Chasing rays:
Distribution and habitat-use of mobulid rays in the northeastern continental shelf of Aotearoa New Zealand

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Abstract

Endangered mobulid rays have a conservative life history associated with long reproductive cycles and subsequent low population growth rates. Targeted fisheries as well as bycatch threaten the survival of mobulid rays. Although attempts have been made to reduce overlap between mobulid rays habitat and fisheries, the lack of robust knowledge surrounding rays distribution and basic ecology remains a hindrance to effective protection. This thesis investigated the spatio-temporal distribution and habitat use of the only two mobulid rays that are known to occur in the northeastern (NE) coast of Te Ika-a-Māui North Island of Aotearoa New Zealand: Spinetail devil ray (*Mobula mobular*) and Oceanic manta ray (*Mobula birostris*), with the overarching aim to contribute this information to conservation and management. Fisheries and citizen science occurrence data were used in a Boosted Regression Tree (BRT) model to investigate mobulid rays' habitat suitability in Aotearoa. Along with a spatial model, using long-term averages of environmental conditions (i.e., static model), this study assessed temporal changes in habitat suitability by considering different years separately (i.e., dynamic model). For both species, the 200m depth contour line outlining the continental shelf edge was predicted to be an important feature – for Spinetail devil rays demarcating their inshore extent and for Oceanic manta rays, their offshore extent. As large filter feeders, this is likely related to prey availability and potential evidence of trophic separation, in that despite presumed similar habitat requirements, there is clear segregation in their distribution. For both static and dynamic models, sea surface temperature and chlorophyll-a concentrations were consistently prevalent. Although the dynamic models demonstrated that there was a change in habitat suitability occurring over time, some of this change was unable to be captured by the variables in the model, especially for Oceanic manta rays. Through this study, important baseline information has been identified in the NE coast. The high coupling of prey availability and distribution for both species poses questions on how their distribution may change with climate change and proposed poleward movement of prey. Further, the contraction of trophic separation with predicted reductions in prey availability create further uncertainties in the future that require additional investigation. Increased data availability and deeper understandings of the processes

that drive mobulid distribution and habitat use are required for their protection and conservation in the wake of current and future threats.

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List of abbreviations

IUCN	The International Union for Conservation of Nature
SDM	Species Distribution Modelling
NE	Northeastern
SST	Sea surface temperature
Chl-a	Chlorophyll-a
ENSO	El Niño Southern Oscillation
EAUC	East Auckland Current
SOI	Southern Oscillation Index
NZTCS	New Zealand Threat Classification System
DOC	Department of Conservation
GLM	Generalised Linear Model
GAM	Generalised Additive Model
CART	Classification and Regression Tree
GBM	Generalised Boosting Model
BRT	Boosted Regression Tree
MaxEnt	Maximum Entropy
RF	Random Forest
MPI	Ministry for Primary Industries
COD	Centralised Observer Database
NFPS	Non-Fish Protected Species
MWNZ	Manta Watch New Zealand
KDE	Kernel Density Estimate
NIWA	National Institute of Water and Atmosphere
NOAA	National Oceanic and Atmospheric Administration
ROC	Receiver Operating Characteristic
AUC	Area Under the ROC Curve
TSS	True Skill Statistic
SD	Standard Deviation
HSI	Habitat Suitability Index
IPO	Interdecadal Pacific Oscillation
MPA	Marine Protected Area

Note:

Majority of place names in Aotearoa New Zealand has two names: a Māori and European name. Different iwi have different conventions in the way that place names should be referred to and this thesis attempts to the best of my knowledge acknowledge the stewardship that Māori people have in the marine space. Therefore, in this thesis, place names will be referred to by both names, the Māori name followed by the European name.

Glossary:

Aotearoa New Zealand
Te Ika-a-Māui North Island
Ko te Pataka kai o Tīkapa Moana Te Moananui a Toi Hauraki Gulf Marine Park
Rākaumangamanga Cape Brett
Te Moana a Toi-te-Huatahi Bay of Plenty
Ruamaahu Alderman Islands
Tawhiti Rahi Poor Knight’s Islands
Otou North Cape
Te Hauturu-o-Toi Little Barrier Island

Chapter 1

General Introduction

Cover for chapter: *Ventral photo of an Oceanic manta ray observed in the Hauraki Gulf Marine Park (photo: Rika Ozaki)*

1.1 INTRODUCTION

Mobulid rays (family Mobulidae) are large, filter-feeding elasmobranchs in which two species: Spinetail devil ray (*Mobula mobular*) and Oceanic manta rays (*Mobula birostris*) are known to occur in Aotearoa New Zealand waters (Paulin et al., 1982). Slow life histories including low reproductive rates, late maturation and slow growth has prevented population growth (Myers & Worm, 2003; Stevens et al., 2000; Ward-Paige et al., 2013) under the pressure of directed and indirect (i.e., bycatch) fisheries (Croll et al., 2016; Francis & Jones, 2016). Combinations of biological traits, presumed declining numbers and unsustainable interaction with fisheries, have resulted in the addition of both mobulid species to be classified as “Endangered” in the IUCN Red List (Marshall et al., 2022a; Marshall et al., 2022b). However, a perennial hindrance to their conservation continues to be the scarcity of data and knowledge, namely on their biology, distribution, habitat preference and abundance (Canese et al., 2011; Hacohen-Domené et al., 2017). In Aotearoa New Zealand, the Department of Conservation has classified both species as “data deficient” (Duffy & Tindale, 2018). Without baseline information, the effectiveness of conservation, and management initiatives is limited. Currently, research associated with dedicated survey effort is limited globally and most studies are based on opportunistic observations (Fortuna et al., 2014). With inferred depletion of mobulid populations worldwide and increasing fishing pressure, the collection of baseline information is urgently required (Couturier et al., 2012).

Understanding the relationship between environmental conditions and a species’ distribution is essential when investigating the habitat requirements of species’ and predicting where they are likely to occur (Guisan & Zimmermann, 2000). Although scarcity of data remains a central issue to both species, the interaction with fisheries and charismatic nature of mobulid rays has meant that observational records do exist, albeit with varying reliability (Fortuna et al., 2014). These observations along with environmental variable layers can be combined in a species distribution model (SDM) (also known as ecological niche models and habitat suitability models) to predict the potential spatial distribution of the species (Hacohen-Domené et al., 2017). SDMs have become widely used in conservation biology to identify priority conservation areas and diversity hot-spots, serving as a critical tool in supporting conservation and management (Chavez-Rosales et al., 2019). The relevance and application of SDMs have grown rapidly in the wake of increasing anthropogenic and climate impacts in the hopes of understanding how this may affect the distribution and survival of future biological communities (Dormann, 2007).

The rest of this Chapter outlines the key concepts behind species distribution, habitat-use and habitat suitability used in this thesis, as well as an introduction to static and dynamic modelling. Study site and study species are introduced and modelling framework and introduction to the methodology used is preliminarily discussed. Thesis aims and rationales are outlined at the end of the Chapter. No published study to date has looked at the distribution and habitat-use of both species in Aotearoa New Zealand.

1.1.1 Species distribution, habitat use and ecological niches

The quantification of species-environment relationships is a key component to marine conservation biology especially for assessing the overlap of distributions within areas with high human activity and presence (e.g., shipping, fishing) (Fiedler et al., 2018). The extent and impact of these human hazards on species and ecosystems can be understood and mitigated. For apex marine predators, key factors impacting their distribution are abundance of prey, driven primarily by dynamic oceanographic conditions (e.g., sea surface temperature), physiologic constraints, as well as physiographic features (e.g., depth, slope) (Ramírez-León et al., 2021).

Species distribution describes the whereabouts of a species in space and time and in this thesis is defined as the geographic range of such species. The investigation of environmental conditions and factors that influence a species' distribution can support insight of ecological processes or physiological constraints that create and affect these patterns (Fiedler et al., 2018). What fundamentally drives distribution of a species is the prevalence of their habitat which Hall et al. (1997) describe as, "*the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism…it is the sum of the specific resources that are needed by organisms*." **Habitat-use** is defined as the way in which an organism uses their habitat to meet its life history needs (Jones, 2001). By contrast, **habitat suitability** refers to the probability of habitat use by an animal, based on their resource requirements (Manly et al., 2002). This thesis will largely be discussing themes of habitat suitability and habitat characterisation and these terms will be used in the context to quantify and characterise habitat-use (Giannoulaki et al., 2014) and identify environmental factors that are conditioning the occurrence of the study species.

It is important to note the differentiation between **fundamental** and **ecological (realised) niche**. A species' fundamental niche is defined as the area where the physiological performance and ecosystem characteristics are within the species' optimum range, characterised by abiotic conditions (Guisan & Zimmermann, 2000). In contrast, the ecological niche additionally includes biotic interactions, competitive exclusion and predation which often results in the fundamental niche being a lot larger in area than the latter (Malanson et al., 1992; Malanson, 1997). Predictive modelling in areas where environmental factors are known but species occurrence is unknown provides a cost-effective and optimal method in understanding species' distributions over large areas (Brotons et al., 2004) however, it is crucial to acknowledge that without field observations which may include more details surrounding associated species, evidence of predation (e.g., markings, scars), the model is unable to provide the full picture and is limited to understanding the fundamental niche and associated theoretical physiological and biological restraints.

1.2 STATIC AND DYNAMIC SDM

Oceans are in constant flux and motion, with movement of marine animals influenced by dynamic environmental and biological variables that change over multiple spatial and temporal scales (Niella et al., 2022). Complex interactions exist between the physical and biological environment including many centred around animals moving to locate prey patches that are unevenly distributed in space and time (Lima, 2002). However, responses of species to dynamic changes in environmental conditions are seldom studied (e.g., seasonal, interannual, long-term). The use of long-term averages (hereafter, "static") remains the dominant form of species distribution modelling within the literature (Guisan & Zimmermann, 2000). The disadvantage of using a static SDM is that it assumes equilibrium, or pseudo-equilibrium, between observed species' patterns and the environment surrounding. This means the model cannot distinguish between the transient or equilibrium response of species to a constantly changing environment and is unable to account for migration, adaptation, and plasticity inherent in individual behaviours (Guisan & Zimmermann, 2000). associated with seasonal or annual events (i.e., breeding) (Robinson et al., 2011). Migratory species may benefit especially from SDMs that take temporal changes into account (hereafter, "dynamic") as they are known to rely on highly productive areas including upwelling zones or temperate regions that tend to change seasonally (Cropper et al., 2014). Sources of interannual variability including El Niño Southern Oscillation (ENSO) are also critical factors of species distribution and have been shown to influence mobulids with a poleward shift away from warmer waters during a strong El Niño event (eastern Pacific) (Feely et al., 1987; Chavez et al., 1999; Lea & Rosenblatt, 2000; Burgess, 2017), which can be investigated further with dynamic SDMs. Dynamic SDMs are becoming more common with the need to incorporate time to investigate the impacts of climate change (Franklin, 2010; Vergés et al., 2016).

