Movements and co-occurrences of white sharks (*Carcharodon carcharias*) at Stewart Island, New Zealand.

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***Figure 1** - White shark (Carcharodon carcharias) tagged with a Vemco V16-5H R-code acoustic tag at East Edwards Island, northeast of Stewart Island, New Zealand. Photo: Kina Scollay.*

Executive Summary

Our understanding of the fine-scale movements and behaviours of white sharks (*Carcharodon carcharias*) at aggregation sites is limited, yet it is central to conservation management and mitigating human-shark conflicts. This thesis examined traditionally understudied behaviours, namely individual variation in movements and sociality, to better understand the fine-scale habitat use of white sharks at Stewart Island, an aggregation site in southern New Zealand. Bayesian statistical modelling and social network analysis were used to analyse an acoustic telemetry dataset published by Francis et al. (2015), consisting of detections of 22 tagged subadult and adult white sharks by 15 acoustic receivers deployed northeast of Stewart Island during April-June 2011. The northern Titi Islands were a hotspot for white shark activity, with the highest estimated probability of occurrence (0.60) and accounting for 89.4% of co-occurrences. Chapter 2 revealed substantial individual variation in movement patterns, with sharks exhibiting unique 'preferences' towards particular receivers, possibly a result of size-related behaviours like variable feeding strategies and competitive exclusion. Chapter 3 found no clear social structure and weak associations among white sharks in this study, indicating that behaviour at aggregation sites is not socially driven. That said, sharks with greater differences in body size tended to form stronger associations. This is possibly a result of smaller sharks, being considered less adept to hunting pinnipeds, associating with larger and more experienced conspecifics to exploit successful kills or to benefit from social learning. Both chapters also identified the potential influence of shark cage diving operations on the occurrences and co-occurrences of white sharks at the northern Titi Islands, particularly East Edwards Island. This thesis highlights the importance of considering white shark behaviour to obtain accurate predictions and estimates of their distribution and abundance. Incorporating measures for individual variation substantially improved model predictions of shark occurrence, and studying sociality revealed aggregations of up to seven individuals at Edwards Island. As aggregations increase the risks of fisheries-related mortality, Edwards Island should be considered for conservation efforts, such as seasonal fishing restrictions. This thesis also recommends the inclusion of individual variation in ecological modelling and further investigation of social behaviour.

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General Introduction and Background

1.1 Introduction

The white shark (*Carcharodon carcharias*), also known as the great white shark and white pointer shark, is an iconic, yet poorly understood, apex predator. Shark research has historically been limited by several factors, including restrictions in the availability of technology required to study large free-ranging marine predators. There is also a misconception that sharks lack behavioural complexity due to their long evolutionary history (Castro, 2016). However, recognition of the species' vulnerability to overexploitation and advancements in data collection and analysis methods have increased white shark research over the past 10-15 years (Dewar et al., 2004; Huveneers et al., 2018), revealing complex behaviours such as basin-scale migrations between ephemeral feeding locations (Domeier & Nasby-Lucas, 2007; Duffy et al., 2012), ontogenetic shifts in habitat use and foraging strategies (Aquino-Baleytó et al., 2021; Gennari et al., 2022; Goldman & Anderson, 1999), and spatial segregation by size and sex (Domeier & Nasby-Lucas, 2007; Jewell et al., 2013).

This chapter reviews current literature on white shark ecology, particularly life history, foraging strategies, and global and local distribution patterns, alongside outlining current threats to white shark populations and discussing common data collection and analysis tools that have facilitated progress in our understanding of these aspects of white shark ecology. It concludes by outlining the aims and objectives of this thesis.

1.2 White Sharks

1.2.1 Threats and Conservation

Populations of white sharks have declined substantially worldwide, with an estimated 30-49% global reduction over the past 159 years (Rigby et al., 2019). In Australia and New Zealand, white shark populations declined throughout the 20th century (Commonwealth of Australia, 2013), with estimated losses of up to 70-90% in some populations in Eastern Australia (Roff et al., 2018). Like other chondrichthyans, white sharks are vulnerable to overexploitation as a consequence of their limited ability to compensate for increased mortality due to their low natural abundance and life history traits, such as slow growth rates, late maturity, and low fecundity (MacArthur & Wilson, 1967; Stevens et al., 2000). Currently, the greatest threats to white shark populations include incidental bycatch by inshore fisheries, the shark finning industry, and beach-protection programmes in Australia and South Africa (Roff et al., 2018). Other threats to white sharks include declines in habitat loss, pollution, and declines in prey abundance due to changes in coastal productivity (Huveneers et al., 2018).

Despite mixed public support, increased recognition for the species' vulnerability to overexploitation and its potential importance in marine ecosystem regulation have resulted in the white shark being among the first shark species listed under several wildlife treaties, including Appendix I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) (Rigby et al., 2019). The white shark is currently listed as 'Vulnerable' under the IUCN Red List (Rigby et al., 2019) and is protected across most of its range through both international and regional legislation (Chapman et al., 2015; Jewell et al., 2013). In New Zealand, white sharks have been listed as 'Threatened – Nationally Endangered' under the New Zealand Threat Classification System since 2016 (Duffy et al., 2018) and have been protected since 2007 under the Wildlife Act 1953, making it illegal to harm/kill white sharks and trade their products.

Though there is a lack of data on population trends in New Zealand, the New Zealand-Eastern Australian (hereafter 'Eastern Australasian') population has been estimated to comprise 5,460 individuals (uncertainty range of 2,909 to 12,802 individuals) (Bruce et al., 2018) with conflicting evidence for population recovery since the implementation of protection measures. For example, a meshing programme in Eastern Australia from 2008 to 2018 saw fluctuating catches of white sharks, with an increase in later years (Reid et al., 2011). Davenport et al. (2021) found evidence that the Eastern Australasian population had not changed significantly between 2010 and 2013, while Bruce et al. (2018) found a slight decline in the abundance of adult white sharks in this population. Although, these authors noted that benefits of protection measures are unlikely to be apparent in the short term.

The lack of information regarding white shark population trends is primarily due to a lack of historical baselines on their population sizes (Roff et al., 2018) and spatial ecology, and the difficulties in studying wide-ranging marine predators (Afonso et al., 2022). Understanding white shark population trends and dynamics, however, is a priority for both conservation management and human safety (Davenport et al., 2021; Huveneers et al., 2018). While the field of white shark research has grown considerably in recent years, further information regarding white shark behaviour, movement, and population dynamics is required for the development of strategies such as non-lethal beach protection measures, dynamic spatial approaches for species conservation that account for the species' high mobility (Mull et al., 2022), and adequate population models for stock assessment and management advice (Huveneers et al., 2021).

1.2.2 Life History and Feeding Ecology

The white shark is one of the largest extant marine predators in the world (Hussey et al., 2012), reaching an estimated maximum size of 600-640cm total length (TL) (Compagno, 2001) and with females growing considerably larger than males (Francis, 1996; Pratt, 1996). Subadult white sharks, defined as those between the size at which they begin to show seasonal residency to specific foraging locations and the size of maturity, range from >3.0m to 3.6m TL and >3.0m to 4.8m TL for males and females, respectively (Bruce & Bradford, 2012; Martin et al., 2005). Adult white sharks, defined as those that have reached sexual maturity, exceed 3.6m TL and 4.5-5.0m TL for males and females, respectively (Francis, 1996; Pratt, 1996), but immature females as large as 5.2m TL have been observed (Duffy et al., 2012).

White sharks undergo an ontogenetic shift in diet and trophic level as they transition from juveniles (<3m TL) to subadults and adults (Aquino-Baleytó et al., 2021; Kim et al., 2012). Ontogenetic variation in diet is common across chondrichthyans and can have multiple drivers, such as age-related changes in size, morphology, and energy requirements, foraging experience, and expanding home ranges (Munroe et al., 2022). Juvenile white sharks are primarily generalist piscivores but are also known to consume cephalopods and other invertebrates (Hussey et al., 2012). As individuals grow into the larger subadult and adult life stages, they develop stronger jaws and broader teeth as they begin to include marine mammal prey in their diet (Ferrara et al., 2011). In particular, pinnipeds are targeted by white sharks presumably for their energy-rich fatty layer (Klimley et al., 2023) to meet shifting nutritional requirements linked with an expanding migratory range (Grainger et al., 2020). That said, large white sharks are not obligate marine mammal predators, also feeding on finfish, elasmobranchs, and invertebrates (Curtis et al., 2012; Hussey et al., 2012). A dietary study by Hussey et al. (2012) found that while the diets of juvenile and subadult/adult white sharks differed significantly, there was a high degree of overlap in the presence of several prey groups, with the inclusion of whale and seal prey in the stomachs of sharks as small as 194cm precaudal length. Besides dentition, variation in preferred foraging habitats is also believed to be a primary reason for the ontogenetic variation in distribution observed in white sharks (Hussey et al., 2012), with a predominance of nearshore, coastal prey in the diets of juveniles, and mesopelagic and oceanic prey in that of adults (Grainger et al., 2020; Smale & Cliff, 2012).

1.2.3 Global Distribution and Movements

White sharks are circumglobally distributed, occupying waters across all major oceans (Bradford et al., 2020; Compagno, 2001; Kanive et al., 2015). Known white shark populations occur at low natural densities (Compagno et al., 2005) in several general regions, including South Africa, western North Atlantic, southwest Atlantic, Mediterranean, northwest Pacific, northeast Pacific, and Australia/New Zealand (Franks et al., 2021; Kanive et al., 2015). Although the population structure is not clearly defined within and among all regions, genetically distinct groups exist at the regional level, such as in the western North Atlantic, southern Africa, and at finer scales such as in southern/western Australia, and eastern Australia/New Zealand (Franks et al., 2021). These groups share patterns of movement ecology and habitat use, likely driven by requirements for foraging and reproduction, environmental conditions, or physical constraints such as shelf structure and width, and landmass size/orientation (Franks et al., 2021).

White sharks occupy a range of habitats (Spaet et al., 2020), from tropical to cool temperate waters (Findlay et al., 2016; Gennari et al., 2022), and from coasts to the open ocean (Grainger et al., 2020). While white sharks were previously considered to predominantly inhabit coastal temperate waters, recent tagging studies have revealed their capability to undertake extensive offshore migrations (e.g., Bruce et al., 2019; Duffy et al., 2012; Hussey et al., 2012), showing long-distance movements along continental shelves, into pelagic waters, and across ocean basins (Franks et al., 2021; Smale & Cliff, 2012). Like other migratory species, these movement patterns are often predictable (Kanive et al., 2015), occurring along “migration corridors” connecting distant and, often, ephemeral resource-rich feeding grounds (Franks et al., 2021; Munroe et al., 2022) where subadult and adult white sharks often exhibit temporary residency (Aquino-Baleytó et al., 2021). Drivers of white shark movements may include abiotic factors, such as temperature, current, or bathymetry, and biotic factors, such as mating, pupping, prey availability or predation risk (Aquino-Baleytó et al., 2021; Franks et al., 2021). Movement and habitat use are also related to ontogeny and sex (Domeier & Nasby-Lucas, 2007; Jewell et al., 2013), whereby subadult and adult white sharks exhibit similar offshore migrations and seasonally aggregate at these resource-rich habitats (Domeier & Nasby-Lucas, 2007; Duffy et al., 2012), while young-of-the-year and juvenile individuals are predominantly distributed close to shore in depths <200m (Anderson et al., 2021a), and females tend to show broader dispersal, spending more time in offshore than males (Bradford et al., 2020; Domeier & Nasby-Lucas, 2013).

1.2.4 White Shark Aggregations

White sharks show seasonal patterns of residency at many known aggregation sites throughout the world, including in western North America, Mexico, South Africa, Australia and New Zealand (Compagno, 2001). The term, ‘aggregation’, refers to a passive process through which individuals of the same species group within a particular area or habitat (Papastamatiou et al., 2022a). Aggregatory behaviour in white sharks may be influenced by several factors, but the primary driver is believed to be the availability of calorie-rich pinniped prey (Hussey et al., 2012; Jewell et al., 2024). Most white shark aggregation sites are centred on dense coastal or oceanic pinniped colonies (Aquino-Baleytó et al., 2021; Domeier & Nasby-Lucas, 2007), with the presence of white sharks correlating with seasonal concentrations of pinnipeds undergoing moulting, mating and pup-rearing (Francis et al., 2015; Goldman & Anderson, 1999; Klimley et al., 2001; Munroe et al., 2022). Young-of-the-year and juvenile white sharks are generally absent from these sites as it is thought they are incapable of consistently capturing marine mammal prey (Jewell et al., 2024; White et al., 2019). The arrival of subadults at aggregation sites, therefore, marks a change in their predatory regime (Bruce & Bradford, 2012). Both sexes visit aggregation sites, though the sex ratio can vary among locations, seasons and years (Bradford et al., 2020; Bruce et al., 2019). The reasons for sexual segregation at pinniped colonies are largely unknown, but females may spend more time foraging offshore than males, potentially as a result of prey availability, differing physiological needs, reproductive habits, or male avoidance (Bradford et al., 2020; Domeier & Nasby-Lucas, 2013; Jewell et al., 2024; Robbins, 2007).

1.2.5 Stewart Island, New Zealand

Stewart Island/Rakiura, located c. 30km south of New Zealand's South Island, is a known aggregation site utilised by the Eastern Australasian white shark population (Duffy et al., 2012; Francis et al., 2015). The Rakiura region, encompassing Stewart Island and its outlying islands, contains more than 50 islands (Watson et al., 2014); some of which harbour major New Zealand fur seal (*Arctocephalus forsteri*) breeding colonies, particularly along the 12-km long Titi (Muttonbird) Islands chain (Watson et al., 2014). Following their extirpation from the Rakiura region by earlier sealers, the first fur seal colonies at the Titi Islands were reported on Bench Island in 1943, before spreading to the Bunker Islets by the 1970s (Wilson, 1981), and to Edwards Island, North Island, and other islands northeast of Stewart Island by 2004 (Watson et al., 2014). These breeding colonies seasonally attract white sharks which are present almost continuously from late spring to early winter, peaking during autumn in March-June (Francis et al., 2015). The arrival of white sharks to Stewart Island coincides with a time in the life cycle of New Zealand fur seals that is believed to optimise foraging success (Francis et al., 2015). Pregnant female fur seals arrive at breeding colonies in southern New Zealand to give birth between mid-November and mid-January (Francis et al., 2015), with a median pupping date of mid to late December (Bradshaw et al., 2000). Pups remain ashore during their weaning period of 7-10 months, during which lactating females regularly alternate between feeding at sea and coming ashore to suckle their pups (Bradshaw et al., 2000; Francis et al., 2015). Female fur seals are constrained to foraging relatively near the breeding colony and, consequently, spend a large proportion of time foraging near the surface in mean depths <100m (Harcourt et al., 2002). Pups begin swimming in exposed tide pools during February-March, venturing further offshore as they grow and begin foraging at ~ 6 months old (Francis et al., 2015). Pups are then weaned by September, approximately, and females depart for 1-2 months to feed before returning to birth again (Francis et al., 2015). The peak in abundance of white sharks at Stewart Island coincides with the peak of adult female fur seal movements between sea and shore, pup activity (Francis et al., 2015) in southern New Zealand. Therefore, this time of year is likely when opportunities for foraging seals are at their peak for subadult and adult white sharks (Francis et al., 2015).

White sharks of both sexes and all sizes, except young-of-the-year individuals, have been directly observed at Stewart Island (Duffy et al., 2012), although males outnumber females 2.5 to 1 (Francis et al., 2015). Mature females are rarely seen or recorded at the Titi Islands, possibly arriving at Stewart Island after the typical aggregatory season (Francis et al., 2015). Most white sharks aggregating at Stewart Island then migrate annually to subtropical and tropical regions of the southwest Pacific, with some showing return migration to Stewart Island (Duffy et al., 2012).

1.3 Research Methods and Data Analysis

1.3.1 Data Collection and Acoustic Telemetry

Our ability to understand marine predators is limited by the difficulties in obtaining ecological and behavioural data (Gennari et al., 2022). Studies on the population estimates and dynamics (Kanive et al., 2015), sociality (Jacoby et al., 2012), and movements of sharks have been largely descriptive due to challenges in observing and tracking large pelagic predators in the marine environment (Grainger et al., 2020; Mull et al., 2022). Understanding the internal and external influences of these aspects of species' ecology also requires the collection of large, high-resolution datasets across multiple conditions at different temporal and spatial scales (Franks et al., 2021; Jewell et al., 2024). Telemetry, or the use of electronic tags, has seen rapid developments since the 1980s (Bruce et al., 2019; Curtis et al., 2018) and has become a common approach for conducting elasmobranch research (Green et al., 2022). Advancements in telemetry and battery lifespans have improved the spatial and temporal resolution of data collected, highlighting many misconceptions about shark ecology (Baremore et al., 2021; Domeier & Nasby-Lucas, 2013; Findlay et al., 2016; Heupel et al., 2015). For example, long-term telemetry studies have reinforced the capabilities of white sharks to undertake extensive offshore migrations (e.g., Bradford et al., 2020; Bruce & Bradford, 2012; Duffy et al., 2012; Francis et al., 2015; Kanive et al., 2015), alongside identifying diel and temporal movements relative to physical parameters (Aquino-Baleytó et al., 2021; Domeier et al., 2012; Fallows et al., 2012; Gennari et al., 2022). Additionally, spatial data collected from high-density arrays have found numerous large pelagic shark species to have organised social structures, after previously being considered solitary (e.g., Findlay et al., 2016; Guttridge et al., 2009a; Jacoby et al., 2010; Klimley & Nelson, 1984; Mourier et al., 2012). Telemetry also has implications for species management, being an important tool for identifying areas of spatiotemporal overlap between sharks and anthropogenic activities (Spaet et al., 2020). As a result, telemetry studies have played an essential role in shark conservation, fisheries management (Curtis et al., 2018; B. G. C. King et al., 2024), and minimising shark-human conflicts (Bruce & Bradford, 2012; Curtis et al., 2012).

Satellite telemetry has provided information on large-scale migrations and population connectivity; however, behavioural decision-making processes often occur at smaller scales than can be observed via satellite telemetry (Gennari et al., 2022). Acoustic telemetry has been used to obtain information on the behaviour and movement of sharks at finer spatiotemporal resolutions, particularly in areas frequented by animals for long periods of time, such as aggregation sites (Baremore et al., 2021), and for animals that do not surface frequently (Mull et al., 2022). Acoustic telemetry involves two-parts: 1) a specialised tag either implanted or externally attached to an animal that transmits acoustic pulses and, 2) a hydrophone, or ‘acoustic receiver’, at a fixed location within a region of interest which records acoustic pulses when within range of a tagged animal (Mull et al., 2022). Although acoustic telemetry studies commonly involve a trade-off between spatial coverage and receiver cost, especially when conducted at larger spatial scales and/or when spatial coverage is difficult to achieve (Dorazio & Price, 2019), this method offers benefits such as allowing nearly uninterrupted long-term monitoring of tagged individuals and unaffected survey capabilities in low visibility conditions (Kraft et al., 2024). Consequently, acoustic telemetry has proven instrumental in understanding the movement and behaviours of sharks (Farine, 2013; Setyawan et al., 2024) and, therefore, the development of management strategies, such as marine protected areas and seasonal fisheries restrictions (Jewell et al., 2013; Kohler et al., 2023).

1.3.2 Data Analysis and Bayesian Statistics

Despite rapid advancements in monitoring technologies, progress in our understanding of species and their ecology has been hindered by a lack of sophisticated statistical modelling techniques (Finn et al., 2014). The use of large datasets produced by ecological monitoring is increasing due to the range of ecological questions they can answer (Kruschke, 2021; Wade et al., 2022). However, these datasets can be difficult to analyse and interpret at both individual and population levels (Finn et al., 2014) not only because of their size, but also because they are often highly variable, contain strong class imbalances (Wade et al., 2022) and often do not conform to the assumptions of linear models, requiring transformations which can alter the relationships between predictor and response variables (Spake et al., 2023; Wade et al., 2022).

Another limitation of traditional statistical approaches is the inability to produce reliable analyses and estimates from limited data (Tsai et al., 2019). This is particularly problematic for studying species with low natural population sizes or low productivity (McElreath, 2020; Tsai et al., 2019), such as the white shark (Bradford et al., 2020; Kanive et al., 2015). Consequently, Bayesian approaches to statistical analysis have become increasingly popular (van de Schoot et al., 2021). Bayesian modelling has been promoted over traditional frequentist methods for various reasons, including its capacity for fitting complex hierarchical models, and the inclusion of prior information from previous research, captured by the prior distributions for model parameters (Kruschke, 2021; van de Schoot et al., 2021). A prior distribution is paired with the observed data via a likelihood function to produce the posterior distribution, from which predictions about future events can be made (van de Schoot et al., 2021).

1.3.3 Social Network Analysis

Sociality and group formation have previously been neglected in elasmobranch research (Papastamatiou et al., 2022a), particularly in large pelagic sharks (Lilly et al., 2020), predominantly due to insufficient data collection and analysis methods (Findlay et al., 2016; Mourier et al., 2017; Papastamatiou et al., 2022a). Recognition of shark social behaviour has grown since the early 2000s due to advancements in tracking technology and the ability to yield higher resolution spatial data, and the development of social network analysis (Farine, 2013; Papastamatiou et al., 2022a). Social network analysis originated in the 1930s for the purpose of understanding human relationships and social processes but has recently become an increasingly common tool for understanding animal social structure and the ecological causes and consequences of social behaviour (Farine & Whitehead, 2015), especially in species that are hard to study or do not explicitly display sociality (Kraft et al., 2024). Long-term studies have since revealed that shark sociality may be more complex than previously thought (Castro, 2016; Porcher, 2023), with some species of large pelagic shark, which were generally regarded as solitary, showing complex and organised social structures (e.g., Guttridge et al., 2009a; Jacoby et al., 2010; Klimley & Nelson, 1984; Mourier et al., 2012).

Social network analysis uses spatiotemporal data, such as the co-occurrence of individuals at the acoustic receivers (B. G. C. King et al., 2024; Lilly et al., 2020), to estimate networks of social interactions (e.g., grooming) or associations between pairs of animals within a population (Farine & Whitehead, 2015). The interactions or associations within a population combine to form a ‘network’. Networks comprise a set of nodes, representing individuals, connected by edges, representing the interactions or associations between a pair of nodes, known as a ‘dyad’ (Farine & Strandburg-Peshkin, 2015). These edges are often weighted corresponding to the strength of an association between a dyad (Farine & Strandburg-Peshkin, 2015), which can be calculated by the extent of spatiotemporal overlap between individuals, such as the frequency of co-occurrences at acoustic receivers (Lilly et al., 2020).

1.3 Thesis Aims & Objectives

1.3.1 Chapter 2 Objectives

Chapter 2 investigates individual variation in white sharks’ spatial and temporal patterns of habitat use at the aggregation site northeast of Stewart Island.

The objectives of this chapter were to assess:

1. The overall spatiotemporal distribution of white shark occurrences northeast of Stewart Island, and whether some acoustic receivers (i.e., sites) are more ‘popular’ with white sharks than others; and
2. The degree to which occurrence at particular sites varied among individual white sharks.

1.3.2 Chapter 3 Objectives

Chapter 3 investigates the co-occurrences and potential social associations of white sharks northeast of Stewart Island.

The objectives of this chapter were to assess:

1. The formation of associations between white sharks aggregating at Stewart Island.
2. If associations existed, whether these associations were formed between white sharks of the same sex and/or similar size (i.e., ontogeny).
3. Where most co-occurrences between white sharks aggregating at Stewart Island occurred.

Chapter 2:

Individual variation in the spatiotemporal occurrences of white sharks (Carcharodon carcharias) around Stewart Island, New Zealand.

2.1 Abstract

Variation in behaviour and movements among individuals within an animal population has recently been recognised for its implications in understanding population-level processes, such as habitat use, dispersal, and predator-prey interactions. The purpose of this study was to investigate the extent to which spatiotemporal distribution varied among individual white sharks (*Carcharodon carcharias*) at Stewart Island, an aggregation site in southern New Zealand, at fine spatial scales of up to tens of kilometres, using an acoustic telemetry dataset collected in April-June 2011. We modelled the probability of observing each shark at each site/receiver on each day using logistic Bayesian hierarchical models, including terms for receivers, individual sharks, days, and their interactions. Variance components of the fitted terms were compared to understand the relative importance of overall differences in receivers, individual sharks, and individual preferences of individual sharks for particular receivers. Substantial variation was found in both the overall presence of white sharks across different receivers in the array and in the preferences of individual white sharks for particular sites as evidenced by greater variation in shark-receiver interaction effect than that of the effects of sharks', averaged over receivers. The northern Titi Islands were highlighted as an area of particularly high white shark activity, potentially due to prey abundance, site fidelity behaviour, and the presence of shark cage diving operations. Larger sharks (with potentially more hunting experience) showed higher probabilities of occurrence at the northern Titi Islands, while smaller white sharks showed broader use of the receiver array. Therefore, size-related behaviours, such as variable feeding strategies, competitive exclusion and predation risk, were identified as potential drivers for the individual variation observed in this study. The inclusion of measures for individual variation produced statistical models with better predictive accuracy regarding the occurrence of white sharks northeast of Stewart Island, highlighting the importance of incorporating individual variation in ecological modelling of movement to obtain a more comprehensive understanding of white shark habitat use and to better inform conservation and human safety initiatives.

2.2 Introduction

Individual variation, a fundamental concept in modern evolutionary theory, has been increasingly applied in ecological research since the early 2000s, particularly in studies of animal behaviour and movement (Roche et al., 2016). Previously, ecological studies had predominantly focused on understanding 'typical' patterns (A. K. Shaw, 2020), considering the variation among individuals as mere "noise" around the mean (Hertel et al., 2020). While the relevance of individual variation to understanding population processes has been questioned, Bennett (1987) suggested that variation in performance among individuals may have profound eco-evolutionary implications for population-, community-, and ecosystem-level processes. A. K. Shaw (2020) also explains that population-level patterns, such as distribution and habitat use, are the sum of individual behaviours. Consequently, ecological studies are beginning to adopt more comprehensive and dynamic approaches that consider individual variation to predict and obtain a more complete understanding of animal behaviour (Estes et al., 2003; Roche et al., 2016). Individual variation may also have important implications for conservation management both in the near-term, such as in the case of evaluating habitat use and areas of overlap with anthropogenic activities, and in the long-term through understanding how and when behavioural differences in populations might become adaptive (Roche et al., 2016). Developing frameworks for studying individual variation, therefore, may be particularly important for marine apex predators, given their potential effects on prey communities within their ecosystem (Kim et al., 2012) and their vulnerability to overexploitation (Roff et al., 2018). However, there continues to be a lack of frameworks for systematically understanding variation in movement patterns, the mechanisms by which this variation arises, and the implications on population- to ecosystem-level processes (Estes et al., 2003; A. K. Shaw, 2020).

