the mean white shark sightings per day significantly increased from 5.11 ± 2.5 (mean ± sd, n = 243) to 8.61 ± 4.5 (n = 289; $F_{47, 1036} = 18.51$ $p<0.05$). In the last six months of 2016, before the first killer whale predation on white sharks on 9 February 2017, mean daily white shark sightings were 6.68 ± 2.4 (n = 152; Figure 3.3). The remaining four dead white sharks washed up between 3 May and 24 June 2017. Six months after the killer whale predations, the mean daily white shark sightings dropped to 1.17 ± 1.43 (n = 138; Figure 2b). The mean daily white shark sightings remained low throughout 2018 and 2019 at 1.40

±1.68 (n = 293) and 1.96 ± 1.50 (n = 225), respectively. The mean monthly white shark sightings from 2017 to 2019 were significantly lower than those of previous years (ANOVA: $F_{143,3220} = 38.1$, $p<0.05$; Appendix Figure AP1). The change-point analysis over the explored period (2008 – 2019) identified a significant change in the mean daily white shark numbers on 19 April 2017 (Box-Ljung: $X^2=2012.9$, $p<0.05$). This date coincided with the second sighting of the killer whale pair, after which predations on white sharks occurred within the following month, starting on 3 May 2017 (Table 3.1).

The duration that white sharks were absent from Gansbaai following the killer whale pair sightings generally increased with each subsequent sighting (Figure 3.3). Initial white shark absences at Gansbaai lasted 4.29 ± 2.56 weeks (mean ± sd; the number of absences = 5, Range: 2 - 9 weeks) in 2017 following the predation events but increased to 8.5 ± 12.34 weeks (n = 4, 2 - 27 weeks) in 2018 and 9.67 ± 8.50 weeks (n = 3, 1 - 18 weeks) in 2019 following additional sightings of the killer whale pair and subsequently straight-finned killer whale pods.

Bronze whaler sharks were rarely observed at the shark dive or research vessels in Gansbaai before 2017. The mean daily number of bronze whaler shark sightings from 2008 to 2016 was 0.00 ± 0.06 (mean ± sd; n = 2572 trips; Figure 3.3). However, six months after the killer whale predations and the subsequent absence of white sharks, the mean daily number of bronze whaler sightings increased to 1.38 ± 1.96 (n = 137). Their presence remained high with the mean daily number of sightings at 3.22 ± 4.48 (n = 292) and 5.90 ± 4.99 (n = 225), throughout 2018 and 2019, respectively ($F = 1632$, $p<0.05$).

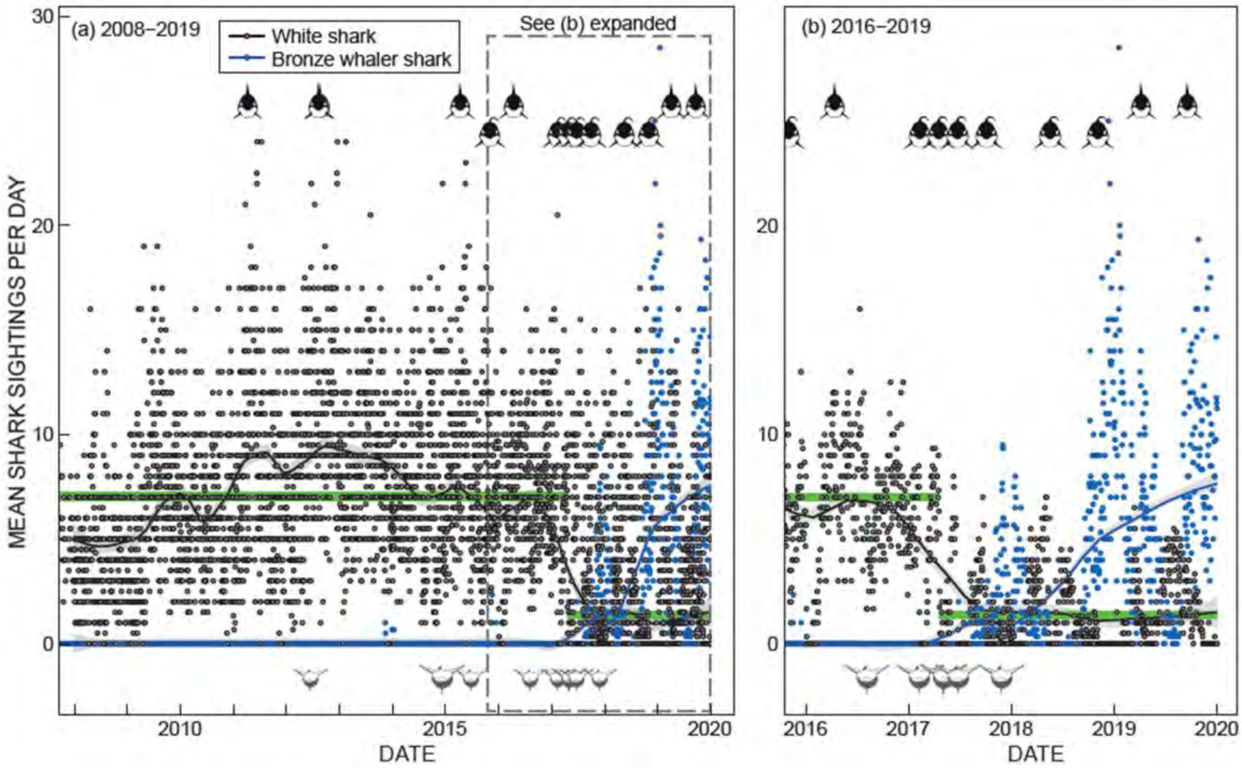

Figure 3.3: Long-term (A: 2008-2019) and short-term (B: 2016-2019) average white shark and bronze whaler sightings per day in Gansbaai, with loess smooth curve (span=0.2) and change-point analysis result, whereby killer whale sightings are represented by icons (curved fin: Port and/or Starboard sighting; straight fin: other killer whale pod sighting), and incidences of white shark strandings with inverted white shark icons.

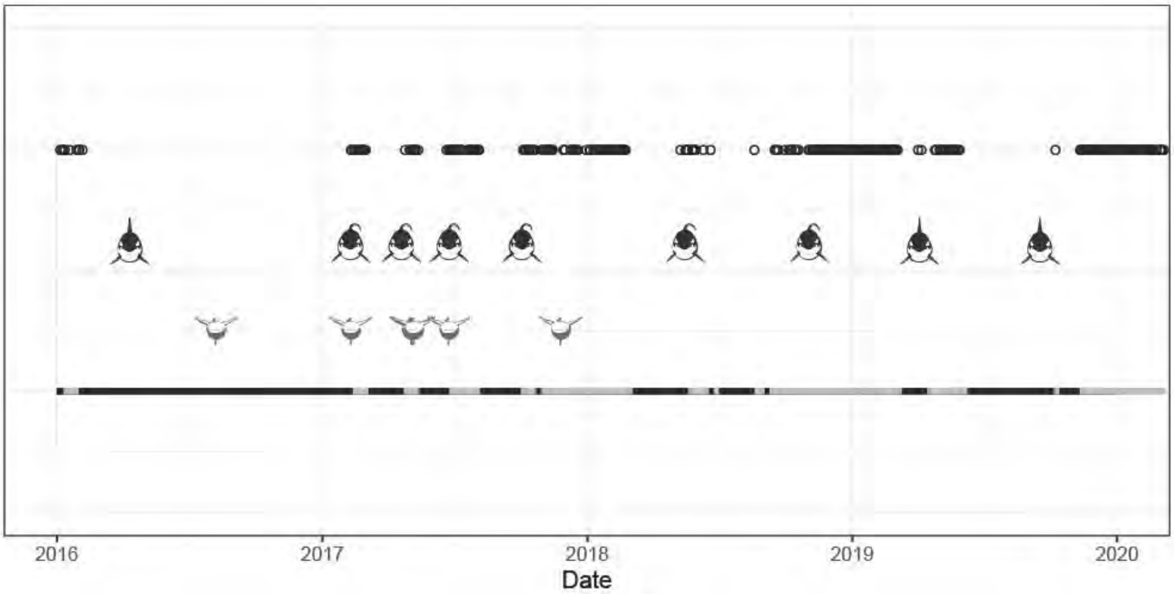

Figure 3.4: Periods of white shark absences in Gansbaai. Black circles (○) indicate dates with no white shark sightings, with light grey bars indicating weeks with average white shark sightings lower than 1 shark/day/week, while black bars indicate weekly periods with average white shark sightings higher than 1 shark/day/week. Killer whale sightings are represented by icons (curved fin: Port and/or Starboard sighting; straight fin: other killer whale pod sighting) and incidences of white shark strandings with inverted white shark icons.

Figure 3.5: Injuries to white sharks included a large clean tear across the pectoral girdle and the missing liver (A). Sharks ranged in size from 2.6 m TL - 4.9 m TL. The first carcass (B) was the largest white shark to be necropsied in South Africa, and results indicated she was reproductively immature. The liver was completely missing from the four larger sharks, with the other organs visible through the tear (C). Killer whale rake marks were present on two carcasses, and shark 3 was missing the heart and testes along with the liver (D). The second shark to wash out had blunt circular impressions on the pectoral fins, which resembled marks made by Orca dentition (E and F). Photos credit Tami Kaschke, Dyer Island Conservation Trust.

3.3.3 Necropsies

Between 8 February and 25 June 2017, five white shark carcasses (three males, two females) ranging in size from 2.6 - 4.9 m TL were washed up between Danger Point and Struisbaai (Figure 3.1; Table 3.1). Four of the five sharks had large tear wounds across the pectoral girdle and were missing their livers (Figure 3.5c and 3.5d). Killer whale rake marks (scratch-like tooth impressions) were visible on two carcasses. Besides these external wounds and missing livers, there were no signs of any capture (hook or net) marks. Shark 1 had fresh scarring from the shallow rocky area it was found, while shark 3 was also missing its testes and heart in addition to its liver. The largest shark (shark 2; Figure 3.5a) weighed ~1100 kg and was identified the previous year at Dyer Island. Shark 3 was identified in Gansbaai by the shark dive vessel three days before washing up (29 April 2017), while sharks 4 and 5 had not been seen in the area before.

3.3.4 Shark movements

Between 2012 and 2019, 106 white sharks were tagged (externally and/or internally) with acoustic transmitters in South Africa. Thirty-six were tagged within the Gansbaai area. However, these animals show wide-ranging movement across South Africa and are known to travel into the Indian Ocean (Bonfil et al. 2005; Kock et al. 2022). Of the tagged white sharks in South Africa with acoustic transmitters, 69 were still active by the end of the study period in South Africa (barring animal death or transmitter loss). Before the killer whale predations in 2017, the number of tagged individual white sharks detected per day across the receivers in Gansbaai ranged from 3 - 8 individuals. After the first shark carcass washed ashore in January 2017, the number of detected individuals dropped to 0. The detections remained between 0 - 2 sharks for the remainder of 2017 (Figure 3.6).

The change-point analysis and Box-Ljung test showed a significant change in the number of concurrent transmitters in the Gansbaai area (Box-Ljung: X^2=2082.7, $p<0.05$, Figure 3.6).

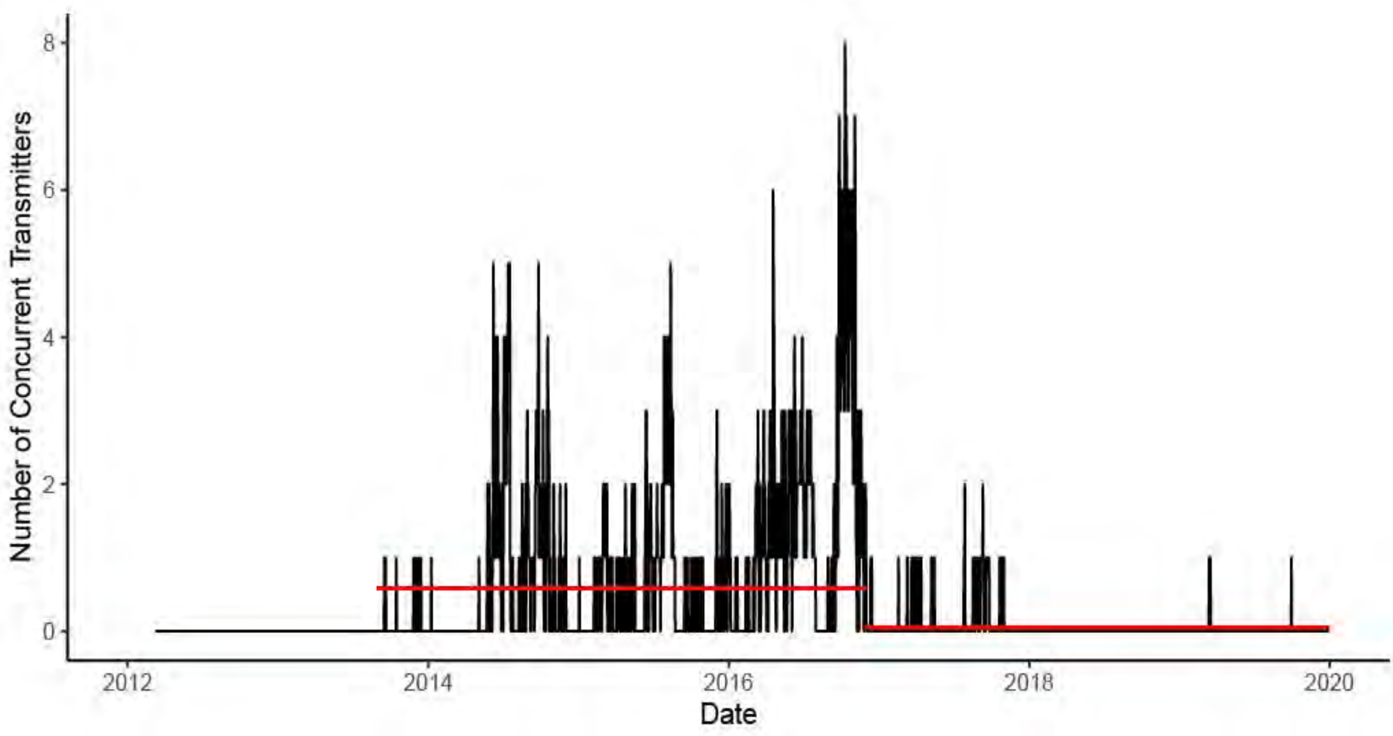

Figure 3.6: Concurrent detected acoustically tagged *Carcharadon. carcharias* in the Gansbaai acoustic receiver network with the change point analysis trend line.

3.4 Discussion

Convincing evidence was documented that killer whale predation induced a departure of white sharks from Gansbaai and that the absence of white sharks led to a corresponding increase in bronze whaler sharks. As such, available evidence is added that white sharks can respond rapidly to the threat of predation by emigrating and that their absence can start to induce some degree of trophic cascade (also see Jorgensen et al. 2019). In southern Africa, two different morpho-types of killer whales can be found, a coastal and an offshore type, which are separated based on differences in diet, size, morphometrics, and dental wear (de Bruyn et al. 2012; Best et al. 2014). While killer whales are known to prey upon white sharks in California, this is the first time it has been documented in South Africa (Pyle et al. 1999; Jorgensen et al. 2019). Previous studies have highlighted that killer whales in South Africa can prey upon large elasmobranch species, including blue sharks (*Prionace glauca*, Best et al. 2010; 2014), sevengill sharks (Engelbrecht et al. 2019), and a basking shark (*Cetorhinus maximus*) in Plettenberg Bay (Kevin O'Donnell, pers. obs, Appendix AP2).

A pair of identifiable killer whales were potentially responsible for preying on at least five white sharks in Gansbaai. Shark carcasses revealed a single large tear across the pectoral girdle and the liver, and in some cases, other internal organs were missing, and rake marks were present on the fins. The wounds recorded on the white shark carcasses were similar to those seen on other chondrichthyans (Hoyt 1990; Fertl et al. 1996; Pyle et al. 1999), where killer whales tore the sharks open across the pelvic girdle, most likely by their pectoral fins, and selectively removed their livers (Engelbrecht et al. 2019). Sharks' livers are energy-rich as they are composed of lipids and may account for up to a third of the sharks' body weight (Kohl et al. 2015; Pethybridge et al. 2014). Selective feeding on energy-rich prey is a hunting strategy frequently used by killer whales (Fertl et al. 1996; Pyle et al. 1996; Heithaus and Dill 2006; Engelbrecht et al. 2019), but there are fewer examples of predators extracting specific organs from their prey (Gende et al. 2001). Harbour seals (*Phoca vitulina*) consumed only the bellies of high-lipid roe-containing pre-spawning female salmon (*Oncorhynchus nerka*) (Hauser et al. 2008), while bears (*Ursus* spp.) targeted the lipid-rich brain tissue and roe of salmon (Gende et al. 2001), and wolves will feed initially on the internal organs of large ungulates (Bosch et al. 2015; Kohl et al. 2015). Although no direct observations were made of the killer whale pair preying on the white sharks, the rake marks and wounds on the carcasses were distinctly those of killer whales, and the same killer whale pair was observed in the area when predations were known to occur. The same killer whale pair were also implicated in predations on sevengill sharks (Engelbrecht et al. 2019) and bronze whaler sharks in False Bay (Elwen et al., SeaSearch, unpublished data; Appendix AP2), indicating a level of experience and skill in hunting large sharks.

White sharks are known to use aggregation sites in South Africa seasonally, with the highest shark numbers occurring during the austral winter (May - September) when Cape fur seal pup abundance is highest (Kock et al. 2013; Towner et al. 2013a). The lowest shark numbers occur during the austral summer (Dec - Feb) when sharks move inshore to forage on other prey species (Kock et al. 2013; Ryklief et al. 2014). Despite this, killer whale predations likely induced the emigration of white sharks from Gansbaai starting during the austral winter months, and avoidance of the Gansbaai area or movement away was documented by several acoustically tagged white sharks that were present in the area at the time of the predations. Boat surveys and telemetry data (Chapter 5) showed that white sharks left the Greater Dyer Island region in May 2017, which is considered the peak season for white shark abundance (Ryklief et al. 2014; Towner et al. 2016), and remained absent from the region for six weeks. White sharks eventually returned, and the numbers stabilised, only to disappear for more prolonged periods after more sightings of the implicated killer whale pair and, subsequently, killer whales with straight fins. Prior to these predations, there were only two instances where white sharks were absent for a week since the start of the data collection: one week in 2007; and one three-week period at the beginning of 2016. The change-point analysis of the white shark sightings data matched the exact date of the second sighting of the killer whale pair, which suggests their presence made a significant impact even before recorded predations occurred.

Concurrent with the emigration of white sharks from Gansbaai was an increase in the number of sightings of bronze whaler sharks in the bay. The timing of the increase is strong evidence that the absence of white sharks was a crucial driver in the immigration of bronze whaler sharks. The increase in bronze whaler sharks may represent competitive release or mesopredator release due to a reduction in risk from white shark predation (Dulvy et al. 2000, Hussey et al. 2012). Stomach content analysis of white sharks >235 cm Pre-caudal length reveals that they will prey on bronze whaler sharks (Cliff et al. 1996, Hussey et al. 2012). In the absence of top predators, mesopredators may be less restricted in their access to resources due to the reduced risk of predation and competition (Ebert 1991; Heithaus et al. 2008; Dicken et al. 2013; Moxley et al. 2019). Similarly, in the adjacent coastal region of False Bay, although sevengill sharks disappeared from the coastal location of Millers Point, their numbers appeared to increase following the extended absence of white sharks at Seal Island, False Bay (Engelbrecht et al. 2019, Hammerschlag et al. 2019). Hence, the absence of white sharks may lead to rapid responses in lower trophic levels, raising the possibility that they can induce trophic cascades (Jorgensen et al. 2019). Additional factors may also play a role in the ability of killer whale induced departure of white sharks to trigger trophic cascades. For example, white sharks in South Africa have been shown to elevate physiological stress levels in seals exposed to high risk of predation (Hammerschlag et al. 2022). The departure of white sharks from aggregation sites in northern California also led to a steep decline in predation rates on pinnipeds, potentially leading to some direct density-dependent changes in seal populations (Jorgensen et al. 2019). Why would killer whale predation on white sharks suddenly increase? While killer whales have previously been incidentally sighted in South Africa (Best et al. 2010), there has been an increase in sightings in the last decade (Elwen et al. SeaSearch, Unpublished data). This change could be related to a decline in prey populations, including pelagic fish and sharks, causing changes in distribution patterns (Englebrecht et al. 2019). However, four behaviourally distinct populations of killer whales now occur around southern Africa, and further research is needed to understand better the relationship between these populations, their spatial ecology, and diets (Elwen et al. SeaSearch, unpublished data).

White sharks appear to use a strategy of large-scale avoidance in response to the threat of predation in lieu of fine-scale avoidance. This may be similar to strategies used by wild dogs in the Serengeti, which abandon dense lion areas for the long term (Swanson et al. 2014). How larger marine predators respond to risk is important for helping to understand the dynamics of coexistence with predator communities. These may also dictate the interactions between competitors or intra-guild predator/prey (Vanak et al. 2013).

As with all correlative studies, alternative explanations for shark declines must be explored beyond just predation risk from killer whales. Sea-surface temperatures (SST) influence white shark sightings, and white shark numbers in Gansbaai decline in the austral summer as water temperatures increase (Towner et al. 2013b). However, SST or seasonality cannot explain the immediate and abrupt decline in sightings at the beginning of 2017 and the extended and increasing absence periods (Appendix, AP4).

The decline in white shark numbers could also be due to direct fishing of white sharks or indirectly due to fishery-induced declines in potential prey (e.g., teleost fishes). For example, the KwaZulu-Natal Shark Board (KZNSB) bather protection nets and drumlines off the Durban coastline may catch up to 32 white sharks annually (Cliff and Dudley 2011; Towner et al. 2013a; Kock et al. 2022). While located further east than our study sites, white shark movements can easily extend into KwaZulu-Natal (Kock et al. 2022). While there is debate about the white shark population size, all studies agree that the low numbers of white sharks are of concern (Andreotti et al. 2016; Irion et al. 2017). Demersal longline fisheries target one of the prey types of white sharks, small shark species <1.3m TL. For example, there are well-documented declines in smoothhound shark (*Mustelus mustelus*) and soupfin shark (*Galeorhinus galeus*) populations in South Africa (da Silva et al. 2019; Winker et al. 2019). Hence, the decline in white shark observations could be due to a decrease in white shark population sizes or emigration due to declines in prey abundance. While these issues could contribute to the declining numbers of white sharks in South Africa, they are unlikely to explain the sudden decline in Gansbaai. The population sizes of soupfin and smoothhound sharks have been steadily declining since the 1990s, while the sudden decline in white shark observations started in 2016 (da Silva et al. 2019; Winker et al. 2019). Furthermore, the fishing areas that demersal longliners operate in are closer to the south and Eastern Cape coasts which are not experiencing rapidly vanishing and extended absence of white sharks since 2017, for example Algoa Bay.

White shark catches from the demersal shark longline fishery's scientific equivalent (presented in Kock et al. 2022) support a low number of white shark captures, similar to the USA and Australia, with only two white sharks caught over eight years and >11 000 set hooks. The demersal shark longline fishery generally uses relatively small baited hooks with nylon traces (no steel) that most white sharks could bite through. Although entanglement in longlines is possible, white sharks show high plasticity in their foraging and can adjust their diets to prey on other species if fisheries pressure is an issue (Kock et al. 2022). Before the killer whale predations, white sharks were regularly sighted foraging around Geyser Rock (Wcisel et al. 2014; Jewell et al. 2014). Gansbaai has a large, permanent Cape fur seal colony of approximately 32 000 individuals, providing a predictable and stable food source in time and space (Kirkman et al. 2013).

Evidence is provided that killer whale predation on white sharks induced a direct emigration of sharks from Gansbaai, and individuals did not return for weeks or months. The absence of white sharks was concurrent with an increase in bronze whaler sharks. Hence, fear responses by animals close to the top of the food chain can rapidly induce changes at lower trophic levels. Intense predation pressure will provide an additional source of mortality that is not considered in white shark demographic or population viability models (Irion et al. 2017). It is unclear how they may impact the population.

CHAPTER 4: DIRECT OBSERVATIONS OF KILLER WHALES PREYING ON WHITE SHARKS AND EVIDENCE OF FLIGHT RESPONSES IN SOUTH AFRICA

Killer whales (*Orcinus orca*) and white sharks (*Carcharodon carcharias*) are marine apex predators which shape prey behaviour and even entire ecosystems, through direct predation effects and indirect fear effects (e.g. Estes et al. 2009, Heithaus et al. 2008). Killer whales are known to occasionally hunt white sharks; although only three studies have formally described this behavior and the associated flight responses in white sharks (Pyle et al. 1999, Jorgensen et al. 2019, Towner et al. 2022). However, direct observation of predation has been lacking, giving rise to speculation on the hunting strategies used by killer whales to capture and kill white sharks, and the subsequent behavioral impact on surviving white sharks in the area where the predation took place, including the cues and timing of shark responses to these events.