Thus, understanding not only static species distributions but distribution shifts associated with changing climates has become an increasing field of study and point of discussion (Milanovich et al., 2010). Furthermore, adequately identifying past and current distributions and how patterns may be shifting over time is critical to assessing how future distributions may change in response to climate change and may reflect the species' vulnerability to such changes (Sequeira et al., 2013).

1.3 STUDY SITE

1.3.1 Region of Study

The study area is in the northeastern (NE) continental shelf of the Te Ika-a-Māui North Island of Aotearoa New Zealand (Fig 1.1). The shelf in this region is characterised by low salinity, high nutrient waters (Zeldis et al., 2010) which are bounded seaward by subtropical, oligotrophic water from the East Auckland Current

(EAUC) (Fig 1.2) (Sharples, 1997; Stanton et al., 1997; Zeldis, 2004). The NE continental shelf is highly sensitive to wind direction with prevalent westerly winds in late winter and spring bringing upwelling favourable conditions (Fig 1.3a) (Sharples & Greig, 1998; Zeldis et al., 2004), associated with an abundance of nutrients to the surface (Chang et al., 2003) and high primary productivity (Stevens et al., 2021). By contrast, easterly winds that increase during late summer and autumn elicit downwelling conditions where warmer nutrient-poor water is brought to the surface, causing a decrease in productivity (Fig 1.3b) (Zeldis et al., 2004). The study site includes Ko te Pataka kai o Tīkapa Moana Te Moananui a Toi Hauraki Gulf Marine Park (hereafter referred to as Tīkapa Moana Hauraki Gulf), a large, semi-enclosed, relatively shallow (< 60m depth) embayment (Fig 1.1) (Wiseman et al., 2011) with one of the highest shelf primary biomass in the country (Murphy et al., 2001). The Tīkapa Moana Hauraki Gulf is a critical habitat for many animals including cetaceans (Constantine et al., 2015; Hupman et al., 2015; O’Callaghan & Baker, 2002; Petrella et al., 2012; Stockin et al., 2008), fish (Campbell et al., 2022; Clearwater, 1994; Colman, 1972) as well as a global seabird biodiversity hotspot (Rayner et al., 2021).

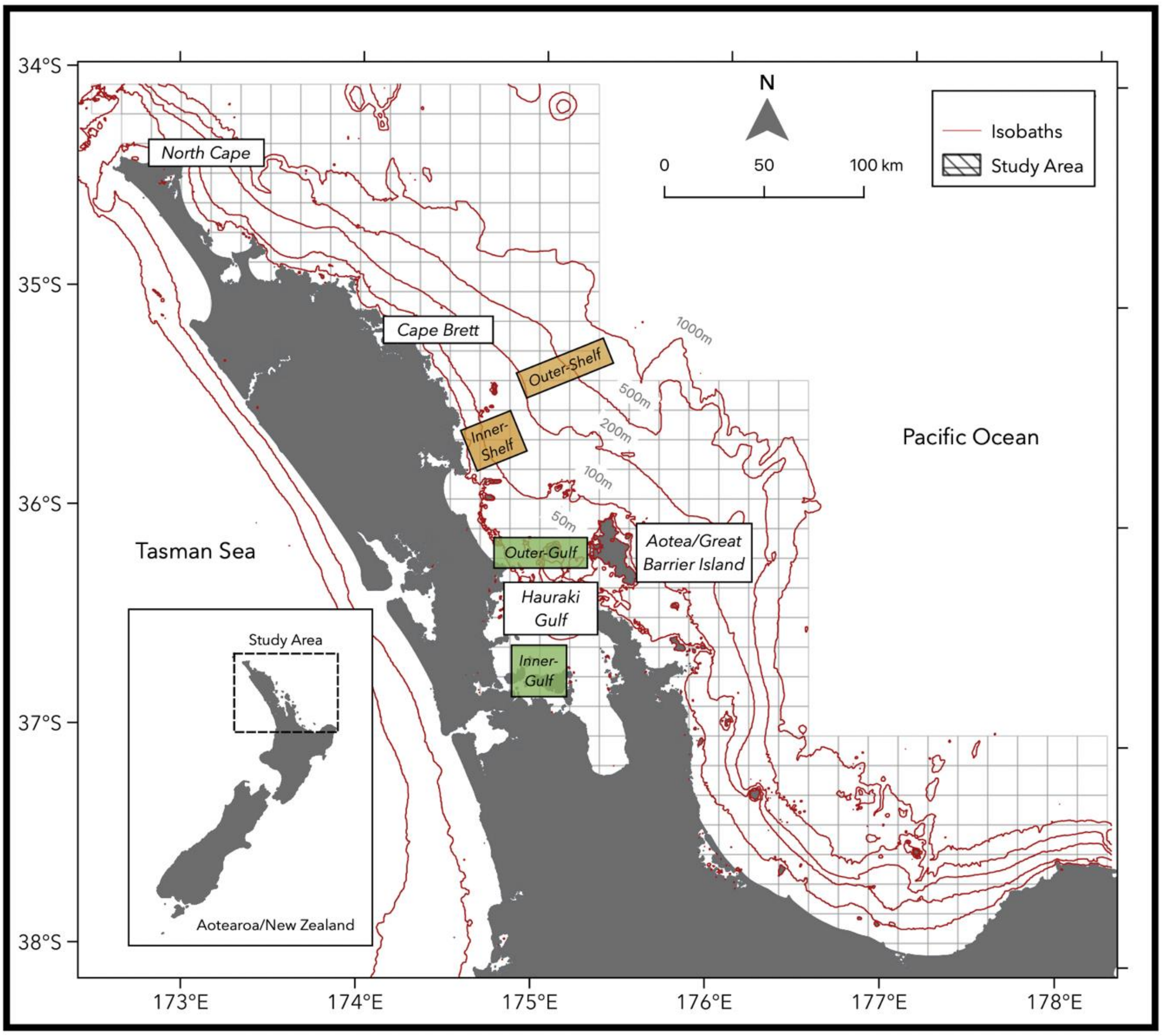

Figure 1.1 *Map of the Ko te Pataka kai o Tīkapa Moana Te Moananui a Toi Hauraki Gulf Marine Park and continental shelf region. Green boxes indicate marine reserves and labels indicate islands within the region. Isobath lines are shown in grey. The boundary starts just past the Mokohinau Islands, around Aotea and down to Ruamaahu Islands.*

The EAUC is a subtropical (i.e., warm, nutrient-poor, high salinity) current travelling from the east coast of Australia, across the Southern Pacific Ocean and down the eastern coastline of Aotearoa New Zealand (Fig 1.2) (Jillet, 1971; Sharples, 1997; Stanton & Sutton, 2003; Zeldis et al., 2004). Semi-permanent eddies near Otou North Cape and East Cape bound the northern and southern extent of the EAUC (Roemmich & Sutton, 1998; Stanton et al., 1997) and it is approximately two degrees warmer than water around the continental shelf (Sharples, 1997).The NE shelf acts as a barrier to this system, causing the EAUC to temporarily intrude across the narrow shelf in late summer, impacting the coastal ecology, with immigration of offshore tropical species and the alteration of phytoplankton and zooplankton assemblages (Francis, 1999; Zeldis et al., 1995). The migration of tropical species in response to these intrusion events suggests that such species could be taking advantage of bordering coastal waters (cold, nutrient-rich, low salinity) while remaining in their optimal temperature ranges (Sharples, 1997; Zeldis et al., 1995). In early summer (Dec) with prevailing westerly winds, the EAUC surface water is located offshore and past the shelf however, in late summer (Feb), along with the shift to easterly winds, the subtropical water moves to the outer shelf, creating a clear boundary between the low salinity water of the inner Gulf and the higher salinity water of the outer shelf (Sharples, 1997). Thus, the influence of the EAUC on the coastal ecology is exacerbated in the late summer with the intrusion of oligotrophic water.

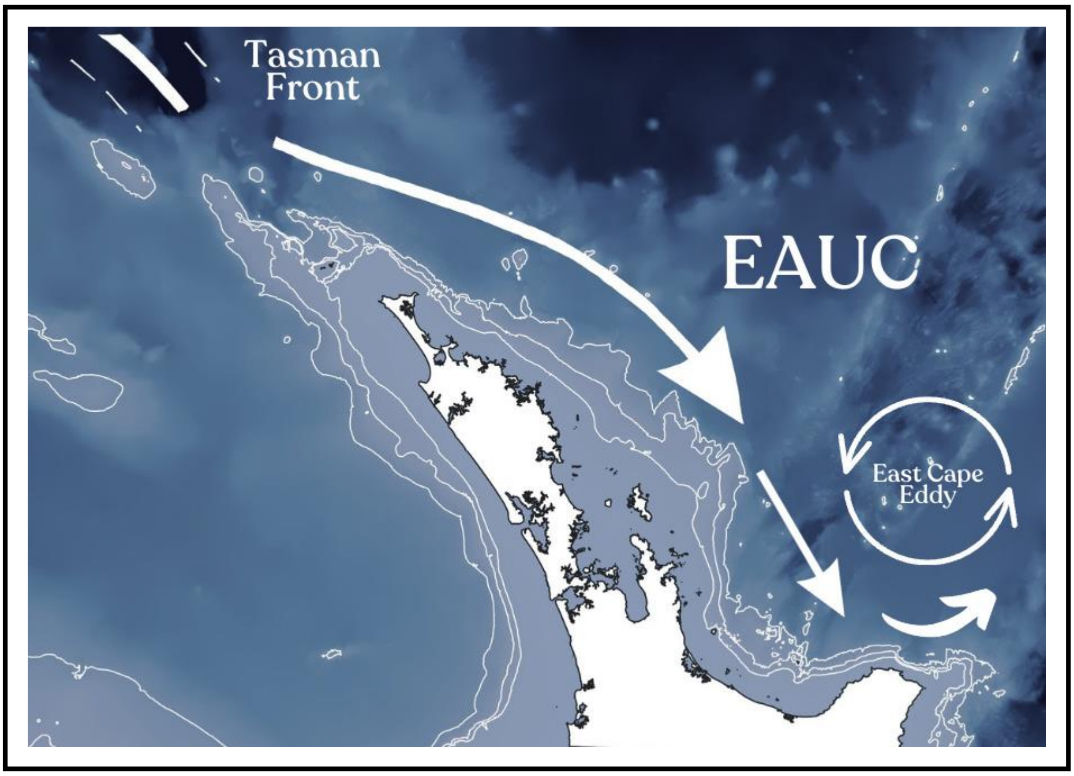

Figure 1.2 *Map of study site showing the generalised path of the East Auckland Current (EAUC) and Tasman Front it originates from. 200m, 500m, 1000m isobars are shown. East Cape Eddy is shown at the southern extent of the EAUC. Adapted from Stevens et al. (2019).*