The white shark (*Carcharodon carcharias*) is a large, highly migratory, marine, apex predator that inhabits coastal and oceanic waters throughout the world (Compagno, 2001; Findlay et al., 2016; Gennari et al., 2022), including New Zealand. Like other chondrichthyan predators, white sharks are particularly vulnerable to overexploitation and have declined globally by 30-49% over the past 159 years (Rigby et al., 2019). Increased scientific effort in understanding the broad-scale distribution and movement of white sharks has been instrumental in the species' conservation, enabling the establishment of management strategies and multi-jurisdictional protection legislation that reflect the species' high mobility (Huveneers et al., 2021). However, local and regional conservation efforts may be hindered by the lack of information regarding movement and habitat use patterns of white sharks at finer scales. Knowledge regarding individual movement variation in white sharks is limited and has not yet been explored in New Zealand. Recent studies elsewhere have revealed unique patterns in diet (Hussey et al., 2012), foraging specialisation (Kim et al., 2012; Sims et al., 2012), and vertical habitat use (Papastamatiou et al., 2022b); although, the extent of individual variation in the fine-scale horizontal movements of white sharks remains understudied.

The purpose of this study was to describe the fine-scale spatiotemporal distribution and extent of individual variation in movements of white sharks around northeastern Stewart Island, an aggregation site in southern New Zealand. We analysed acoustic telemetry data collected by Francis et al. (2015), who used it to assess the broader spatial and temporal patterns of occupancy of white sharks at this location. Here, we build upon this previous research by using Bayesian analyses to investigate spatial and temporal patterns of habitat use at the individual level, to predict 'hotspots' of white shark activity, and to determine how important understanding individual variation is in making these predictions. More specifically, our objectives were to:

1. Assess the overall spatiotemporal distribution of white shark occurrences northeast of Stewart Island, and whether some acoustic receivers (sites) are more 'popular' with white sharks than others; and
2. Quantify the degree to which occurrence at particular sites varied among individual white sharks.

2.3 Methods

2.3.1 Study Site

Stewart Island/Rakiura is located c. 30km south of New Zealand's South Island (Williams, 1936). It sits on a shallow continental shelf (S. D. King et al., 2012), with average depths of c. 27m in Foveaux Strait. The area is frequently exposed to prevailing south-westerly winds (S. D. King et al., 2012; Stead, 1971) and southerly ocean swells (S. D. King et al., 2012). Annual sea surface temperatures average c. 13.5°C, with a thermal range of 7.5°C (Tait et al., 2021).

Stewart Island and its outlying islands are also influenced by the Subtropical Front (Duffy et al., 2012), making it a region of high biological productivity due to the mixing of micronutrient-rich subtropical waters with macronutrient-rich subantarctic waters (Bostock et al., 2015). The Rakiura region supports dense New Zealand fur seal (*Arctocephalus forsteri*) breeding colonies, particularly along the Titi (Muttonbird) Islands chain and Ruapuke Island (Watson et al., 2014), which seasonally attract white sharks to the region (Francis et al., 2015). White sharks are present at Stewart Island from late spring to early winter, with presence peaking in March-June (Francis et al., 2015), before making long-distance migrations to other areas of New Zealand, Australia, or the southwest Pacific (Duffy et al., 2012).

Vemco VR2W acoustic receivers (*Figure 2.2*) were mounted approximately 5m above the seabed at 15 different locations northeast of Stewart Island in late March 2011 near fur seal colonies, or at headlands and rocky islands potentially used as ‘waypoints’ for travelling sharks (Francis et al., 2015). Of the 15 receivers, seven were situated along the 12km-long Titi Islands chain, five at Ruapuke Island, and three at the mouth of the Paterson Inlet/Whaka a Te Wera (*Figure 2.1*). When present, the orientation at the start of a receiver name (e.g., West Edwards Island, East Edwards Island) indicates the side of the island where a receiver was deployed.

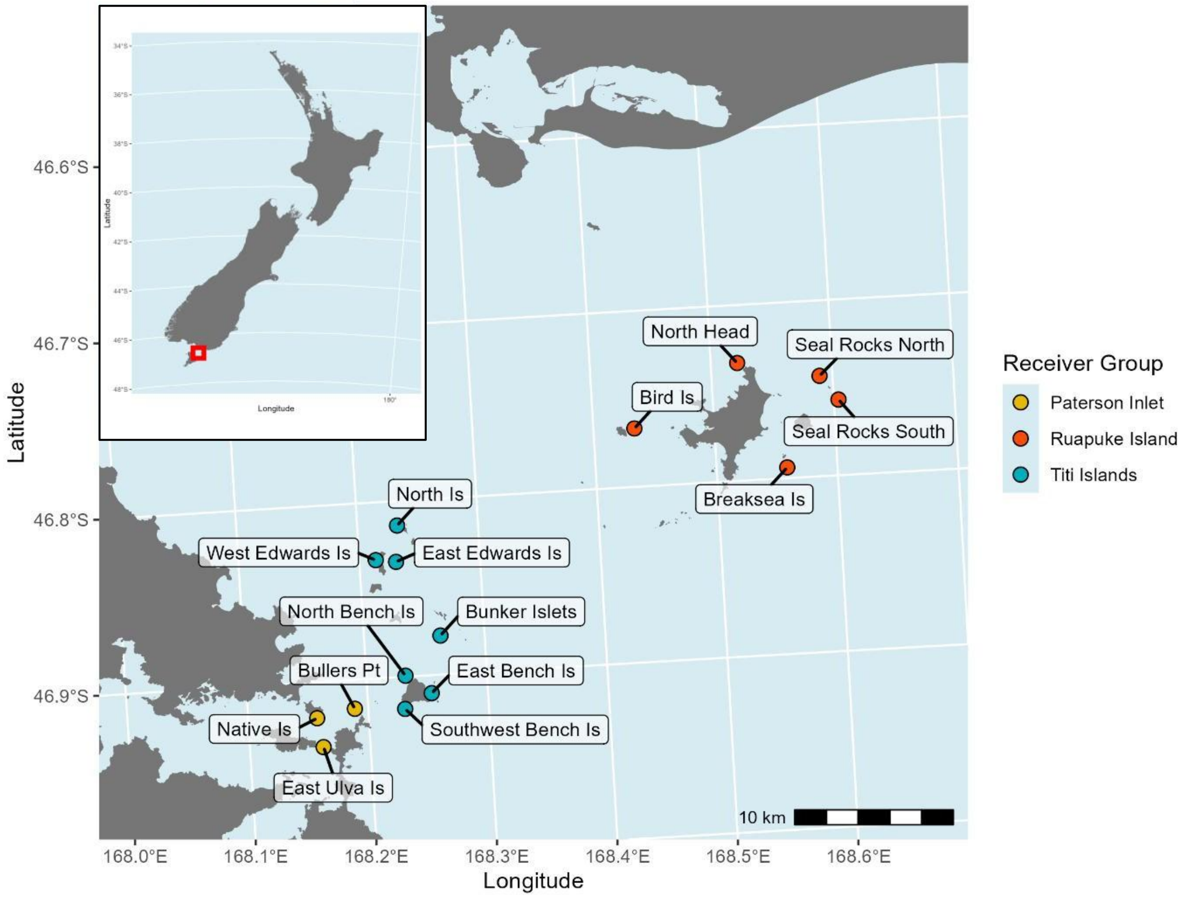


Figure 2. 1 *– Locations of acoustic receivers deployed northeast of Stewart Island.*

2.3.2 Data Collection

A total of 22 sharks were tagged with Vemco Ltd V16-5H acoustic R-code tags in March (early autumn) within the network of acoustic receivers (*Figure 2.2*), hereafter referred to as the 'receiver array' (Francis et al., 2015). All white sharks in this study were tagged around the Titi Islands (Francis et al., 2015). During the tagging process, the individual identification, sex, and estimated minimum and maximum total length (TL) of the shark was recorded (Francis et al., 2015; *see Appendix A, Table A.1 for more details*). In this chapter, the average between the minimum and maximum TL measurements will be reported when referring to the size of a shark. One shark, CC30, lacked minimum and maximum TL measurements (*see Table A.1 in Appendix A*). For more details on tagging and data collection, see Francis et al. (2015).

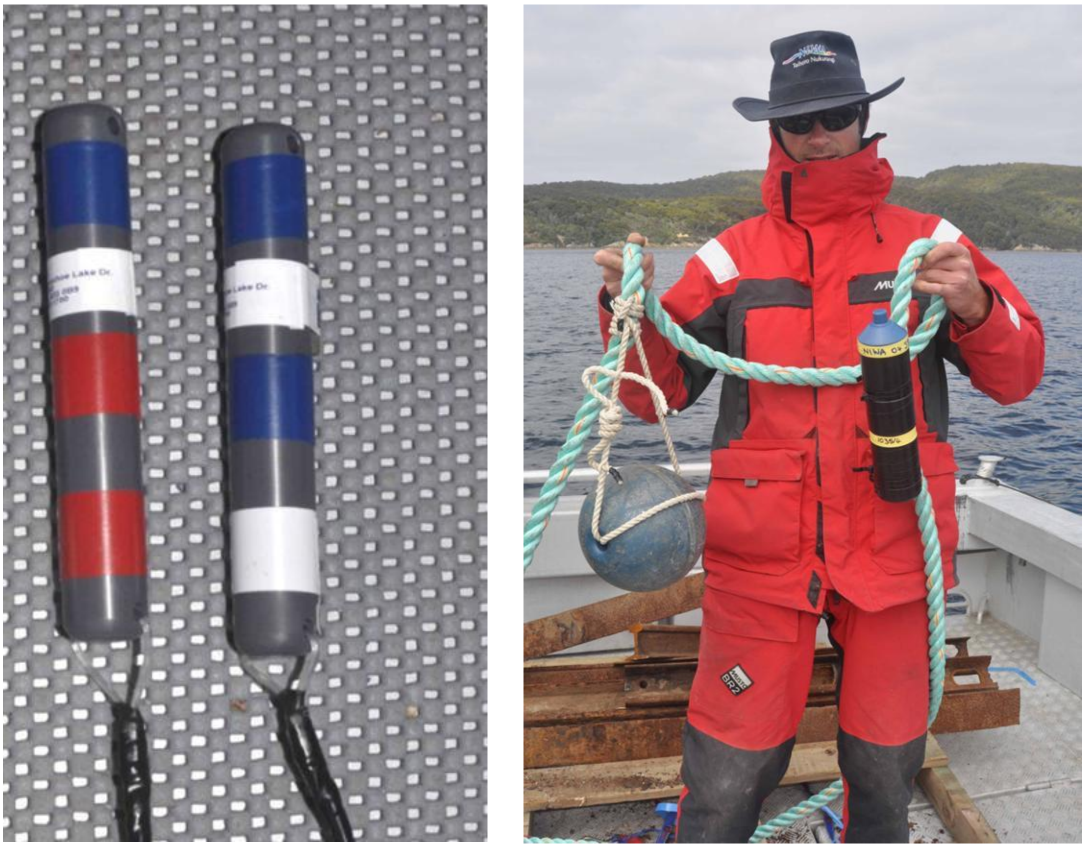


Figure 2. 2 *- Acoustic tag and receiver. Left: Vemco V16-5H R-code acoustic tag. Right: Vemco VR2W acoustic receiver attached to mooring prior to deployment northeast of Stewart Island, New Zealand. Photos: Malcolm Francis.*

2.3.3 Statistical Analysis

Detections recorded between 1 April 2011 and 25 June 2011 were analysed to ensure all receivers were active in the array. All 15 receivers deployed were included in the dataset and sorted into three geographical 'receiver groups' based on the broader area in which they were located, namely Paterson Inlet, Titi Islands, and Ruapuke Island (*Figure 2.1*). Detections from four shark tags were removed from the dataset for the following reasons. One was lost during the tagging process and was, consequently, not attached to a shark (Francis et al., 2015). Detections from the remaining three tags, attached to two 3.0m TL females and one 3.0m TL male, were removed due to their detections ending prematurely, as early as two weeks post tagging. It is uncertain whether this is a result of the sharks leaving the area or losing their tags, though the male individual was observed without its tag in March 2012 (Francis et al., 2015).

The data were summarised to represent daily occurrences, so that each row of the data represented a unique combination of day, shark, and receiver. Rows for dates before an individual shark was tagged and after their last detection in the receiver array were removed. Each row was then assigned an *occurrence* $y_{ijk} \in \{0, 1\}$, where 0 and 1, respectively, indicate the non-detection or detection of shark_i at receiver_j on day_k. All statistical analyses were conducted in R version 4.3.1 (R Development Core Team, n.d.) and used the packages, *brms* (Bürkner, 2017), *marginaleffects* (Arel-Bundock et al., 2024) and *ggplot2* (Wickham, 2016), for modelling, extracting the model's average predictions and 90% credible intervals (CI) for a given effect, and plotting respectively.

2.3.3.1 Model Definitions

To understand the extent of individual variation in the spatiotemporal distribution of occurrences of white sharks across the receiver array, we fit eight hierarchical logistic models. The models were compared in terms of their out-of-sample predictive accuracy, and the most accurate model was then used to make predictions and inferences. All eight models included the main effects of receiver, shark, and date, but they differed with respect to which of the following two-way interaction terms were included: shark and receiver; shark and date; receiver and date (*Table 2.1*). The most complex model, containing all two-way interactions, was defined as:

$$y_{ijk} \sim \text{Bernoulli}(\pi_{ijk})$$

$$\text{logit}(\pi_{ijk}) = \mu + \alpha_i + \beta_j + \gamma_k + \kappa_{ij} + \iota_{ik} + \nu_{jk}$$

$$\mu \sim \text{Normal}(0, 1.5)$$

$$\alpha_i \sim \text{Normal}(0, \sigma_\alpha)$$

$$\beta_j \sim \text{Normal}(0, \sigma_\beta)$$

$$\gamma_k \sim \text{Normal}(0, \sigma_\gamma)$$

$$\kappa_{ij} \sim \text{Normal}(0, \sigma_\kappa)$$

$$\iota_{ik} \sim \text{Normal}(0, \sigma_\iota)$$

$$\nu_{jk} \sim \text{Normal}(0, \sigma_\nu)$$

$$\sigma_\alpha , \sigma_\beta , \sigma_\gamma , \sigma_\kappa, \sigma_\iota, \sigma_\nu \sim \text{Exponential}(1)$$

where π_{ijk} is the probability $shark_i$ was detected at $receiver_j$ on day_k, μ is the intercept, α_i are the random effects for shark, β_j are the random effects for receivers, γ_k are the random effects for days, and κ_{ij}, ι_{ik}, and ν_{jk} are the interaction effects for shark and receiver, shark and date, and receiver and date, respectively.

2.3.3.2 Prior Predictive Checks

The model priors were checked to ensure they generated data that were reasonable and consistent with prior knowledge (Kruschke, 2021). Five different prior distributions were checked, and results were relatively consistent. The priors from the fifth prior predictive check (*see Figures B.1 and B.2 for more details*) were selected for several reasons. Firstly, McElreath (2020) explains that using "flatter" intercept priors on logit-transformed probabilities can cause the model to "pile" likelihood at 0 or 1. This means the model assumes a white shark is almost never or almost always likely to be present at a single receiver, which is inappropriate. Secondly, an Exponential (1) standard deviation prior makes the model more sceptical of large differences between receivers and sharks, for example, and makes smaller differences more likely. It is also a weakly informative prior, allowing posterior predictions to be largely a result of patterns in the data, rather than the prior.

2.3.3.2 Model Comparison and Interaction Term Analysis

The purpose for including interaction terms was to assess whether the probability of an individual shark being present at a particular receiver on a given day could be accurately predicted by the main effects of shark, receiver and/or date alone (indicating relatively consistent patterns of occurrence across all sharks, receivers and days), or whether predictions required interaction terms that allowed sharks to have individual 'preferences' for particular receivers, or different probabilities of occurrences on different days.

To assess the importance of these interaction terms, the eight models were compared using Pareto-smoothed importance sampling (PSIS-LOO) cross-validation and expected log pointwise predictive density (ELPD) estimates. Cross-validation assesses a model's out-of-sample predictive performance by fitting it to a subset of the data and predicting the withheld data (Vehtari, 2020); lower ELPD estimates indicate better out-of-sample predictions.

We assessed the magnitude of the effects of each term – main effects of sharks, receivers, dates, and their interactions – by comparing the terms' standard deviations of effects (i.e., the square-root of the variance components). A larger standard deviation indicates that a term has a greater effect on the probability of occurrence. For example, a large standard deviation for the main effect of receiver would suggest there is large variation in the overall mean probability of shark occurrence among receivers, irrespective of individual sharks or individual days. In the case of interaction terms, the standard deviation shows the degree of variation that is explained by the specific combination of shark, receiver, and/or date, after accounting for the main effects. For example, a standard deviation for the interaction of shark and receiver that is larger than the standard deviations for the main effects of sharks and receivers would suggest that the degree to which individual sharks vary in their probability of occurrence at particular receivers is greater than the overall variation among sharks and receivers (when averaged over receivers and sharks, respectively). Alternatively, if the standard deviation of the interaction were less those of the main effects, this would suggest that the occurrences of sharks at receivers were relatively consistent, with relatively little in the way individual preferences of sharks for particular receivers.

2.3.3.3 Inferences

Spatial Distribution

The selected model was used to make various predictions of the probability of the occurrence of sharks, and these predictions were used to make inferences about the spatiotemporal distribution and individual variation exhibited by white sharks at Stewart Island. Posterior distributions of the predicted probabilities were obtained via the *avg_predictions()* function from the *marginaleffects* package (Arel-Bundock et al., 2024) and then summarised as means and 90% credible intervals. To understand the overall spatial distribution of sharks across the array and identify areas of high activity, we estimated the probability of white shark occurrence at each receiver, averaged over sharks and days.

Individual Variation in White Sharks

The average predictions of the main effects of sharks were plotted to show how individual white sharks varied in their overall occurrence rates across the array, averaged over receiver and date. Next, the average predictions for the shark-by-receiver interaction effect were plotted to examine individual variability in the probability of white shark occurrences at a given receiver.

Temporal Variation

The receiver-by-date interaction term assessed how the popularity of different receivers varied from day to day. To examine this, the predicted probabilities of occurrence for each receiver on each day, averaged across sharks, were extracted and plotted. The average predictions for the main effect of date were also shown to assess how white shark presence varied from day to day over the study period, averaged over sharks and receivers.

The shark-by-date interaction term was included to assess whether the occurrence of individual white sharks also varied over the study period, averaged across receivers, whereby low probabilities of occurrence for a given day implied the use of habitats outside the receiver array. To test this, the average predictions for this effect were plotted.

2.4 Results

Across the 86 days, from 1 April 2011 to 25 June 2011, a total of 56,307 detections occurred across the 22 tagged sharks (18 males, 4 females) and 15 receivers. The total lengths of the sharks ranged from 2.5m to 4.0m (mean 3.4m TL), with both subadults and adults present in the sample (*see Appendix A, Table A.1 for more details*).

2.4.1 Model and Term Comparison

According to PSIS-LOO cross-validation, the model including all three two-way interaction terms had the greatest predictive accuracy, when compared to seven other reduced models that omitted various combinations of interactions (*Table 2.1; see Appendix B, Figure B.3 for Markov Chain Monte Carlo trace plots*). The three reduced models with the greatest predictive accuracy all included the shark-by-receiver interaction term and two included either the receiver-by-date or shark-by-date terms (*Table 2.1*). The model with the lowest predictive accuracy was the model that included no interaction terms, indicating that all the interaction terms were important for predicting the presence of white sharks in the receiver array.

The main effect of receivers had the largest standard deviation (*Figure 2.3*) of all terms, meaning that the spatial effects of the different receivers had the greatest influence on the probability of occurrences of white sharks; that is, individual receivers varied considerably in their overall 'popularity'. The standard deviation of the shark-by-receiver interaction term exceeded that of the main effect of sharks, indicating that individual white sharks varied more in occurrences at particular receivers than they did in their overall occurrences, averaged across receivers. The receiver-by-date and shark-by-date interaction terms had similar standard deviations, but both had greater variation than the main effect of date (*Figure 2.3*), indicating that the daily variation in individual sharks and receivers was greater than the overall daily variation (averaged across sharks and receivers).

Table 2. 1 *– Bayesian model interaction terms and comparison. Models are ordered from greatest predictive accuracy to lowest predictive accuracy according to their ELPD estimates. 'SE' refers to the 'Standard Error' of ELPD estimates.*

Model Rank	Interaction Terms	ELPD Estimate ± SE	ELPD Difference
1	Shark : Receiver Shark : Date Receiver : Date	-5963.2 ± 83.0	0.0
2	Shark : Receiver Receiver : Date	-6032.7 ± 83.4	-69.5
3	Shark : Receiver Shark : Date	-6075.7 ± 83.7	-112.5
4	Shark : Receiver	-6126.9 ± 83.9	-163.7
5	Shark : Date Receiver : Date	-6542.4 ± 86.3	-579.3
6	Receiver : Date	-6566.5 ± 86.5	-603.3
7	Shark : Date	-6619.5 ± 86.5	-656.3
8	None	-6636.0 ± 86.6	-672.8

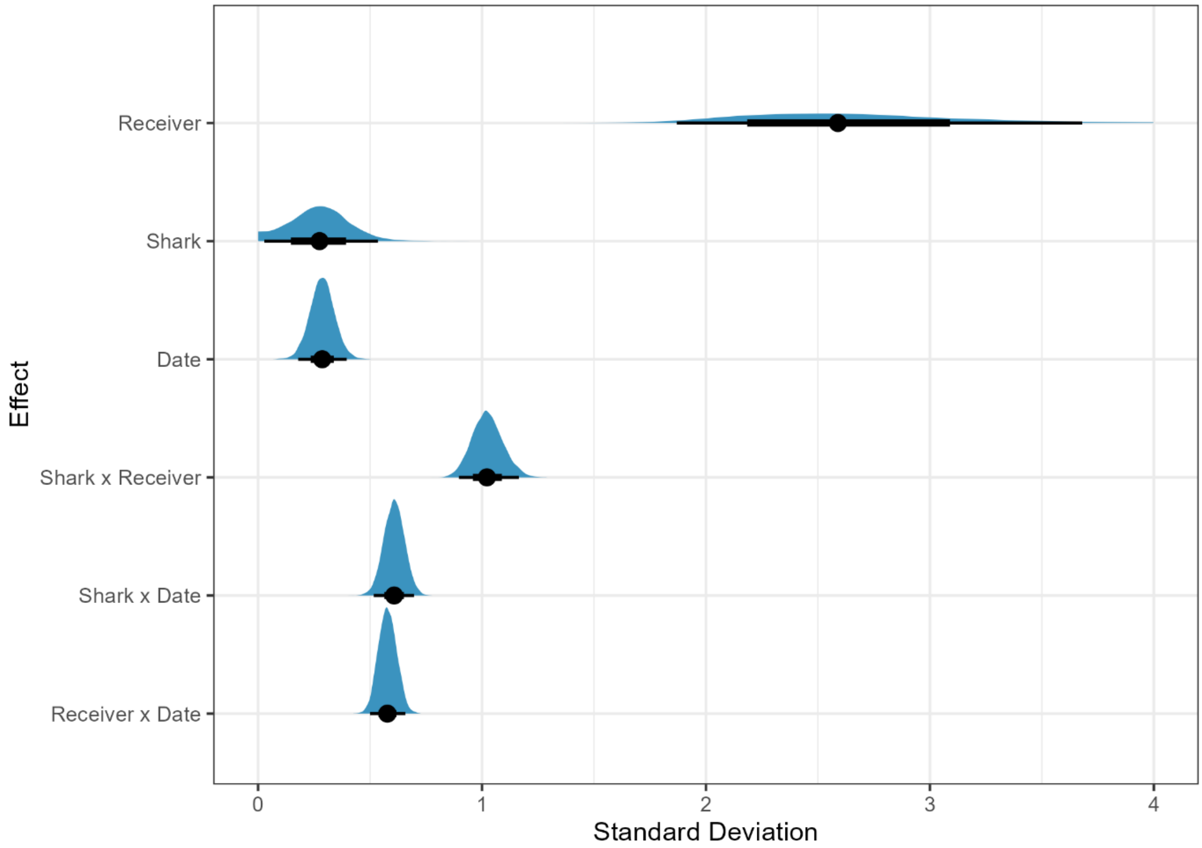


Figure 2. 3 *- Half-eye plots of the posterior distributions of the standard deviations (square-root of the variance components) of main and interaction effects on the probability of sharks being observed in the receiver array.*

2.4.2 Overall Spatiotemporal Distribution

2.4.2.1 Spatial Distribution

Overall, the Titi Islands had the highest probabilities of white shark co-occurrence, with an average estimate across all seven receivers of 0.29 (*Figure 2.4; Figure 2.5*). This was followed by the Paterson Inlet group with an average estimate of 0.029 across three receivers, and the Ruapuke Island group with an average estimate of 0.0008 across five receivers (*Figure 2.4; Figure 2.5*).

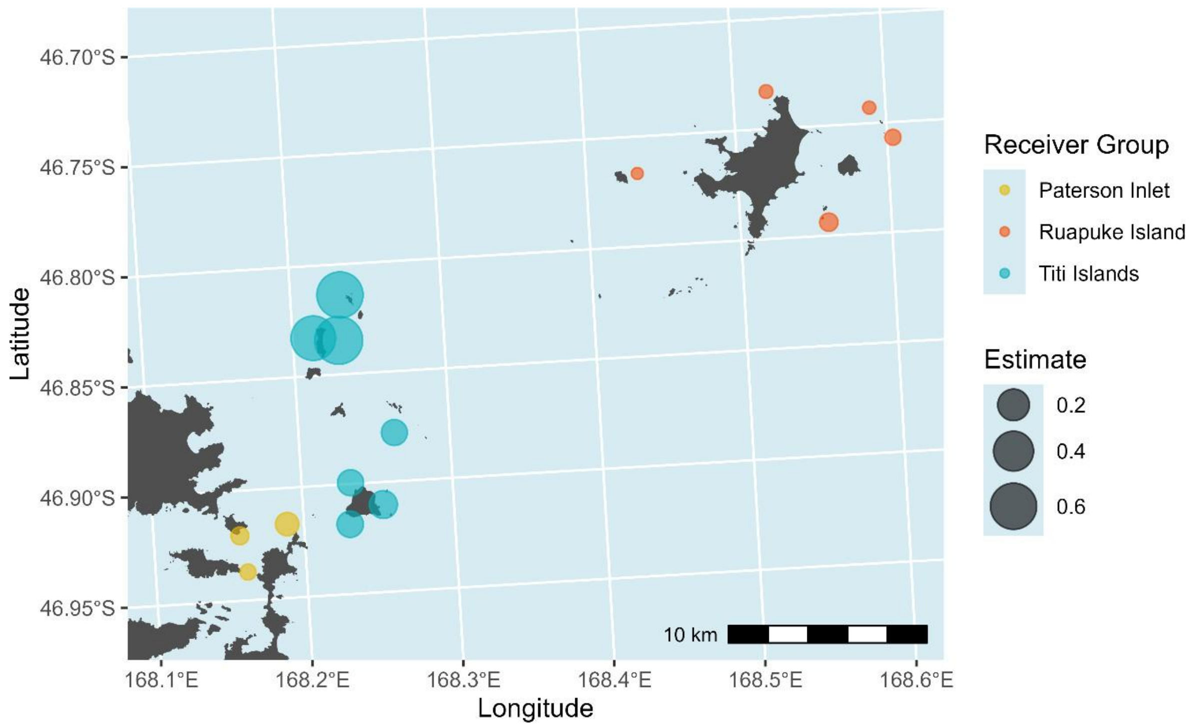


Figure 2. 4 *– Overall estimated probability of occurrence (i.e., 'popularity') of receivers in the Stewart Island receiver array, averaged over sharks and days. The size of the points represents the estimated (mean of the posterior distribution) probability of white shark occurrence per receiver, averaged across sharks and days.*

The three northernmost Titi Island receivers – East Edwards Island, North Island, and West Edwards Island – were the most popular overall, with probability estimates of 0.66 (90% Credible Interval: 0.64, 0.67), 0.60 (90% CI: 0.58, 0.61) and 0.54 (90% CI: 0.52, 0.56), respectively (*Figure 2.5*). The probabilities of white shark occurrence at the southern Titi Islands receivers (East Bench, Southwest Bench, North Bench, and Bunker Islets) were all similar to each other, but were considerably lower than the northern receivers (*Figure 2.5*). East Bench had the greatest probability with an estimate of 0.13 (90% CI 0.12, 0.14) and Bunker Islets had the lowest estimate of 0.10 (90% CI: 0.09, 0.11). All sharks were detected at least once at all Titi Islands receivers, except one individual (CC38, 2.9m male) was not detected at the North and Southwest Bench receivers across the season.