4.1 Behavioral observations recorded by a drone

On the 16th of May 2022 at 14.36 pm, a hobbyist drone pilot, filmed a group of killer whales at Hartenbos Beach and river mouth, Mossel Bay, South Africa (34° 07' S, 22° 07' E) using a private drone (DJI Mavic Air2S with a 1" CMOS sensor and 20 MP camera). Five killer whales were observed for around 40 minutes, and the drone followed them for 30 minutes. Due to drone memory and battery constraints, only the two segments described here were recorded. Initially, the group of five killer whales was together. However, they separated as direct observations began, with KW1 ("*Starboard,"* a male killer whale implicated in earlier shark predations in South Africa) (Figure 4.1 inset.) and KW2 (unidentified) began moving ~500 m east towards the Hartenbos River mouth, a known high use area for white sharks (Jewell et al. 2013). The drone first flew over three of the five killer whales, ~400 m off Hartenbos beach, and started recording. The following event was filmed as a single clip with all three whales continuously visible in the frame: KW3 and KW4 were observed swimming together on the surface but facing opposite directions. After seven seconds, KW5 appeared from depth between KW3 and KW4 and used its rostrum to push an estimated ~3 m total length white shark to the surface from the ventral side while rolling the shark to its right side (Figure 1 Panel 1a). The shark appeared dead as KW5 brought it up to the surface, with its white underbelly partially visible (Figure 4.1b). KW5 bit into the shark in the region of the pectoral fins, and a large cloud of blood appeared (Figure 4.1c). KW5 then dove down with the shark still in its mouth but released it and began to move off when KW3 rapidly approached and made a very close pass by the white shark's caudal fin, appearing to bite the caudal fin before diving out of sight (Figure 4.1d). KW3 surfaced again away from the last observed location of the white shark then all three KWs moved offshore to the west. At 15.17 pm, the drone flew east to the river mouth and filmed KW1 and KW2 before moving in the same direction as KWs 3, 4, and 5. The group remained spread out and swam off towards Diaz Point, the western headland of the bay. No shark carcasses were observed or recovered during this or subsequent weeks.

4.2 Behavioral observations recorded from a helicopter

On the 16th of May 2022, between 14h00 and 15h00, Mr D. Archer of Mossel Bay Helicopters flew a series of short tourist flights over the same area of Hartenbos (34° 07' S, 22° 07' E). The pilot witnessed two white sharks being killed by killer whales, but neither was fully captured on film. However, using a Samsung S21 cell phone, the pilot captured a series of images and short video clips, partially capturing the interactions between four killer whales described above and several white sharks (Figure 4.1, panels 2 and 3). Given the overlap in time and area, it is assumed that the drone footage captured the same group. Two video sequences at 14:07 and 14:27 showed two killer whales (one *Starboard*) closely following a large white shark at <1 body length. The shark displayed evasive behaviours, circling back tightly with the whale following, but both moving slowly. A second killer whale is directly seen approaching the first killer whale and white shark to within five body lengths before visuals are lost. In these videos, one and two other white sharks swam <100 m from the killer whales without noticeable reactions. In another sequence, four different killer whales are seen at the surface, but only *Starboard* can be identified because of his collapsed dorsal fin. Between these video clips, a series of three images over four seconds showed what appears to be the consumption of a free-floating shark liver. The liver is roughly the size of the killer whale's head and appears at the surface before being taken into the killer whale's mouth.

Panel 1 Drone
a
KW4
KW5 & WS
KW5 releases bubbles as it pushed WS towards surface
b
KW5 attempts to invert WS and pushes it sideways
c
KW5 bites into WS behind pectoral fin, blood cloud seen
d
KW5 takes WS to depth and moves off.
KW3 rapidly approaches
Panel 2 Helicopter
e
14:19:14
f
Liver?
14:19:16
g
14:19:17
Panel 3 Helicopter
h
14:27:06
i
14:27:07

Figure 4.1: Series of images taken off Hartenbos Beach, Mossel Bay, South Africa. PANEL 1: screen grabs from a video filmed on a drone by author CS showing the first confirmed observation of a group of killer whales killing a white shark. Inset in (d) shows KW1, an animal with a bent dorsal fin known as "Starboard," one of the pair of killer whales previously implicated in shark predations in South Africa, which was part of the group. PANEL 2: Series of photographs taken on a mobile phone from a helicopter (D. Archer, Mossel bay Helicopters) showing the potential consumption of a free-floating shark liver. PANEL 3: screen grabs from a video taken on a mobile phone showing the circling behaviour of a white shark avoiding a killer whale while a second whale approaches.

4.3 Flight response of surviving white sharks

Three lines of evidence suggest that white sharks fled the area immediately and remained away for at least seven weeks (Figure 4.2). Firstly, four minutes before the predation occurred, the drone pilot and other beach-based observers reported seeing white sharks fleeing the area in several directions, some swimming into extremely shallow water less than 2 m deep. Secondly, opportunistic drone flight data were available from the 2nd of April 2022 to the 7th of July 2022 (52 flights; 1477 minutes of drone footage) from the same area. The average drone flight before the predation on the 16th of May lasted 48 minutes, covered 12.4 km of coastline, and counted an average of four white sharks (range 1 to 8, Figure 4.2a). Based on the sharks' size, individuals in one frame, and their location during the drone flight, ten different sharks were observed during the 75 minutes of flight time on the 16th of May. During the eight days after the predation event (8 drone flights, average flight duration of 59 minutes covering 6.6 km), only one shark was recorded the day after the predation (Figure 4.2a). Thirdly, commercial white shark cage diving operators, White Shark Africa, operating in Mossel Bay, conducted 38 trips on 31 days between the 6th of May and the 6th of July 2022. They encountered an average of 3.3 individual sharks per trip (range 0.5 to 6 sharks per trip, Figure 2b) before the predations and 0 sharks for 45 days after. The first white shark was seen again on the 1st of July (Figure 4.2b). Four sharks (identified by their size and body patterns) were observed on the day of the predation. Given the well-documented, predictable year-round presence of white sharks in Mossel Bay (Jewell et al. 2013; Ryklief et al. 2014), the sudden absence of white sharks for several weeks immediately after the predation event supports a flight response by surviving white sharks in the area.

4.4 Hunting strategy of killer whales

A group of killer whales killed at least two, possibly three, white sharks on the 16th of May in Mossel Bay during 71 minutes of footage. Prior evidence of white shark deaths from killer whale predation has been limited to recovered carcasses (Towner et al. 2022). The combined footage and events described here provide novel insights into how killer whales cornered, captured, and incapacitated white sharks and how sharks responded. In one case, although we suspect the shark was already dead, a killer whale attempted to roll and invert a white shark into a position that would result in tonic immobility (Henningsen 1994, Pyle et al. 1999) before biting into its abdomen just behind the pectoral fins. This confirms the strategy hypothesised from examining previous shark carcasses based on missing livers and bite marks on pectoral fins and torn pectoral girdles (Engelbrecht et al. 2019, Towner et al. 2022). The consumption of what appears to be a large piece of drifting liver confirms that the liver is positively buoyant and may escape the torn open body cavity of the shark and float to the surface.

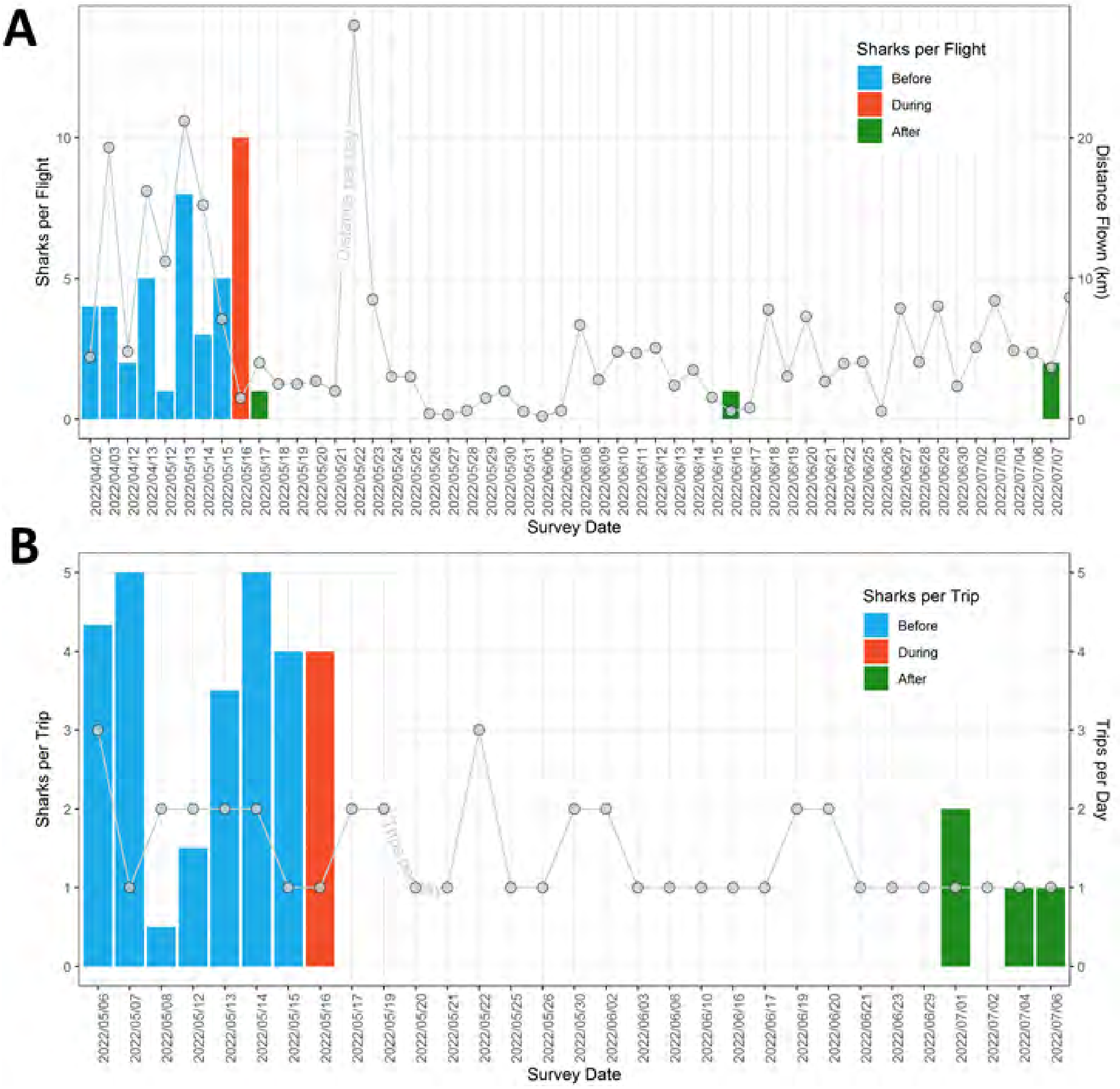

Figure 4.2: (A) Bars show the number of white sharks observed per drone flight by author CS in the Hartenbos, Mossel Bay area before, during, and after the predation event described here. The line shows the total flight distance per day for the drone from the pilot log books. (B) Bars show the average number of white sharks observed per trip by a commercial cage diving operator working in Mossel Bay before, during, and after the predation event described here. The line shows the number of trips per day. Note that day without surveys are not included in either plot.

The videos also provided new insight into the evasive behaviour employed by white sharks. Killer whales closely but slowly followed white sharks, which in turn displayed evasive action by tightly circling the killer whale while keeping it within sight. Similarly, Cape fur seals have a better chance of evading white sharks by staying close to them and keeping the shark within sight (Martin et al. 2005). Turtles successfully evaded tiger sharks by swimming in tight circles around the shark (Andrzejaczek et al. 2019). However, because killer whales are social and hunt in groups, this evasive tactic may not be effective, as a shark cannot keep sight of more than one killer whale at a time. Combined, these behaviors reveal a specialised foraging tactic that killer whales have learned to catch, incapacitate and eat large white sharks.

4.5 Cultural transmission of shark hunting behavior

In southern Africa, killer whales mainly hunt cetaceans, and shark predation was extremely rare, with only two known records before 2010 (Best et al. 2010). Since *Port* and *Starboard* were first recorded regularly in South African waters in 2015, both as adults, they have been linked through a high correlation with discovered carcasses to preying on large coastal sharks (Engelbrecht et al. 2019, Towner et al. 2022). The two killer whales have almost exclusively been seen together (63 of 66 records to the end of 2021), with no other killer whales, suggesting relative social isolation from other killer whales and the potential introduction of this novel predation strategy to the region (Elwen et al. in prep). The participation in the events here of killer whales not previously known to hunt sharks suggests that shark-eating behaviour is more widespread than previously thought or that more killer whales have begun targeting sharks. Cultural transmission of specialist feeding behaviour occurs rapidly in killer whales (Amelot et al. 2021). Given that Starboard at least was seen as part of the group described here, it is feasible that other killer whales may be learning this novel predation strategy.

4.6 Socio-ecological impacts

The South African white shark population is estimated to be small, with between 500-2000 individuals (Andreotti et al. 2016, Towner et al. 2013). Natural mortality is typically considered low for the species (Bowlby and Gibson 2020). The current mortality caused by killer whales is unknown, but the number of deaths is likely underestimated because shark carcasses, particularly those without livers, are negatively buoyant and typically sink to the ocean floor. Furthermore, adult male killer whales measuring ~5.7 tons (7.26 m total length) require 1 394 MJ of energy per day (Reisinger et al. 2011), and the energetic value of a 428 kg white shark liver is estimated to contain around 1425 MJ of energy (Pethybridge et al. 2014). This suggests that an adult male killer whale needs to consume the equivalent of one white shark liver per day to survive. It is, therefore, feasible that killer whales could exert population-level effects on the white shark population, which need to be accounted for in population modelling.

Indirect (fear) effects of predation can have more significant impacts on ecosystems than direct predation (Heithaus et al. 2008). Shark hunting specialists, *Port* and *Starboard,* have already triggered white sharks' short and long-term displacement at the largest South African white shark aggregation site (Chapter 3). Subsequently, mesopredator species (sevengill and bronze whaler sharks) have replaced white sharks at this site (Towner et al. 2022), and shark tour operators have had to adapt their tours accordingly, with socio-economic consequences. Displacement of white sharks from additional white shark aggregation sites may further transform the ecosystem and the white shark-based tourism industry in South Africa.

4.7 Conclusion

Since 2017, scientists and the public have debated the causes, impacts, and potential mitigation actions of killer whale predation on white sharks in South Africa. In the terrestrial environment, translocation or removal of so-called 'problem predators' is a typical response (e.g., lions eating cattle, leopards eating penguins) (Nyhus 2016). However, the solutions are unclear when the' problem predator' is an endangered, charismatic, intelligent, large-bodied, and wide-ranging marine mammal. If shark predation is not (or no longer) limited to two unusual individuals (*Port* and *Starboard*), even lethal control options may now be moot. Solutions must focus on understanding the ecological drivers of this behaviour, the degree and extent of its transmission across the killer whale population, and an improved understanding of the long-term impacts on the socio-ecological landscape.

CHAPTER 5: COASTAL MOVEMENTS AND CONNECTIVITY OF WHITE SHARKS EXPOSED TO KILLER WHALE PREDATION IN SOUTHERN AFRICA 2012-2021

5.1 Introduction

As human impacts on natural habitats become more widespread, understanding animal movement and the reasons for it is vital to identifying and potentially mitigating anthropogenic disruption (Jacoby et al. 2012). The decision by an animal to move or reside is driven by various physical, environmental, and biological factors (Patterson et al. 2008). Evolutionarily successful behaviours in response to these factors determine the temporal and spatial structure of such movement patterns (Jacoby et al. 2012). Advances in biologging technology and analytical methods for large datasets have improved the quantification of animal aggregation and association, species interactions, or animal-mediated habitat connectivity (Fletcher et al. 2011, Farine and Whitehead, 2015).

White sharks *Carcharadon carcharias* make extensive migrations longitudinally and latitudinally throughout their global distribution range, yet they show temporary residency and site fidelity to specific coastal aggregation sites (Huveneers et al. 2018). In southern African white sharks, movement trajectories vary between males and females and different life history phases (Kock et al. 2022). From the inception of white shark research in South Africa, the Western Cape of South Africa was established as the 'epicenter' of their coastal distribution, with False Bay in Cape Town and Gansbaai/Dyer Island considered core areas, making them excellent research and cage dive tourism sites (Bonfil et al. 2005, Towner et al. 2013a, Kock et al. 2022).

Satellite and acoustic tagging studies confirmed these bays offer key areas to hunt Cape fur seal *Arctocephalus pusillus pusillus* prey in winter months and access other prey, including teleost, elasmobranch and cetacean species throughout the rest of the year (Jewell et al. 2013, Towner et al. 2016, Kock et al. 2018). Seasonality influences environmental conditions within these coastal bays. With cooler upwelled water occurring in summer months, smaller sharks are seen more frequently closer to shore, with a mixture of larger sharks of both sexes at the seal colonies in winter (Weltz et al. 2013, Towner et al. 2013b).

In 2015, False Bay experienced a site abandonment by white sharks (Engelbrecht et al. 2019). Although the driver for this emigration has been debated inferring causes such as declines in smaller sharks as prey species (Hammerschlag et al. 2019), strong evidence suggests that killer whales triggered this movement (Engelbrecht et al. 2019, DFFE report). Gansbaai experienced abrupt declines in white shark numbers in 2017. Acoustic tag data, boat-based observations together with necropsy data on stranded dead white sharks, have provided evidence that an increase in killer whales in the Western Cape was responsible for the white sharks moving away (Chapter 3 and 4, Elwen et al.in prep).

More recently, at least three white sharks were hunted by these killer whales, at a third more easterly aggregation site, Mossel Bay, with direct evidence via drone footage captured in 2022 after the study period of this Chapter (Chapter 3 and 4). Following each killer whale-white shark interaction incident, white sharks abandoned the Western Cape attack sites for weeks to months. Increased sightings of white sharks are now being reported by water users in Eastern Cape localities of South Africa, such as Plettenberg Bay and Jeffreys Bay, including increased catches of white sharks by recreational anglers in Algoa Bay as well as along the Transkei coastline (Dicken, unpublished data). Both ecologically and economically, there is an urgent need to establish if the South African white shark population has undergone an eastward shift or fled offshore in response to killer whale predation.

Network methods offer a robust framework to quantify and analyse components of animal behavior that until recently have proven difficult (Mourier et al. 2019). The repeated aggregation of movement steps through time and/or the correlation of edges among individuals can enable the extraction of fundamental behavioural insights from long-term tracking data (Mourier et al. 2019). Spatial networks in animal movement ecology have been particularly useful in systems where connectivity and multi-individual ranging behaviour are difficult to study, such as marine systems, where movement is often inferred between discrete locational fixes (Jacoby et al 2016). To date, acoustic telemetry has mainly been employed to build movement networks in sharks and analyse the properties of the movement patterns in a population (Espinoza et al. 2015; Lédée et al. 2015, Papastamatiou et al. 2015). Network analyses, alongside several other burgeoning methodologies (e.g., Bayesian bridges; step-selection methods; behavioural state modelling), now offer more integrative, comparative, and hypothesis-driven approaches to movement ecology (Jacoby et al. 2016, Mourier et al. 2019).

In this study, the following hypothesis were drawn from the conclusions of Chapters 2, 3 and 4 and were investigated: killer whale predation will cause displacement of white sharks from former traditional aggregation sites in the Western Cape such as False bay and Gansbaai between 2012-2022; and the remaining cohort of white sharks in coastal South Africa will shift to Easterly locations to evade the risk of killer whale predation further.

5.2 Materials and Methods

5.2.1 Tagging of sharks

Between 2012 and 2021, 118 white sharks were tagged with Vemco V16 acoustic transmitters between Algoa Bay (n = 39), Arniston (n = 2), False Bay (n = 4), Gansbaai (n = 42), Mossel Bay (n = 20), Port St Johns (n = 3) and Struisbaai (n = 8) (Figure 5.1).

Of these sharks, 42 individuals were tagged internally by catching the shark with a bait and circle hook and either bringing the shark on board a purpose-designed hydraulic cradle on the Research vessel *Ocearch* or into a sling next to a smaller research vessel to induce tonic immobility (Klimley 1986, Skomal et al. 2018). In the hydraulic cradle, the shark's eyes were covered with a wet towel, its gills were irrigated with seawater, hooks were removed, and antibiotic was administered via injection into the dorsal muscle (Skomal et al. 2019). A V16 transmitter was then inserted into the peritoneal cavity through a small (< 4cm) surgical incision, which was then sutured back together using proline monofilament (Klimley, 1983; Hearn et al., 2010, Skomal et al. 2018). Sharks were released within 10-20 minutes and, where possible, were fitted with both SPOT and Pop off Archival satellite tags.

External acoustic tags were deployed on the remaining 76 individual sharks from small research vessels at the different locations in Figure 5.1, either at seal colonies or inshore reefs in depths between 10-25 m. The externally cased V16 transmitters were attached to umbrella dart heads fitted with sterilised (80% ethanol) dacron, followed by a second soak in diluted disinfectant and rinsed with water directly before tagging. Nylon fishing trace connected the tag to the dart head via double knots in the line or stainless-steel crimps and a rubber sheath over the fishing line. A teleost bait was used to draw the shark close enough to deploy the tag next to the dorsal fin, using either a tagging pole or modified speargun to insert the tag head at the base of the shark's dorsal fin (Kock et al. 2013; Towner et al. 2016). All research was conducted under a DFFE research permit (RES2018/31).

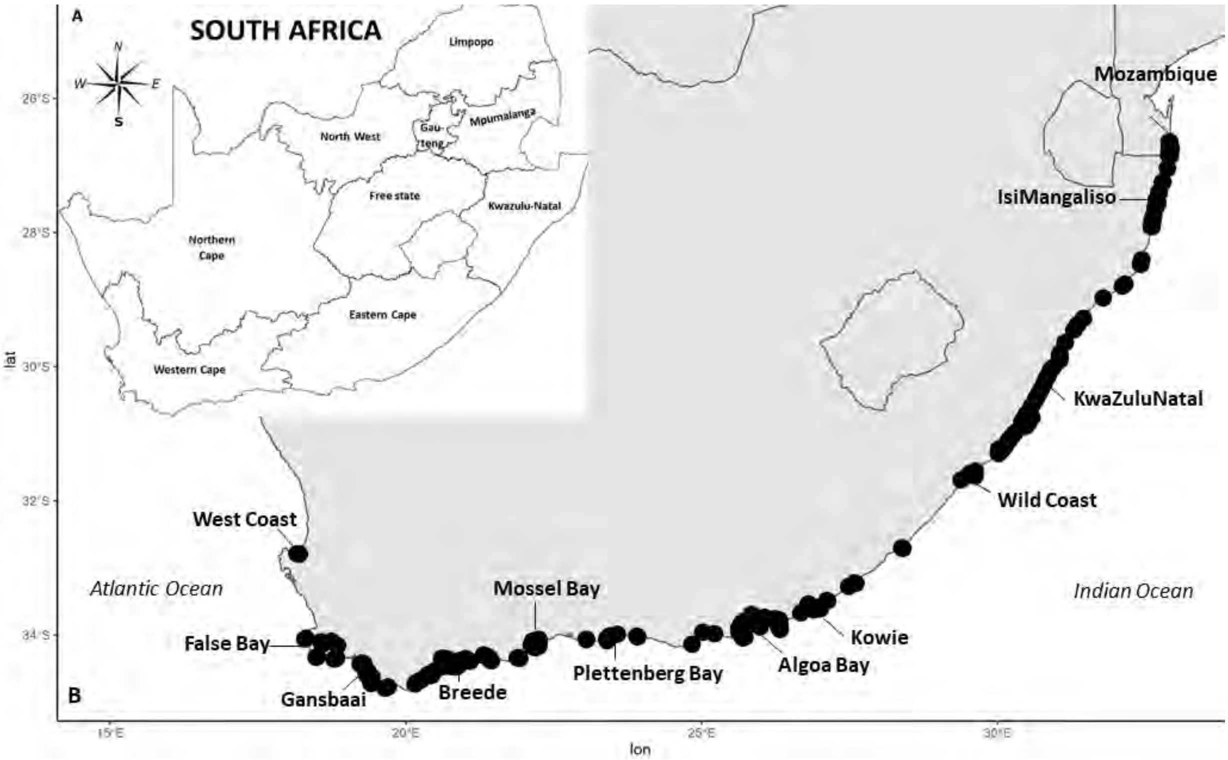

Figure 5.1 Map of South Africa with each province labelled. Locations of the acoustic receivers are denoted as black circles in groupings of main locations groupings.