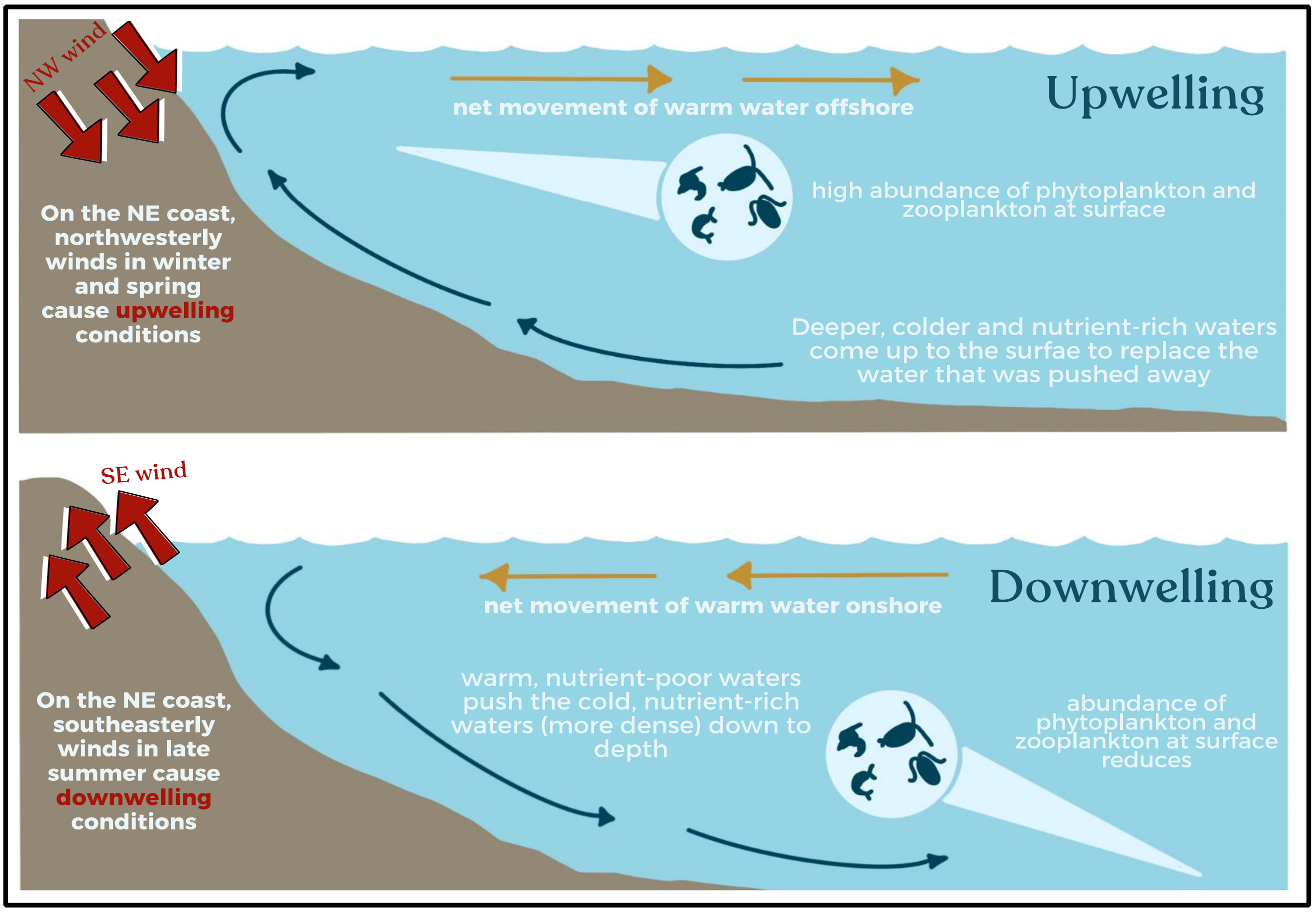

***Figure 1.6 a)** Diagram of downwelling on the eastern coast of the North Island **b)** diagram illustrating upwelling at the eastern coast of the Te Ika-a-Māui North Island.*

1.3.2 Drivers of inter-annual variability

1.3.2.1 El Niño Southern Oscillation (ENSO)

The wind-dependence of nutrient supply to the shelf suggests that new nutrient supply and productivity will ultimately covary with wind patterns, which are in turn forced by large-scale processes such as El Niño Southern Oscillation (ENSO) (Broekhuizen et al., 2002; Gordon, 1985). In a typical year, trade winds blow westwards over the Equatorial Pacific, causing increased SST and rainfall over the Western Pacific (e.g., Indonesia), and decreased SST and increased productivity in the Eastern Pacific (e.g., Peru) (Philander, 1983). El Niño events are characterised by a weakening in the trade winds causing the West Pacific Warm Pool to disperse east. La Niña events are the opposite: trade winds strengthen forcing the West Pacific Warm Pool to remain in the south-west Pacific (Hill et al., 2016) (Fig 1.4). These variations at the scale of the Pacific basin affect the local circulation of the NE of Aotearoa New Zealand and in particular, of the Tīkapa Moana Hauraki Gulf. The interannual variability in physical conditions, nutrient supply and productivity is attributed to shifting cycles of ENSO and subsequently, it affects phytoplankton abundance, prey availability and ultimately, the distribution of animal communities within the Gulf (Mann & Lazier, 1991). During El Niño conditions, there is an increased prevalence of north-westerly winds causing upwelling around the shelf and a subsequent reduction in sea surface temperature. Conversely, La Niña conditions bring south-easterly winds towards to coast, causing downwelling at the shelf and higher sea surface temperatures (Broekhuizen et al., 2002; Gordon, 1985; Rhodes et al., 1993; Srinivasan et al., 2015). In the Tīkapa Moana Hauraki Gulf, studies investigating the impact of ENSO on mammals (Neumann, 2001) and birds (Srinivasan et al., 2015) have been conducted however, there is a lack of understanding on how it may affect ectothermic (i.e., cold-blooded) fish.

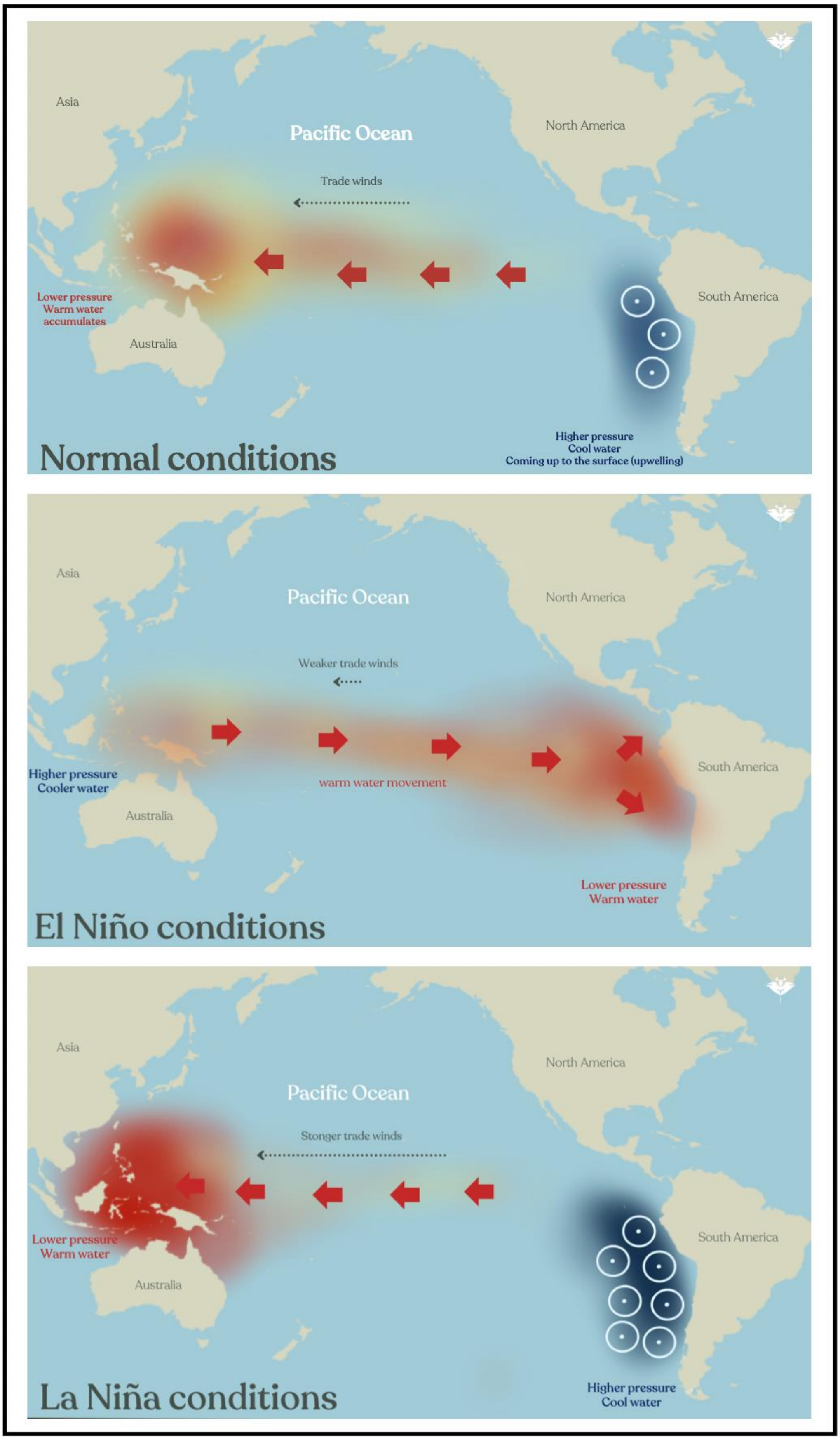

***Figure 1.4** Schematic illustrations of normal (top), El Niño (middle) and La Niña conditions. White circles with a dot indicate areas with upwelling conditions. Red arrow represents the movement of warm water.*

The Southern Oscillation Index (SOI), a measure of surface air pressure difference between Tahiti and Darwin, is often used as an indication of the development or intensity of a El Niño or La Niña event (Srinivasan et al., 2015). A negative SOI indicates a El Niño event, and a positive SOI indicates a La Niña, with the intensity indicated by the value of the SOI. When neither La Niña nor El Niño event occurs, the conditions are considered to be neutral.