The Paterson Inlet and Ruapuke Island receivers had substantially lower estimates of white shark occurrence in comparison to the Titi Islands receivers (*Figure 2.5*). Of these receivers, Bullers Point (Paterson Inlet) had the highest estimate of 0.068 (90% CI: 0.06, 0.08). All

Ruapuke Island receivers, except Breaksea Island, were the least 'popular' of all 15 receivers in the array, having estimates of c. 0.1 or less (*Figure 2.5*). Bird Island, the westernmost Ruapuke Island receiver, was the least 'popular' of all receivers, with an estimated probability of shark presence of 0.002 (90% CI: 0.0007, 0.004) and only three detections from two white sharks (CC25, 2.8m male; CC28, 3.5m male) across the season.

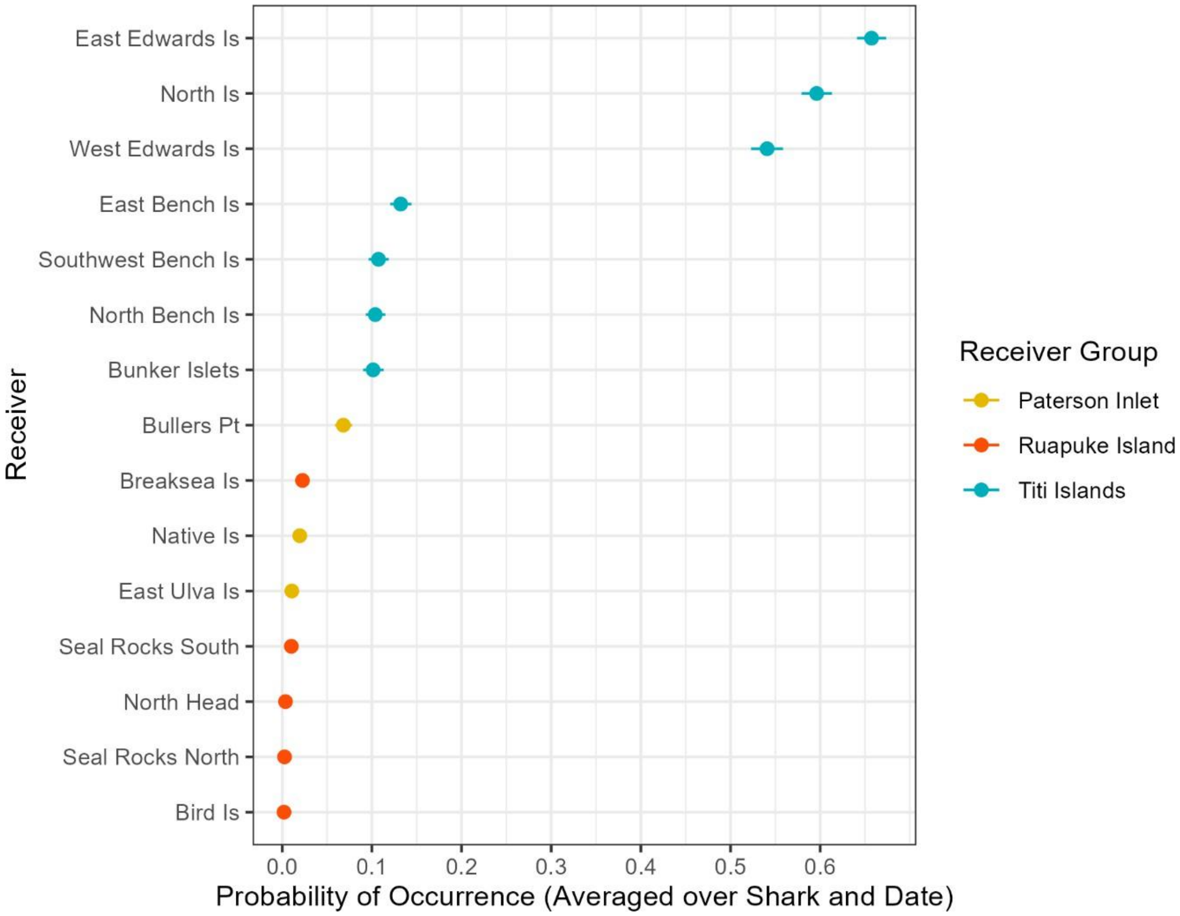


Figure 2. 5 *- Estimated model predictions for the probability of white shark occurrence per receiver, averaged across sharks and days (means and 90% credible intervals).*

2.4.4.2 Temporal Variation

The average probability of white shark occurrence in the receiver array fluctuated across days but did not vary greatly, with a minimum estimate of 0.13 (90% CI: 0.11, 0.15) on 8 April and a maximum estimate of 0.213 (90% CI: 0.18, 0.24) on 25 June (*Figure 2.6*); however, the latter estimate may have been affected by several sharks being 'absent' from the array (i.e., their final detection at any receiver was prior to this date). The second highest estimate was on 9 May with an estimate of 0.209 (90% CI: 0.18, 0.24); all tagged sharks except one (CC33, 3.4m female) were detected on this day. The mean estimated probability of occurrence across the season, averaged over receiver and shark, was 0.16.

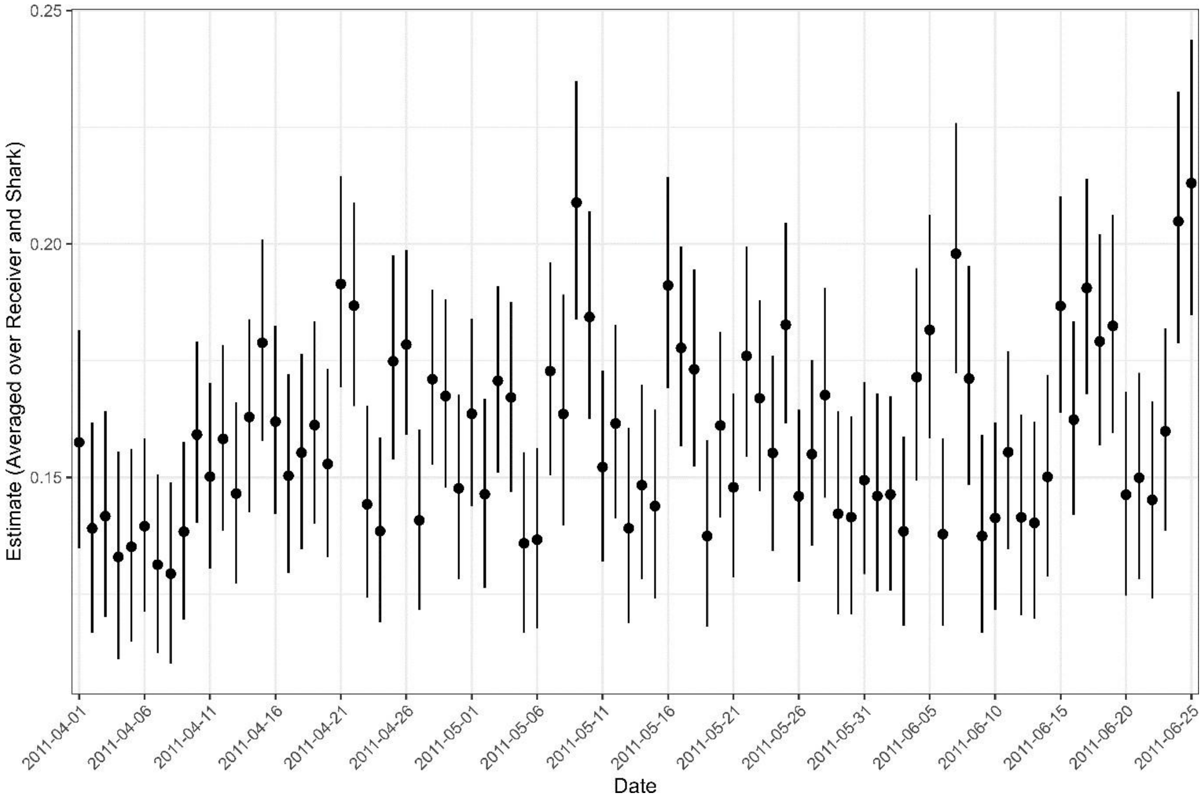


Figure 2. 6 *- Daily variation in the estimated probabilities of white shark occurrence at receivers deployed northeast of Stewart Island, averaged over sharks and receivers (means and 90% credible intervals).*

The Titi Islands receivers showed the most variable probabilities of white shark occurrence per day, averaged across sharks, with an average difference between the lowest and highest days of white shark occurrence of 0.42 (*Figure 2.7*). East Edwards saw the highest daily estimate of 0.86 (90% CI: 0.75, 0.94) on 25 June, and Bird Island (Ruapuke Island group) saw the lowest daily estimate of 0.0001 (90% CI: 0.0002, 0.004) on 8 April. While daily estimates at the Titi Islands remained high throughout the season, there were two periods, 7-10 May and 6-7 June, where there was slight decrease in the probability of white shark occurrence at these receivers and a noticeable increase in that of other receivers in the array (*Figure 2.7*). For example, all Paterson Inlet and Bench Island (southern Titi Islands) receivers recorded some of their highest estimates, while all three northern Titi Islands receivers recorded their lowest estimates on 8 May, and use of the Ruapuke Island and Paterson Inlet receivers was considerably higher on 7 June (*Figure 2.7*).

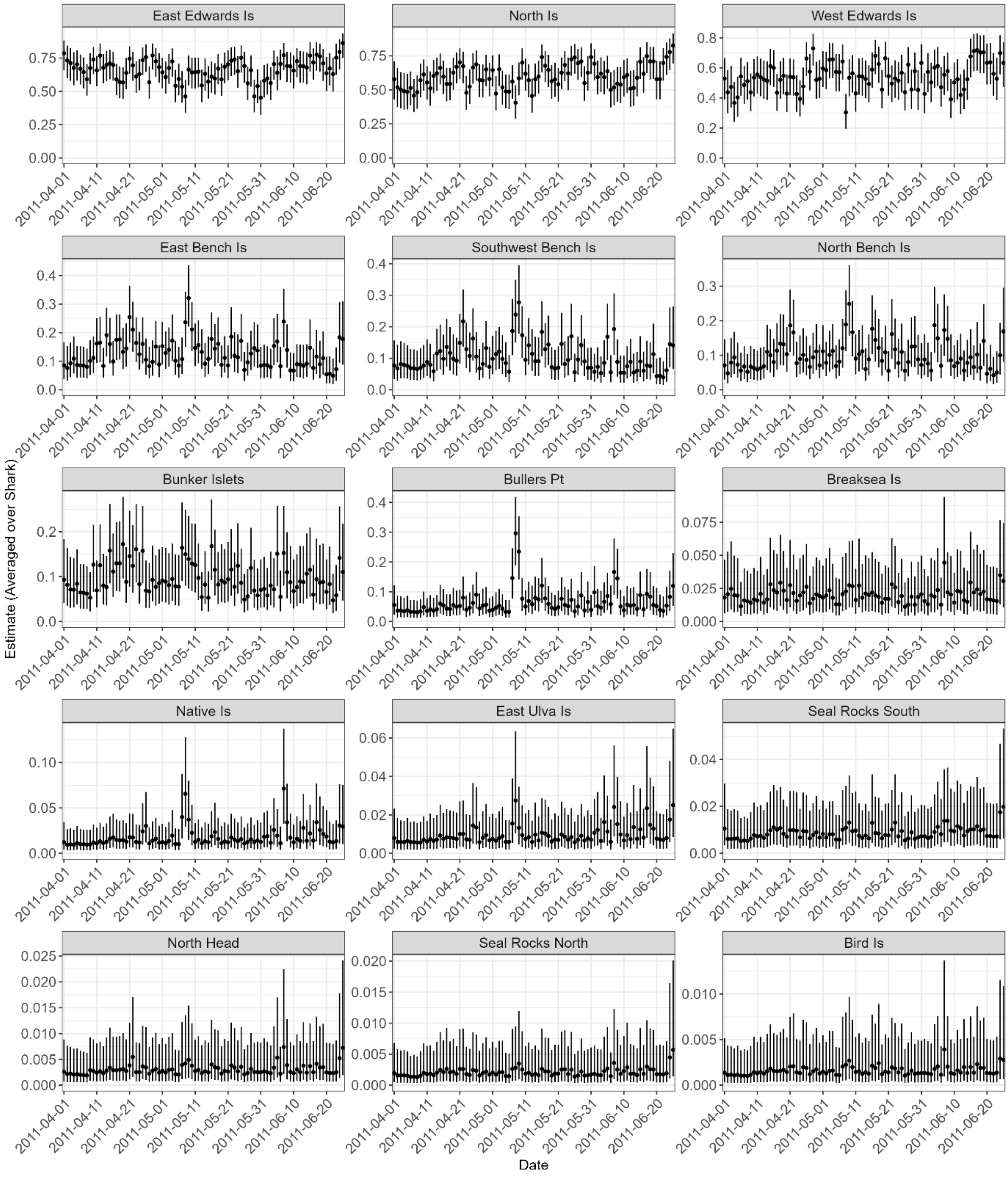


Figure 2. 7 *- Daily variation in the estimated probabilities of white shark occurrence at receivers deployed northeast of Stewart Island, averaged over shark (means and 90% credible intervals). Receivers are ordered by their overall 'popularity'.*

2.4.3 Individual Variation

2.4.3.1 Spatial Distribution

On average, white sharks were detected in the array for 72 of the 86 days in the season, visiting between one and eight receivers per day (*see Figure B.4 in Appendix B*). There was some variation among individual white sharks in their estimated probabilities of occurrence, when averaged across receivers and days (*Figure 2.8*). Of the 22 sharks, 15 had average probabilities of occurrence between 0.15 and 0.2. CC32 (4.0m female) had the highest average probability of occurrence of 0.197 (90% CI: 0.18, 0.21). Only two sharks had average probabilities of occurrence less than 0.1 (CC33, 3.4m female; CC44, 3.0m male); CC44 had the lowest estimate of 0.084 (90% CI: 0.07, 0.09), having not been detected by the array for 29 days of the season (*see Figure B.4 in Appendix B for more details*).

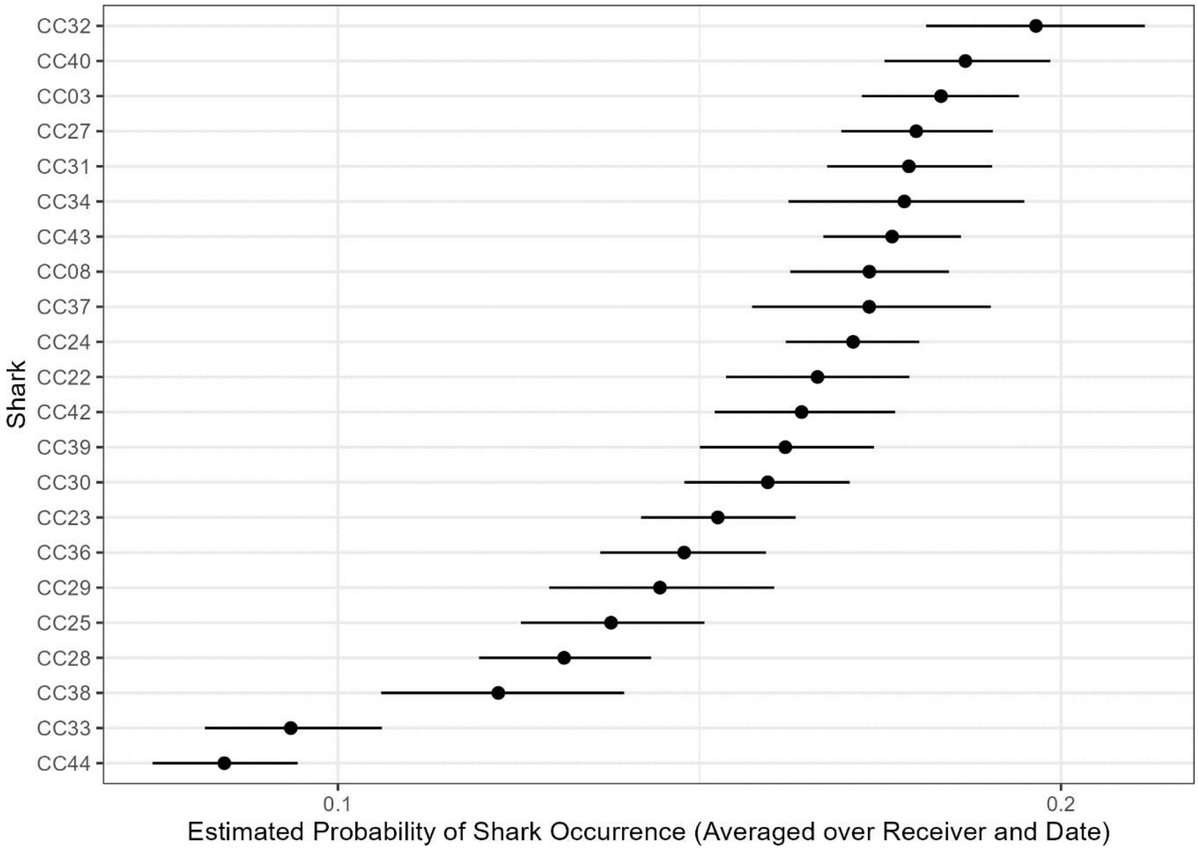


Figure 2. 8 *- The estimated probabilities of individual white shark occurrence in the Stewart Island receiver array, averaged across receivers and days (means 90% credible intervals).*

Comparing the standard deviations of effects, the main effects of sharks (averaged over receiver and day) accounted for less variation than the shark-by-receiver interaction term

(*Figure 2.3*). This shows that the degree to which white sharks at Stewart Island exhibit unique preferences for different receivers was greater than the variation among sharks overall, meaning that individual sharks varied substantially in the rates at which they visited particular receivers.

Occurrence at the Titi Islands receivers varied the most among individual sharks (*Figure 2.9*). Of the 22 sharks in the sample, 10 showed higher-than-average preferences for at least two of the northern Titi Island receivers (*Figure 2.9*). These sharks also had estimated probabilities of occurrence of less than 0.17, averaged over the season, at all other receivers in the array (*Figure 2.8*). These individuals comprised eight males (2.8m to 4.0m TL) and two of the four females (CC08, 2.8m; CC27, 4.0m). Only two individuals were smaller than 3.0m TL (CC08; CC43, 2.9m male). By contrast, seven individuals showed lower-than-average preferences for at least two of the northern Titi Islands receivers, all of which were 3.5m TL or smaller, except for one female (CC32, 4.0m). CC32 was also the only individual to show distinctly higher preferences to all southern Titi Islands receivers (*Figure 2.9*).

Variation was universally limited amongst the Paterson Inlet and Ruapuke Island receivers (*Figure 2.9*). Although, sharks CC31 (3.9m male) and CC25 (2.8m male) showed slightly higher probabilities of occurrence at the Paterson Inlet receivers, and CC28 (3.5m male) showed a higher affinity to the Breaksea Island and Seal Rocks South receivers of the Ruapuke Island group (*Figure 2.9*).

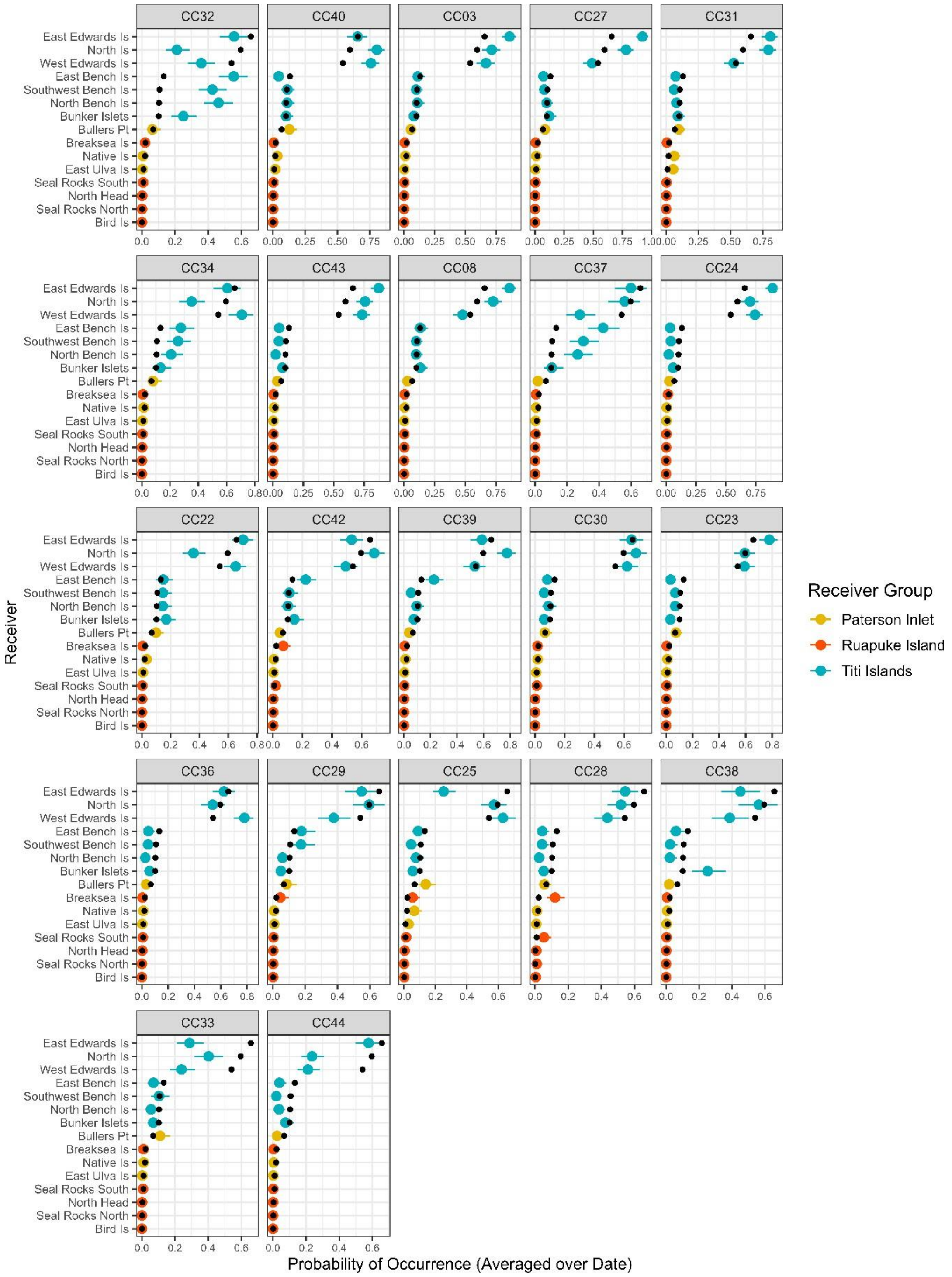


Figure 2. 9 *- Estimated model predictions for the probability of individual white shark occurrences at each receiver deployed northeast of Stewart Island, averaged over days (means and 90% credible intervals). Receivers are ordered by their overall popularity (averaged over sharks and days). Sharks are ordered by their overall probability of occurrence (averaged over receivers and days). Coloured points represent the estimate for the individual shark; black points represent the overall popularity of a given receiver.*

2.4.3.1 Temporal Variation

Temporal variation existed at the individual-level also, with all white sharks in the sample showing fluctuating daily estimated probabilities of occurrence across the season, averaged over receiver (*Figure 2.10*). CC31 (3.9m male) had the highest daily estimate of occurrence of 0.33 (90% CI: 0.24, 0.43) on 7 June, while CC44 (3.0m male) had the lowest daily estimate of occurrence of 0.05 (90% CI: 0.02, 0.1) on 29 May.

Daily variation among sharks was similar to that among receivers (*Figure 2.7*) and similar temporal patterns became apparent (*Figure 2.7; Figure 2.10*). For example, on 9 May all white sharks saw an increase in their individual daily estimates of occurrence, with 17 of the 22 sharks producing their first to third highest daily estimates between 7 May and 10 May. Given these estimates are averaged over all receivers, high estimates of occurrence imply broader use of the receiver array (i.e., the probability of an individual being detected by multiple receivers is greater). Furthermore, on 7 June all tagged sharks, excluding the four individuals whose final detections in the array occurred prior to this date (CC29, CC34, CC37, CC38), were detected by at least two receivers, with one individual (CC31, 3.9m male) visiting eight receivers, the largest number of receivers visited in a single day (*see Figure B.4 in Appendix B for more details*).