5.2.2 Acoustic receivers

Between 2011 and 2022, a network of biologging acoustic receivers (Vemco VR2Ws) was deployed along the South African coastline into Mozambique, and the Acoustic Tracking Array Platform (ATAP) was established. Since its inception, the ATAP has had a mean of 179 (± 43) active acoustic receiver stations per year and currently spans approximately 2200 km of the South African coastline (for further details on equipment and deployment, see Cowley et al.

(2017). Together these receivers allow for the assessment of residency, site fidelity, localised movement patterns, habitat connectivity, large-scale coastal movements, migration biology, and estuarine-marine connectivity of marine animals (Cowley et al. 2017). The VR2W receivers were deployed in depths ranging from 5-60 m (Figure 5.1). The ATAP network was then supplemented with additional VR2W receivers as part of private arrays in the study sites of Gansbaai to Struisbaai (n = 10), Mossel Bay (n = 7), and Algoa Bay (n = 20). The ATAP receivers were fitted with VAR acoustic releases and "rolled over" (retrieved, downloaded, and redeployed) every six to nine months with an interrogator system that, causes the receiver to detach the release (Figure 5.2). All moorings and receivers were painted with anti-fouling paint and marked with the institute's contacts if found washed ashore. (Figure 5.2). The private array receivers were serviced using SCUBA divers every 9-12 months.

Range tests were conducted in each region during the initial deployment of receivers and again throughout the study periods to determine detection ranges in different topographies and conditions, which varied from 200 – 1000 m detection ranges dependent on sites (Hearn et al. 2010; Bessudo et al. 2011; Huveneers et al. 2015).

5.2.3 Spatial Network Analysis

Data were analysed through a combination of network analysis (Pedersen 2022). _tidygraph: A Tidy API for Graph Manipulation_. R package version 1.2.1, <https://CRAN.R project.org/package=tidygraph>

Spatial network analysis was used to investigate the relatedness of the shark detections from the receivers. The nodes (an element of a network with a known relationship to others in the network) are the receivers that detected shark presence. The network was undirected yet weighted. Undirected means that there is no direction on the edges and weighted in that the network's edges have differing strengths based on the number of individuals detected. A weighted network has an adjacency matrix with entries that are not simply zero or one but are equal to the weights of the edges, such that

$$A_{ij} = \text{weight of the connection from } i \text{ to } j$$

The measures used to interpret the network are the number of individuals detected at each node, and therefore the most important receivers in the network; the *Degree* centrality measures number of direct neighbours connected through a path and indicates the interaction between the nodes in terms of detections; and *Betweenness* quantifies the number of times a receiver acts as a connector along the shortest path between two other receivers.

Which sites function as key connectivity nodes?

To assess connectivity and relative importance of location to white shark movements, detections were formulated as a network where receivers were considered to be the nodes and edges described movements of individual white sharks between the nodes (movement corridors). For each node, several measures of centrality were calculated. Specifically, for each node, the *Degree* was calculated, i.e., the number of incoming and outgoing edges linked to a node, and *Betweenness*, i.e., the number of shortest paths each node lies on. In addition, the number of individuals detected on each node was calculated. These measures were then summarized across groups of receivers at particular locations (e.g., False Bay, Gansbaai, Mossel Bay, Plettenberg Bay, Algoa Bay, Kowie, Wild Coast, KZN, IsiMangaliso and Mozambique).

How does movement differ across location?

Detection data were summarised to count the number of individual sharks detected at each receiver in each year. Acoustic telemetry data were collected between 2012 and 2021 on white sharks and filtered to remove any singular detections on receivers within 24 hours (to avoid false detections) and concurrent detections on two neighbouring receivers to clarify movement. Any Westward-Eastward movements were plotted along the South African coastline to see if tagged sharks from the Gansbaai and Mossel Bay areas moved to other areas with acoustic listening coverage along the coast.

5.2.4 Killer whale observations

Killer whale observations were obtained from multiple sources (opportunistic, ecotourism vessel, scientific and social media surveys) in South Africa between 2008 and 2021 (Elwen et al. 2022). Coastal records of killer whales, including the highly distinctive shark-eating pair *Port* and *Starboard,* were standardised and analysed over the time period. Values were plotted into time series figures to reflect monthly and annual values. ID counts of white sharks from the spatial network data were then combined with killer whale data to assess trends in the distribution of both species that occurred annually between 2012 and 2021.

5.2.5 White shark annual catches by recreational anglers in Algoa Bay

Data were collected on incidental captures of white sharks between 2013 and 2019 from voluntary interviews with four anglers in Algoa Bay. The sharks were released alive. These anglers were a subset of those initially interviewed by Dicken and Booth (2013) and were identified as those with the necessary knowledge of when and where incidental catches of white sharks occurred in the bay. Respondents detailed the location and time of year of captures, the number caught, the size of each animal, and their approximate number of fishing days. Because of general consistency among participants in fishing locations and the number of days fished per annum (~100), capture data was used as a proxy for catch-per-unit effort in Algoa Bay. However, for this study simple catches were plotted annually to assess any changes pre and post 2017. Data were provided by Dicken (unpublished data).

5.3. Results

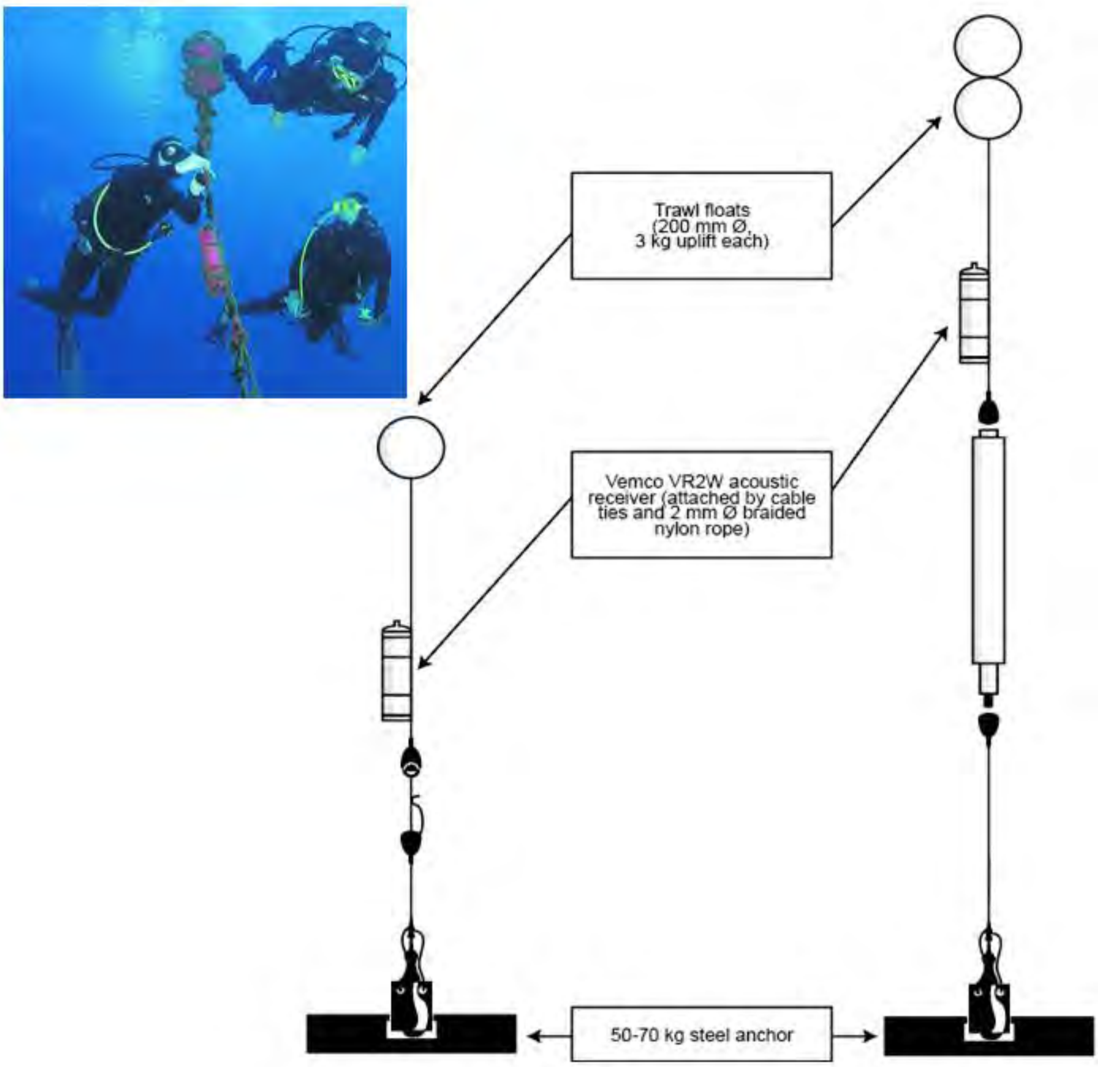

Figure 5.2: Acoustic receiver design, showing the release and non-release design.

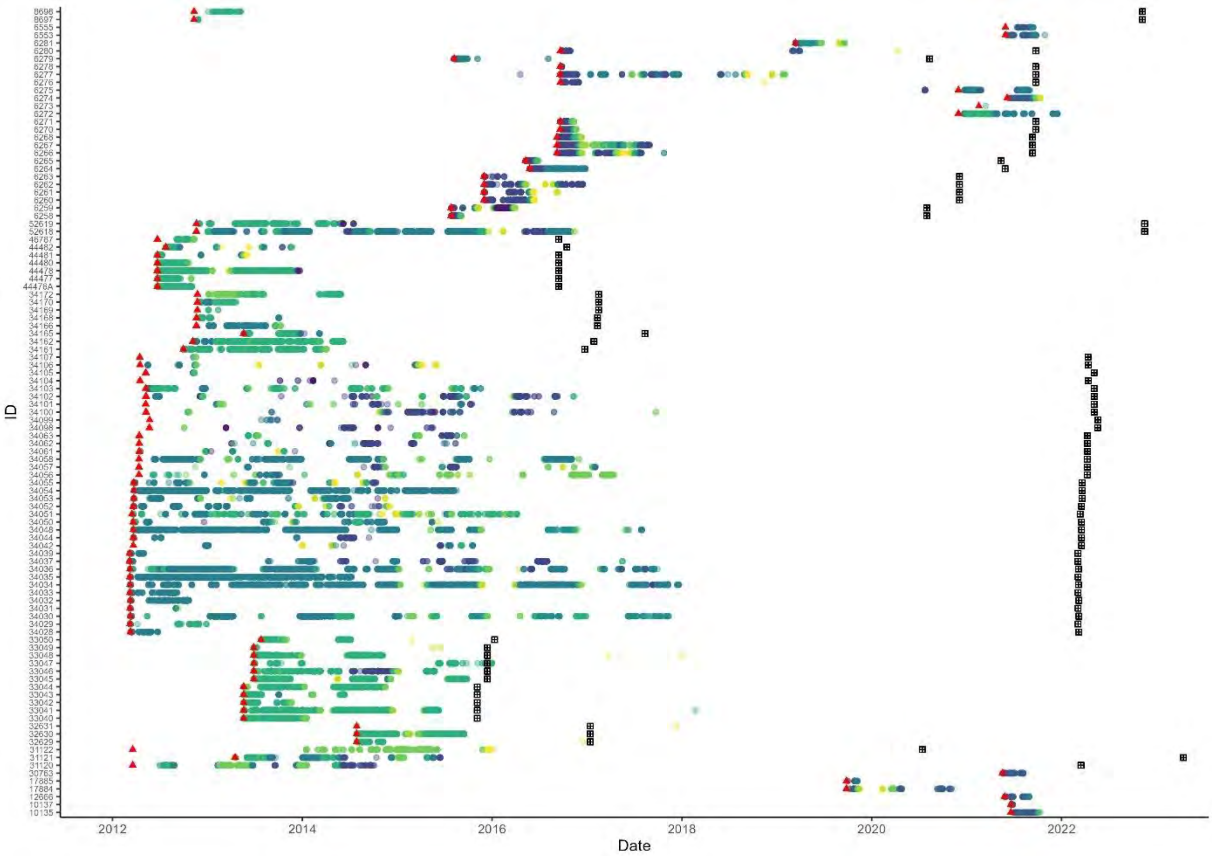

Figure 5.3: Abacus plot of 118 acoustic transmitters (battery expiration dates demonstrated by a black square, colours represent locations), 2012-2022. See Appendix AP6a,b for abacus plot of tag detections 2021-2022 on white sharks, sevengill *Notorynchus cepedianus* and raggedtooth *Carcharias taurus* sharks from OCEARCH and AP6b for an abacus plot of VR2w receiver coverage and soak time 2012-2022.

5.3.1 Spatial Network Analysis

Table 5.1. Mean (standard deviation) values of the number of individuals detected, *Degree*, and *Betweenness*, over multiple receivers deployed at 18 locations along the South African coast from 2012-2021.

Location	**Individuals**	***Degree***	***Betweenness***
Mossel Bay	25 (16.2)	36.4 (24.2)	259.4 (517.4)
Kowie	22.2 (13.3)	7.6 (17)	109 (357.1)
Algoa Bay	19.8 (13.7)	34.7 (24.9)	179 (380.6)
Wild Coast	13.1 (13.3)	16.4 (18.9)	402.8 (613.1)
Gansbaai	11.7 (9.2)	22 (15.5)	325.2 (626.6)
Plettenberg Bay	8 (4.5)	21 (10.2)	504.8 (898.6)
Stilbaai	8 (NA)	1.7 (5.8)	2.6 (9.1)
Breede	4 (3.3)	4.6 (7)	56.4 (126.2)
Mozambique	3.7 (3.2)	5.6 (6.2)	50.8 (95.1)
IsiMangaliso	3.3 (3.2)	6.3 (7.3)	137 (243.2)
KZN	2.9 (2.1)	4.8 (5.2)	62.8 (126.9)
False Bay	2.2 (1.4)	6 (3.3)	117.6 (175)
Hout Bay	1 (NA)	0.8 (1.8)	0.9 (2.1)
TNP	1 (0)	7.3 (3.3)	173.5 (292.3)
Walker Bay	1 (0)	4 (2.9)	34.6 (66.1)
Knysna	NaN (NA)	0 (0)	0 (0)
StFrancis	NaN (NA)	0 (0)	0 (0)
West Coast	NaN (NA)	0 (0)	0 (0)

Individuals

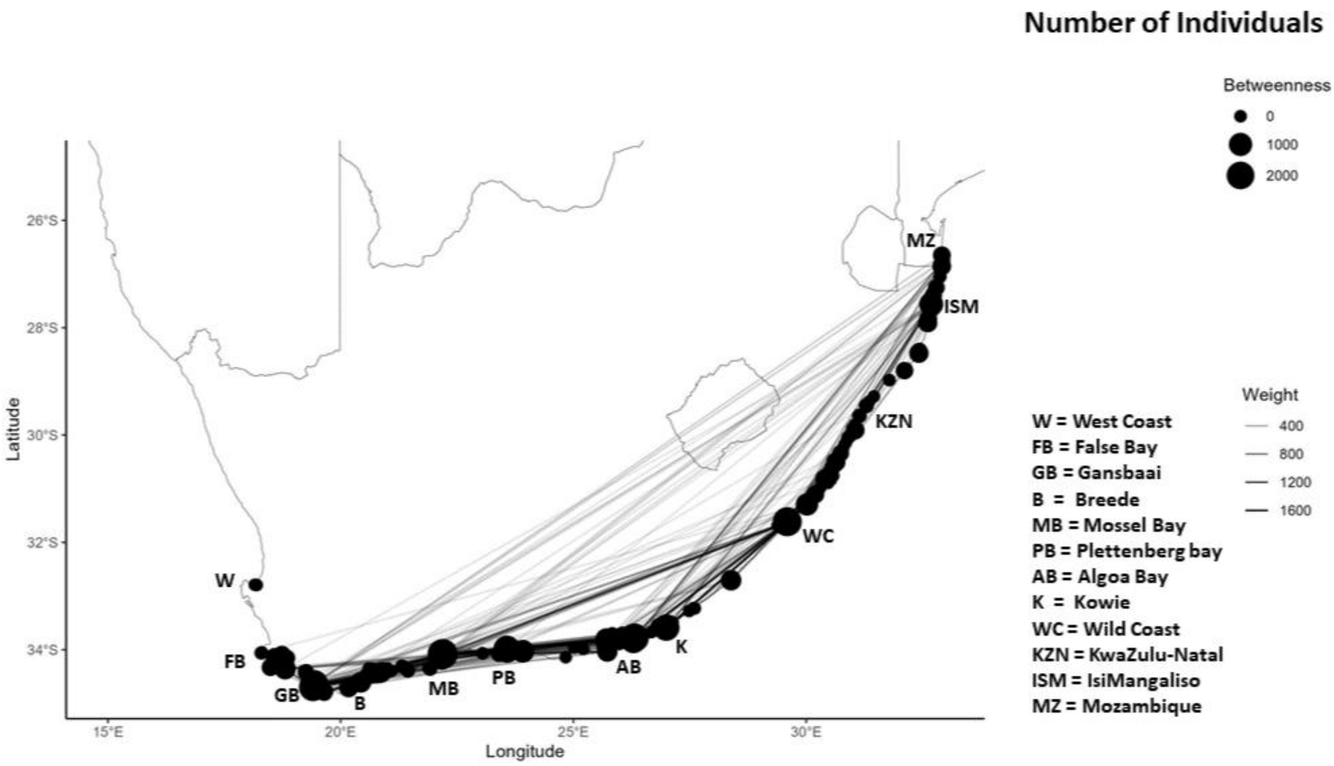

Figure 5.4(a): Network of white shark acoustic detections collected between 2012 and 2021 in South Africa. Each node represents a receiver, and each edge describes successive detections (movement) between each pair of receivers. The nodes are weighted by the total number of individuals, i.e., the number of incoming and outgoing edges, and labelled by location of interest. Edges are weighted by the total number of connections between nodes.

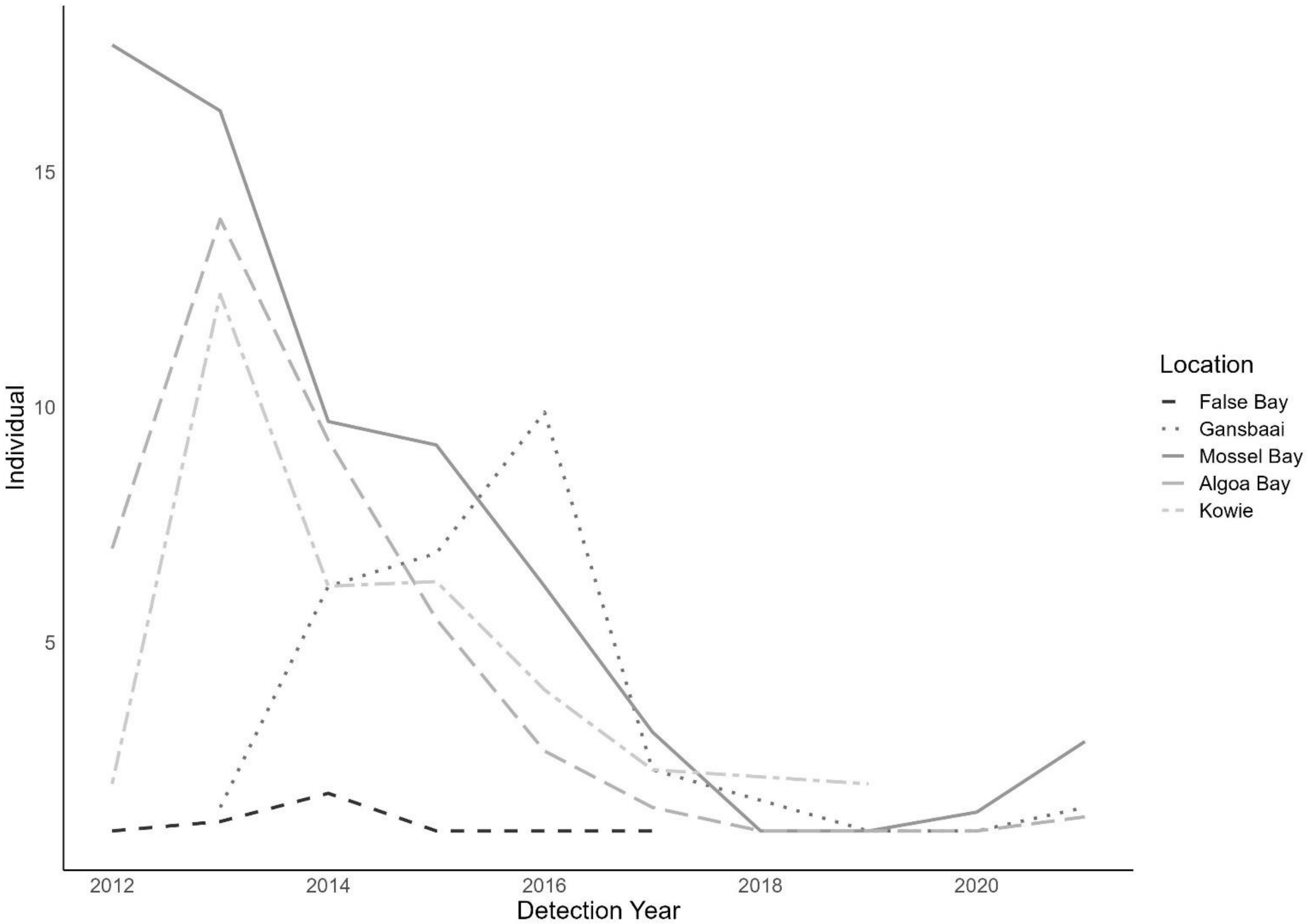

Figure 5.4 (b): Timeline of the number of individuals detected 2012-2021. This is the same metric as Figure **5.4(a)** but extracted for networks run annually. Only a subset of the data were plotted and illustrate those locations with the highest numbers of sharks detected.

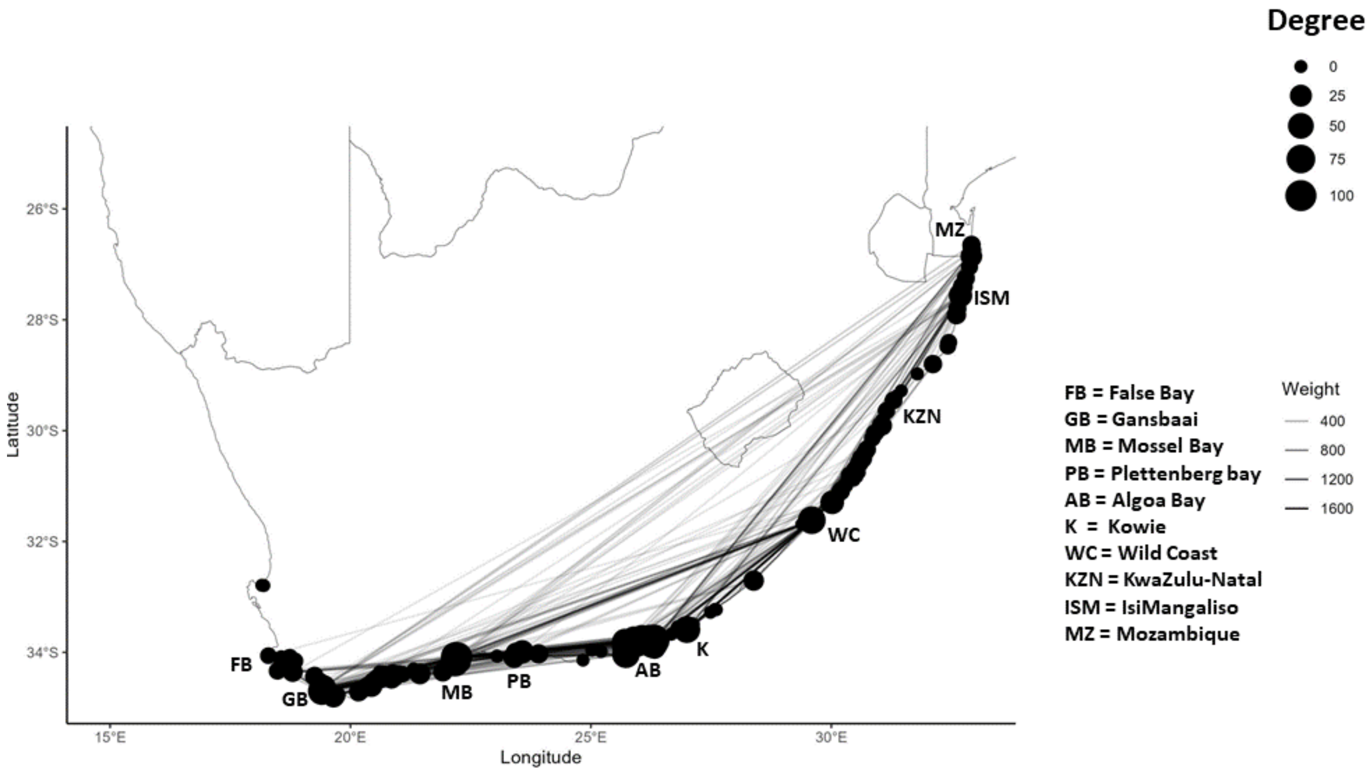

Figure 5.5 (a): Network of white shark acoustic detections collected between 2012 and 2021 in South Africa. Each node represents a receiver, and each edge describes successive detections (movement) between each pair of receivers. Node is weighted by *Degree*, the number of incoming and outgoing edges, and labelled by location of interest. Edges are weighted by the total number of connections between nodes.