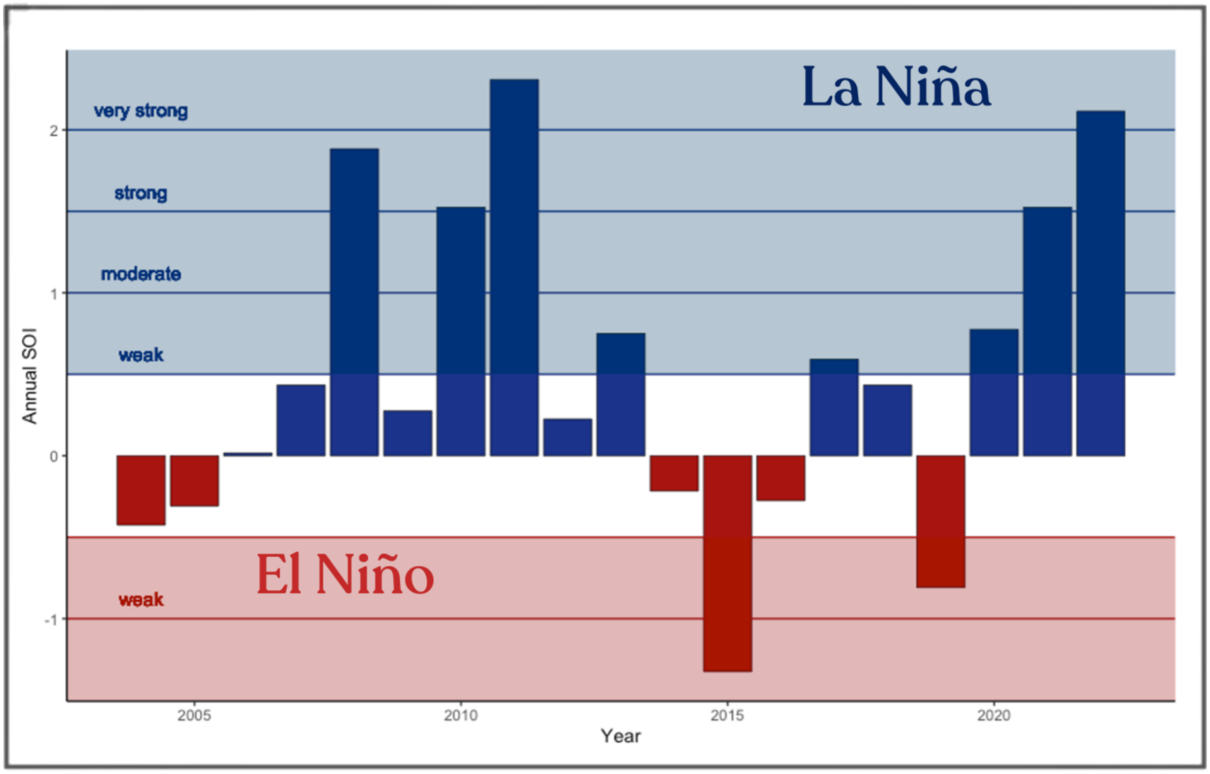

Figure 1.5 *Annual Southern Oscillation Index (SOI) values from 2004 to 2022. Values greater than 0.5 indicate La Niña conditions (blue), while values less than -0.5 indicate the presence of El Niño conditions (red). Data source: NOAA.*

During the study years 2004 to 2022, most years have been dominated by La Niña conditions, especially 2008, 2010, 2011, 2021 and 2022 (Fig 1.5). Although the presence of El Niño conditions is relatively rare in comparison, there is a signal for a moderate event in 2015 (Fig 1.5). Variability associated with the EAUC during ENSO conditions is still relatively unknown and understudied (Willis et al., 2007).

1.3.2.2 Climate change

On top of the uncertainty in how natural variability in oceanographic features are affecting animal movement, there is a long-term shift that is being forced by anthropogenic climate change. The combination of various climate influences such as these are creating immense uncertainty and variability in the understanding of how species' distributions are responding to these changes (Hill et al., 2016). Further, the rate of change in response to climate change is nuanced and species specific, with some species showing no response (i.e., potential evolutionary adaptation) and some showing evidence of range shifts (Poloczanska et al., 2013). Thus, in amongst unprecedented uncertainty, it is ever more critical to identify mobulids' distributions and understand how it may have changed overtime to infer how it may continue to change into the future.

1.4 STUDY SPECIES

This thesis focusses on two species of elasmobranchs that are seldom studied within the study region and the only known mobulid species to occur in Aotearoa New Zealand waters: Spinetail devil rays (*Mobula mobular*) and Oceanic manta rays (*Mobula birostris*).

1.4.1 Spinetail devil ray (*Mobula mobular*)

1.4.1.1 Taxonomic description

The *Mobuilidae* family consists of two manta (*Manta* spp.) species and nine devil (*Mobula* spp.) ray species (Couturier et al., 2012). Spinetail devil rays (*Mobula mobular*) (Bonnaterre, 1788) are pelagic marine fish. Although there are nine recognised species within the genus *Mobula*, to date there is only confirmed occurrence of one, Spinetail devil ray, in Aotearoa New Zealand waters (Francis & Lyon, 2012). The correct taxonomy of this species has remained challenging due to the observational similarities between the Oceanic manta ray, with many descriptions not being taken into the wider taxonomic context, resulting in several different names for this species (Notarbartolo di Sciara, 2020). Notably, it was believed to be two separate species: Spinetail devil ray (*Mobula japonica*) and Giant devil ray (*Mobula mobular*). Due to the misconception that Oceanic manta rays were not habitants of the Mediterranean Sea and the misidentification of Spinetail devil rays with Oceanic manta rays this resulted in the name, Giant devil ray (*Mobula mobular*) (Notarbartolo di Sciara, 1987). Only recently has molecular methods provided strong evidence that these two species are in fact one, which has resulted in the revised taxonomic renaming of the Spinetail devil ray as *Mobula mobular* and discontinuation of the Giant devil ray (Notarbartolo di Sciara, 2020).

Spinetail devil rays have a disc width of 2 to 4 metres with a dark stripe stretching across the head, with two cephalic fins on either side, giving the species the iconic “devil horns” that the name devil ray originates from (Fig 1.6) (Francis & Jones, 2016). When observed dorsally, the species appears to be a brown to black colour with a distinctive purple and blue iridescent shimmer (Fig 1.8) (Fortuna et al., 2014). Compared to other Mobula species, they have a spine on the base of their long tail which describes their forename, “Spinetail” (Notarbartolo-di-Sciara, 1988). Pectoral fins extend outwards, and the species locomotion is driven by the flapping of these fins in a wing-like manner, with a sub-terminal or inferior mouth to assist with water-column filter feeding (Bradaii & Capapé, 2001; Gill, 1910).

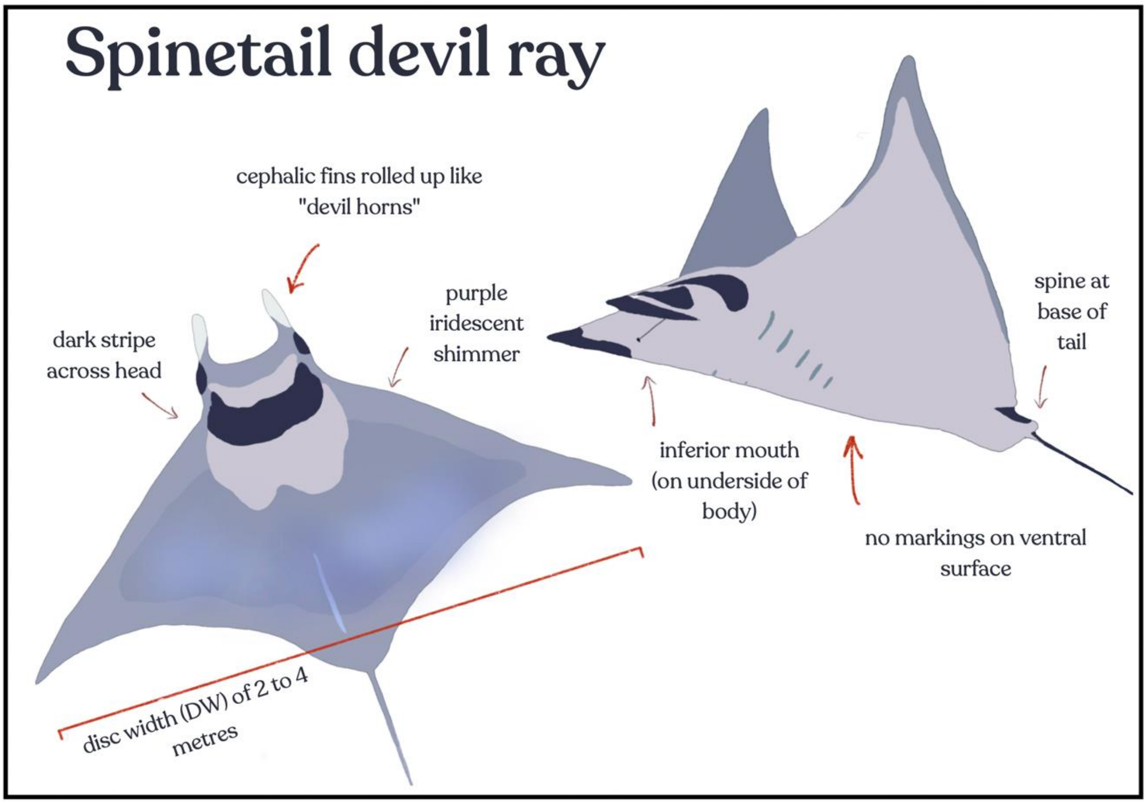

Figure 1.6 *Schematic illustration of the physical and visual characteristics of Spinetail devil rays (Mobula mobular).*

1.4.1.2 Distribution

Spinetail devil rays have a worldwide distribution in tropical and warm-temperate waters with sightings in the Atlantic, Pacific and Indian Ocean (Fig 1.7) (Last & Stevens, 1994; Lawson et al., 2017; White et al., 2006). However, most of the studies within the literature are focussed only a few locations: Mediterranean Sea (Bradaii and Capapé, 2001; Canese et al., 2011; Fortuna et al., 2014; Holcer et al., 2013; Notarbartolo di Sciara & Serena, 1988; Notarbartolo di Sciara et al., 2015; Scacco et al., 2009) and in the Eastern Pacific Ocean (Croll et al., 2012; Griffiths & Lezama-Ochoa, 2021; Lezama-Ochoa et al., 2019a; Lezama-Ochoa et al., 2019b; Lezama-Ochoa et al., 2020a; Lezama-Ochoa et al., 2020b; Notarbartolo di Sciara, 1988), and based on a literature review by Lawson et al. (2017) found that there were 2.5 times less publications with the name “devil ray” compared to “manta”.