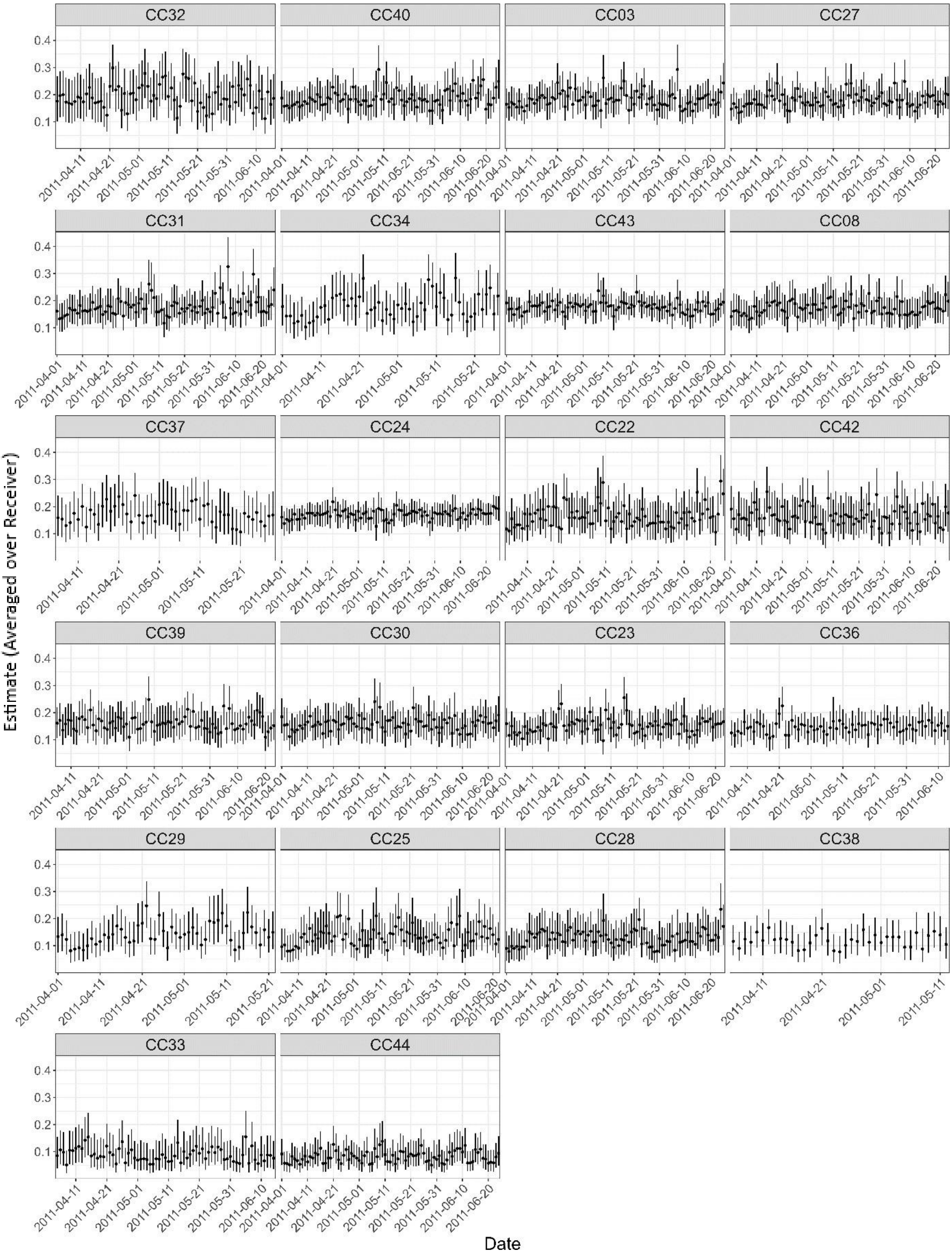


Figure 2. 10 *- Daily variation in the estimated probabilities of occurrence of individual white sharks at receivers northeast of Stewart Island, averaged over receiver (means and 90% credible intervals). Sharks are ordered by the overall estimated probability of occurrences. Individuals with fewer daily estimates were present in the receiver array for a shorter period.*

2.5 Discussion

2.5.1 Overall Spatiotemporal Distribution

This study investigated the overall patterns and individual variation in the occurrences of white sharks across various islands northeast of Stewart Island between April and June 2011 at scales of up to tens of kilometres. Overall, the Titi Islands group had the highest probabilities of white shark occurrence (mean of 0.29, averaged across sharks and days), with relatively low probabilities at the Ruapuke Island (mean of 0.0008) and Paterson Inlet receivers (mean of 0.029) (*Figure 2.4; Figure 2.5*). The affinity with the Titi Islands over other locations was also consistent across the sample of white sharks (*Figure 2.9*). While spatial variation in site use can have numerous drivers, these results may reflect the distribution and abundance of pinniped prey and/or site fidelity behaviour. Breeding colonies of New Zealand fur seals exist throughout the Rakiura region but are particularly dense along the Titi Islands (Watson et al., 2014), making this an important foraging habitat for white sharks. As the primary reason behind aggregatory behaviour at Stewart Island is believed to be the abundance of pinniped prey (Francis et al., 2015), the presence of dense fur seal colonies at the Titi Islands most likely explains the strong affinity of white sharks for these receivers. Although, large fur seal breeding colonies also exist on Ruapuke Island (Watson et al., 2014) and white sharks are often observed there (C. Duffy, personal communication, 13 March 2025), despite the observed low probability of white shark occurrence (0.0008). White sharks have previously shown to exhibit strong site fidelity behaviour (Domeier & Nasby-Lucas, 2007; Duffy et al., 2012; Jewell et al., 2013); therefore, given that all white sharks in this study were tagged in the Titi Islands, site fidelity may explain the strong affinity to the Titi Islands compared to the limited use of other sites in the receiver array, regardless of prey abundance.

The southern Titi Islands harbour the oldest established fur seal colonies in the Titi Islands, although these receivers were favoured substantially less than the northern receivers, with average probabilities of white shark occurrence of 0.11 and 0.60, respectively (*Figure 2.5*). This variation may be a result of factors besides prey availability likely influenced the stronger affinity towards the northern receivers, such as the presence of shark cage diving operators (SCDOs). Almost all SCDO effort (97-100%) over the study period was focused around Edwards Island, particularly the eastern side (C. Duffy, personal communication, 13

March 2025; Francis et al., 2015). Previous studies have demonstrated that the presence of SCDOs can alter the diel activity patterns and behaviours of white sharks, including the arrival of sharks in anticipation of the arrival of SCDOs and ‘lingering’ at cage sites after operations cease for the day (Bruce & Bradford, 2013; Francis et al., 2015; Huveneers et al., 2013; Laroche et al., 2007; Meyer et al., 2009; Strong et al., 1996). Although the presence of SCDOs unlikely affected the ‘popularity’ of the northern Titi Islands, as high abundances of white sharks were observed prior to 2008 when SCDOs began operating (Francis et al., 2015), similar behaviours may have resulted in white sharks spending more time at East Edwards Island, leading to the high probabilities of occurrence observed in this study.

The estimated daily probabilities of occurrence, averaged over sharks and receivers, varied throughout the study period from a minimum daily estimate of 0.1 to a maximum of 0.21 (*Figure 2.6*), though both interactions (between day and shark, and between day and receiver) were greater than the main effect of day (*Figure 2.3*). Across two particular time periods, 7-10 May and 6-7 June, the daily probabilities of occurrence were relatively low at the northern Titi Islands receivers and relatively high at other receivers in the array (*Figure 2.7*). Additionally, the probability of occurrence of individual sharks, averaged over receiver, increased over these periods (*Figure 2.6*), indicating broader use of the array. Several factors may have contributed to these short-term changes in distribution, such as the presentation of alternative foraging opportunities (e.g., whale carcasses), predator avoidance (Finn et al., 2014; Gennari et al., 2022), the presence of fishing vessels or other anthropogenic activities (Gleiss et al., 2022), or changes in environmental conditions affecting foraging success (Mourier et al., 2024), leading to reduced use of regularly visited sites and increased occurrence elsewhere in the array.

2.5.2 Individual Variation

Growing recognition of the importance of understanding individual variation in animal behaviour has led to an increasing number of studies (e.g., Baremore et al., 2021; Estes et al., 2003; Huveneers et al., 2021; Mourier et al., 2024; Spaet et al., 2020, 2022) suggesting that individual differences in movement, foraging and diet can influence population dynamics and processes through various factors, such as habitat-specific variation in prey availability, differences in the cost-benefit trade-offs among sex and age/size classes (Kim et al., 2012), and local abiotic conditions (A. K. Shaw, 2020). In the case of white sharks, Kim et al. (2012) suggested that individual differences in foraging behaviour can be attributed to changes in prey preference and foraging location as a result of ontogeny. Ontogenetic segregation in white sharks has been reported across several studies, whereby larger individuals over ~ 4.0m TL occupy smaller, more specific foraging habitats than juvenile and subadult conspecifics to optimise foraging success (Goldman & Anderson, 1999; Jewell et al., 2013, 2024). The effects of size-related behaviours, including variation in feeding strategies and/or diet, competitive exclusion, and predation risk, therefore may also explain the individual variation observed in this study.

White sharks that exhibited higher-than-average 'preferences' towards the northern Titi Islands receivers tended to be larger individuals that exhibited less use of other areas within the array (*Figure 2.9; see Appendix A, Table A.1 for more details on shark size*). Larger sharks have been found to show stronger site fidelity (Goldman & Anderson, 1999) and may utilise more restricted activity spaces, focusing on foraging at particular sites to minimise energy expenditure and maximise foraging success (Goldman & Anderson, 1999). In contrast, smaller sharks showed greater use of habitats outside the receiver array, as all sharks that spent more days 'absent' from the array (i.e., undetected by any receiver) were under 3.0m TL, except one individual (CC33; 3.4m female; *Figure B.4 in Appendix B*). This suggests that the smaller, less experienced, individuals in this study utilised broader activity spaces than larger conspecifics, potentially as they learn the foraging locations and strategies to optimise foraging success (Goldman & Anderson, 1999; Hussey et al., 2012; Munroe et al., 2022) and/or to exploit different habitats to supplement their diet with non-mammalian prey (Curtis et al., 2018; Hussey et al., 2012).

Differences in size can also drive individual variation through social interactions (Hertel et al., 2020; A. K. Shaw, 2020). Larger adult white sharks pose a predation risk to smaller conspecifics (Findlay et al., 2016; *see Appendix B, Figure B.5*); so, smaller individuals may forage in spatially separate areas to avoid competition or predation (Hertel et al., 2020; A. K. Shaw, 2020). In this study, six of the seven white sharks that showed lower-than-average preferences for the northern Titi Islands were under 3.5m TL (*Figure 2.9; see Appendix A, Table A.1*), with these individuals showing greater use of other receivers in the array (*Figure 2.9*). For example, three of the four individuals showing higher-than-average preferences for the southern Titi Islands receivers were 3.5m TL or smaller (*Figure 2.9*). This may be a consequence of white sharks avoiding more popular foraging areas frequented by larger conspecifics (i.e., the northern Titi Islands), trading off the benefits of prey availability against the costs of competition and predation risk (Hertel et al., 2020; A. K. Shaw, 2020).

Ontogeny has often been linked to variation in white shark movement patterns; however, individual variation arises from complex interactions of numerous drivers that may have influenced the spatiotemporal patterns observed in this study, such as the animals' internal state (e.g., sex, hunger, condition), life history, the biotic and abiotic environment (A. K. Shaw, 2020), or response differences towards anthropogenic activities like commercial fishing vessels or SCDOs (Bruce & Bradford, 2013; Duffy, 2016; Huveneers et al., 2013; Laroche et al., 2007). In some cases, individual variation cannot be explained by phenotypic or environmental variation (Estes et al., 2003). Given this complexity and the inherent difficulties in studying marine predators, individual variation has largely been neglected in ecological modelling of population-level patterns (Estes et al., 2003; Grainger et al., 2020). Nevertheless, the strength of the interaction terms (especially the term representing individual preferences for particular receivers) in this study (*Figure 2.3*) demonstrates a high degree of variability in movement patterns among individuals. The ability to obtain reliable estimates of the occurrences of protected species, like the white shark, is fundamental for conservation and will inform strategies to minimise potential threats, such as temporary fishing restrictions. Understanding the distribution of large marine predators is, also, currently at the forefront of human safety initiatives, with conservationists concerned that recovering white shark populations could increase the frequency of shark-human conflicts, thereby reducing public support for white shark conservation (Acuña-Marrero et al., 2018; Kock et al., 2012; Winton et al., 2023). The results of this study demonstrate that understanding individual-level spatiotemporal variation is necessary for accurately predicting white shark occurrence (*Table 2.1*) and that ignoring individual variation will offer an incomplete picture of their movements and ecology.

2.6 Conclusion

This study highlights substantial individual variation in the spatiotemporal distribution of white sharks aggregating at Stewart Island and surrounding island groups. While overall patterns were apparent, white sharks varied in their individual 'preferences' for particular sites, potentially as a result of factors such as size-related differences in activity space and feeding strategies, and intraspecific interactions, such as competitive exclusion and predation risk. Comparisons of the model terms revealed that understanding interactions between individual white sharks and individual receivers was necessary to accurately predict the occurrence of white sharks. Given that obtaining reliable estimates of white shark occurrence is crucial for conservation management and relevant to the human-shark conflict mitigation, individual variation should be considered in future ecological modelling to provide a more comprehensive understanding of white shark habitat use at aggregation sites.

Chapter 3:

Co-occurrences and associations of white sharks (*Carcharodon carcharias*) aggregating at Stewart Island, New Zealand.

3.1 Abstract

The development of acoustic telemetry and social network analysis has allowed greater exploration of shark social behaviour not immediately associated with feeding events, although the literature on white shark social behaviour remains limited. The purpose of this study was to investigate the extent to which white sharks formed social associations and the spatiotemporal distribution of their co-occurrences during an aggregation northeast of Stewart Island, New Zealand. Social network analysis was conducted on an acoustic telemetry dataset of detections collected at the minute-scale between April and June 2011. No evidence of any clear social structure was found as white sharks formed weak associations with one another, with an average simple ratio index score of 0.036. Nearly all co-occurrences (99.5%) were recorded in the Titi Islands, with the northern receivers accounting for 89.4%, capturing aggregations of up to seven individuals within a single 15-minute sampling period. Most co-occurrences at the northern receivers occurred during night/twilight and during the day at the southern receivers, except East Edwards which was the only northern receiver to also record a high frequency of co-occurrences during the day. This receiver also accounted for 45.4% of all co-occurrences, suggesting the potential role of shark cage diving operators in the diel activity patterns of sharks and facilitating social interactions. No evidence was found for a relationship between association strength and sex, likely due to the few females in the dataset (four out of 22); however, there was strong evidence that pairs with greater differences in total length co-occurred more often ($p < 0.01$). This may be a result of smaller white sharks following larger conspecifics to learn the locations of prey and/or to take advantage of successful kills. This study has demonstrated that measuring animal sociality and their encounter rates can yield insights into biological processes besides social structure, such as habitat use, abundance, and the potential effects of anthropogenic activities; likely serving for improved conservation and human safety management strategies.

3.2 Introduction

Sociality, or the extent to which conspecifics deliberately associate with one another (Hinde, 1976), has been well-documented in marine predators such as toothed whales (e.g., Augusto et al., 2017; Díaz López, 2020; Jordaan et al., 2021) and smaller elasmobranchs (e.g., Jacoby et al., 2012; Mourier et al., 2017; Myrberg & Gruber, 1974; Porcher, 2023). In contrast, due to their cryptic nature and the challenges of studying social interactions in aquatic environments, previous understanding of social behaviour in large pelagic sharks has largely derived from descriptive and observational studies, as opposed to hypothesis testing (Findlay et al., 2016). Advancements in acoustic telemetry and social network analysis methods in the early 2000s have since facilitated research on shark sociality (e.g., Jacoby et al., 2012; Kraft et al., 2024; Mourier et al., 2024; Papastamatiou et al., 2022b), whereby indirect estimates of social structure can be obtained through measuring the co-occurrences of individuals in a population (Jacoby et al., 2012; Mourier et al., 2017).
These studies have refuted previous misconceptions on the lack of sociality in several large pelagic species, including lemon sharks (Guttridge et al., 2009a), scalloped hammerhead sharks (Klimley & Nelson, 1984), blacktip reef sharks (Mourier et al., 2012), bull sharks (Loiseau et al., 2016), and tiger sharks (Jacoby et al., 2021), which instead show structured social networks and a wide range of gregariousness.

Subadult and adult white sharks (*Carcharodon carcharias*) are generally regarded as solitary, except when individuals aggregate at feeding sites presumably driven by the common attraction of prey availability (Findlay et al., 2016; Klimley et al., 1996). While many animal aggregations do not involve a social attraction (Johnson et al., 2002), these events facilitate non-random proximity to conspecifics – a prerequisite for most social behaviours (Findlay et al., 2016; Jacoby et al., 2012; Kraft et al., 2024). White sharks also possess anatomical specialisations comparable to that of social birds and mammals, such as a large brain-to-body mass ratio and acute sensorial apparatus (Northcutt, 1977), which researchers argue are indicative of potential social complexity (Dunbar & Shultz, 2007; Findlay et al., 2016). Several studies have suggested that white sharks may form sex-based associations (e.g., Findlay et al., 2016) and/or size-related dominance hierarchies, such as that based on observations at feeding events whereby social interactions more often occurred between sharks of similar sizes (e.g., Sperone et al., 2010) and smaller individuals were excluded from prey by larger conspecifics (e.g., Duffy et al., 2012). Furthermore, a study conducted in southern California found evidence for sociality, whereby juvenile white sharks formed between one and 10 preferential associations with conspecifics (Anderson et al., 2021b). While the extent to which subadult and adult white sharks are social hunters is uncertain (Klimley et al., 2001), this emerging evidence suggests that this species is more socially complex than previously understood (Martin et al., 2005).

Understanding the social behaviour of white sharks at aggregation sites will likely serve to improve conservation and human safety initiatives. Aggregations can increase white sharks' susceptibility to fisheries-related mortality and increase the potential risk of human-shark conflicts due to the higher concentration of individuals in a restricted area (R. L. Shaw et al., 2021). Conservation and human safety management have been described as key focuses for white shark research; both of which are dependent on reliable estimates of white shark distribution and abundance (Davenport et al., 2021; Huveneers et al., 2018). Understanding the social structure and spatiotemporal distribution of individuals' co-occurrence can contribute to a more comprehensive understanding of how white sharks utilise aggregation sites by providing insights into biological processes such as population structure, predator-prey interactions, mating behaviour, and information or disease transmission (Jacoby et al., 2012; Mourier et al., 2017). Understanding white shark sociality can also identify areas of high activity and/or overlap with anthropogenic activities (Jacoby et al., 2012; Spaet et al., 2020), highlighting areas for potential conservation action, such as the establishment of seasonal fishing restrictions, or human safety management.

The purpose of this study was to use social network analysis to investigate the extent of sociality exhibited by white sharks aggregating northeast of Stewart Island, New Zealand, using an acoustic telemetry dataset published by Francis et al. (2015). This study also investigated the influence of sex and body size on the strength of associations between pairs of white sharks, and the spatiotemporal distribution of co-occurrences. The specific objectives of this chapter were to:

1. Investigate the extent to which white sharks aggregating at Stewart Island co-occur and associate with one another.
2. Examine whether the strength of associations are influenced by sex and/or body size.
3. Investigate the spatiotemporal distribution of white shark co-occurrences.

3.3 Methods

3.3.1 Dataset

This study used the same acoustic telemetry dataset analysed in the previous chapter. This included all 15 Vemco VR2W acoustic receivers (*Figure 2.1; Figure 2.2*) and 22 individual white sharks (*see Appendix A, Table A.1*). The sharks were tagged with Vemco Ltd V16-5H acoustic R-code tags (Francis et al., 2015; *Figure 2.2*). Individual identification, sex, and estimated minimum and maximum total length (TL) of each shark were recorded during the tagging process (Francis et al., 2015; *see Appendix A, Table A.1*). In this chapter the average between the minimum and maximum TL measurements will be reported when referring to the size of a shark. Vemco VR2W acoustic receivers can have a detection range of up to 800m in good conditions (Vemco, 2018); however, Francis et al. (2015) found that the receivers in this study detected 58-71% (mean 67%) of tag transmissions at distances less than 200m, 20-70% (mean 53%) at 300m, and 0-35% (mean 12%) at 500m. All receivers were located at least 1200m apart meaning it is unlikely that any shark could be detected by multiple receivers at the same time. Only data collected between 1 April 2011 and 25 June 2011 was used to ensure that all receivers were active over the period analysed.

For the purpose of social network analysis, dates and times were extracted from the timestamp of a detection, and time was converted to minutes from midnight (i.e., a timestamp of 3:00am was converted to 180 minutes from midnight). These times were then binned into 15-minute intervals, hereafter referred to as ‘sampling periods’. A 15-minute sampling period duration was selected to minimise the potential for false co-occurrences, whilst still capturing meaningful data on the association between sharks. False co-occurrences are recorded when two sharks are detected by the same receiver within the same sampling period, but their presence did not overlap. The likelihood of false co-occurrences increases with longer sampling periods, as there is a greater possibility of a shark departing the vicinity of a receiver prior to another arriving, making this event not truly representative of association. Conversely, a sampling period duration shorter than 15 minutes may not capture associations from behaviours, such as following, which may occur over longer intervals. Finally, the dataset was filtered to include only single detections from one shark at one receiver during one sampling period.

3.3.2 Social Network Analysis

Social network analyses were conducted using the *asnipe* package (Farine, 2016) in R version 4.3.1 (R Development Core Team, n.d.). The *asnipe* package provides tools for analysis of social networks from spatial data, such as acoustic telemetry, consisting of observations of individuals co-occurring in time and space (Farine, 2013). The social network analysis run in this study was interpreted as a co-occurrence network and used a gambit-of-the-group approach, whereby all individuals co-occurring were assumed to have interacted and, therefore, associated (Whitehead & Dufault, 1999). This does not necessarily represent socialisation, given the resolution and data required to confidently deduce true association were lacking (Kraft et al., 2024), so associations must be interpreted with this caution in mind.

First, the *gmmevents()* function was used to identify instances when at least two tagged white sharks co-occurred at the same receiver during the same 15-minute sampling period, hereafter referred to as 'events'. This function requires three inputs: time, identity (i.e., the individual shark) and location. A new variable representing the combination of the location (i.e., receiver), date, and time interval of a detection, was created for the 'location' input to ensure that the *gmmevents()* function could distinguish between different sampling periods, as any divisions or gaps in the data at a given receiver (e.g., when no white sharks were detected) will be treated as a continuous stream of observations, and therefore one event, if not accounted for (Farine, 2016).

A group-by-individual (GBI) matrix was then extracted from the *gmmevents()* output, where each row represented a 'group', or in this case the combination of receiver and sampling period, each column represented an 'individual' (i.e., shark), and each cell contained a value of 1 if an individual was observed at an event, or 0 if not (Farine, 2016). The GBI matrix was then used to create a N x N association matrix using the *get_network()* function from the *asnipe* package, where *N* represents an individual white shark. The simple ratio index (SRI) was selected to calculate the rate at which a dyad, or pair of white sharks, associate or interact over time (Farine & Strandburg-Peshkin, 2015). The SRI is commonly used in social network analyses (Farine & Whitehead, 2015) as it is considered one of the most suitable indices for estimating association rate (Ginsberg & Young, 1992). Furthermore, the properties of acoustic telemetry data make it unlikely to violate the assumptions of the SRI, being that recorded associations (i.e., detections of different individuals) are accurate and that the likelihood of identifying an individual is independent of whether it associated with other individuals or not (Whitehead, 2008). The SRI calculates the probability that individuals were observed together given that at least one was observed during the sampling period using the following equation:

$$E_{AB} = \frac{x}{x + y_{AB} + y_A + y_B}$$

where E_{AB} is the 'undirected edge weight' or association between individuals *A* and *B*; *x* is the number of sampling periods where *A* and *B* co-occurred; y_{AB} is the number of sampling periods where both *A* and *B* were observed but did not co-occur; and y_A and y_B are the number of sampling periods where only *A* or only *B* were observed, respectively (Farine & Whitehead, 2015). The SRI scores a dyad's strength of association between 0 and 1, where 0 indicates no co-occurrence and 1 indicates complete co-occurrence (B. G. C. King et al., 2024).

The associations for each dyad were plotted using the *igraph* (Csárdi et al., 2025) and *pheatmap* (Kolde, 2019) packages in R. For plotting purposes, receivers were colour-coded by their geographical 'receiver group': Titi Islands (blue), Ruapuke Island (red), and Paterson Inlet (yellow).

3.3.3 Influence of Ontogeny and Sex

The software PRIMER version 7 (Clarke et al., 2014) was used to assess whether sharks had stronger associations with conspecifics of the same sex or of similar size. To test the effect of sex, we ran an analysis of similarities, or ANOSIM (Clarke & Green, 1988).
ANOSIM works by calculating the difference between the average rank of the 'within-group' associations (i.e., those between individuals of the same sex) and the average rank of the 'between-group' associations (i.e., those between individuals of different sexes) as follows:

$$R = \frac{\bar{R}_B - \bar{R}_W}{{}^{M}/_{2}}$$

where $\bar{R}_B$ is the average rank of the between-group associations, $\bar{R}_W$ is the average range of the within-group associations; the denominator *M/2* ensures the test statistic is constrained between the values of -1 and +1. An *R*-statistic value of +1 would arise if all within-sex associations were greater than all between-sex associations and vice versa would result in an *R*-statistic of -1. To test for a statistically significant relationship between the associations and sex, the ANOSIM was calculated using 99,999 permutations of the sex labels; the p-value representing the number of *R*-statistics, generated under permutation, that were greater or equal to the observed *R*-statistic.

We tested whether associations were related to body size using the RELATE test in PRIMER version 7 (Clarke et al., 2014). The Spearman rank correlation coefficient (ρ) was calculated between the associations *vs* the differences in the lengths for each pair of sharks. The p-value of the test was obtained by permuting the individuals 99,999 times and, in each case, recalculating the test statistic ρ, and finding the proportion of values of ρ obtained under permutation that were as or more extreme than the observed value of ρ. Since there was no prior expectation regarding the direction of the relationship (i.e., sharks of similar size were more or less likely to associate), a two-tailed test was applied.

3.3.4 Spatiotemporal Distribution of Events

To understand how white shark co-occurrences varied across the study period, the number of events that occurred per day was tallied across all receivers and plotted. To understand the temporal distribution of co-occurrences at a finer scale, the number of events that occurred per 15-minute sampling period was tallied across all receivers and individually, then plotted. Sampling periods were grouped and colour-coded by their ‘day period’, namely night, twilight, morning and afternoon. The temporal boundaries for each period were defined from data obtained from the website, ‘Time and Date’ (Time and Date, 2011), using the middle of the study period (mid-May) as a reference point. These were rounded to the nearest quarter-hour (*see Table C.1 in Appendix C for more details*).

3.4 Results

A total of 2,992 events occurred between 1 April and 25 June 2011 across 9 of the 15 acoustic receivers. The largest number of sharks co-occurring during one sampling period was seven, occurring twice at East Edwards Island and once at West Edwards Island.

3.4.1 Social Associations

Overall, we found little evidence of social structure in subadult and adult white sharks aggregating northeast of Stewart Island, as exhibited by the lack of structure in *Figure 3.1*. Although all but two dyads (CC38, 2.9m male, and CC25, 2.8m male; CC38 and CC34, 3.5m male) co-occurred with one another, the association scores were generally very low (*Figure 3.2*). The average association across all dyads was 0.036, with the strongest association occurring between sharks CC37 (2.8m male) and CC39 (2.5m male), with a value of 0.115 (*Figure 3.2*).