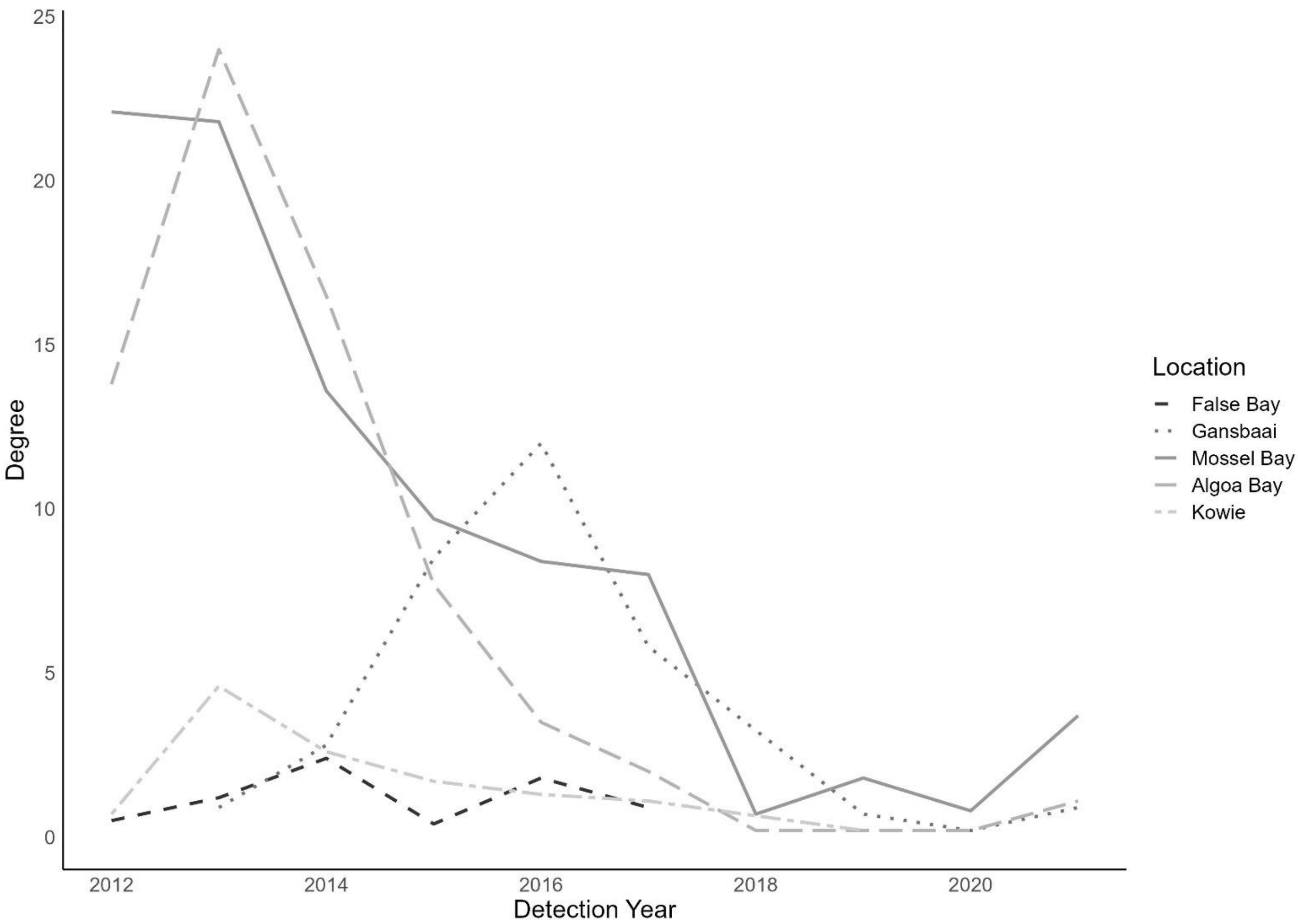

Figure 5.5 (b): Timeline of the centrality metric *Degree* 2012-2021 This is the same metric as Figure 5.5(a) but extracted for networks run annually.

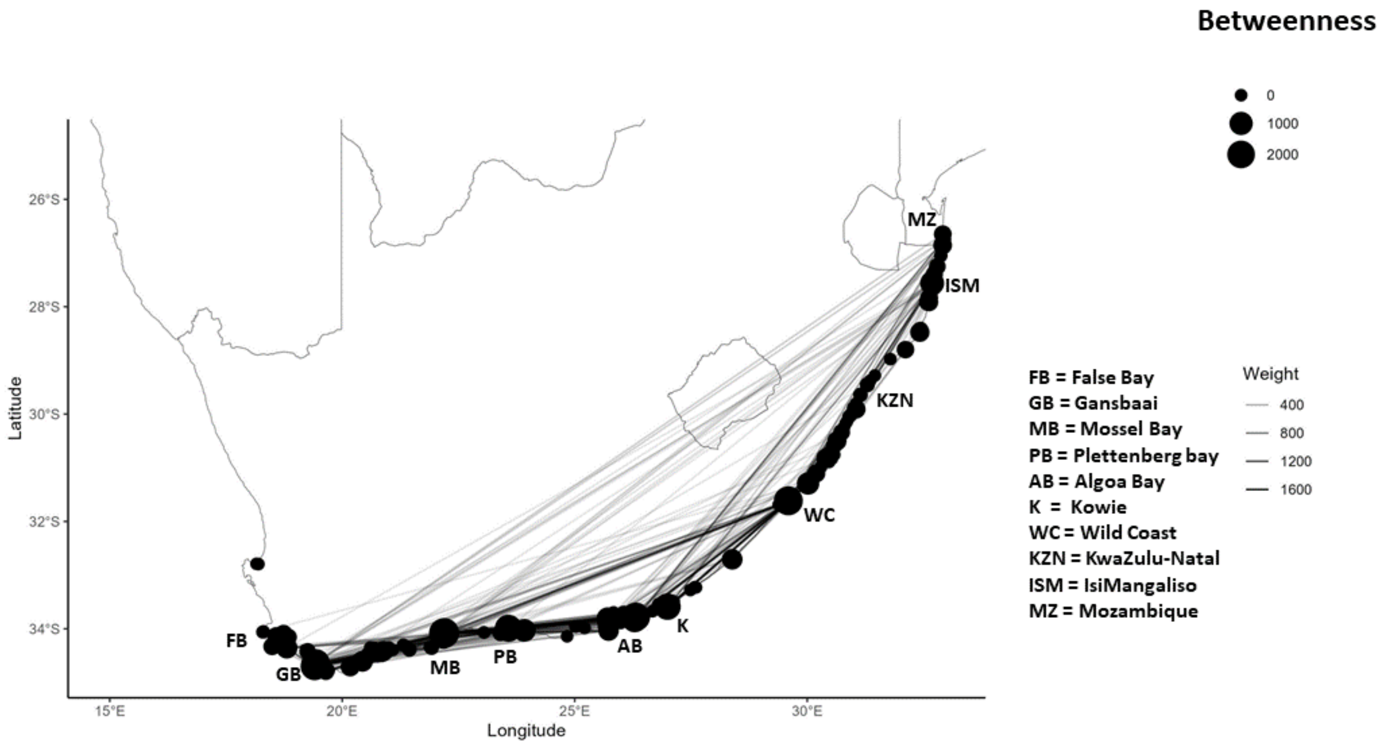

Figure 5.6(a): Network of white shark acoustic detections collected between 2012 and 2021 in South Africa. Each node represents a receiver, and each edge describes successive detections (movement) between each pair of receivers. Node is weighted by *Betweenness*, the number of shortest paths that each node lies on and labelled by location of interest. Edges are weighted by the total number of connections between nodes.

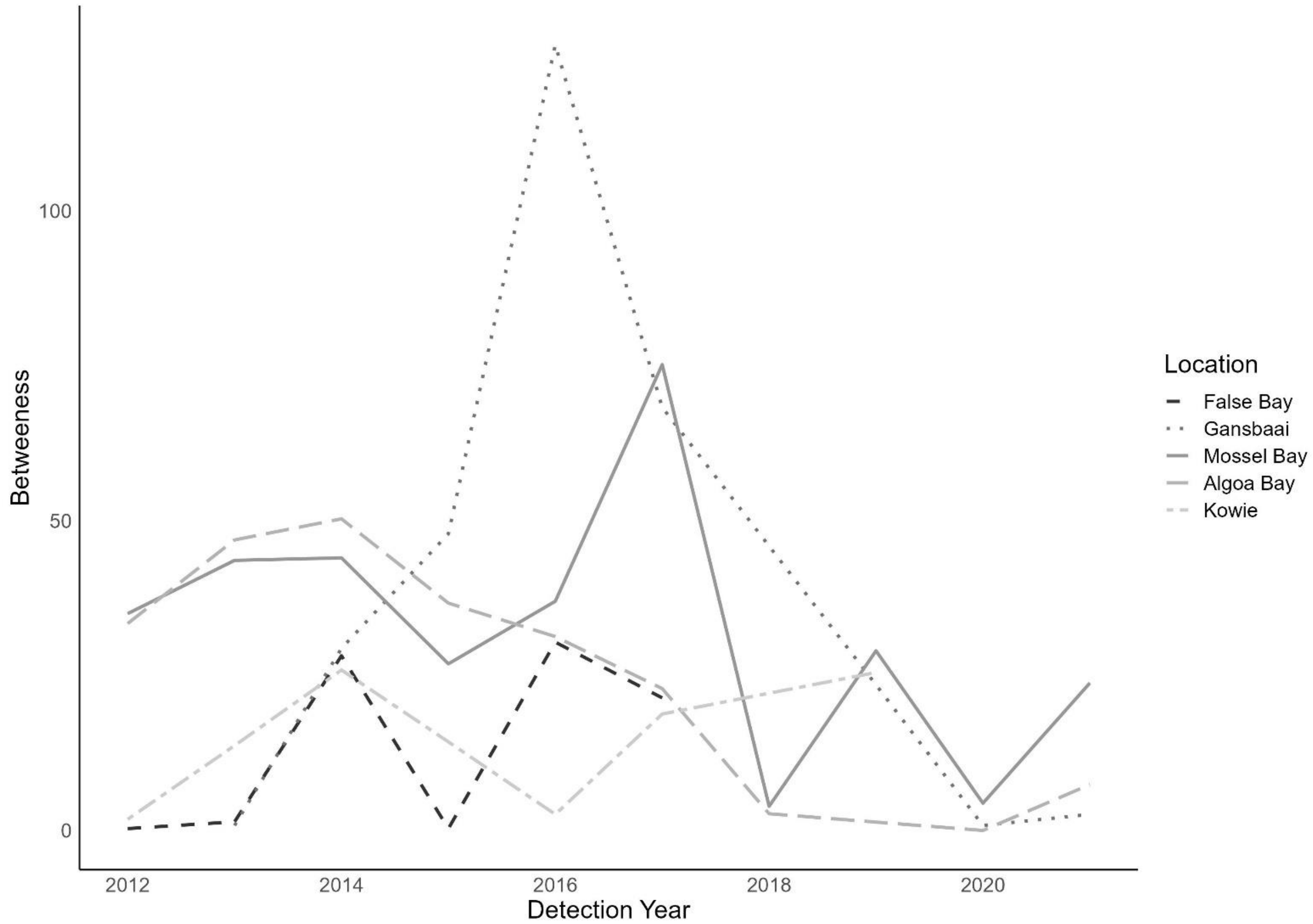

Figure 5.6(b): Timeline of centrality metric *Betweenness* 2012-2021. This is the same metrics as figure 5.6(a) but extracted for networks run annually.

Which sites function as key connectivity nodes?

While variation between sites occured, Mossel Bay, Kowie, and Algoa Bay, had the largest mean total number of individuals detected (Table 5.1, Figure 5.4). The top three sites with the highest average *Degree* and *Betweenness* were Mossel Bay, Algoa Bay, and Gansbaai (Table 5.1).

Individual detections 2012-2021

When the metric data were calculated for annual networks for individuals (Figure 5.4), an initial increase in all detections occurred in 2012, across all locations, due to high tagging effort in 2012. In 2015, False Bay abruptly dropped to zero and remained with no detections at this site or West of it for the following seven years. Conversely, individual detections in Gansbaai increased in 2015, peaked in 2016 then dropped abruptly in 2017. Mossel Bay and all receivers at locations further east continued to log few detections after 2017, with a very slight increase in 2021, as opposed to the west, between False Bay to Gansbaai, where detections remained consistently between 0 and 1 per year.

Centrality metric: Degree 2012-2021

The centrality metric of node *Degree* represents the connections that a specific node has varied across sites and between years (Table 5.1, Figure 5.5). The highest average *Degree* was 36.4 and occurred at Mossel Bay, followed closely by an average of 34.7 at Algoa Bay (Table 5.1, Figure 5.5). The third highest average *Degree* (22.0) occurred at Gansbaai.

When *Degree* was explored per year, all regions dropped sharply between 2016-2018. Mossel Bay was the only location that increased after 2020. False Bay dropped to 0 in 2017, Gansbaai peaked in 2016, then dropped to between 0 and 1 post-2019. Breede increased after 2019 with *Degree* the highest east of Breede until 2021.

Centrality metric: Betweenness 2012-2021

The highest average *Betweenness*, the centrality metric representing 'passing through a location, was at Plettenberg Bay 504.8 (Table 5.2, Figure 5.6). The second and third highest average *Betweenness* were 402.8 and 325.2 and were observed at the Wild Coast and Gansbaai, respectively. When broken down yearly, *Betweenness* peaked in False Bay and Gansbaai before 2016, then dropped abruptly to zero for False Bay in 2017. *Betweenness* declined steadily for Algoa Bay and increased in Mossel Bay and Kowie after 2016. Furthermore, this metric increased in Algoa Bay in 2021.

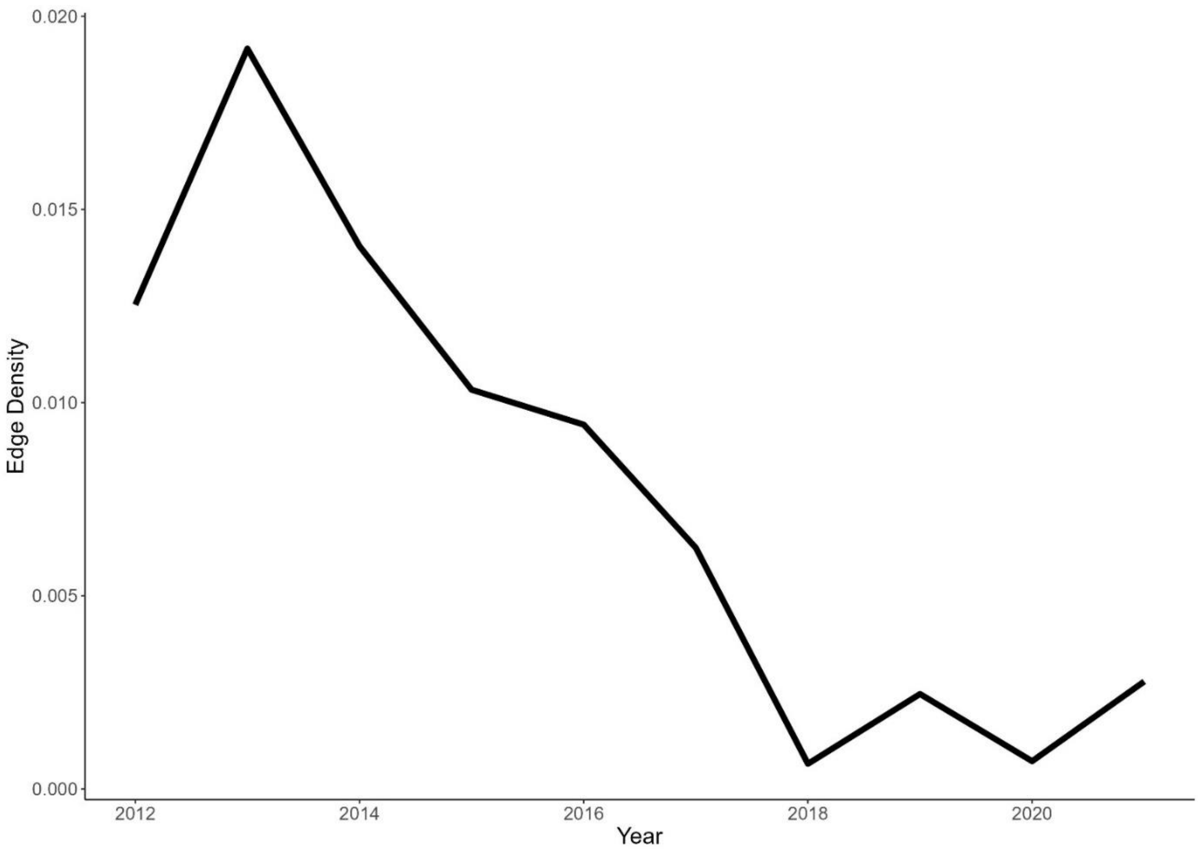

Figure 5.7: Edge density plot showing tag detections through the network over time.

5.3.2 Individual flight responses

In November 2016, prior to the white shark carcasses washing on shore in Gansbaai (Chapter 3, Towner et al 2022a), there was an additional migration of white sharks from the area (ID 34037, 34102, 56102, 6264, 6266, 6267, 6268, 6270, 6271, 6277, 6280; Figure 5.8), that coincided with the sightings of killer whales in False Bay (D. Hurwitz, pers. comm.) in October 2016.

Three white sharks (ID 6266, 6267, and 6277) returned to Gansbaai in early 2017. Data from these three acoustically tagged white sharks (ID 6266, 6267, and 6277), which were present at the time the first carcass washed up, showed departures of those individuals from the area after killer whale predations took place (Figure 5.8). A 3 m TL female shark was tagged in Gansbaai on 7 September 2016 and was present until 9 November 2016. It returned seven months later, on 3 April 2017, and was detected until 13 April 2017 in Gansbaai. Then five days later, it was detected 400 km east in Plettenberg Bay, swimming at an average speed of 3.3kms/hr. It then continued eastwards towards Port St. Johns, a total distance of 1058 km. A 3.2 m TL male white shark was tagged in Gansbaai on 11 September 2016 and was present until 21 November 2016. It was then detected in Gansbaai six months later on 9 May 2017, two days after the fourth white shark washed up. Then five days later, the shark was detected 200 km away in Mossel Bay (Figure 5.11). Another 3.2 m TL male white shark was tagged in Gansbaai on 20 September 2016 and was present until 21 November 2016. It returned to Gansbaai on 9 May 2017. Like the other tagged white sharks, it did spend time in Gansbaai but moved rapidly eastwards over the subsequent four weeks. It was then detected 50 km north of East London, 900 km east of Gansbaai (Figure 5.8).

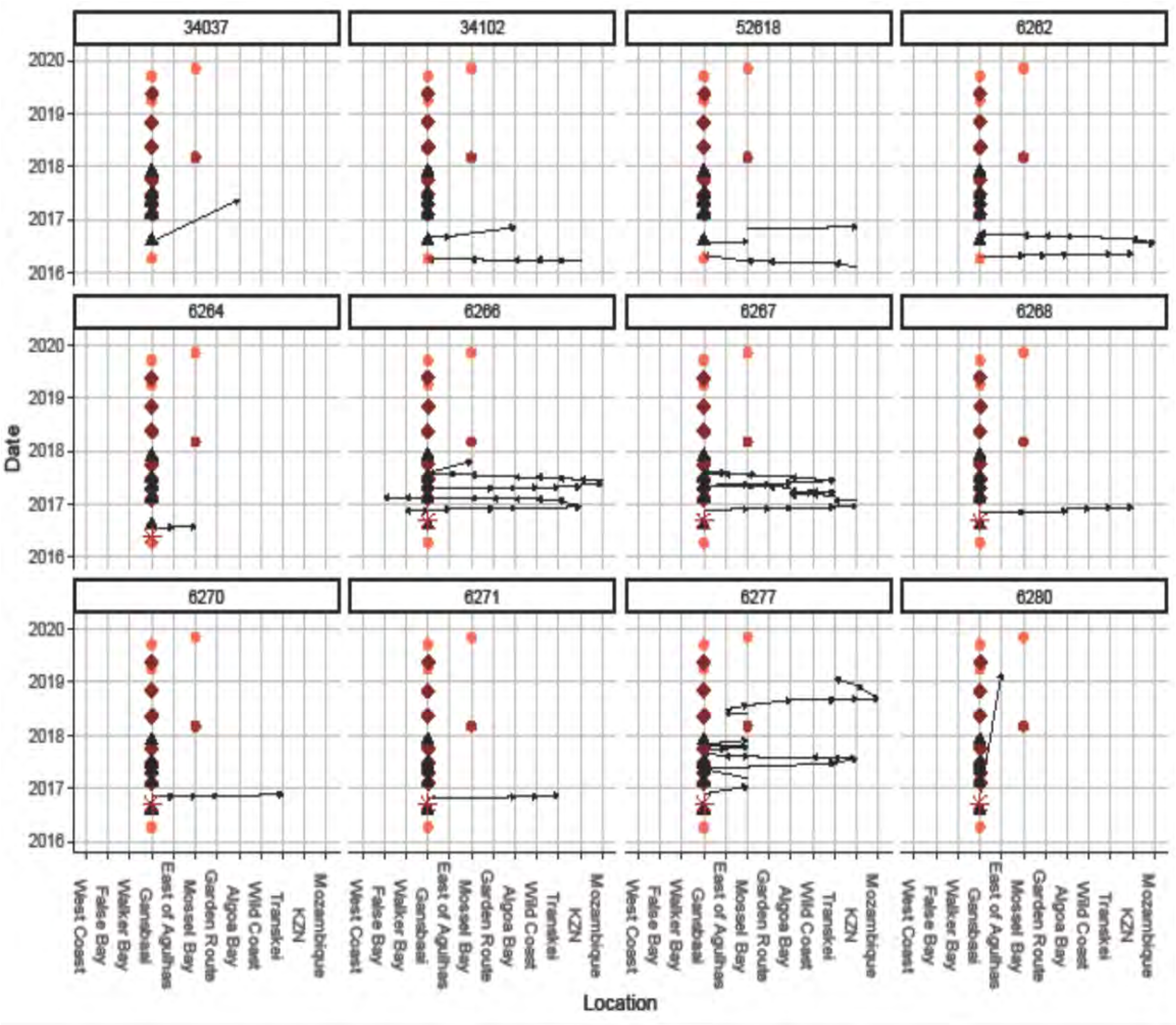

Figure 5.8: Movement data on *Carcharadon carcharias* tagged in Gansbaai (except 34037 and 52618, which were tagged in Mossel Bay and Algoa Bay, respectively) demonstrating departures at the time of *Orcinus orca* sightings and predations, 2016 - 2019. Brown stars represent shark tagging date (unless the animal was tagged prior to 2016), black triangles represent dead *C. carcharias*, dark red diamonds represent *Port* and/or *Starboard* sightings and light red dots represent other *O. orca* pods. Sites are distributed as per Figure 5.1. Black lines with arrows represent movements approximated by receiver detections at other locations.