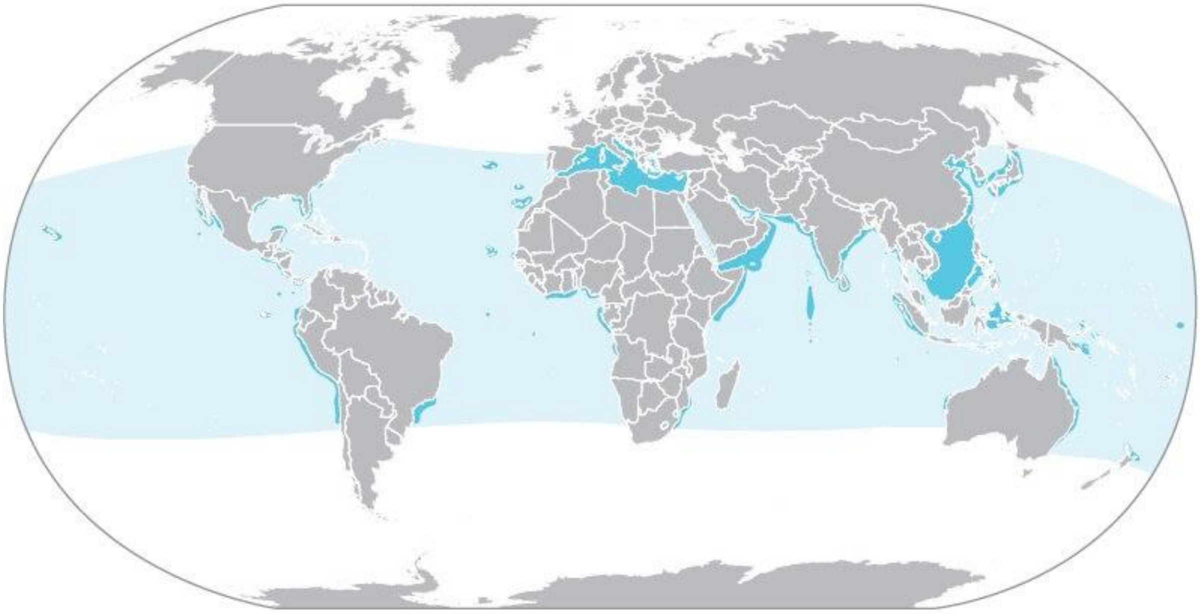

Figure 1.7 *Global distribution of Spinetail devil ray (Mobula mobular). Darker blue areas indicating confirmed range while lighter areas indicate expected range. Source: Manta Trust.*

Although migration routes of Spinetail devil rays have not yet been identified, it is hypothesised that individuals take part in seasonal latitudinal migrations to exploit productive waters towards the temperate areas in summer, and warmer waters towards the equator in winter (Notarbartolo di Sciara et al., 2015). For example, two satellite tagged individuals in Aotearoa New Zealand migrated 1400-1800km northward to tropical waters around Vanuatu and Fiji near the end of summer (Francis & Jones, 2016).

There have been recorded sightings of Spinetail devil rays in Aotearoa New Zealand since the late 1950s (first known as manta rays and later identified as Spinetail devil ray) (Muller & Henle, 1841). In Aotearoa New Zealand, the distribution of Spinetail devil rays is known to be spatially and temporally localised. Observations are mainly restricted to the northern Te Ika-a-Māui North Island along the eastern shelf edge between Aotea Great Barrier Island and Rākaumangamanga Cape Brett and temporally constrained between January and March (Francis & Jones, 2016).

Studies on Spinetail devil rays in Aotearoa New Zealand have been intimately linked to fisheries, namely the skipjack tuna (*Katsuwonus pelamis*) purse seine fisheries, which is operational since the mid 1970s, especially around January to March (West, 1975; Kendrick, 2006; Langley, 2011). Therefore, the lack of thorough investigation on their distribution across the whole country has resulted in apparent gaps in their occurrence and may be true absences or a manifestation of detection bias (Francis & Jones, 2016). However, Francis and Lyon (2012) point out that their distribution should not be an artefact of the effort or distribution of purse seine operations as the latter is operational over a wider geographic extent, namely around the northern Te Ika-a-Māui North Island (east and west coast), Te Moana a Toi-te-Huatahi Bay of Plenty and North Taranaki Bight, whereas the observations of Spinetail devi rays are more locally constrained in the NE shelf of the Te Ika-a-Māui North Island (Jones & Francis, 2012). Spinetail devil rays breed within Aotearoa New Zealand waters with the occurrence of late-term pregnant females, mating behaviour and near-term embryos off the eastern coast of the northern Te Ika-a-Māui North Island (Duffy & Tindale, 2018; Paulin et al., 1982; Stewart, 2002).

1.4.1.3 Habitat use

Spinetail devil rays occupy pelagic habitats with a preference for warmer waters between 18 and 29 °C (Canese et al., 2011; Francis & Jones, 2016). As a filter feeder, Spinetail devil rays strain and trap food from the water column with specialised gill plates and in the Mediterranean, have a highly specialised diet of macro-zooplankton, specifically euphasiids (also known as krill) (*Meganyctuphanes norvegica*) (Abudaya et al., 2018; Canese et al., 2011; Fortuna et al., 2014; Francis & Jones, 2016; Holcer et al., 2013), in the Philippines they feed on a different species of euphasiid (*Pseudeuphausia latifrons*) and in the Gulf of California, a different euphasiid species called *Nyctiphanes simplex* (Sampson et al., 2010), suggesting subtle geographical foraging differences. Spinetail devil rays have also been observed consuming small mesopelagic and clupeid fishes (Celona, 2004; Thorrold et al., 2014). Their highly specialised diet is assumed to explain their well-documented ability to dive deep to forage and exploit significant mesopelagic fish and euphasiid populations concentrated in deep scattering layers up to 1000m deep (Sardou et al., 1996; Sutton et al., 2008). Spinetail devil rays undergo diel vertical migration, making deep dives during the day and spending more time at the surface during night. This behaviour is most likely to follow the movement of their main prey, euphausiids, who exhibit diel vertical migration behaviour in response to changing light intensity and to avoid visual predators (Canese et al., 2011; Francis & Jones, 2016; Shirlamaine et al., 2018). However, time spent deeper than 200m during dives is low and most time is spent in the upper 50m, especially at the surface, possibly linked to physiological constraints and thermoregulation (Alexander, 1996; Andrzejaczek et al., 2022).

Locations which Spinetail devil rays are known to frequent are synonymous with upwelling zones such as the Angolan upwelling system and coast of Ghana (Lezama-Ochoa et al., 2020a), Gulf of California (Croll et al., 2012; Notarbartolo di Sciara, 1988; Sampson et al., 2010), northern Peru and area close to the Costa Rica Dome (Lezama-Ochoa et al., 2019a). This is further corroborated by modelling results by Lezama-Ochoa et al. (2019b) that identified chlorophyll (Chl-a) (proxy of phytoplankton abundance) and sea surface height (proxy of upwelling), as the most important variables for variation in the seasonal distribution of Spinetail devil rays. The prevalence of these variables makes sense as for all filter feeding vertebrates (Croll et al., 2012).

In Aotearoa New Zealand, Spinetail devil rays occur in SST ranging from 18 to 22 °C and their preferred diet is still unknown (Francis & Jones, 2016). Results from a satellite tagging study showed that tagged Spinetail devil rays reached depths of 1112m and the occurrence of Spinetail devil rays peaked at a bathymetric range of 300 to 350m (Francis & Jones, 2016).

1.4.2 Oceanic manta ray (*Mobula birostris*)

1.4.2.1 Taxonomic description

Oceanic manta rays (*Mobula birostris*) (Walbaum, 1792), are one of the largest known elasmobranchs globally. They are known to be one of the last additions to the chondrichthyan family (including all sharks, rays, and skates), with their first recorded appearance in the fossil record only five million years ago (Bourdon, 1999) and regarded as one of the most evolved and highly derived of all living elasmobranchs (Compagno, 1999). Oceanic manta rays have a circumtropical distribution with their range extending from tropical waters to semi-temperate waters of the Atlantic, Pacific and Indian Oceans (Fig 1.8) (Bigelow and Schroeder, 1953; 2009; Ebert, 2003; Gordon & Vierus, 2022; Last and Stevens, 1994; Marshall et al., 2009).