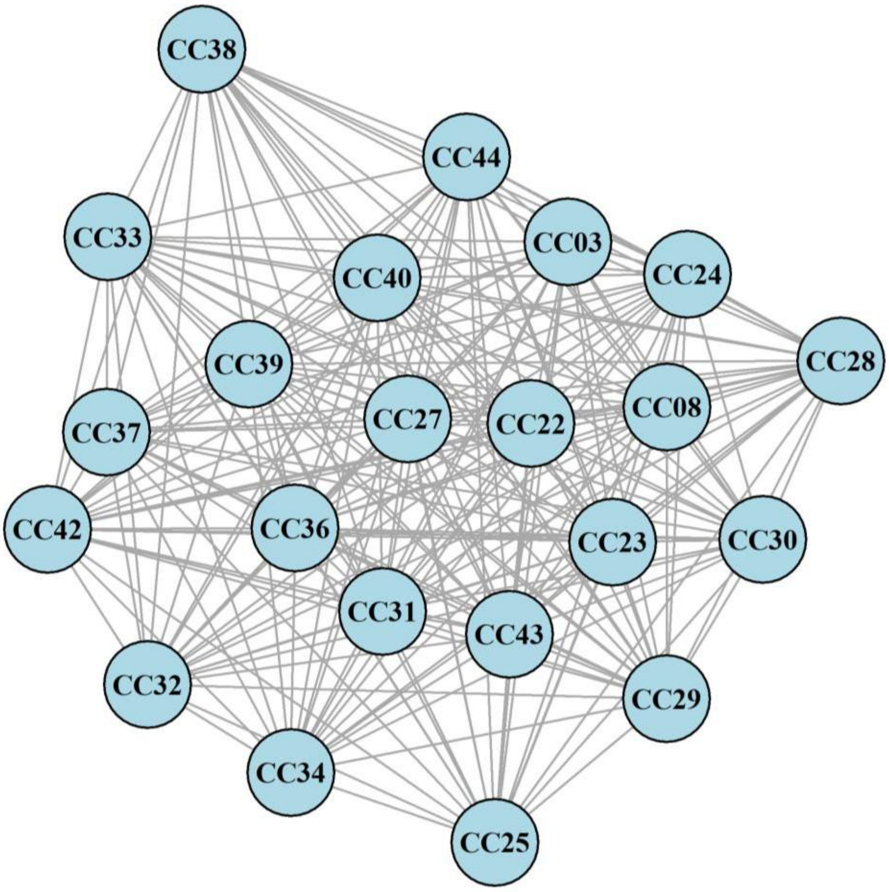
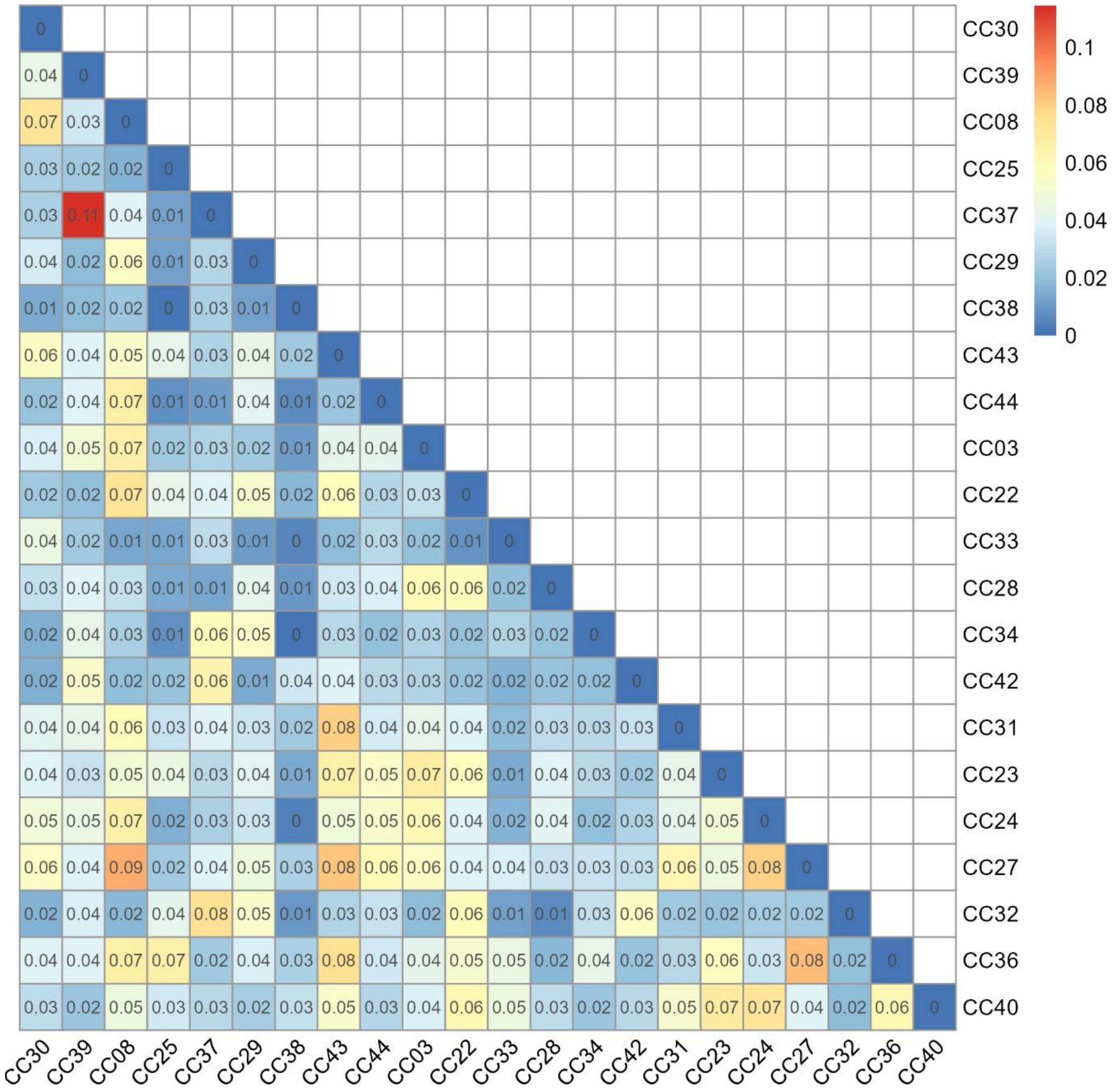


Figure 3. 1 *- Network plot of the social associations between white sharks aggregating northeast of Stewart Island, New Zealand, between April and June 2011.*



CC30	CC39	CC08	CC25	CC37	CC29	CC38	CC43	CC44	CC03	CC22	CC33	CC28	CC34	CC42	CC31	CC23	CC24	CC27	CC32	CC36	CC40	
0																						CC30
0.04	0																					CC39
0.07	0.03	0																				CC08
0.03	0.02	0.02	0																			CC25
0.03	0.11	0.04	0.01	0																		CC37
0.04	0.02	0.06	0.01	0.03	0																	CC29
0.01	0.02	0.02	0	0.03	0.01	0																CC38
0.06	0.04	0.05	0.04	0.03	0.04	0.02	0															CC43
0.02	0.04	0.07	0.01	0.01	0.04	0.01	0.02	0														CC44
0.04	0.05	0.07	0.02	0.03	0.02	0.01	0.04	0.04	0													CC03
0.02	0.02	0.07	0.04	0.04	0.05	0.02	0.06	0.03	0.03	0												CC22
0.04	0.02	0.01	0.01	0.03	0.01	0	0.02	0.03	0.02	0.01	0											CC33
0.03	0.04	0.03	0.01	0.01	0.04	0.01	0.03	0.04	0.06	0.06	0.02	0										CC28
0.02	0.04	0.03	0.01	0.06	0.05	0	0.03	0.02	0.03	0.02	0.03	0.02	0									CC34
0.02	0.05	0.02	0.02	0.06	0.01	0.04	0.04	0.03	0.03	0.02	0.02	0.02	0.02	0								CC42
0.04	0.04	0.06	0.03	0.04	0.03	0.02	0.08	0.04	0.04	0.04	0.02	0.03	0.03	0.03	0							CC31
0.04	0.03	0.05	0.04	0.03	0.04	0.01	0.07	0.05	0.07	0.06	0.01	0.04	0.03	0.02	0.04	0						CC23
0.05	0.05	0.07	0.02	0.03	0.03	0	0.05	0.05	0.06	0.04	0.02	0.04	0.02	0.03	0.04	0.05	0					CC24
0.06	0.04	0.09	0.02	0.04	0.05	0.03	0.08	0.06	0.06	0.04	0.04	0.03	0.03	0.03	0.06	0.05	0.08	0				CC27
0.02	0.04	0.02	0.04	0.08	0.05	0.01	0.03	0.03	0.02	0.06	0.01	0.01	0.03	0.06	0.02	0.02	0.02	0.02	0			CC32
0.04	0.04	0.07	0.07	0.02	0.04	0.03	0.08	0.04	0.04	0.05	0.05	0.02	0.04	0.02	0.03	0.06	0.03	0.08	0.02	0		CC36
0.03	0.02	0.05	0.03	0.03	0.02	0.03	0.05	0.03	0.04	0.06	0.05	0.03	0.02	0.03	0.05	0.07	0.07	0.04	0.02	0.06	0	CC40

Figure 3. 2 *– Association (simple ratio index) values between white sharks co-occurring at receivers deployed northeast of Stewart Island, New Zealand. Shark IDs are ordered by ascending body size (total length), except CC30 which lacked a measurement. No association occurred between dyads CC38 and CC25, and CC38 and CC34; other SRI values of 0 indicate an association of less than 0.01.*

3.4.2 Influence of Ontogeny and Sex

The ANOSIM test found no evidence for a relationship between the sex of sharks within a dyad and their association value (ANOSIM *R*-statistic = -0.65, p = 0.635). This result was corroborated by a lack of assortment by sex in *Figure 3.3*. There were a total of six female-

female associations, 153 male-male associations, and 72 male-female associations, with average SRI values of 0.34, 0.36, and 0.36, respectively.

The RELATE test found strong evidence for a positive relationship between the difference in total length of sharks within a dyad and their association value (*Figure 3.3*). This suggests that, on average, sharks that had a greater difference in body size were likely to be more strongly associated. This result was evidenced by a negative rank-correlation coefficient of $\rho = -0.175$ and p-value < 0.01.

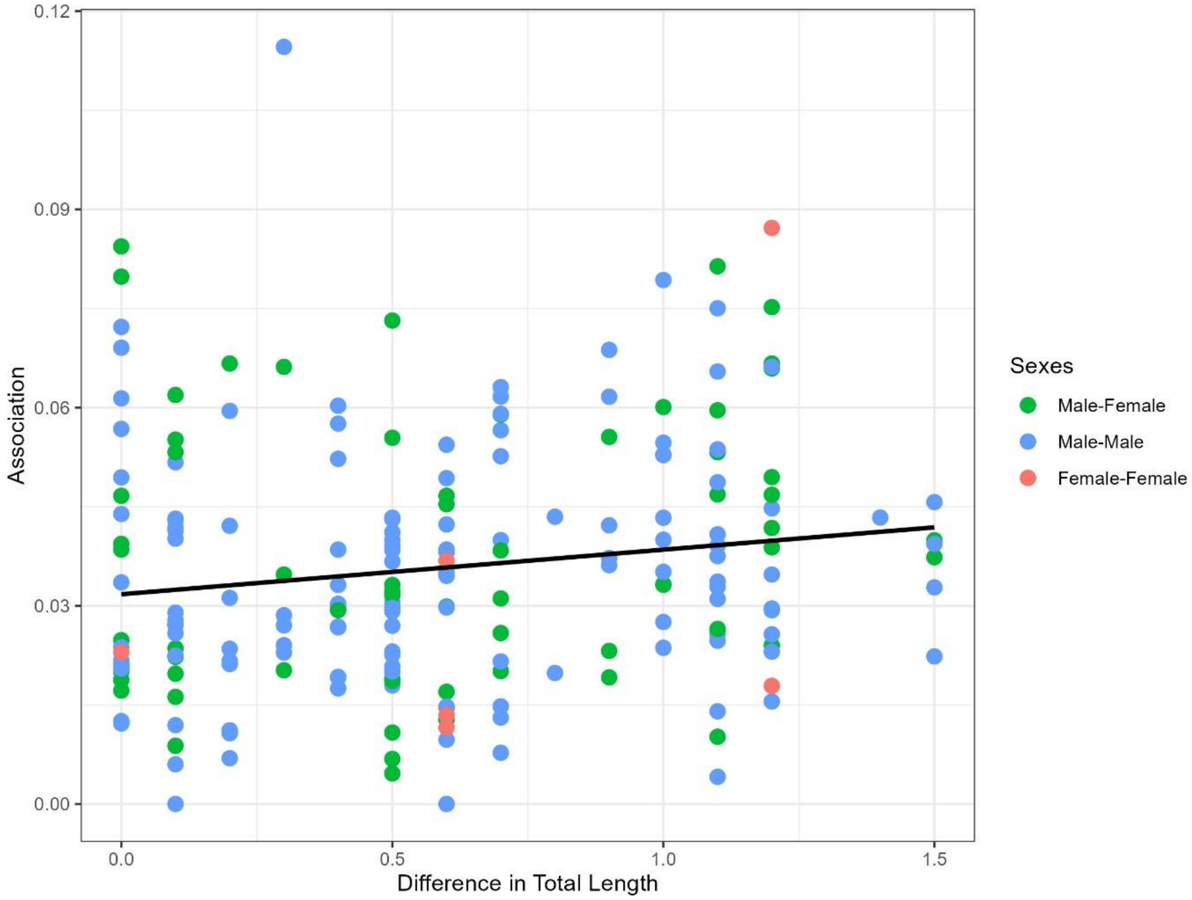


Figure 3. 3 *- The relationship between the association strength, sex, and difference in total length between pairs of white sharks aggregating northeast of Stewart Island, New Zealand.*

3.4.3 Spatiotemporal Distribution of Events

3.4.3.1 Spatial Distribution

White sharks co-occurred at 9 of the 15 receivers in the acoustic array (*Figure 3.4*). No events were recorded at East Ulva Island (Paterson Inlet) and all Ruapuke Island receivers (Bird Island, Breaksea Island, North Head, Seal Rocks North, and Seal Rocks South). Almost all co-occurrences (99.5%) were recorded at Titi Island receivers, with the three northern receivers (East Edwards, West Edwards, North Island) accounting for 89.4% of all co-occurrences. West Edwards and North Island had a similar number of co-occurrences with 677 and 642 respectively, whereas East Edwards had over twice as many, with 1,357 co-occurrences, accounting for 45.4% of all co-occurrences (*Figure 3.4*). In contrast, Native Island (Paterson Inlet) had the lowest of co-occurrences, with only 3 events (*Figure 3.4*) occurring across two consecutive days during the study period.

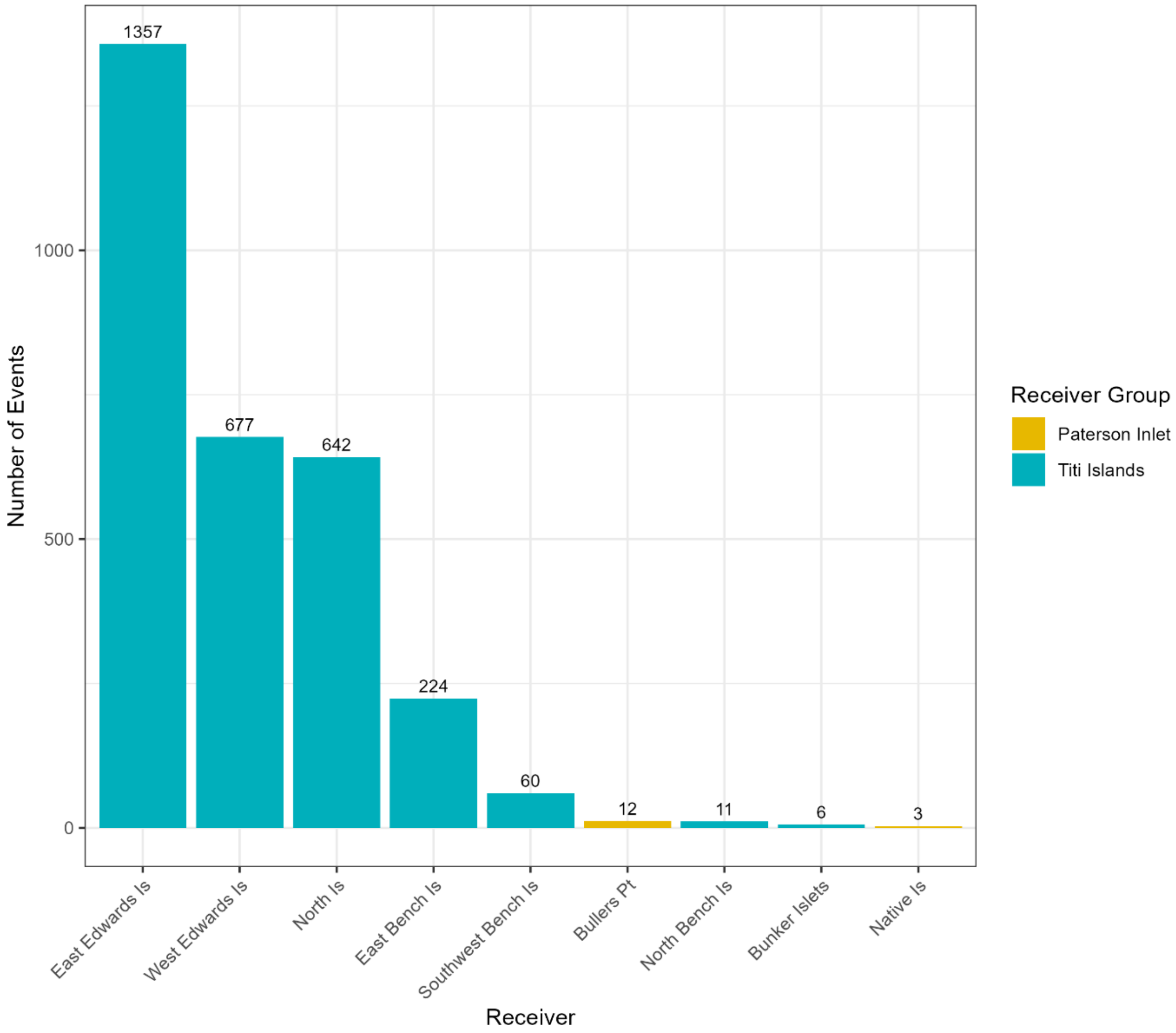


Figure 3. 4 *- The number of 'events' (white shark co-occurrences) per receiver in the array deployed northeast of Stewart Island. Five receivers are absent from this plot as no events occurred: Bird Island, North Head, Seal Rocks North, Seal Rocks South (Ruapuke Island), and East Ulva Island (Paterson Inlet).*

3.4.3.2 Temporal Distribution

Co-occurrences were recorded on all 86 days of the study period. The daily maximum was 84 events on 28 April; the daily minimum was 10 events on 19 May (*see Appendix C, Figure C.1*). Co-occurrences occurred during all times of the day (by 15-minute sampling periods), but peaked during the night (52 events during 1:30am-1:45am). The minimum occurred during mid-afternoon (16 events during 2:30pm-2:45pm) (*see Appendix C, Figure C.2*).

After analysing the temporal distribution of events at the five recievers with the greatest number of events (East Edwards, West Edwards, North Island, East and Southwest Bench Island), there was a distinct difference in the frequency of white shark co-occurrences between the northern Titi Island and southern Bench Island receivers (*Figure 3.5*). Both West Edwards and North Island had their highest average frequency of events per sampling period during night and twilight periods (*Figure 3.5*), with combined averages of 8.1 and 7.8 events per sampling period, respectively. In contrast, East Bench Island had its highest average frequency of events during daytime sampling periods (*Figure 3.5*), with an average of 4.5 events. Although Southwest Bench Island had fewer white shark co-occurrences comparatively, this receiver showed a similar pattern, with all but 4 events occurring between 5:00am and 7:00pm (*Figure 3.5*). East Edwards Island had its highest average frequency of events during daytime sampling periods, with 15.2 events, but this receiver also showed a more consistent temporal pattern of events, with an average of 13.3 events during night/twilight sampling periods.

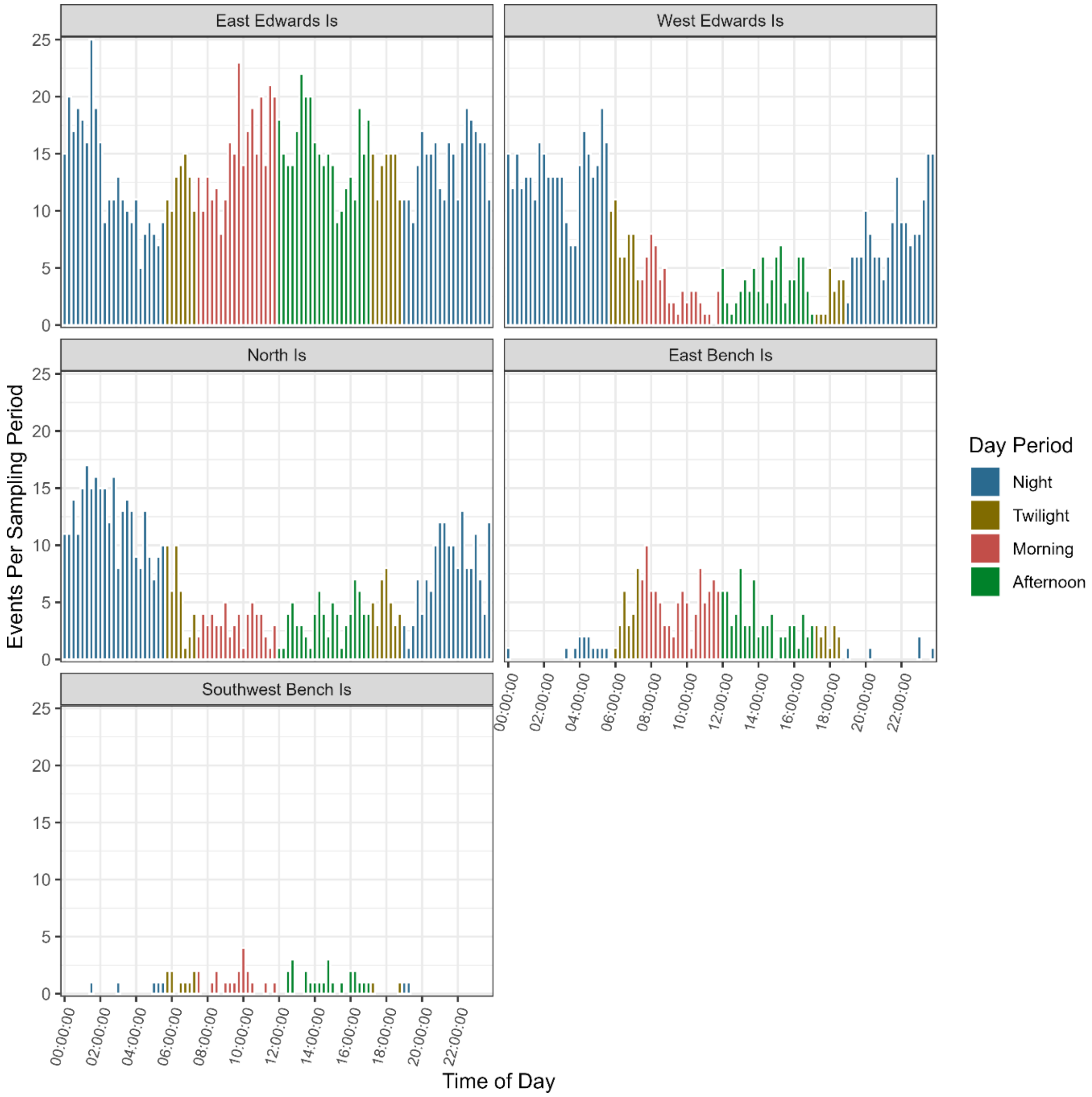


Figure 3. 5 *- Frequency of events (white shark co-occurrences) during 15-minute sampling periods at acoustic receivers deployed northeast of Stewart Island. This plot excludes four receivers with recorded events due to low frequencies of events: North Bench Island, Bullers Point, Bunker Islets (southern Titi Islands), Native Island (Paterson Inlet).*

3.5 Discussion

Aggregations form when individuals cluster due to synchronised activity patterns or a common attractant, such as prey availability (Johnson et al., 2002). Many elasmobranch aggregations are not considered to involve a social attraction, yet aggregations may facilitate sociality in sharks (Jacoby et al., 2012; Papastamatiou et al., 2022a). During an aggregation northeast of Stewart Island from April to June 2011, white sharks exhibited no clear social structure and formed only weak associations with conspecifics (*Figure 3.2*). The lack of social structure observed in this study supports the idea that white sharks aggregate for asocial reasons, particularly to exploit seasonal abundances of pinniped prey (Hussey et al., 2012; Jewell et al., 2024). Sociality arises then the benefits of forming social relationships, such as predator avoidance, increased foraging efficiency, and navigational capabilities, outweigh the costs, such as increased intra-specific competition (Anderson et al., 2021b; Kraft et al., 2024; Krause & Ruxton, 2002). White sharks likely experience low probabilities of encountering conspecifics outside aggregation events due to the species' low natural population sizes and broad dispersal across shelf and oceanic environments (Domeier & Nasby-Lucas, 2013; Duffy et al., 2012; Findlay et al., 2016; Franks et al., 2021). Consequently, white sharks are likely under stronger selective pressures to be efficient solitary hunters than to form multiple and/or lasting social relationships (Findlay et al., 2016; Krause & Ruxton, 2002). This may explain the lack of social structure observed at Stewart Island.

The idea that white sharks aggregate at Stewart Island for asocial reasons is further supported by the spatial distribution of co-occurrences observed in this study. For example, 89.4% of all co-occurrences were recorded in the northern Titi Islands, with less than 1% recorded outside the Titi Islands group (*Figure 3.4*). The Titi Islands have been identified as an important foraging habitat and area of high white shark activity, presumably due to the presence of dense breeding colonies of New Zealand fur seal (*Arctocephalus forsteri*). White sharks have also been found to exhibit strong site fidelity behaviour (Domeier & Nasby-Lucas, 2007; Duffy et al., 2012; Jewell et al., 2013) which, given that all sharks in this study were tagged in the Titi Islands, may explain the lack of co-occurrences elsewhere in the array. The high proportion of co-occurrences at the Titi Islands, therefore, was likely driven by overlapping patterns of individuals' spatiotemporal habitat use, influenced by prey availability and site fidelity behaviour.

Although prey availability and site fidelity likely led to the high co-occurrences at the Titi Islands overall, the proportion accounted for by the three northern receivers suggests that other influences, such as the presence of shark cage diving operators (SCDOs), may have contributed to the spatiotemporal patterns observed here. A previous study conducted at Guadalupe Island, Mexico, found that 68% of associations between white sharks occurred at regular cage sites (Papastamatiou et al., 2022b). The present study found similar results, whereby 45.4% of all co-occurrences were recorded at East Edwards Island (*Figure 3.4*), the site most heavily used by SCDOs over the study period (C. Duffy, personal communication, 13 March 2025; Francis et al., 2015). Furthermore, the majority of co- occurrences at East Edwards Island were recorded during the day, aligning with hours of SCDO operation (*Figure 3.5*). We note that the eastern and southwestern Bench Island receivers also recorded the majority of co-occurrences during the day (*Figure 3.5*); however, this site was not used by SCDOs during the study period, so the temporal patterns of co- occurrences here likely represent a more natural pattern of white shark abundance and were possibly driven by factors that optimise foraging during the day (Byrnes et al., 2021; Jewell et al., 2024). Similar to feeding events (e.g., on whale carcasses), SCDOs and other anthropogenic activities (e.g., research or fishing vessels) that can attract sharks to a localised area may still facilitate social interaction even though the reasons for white shark movement are not inherently social. Due to the resolution of the data, we cannot conclude that white sharks were interacting at cages if present at East Edwards during hours of SCDO operation, although observations during data collection (*see Appendix C, Figure C.3 and C.4*) support the idea that aggregation sites, and the anthropogenic activities that may occur, can facilitate white shark sociality through enabling spatial proximity of individuals.