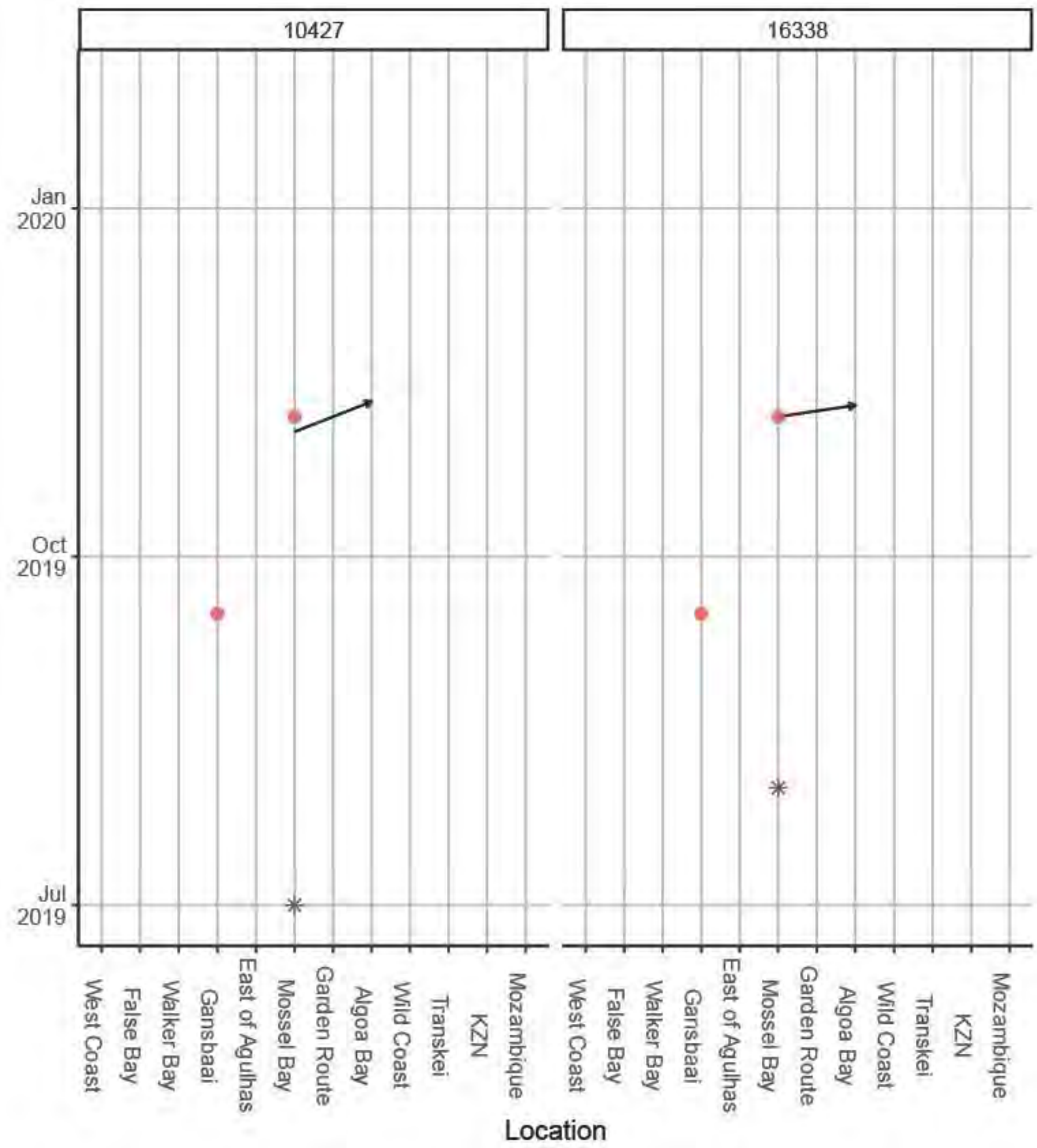

Figure 5.9: Movement data on two *Carcarodon carcharias* tagged in Mossel Bay demonstrating departures at the time of *Orcinus orca* sightings and predations between July 2019 and January 2020. Brown stars represent shark tagging date, and light red dots represent *O. orca* pods. Black lines with arrows represent movements approximated by receiver detections at other locations.

5.3.3 Killer whale observations

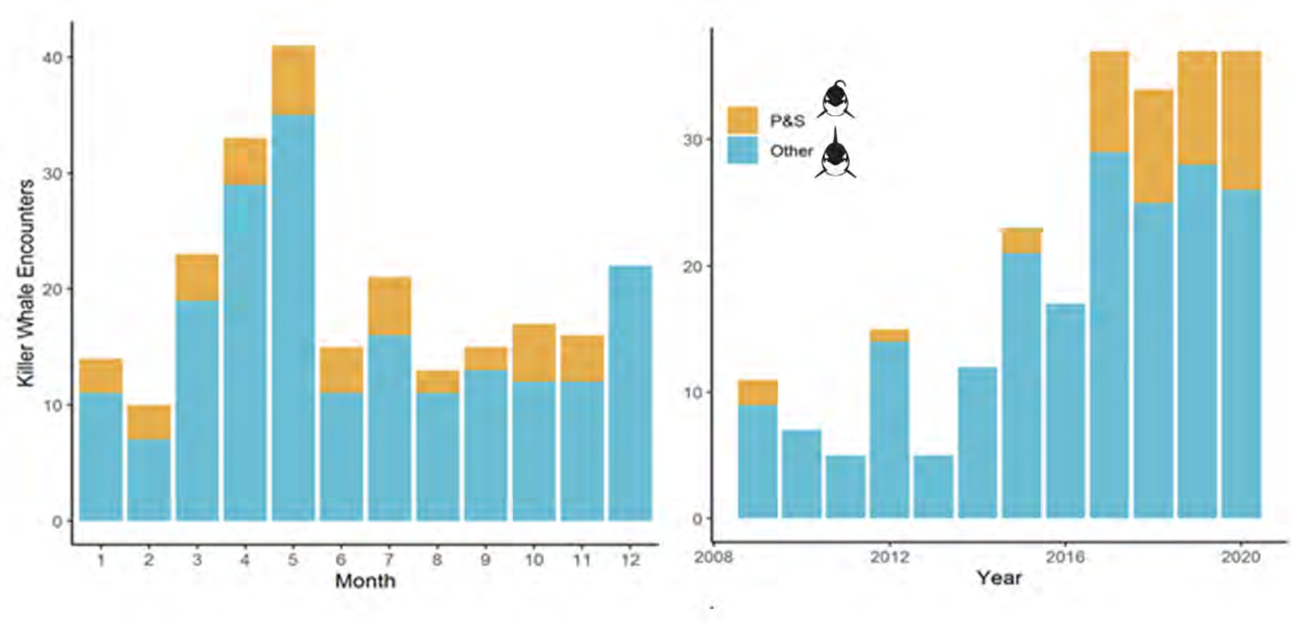

Figure 5.10: Temporal patterns in available records of killer whales *Orcinus orca* in southern Africa between January 2008 and December 2020. Data are disaggregated between the highly distinctive killer whales *Port* and *Starboard* (P&S) and other whales. (Data are from Elwen et al. 2022).

The number of killer whale reports in South Africa increased from 2008 to 2020, with a noticeable increase in 2017 in all killer whales and a striking increase in reports of *Port* and *Starboard* (Fig 5.10). Within years, the timing of sightings showed a distinct peak of killer whale sightings between April to May (Autumn) but year-round presence of *Port* and *Starboard*, specifically between 2015 and 2020 (Figure 5.10).

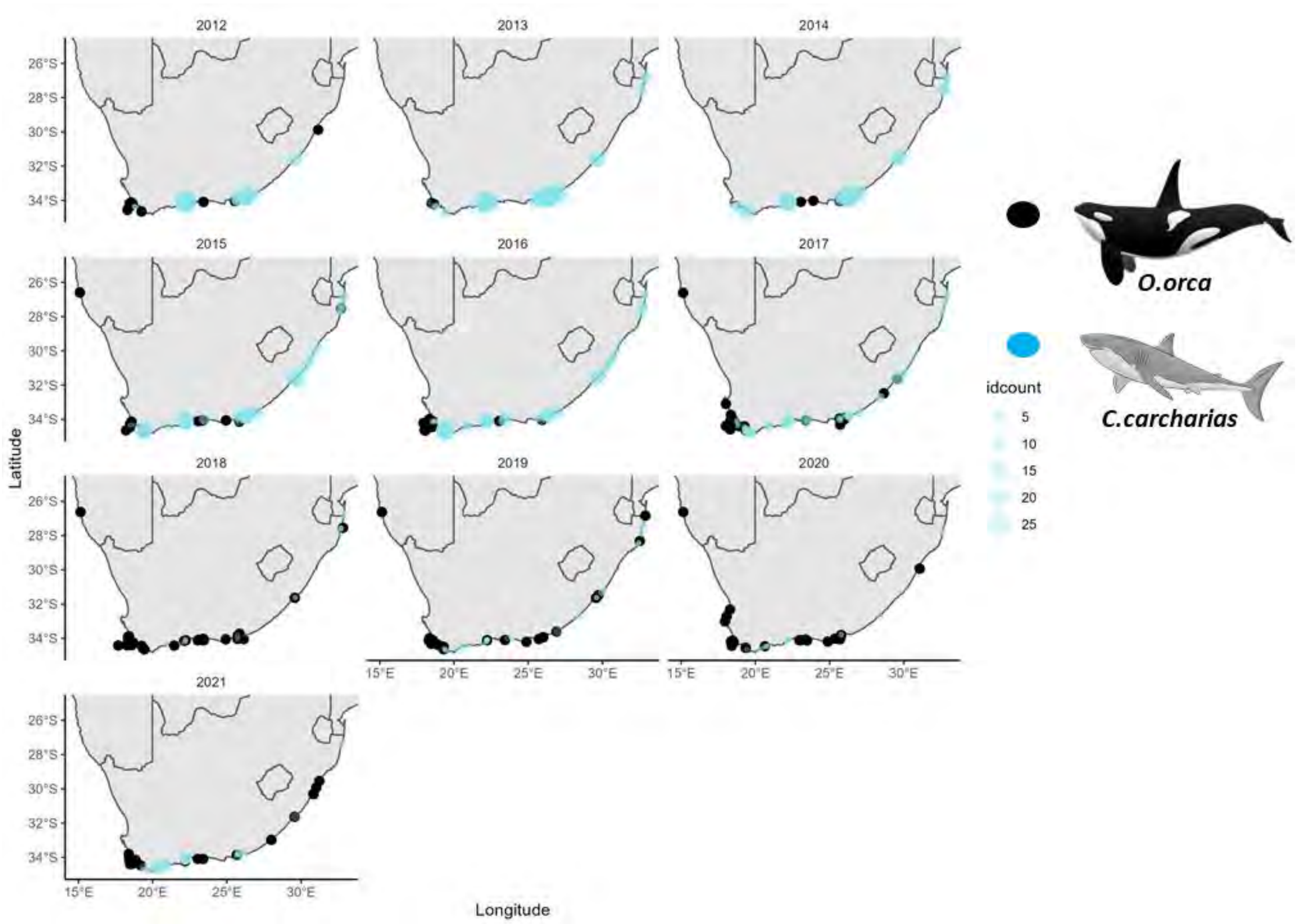

Figure 5.11: Distribution of all available records of killer whales, *Orcinus orca,* and the number of individuals detected from 118 acoustic-tagged white sharks, *Carcharadon carcharius* in southern Africa between January 2012 and December 2021 (Data Elwen et al. unpublished).

White sharks were present (between 5 and 10 individuals) in False Bay between 2012 to 2015, yet were not detected or sighted by cage dive operators or scientists from 2018-2021 (Figure 5.11) Conversely, Killer whale sightings occurred in False Bay in 2012 but remained primarily to the West around the Cape Peninsula. In 2015, killer whale presence spread into False Bay (largely *Port* and *Starboard*), and in 2017 sightings began to increase further East towards Gansbaai. Between 2018 and 2021 killer whale sightings spread further east but with a pronounced presence between False Bay and Gansbaai (Figure 5.11)

5.3.4 White shark annual catches Algoa Bay

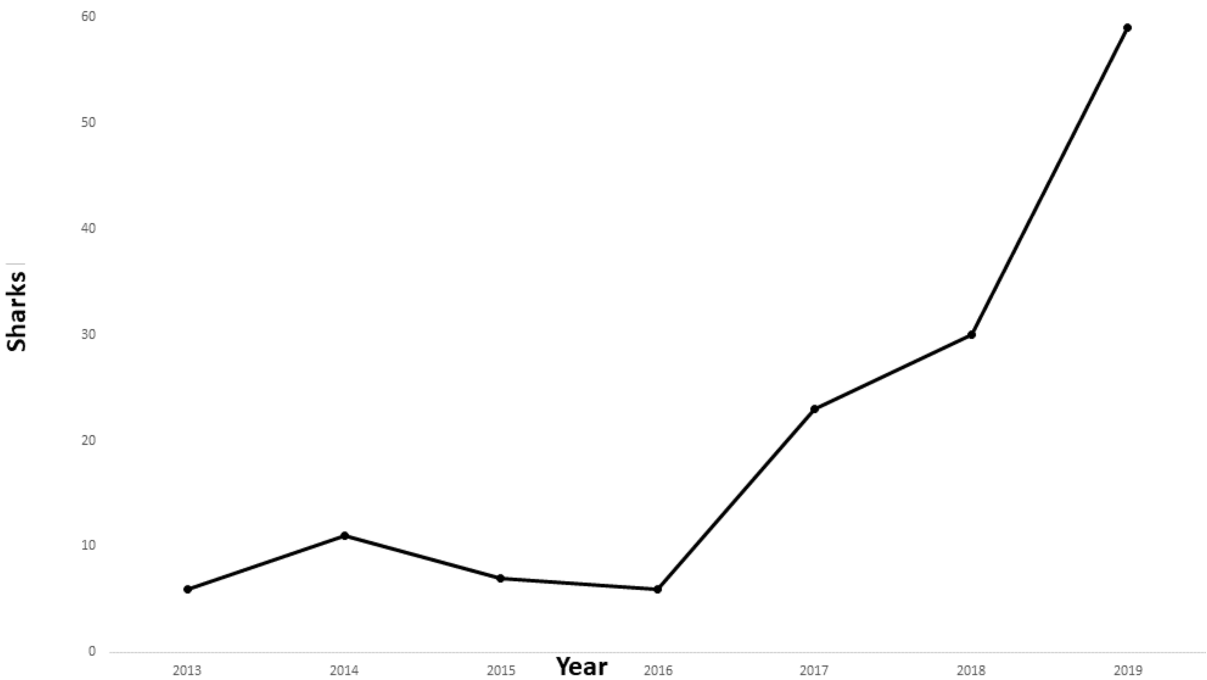

Figure 5.12 Catches of white sharks (released alive) by five recreational anglers inshore of Algoa Bay between 2013 and 2019.

Between 2013 and 2016 annual white shark catches on the inshore of Algoa Bay remained between 6 and 11 sharks (Figure 5.12). However, there was a steep increase of 23 sharks caught in 2017. In 2018 and 2019, 30 and 59 white sharks were caught, respectively (Figure 5.12).

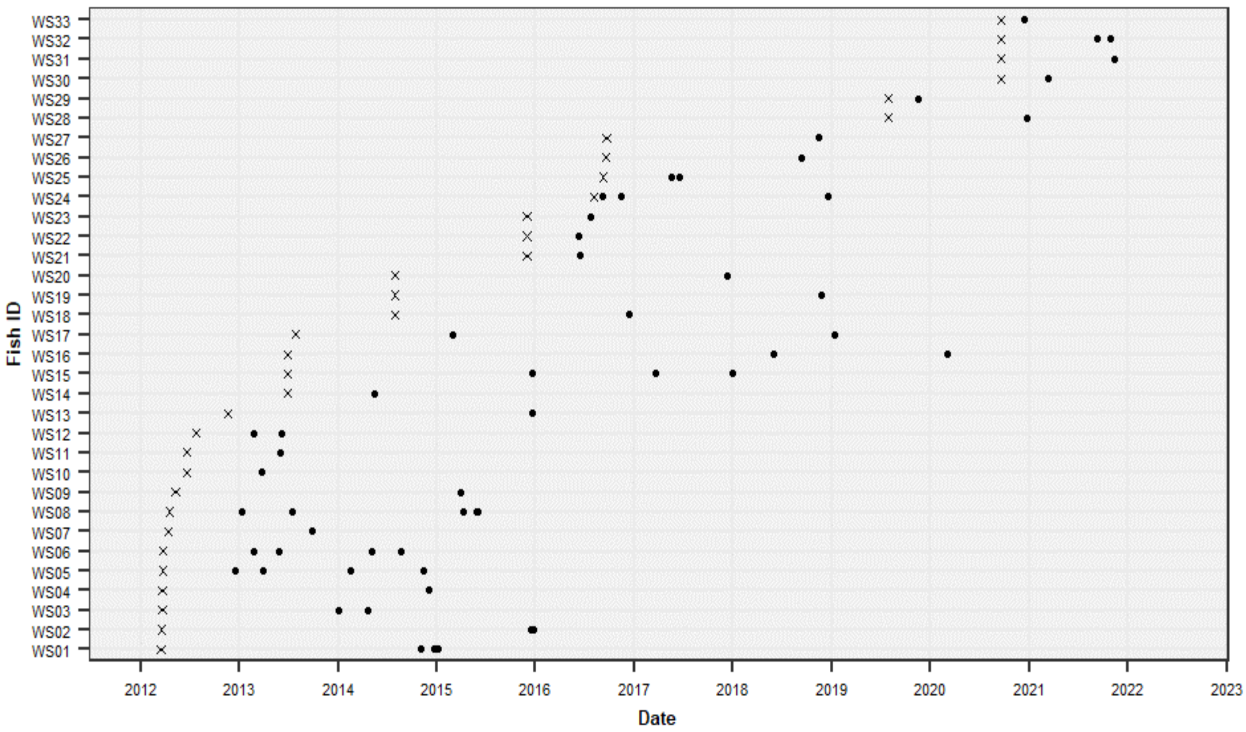

Figure 5.13: Detections of individual acoustically tagged white sharks, tagged in SA on Mozambique receivers (ATAP) 2012-2022. × represents tagging date**.** Thirty-three white sharks were recorded in Mozambique, with detections of 15 individuals after 2017 (Data courtesy of Taryn Muray, ATAP).

5.4 Discussion

Spatial network analysis showed that individual white shark detections ceased after 2018 in most coastal areas of South Africa. Many edges were observed within the network between non-neighboring nodes, which could suggest some offshore movement. While Kock et al. 2022 described the offshore movement of Southern African white sharks, tag transmissions ceased in 2014 with very little data on offshore movement collected after this time period. One juvenile male white shark externally acoustic tagged in May 2022, swam from the tagging site of Struisbaai (WC of SA) to Chidenguele, Mozambique, a distance of approximately 1,800 km in 4 months. The sharks' identification was confirmed by Baited Remote Underwater Video survey (BRUV) footage, yet no detections of the tag ID were recorded on the ATAP receiver network in South Africa. Although this is only one individual, it confirms that a white shark remained outside the network range (as it would have been detected) and thus likely utilised a more offshore migratory corridor eastwards (Appendix, AP6).

Other explanations for the loss of individual white shark tag detections in South Africa are that the tags were shed or programmed to end transmitting earlier than expected. Thirty-eight animals were internally tagged with ten-year tags in 2012, which eliminates shedding. The raw tag data from this batch was carefully examined by a scientist involved in the development of the V16 transmitter. The results confirmed that the tag battery life would have lasted until 2022, with no significant decay, as evidenced by another shark species tagged internally with the same batch of tags (Appendix AP6). The conclusion was that the large disappearance of these tags from the SA coast is likely biologically driven (Webber pers. comm.) The technology is robust enough that for so many tags to have manufacturing issues is very unlikely.

Of the few remaining tagged white sharks that were detected after 2018, the epicenter of the species distribution was no longer centered in the historical Western Cape hotspots as described in all previous satellite tagging and boat-based studies (Ferreira and Ferreira 1996, Dudley 2012, Bonfil et al. 2006, Kock et al. 2022). Interannual trends of the network metrics at each location did not reflect a gradual decline in numbers but rather abrupt declines in white shark space use in the western locations of False Bay and Gansbaai in 2015 and 2017, respectively. Conversely, isolating white shark detection data for Mozambique alone showed that fifteen white sharks tagged in South Africa were detected on ATAP receivers after 2017, contrasting the patterns reflected in the Western Cape of South Africa (Figure 5.13)

The arrival in the Western Cape of killer whales *Port* and *Starboard* timed precisely with the white sharks disappearing in the Western Cape locations confirmed by white shark dive operations sightings data and telemetry (Towner et al. 2022a, Chapter 3). Conversely, the movements of the killer whales *Port* and *Starboard* did not extend into eastern locations during this study period (although they did enter Mossel Bay repeatedly later in 2022), and the pair have never been sighted in Mozambique (Chapter 4).

A location with high *Betweenness* indicates that it is a crucial site for population connectivity (Mourier et al. 2019). Plettenberg Bay and the Wild Coast locations in the Eastern Cape were overall the highest regions of connectivity post 2018. Similarly, node *Degree* (the number of incoming and outgoing edges linked to a node, i.e., the highest movement to and from a location) was highest at Mossel Bay, followed by Algoa Bay. These centrality metrics indicated that central South Coast and Eastern Cape sites became key movement corridors and areas for connectivity for white sharks over the study period in South Africa, in contrast to the Western Cape sites. While this is the first spatial network analysis to be conducted on white shark data in South Africa, earlier satellite tracking papers indicated that the Western Cape was utlised significantly more by white sharks before 2015 (Bonfil et al. 2005, Kock et al. 2022).

Changes in patterns of white shark distribution have been demonstrated elsewhere. Post-2014, in the North West Atlantic, numbers of white sharks increased off the West coast of the US. This was in response to recovering populations of North Atlantic Gray seals *Halichoerus grypus* and enforced protection of the white shark population from 1997 (Curtis et al. 2014, Burgess et al. 2014, Winton et al. 2021). Likewise, an increase in juvenile white sharks was recorded in coastal California from 2014 to 2019. The space use shift was due to a significant marine heatwave associated with persistent El Nino conditions in the North Pacific (Tanaka et al. 2019). While other physical and biological driving factors could be responsible for changes in white shark space use in South Africa between 2012-2021, these factors were examined (see appendix AP10,11,12, DFFE report, Towner et al. 2022a, Kock et al. 2022) and no significant trends are apparent that would justify such abrupt disappearances of white sharks between 2015 and 2018. However, the time periods that white sharks vanished in the Western Cape sites coincided precisely with the timing of the known shark-eating killer whales' presence increasing, strongly suggesting that predation and consequent escape responses from killer whales were the main driving factors triggering shifts in white shark space use.

The findings of this work support those of Jorgensen et al. (2019), who documented the displacement of acoustic-tagged white sharks by killer whales in California. Even though offshore killer whales were considered infrequent visitors to the region, killer whale presence was enough to elicit flight responses in tagged white sharks and a site abandonment for an entire season. Convincing evidence of flight responses in acoustic-tagged white sharks from Gansbaai and Mossel bay occurred demonstrating that individuals departed east at the time killer whales were sighted in both locations. Similarly, predation events by killer whales on sevengill sharks in False Bay in 2015 and 2016 led to the departure from the bay for several months (Engelbrecht et al. 2019) with similar flight responses to the sharks in this study documented using telemetry (Engelbrecht et al., unpublished data).

These data are also consistent with the findings of Pyle et al. (1999), who observed a killer whale hunt a white shark at the Farallon's on the 4th of October 1997. They subsequently saw only two white sharks through the duration of observations until the 1st of December 1997 (Weng et al. 2007). Similarly, in 2019 off the Neptune islands in South Australia, white sharks disappeared abruptly for three months after killer whales preyed on one white shark in front of a cage diving boat (Huveneers unpublished data). Acoustic tagging data supported these observations.

Changes in distribution may also relate to their using deeper waters to avoid predation threats. On the 16th of October 2000, an adult white shark (457cm TL) was satellite tagged in the Farallon islands, California. It remained at depths shallower than 77 m until the day of an observed killer whale attack, when a dive to 484 m occurred, indicating that the shark had left shelf waters close to the Farallon Islands (Weng et al. 2007). Geolocation data showed that the shark traveled in a westerly direction until it reached the main Hawaiian Islands, a distance of approximately 4,000km (Weng et al. 2007). Likewise, in May 2022, when killer whales preyed on white sharks in Mossel Bay, a 3.8m female white shark with a towed satellite tag displayed similar behavior. Her tag was only detected a month later >400km to the east, suggesting limited surface swimming behaviour and a flight response (A Towner unpublished data, Towner et al. 2022b, Chapter 4).

A sub-sample (n = 38) of white sharks from this study was also satellite-tagged (OCEARCH) in 2012. Large scale movement of these white sharks between 2012 and 2014 revealed that space use differed between sizes and sexes, with males and juveniles more resident and coastal and larger females more transient and offshore (Kock et al. 2022). In response to the pressure of being preyed on by killer whales, it is possible that larger white sharks, specifically females, reverted to predominantly offshore environments (Kock et al. 2022). Younger sharks could have been forced to move into other coastal areas, further to the east of South Africa, areas with less threat of encountering killer whales, specifically hunting sharks. However the range capability (<60 m depth, < 1 km detection range) of the receiver network was a limitation to this study, thus future work will focus on the use of satellite tags for tracking white sharks to overcome this caveat.