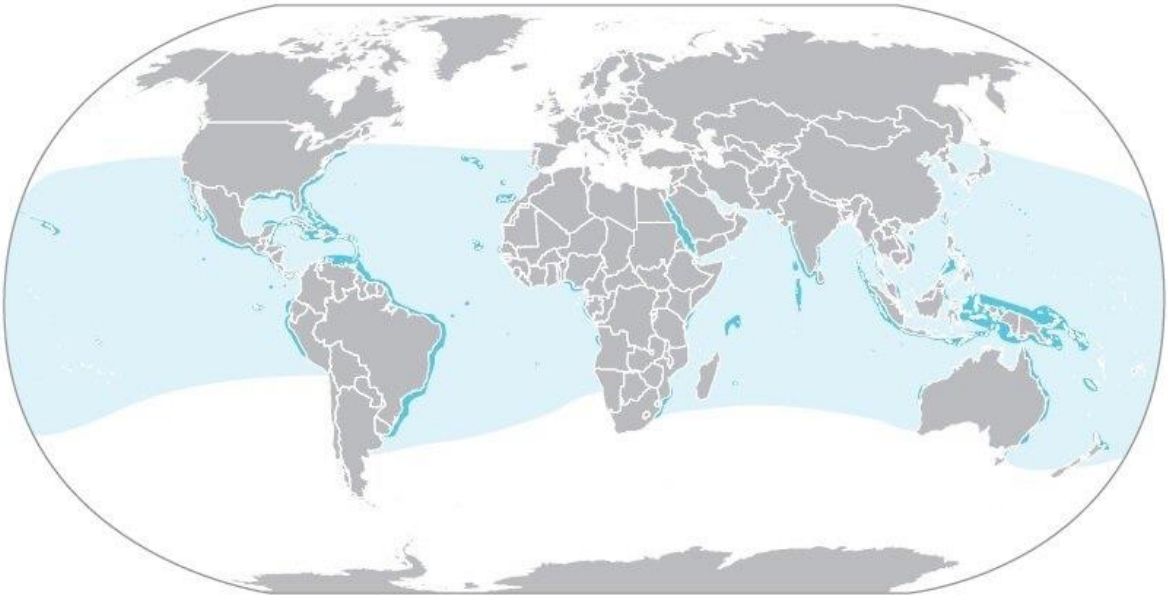

Figure 1.8 *Global distribution of Oceanic manta ray (Mobula birostris). Darker blue areas indicating confirmed range while lighter areas indicate expected range. Source: Manta Trust.*

Observations in Aotearoa New Zealand waters are restricted to the larger, migratory, and more pelagic *Manta* spp. species, Oceanic manta rays (*Manta birostris*) (Fig 1.9; Compagno, 1999; White et al., 2006; Marshall et al., 2009). Oceanic manta rays have a disc width exceeding 7.1m (Last & Stevens, 2009) with some anecdotal reports of up to 9.1m (Compagno, 1999) and weigh more than 1360kg (Bigelow & Schroeder, 1953). Compared to their close relative stingrays, they have a terminal mouth and a broad head (Bigelow & Schroeder, 1953), paddle-like lobes that extend in front of their mouth called “cephalic lobes”, that unravel when individuals are feeding with their mouth open wide (Fig 1.9) (Girondot et al., 2015; Sanderson & Wassersug, 1990). Like all planktivorous elasmobranchs, they have gill plates that are adapted to filter plankton out of the water column (Bigelow & Schroeder, 1953) where cephalic lobes guide water into their mouth and prey gets sieved out before water exists through gill slits (Coles, 1916; Paige-Tran et al., 2011). The black diamond-shaped dorsal surface has white shoulder patches and distinctive patterns on the dorsal surface however, spot patterns on the ventral side have been used to identify individual manta rays (Kitchen-Wheeler, 2010). These patterns are unique to each manta and change little over a period of 20 years allowing researchers to distinguish between individuals and easily track population dynamics (Ishihara & Homma, 1995; White et al., 2006) (Homma, 1999; Kitchen-Wheeler, 2010; Yano et al., 1999). Further, observations of a black morph or melanistic form of the species have been made worldwide (Barton, 1948; Homma, 1999;; Ebert, 2003) where the dorsal surface of the individual is completely black with no white colouration and the ventral surface is largely white.

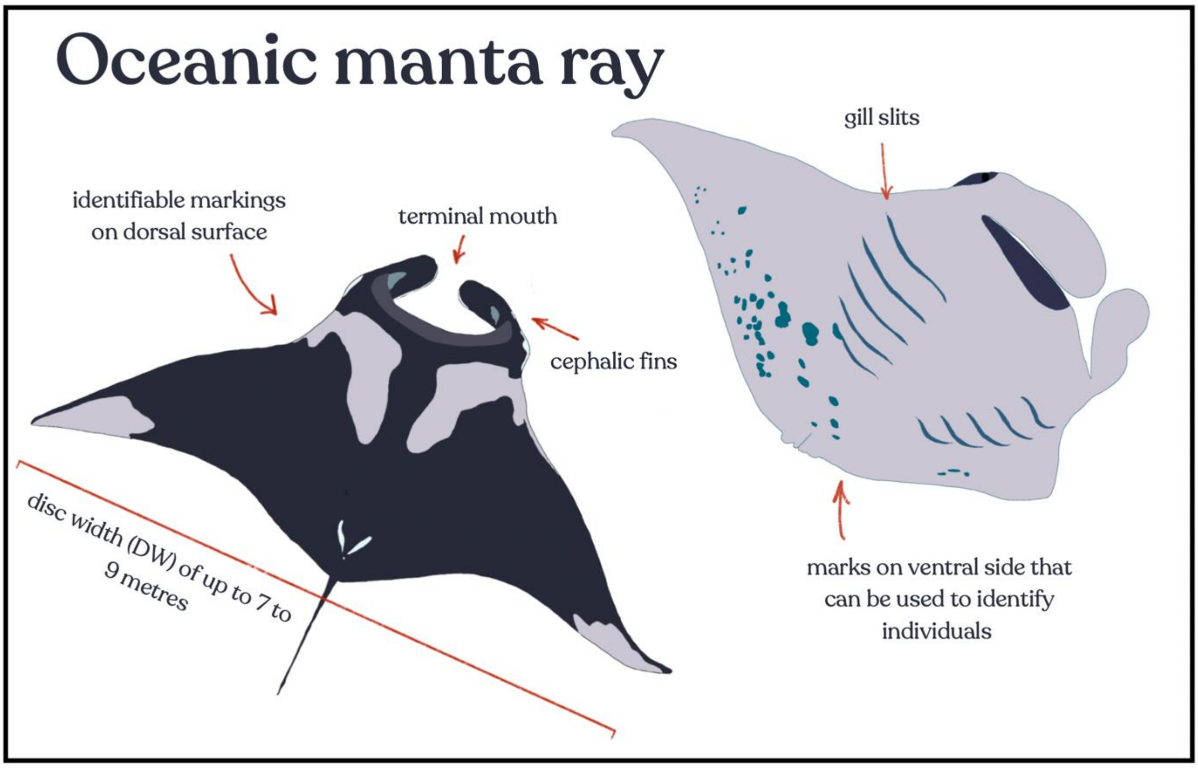

Figure 1.9 *Schematic illustration of the physical and visual characteristics of Oceanic manta rays (Mobula birostris).*

1.4.2.2 Distribution

Oceanic manta rays are often sighted around offshore islands, oceanic seamounts, and submarine ridge systems (Homma, 1999; 1999; Kashiwagi et al., 2011; Kitchen-Wheeler, 2010; Marshall et al., 2009; Yano et al., 1999). Rare and seasonal sightings of Oceanic manta rays in southern Brazil (Luiz et al., 2009), the Azores and Similan Islands (Couturier et al., 2012), Gulf of Mexico (Graham et al., 2012), Komodo National Park in Indonesia (Dewar et al., 2008), Venezuela (Notarbartolo di Sciara &

Hillyer, 1989), Yucatan Peninsula (Hacohen-Domené et al., 2017), eastern Australia (Couturier et al., 2011) and northern Aotearoa New Zealand (Duffy & Abbott, 2003) suggest that this species may be highly migratory, with evidence of migrations of more than 1400km recorded (Dewar et al., 2008; Hearn et al., 2014; Homma, 1997; Marshall et al., 2010). However, recent studies have demonstrated that although they are capable of long-distance migration, Oceanic manta rays remain in restricted geographic locations and show high site fidelity worldwide (Graham et al., 2012; Hearn et al., 2014; Homma et al., 1997; Stewart et al., 2016a). Further, stable isotope and genetic data show that long-distance migration is rare and does not generate substantial gene flow or interpopulation interaction, demonstrating that Oceanic manta rays may form unique and distinct sub-populations in areas they occur, with movements only describing areas from coastal aggregation sites to offshore habitats (i.e., shorter distance migrations) (Stewart et al., 2016a).

In Aotearoa New Zealand, seasonal sightings of Oceanic manta rays in summer (December to April) have been made around the NE shelf of the Te Ika-a-Māui North Island around Tawhiti Rahi Poor Knight’s Islands, outer Tīkapa Moana Hauraki Gulf, and the Ruamaahu Alderman Islands (Duffy & Abbott, 2003). The temporal window within which Oceanic manta rays are observed suggest that they migrate to Aotearoa New Zealand waters in summer and move further north toward tropical waters during winter (Duffy & Abbott, 2003). Whether they are a resident population is unknown however, observations of heavily pregnant individuals, courting behaviour and a resighting of an individual (Lydia Green pers comm.) indicate that breeding may occur in Aotearoa New Zealand waters making it a location of site fidelity.

1.4.2.3 Habitat use

Oceanic manta rays are frequent in warmer waters around 20 to 26 °C (Burgess, 2017; Clark, 2010; Dewar et al., 2008; Marshall et al., 2011) with a high correlation of aggregation sites with high productivity, along coastlines, island groups, offshore pinnacles, and seamounts with regular upwelling (forcing of deep, cold, nutrient-dense waters towards the surface) (Dewar et al., 2008; Luiz et al., 2009; Marshall et al., 2009).

Oceanic manta rays show a sophisticated ability to select favourable habitats in terms of their physiology (e.g., temperature) and energetics (e.g., prey density) shown through habitat site fidelity and seasonal aggregations (Dewar et al., 2008; Luiz et al., 2009; Marshall et al., 2009). As filter feeders, due to the energetic cost of feeding, foraging is likely observed only where prey density is above a certain threshold and a strong argument for why this species forms relatively predictable aggregations in these high productivity zones (Sims & Quayle, 1998; Sims, 1999; Etnoyer et al., 2006; Dewar et al., 2008; Marshall et al., 2009; Papastamatiou et al., 2012). Oceanic manta rays' stomachs can hold up to 631,167 kilocalories (kcal) (Rohner et al., 2017), thus, given that capacity it is likely that their target zooplankton blooms comprised of euphasiids, myctophid fishes, Sakura shrimp (*Sergestes lucens*) that occur in swarms and blooms in high densities to obtain high energy net gain relative to time spent foraging (Bigelow & Schroeder, 1953; Homma, 1999; Wilson et al., 2002; Rohner et al., 2017). This sophistication also links to their high degree of behavioural plasticity as they can change the depths, they access in relation to zooplankton density as well as feeding mode (Blackburn et al., 1970; Stewart et al., 2016b). Recent molecular evidence demonstrates a large reliance on demersal or mesopelagic zooplankton food sources, similar to that of other mobulid rays, particularly Spinetail devil rays (Borrell et al., 2011; Burgess, 2017).

Zooplankton abundance has strong negative correlation with temperature (Wilson et al., 2003) thus, temperature is considered an indirect driver of planktivorous elasmobranch aggregative behaviour (Rohner et al., 2013; Wilson et al., 2001). However, as Oceanic manta rays are ectotherms whose physiology is dependent on optimal temperature ranges, it is also considered a direct driver of distribution (Wilson et al., 2003). This is evidenced by the strong seasonal patterns in occurrence and subsequent aggregative behaviour (Anderson et al., 2011; Graham et al., 2012; Hacohen-Domené et al., 2017).