While asocial factors are likely the primary driver behind the seasonal aggregation of white sharks at Stewart Island, individuals may still benefit from being in close proximity to each other. Some species of large sharks have demonstrated the capability for social learning (e.g., Guttridge et al., 2013; Guttridge et al., 2009b; Jacoby et al., 2012), with several studies suggesting that associations between white sharks may be a result of individuals 'listening in' on conspecifics to learn the locations or remains of prey, or to take advantage of kills by other sharks (Klimley et al., 2001; Papastamatiou et al., 2022b). This may be particularly beneficial for younger sharks. Anderson et al. (2021a) found that 64% of juvenile white sharks tagged in southern California exhibited sociality, forming between one and 10 (mean of 2.21) preferential associations. The strongest association in this present study (SRI = 0.115) was between two of the smallest individuals in the sample (*Figure 3.2; see Appendix A, Table A.1 for more details on shark body size*). Small sharks are thought to be less experienced at hunting mammalian prey (Jewell et al., 2013) and, consequently, may be more likely to associate with conspecifics for benefits such as increased hunting efficiency and scavenging opportunities, as well as social learning.

The benefit of increased access to food resources may also explain the positive relationship observed between body size and association strength, whereby dyads with greater differences in their total length tended to be more strongly associated ($p < 0.01$; *Figure 3.3*). While analyses presented in the previous chapter suggest that small white sharks at Stewart Island generally avoid areas frequented by larger sharks, it is possible that some may follow larger and more experienced individuals to take advantage of their kills and other scavenging opportunities (Findlay et al., 2016; Papastamatiou et al., 2022a). The detection range of the acoustic receivers used in this study means that the observed association is not necessarily an indication of direct interaction between white sharks; therefore, it is possible that smaller individuals only remained within sensory range of conspecifics. If social interactions did occur, such as at feeding events or dive cages, smaller sharks may have avoided agonistic interactions through established size-related dominance hierarchies (Sperone et al., 2010; *see Appendix C, Figure C.4*). White sharks possess an acute sensorial apparatus, which is thought to allow them to 'listen in' on conspecifics but also maintain complex social behaviours, such as size-related dominance hierarchies (Dunbar & Shultz, 2007; Northcutt, 1977). These hierarchies have been described across several elasmobranch species (e.g., Allee & Dickinson, 1954; Myrberg & Gruber, 1974), including the white shark (e.g., Duffy et al., 2012; Findlay et al., 2016; Sperone et al., 2010). Maintaining social hierarchy through body size may have allowed smaller white sharks to co-occur with larger conspecifics at Stewart Island, potentially benefitting from increased foraging opportunities and/or social learning, whilst avoiding conflict and injury (Sperone et al., 2010).

This study found no evidence for a relationship between the sex of individuals in a dyad and the strength of their association (*Figure 3.3*), consistent with previous reports of a lack of a relationship between sex and shark sociality (Allee & Dickinson, 1954; Sperone et al., 2010). Increased reproductive opportunities have been described as another social benefit of aggregation (Anderson et al., 2021b); however, large, mature females are rarely recorded at Stewart Island (Francis et al., 2015) and it is unlikely that any of the tagged females in this study were large enough to be sexually mature (*see Appendix A, Table A.1*).

Mature females have been shown to avoid male-dominated sites (Bradford et al., 2020; Domeier & Nasby-Lucas, 2013; Robbins, 2007), as demonstrated by the observed sex ratio at Stewart Island of 2.5 males to one female (Francis et al., 2015). While these results suggest that white sharks do not aggregate at Stewart Island for reproductive purposes, due to the lack of females in the dataset we cannot conclude that a relationship between sex and sociality does not exist.

Although this study has demonstrated that white sharks likely aggregate for asocial reasons, namely prey availability, these events may still play an important role in facilitating social behaviour by increasing proximity of individuals who may otherwise experience limited encounters with conspecifics (Findlay et al., 2016). This study has also demonstrated that measuring the frequency and spatiotemporal distribution of co-occurrences can provide insights into processes relevant for conservation, such as habitat use, abundance, and the effects of SCDOs on activity patterns. Aggregations can increase white sharks' susceptibility to fisheries-related injury or mortality due to the high concentration of individuals in a restricted area (R. L. Shaw et al., 2021). Given the high abundance of white sharks and potential contributions of SCDOs, Edwards Island may, therefore, be an important area to focus white shark conservation at Stewart Island. Aggregations at Edwards Island may also pose a greater safety risk to commercial pāua (*Haliotis iris*) divers and recreational divers and spear fishers who use the area. Both conservation and human safety have been described as key priorities for white shark research (Davenport et al., 2021; Huveneers et al., 2018), so considering measures for sociality and encounter rates may provide greater insight into white shark habitat use, on which effective species and human safety management are highly dependent (Winton et al., 2023).

3.6 Conclusion

This study supports previous findings that white sharks are generally solitary animals that exhibit resource-driven patterns of behaviour. White sharks aggregating at Stewart Island between April and June 2011 showed minimal social structure, weak associations, and spatiotemporal co-occurrence patterns consistent with foraging behaviour and the potential influence of SCDOs. This suggests that co-occurrences, and in turn social interactions, are likely a result of shared habitat use, driven by prey availability and processes associated with predatory success. While there was no evidence for a relationship between sex and association strength, white sharks with greater variation in body size tended to be more strongly associated. White sharks, particularly smaller and less experienced individuals, may have associated with larger conspecifics to exploit successful kills and find prey. Although the white sharks in this study showed minimal evidence for sociality, aggregations may have an important role in facilitating social interaction. Understanding the frequency and spatiotemporal distribution of their co-occurrences has also identified areas of high white shark activity and, therefore, potential areas to focus conservation and human safety strategies at Stewart Island.

Chapter 4:

Overall Conclusions and Recommendations

4.1 Conclusions

White shark (*Carcharodon carcharias*) behaviour during aggregation events is considered to be predominantly driven by the biological demand for food resources (Hussey et al., 2012; Jewell et al., 2024). At Stewart Island, the reason for aggregations is believed to be the presence of large breeding colonies of New Zealand fur seal (*Arctocephalus forsteri*) (Francis et al., 2015; Watson et al., 2014). While prey availability may largely influence the behavioural decisions of white sharks, it is the interaction between numerous internal and external processes that gives rise to individuals' spatiotemporal patterns in habitat use (Jewell et al., 2024). This thesis has demonstrated that modelling individual variation in occurrence and sociality can provide a more complete understanding of how white sharks use aggregation sites at fine spatial and temporal scales.

Based on a dataset of acoustic telemetry detections collected northeast of Stewart Island between April and June 2011, the northern Titi Islands were identified as an area of particularly high white shark activity. Chapter 2 found the northern Titi Islands had the highest estimated probability of white shark occurrence (averaged across sharks and days), with an estimate of 0.60 (*Figure 2.3; Figure 2.4*), and Chapter 3 found that these islands accounted for 89.4% of all co-occurrences, with less than 1% recorded outside the Titi Islands group (*Figure 3.4*). The Titi Islands harbour dense New Zealand fur seal breeding colonies (Francis et al., 2015; Watson et al., 2014); consequently, the high estimates of occurrence and large proportion of co-occurrences are likely due to white sharks utilising habitats with abundant prey and overlapping spatiotemporally with conspecifics as a result.

Site fidelity behaviour likely also contributed to the spatiotemporal patterns of occurrence and co-occurrence observed in this study. New Zealand fur seal breeding colonies exist throughout the Rakiura region, including Ruapuke Island (Watson et al., 2014) which observed the lowest estimated probability of occurrence of 0.0008, averaged across five receivers (*Figure 2.4; Figure 2.5*). Despite this, white sharks are often observed at Ruapuke Island (C. Duffy, personal communication, 13 March 2025). Chapter 2 revealed substantial variation among the occurrences of white sharks northeast of Stewart Island, indicating that sharks exhibited individual ‘preferences’ towards different sites (*Figure 2.9*). Given that all white sharks in this study were tagged in the Titi Islands, it is possible that the white sharks included in the sample exhibited stronger site fidelity and preferences towards the Titi Islands compared to Ruapuke Island. This suggests that individual variation and ‘preferences’ may influence white shark habitat use at relatively small (i.e., site-level) and larger (i.e., island-level) spatial scales.

Both chapters also identified the potential role of shark cage diving operators (SCDOs) on the diel activity patterns of white sharks at Stewart Island. Over the study period, nearly all SCDO effort (97-100%) was directed at East Edwards Island, particularly the eastern side (Francis et al., 2015; C. Duffy, personal communication, 13 March 2025). The effects of SCDO presence at East Edwards was potentially reflected in the results of Chapter 2, whereby white sharks showed a stronger affinity towards the northern Titi Islands receivers, particularly East Edwards Island, despite large and well-established fur seal colonies existing on the southern Bench Island and Bunker Islets (Francis et al., 2015; Wilson, 1981). Furthermore, Chapter 3 found that East Edwards Island accounted for the most co-occurrences at a single receiver (45.4%), the majority of which occurring during the day and hours of SCDO operation (*Figure 3.5*). East Edwards Island was also the only northern receiver with this temporal pattern of co-occurrences (*Figure 3.5*), as both West Edwards Island and North Island recorded the majority of co-occurrences during night sampling periods. This may have been a consequence of white sharks being drawn towards East Edwards Island and away from the other northern receivers when SCDOs were present. Previous studies have shown that SCDOs can affect the diel activity patterns of white sharks, with white shark presence aligning with that of SCDOs (Bruce & Bradford, 2013; Francis et al., 2015; Huveneers et al., 2013). It is unlikely that SCDOs affected the abundance of white sharks at the northern Titi Islands, as no significant change in the abundance of white sharks was observed at Stewart Island prior to and post the beginning of SCDO operations in 2008 (Francis et al., 2015). However, SCDOs may have affected the diel activity patterns of sharks, whereby their occurrence at Edwards Island coincided with the presence of SCDOs and encouraged individuals to spend more time at this site, leading to the spatiotemporal patterns of occurrences and co-occurrences observed in this study.

Social network analysis found that white sharks aggregating northeast of Stewart Island formed only weak associations with conspecifics (mean of 0.036; *Figure 3.2*) and lacked a clear social structure (*Figure 3.1*). In combination with the individual variation observed in Chapter 2, these results are consistent with the idea that white sharks exhibit unique patterns in habitat use that are unlikely to be socially driven but are, instead, influenced by asocial processes such as prey availability, local abiotic and biotic conditions, and the animals' internal state. Many elasmobranch aggregations are not considered to involve a social attraction (Johnson et al., 2002) but these events may still facilitate sociality by enabling spatial proximity of individuals that are otherwise wide-ranging and possibly experience low probabilities of encountering conspecifics (Findlay et al., 2016). White sharks have previously been observed interacting at feeding events, dive cages and research vessels (Duffy et al., 2012; Findlay et al., 2016; Martin et al., 2005), ranging from agonistic displays to following and tolerance (*see Appendix C, Figure C.3*). Therefore, while the reasons for social interaction may be asocial, aggregations may play an important role in white shark sociality and related behaviours, such as the formation of associations and size-related dominance hierarchies (*see Appendix C, Figure C.4*).

Ontogeny and size-related differences in behaviour are often linked to the behavioural and movement patterns of white sharks (Gennari et al., 2022; Jewell et al., 2024; Kim et al., 2012) and may have influenced the patterns and individual variation observed in this thesis. Larger white sharks are thought to be more experienced at hunting pinnipeds due to increased familiarity with the foraging locations and strategies to optimise predatory success (Franks et al., 2021; Goldman & Anderson, 1999). Consequently, larger white sharks tend to utilise more restricted activity spaces, focusing on favoured habitats that provide the best foraging opportunities (Goldman & Anderson, 1999). This idea was corroborated in Chapter 2, whereby individuals showing higher-than-average preferences for the northern Titi Islands receivers tended to be larger in size and showed limited use of other receivers in the array, while those showing lower-than-average preferences tended to be smaller (*Figure 2.9*). Furthermore, all but one of the sharks that were 'absent' from the array (i.e., undetected by any receiver) more often than they were detected by at least one receiver were under 3.0m total length. This may be a result of white sharks utilising a broader activity space as they learn the locations that provide the best foraging opportunities (Goldman & Anderson, 1999), exploit different habitats to supplement their diet with non-mammalian prey, such as teleosts, cephalopods, and other elasmobranchs (Curtis et al., 2012; Hussey et al., 2012), or due to competitive exclusion from favoured habitats by larger conspecifics (Baremore et al., 2021; Munroe et al., 2022).

Body size may also explain the associations observed in Chapter 3, whereby the strongest association (SRI = 0.115) was formed between two of the smallest sharks in the sample (CC37, 2.8m male; CC39, 2.5m male; *Figure 3.2*), and sharks with greater differences in body size (TL) tended to be more strongly associated ($p < 0.01$; *Figure 3.3*). These results suggest that smaller white sharks may be more likely to associate with conspecifics, including larger and more experienced individuals, due to benefits such as exploitation of successful kills by conspecifics, thereby increasing their access to food resources relative to when foraging solitarily, and social learning (Klimley et al., 2001; Papastamatiou et al., 2022b). White sharks, like other sharks, are considered to be capable of social learning due to anatomical specialisations, such as a large brain-to-body mass ratio and acute sensorial apparatus, comparable to that of social birds and mammals (Dunbar & Shultz, 2007; Northcutt, 1977). While these anatomical specialisations may be better related to foraging efficiency (Findlay et al., 2016), the ability to engage in social learning and 'listen in' on conspecifics may be beneficial for smaller, less experienced white sharks in particular, and may explain the relationships between body size and sociality observed in Chapter 3.

Sex has also been described as a potential mechanism behind white shark movements (Bradford et al., 2020; Domeier & Nasby-Lucas, 2007, 2013; Jewell et al., 2024); however, sex was not an important driver in this case. No evidence for a relationship between association strength and sex was found (*Figure 3.3*), possibly a result of the small number and size of the females tagged in this study (*see Appendix A, Table A.1 for more information*). Though large females are present in New Zealand, they are rarely recorded or observed at Stewart Island (Francis et al., 2015). This is potentially a result of sex-based differences in dispersal patterns, whereby females tend to occupy offshore waters more often than males and avoid male-dominated aggregation sites (Bradford et al., 2020; Domeier & Nasby-Lucas, 2013). While this work cannot determine if sex influences sociality or individual variation in white sharks, these results are consistent with reproduction not being a primary reason for aggregatory behaviour at Stewart Island.

The ability to obtain reliable estimates of white shark occurrence and abundance is central to effective conservation and human safety initiatives – two key focuses for white shark research (Davenport et al., 2021; Huveneers et al., 2018). This thesis has demonstrated that integrating different aspects of white shark behaviour into ecological modelling can be highly valuable in providing a more complete overview of how white sharks utilise aggregation sites at fine spatial and temporal scales. For example, Chapter 2 found that the Bayesian logistic models that could most accurately predict the occurrences of white sharks northeast of Stewart Island all included terms for individual variation (*Table 2.1*). Chapter 3 found that white sharks most often aggregated at Edwards Island (*Figure 3.4*) with up to seven individuals co-occurring during one sampling period. Fisheries-related mortality is a risk at aggregation sites as the high concentration of individuals can increase their susceptibility to bycatch and lead to the removal of mature or near-mature from the population. Aggregatory behaviour can also increase the risk of shark-human conflicts, potentially leading to reduced public support for white shark conservation (Kock et al., 2012; Winton et al., 2023). Therefore, incorporating white shark behaviour, such as individual variation and sociality, into understanding the fine-scale use of aggregation sites can provide a more accurate understanding of their spatiotemporal movements and abundances, likely serving for more effective conservation management, such as seasonal fishing restrictions, and human-shark conflict mitigation.

4.2 Recommendations for Management and Future Research

4.2.1 Recommendations for Management

White sharks are currently listed on Appendix I and Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), making it so that Range States, including New Zealand, have a statutory obligation to prohibit the taking of the species, conserve their habitats, and control factors that might further endanger them (Convention on the Conservation of Migratory Species, 2024). Due to their listing on Appendix I of CMS, white sharks have been protected in New Zealand since 2007 under the Wildlife Act 1953 and have had the conservation status of 'Threatened – Nationally Endangered' under the New Zealand Threat Classification System since 2016 (Duffy et al., 2018). While information on the recovery of the Eastern Australasian white shark population and effectiveness of current conservation strategies is scarce, this thesis has highlighted a few areas where species management could potentially be improved.

While this study cannot speak to the relevant importance of Ruapuke Island and other areas northeast of Stewart Island not covered by the acoustic array, Edwards Island should be considered as an area to implement seasonal fishing restrictions due to the high presence and concentration of white sharks at this site. Between 2007 and 2016, 15 white sharks were reported caught by set nets deployed in the Foveaux Strait, four of which were retrieved dead (Francis, 2017). All white sharks were caught during summer-autumn (Francis, 2017), coinciding with the aggregatory season (Francis et al., 2015). Therefore, the establishment of seasonal set netting restrictions, at least at Edwards Island, during the summer-autumn months will likely reduce the risk of bycatch and fisheries-related mortality (Francis, 2017).

The potential effects of SCDOs on the diel activity patterns of white sharks should also be considered. The use of berley odour trails to attract sharks to cages has shown to be effective over several kilometres (Strong et al., 1996). The southern Titi Islands were not used by SCDOs over the study period and are located 7-11km away from the cage sites, so white shark presence at these receivers may not have been affected by SCDOs or odour trails and, instead, may have represented a more natural pattern of abundance. White sharks' diurnal presence at the northern Titi Islands, however, may have been affected by SCDOs, whereby sharks could have potentially been attracted to East Edwards Island during times of operation, resulting in the fewer co-occurrences recorded at West Edwards and North Island during the day observed in Chapter 3. Financially viable shark tourism operations rely on being able to successfully attract sharks (Bruce & Bradford, 2013) and thereby potentially elicit changes to their natural behaviour and patterns of habitat use. Future management strategies should consider the influence of SCDOs on white shark behaviour and habitat use and the implications for potential threats to the aggregatory population, such as fisheries interactions.

4.2.2 Recommendations for Future Research

Both chapters demonstrated the importance of analysing spatial data at the individual-level of both sharks and receivers. Chapter 2 revealed white sharks showed individually unique patterns of habitat use, and including measures for this variation in modelling substantially improved the predictive accuracy regarding their distribution northeast of Stewart Island (*Table 2.1*). Additionally, temporal variation found in Chapter 3 found that co-occurrences, across all receivers, predominantly occurred at night (*see Appendix C, Figure C.2*), although analysis of each receiver showed that the northern and southern Titi Islands receivers exhibited unique temporal patterns in the frequency of co-occurrences, leading to the identification of the influences of SCDOs on the northern Titi Islands receivers. Given the dependency of conservation and human safety initiatives on reliable estimates of white shark distribution and habitat use, particularly at aggregation sites where individuals occur in higher concentrations, I strongly recommend that individual variation is considered in studies going forward.

Further research is required into the social behaviour of white sharks. The combination of acoustic telemetry and social network analysis will likely provide a truer representation of white shark sociality in the absence of provoked behaviour, such as that at feeding events; however, acoustic receivers with smaller detection ranges should be used to improve the confidence of whether sharks are truly interacting (Mourier et al., 2017). Alternatively, CHAT tags, which record encounters with other tagged sharks, could be used (Mourier et al., 2017).

Future research at Stewart Island should also consider tagging white sharks at locations separate from the Titi Islands, such as Ruapuke Island, to understand whether site fidelity and/or preferences towards island groups influences habitat use.

Reference Materials

Bibliography

Acuña-Marrero, D., de la Cruz-Modino, R., Smith, A. N. H., Salinas-de-León, P., Pawley, M. D. M., & Anderson, M. J. (2018). Understanding human attitudes towards sharks to promote sustainable coexistence. *Marine Policy*, *91*, 122–128. https://doi.org/10.1016/j.marpol.2018.02.018

Afonso, P., Gandra, M., Graça, G., Macena, B., Vandeperre, F., & Fontes, J. (2022). The multi-annual residency of juvenile smooth hammerhead shark in an oceanic island nursery. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.844893

Allee, W. C., & Dickinson, J. C. (1954). Dominance and subordination in the smooth dogfish Mustelus canis (Mitchill). *Physiological Zoology*, *27*(4), 356–364.

Anderson, J. M., Burns, E. S., Meese, E. N., Farrugia, T. J., Stirling, B. S., White, C. F., Logan, R. K., O'Sullivan, J., Winkler, C., & Lowe, C. G. (2021a). Interannual nearshore habitat use of young of the year white sharks off Southern California. *Frontiers in Marine Science*, *8*, Article 645142. https://doi.org/10.3389/fmars.2021.645142

Anderson, J. M., Clevenstine, A. J., Stirling, B. S., Burns, E. S., Meese, E. N., White, C. F., Logan, R. K., O'Sullivan, J., Rex, P. T., May, J., Lyons, K., Winkler, C., García-Rodríguez, E., Sosa-Nishizaki, O., & Lowe, C. G. (2021b). Non-random co-occurrence of juvenile white sharks (Carcharodon carcharias) at seasonal aggregation sites in Southern California. *Frontiers in Marine Science*, *8*, Article 688505. https://doi.org/10.3389/fmars.2021.688505

Aquino-Baleytó, M., Leos-Barajas, V., Adam, T., Hoyos-Padilla, M., Santana-Morales, O., Galván-Magaña, F., González-Armas, R., Lowe, C. G., Ketchum, J. T., & Villalobos, H. (2021). Diving deeper into the underlying white shark behaviors at Guadalupe Island, Mexico. *Ecology and Evolution*, *11*(21), 14932–14949. https://doi.org/10.1002/ece3.8178

Arel-Bundock, V., Greifer, N., & Heiss, A. (2024). How to interpret statistical models using `marginaleffects` for R and Python. *Journal of Statistical Software*, *111*(9), 1–32. https://doi.org/10.18637/jss.v111.i09

Augusto, J. F., Frasier, T. R., & Whitehead, H. (2017). Social structure of long-finned pilot whales (Globicephala melas) off northern Cape Breton Island, Nova Scotia. *Behaviour*, *154*(5), 509–540. https://doi.org/10.1163/1568539X-00003432

Baremore, I. E., Graham, R. T., Burgess, G. H., & Castellanos, D. W. (2021). Movements and residency of Caribbean reef sharks at a remote atoll in Belize, Central America. *Royal Society Open Science*, *8*(8), Article 201036. https://doi.org/10.1098/rsos.201036

Bennett, A. F. (1987). Interindividual variability: An underutilized resource. In M. Feder, A. F. Bennett, W. Burggren, & R. Huey (Eds.), *New Directions in Ecological Physiology* (pp. 147–169). Cambridge University Press.

Bostock, H. C., Hayward, B. W., Neil, H. L., Sabaa, A. T., & Scott, G. H. (2015). Changes in the position of the Subtropical Front south of New Zealand since the last glacial period. *Paleoceanography*, *30*(7), 824–844. https://doi.org/10.1002/2014PA002652

Bradford, R., Patterson, T. A., Rogers, P. J., McAuley, R., Mountford, S., Huveneers, C., Robbins, R., Fox, A., & Bruce, B. D. (2020). Evidence of diverse movement strategies and habitat use by white sharks, Carcharodon carcharias, off southern Australia. *Marine Biology*, *167*(7), Article 96. https://doi.org/10.1007/s00227-020-03712-y

Bradshaw, C. J. A., Lalas, C., & Thompson, C. M. (2000). Clustering of colonies in an expanding population of New Zealand fur seals (Arctocephalus forsteri). *Journal of Zoology*, *250*(1), 105–112. https://doi.org/10.1111/j.1469-7998.2000.tb00581.x

Bruce, B. D., & Bradford, R. (2013). The effects of shark cage-diving operations on the behaviour and movements of white sharks, Carcharodon carcharias, at the Neptune Islands, South Australia. *Marine Biology*, *160*(4), 889–907. https://doi.org/10.1007/s00227-012-2142-z

Bruce, B. D., Bradford, R., Bravington, M., Feutry, P., Grewe, P., Gunasekera, R., Harasti, D., Hillary, R., & Patterson, T. A. (2018). *A national assessment of the status of white sharks*. National Environmental Science Program Marine Biodiversity Hub. https://www.researchgate.net/profile/Russell-Bradford/publication/323019297_A_national_assessment_of_the_status_of_white_sharks/links/5a7ccb54aca272341aed7c8f/A-national-assessment-of-the-status-of-white-sharks.pdf

Bruce, B. D., & Bradford, R. W. (2012). Habitat use and spatial dynamics of juvenile white sharks, Carcharodon carcharias, in Eastern Australia. In M. L. Domeier (Ed.), *Global Perspectives on the Biology and Life History of the White Shark* (pp. 225–253). CRC Press.

Bruce, B. D., Harasti, D., Lee, K., Gallen, C., & Bradford, R. (2019). Broad-scale movements of juvenile white sharks Carcharodon carcharias in eastern Australia from acoustic and satellite telemetry. *Marine Ecology Progress Series*, *619*, 1–15. https://doi.org/10.3354/meps12969

Bürkner, P.-C. (2017). `brms`: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1–28. https://doi.org/10.18637/jss.v080.i01

Byrnes, E. E., Daly, R., Leos-Barajas, V., Langrock, R., & Gleiss, A. C. (2021). Evaluating the constraints governing activity patterns of a coastal marine top predator. *Marine Biology*, *168*(1), 1–15. https://doi.org/10.1007/s00227-020-03803-w

Castro, J. I. (2016). The origins and rise of shark biology in the 20th century. *Marine Fisheries Review*, *78*(1–2), 14–33. https://doi.org/10.7755/MFR.78.1â€“2.2

Chapman, D. D., Feldheim, K. A., Papastamatiou, Y. P., & Hueter, R. E. (2015). There and back again: A review of residency and return migrations in sharks, with implications for population structure and management. *Annual Review of Marine Science*, *7*, 547–570. https://doi.org/10.1146/annurev-marine-010814-015730

Clarke, K. R., & Green, R. (1988). Statistical design and analysis for a 'Biological Effects' study. *Marine Ecology Progress Series*, *46*, 213–226. https://doi.org/10.3354/meps046213

Clarke, K. R., Gorley, G. N., Somerfield, P. J., & Warwick, R. M. (2014). *Change in marine communities: An approach to statistical analysis and interpretation* (3rd ed.). PRIMER-E.

Commonwealth of Australia. (2013). *Recovery plan for the white shark (Carcharodon carcharias)*. Department of Sustainability, Environment, Water, Population and Communities. http://tinyurl.com/zylhrnx

Compagno, L. J. V. (2001). *Sharks of the world: An annotated and illustrated catalogue of shark species known to date* (Vol. 2). Food & Agriculture Org.

Compagno, L. J. V., Dando, M., & Fowler, S. (2005). *Sharks of the world*. Princeton University Press. https://research.ebsco.com/linkprocessor/plink?id=a9099f8f-127d-34e9-9234-5819088c2c89

Csárdi, G., Nepusz, T., Müller, K., Horvát, S., Traag, V., Zanini, F., & Noom, D. (2025). *igraph for R: R interface of the `igraph` library for graph theory and network analysis* (Version v2.1.4) [Computer software]. Zenodo. https://doi.org/10.5281/zenodo.14736815

Curtis, T. H., Bruce, B. D., Cliff, G., Dudley, S. F. J., Klimley, A. P., Kock, A., Lea, R. N., Lowe, C. G., McCosker, J. E., Skomal, G. B., Werry, J. M., & West, J. G. (2012). Responding to the risk of white shark attack: Updated statistics, prevention, control methods, and recommendations. In M. L. Domeier (Ed.), *Global Perspectives on the Biology and Life History of the White Shark* (pp. 477–509). CRC Press.