Algoa Bay is the white shark's most eastern aggregation site in South Africa, with a Cape Fur Seal colony. Dicken and Booth (2013) have suggested that the bay serves as a nursery area in the austral summer. The fact that during 2016-2019 the catches of white sharks by recreational anglers increased could support the hypothesis that juveniles move into the bay from the West. However, verification from tagging data, Photo ID, genetics and Catch per unit effort data data would be needed to verify this. Nonetheless, Kock et al. 2022 showed that False Bay and Gansbaai were critical hotspots of white shark movement in the Western Cape between 2012-2014, the period before *Port* and *Starboard* appeared and started to hunt white sharks in False Bay and Gansbaai.

The pair of killer whales (*Port* and *Starboard*) have effective hunting strategies for sharks, and others appear to have joined their group (at least periodically) and have similar hunting tactics (Towner et al. 2022b, Chapter 4). This is concerning for the white shark population in SA. There are no clear-cut answers to managing killer whales preying extensively upon large shark species in coastal waters. This Chapter provides evidence of one marine apex predator species being displaced by another in less than a decade. Marine apex predator loss can lead to the collapse of fragile coastal ecosystems due to trophic cascades (Estes et al. 2011, Towner et al. 2022a, Chapter 3). Given the rate at which these interactions are increasing in South Africa (in less than seven years, white sharks have moved away from all three main western Cape sites), actions should be put in place to prevent even more economic, ecological, and bather safety impacts.

CHAPTER 6: SYNTHESIS

6.1 Overview of research findings

The objective of this thesis was to investigate the movement patterns of a population of white sharks in southern Africa and analyse their behavior on both fine and large scales (Chapter 2 and Chapter 5). Not all predators exert pressures on ecosystems in the same way (Heupel et al. 2014) and Chapter 2 provided novel evidence that individual white sharks not only display preferences for specific hunting modes, but also switch between them, while hunting pinnipeds. These behaviours were not previously documented in white sharks (Le Boeuf et al. 1992, Hammerschlag et al. 2006, Martin et al. 2009) and it is suggested that future ecosystem models consider it. This work also provided important baseline data on habitat use of white sharks at a key Western Cape location, Gansbaai, before displacement of the species occurred. Most research outputs on white sharks from Gansbaai prior to this study were observations collected from chumming vessels (Ferreira and Ferreira et al. 1996, Johnson and Kock 2005, Towner et al. 2013) and this study, together with Jewell et al. 2014, explored the natural fine scale movement of white sharks in the region by both active tracking and deploying acoustic receivers within the bay (Chapter 2 and Chapter 5). Tracking white sharks for over 400 hours established core hotspots for white shark habitat use (Jewell et al 2014, Towner et al. 2016) how they capture prey (Chapter 2, Towner et al. 2016) and the time they spend at chumming vessels (Chapter 2, Towner et al. 2016). In support of other studies, white sharks displayed less time at cage dive vessels, over time (Johnson and Kock 2005, Laroche et al. 2009). Recent work in the Neptune islands, South Australia, determined that when effort of chumming vessels increases over time, the white sharks residency periods in the region extended (Niella et al. 2023). However, when management regulations were implemented, such as restriction on vessel access days, white shark residency returned to baseline, even with the presence of cage-dive vessels (Niella et al. 2023). It was not possible to determine the impacts of cage-dive vessel presence on overall white shark residency in Gansbaai, as the white sharks abandoned the site of Dyer Island shortly after the acoustic receivers were deployed in 2015 and such studies require long term monitoring over minimum two years (Chapter 3). It is certainly worth investigating this further if white sharks do return, specifically with marine wildlife tourism increasing in popularity (Niella et al. 2023).

Killer whales appeared and began hunting white sharks in the research site(s) during the middle of the study and provided a unique opportunity to investigate these rare behavioral interactions together with examining how white shark movement and habitat use changed in response to predation pressure (Chapter 3, 4 and 5). There is an increasing need to better understand why and how various factors affect the relative strengths of contrasting pressures and interactions within ecosystems (Schmitz et al. 2004, Borer et al. 2005). Direct observations of predator-prey encounters are rare, especially in aquatic environments (Heithaus 2009, Estes et al. 2011). Although white sharks' distribution and habitat preferences have been the subject of numerous research papers (Bonfil et al. 2005, Block et al. 2011, Spaet et al. 2021) there have been few studies on the impacts that killer whales have had on white sharks; specifically, how they hunt the sharks and influence their behaviour together with the impacts on coastal ecosystems caused by the sharks being displaced (Chapter 3, Pyle et al. 1999, Jorgensen et al. 2019, Moxley et al. 2019). Top-down influences upon community structure have been identified in both terrestrial and aquatic ecosystems (Shurin et al. 2002, Schmitz et al. 2000), yet a particularly troubling aspect of trophic cascade research is the paucity of studies involving top predators, largely due to the difficulty of assessing their effects at long temporal and large spatial scales (Beschta and Ripple 2009). This work provided important insights into the mechanisms behind one wild oceanic apex predator species displacing another, which is a valuable contribution to the ecological literature, specifically regarding marine predators.

The strategies killer whales employ while hunting white sharks had never been documented or filmed in detail, neither had the strategies white sharks used to try and evade killer whale predation (Chapter 4). This research analysed novel aerial footage confirming that killer whales worked together to subdue and handle the white sharks in coastal bays within South Africa (Chapter 4). Group size in the carnivores is adjusted to prey size, with the larger hunting groups attacking larger prey. Social hunting behaviour in arachnids revealed that the agelenid spider *Agelena consociate* captured small prey, yet when large prey entered the web, individual spiders co-operated, hunting prey together (Burgess et al. 1976). Pack hunters target the largest prey of all predators (Enders 1975). Among the Carnivora, the solitary species, e.g., cheetahs *Acinonyx jubatus*, leopards *Panthera pardus*, striped hyenas *Hyaena hyaena*, hunt prey smaller than themselves as opposed to the group hunters, e.g., spotted hyenas *Crocuta crocuta*, wild dogs *Lycaon pictus* and wolves *Canis lupus*, which all hunt prey larger than themselves (Kruuk 1975, Schaller 1972). Groups of animals exhibit higher foraging success in capturing prey compared with solitary individuals. It is only among fishes that pack-hunting is not associated with an increase in prey size. Piranha *Serrasalmus* spp. are the only group of pack-hunting fish that attack prey larger than themselves (Griffiths 1978). While some solitary killer whales have occasionally been recorded forging alone in Cape Town (Elwen et al. in prep) this research has documented that when killer whales are hunting white sharks in South Africa, they often use social and cooperative hunting tactics, presumably due to the large size of white sharks and the difficulty of restraining and handling them. However, it is likely they are capable of hunting sharks alone too.

Wild predators feed on specific body parts according to their macronutrient composition, which may have significant implications for applied wildlife and conservation management as well as ecological and foraging theory (Kohl et al. 2015). The majority of direct studies on vertebrate predators have been undertaken on domesticated animals with a paucity of information on wild predators. This raises the questions of how widespread similar responses are among non-domesticated vertebrate predators, under what ecological circumstances they are expressed, and how they influence individual performance (Wilder et al. 2013, Simpson et al. 2010). Answers to such questions will have significant implications for managing predator populations and the ecological communities of which they inhabit (Kohl et al. 2015).

This study gave novel insights into the condition of white shark carcasses, directly after they were preyed on by killer whales, revealing how the killer whales extract the sharks livers for consumption (Chapter 3 and Chapter 4). Killer whales first immobilise white sharks, then either tear open or bite into the area of the pectoral girdle, to directly access the lipid rich liver (Chapter 3 and Chapter 4). Predatory gastropods *Nucella lapillus* learned to handle and drill into European black mussel shells *Mytilus edulis* in the best position to reach the most energy dense part of the mussel, this allowed close access to the underlying digestive gland, which is the richest source of glycogen and is softer, thus more easily ingested, than muscular tissue (De Zwaan & Zandee, 1972, Hughes and Dunkin 1984). This study confirmed that killer whales are most often selectively removing the white sharks livers and discarding the rest of the carcass. Various carnivores selectively consume specific body parts of their prey, Harbour seals *Phoca vitulina* consume the bellies of pre-spawning female salmon *Oncorhynchus nerka* containing high-lipid roe (Hauser et al. 2008), brown bears target the lipid-rich brain tissue and roe of salmon (Erlenbach et al. 2014), Cape fur seals selectively feed on the stomach contents and livers of blue sharks *Prionace glauca* (Reynolds 2013), while wolves first feed on the internal organs of large ungulates (Bosch et al. 2015). In order to effectively address conservation of vertebrate predators, it is critical to understand not only their hunting dynamics but also their nutritional ecology (Kohl et al. 2015).

Lipids are the most energy dense macronutrient and in addition to serving as an energy source play important roles in cellular processes and membrane fluidity (Kohl et al. 2015). Due to a normally lipid rich diet, some carnivores have lost the ability to convert fatty acids, making some of them essential nutrients that carnivores must consume (Rivers et al. 1975). Flaccid dorsal fins are features that both *Port* and *Starboard* have and can be attributed to various factors, including immune suppression and nutrient deficiency in wild killer whales (Visser 1998). Lipids may be a high priority nutrient they need to ingest. While determining this was beyond the scope of the study, muscle tissue biopsy samples have been obtained from the killer whale pair in Cape Town, along with other killer whales in South Africa (Elwen et al. in prep). Stable isotope analysis will reveal if other nutrient sources are being supplemented in the killer whales diet, additional to shark livers. *Port* and *Starboard* have been observed hunting other species such as sunfish *Mola mola* and Cape Fur Seals, however consumption was not confirmed in each interaction (Elwen et al. in prep).

The fact that other killer whales were observed hunting white sharks, additional to *Port* and *Starboard*, raises the issue of whether these animals have transferred knowledge through cultural transmission (Amelot et al. 2021, Chapter 4). This study implicated at least five individual killer whales working together to hunt white sharks in 2022 (Chapter 4). How the use of food may spread as a new behaviour, across individuals within populations over time, is poorly understood (Amelot et al. 2022). Longline fisheries in the subantarctic Crozet islands, began targeting Patagonian toothfish *Dissostichus eleginoides* in 1996. It took approximately 16 years for all 80 - 100 individuals of the killer whale population to start depredating the tooth fish directly from the set lines (Amelot et al. 2022). The capacity of predators to acquire new feeding strategies and/or to switch diet to new prey may depend on their level of specialisation with some individuals being more opportunistic and innovative than others in their feeding strategies. Amelot et al.'s (2022) findings show how changes in prey availability caused by human activities lead to rapid, yet progressive, innovations in killer whales, likely altering the ecological role of the killer whales as top predators. It remains to be seen where *Port* and *Starboard* along with the other shark specialists have learned their shark depredation behaviour, but it could be possible this was at pelagic longline fisheries which may have either depleted the pelagic chondrichthyan food resources offshore or displaced the killer whales through deterrence. This is currently being examined by Elwen et al. (in prep) using observational data from pelagic longline fisheries and distribution data of killer whales in South Africa.

This thesis has therefore helped fill significant gaps in the regional and global knowledge about how white sharks respond to the threat of killer whale predation and how this may shape their respective marine communities (Chapter 3, Chapter 5). The spatial network analysis has shown that white sharks in southern Africa are not aggregating in the same historic hotspots due to intraguild predation and fear effects. They have likely shifted their space use to avoid being preyed on and the data reflects some of the largest largest-scale avoidance of white sharks by killer whales (Chapter 5). Displacements represent natural experiments, which, if found at the appropriate time and empirically examined in depth, can provide insight into competitive processes, ecological impacts, and evolutionary change (Reitz and Trumble, 2002). Recovering carnivores, can increase direct and indirect top-down effects (Stier et al. 2016) that may inhibit the recovery of protected prey species and thus interfere with the recovery of an ecosystem (Marshall et al. 2016, Samhouri et al. 2017). Further investigation is required to determine the spatial and temporal scales of white shark movements and associated ecological impacts in South Africa. This new knowledge has important implications for the conservation management of white sharks, bather safety, and the coastal ecology of the entire southern African region.

6.2 Ecological impacts of white shark displacement in South Africa

Most displacements cause negative impacts, particularly keystone species, which adversely impact other native species (Reitz and Trumble 2002). Various prey species of killer whales show abrupt shifts in habitat use, both fine and large scale, to spatially avoid predation. For example, Southern Right whale *Eubaelena australis* cow-calve pairs in Argentina moved to very shallow waters when killer whales began to hunt their calves, as echo-location is less effective (Sironi et al. 2008). Killer whale mediated population declines have been documented in sea otters *Enhydra lutris* in the eastern North Pacific (Estes et al. 2009), as well as pinnipeds in the subantarctic *Arctocephalus gazella* and *Mirounga leonina* (Reisinger, de Bruyn, & Bester, 2011). In the Canadian Arctic, climate change has accelerated the melting of sea ice, driving range expansion north in killer whales thus having substantial impacts on and displacing Narwhal *Monodon monoceros* populations (Breed et al. 2017, Lefort et al. 2020).

One direct effect of white shark loss in Western Cape historical hotspots was that the Cape Fur seal populations (in False Bay and Gansbaai) had no fear effects shaping their behaviour at the colonies for the past 5-7 years (de Vos et al. 2010, Wcisel et al. 2014). With no white sharks around, the seals became bolder in their movements directly around the colony and more prevalent in number. A study examining seal scats in False Bay revealed that their stress hormones are significantly reduced without white sharks in the region (Hammerschlag et al. 2020). This increases seal predation on critically endangered African penguins and inter-specific competition for already limited resources such as small pelagic fish species (Van der Lingen et al. 2020). These top-down shifts can lead to trophic cascades, where entire ecosystems can eventually suffer from top predator loss (Estes et al. 2009). Tri-trophic cascade studies involving the presence and absence of large predators for five national parks in the western United States indicated major impacts to woody plant communities by ungulates following the extirpation or displacement of large predators (Beschta and Ripple 2009) demonstrating how far alterations in top predator dynamics can influence the entire ecosystem down to the floral composition. Similar observations were recorded by Estes et al. 2009 with killer whales causing reductions in sea otter *Enhydra lutris* numbers, driving sea urchin *Mesocentrotus franciscanus* expansions thus degrading kelp *Nereocystis luetkeana* forest coverage.

6.3 Economic impacts of white shark displacement in South Africa

A recent financial analysis by NGO's *Endangered Wildlife Trust* and *Shark Allies* examined the live worth of white sharks at Guadalupe Island, Mexico, in the North East Pacific. The report concluded that the total conservation worth of the white shark population at Guadalupe over 30 years was valued at $123.1M and in South Australia white shark cage-diving was valued at $15M a year (Huveneers et al. 2018). The analysis was repeated for southern African white sharks using the same criteria and valued the species conservation worth at $241.7M over 30 years.

The loss of the predictable presence of white sharks from each primary aggregation site in the Western Cape has resulted in significant financial losses for the white shark-based tourism and filming industries in False Bay, Gansbaai, and now in Mossel Bay. Businesses are struggling to survive on the smaller shark species such as bronze whaler and sevengill sharks which have taken over these sites in the absence of white sharks. In Mossel bay, other mesopredator shark species have not shown at cage diving/research boats in the white sharks' absence. Short or long-term displacement of sharks from the remaining aggregation sites may ultimately collapse the entire white shark-based tourism industry in South Africa. Shark tour operators have had to adapt their tours accordingly. In Gansbaai, half the permitted boats are in operation in 2022 versus in 2017, with the added pressure of the Coronavirus pandemic on tourism, there are more operations likely to close. This has had wide reaching consequences for the coastal regions 'Blue Economy'. Local guest houses and restaurants within these communities are highly dependent on shark tourism for income as are the large number of people employed within the industry and as a consequence, various businesses closed down or reduced the number of their employees.

6.4 Bather safety impacts of white shark displacement in South Africa

Large carnivore attacks on humans are the most dramatic form of human-wildlife conflicts (Bombieri et al. 2019). Although rare compared to attacks by other wildlife and domestic species, such incidents often undermine large carnivore conservation efforts, raise human safety concerns, as well as hinder the recovery of several species around the world (Bombieri et al. 2019). Urbanisation of areas in North America reduced natural habitat for brown bears *Ursus arctos* causing increases in human incidents (Conover 2008). The construction of a large coastal port in Recife, Brazil, displaced a population of bull sharks *Carcharhinus leucas* which resulted in 47 bite incidents on humans over 14 years, of which 17 were fatal (Hazin et al. 2008). Increased building of dams in Brazilian rivers resulted in an increase in human bathers bitten by speckled Pirhana *Serrasalmus spilopleura* (Haddad and Sazima 2003) and polar bears *Ursus maritimus* in the Arctic were displaced by climate change induced melting sea ice, forcing them to forage closer to urban settlements, which increased bite incidents and fatalities on humans (Wilder et al. 2017). Conflicts become extremely controversial when people are attacked by species that are endangered and legally protected (Acharya et al. 2016).

During this study, one fatal bite incident occurred on a male triathlon swimmer training in Plettenberg bay in June 2022 (the first fatal white shark incident in South Africa in over seven years). This was a month after killer whales displaced white sharks from Mossel Bay, and one of the white shark's photo identified in Plettenberg Bay was previously recorded in Mossel Bay, confirming connectivity between sharks at these sites. Four months later, on September 25th, six weeks after killer whales displaced white sharks for a second time from Mossel Bay (on August 2nd), a second fatal bite incident occurred in Plettenberg Bay on a female swimmer. Three days later, aerial surveys by the Marine Mammal Research Institute (MRI) and the National Sea Rescue Institute (NSRI) confirmed an abnormally high number of white sharks patrolling the coastline between Knysna and Plettenberg Bay. The flight by the MRI counted 34 individual large sharks, and the scientist who has partaken in the annual Southern Right Whale surveys for several years remarked they had "never witnessed so many large sharks along this short stretch of the coast" (Vermeulen et al. 2022.).

If a cohort of white sharks has been displaced into Eastern Cape coastal regions post-2017 (as suggested in Chapter 5), water users should be alerted to this, and there are currently few measures in place to do so and bather safety is compromised. Many of the Eastern Cape beaches are popular for surfing, diving, and general recreational beach activities due to the warmer Indian ocean.

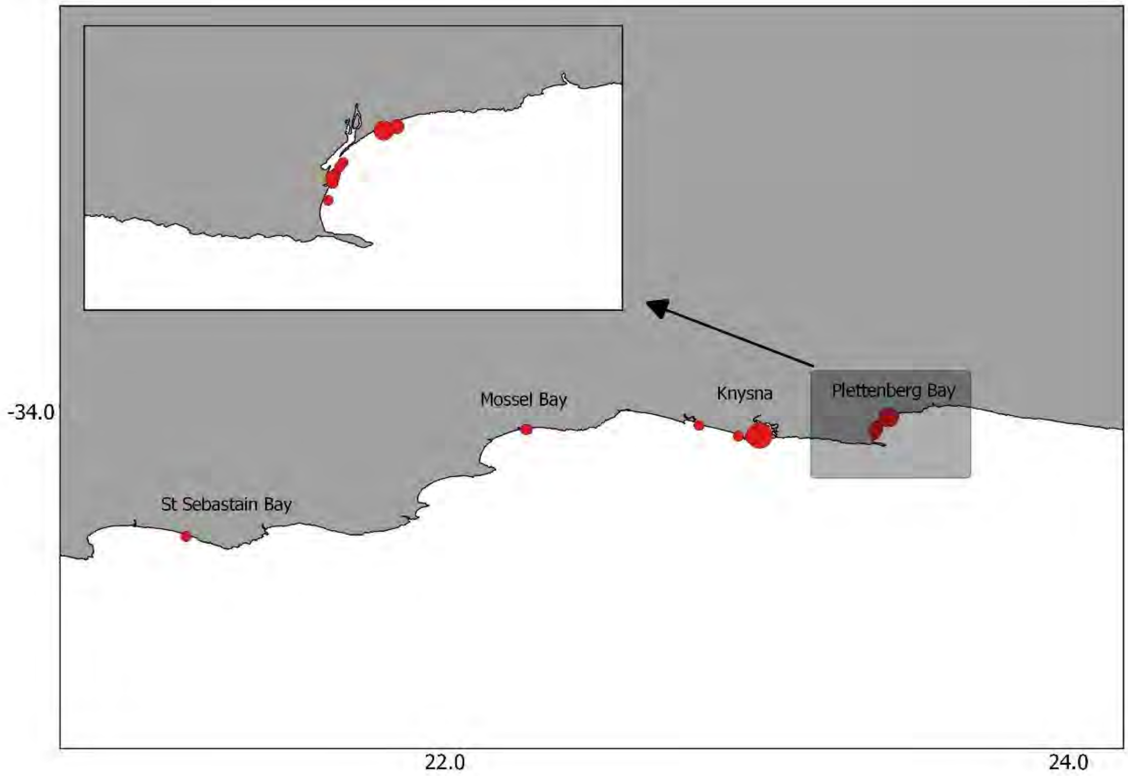

Figure: 6.1: Distribution of large sharks between Mossel and Plettenberg Bay on October 10th, 2022 a week after Plettenberg Bay's second fatal bite incident (data from Vermulen et al. 2022)

Several measures, ranging from the compensation and promotion of wildlife deterrents to supporting the livelihoods of people, have been implemented to foster the co-existence of humans and wildlife in terrestrial environments (White and Ward, 2011). However, the efficacy of such measures is largely uncertain due to the absence of information about the patterns of conflicts across various landscapes (Acharaya et al. 2016).

There are various effective ways to educate and warn the public about shark presence and higher risk times for entering the water. In Australia and the USA; drones, sonar buoys connected to receivers, and even cell phone apps with live notifications are in place, to warn the public of high shark presence. Given the fatal bite incidents in Plettenberg Bay, local authorities and government have recently authorised a Shark Spotters program (similar to Cape Town) combined with an exclusion net at the main 'Central beach' in Plettenberg Bay where the fatal incidents occurred (Sarah Waries, CEO of Shark Spotters, pers comm). While these measures cover one location, other urbanised coastal regions in the Eastern Cape, such as East London and Gqeberha, will need similar measures in place, as well as signage, awareness, and education to prevent further incidents. Queensland in Australia spends 1.9M $AUD annually on shark mitigation device trialing, a combination of lethal, non-lethal, and personal (worn by the water user). Given the rise in fatal white shark bites in South Africa's Eastern Cape, it would be wise for local municipalities and governments to invest in testing several potential methods to prevent more incidents and damage to tourism due to closed beaches.

6.5 Suggestions for future research, lessons learned, and concluding remarks

Acoustic telemetry has provided important information on white shark movement in this study, but it has also resulted in some conspicuous gaps in the data that are challenging to interpret. Satellite tagging would have provided more explicit evidence of white shark space use, specifically at broader scales away from coastal areas if they lasted over multiple years. This thesis's main limitation was that the satellite tags deployed on white sharks expired before 2014 (Kock et al. 2022). Future tagging work on white sharks should be continued in southern Africa, specifically satellite tagging methods. Permitted researchers should be allowed access to tag white sharks in the more eastern parts of their range.

Additionally, satellite tagging killer whales would be beneficial to see how the two species overlap spatially and temporally. Such data could then be used to help predict seasonality and times when the potential for overlap between the species is most likely to occur, supported by the extensive history of sightings and previous tagging data archived. This information could inform operators, bather protection measures, and overall management. Additional future work could utilise abundance estimates on killer whales through mark recapture methods and parameterize a bioenergetics model to explore the potential consumptive effects of killer whale predation on large coastal sharks in South Africa (Lefort et al. 2020).

In order to understand changes in white shark fine-scale behaviour, after the pressure of killer whale presence, CATs tags would be a valuable method to use in future work. These devices have recently quantified white sharks' habitat use (including metabolic expenditure and acceleration) through different seascapes globally, revealing how they have specific circadian rhythms and how they hunt seals within kelp forests (Jewell 2022). Displacement has caused white sharks to abandon core areas of habitat use near seal colonies in the West Coast of South Africa; however, stomach contents have revealed that they are still hunting cape fur seal prey. CATs tags may be able to show if any alteration of circadian rhythm has occurred, i.e., white sharks have shifted to hunting nocturnally or if they are foraging in different environments to access seals as prey. This information is essential to adequately protect critical habitat for white sharks to try and prevent overlap with anthropogenic pressures or popular swimming beaches.

Despite the white sharks potentially becoming more prevalent along Eastern Cape beaches, it is suspected that the population in southern Africa is not showing recovery (Bowlby et al. 2022). One notable impact of the killer whales' presence, is that if they enter a region and successfully hunt a white shark, this triggers a flight response in other white sharks, which can last for several months. This relatively new source of mortality for South African white sharks saw at least five sharks killed in 2022, these are only the documented events, the number of dead sharks is likely much higher.