Oceanic manta rays tend to aggregate near cleaning habitats, often called 'cleaning stations', characterised by shallow coral or rocky reefs that have high abundance of cleaner fish (Youngbluth, 1968; O'Shea et al., 2010; Marshall et al., 2011; Jaine et al., 2012). Due to their dorso-ventrally compressed body, this species has a high surface area to volume ratio (Gray, 1953) making them vulnerable to parasitic load (Grutter,

1995) which can impact their fitness. This aggregative behaviour which is more observed and studied in Reef manta rays potentially due to these habitats being easier to access however, cleaner-client interactions have been observed in Oceanic manta rays as well (Burgess, 2017). Nonetheless, prevalence of cleaning stations remains an understudied potential driver of aggregative behaviour and distribution in Oceanic manta rays.

In Aotearoa New Zealand, habitat-use and selection of Oceanic manta rays remains elusive however, their sightings appear to coincide with the EAUC (Duffy & Abbott, 2003). Researchers part of a citizen-science conservation project, Manta Watch New Zealand, observe most sightings occur at a falling tide, with SST between 18 and 24 °C and where dense patches of euphausiids occur in the Tīkapa Moana Hauraki Gulf (Lydia Green pers comm.).

1.5 CONSERVATION AND MANAGEMENT

Globally, Oceanic manta rays and Spinetail devil rays (collectively and hereafter, mobulids) populations are in decline (Dewar et al., 2008; Marshall et al., 2011). Both species have been listed by the International Union for Conservation of Nature (IUCN) Red List with a status of "Endangered" for both indicating population decline and a high risk of extinction in the wild (Marshall et al., 2022a; Marshall et al., 2022b) which has been evidenced in aggregation sites in Mozambique (Rohner et al., 2013), the Philippines, Indonesia and Mexico (Marshall et al., 2011). Although the existence of mobulids have been known since at least the 17th century (Willughby, 1686) and likely earlier due to the cultural significance of rays in indigenous communities (Campbell et al., 2022; McDavitt, 2005), there is a lack of baseline knowledge on their basic ecology and biology, restricting the efficacy of conservation and management efforts (Alava et al., 2002; Dewar et al., 2002; White et al., 2006; Couturier et al., 2012).

The affinity of mobulids to occur in productive habitats in epipelagic zones means that their distribution often overlaps with commercial species such as skipjack tuna (Croll et al., 2012; Croll et al., 2016). Due to this overlap, mobulids (specifically

Spinetail devil rays) are often caught as bycatch in the Mediterranean Sea, eastern Atlantic Ocean, central western Pacific Ocean, western Indian Ocean and northern Aotearoa New Zealand, especially in tuna purse-seine fisheries (Celona, 2004; Croll et al., 2016; Paulin et al., 1982; Scacco et al., 2009). Purse-seine nets are trapezoid shaped large nets with a steel cable at the bottom of the net to keep it vertical in the water column. When a dense school is present within the confines of the net, the cable is pulled tight to close the bottom of the net and prevent fish from escaping and incidentally, mobulids are trapped within these nets as well.

Further, there is a growing international market for their gill plates which are cartilaginous, thin filaments that mobulids use to sieve zooplankton out of the water column, commonly traded as Peng Yu Sai (translated as “Fish Gill of Mobulid Ray”) (Fig 1.10; Lawson et al., 2017; White et al., 2006), especially popular in Asia (Dewar, 2002; Rubin, 2002; White et al., 2006; Rajapackiam et al., 2007; Mohanraj et al., 2009). The gill plates are used in Chinese medicines and tonics that are believed to boost the immune system to prevent sickness and increase blood circulation despite practitioners providing no evidence of this (O’Malley et al., 2016). The rise in popularity despite many of these health benefits being disproved, is presumed to be the responsibility of industry marketing (Whitcraft et al., 2014). A single mature mobulid can yield up to 7kg of gill plates, worth up to $680 per kilogram in Chinese markets (Heinrichs et al., 2011).

Figure 1.10 *Photograph of mobulid gill plates (left); photograph of an entangled Oceanic manta ray (right, top and bottom). Source: Manta Trust.*

Mobulids are also recorded to be incidentally caught in shark-control nets off Australian and South African coasts (Paterson, 1990; Dudley & Cliff, 1993; Dudley et al., 1999; Young, 2001; Sumpton et al., 2011); entangled in fishing lines (Fig 1.10; Marshall & Bennett, 2010; Deakos et al., 2011); ingesting plastic debris and microplastics (Boerger et al., 2010; Germanov et al., 2018).

Both species are known to have slow (also known as K-selected) life histories that are characterised by low fecundity, late age of maturity and slow growth rates, a commonality between all elasmobranch life histories where investment is put into juvenile survival and growth (Frisk et al., 2001), rather than fecundity (Cortés, 2002; Dulvy et al., 2014; Croll et al., 2015). However, compared to other elasmobranchs, mobulids have extremely low fecundity or reproductive output (Dulvy et al., 2014), only birthing one pup (very rarely two) (Hoenig, 1990; Stevens et al., 2000) with intervals between each birth being estimated at 1-3 years (Compagno & Last, 1999; Homma et al., 1999; Marshall & Bennett, 2010; Notarbartolo di Sciara, 1988). Each pup is relatively large at birth, around 27-49% of maternal size (Marshall et al., 2009; Notarbartolo di Sciara, 1988; White et al., 2006) with maximum population increase also limited by the presumed late age at maturation, the age at which individuals will start to reproduce (Croll et al., 2015). Although there are no direct measurements of lifespan, gestation period or age at maturation (Croll et al., 2015), mobulids are presumed to be long-lived (up to 40 years for Oceanic manta rays) and gestation period is estimated to be just over a year (Ward-Paige et al., 2013). This makes them especially vulnerable to overexploitation and the high landing rates of mobulids in fisheries and expanding gill plate market raise serious concerns and a high risk of destabilising populations worldwide (Croll et al., 2015). A study by Dulvey et al. (2014) uncovered that the low productivity of Oceanic manta rays means that even a moderate level of fishing mortality would lead to a serial depletion of individuals in a short amount of time which solidifies the argument for the need of urgent, effective conservation management responses globally.

In Aotearoa New Zealand, Oceanic manta rays and Spinetail devil rays are protected under Schedule 7A of the Wildlife Act (1953) since July 2011. This means that they receive absolute protection such that unless granted permission, no one may kill or have in possession such animal (Francis & Lyon, 2012). Under the New Zealand Threat Classification (NZTCS) by the Department of Conservation (DoC), Oceanic manta rays and Spinetail devil rays are classified as data-deficient (Duffy et al., 2018) indicating that there is a lack of current information on their abundance and distribution.

A known threat to mobulid populations in Aotearoa New Zealand waters is the domestic skipjack tuna purse-seine fisheries operational since the 1970s, as mobulids are reportedly caught as bycatch (Francis & Lyon, 2012). Observational accounts from purse-seine fleets estimate 40-50% of skipjack tuna schools have mobulid rays within them with some commenting that this association being more frequent in Aotearoa New Zealand than anywhere else (Francis & Lyon, 2012). Furthermore, the frequency of mobulid occurrence as bycatch in the NE shelf of the Te Ika-a-Māui North Island based on observer records are estimated to be as high as 23% of purse-seine sets (Francis & Lyon, 2012). Most if not all mobulid rays that are caught in commercial fisheries are likely to be Spinetail devil rays (Paulin et al., 1982) as no Oceanic manta ray have been confirmed to have been caught in Aotearoa New Zealand waters (Jones & Francis, 2012). However, correct identification of mobulids have been of great debate due to the morphological similarities and unavailability of suitable field identification guides on purse-seine fleets thus, it is possible that some individuals caught are Oceanic manta rays (Francis & Lyon, 2012). For Oceanic manta rays, entanglement and ship strikes seem to be a more significant source of mortality with many individuals seen with fishing line scars and one record of an individual dying from a presumed ship strike (Lydia Green pers comm.).

The lack of abundance and distributional information in Aotearoa New Zealand prevents the assessment of their current conservation status however, based on population declines reported globally (Couturier et al., 2012; Homma et al., 1997; Marshall et al., 2006; White et al., 2015), it is probable that populations in Aotearoa New Zealand may be facing the same serial depletions.

Currently, there are no systematic international or national management plans in place to ensure future of mobulid populations (Canese et al., 2011; Graham et al., 2012; Holcer et al., 2013; Ward-Paige et al., 2013) and due to their migratory nature and potential to move out of domestically protected waters (Bonfil et al., 2005), international cooperation is likely to be necessary. Further, a recent publication, the Global Devil and Manta Ray Conservation Strategy, outlines goals, aims, objectives and actions to guide governmental agencies, scientists and conservationists and addresses the apparent “charisma-gap” that exists in that devil rays are significantly lesser known than manta rays, creating a barrier for equal conservation (Lawson et al., 2017). This gap can be clearly seen in the number of peer-reviewed publications for both species: both species are understudied however, the gap between Oceanic manta rays and Spinetail devil rays is evident and seems to be increasing (Fig 1.11). The need for coordinated action and the closing of the charisma-gap is required for successful management and conservation of mobulids for generations to come.