Curtis, T. H., Metzger, G., Fischer, C., McBride, B., McCallister, M., Winn, L. J., Quinlan, J., & Ajemian, M. J. (2018). First insights into the movements of young-of-the-year white sharks (Carcharodon carcharias) in the western North Atlantic Ocean. *Scientific Reports*, *8*(1), Article 10794. https://doi.org/10.1038/s41598-018-29180-5

Davenport, D., Butcher, P., Andreotti, S., Matthee, C., Jones, A., & Ovenden, J. (2021). Effective number of white shark (Carcharodon carcharias, Linnaeus) breeders is stable over four successive years in the population adjacent to eastern Australia and New Zealand. *Ecology and Evolution*, *11*(1), 186–198. https://doi.org/10.1002/ece3.7007

Dewar, H., Domeier, M., & Nasby-Lucas, N. (2004). Insights into young of the year white shark, Carcharodon carcharias, behavior in the Southern California Bight. *Environmental Biology of Fishes*, *70*(2), 133–143. https://doi.org/10.1023/B:EBFI.0000029343.54027.6a

Díaz López, B. (2020). When personality matters: Personality and social structure in wild bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour*, *163*, 73–84. https://doi.org/10.1016/j.anbehav.2020.03.001

Domeier, M. L., & Nasby-Lucas, N. (2007). Annual re-sightings of photographically identified white sharks (Carcharodon carcharias) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). *Marine Biology: International Journal on Life in Oceans and Coastal Waters*, *150*(5), 977–984. https://doi.org/10.1007/s00227-006-0380-7

Domeier, M. L., & Nasby-Lucas, N. (2013). Two-year migration of adult female white sharks (Carcharodon carcharias) reveals widely separated nursery areas and conservation concerns. *Animal Biotelemetry*, *1*(1), 2. https://doi.org/10.1186/2050-3385-1-2

Domeier, M. L., Nasby-Lucas, N., & Lam, C. H. (2012). Fine-scale habitat use by white sharks at Guadalupe Island, Mexico. In M. L. Domeier (Ed.), *Global Perspectives on the Biology and Life History of the White Shark*. CRC Press.

Dorazio, R. M., & Price, M. (2019). State-space models to infer movements and behavior of fish detected in a spatial array of acoustic receivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(4), 543–550. https://doi.org/10.1139/cjfas-2018-0067

Duffy, C. A. J. (2016, April 22). *Affidavit of Clinton Anthony John Duffy on behalf of the Director-General of Conservation, PauaMac5 Incorporated v. Director-General of Conservation, Shark Dive New Zealand Limited, & Shark Experience Limited, CIV-2015-485-1033* [Court filing]. High Court of New Zealand, Wellington Registry.

Duffy, C. A. J., Francis, M., Dunn, M., & Finucci, B. (2018). *Conservation status of New Zealand chondrichthyans (chimaeras, sharks and rays), 2016* (New Zealand Threat Classification Series 23). Department of Conservation.

Duffy, C. A. J., Francis, M. P., Manning, M. J., & Bonfil, R. (2012). Regional population connectivity, oceanic habitat, and return migration revealed by satellite tagging of white sharks, Carcharodon carcharias, at New Zealand aggregation sites. In M. L. Domeier (Ed.), *Global Perspectives on the Biology and Life History of the White Shark* (pp. 301–318). CRC Press.

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, *317*(5843), 1344–1347. https://doi.org/10.1126/science.1145463

Estes, J. A., Riedman, M. L., Staedler, M. M., Tinker, M. T., & Lyon, B. E. (2003). Individual variation in prey selection by sea otters: Patterns, causes and implications. *Journal of Animal Ecology*, *72*(1), 144–155.

Fallows, C., Martin, R. A., & Hammerschlag, N. (2012). Comparisons between white shark–pinniped interactions at Seal Island (South Africa) with other sites in California. In M. L. Domeier (Ed.), *Global Perspectives on the Biology and Life History of the White Shark*. CRC Press.

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using `asnipe`. *Methods in Ecology and Evolution*, *4*(12), 1187–1194. https://doi.org/10.1111/2041-210X.12121

Farine, D. R. (2016). *`asnipe`: Animal Social Network Inference and Permutations for Ecologists* (p. 1.1.17) [Dataset]. https://doi.org/10.32614/CRAN.package.asnipe

Farine, D. R., & Strandburg-Peshkin, A. (2015). Estimating uncertainty and reliability of social network data using Bayesian inference. *Royal Society Open Science*, *2*(9), Article 150367. https://doi.org/10.1098/rsos.150367

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, *84*(5), 1144–1163. https://doi.org/10.1111/1365-2656.12418

Ferrara, T. L., Clausen, P., Huber, D. R., McHenry, C. R., Peddemors, V., & Wroe, S. (2011). Mechanics of biting in great white and sandtiger sharks. *Journal of Biomechanics*, *44*(3), 430–435. https://doi.org/10.1016/j.jbiomech.2010.09.028

Findlay, R., Gennari, E., Cantor, M., & Tittensor, D. P. (2016). How solitary are white sharks: Social interactions or just spatial proximity? *Behavioral Ecology and Sociobiology*, *70*(10), 1735–1744. https://doi.org/10.1007/s00265-016-2179-y

Finn, J. T., Brownscombe, J. W., Haak, C. R., Cooke, S. J., Cormier, R., Gagne, T., & Danylchuk, A. J. (2014). Applying network methods to acoustic telemetry data: Modeling the movements of tropical marine fishes. *Ecological Modelling*, *293*, 139–149. https://doi.org/10.1016/j.ecolmodel.2013.12.014

Francis, M. P. (1996). Observations on a pregnant white shark with a review of reproductive biology. In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks* (pp. 157–172). Academic Press. https://doi.org/10.1016/B978-012415031-7/50016-1

Francis, M. P. (2017). *Bycatch of white sharks in commercial set nets* (No. 2017113WN). NIWA Client Report 2017113WN prepared for the Department of Conservation.

Francis, M. P., Duffy, C., & Lyon, W. (2015). Spatial and temporal habitat use by white sharks (Carcharodon carcharias) at an aggregation site in southern New Zealand. *Marine and Freshwater Research*, *66*(10), 900–918. https://doi.org/10.1071/MF14186

Franks, B. R., Tyminski, J. P., Hussey, N. E., Braun, C. D., Newton, A. L., Thorrold, S. R., Fischer, G. C., McBride, B., & Hueter, R. E. (2021). Spatio-temporal variability in white shark (Carcharodon carcharias) movement ecology during residency and migration phases in the Western North Atlantic. *Frontiers in Marine Science*, *8*, Article 744202.

Gennari, E., Irion, D. T., & Cowley, P. D. (2022). Active acoustic telemetry reveals ontogenetic habitat-related variations in the coastal movement ecology of the white shark. *Animal Biotelemetry*, *10*(1), Article 25. https://doi.org/10.1186/s40317-022-00295-x

Ginsberg, J. R., & Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, *44*, 377–379. https://doi.org/10.1016/0003-3472(92)90042-8

Gleiss, A. C., Treberg, J. R., Byrnes, E. E., & Lear, K. O. (2022). Physiological and applied energetics of elasmobranch fishes. In *Biology of Sharks and Their Relatives* (3rd ed.). CRC Press.

Goldman, K. J., & Anderson, S. D. (1999). Space utilization and swimming depth of white sharks, Carcharodon carcharias, at the South Farallon Islands, Central California. *Environmental Biology of Fishes*, *56*(4), 351–364. https://doi.org/10.1023/A:1007520931105

Grainger, R., Peddemors, V. M., Raubenheimer, D., & Machovsky-Capuska, G. E. (2020). Diet composition and nutritional niche breadth variability in juvenile white sharks (Carcharodon carcharias). *Frontiers in Marine Science*, *7*, Article 422. https://doi.org/10.3389/fmars.2020.00422

Green, M. E., Simpfendorfer, C. A., & Devloo-Delva, F. (2022). Population structure and connectivity of chondrichthyans. In *Biology of Sharks and Their Relatives* (3rd ed.). CRC Press.

Guttridge, T. L., Gruber, S. H., Gledhill, K. S., Croft, D. P., Sims, D. W., & Krause, J. (2009a). Social preferences of juvenile lemon sharks, *Negaprion brevirostris*. *Animal Behaviour*, *78*(2), 543–548. https://doi.org/10.1016/j.anbehav.2009.06.009

Guttridge, T. L., Myrberg, A. A., Porcher, I. F., Sims, D. W., & Krause, J. (2009b). The role of learning in shark behaviour. *Fish & Fisheries*, *10*(4), 450–469. https://doi.org/10.1111/j.1467-2979.2009.00339.x

Guttridge, T. L., van Dijk, S., Stamhuis, E. J., Krause, J., Gruber, S. H., & Brown, C. (2013). Social learning in juvenile lemon sharks, Negaprion brevirostris. *Animal Cognition*, *16*(1), 55–64. https://doi.org/10.1007/s10071-012-0550-6

Harcourt, R. G., Bradshaw, C. J. A., Dickson, K., & Davis, L. S. (2002). Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology Progress Series*, *227*, 11–24. https://doi.org/10.3354/meps227011

Hertel, A. G., Niemelä, P. T., Dingemanse, N. J., & Mueller, T. (2020). A guide for studying among-individual behavioral variation from movement data in the wild. *Movement Ecology*, *8*(1), Article 30. https://doi.org/10.1186/s40462-020-00216-8

Heupel, M. R., Simpfendorfer, C. A., Espinoza, M., Smoothey, A. F., Tobin, A., & Peddemors, V. (2015). Conservation challenges of sharks with continental scale migrations. *Frontiers in Marine Science*, *2*, Article 12. https://doi.org/10.3389/fmars.2015.00012

Hussey, N., Christiansen, H., Cliff, G., Dudley, S., Wintner, S., & Fisk, A. (2012). Size-based analysis of diet and trophic position of the white shark, Carcharodon carcharias, in South African Waters. In M. L. Domeier (Ed.), *Global Perspectives on the Biology and Life History of the White Shark* (pp. 27–45). https://doi.org/10.1201/b11532-5

Huveneers, C., Apps, K., Becerril-García, E. E., Bruce, B. D., Butcher, P. A., Carlisle, A. B., Chapple, T. K., Christiansen, H. M., Cliff, G., Curtis, T. H., Daly-Engel, T. S., Dewar, H., Dicken, M. L., Domeier, M. L., Duffy, C. A. J., Ford, R., Francis, M. P., French, G. C. A., Galván-Magaña, F., … Werry, J. M. (2018). Future research directions on the "elusive" white shark. *Frontiers in Marine Science*, *5*, Article 455. https://doi.org/10.3389/fmars.2018.00455

Huveneers, C., Niella, Y., Drew, M., McAuley, R., Butcher, P., Peddemors, V., Waltrick, D., Dowling, C., Mountford, S., Keay, I., & Braccini, M. (2021). Continental-scale network reveals cross-jurisdictional movements of sympatric sharks with implications for assessment and management. *Frontiers in Marine Science*, *8*, Article 697175. https://doi.org/10.3389/fmars.2021.697175

Huveneers, C., Rogers, P., Beckmann, C., Semmens, J., Bruce, B., & Seuront, L. (2013). The effects of cage-diving activities on the fine-scale swimming behaviour and space use of white sharks. *Marine Biology*, *160*(11), 2863–2875. https://doi.org/10.1007/s00227-013-2277-6

Jacoby, D. M. P., Busawon, D. S., & Sims, D. W. (2010). Sex and social networking: The influence of male presence on social structure of female shark groups. *Behavioral Ecology*, *21*(4), 808–818. https://doi.org/10.1093/beheco/arq061

Jacoby, D. M. P., Croft, D. P., & Sims, D. W. (2012). Social behaviour in sharks and rays: Analysis, patterns and implications for conservation. *Fish & Fisheries*, *13*(4), 399–417. https://doi.org/10.1111/j.1467-2979.2011.00436.x

Jacoby, D. M. P., Fairbairn, B. S., Frazier, B. S., Gallagher, A. J., Heithaus, M. R., Cooke, S. J., & Hammerschlag, N. (2021). Social network analysis reveals the subtle impacts of tourist provisioning on the social behavior of a generalist marine apex predator. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.665726

Jewell, O. J. D., Chapple, T. K., Jorgensen, S. J., Kanive, P., Moxley, J. H., Tweedley, J. R., Anderson, S., Block, B. A., & Gleiss, A. C. (2024). Diverse habitats shape the movement ecology of a top marine predator, the white shark Carcharodon carcharias. *Ecosphere*, *15*(4), e4825. https://doi.org/10.1002/ecs2.4825

Jewell, O. J. D., Johnson, R. L., Gennari, E., & Bester, M. N. (2013). Fine scale movements and activity areas of white sharks (Carcharodon carcharias) in Mossel Bay, South Africa. *Environmental Biology of Fishes*, *96*(7), 881–894. https://doi.org/10.1007/s10641-012-0084-4

Johnson, D. D. P., Kays, R., Blackwell, P. G., & Macdonald, D. W. (2002). Does the resource dispersion hypothesis explain group living? *Trends in Ecology & Evolution*, *17*(12), 563–570. https://doi.org/10.1016/S0169-5347(02)02619-8

Jordaan, R. K., Reisinger, R. R., Oosthuizen, W. C., & de Bruyn, P. J. N. (2021). Seasonal fission and fusion of killer whale, *Orcinus orca*, social structure at sub-Antarctic Marion Island. *Animal Behaviour*, *177*, 223–230. https://doi.org/10.1016/j.anbehav.2021.05.007

Kanive, P. E., Rotella, J. J., Jorgensen, S. J., Chapple, T. K., Anderson, S. D., Klimley, A. P., & Block, B. A. (2015). Estimating apparent survival of sub-adult and adult white sharks (Carcharodon carcharias) in central California using mark-recapture methods. *Frontiers in Marine Science*, *2*, Article 19. https://doi.org/10.3389/fmars.2015.00019

Kim, S. L., Tinker, M. T., Estes, J. A., & Koch, P. L. (2012). Ontogenetic and among-individual variation in foraging strategies of Northeast Pacific white sharks based on stable isotope analysis. *PLOS ONE*, *7*(9), e45068. https://doi.org/10.1371/journal.pone.0045068

King, B. G. C., Morris, C. J., Green, J. M., Gregory, R. S., Snelgrove, P. V. R., Cote, D., & Pennell, C. J. (2024). Acoustic telemetry and network analysis reveal seasonal spatial overlap between gadid species in a subarctic coastal marine protected area. *Canadian Journal of Fisheries and Aquatic Sciences*, *81*(11), 1547–1559. https://doi.org/10.1139/cjfas-2023-0272

King, S. D., Harper, G. A., Wright, J. B., McInnes, J. C., van der Lubbe, J. E., Dobbins, M. L., & Murray, S. J. (2012). Site-specific reproductive failure and decline of a population of the endangered yellow-eyed penguin: A case for foraging habitat quality. *Marine Ecology Progress Series*, *467*, 233–244. https://doi.org/10.3354/meps09969

Klimley, A. P., Le Boeuf, B. J., Cantara, K. M., Richert, J. E., Davis, S. F., Van Sommeran, S., & Kelly, J. T. (2001). The hunting strategy of white sharks (Carcharodon carcharias) near a seal colony. *Marine Biology*, *138*(3), 617–636. https://doi.org/10.1007/s002270000489

Klimley, A. P., & Nelson, D. R. (1984). Diel movement patterns of the scalloped hammerhead shark (Sphyrna lewini) in relation to El Bajo Espiritu Santo: A refuging central-position social system. *Behavioral Ecology and Sociobiology*, *15*(1), 45–54. https://doi.org/10.1007/BF00310214

Klimley, A. P., Porcher, I. F., Clua, E. E. G., & Pratt Jr., H. L. (2023). A review of the behaviours of the chondrichthyes: A multi-species ethogram for the chimaeras, sharks, and rays. *Behaviour*, *160*(11), 967–1080. https://doi.org/10.1163/1568539X-bja10214

Klimley, A. P., Pyle, P., & Anderson, S. (1996). Tail slap and breach: Agonistic displays among white sharks? In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks: The Biology of Carcharodon carcharias* (pp. 241–255). Academic Press. https://doi.org/10.1016/B978-012415031-7/50023-9

Kock, A., Titley, S., Peterson, W., Sikweyiya, M., Tsotsobe, S., Colenbrander, D., Gold, H., & Oelofse, G. (2012). Shark spotters: A pioneering shark safety program in Cape Town, South Africa. In M. L. Domeier (Ed.), *Global Perspectives on the Biology and Life History of the White Shark* (pp. 447–466). CRC Press.

Kohler, J., Gore, M., Ormond, R., Johnson, B., & Austin, T. (2023). Individual residency behaviours and seasonal long-distance movements in acoustically tagged Caribbean reef sharks in the Cayman Islands. *PLOS ONE*, *18*(11), e0293884. https://doi.org/10.1371/journal.pone.0293884

Kolde, R. (2019). `pheatmap`*: Pretty heatmaps* (Version 1.0.12) [Computer software]. https://cran.r-project.org/web/packages/pheatmap/index.html

Kraft, S., Winkler, A. C., Abecasis, D., & Mourier, J. (2024). Long-term co-occurrence and gregariousness in the migratory common stingray using network analysis. *Marine Biology*, *171*(9), Article 176. https://doi.org/10.1007/s00227-024-04498-z

Krause, J., & Ruxton, G. D. (2002). Living in groups. *Oxford University Press*.

Kruschke, J. K. (2021). Bayesian analysis reporting guidelines. *Nature Human Behaviour*, *5*(10), 1282–1291. https://doi.org/10.1038/s41562-021-01177-7

Laroche, R. K., Kock, A. A., Dill, L. M., & Oosthuizen, W. H. (2007). Effects of provisioning ecotourism activity on the behaviour of white sharks Carcharodon carcharias. *Marine Ecology Progress Series*, *338*, 199–209. https://doi.org/10.3354/meps338199

Lilly, J., McLean, M. F., Dadswell, M. J., Wirgin, I., Comolli, P., & Stokesbury, M. J. W. (2020). Use of social network analysis to examine preferential co-occurrences in Atlantic sturgeon Acipenser oxyrinchus oxyrinchus Mitchill, 1815. *Animal Biotelemetry*, *8*(1), Article 14. https://doi.org/10.1186/s40317-020-00201-3

Loiseau, N., Kiszka, J. J., Bouveroux, T., Heithaus, M. R., Soria, M., & Chabanet, P. (2016). Using an unbaited stationary video system to investigate the behaviour and interactions of bull sharks Carcharhinus leucas under an aquaculture farm. *African Journal of Marine Science*, *38*(1), 73–79. https://doi.org/10.2989/1814232X.2016.1156578

MacArthur, R. H., & Wilson, E. O. (1967). *The equilibrium theory of island biogeography*. Princeton University Press.

Martin, Aidan, R., Hammerschlag, N., Collier, R., & Fallows, C. (2005). Predatory behaviour of white sharks (Carcharodon carcharias) at Seal Island, South Africa. *Journal of the*

Marine Biological Association of the United Kingdom, *85*, 1121–1135. https://doi.org/10.1017/S002531540501218X

McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and STAN*. CRC Press LLC. http://ebookcentral.proquest.com/lib/massey/detail.action?docID=6133700

Meyer, C. G., Dale, J. J., Papastamatiou, Y. P., Whitney, N. M., & Holland, K. N. (2009). Seasonal cycles and long-term trends in abundance and species composition of sharks associated with cage diving ecotourism activities in Hawaii. *Environmental Conservation*, *36*(2), 104–111. https://doi.org/10.1017/S0376892909990038

Mourier, J., Bass, N. C., Guttridge, T. L., Day, J., & Brown, C. (2017). Does detection range matter for inferring social networks in a benthic shark using acoustic telemetry? *Royal Society Open Science*, *4*(9), Article 170485. https://doi.org/10.1098/rsos.170485

Mourier, J., Soria, M., Silk, M., Demichelis, A., Dagorn, L., & Hattab, T. (2024). Both environmental conditions and intra- and interspecific interactions influence the movements of a marine predator. *Ecology and Evolution*, *14*(12), e70659. https://doi.org/10.1002/ece3.70659

Mourier, J., Vercelloni, J., & Planes, S. (2012). Evidence of social communities in a spatially structured network of a free-ranging shark species. *Animal Behaviour*, *83*(2), 389–401. https://doi.org/10.1016/j.anbehav.2011.11.008

Mull, C. G., Andrzejaczek, S., Udyawer, V., & Dwyer, R. G. (2022). Advances in methods, understanding, and applications of elasmobranch movement ecology. In J. C. Carrier, C. A. Simpfendorfer, M. R. Heithaus, & K. E. Yopak (Eds.), *Biology of Sharks and Their Relatives* (3rd ed., pp. 357–399). CRC Press.

Munroe, S., Meyer, L., & Heithaus, M. R. (2022). Elasmobranch foraging strategies and tactics. In J. C. Carrier, C. A. Simpfendorfer, M. R. Heithaus, & K. E. Yopak (Eds.), *Biology of Sharks and Their Relatives* (3rd ed., pp. 323–355). CRC Press.

Myrberg, A. A., & Gruber, S. H. (1974). The behavior of the bonnethead shark, Sphyrna tiburo. *Copeia*, *1974*(2), 358–374. https://doi.org/10.2307/1442530

Northcutt, R. G. (1977). Elasmobranch central nervous system organization and its possible evolutionary significance. *American Zoologist*, *17*(2), 411–429. https://doi.org/10.1093/icb/17.2.411

Papastamatiou, Y. P., Mourier, J., Pouca, C. V., Guttridge, T. L., & Jacoby, D. M. P. (2022a). Shark and ray social lives: Form, function, and ecological significance of associations and grouping. In J. C. Carrier, C. A. Simpfendorfer, M. R. Heithaus, & K. E. Yopak (Eds.), *Biology of Sharks and Their Relatives* (3rd ed., pp. 545–566). CRC Press.

Papastamatiou, Y. P., Mourier, J., TinHan, T., Luongo, S., Hosoki, S., Santana-Morales, O., & Hoyos-Padilla, M. (2022b). Social dynamics and individual hunting tactics of white sharks revealed by biologging. *Biology Letters*, *18*(3), Article 20210599. https://doi.org/10.1098/rsbl.2021.0599

Porcher, I. F. (2023). Ethogram for blacktip reef sharks (Carcharhinus melanopterus). *Behaviour*, *160*(11–14), 1167–1204. https://doi.org/10.1163/1568539X-bja10213

Pratt, H. L. (1996). Reproduction in the male white shark. In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks. The Biology of Carcharodon carcharias* (pp. 131–138). Academic Press.

R Development Core Team. (n.d.). *R: The R Project for statistical computing*. Retrieved 14 January 2025, from https://www.r-project.org/

Reid, D. D., Robbins, W. D., & Peddemors, V. M. (2011). Decadal trends in shark catches and effort from the New South Wales, Australia, shark meshing program 1950–2010. *Marine and Freshwater Research*, *62*(6), 676–693. https://doi.org/10.1071/MF10162

Rigby, C., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M., Herman, K., Jabado, R., Liu, K.-M., Lowe, C., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R., & Winker, H. (2019). *Carcharodon carcharias-White Shark. The IUCN Red List of Threatened Species 2019*. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T3855A2878674.en

Robbins, R. L. (2007). Environmental variables affecting the sexual segregation of great white sharks Carcharodon carcharias at the Neptune Islands South Australia. *Journal of Fish Biology*, *70*(5), 1350–1364. https://doi.org/10.1111/j.1095-8649.2007.01414.x

Roche, D. G., Careau, V., & Binning, S. A. (2016). Demystifying animal 'personality' (or not): Why individual variation matters to experimental biologists. *Journal of Experimental Biology*, *219*(24), 3832–3843. https://doi.org/10.1242/jeb.146712

Roff, G., Brown, C. J., Priest, M. A., & Mumby, P. J. (2018). Decline of coastal apex shark populations over the past half century. *Communications Biology*, *1*(1), Article 223. https://doi.org/10.1038/s42003-018-0233-1

Setyawan, E., Erdmann, M. V., Mambrasar, R., Ambafen, O., Hasan, A. W., Izuan, M., Mofu, I., Putra, M. I. H., Sianipar, A. B., Constantine, R., Stevenson, B. C., & Jaine, F. R. A. (2024). Spatial connectivity of reef manta rays across the Raja Ampat archipelago, Indonesia. *Royal Society Open Science*, *11*(4), Article 230895. https://doi.org/10.1098/rsos.230895

Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. *Movement Ecology*, *8*(1), Article 12. https://doi.org/10.1186/s40462-020-0197-x

Shaw, R. L., Curtis, T. H., Metzger, G., McCallister, M. P., Newton, A., Fischer, G. C., & Ajemian, M. J. (2021). Three-dimensional movements and habitat selection of young white sharks (Carcharodon carcharias) across a temperate continental shelf ecosystem. *Frontiers in Marine Science*, *8*, Article 643831. https://doi.org/10.3389/fmars.2021.643831

Sims, D. W., Humphries, N. E., Bradford, R. W., & Bruce, B. D. (2012). Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. *Journal of Animal Ecology*, *81*(2), 432–442. https://doi.org/10.1111/j.1365-2656.2011.01914.x

Smale, M. J., & Cliff, G. (2012). White sharks and cephalopod prey: Indicators of habitat use? In M. L. Domeier (Ed.), *Global Perspectives on the Biology and Life History of the White Shark* (pp. 51–57). CRC Press.

Spaet, J. L. Y., Butcher, P. A., Manica, A., & Lam, C. H. (2022). Spatial dynamics and fine-scale vertical behaviour of immature Eastern Australasian white sharks (Carcharodon carcharias). *Biology*, *11*(12), Article 1689. https://doi.org/10.3390/biology11121689

Spaet, J. L. Y., Patterson, T. A., Bradford, R. W., & Butcher, P. A. (2020). Spatiotemporal distribution patterns of immature Australasian white sharks (Carcharodon carcharias). *Scientific Reports*, *10*(1), Article 10169. https://doi.org/10.1038/s41598-020-66876-z

Spake, R., Bowler, D. E., Callaghan, C. T., Blowes, S. A., Doncaster, C. P., Antão, L. H., Nakagawa, S., McElreath, R., & Chase, J. M. (2023). Understanding ‘it depends’ in ecology: A guide to hypothesising, visualising and interpreting statistical interactions. *Biological Reviews*, *98*(4), 983–1002. https://doi.org/10.1111/brv.12939

Sperone, E., Micarelli, P., Andreotti, S., Spinetti, S., Andreani, A., Serena, F., Brunelli, E., & Tripepi, S. (2010). Social interactions among bait-attracted white sharks at Dyer Island (South Africa). *Marine Biology Research*, *6*(4), 408–414. https://doi.org/10.1080/17451000903078648

Stead, D. H. (1971). *Survey of Foveaux Strait* (No. 59). New Zealand Marine Department.