Killer whales are profoundly vocal and can be heard underwater over long distances (Miller 2006). Specific avoidance responses to killer whale sounds have been demonstrated experimentally in fish (Doksaeter et al. 2009), pinnipeds (Deecke et al. 2002), and various cetacean species (Cure et al. 2013). One interesting potential avenue of research would be to 'playback" the vocalisations of *Port* and *Starboard* (which have already been recorded in False Bay) to potentially reduce white shark catches at the KwaZulu-Natal Sharks Board, the highest known targeted source of mortality of white sharks in South Africa (Kock et al. 2022). While Chaphuis et al. 2018 found no responses from white sharks to killer whale vocal playbacks (recorded from Australia) in Mossel Bay, the results could well be different now given the white shark populations repeat exposure to the shark specialist pair in South Africa. Even if catches could be reduced at some sites, this could go towards offsetting the additional pressure of killer whale predation on the white shark population. However, while this experiment is worth looking at, playing the vocals of killer whales in coastal environments can negatively impact other species and would need to be tested very carefully with the correct expertise involved (S. Elwen pers. comm).

In terrestrial environments ‘problem predators’ are often culled, for example wolves depredating livestock (Krofel et al. 2011). Cultural transmission (adult to adult learning) may have already begun in the killer whales, thus removing any one individual would be ineffective as well as highly sensitive and unethical. There is a plethora of ‘anti-orca deterrent devices’(ADDs) such as pingers, on the market that are used by fisheries, although- each one has its own set of limitations. Killer whales are highly intelligent, adaptable predators and attempts at deterrence have failed in the past. For example, one attempt to prevent long-line depredation was to try and "trick" killer whales using two longline boats, but this failed as the whales quickly out-smarted the tactic and split into two groups (Petras 2003, Matkin 1994). Beyond the inherent difficulties of trying to affect the behaviour of killer whales, the cautions that must be considered if using deterrents, include potential impacts on non-target species. Hearing damage to other cetacean species, or alteration of the marine environments and composition of fauna within them have all been reported as issues with ADDs (Petras et al. 2003).

There are no clear solutions on how to manage the sudden arrival of shark-specialist adult killer whales in the coastal regions of South Africa and the subsequent impacts on other species. A recent workshop at DFFE using the data from this thesis, concluded that bolstering efforts to satellite tag both species, and improve knowledge of their distributions is one short term plan, however the long-term plans need to be workshopped to consider broader ecosystem impacts with participants from oceanographic, biological and anthropogenic disciplines. Unprecedented interactions between protected species that have only recently arisen, and did not contribute to the historical population declines themselves are challenging to manage (Moxley et al. 2019). Such complex dynamics may increasingly become common as ecosystems are transformed and disrupted by climate change (Carnicer et al. 2011; Moritz et al. 2012) and other athropogenic pressures.

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APPENDIX

CHAPTER 3: KILLER WHALES DRIVE WHITE SHARK ABSENCE AT SOUTH AFRICAS LARGEST AGGREGATION SITE

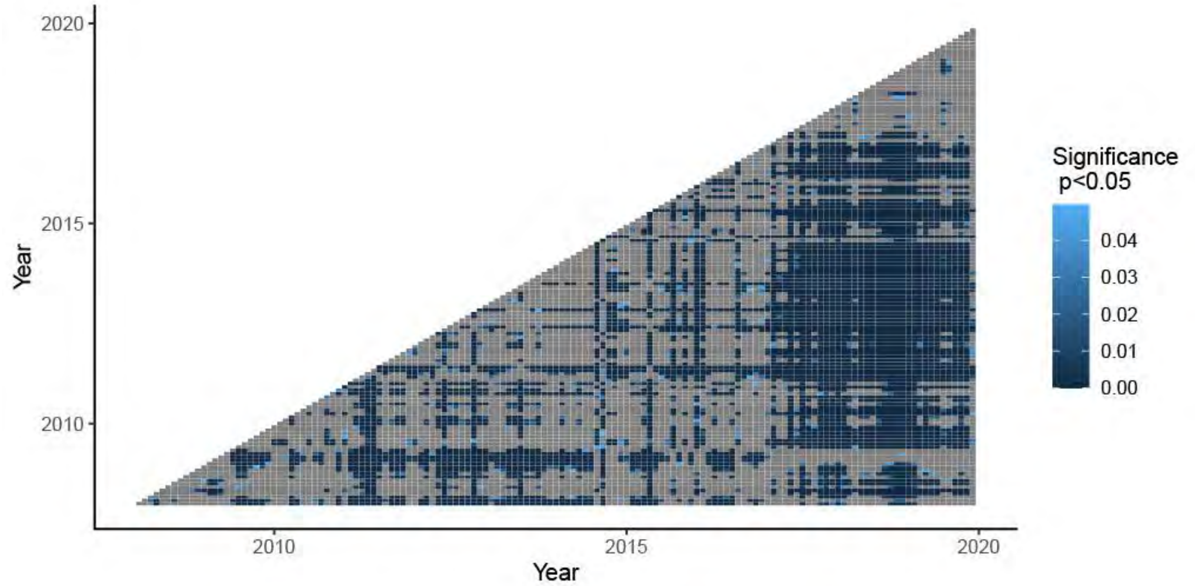

Figure AP1: TukeyHSD results of average monthly *Carcharodon carcharias* abundance in Gansbaai between 2008 and 2020.

Figure AP2(a): Port with a dead bronze whaler shark in his mouth (Photo credit S. Elwen).

Figure AP2(b): Six killer whales (not Port and Starboard) killed a Basking Shark in Plettenberg Bay in 2010. Photo credit Ocean Odyssey.

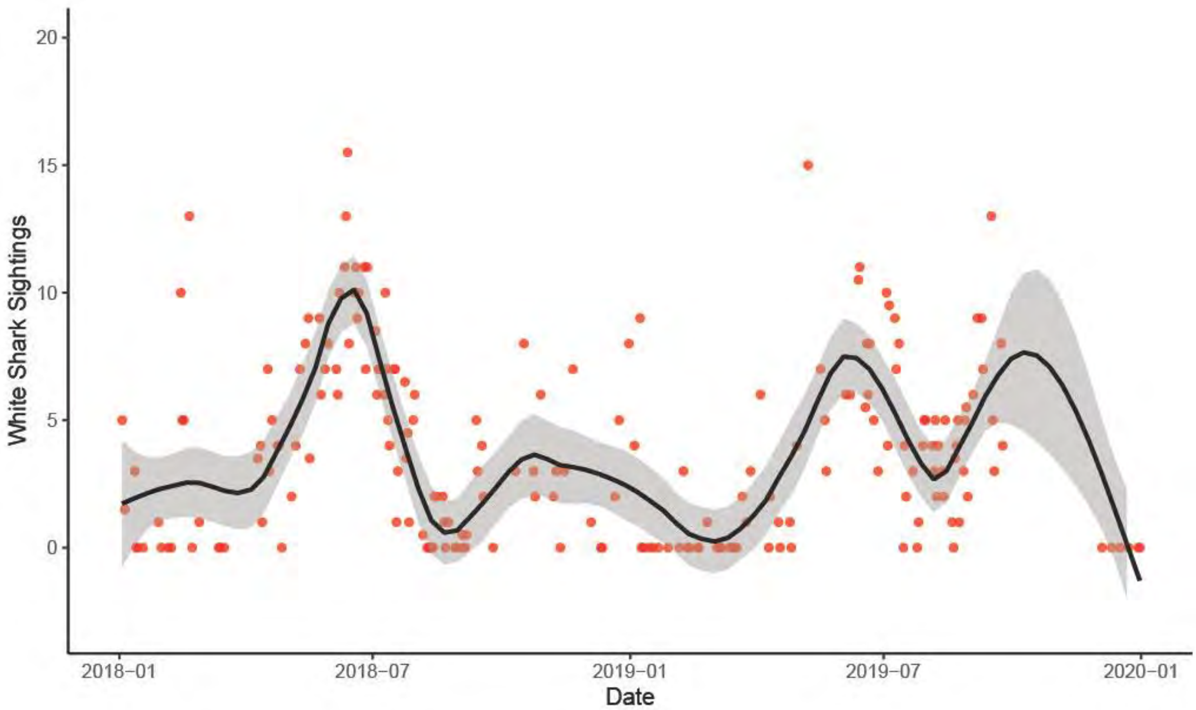

Figure AP3: Long term daily *Carcharodon carcharias* sightings (red) in Mossel Bay between 2008 and 2020, with loess smooth curve (span=0.2).

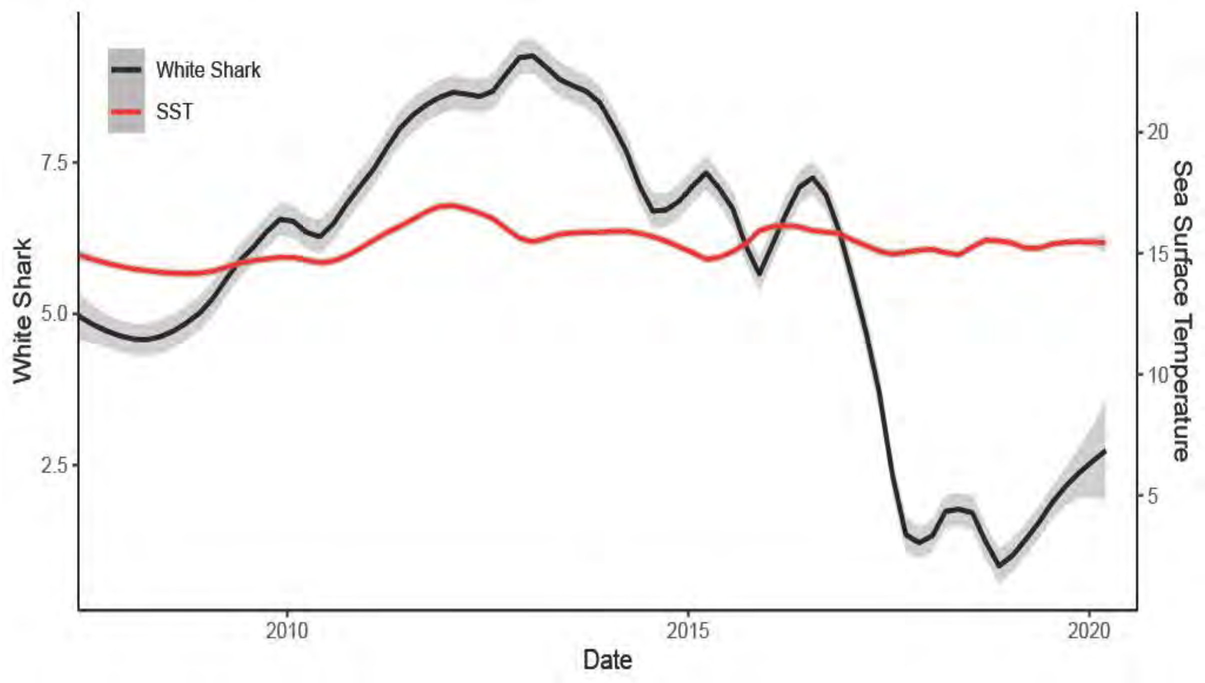

Figure AP4: Average *Carcharodon carcharias* abundance and Sea-Surface Temperature in Gansbaai between 2008 and 2020.

CHAPTER 5: DISAPPEARANCE OR DISTRIBUTION SHIFT? COASTAL MOVEMENTS AND CONNECTIVITY OF WHITE SHARKS EXPOSED TO KILLER WHALE PREDATION IN SOUTHERN AFRICA 2012-2021.

Table AP5: Tagging information for *Carcharodon carcharias* 2012-2022. Tag number, ID, Date of tag deployment, regions tagged, size, sex and tag specifications are detailed.

Tag No.	Tag ID	Tag Date	Region	Size	Sex	Int/Ext	Battery Life	Tag Type
1	34051	2012/03/16	Algoa Bay	265	F	Internal	3650	V16-6L
2	44476	2012/06/22	Algoa Bay	350	F	External	1544	V16-5H
3	44477	2012/06/22	Algoa Bay	300	M	External	1544	V16-5H
4	44478	2012/06/22	Algoa Bay	300	F	External	1544	V16-5H
5	44479	2012/06/22	Algoa Bay	350	F	External	1544	V16-5H
6	44480	2012/06/22	Algoa Bay	300	F	External	1544	V16-5H
7	44481	2012/06/22	Algoa Bay	250	F	External	1544	V16-5H
8	46787	2012/06/22	Algoa Bay	350	F	External	1544	V16-5H
9	44482	2012/07/24	Algoa Bay	300	M	External	1544	V16-5H
10	34161	2012/09/30	Algoa Bay	200	F	External	1544	V16-5H
11	34162	2012/11/05	Algoa Bay	180	F	External	1544	V16-5H
12	8697	2012/11/10	Algoa Bay	220	F	External	3650	V16-6H
13	8698	2012/11/10	Algoa Bay	240	F	Internal	3650	V16-6H
14	34164	2012/11/10	Algoa Bay	300	F	External	1544	V16-5H
15	34166	2012/11/19	Algoa Bay	280	M	External	1544	V16-5H
16	34168	2012/11/19	Algoa Bay	320	M	External	1544	V16-5H
17	52618	2012/11/19	Algoa Bay	230	F	External	3650	V16-6H
18	52619	2012/11/19	Algoa Bay	200	M	External	3650	V16-6H
19	34169	2012/11/23	Algoa Bay	350	F	External	1544	V16-5H
20	34170	2012/11/23	Algoa Bay	300	F	External	1544	V16-5H
21	34171	2012/11/23	Algoa Bay	300	F	External	1544	V16-5H
22	34172	2012/11/23	Algoa Bay	350	F	External	1544	V16-5H
23	33040	2013/05/20	Algoa Bay	300	F	External	899	V16-5H
24	33041	2013/05/20	Algoa Bay	200	F	External	899	V16-5H
25	33042	2013/05/20	Algoa Bay	300	F	External	899	V16-5H
26	33043	2013/05/20	Algoa Bay	220	M	External	899	V16-5H
27	33044	2013/05/20	Algoa Bay	300	F	External	899	V16-5H
28	34163	2013/05/20	Algoa Bay	280	F	External	1544	V16-5H
29	34165	2013/05/20	Algoa Bay	250	F	External	1544	V16-5H
30	33045	2013/06/28	Algoa Bay	300	M	External	899	V16-5H
31	33046	2013/06/28	Algoa Bay	220	M	External	899	V16-5H
32	33047	2013/06/28	Algoa Bay	320	F	External	899	V16-5H
33	33048	2013/06/28	Algoa Bay	350	M	External	899	V16-5H
34	33049	2013/06/28	Algoa Bay	250	M	External	899	V16-5H

35	33050	2013/07/26	Algoa Bay	250	F	External	899	V16-5H
36	32629	2014/07/29	Algoa Bay	300	F	External	899	V16-5H
37	32630	2014/07/29	Algoa Bay	280	F	External	899	V16-5H
38	32631	2014/07/29	Algoa Bay	520	F	External	899	V16-5H
39	34098	2012/05/22	Arniston	441	F	Internal	3650	V16-6L
40	34099	2012/05/23	Arniston	382	M	Internal	3650	V16-6L
41	34107	2012/04/15	False Bay	417	F	Internal	3650	V16-6L
42	34038	2012/04/16	False Bay	437	F	Internal	3650	V16-6L
43	34104	2012/04/16	False Bay	457	F	Internal	3650	V16-6L
44	34106	2012/04/16	False Bay	431	F	Internal	3650	V16-6L
45	34056	2012/04/12	Gansbaai	297	M	Internal	3650	V16-6L
46	34057	2012/04/12	Gansbaai	318	M	Internal	3650	V16-6L
47	34058	2012/04/12	Gansbaai	360	F	Internal	3650	V16-6L
48	34059	2012/04/12	Gansbaai	355	M	Internal	3650	V16-6L
49	34060	2012/04/12	Gansbaai	452	F	Internal	3650	V16-6L
50	34061	2012/04/13	Gansbaai	330	M	Internal	3650	V16-6L
51	34062	2012/04/13	Gansbaai	251	M	Internal	3650	V16-6L
52	34063	2012/04/13	Gansbaai	441	F	Internal	3650	V16-6L
53	34101	2012/05/08	Gansbaai	290	M	Internal	3650	V16-6L
54	34103	2012/05/08	Gansbaai	295	M	Internal	3650	V16-6L
55	34105	2012/05/08	Gansbaai	320	M	Internal	3650	V16-6L
56	34100	2012/05/09	Gansbaai	420	M	Internal	3650	V16-6L
57	34102	2012/05/09	Gansbaai	418	F	Internal	3650	V16-6L
58	6258	2015/07/28	Gansbaai	320	F	External	1830	V16-6X
59	6259	2015/07/28	Gansbaai	400	M	External	1830	V16-6X
60	6279	2015/08/08	Gansbaai	350	M	External	1830	V16-6X
61	6260	2015/12/01	Gansbaai	280	M	External	1830	V16-6X
62	6261	2015/12/01	Gansbaai	380	M	External	1830	V16-6X
63	6262	2015/12/01	Gansbaai	330	F	External	1830	V16-6X
64	6263	2015/12/01	Gansbaai	200	M	External	1830	V16-6X
65	6265	2016/05/09	Gansbaai	400	F	External	1830	V16-6X
66	6264	2016/05/25	Gansbaai	320	F	External	1830	V16-6X
67	6269	2016/05/25	Gansbaai	400	F	External	1830	V16-6X
68	6266	2016/09/07	Gansbaai	300	F	External	1830	V16-6X
69	6267	2016/09/07	Gansbaai	320	M	External	1830	V16-6X
70	6268	2016/09/07	Gansbaai	400	F	External	1830	V16-6X
71	6270	2016/09/19	Gansbaai	350	M	External	1830	V16-6X
72	6277	2016/09/19	Gansbaai	320	M	External	1830	V16-6X
73	6278	2016/09/19	Gansbaai	300	M	External	1830	V16-6X
74	6271	2016/09/20	Gansbaai	400	M	External	1830	V16-6X
75	6276	2016/09/20	Gansbaai	350	F	External	1830	V16-6X
76	6280	2016/09/20	Gansbaai	320	F	External	1830	V16-6X
77	6281	2019/03/14	Gansbaai	380	F	External	1830	V16-6X
78	6282	2019/03/14	Gansbaai	420	F	External	1830	V16-6X

79	17884	2019/09/26	Gansbaai	350	F	External	1830	V16-6X
80	17884	2019/09/26	Gansbaai	350	F	External	730	V16
81	17885	2019/09/26	Gansbaai	480	F	External	1830	V16-6X
82	17885	2019/09/26	Gansbaai	480	F	External	730	V16
83	6273	2021/02/17	Gansbaai	450	M	External	1830	V16
84	30763	2021/05/19	Gansbaai	500	F	External	1830	V16
85	12666	2021/05/27	Gansbaai	450	F	External	1830	V16
86	6274	2021/06/06	Gansbaai	350	M	External	1830	V16
87	34037	2012/03/07	Mossel Bay	340	F	Internal	3650	V16-6L
88	34039	2012/03/07	Mossel Bay	299	F	Internal	3650	V16-6L
89	34029	2012/03/08	Mossel Bay	295	M	Internal	3650	V16-6L
90	34031	2012/03/08	Mossel Bay	371	F	Internal	3650	V16-6L
91	34033	2012/03/08	Mossel Bay	310	F	Internal	3650	V16-6L
92	34035	2012/03/08	Mossel Bay	351	F	Internal	3650	V16-6L
93	34034	2012/03/09	Mossel Bay	210	F	Internal	3650	V16-6L
94	34036	2012/03/09	Mossel Bay	283	F	Internal	3650	V16-6L
95	34028	2012/03/10	Mossel Bay	350	F	Internal	3650	V16-6L
96	34030	2012/03/10	Mossel Bay	228	F	Internal	3650	V16-6L
97	34032	2012/03/10	Mossel Bay	271	F	Internal	3650	V16-6L
98	34042	2012/03/21	Mossel Bay	297	F	Internal	3650	V16-6L
99	34044	2012/03/21	Mossel Bay	292	F	Internal	3650	V16-6L
100	34048	2012/03/21	Mossel Bay	251	F	Internal	3650	V16-6L
101	34050	2012/03/21	Mossel Bay	259	F	Internal	3650	V16-6L
102	34052	2012/03/21	Mossel Bay	266	M	Internal	3650	V16-6L
103	34053	2012/03/23	Mossel Bay	340	F	Internal	3650	V16-6L
104	34054	2012/03/23	Mossel Bay	309	M	Internal	3650	V16-6L
105	34055	2012/03/23	Mossel Bay	312	M	Internal	3650	V16-6L
106	6272	2020/11/30	Mossel Bay	280	F	External	1830	V16
107	6275	2020/11/30	Mossel Bay	350	F	External	1830	V16
108	31120	2012/03/19	Port St Johns	340	F	Internal	3650	V16-6L
109	31122	2012/03/19	Port St Johns	320	M	Internal	3039	
110	31121	2013/04/17	Port St Johns	290	F	Internal	3650	V16-6L
111	6553	2021/05/30	Struisbaai	260	F	External	1830	V16
112	6555	2021/05/30	Struisbaai	300	F	External	1830	V16
113	10135	2021/06/20	Struisbaai	380	M	External	1830	V16-6X
114	10137	2021/06/20	Struisbaai	400	M	External	1830	V16-6X
115	14693	2021/06/20	Struisbaai	350	M	External	1830	V16-6X
116	10141	2022/05/20	Struisbaai	270	F	External	1830	V16
117	10132	2022/05/22	Struisbaai	300	F	External	1830	V16
118	10142	2022/05/22	Struisbaai	450	F	External	1830	V16

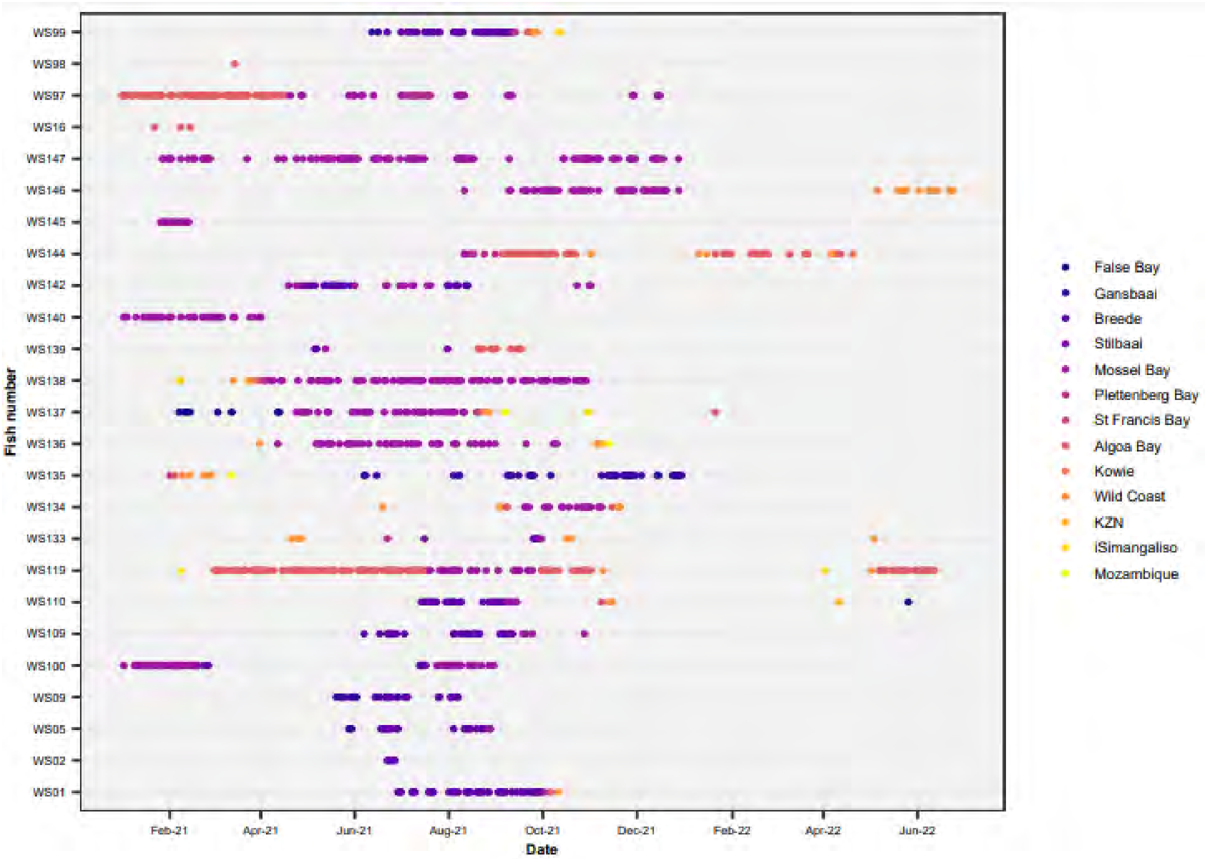

Figure AP6(a): Shows all active transmitters 2021-2022. Note only one tag was detected west of Gansbaai out of 27 tags (data courtesy of Taryn Murray, ATAP).

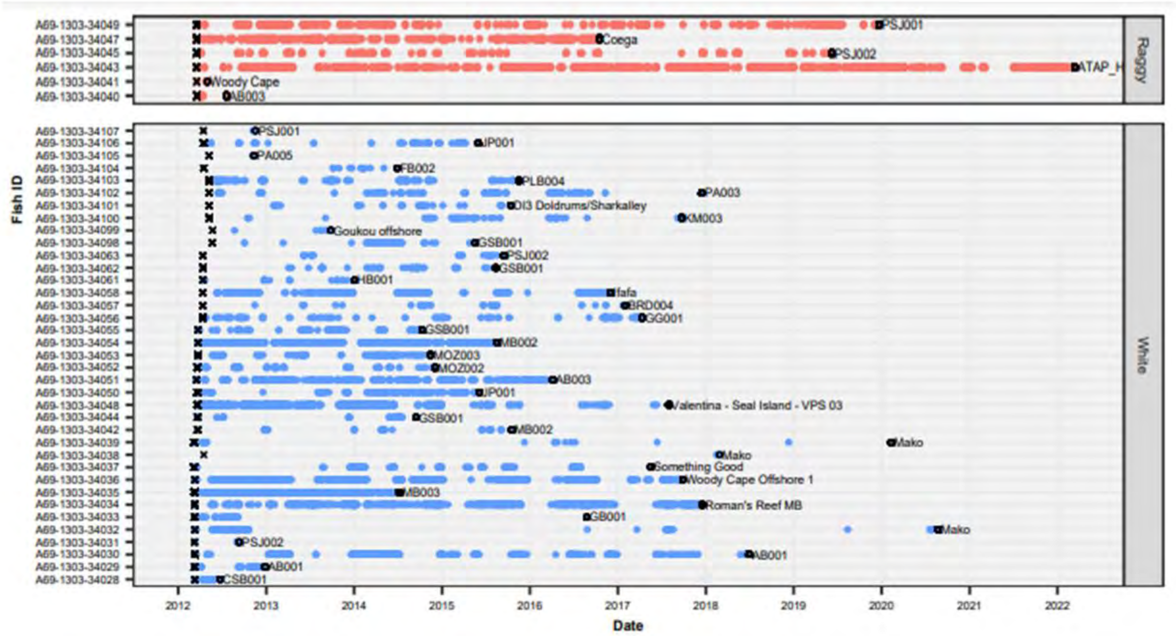

Figure AP6(b): Ocearch tags deployed between 2012-2022. While detections on white sharks disappeared abruptly post 2018, Ragged tooth sharks kept on being detected through until 2022. This may support the idea that the drop off in detections in 2018 on white sharks was not a function of battery expiration or programming but something else, perhaps biological. Data courtesy of Taryn Murray, ATAP.

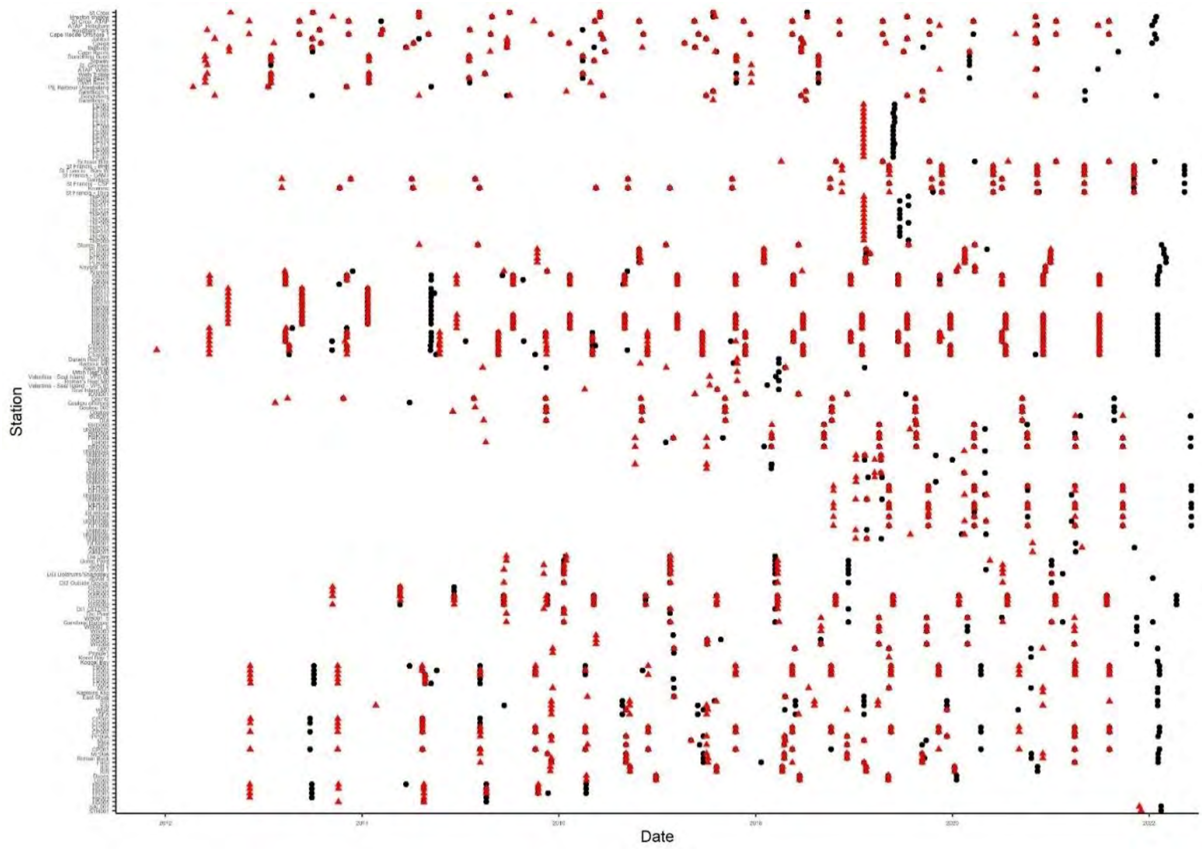

Figure AP7(a): Abacus plot of ATAP receivers over time 2012-2021 Red triangles represent deployment date and black circles retrieval date.

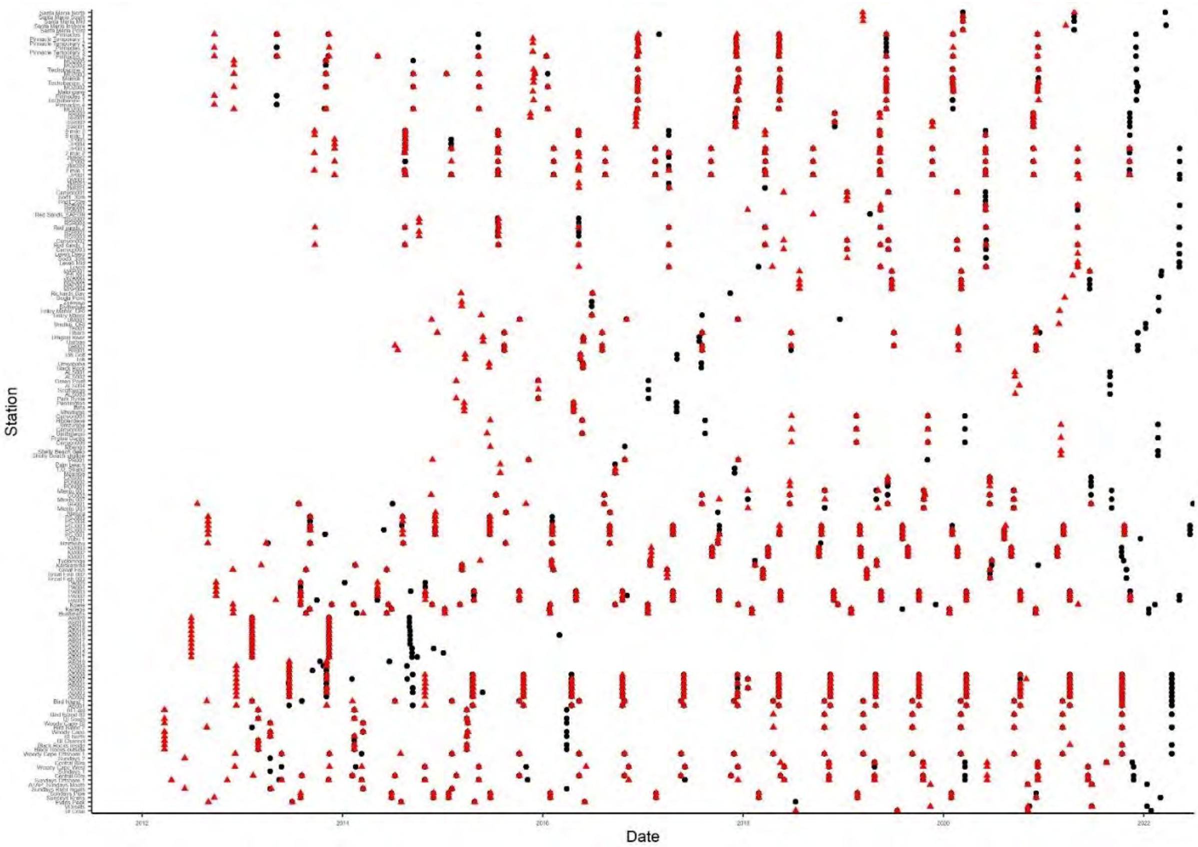

Figure AP7(b): Abacus plot of ATAP receivers over time 2012-2021 Red triangles represent deployment date and black circles retrieval date.

Figure AP8: A 2.6m male white shark acoustic tagged in Struisbaai (Western Cape) South Africa in May 2022 by A. Towner, was matched on a Baited Remote Underwater Video (BRUV) in Mozambique October 2022 (almost 1,800km in 4 months). It was not picked up by the ATAP network of receivers in South Africa.

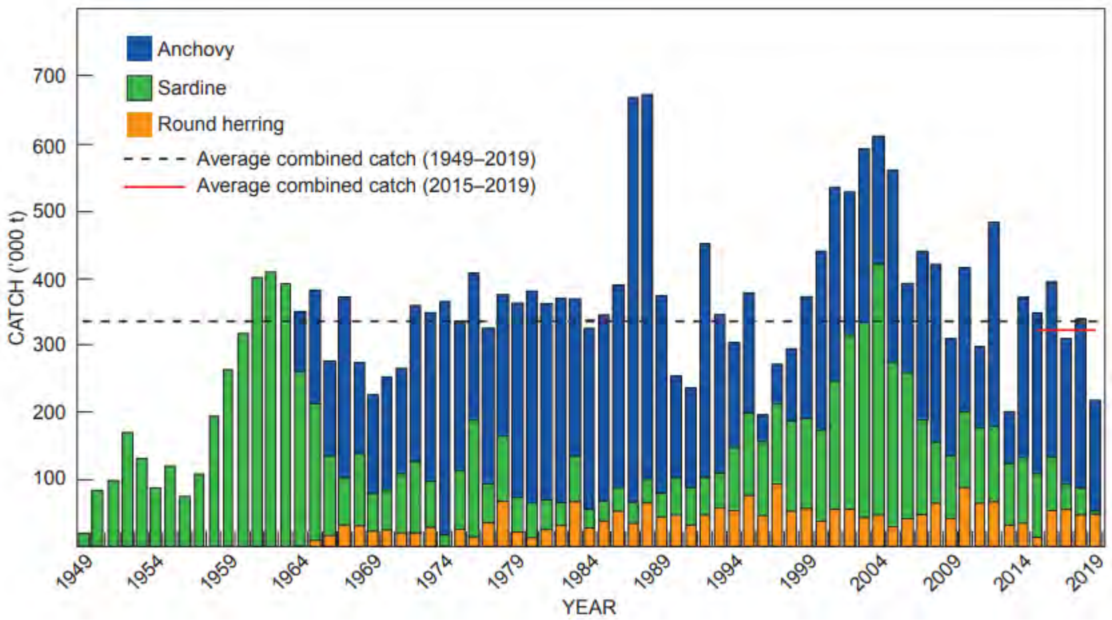

Figure AP9: Data on small pelagic fish species 1949-2019. Sardine and anchovy are important indicators of productivity. No significant or abrupt declines occurred during the time white sharks disappeared 2015-2022. Data from DFFE.

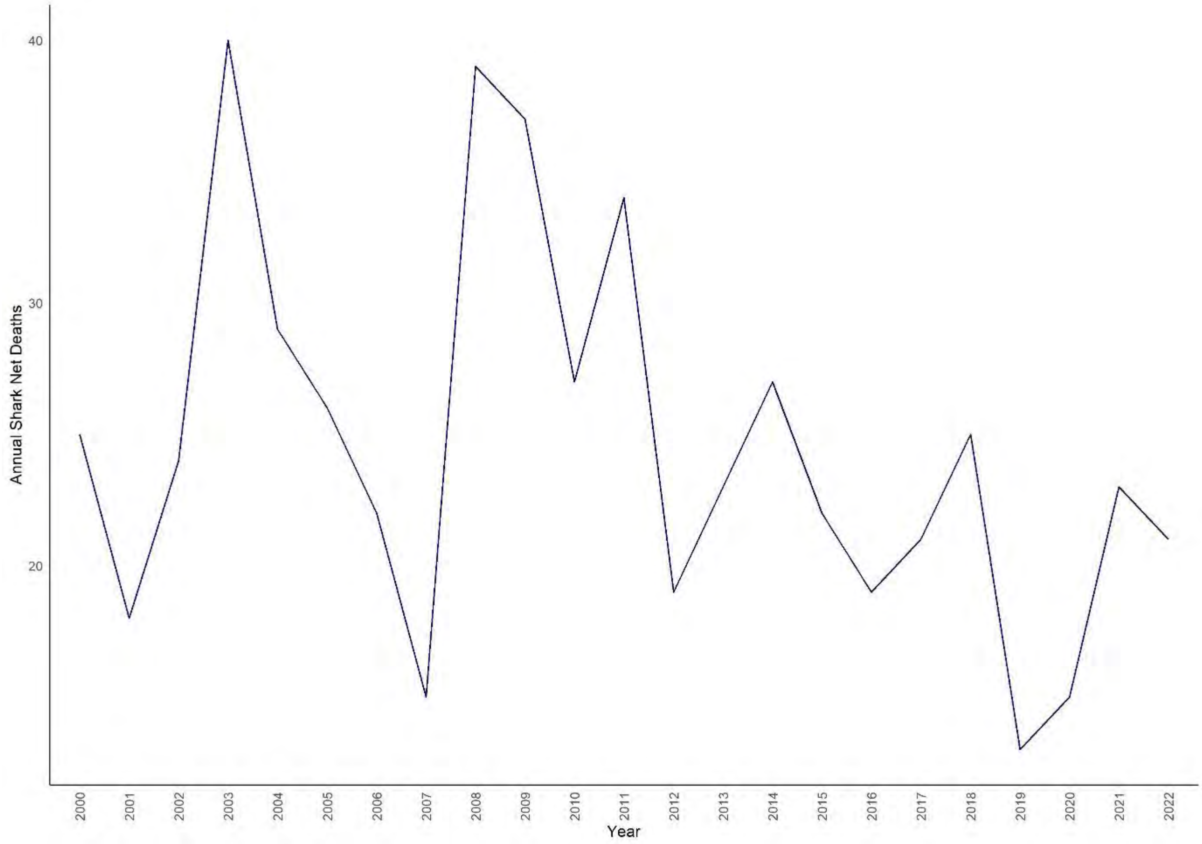

Figure AP10: Catch data at the KZNSB program 2000-2022. Catches did not decrease drastically at the time white sharks began to disappear 2015-2017. Although a drop occurred in 2019, numbers increased again to >20 individuals caught in 2021 and 2022.

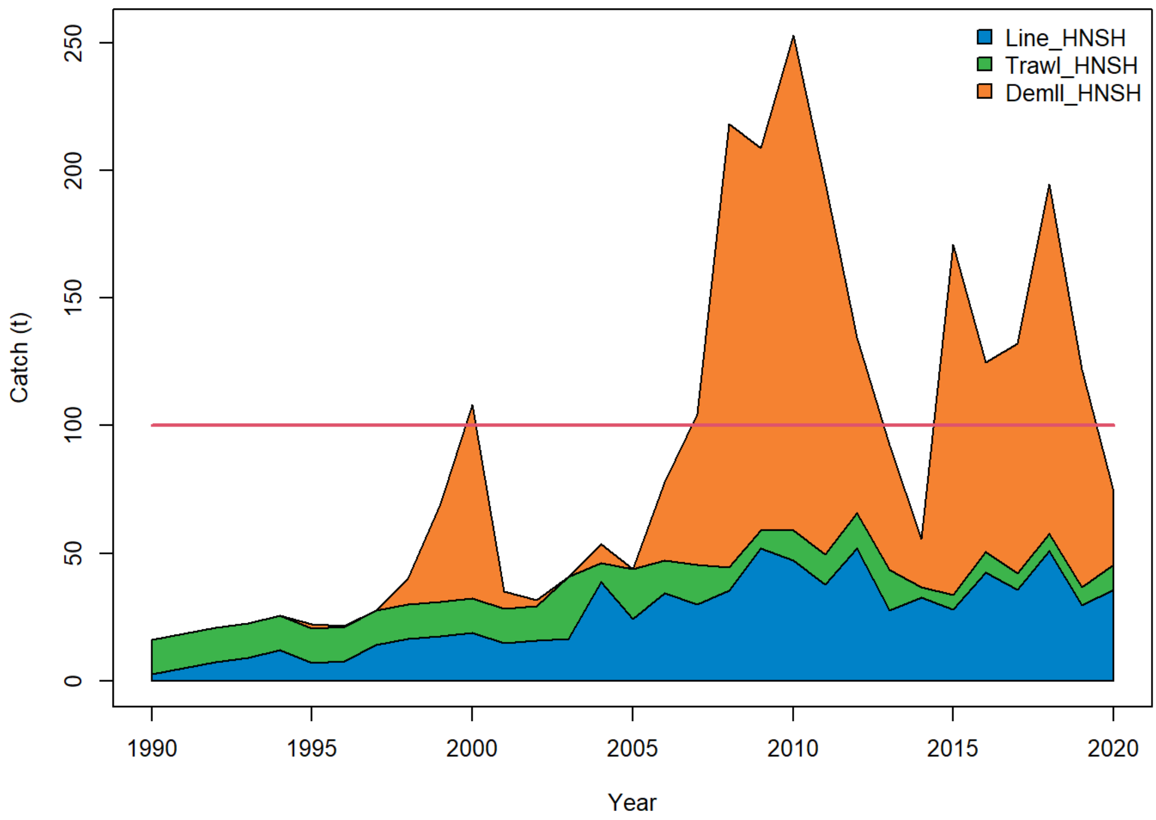

Figure AP11(a): Fisheries data (Trawl, Linefish and Demersal longline) on Smoothound sharks 1990-2020. (data from Charlene da Silva, DFFE).

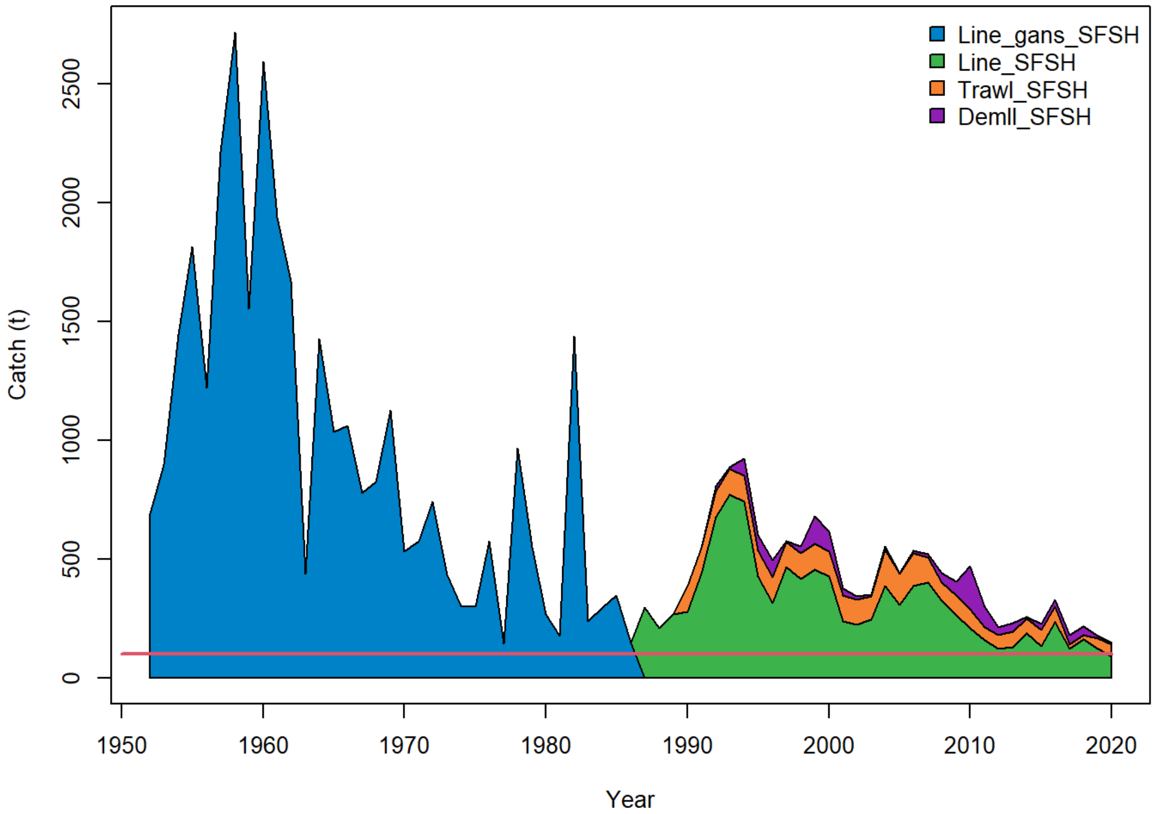

Figure AP11(b): Fisheries data (Trawl, Linefish, Demersal Longline) and Gansbaai Linefish for Soupfin sharks 1950-2020. (Data from Charlene da Silva, DFFE).

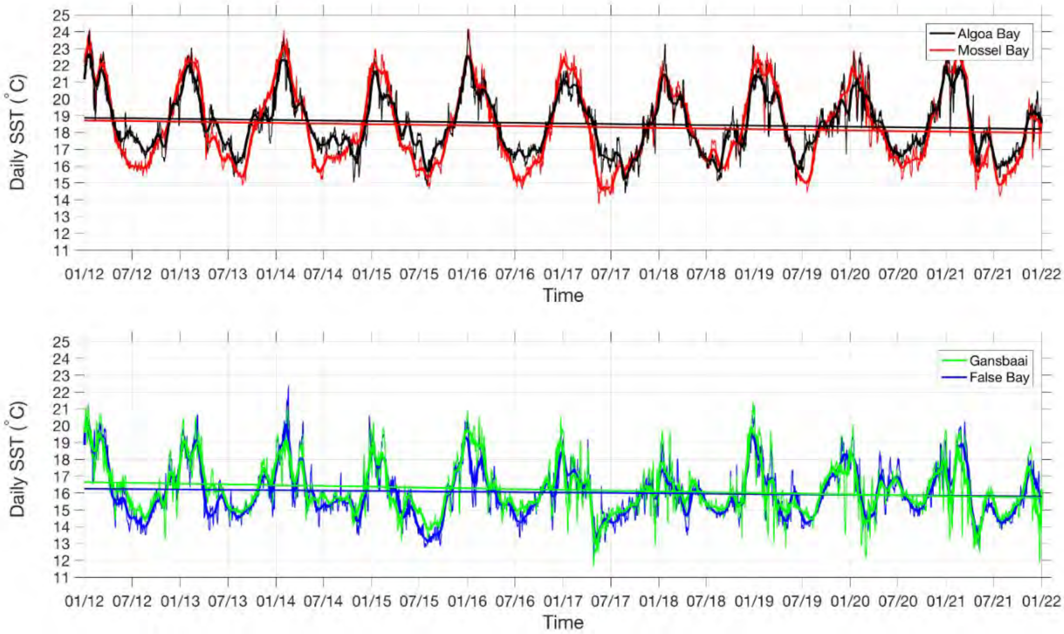

Figure AP12: Sea surface temperature data for four key locations False Bay, Gansbaai, Mossel Bay and Algoa Bay 2012-2022. The SST product used to compute these analyses is OSTIA (available at Marine Copernicus). Credit: Borja Aguiar-Gonzalez.