Stevens, J. D., Bonfil, R., Dulvy, N. K., & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, *57*(3), 476–494. https://doi.org/10.1006/jmsc.2000.0724

Strong, W. R., Nelson, D. R., Bruce, B. D., & Murphy, R. D. (1996). Population dynamics of white sharks in Spencer Gulf, South Australia. In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks* (pp. 401–414). Academic Press. https://doi.org/10.1016/B978-012415031-7/50038-0

Tait, L. W., Thoral, F., Pinkerton, M. H., Thomsen, M. S., & Schiel, D. R. (2021). Loss of giant kelp, Macrocystis pyrifera, driven by marine heatwaves and exacerbated by poor water clarity in New Zealand. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.721087

Time and Date. (2011). *Weather in May 2011 in Stewart Island, New Zealand*. Past Weather in Stewart Island, New Zealand - May 2011. https://www.timeanddate.com/weather/@2182334/historic?month=5&year=2011

Tsai, W., Chang, Y., & Liu, K. (2019). Development and testing of a Bayesian population model for the bigeye thresher shark, Alopias superciliosus, in an area subset of the western North Pacific. *Fisheries Management & Ecology*, *26*(3), 269–294. https://doi.org/10.1111/fme.12347 van de Schoot, R., Depaoli, S., King, R., Kramer, B., Märtens, K., Tadesse, M. G., Vannucci, M., Gelman, A., Veen, D., Willemsen, J., & Yau, C. (2021). Bayesian statistics and modelling. *Nature Reviews Methods Primers*, *1*(1), 1–26. https://doi.org/10.1038/s43586-020-00001-2

Vehtari, A. (2020). *Cross-validation FAQ*. Stan. https://mc-stan.org/loo/articles/online-only/faq.html#elpd_interpretation

Vemco. (2018, July 28). *VR2W User Manual*. https://www.oceans-research.com/wp-content/uploads/2016/09/vr2w-manual-1.pdf

Wade, M. W., Fisher, M., & Matich, P. (2022). Comparison of two machine learning frameworks for predicting aggregatory behaviour of sharks. *Journal of Applied Ecology*, *59*(11), 2767–2778. https://doi.org/10.1111/1365-2664.14273

Watson, D., Beaven, B., & Bradshaw, C. (2014). Population trends of New Zealand fur seals in the Rakiura region based on long-term population surveys and traditional ecological knowledge. *New Zealand Journal of Marine and Freshwater Research*, *49*(1), 106–118. https://doi.org/10.1080/00288330.2014.953184

White, C. F., Lyons, K., Jorgensen, S. J., O’Sullivan, J., Winkler, C., Weng, K. C., & Lowe, C. G. (2019). Quantifying habitat selection and variability in habitat suitability for juvenile white sharks. *PLOS ONE*, *14*(5), 1–20. https://doi.org/10.1371/journal.pone.0214642

Whitehead, H. (2008). *Analyzing animal societies: Quantitative methods for vertebrate social analysis*. University of Chicago Press.

Whitehead, H., & Dufault, S. (1999). Techniques for analyzing vertebrate social structure using identified individuals: Review and recommendations. In P. J. B. Slater, J. S. Rosenblat, C. T. Snowden, & T. J. Roper (Eds.), *Advances in the Study of Behavior* (Vol. 28, pp. 33–74). Academic Press. https://doi.org/10.1016/S0065-3454(08)60215-6

Wickham, H. (2016). *`ggplot2`: Elegant graphics for data analysis*. Springer-Verlag. ISBN https://ggplot2.tidyverse.org/

Williams, G. (1936). The geomorphology of Stewart Island, New Zealand. *The Geographical Journal*, *87*(4), 328–337. https://doi.org/10.2307/1785559

Wilson, G. J. (1981). *Distribution and abundance of the New Zealand fur seal, Arctocephalus forsteri*. Ministry of Agriculture and Fisheries, Fisheries Research Division.

Winton, M., Fay, G., & Skomal, G. (2023). An open spatial capture-recapture framework for estimating the abundance and seasonal dynamics of white sharks at aggregation sites. *Marine Ecology Progress Series*, *715*, 1–25. https://doi.org/10.3354/meps14371

Appendices

Appendix A – White Shark Metadata

Table A. 1 *- Metadata of tagged white sharks. All white sharks were tagged in the Titi Islands. CC30 lacked both minimum and maximum total length measurements.*

Shark ID	Acoustic Tag Number	Sex	Minimum Total Length (m)	Maximum Total Length (m)
CC03	27032	M	3.0	3.2
CC08	27026	F	2.8	2.8
CC22	40961	M	3.3	3.3
CC23	27028	M	4.0	4.0
CC24	40963	M	4.0	4.0
CC25	40962	M	2.8	2.8
CC27	27025	F	4.0	4.0
CC28	27027	M	3.5	3.5
CC29	27029	M	2.8	3.0
CC30	27031	M	-	-
CC31	27033	M	3.8	4.0
CC32	40964	F	4.0	4.0
CC33	40965	F	3.3	3.5
CC34	40966	M	3.5	3.5
CC36	40968	M	4.0	4.0
CC37	40969	M	2.8	2.8
CC38	40970	M	2.8	3.0
CC39	40972	M	2.5	2.5
CC40	40973	M	4.0	4.0
CC42	40975	M	3.5	3.5
CC43	40976	M	2.8	3.0
CC44	40977	M	3.0	3.0

Appendix B – Chapter 2 Supplementary Tables and Figures

Table B. 1 *– Chapter 2: Prior predictive check. The priors from the final test, prior predictive check five, were used in the eighth logistic model.*

Prior Predictive Check	Intercept	Standard Deviation
1	Student T (3, 0, 3.5)	Student T (3, 0, 3.5)
2	Normal (0, 10)	Normal (0, 10)
3	Normal (0, 1.5)	Normal (0, 0.5)
4	Normal (0, 1.5)	Cauchy (0, 1)
5	Normal (0, 1.5)	Exponential (1)

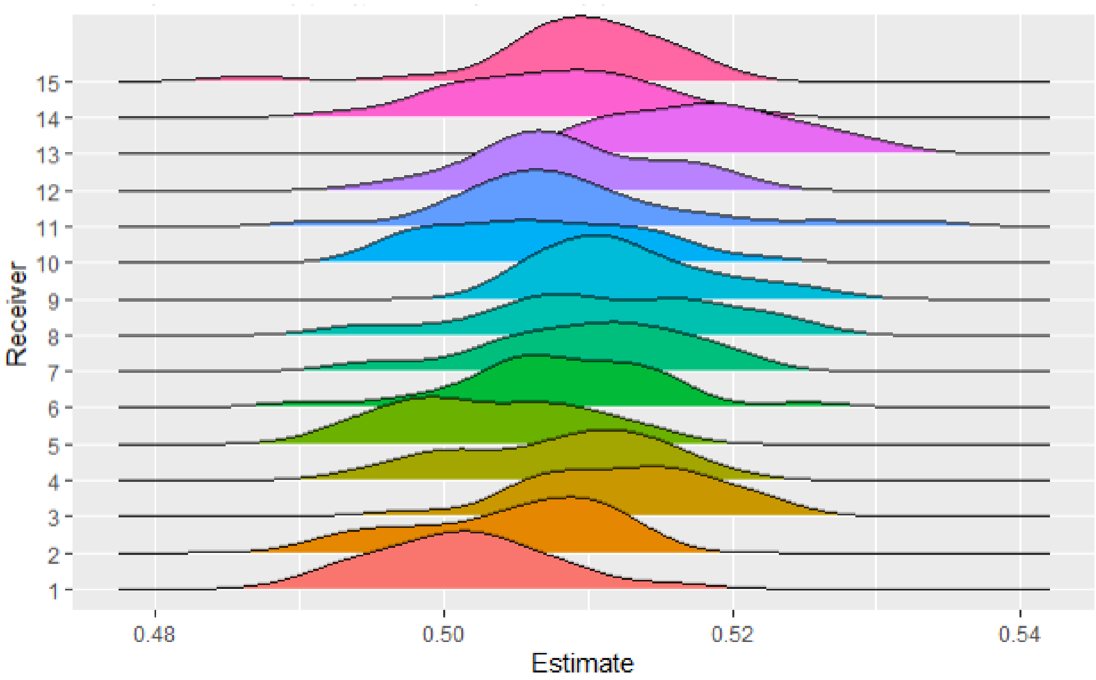


Figure B. 1 *– Chapter 2: Prior distributions for the main effects of receivers produced from a prior predictive check on the prior used in the full Bayesian model: Intercept = Normal(0, 1.5), Standard deviation = Exponential(1).*

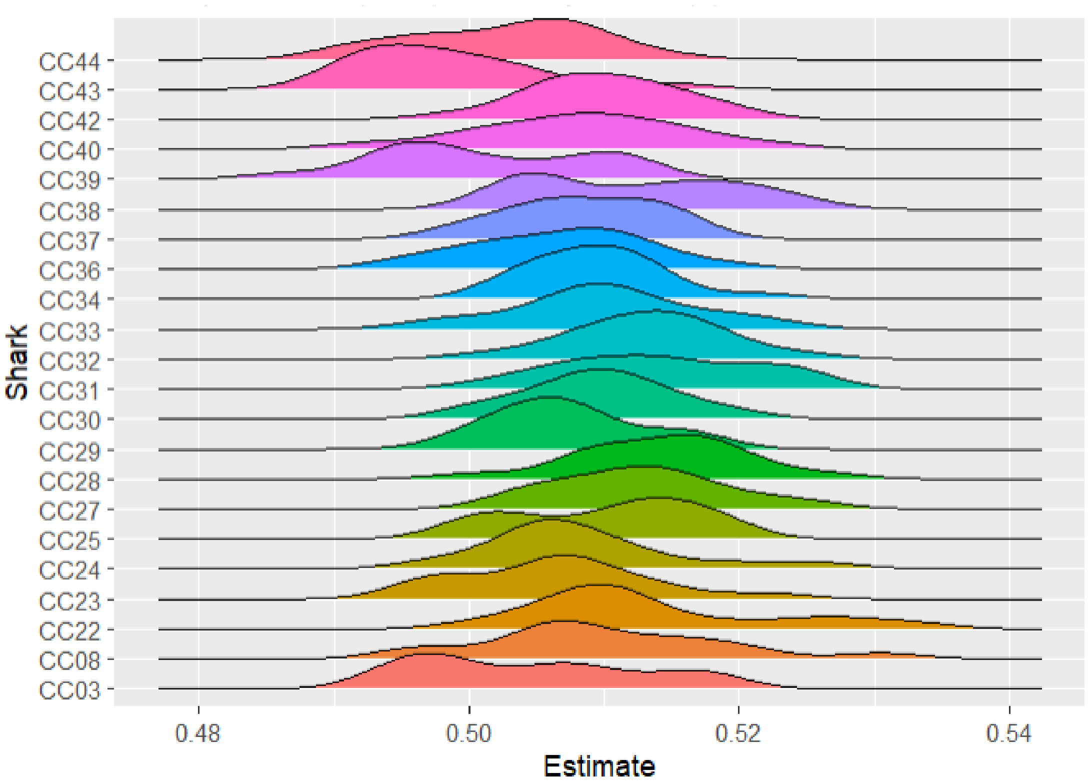


Figure B. 2 *– Chapter 2: Prior distributions for the main effects of sharks produced from a prior predictive check on the prior used in the full Bayesian model: Intercept = Normal(0, 1.5), Standard deviation = Exponential(1).*

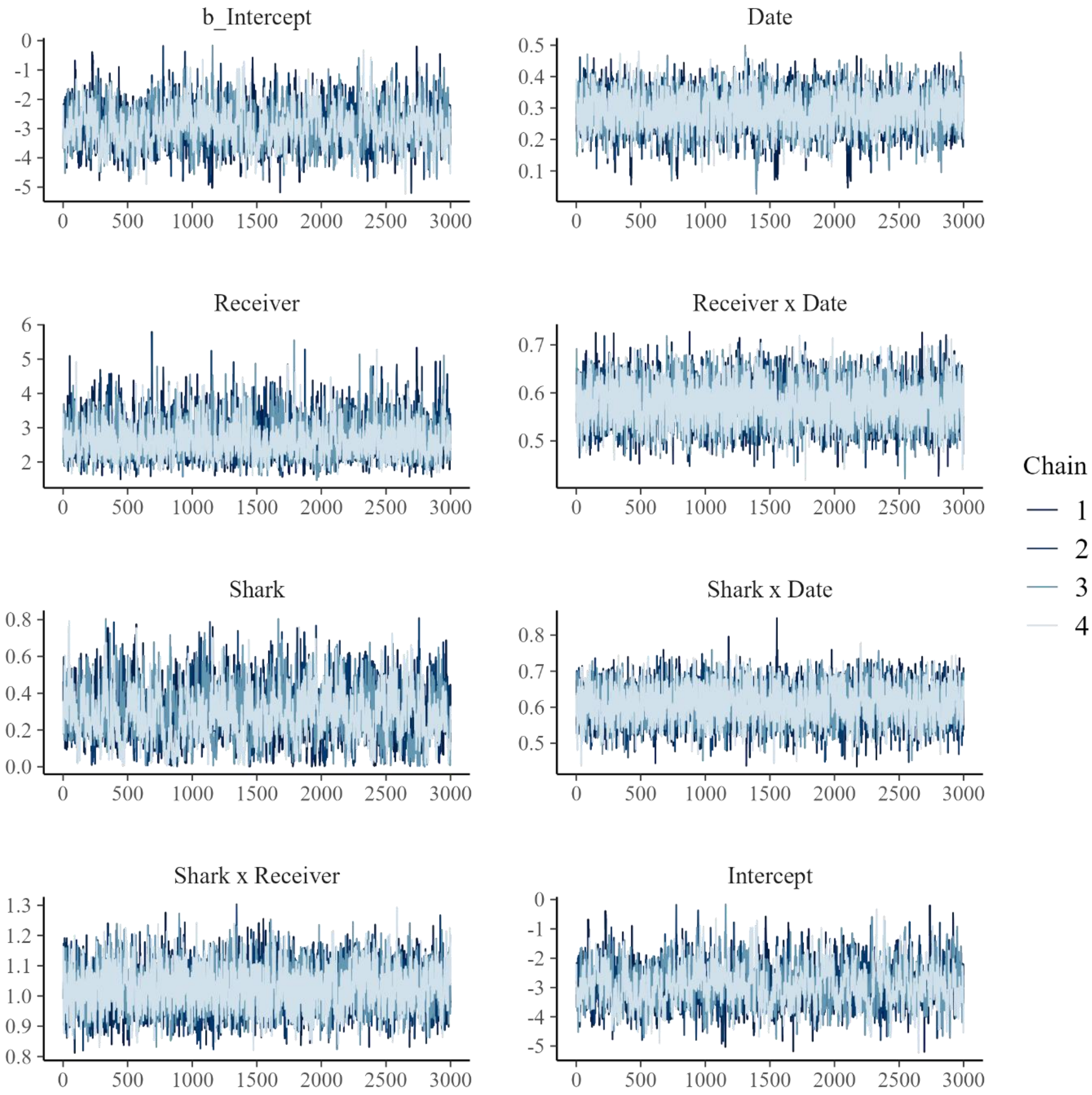


Figure B. 3 *– Chapter 2: Markov Chain Monte Carlo (MCMC) trace plots for full Bayesian model. This model included all interaction terms.*

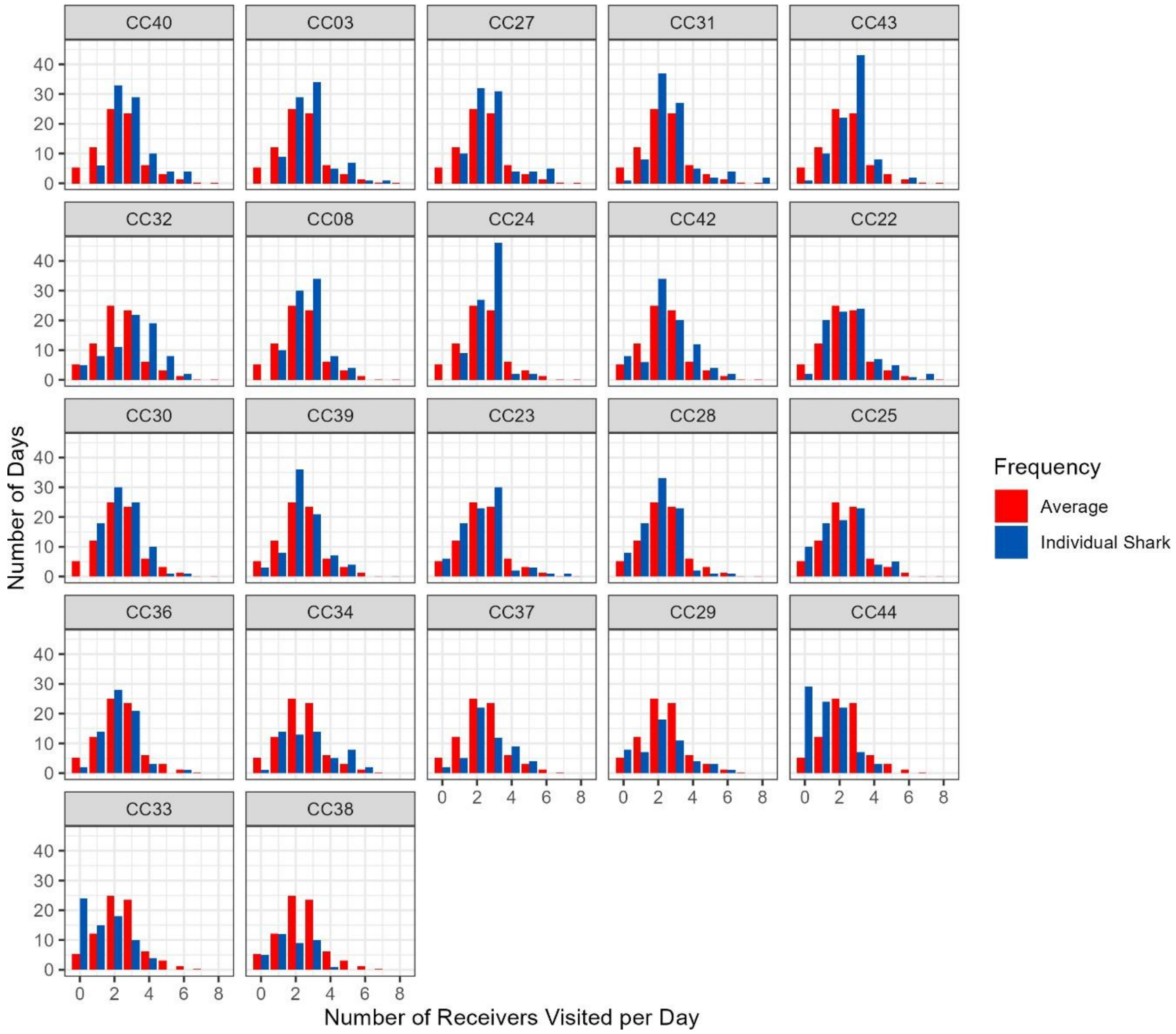


Figure B. 4 *– Chapter 2: The number of receivers (1-8) visited per day by individual white sharks aggregating northeast of Stewart Island between April and June 2011.*

Figure B. 5 *– Chapter 2: White shark (CC25; 2.9m male) displaying a healed bite wound posterior to the right pectoral fin from a larger conspecific at East Edwards Island, northeast of Stewart Island, New Zealand, 4 April 2011. Photo: Clinton Duffy.*

Appendix C – Chapter 3 Supplementary Tables and Figures

Table C. 1 *– Chapter 3: The temporal boundaries for each 'day period', obtained from Time and Date and using mid-May as a reference point.*

Day Period	Time Boundaries
Night	19:00 to 5:44
Dawn	5:45 to 7:29
Morning	7:30 to 11:59
Afternoon	12:00 to 17:14
Dusk	17:15 to 18:59

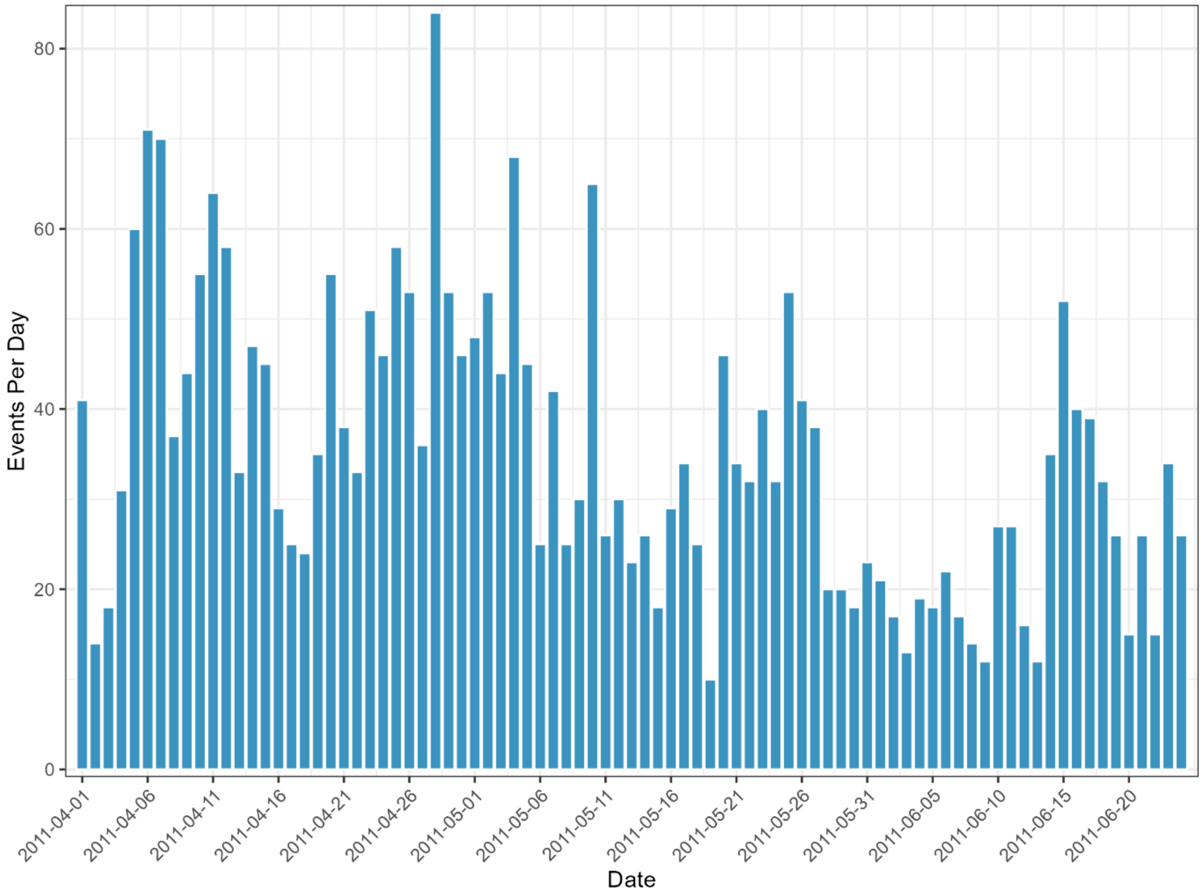


Figure C. 1 *– Chapter 3: Frequency of events (white shark co-occurrences) per day between 1 April 2011 and 25 June 2011 across all acoustic receivers deployed northeast of Stewart Island.*

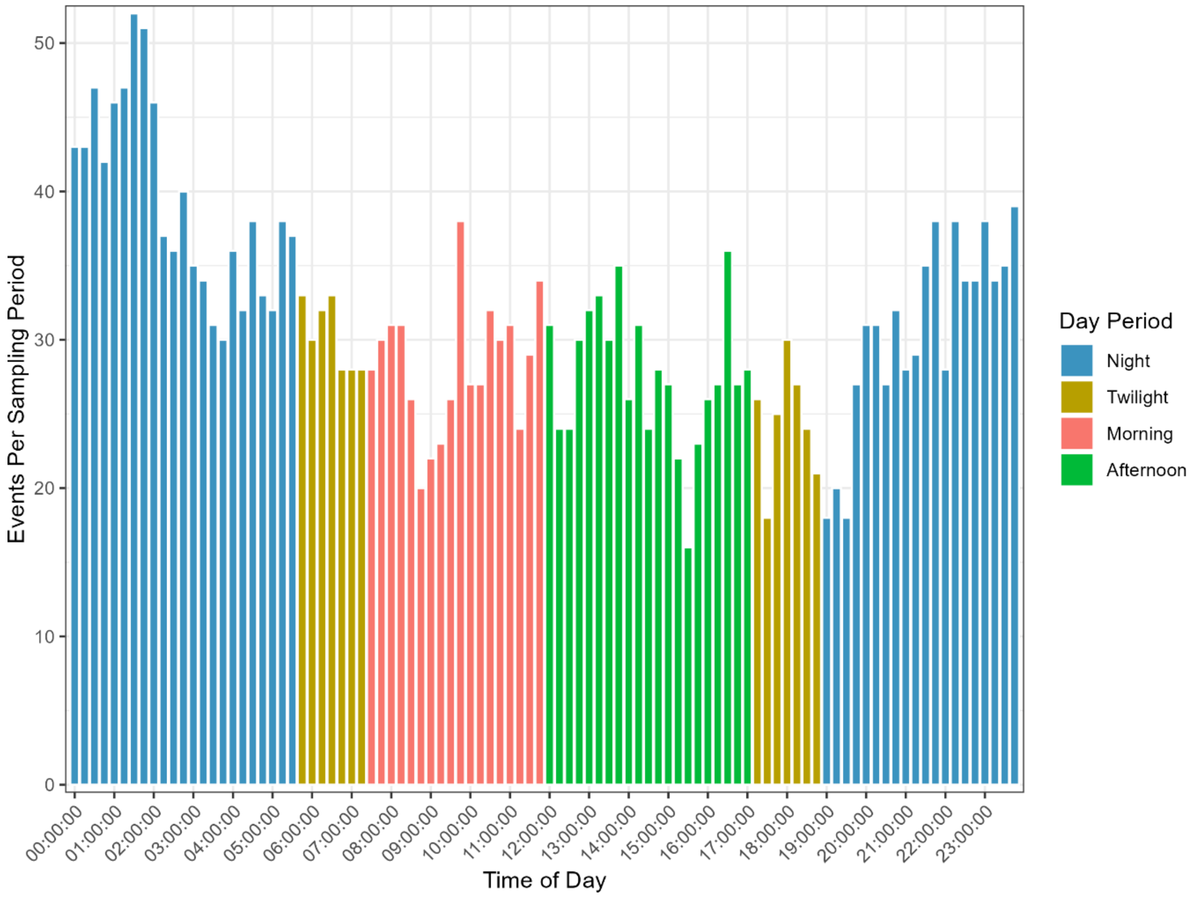


Figure C. 2 *– Chapter 3: Frequency of events (white shark co-occurrences) per 15-minute sampling period at all receivers deployed northeast of Stewart Island.*

Figure C. 3 *– Chapter 3: Tolerance for conspecifics displayed by three white sharks (Front: CC03, 3.1m male; Middle: CC27, 4.0m female; Back: CC44, 3.0m male) at East Edwards Island, northeast of Stewart Island, New Zealand, 29 March 2011. Only the tip of the caudal fin of CC44 can be seen behind CC27. Photo: Kina Scollay.*

Figure C. 4 *– Chapter 3: Size-related dominance behaviour exhibited by two white sharks (CC24, 4.0m male; CC22, 3.3m male) at Herekopare Island, northeast of Stewart Island, New Zealand, 2 April 2011. Top Left: CC22 enters from the right and is approached by the larger male, CC24. Top Right: In response, CC22 does a rapid* 180^{o} *turn and is followed by CC24 so that both sharks are swimming parallel. Bottom Left: CC24 rolls on its side and turns its head to watch CC22. Bottom Right: Both sharks leave, swimming in different directions. Photos: Kina Scollay.*