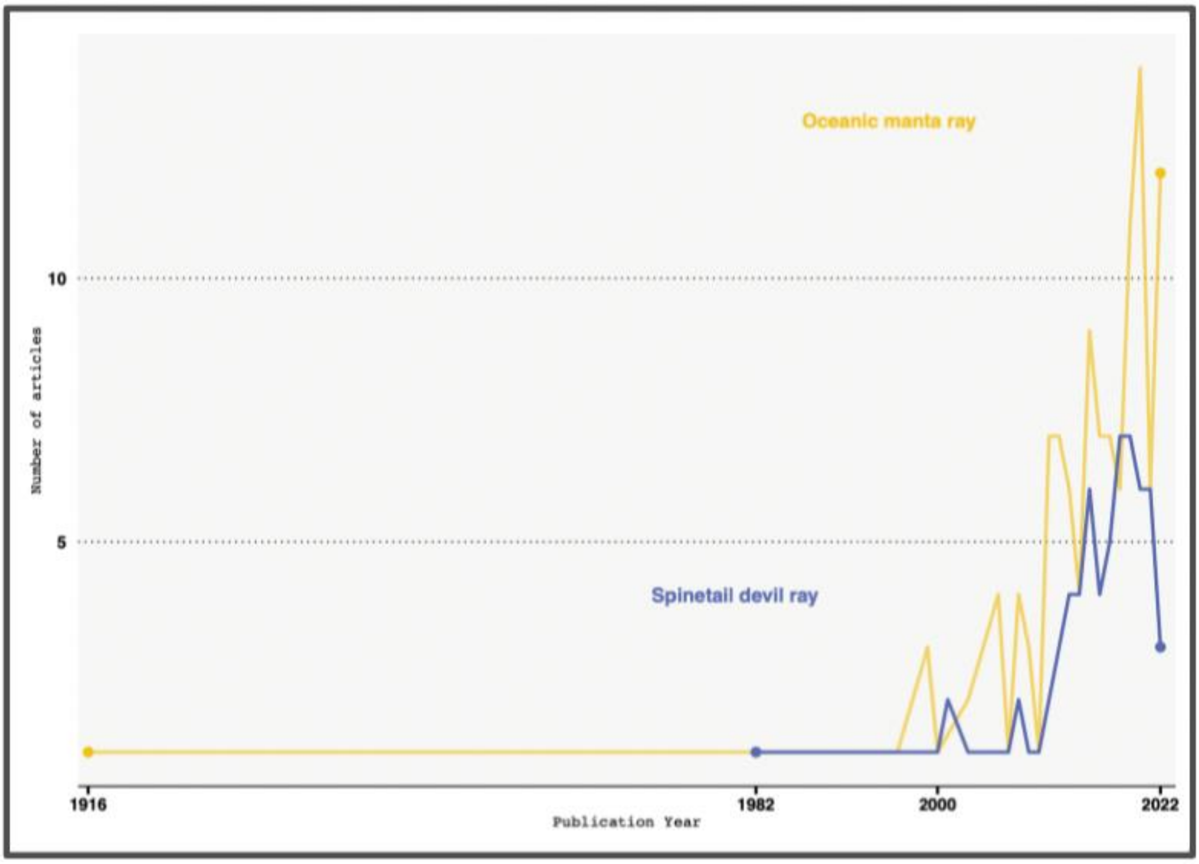

Figure 1.11 *Number of peer-reviewed publications for Spinetail devil rays (blue) and Oceanic manta rays (yellow) on the Web of Science. Spinetail devil ray publications showing results for "mobula mobular", "spinetail devil ray", "mobula japonica", "giant devil ray". Oceanic manta ray publications showing results for "mobula birostris", "manta birostris", "oceanic manta ray", "giant manta ray".*

1.6 SPECIES DISTRIBUTION MODELLING

1.6.1 Introduction

For centuries, people have noted the relationships between species distributions and the physical environment with early scientific writings focussed around qualitative and observational accounts (e.g., Grinnell, 1904). Indigenous peoples have been observing these relationships and learning which activities such as hunting, fishing, and gathering should take place at given times and locations (Chisholm-Hatfield et al., 2018). The relationship between the environment and organisms is not a new concept however, until recently, only qualitative methods were employed to describe these patterns. The study of SDMs is a growing field, owing to the recognised importance of understanding the habitat requirements and ecological and geographic distribution of species for conservation planning and forecasting and understanding evolutionary determinants of spatial patterns that manifest (Brown & Lomolino, 1998; Ferrier, 2002; Funk & Richardson, 2002; Graham et al., 2006; Ricklefs, 2004; Rosenzweig, 1995; Rushton et al., 2004). SDMs are a tool that allows researchers to ask diverse questions in ecology, evolution, and conservation despite the often-sparse availability of occurrence datasets for most species (Elith et al., 2006). Although there are two types of models (mechanistic and correlative), mechanistic models require detailed information on the physiological limits for a well- understood species to environmental factors (Pearson, 2010). Due to the limited knowledge on mobulids, a correlative approach to distribution modelling is the focus of this thesis.

Correlative models utilise associations between known species' occurrence records and environmental factors to identify areas where the suite of environmental variables deemed to affect the species' physiology and probability of occurrence is favourable or not (Pearson, 2010). Known records provide useful information of the environmental requirements of the species and the suitability of conditions between each occurrence point can be predicted to fill the gaps or can be predicted to new regions (i.e., invasive species' potential range expansion, e.g., Peterson, 2003) or a new time period (i.e., predict potential impact of climate change on species' distribution) (Pearson, 2010). Thus, instead of a species' actual distribution being predicted, the distribution of environmentally suitable areas is being modelled to understand where a species' is likely be (Pearson, 2010). The applicability of these models cannot be overstated as information on species distributions is used for nearly every conservation decision to conserve a rare species, manage biodiversity, identify biodiversity hotspots, and anticipate potential invasions at the governmental and policy-making level (Franklin, 2010; Sofaer et al., 2019).

1.6.2 History of SDMs

Traditional indigenous knowledge bases activities and movements around the relationship between environmental and/or geographical gradients and the distribution of species of cultural, economic, and ecological importance (Berkes, 1993). However, the first quantification of these relationships occurred during the

20th century, with a large focus on the shape of species-habitat associations using techniques such as simple geographic envelopes, convex hulls, and environmental matching (e.g., Nix, 1986, Austin, 1987), especially as computing capacity was largely limited (Zimmerman et al., 2010).

Quantitative methods as we know them today emerged in the early 2000s from the convergence of field-based studies with new regression methods and geospatial environmental layers (Elith & Leathwick, 2009; Turner et al., 2003). New technology to measure and model environmental properties with high temporal resolution stands in stark contrast to tools available to early researchers where environmental conditions (e.g., depth, slope, latitude, and longitude) were all measured as a one-time measurement on site (Elith & Leathwick, 2009). Generalised Linear Models (GLM) were one of the earliest SDM algorithms and were used to deal with presence-absence data assuming a linear dependency between species' data and environmental variables (Guisan et al., 2002; Hastie & Tibshirani, 1990). However, the acknowledgement of nonlinear species' responses to the environment necessitated alternative algorithms. Generalised Additive Models (GAM) are an extension on GLMs where smooth functions are used to fit non-linear responses, making it a more flexible option compared to GLMs and suitable when modelling ecological relationships albeit, interactions between environmental variables are not easily incorporated (Elith & Leathwick, 2009).

Although statistical methods such as GLMs and GAMs have proven useful in ecology and are still used today, the shift from using SDMs to understand species-habitat associations to predictions of suitable habitats has given rise to alternative methods, in particular, machine learning algorithms (Drake et al., 2006; Elith et al., 2008; Phillips et al., 2006). In particular, tree-based classification and regression models (CARTs) have been gaining popularity in ecology due to the model's ability to deal with complex, unbalanced data with non-linear relationships and higher-order interactions between variables (De'ath & Fabricus, 2000). Nonetheless, large variations exist between different models based on how distributional response is modelled, how the model is fitted, how selection process of important predictor variables works, if the model allows interactions and predicts patterns of distribution spatially. With the recognition that one model is not superior over the other (Hao et al., 2020; Melo-Merino et al., 2020), it is important to understand study context and objectives to select the appropriate model.

At present, due to well-tested algorithms, increasing availability of occurrence and environmental data and the continuous advancement of computational resources that allow effective model fitting and visualisation, SDMs are considered important tools in conservation biology (Thuiller et al., 2009; Guisan et al., 2013; Sofaer et al., 2019). In settings where an appropriate model is used with reliable data, SDMs can provide useful ecological insight especially for species that are ill-understood.

1.6.3 Applications in terrestrial and marine contexts

Early SDMs focussed largely on terrestrial applications, especially on vascular plants followed by studies of terrestrial animals (Elith & Leathwick, 2009; Robinson et al., 2011). The main differences in modelling approaches were based on the animal's mobility with the environment of sessile species being relatively easier to characterise compared to mobile species that utilise the uneven distribution of resources in space and time (Elith & Leathwick, 2009; Leathwick et al., 2008). In comparison, until the past 10-15 years, marine and freshwater applications of SDMs were relatively rare (Robinson et al., 2011). This is mainly due to the predictive performance and model assumptions being affected by the unique biological and physical properties of marine habitats and organisms (Robinson et al., 2011). Further, the three-dimensionality of marine habitats remains a challenge largely due to many of the environmental layers describing the surface of the ocean (Andrzejaczek et al., 2022; Bentlage et al., 2013; Dambach & Rödder, 2011), a critical limitation as pelagic species primarily inhabit middle layers of the water column. As a result, pelagic organisms' ecology and behaviour are still seldom understood (Bentlage et al., 2013). Models in the marine realm are also required to deal with highly temporally dynamic oceanographic features (e.g., fronts) and the animals that move in response, with static model's incapable of preserving these interactions (Scales et al., 2014). This issue is exacerbated as migratory and highly mobile animals make observation and survey logistically and financially challenging (Redfern et al., 2006; Scales et al., 2017).

Fish are the most common taxonomic group that are modelled, reflecting both the commercial value and abundance of data available and these models have been used to plan marine protected areas and designate critical fish habitats (Robinson et al., 2011). Marine mammals have received some attention in the SDM space especially due to their endangered status, habitat degradation and high fisheries by-catch mortality coupled with their charismatic nature (Panigada et al., 2008; Redfern et al., 2006; Robinson et al., 2011). SDMs have helped researchers inform habitat conservation (Bailey & Thompson, 2009; Embling et al., 2010); understand fisheries interactions (Torres et al., 2003; Howell et al., 2008; Howell et al., 2015), and assist in determining impacts of climate change (Freitas et al., 2008).

The application of SDMs on marine organisms that are endangered and elusive has important implications especially with climate change altering many oceanographic and climatic conditions, influencing behaviour, and leading to alterations in ecosystem structures (Vergés et al., 2016). With temperatures increasing globally, studies have shown that large elasmobranchs have changed dispersion and residency patterns in response (Hill et al., 2016; Niella et al., 2020). Further understanding on how marine organisms adapt and move as seas warm is necessary to understand broader ecosystem impacts of climate change (Niella et al., 2022).

1.6.4 SDM for Spinetail devil rays

The literature on SDMs on Spinetail devil rays has been limited in terms of quantity and methodologies employed are consistent with most studies (Lezama-Ochoa et al., 2019a; Lezama-Ochoa et al., 2019b; Lezama-Ochoa et al., 2020a; Guirhem et al., 2021) employing a GAM, with the exception of one study which used MaxEnt (Putra et al., 2021), a presence-only model only requiring occurrence records and environmental variables (Phillips et al., 2006). Oceanic manta ray data largely consist of decadal sightings data and survey effort, Spinetail devil ray SDMs have a commonly use fisheries-dependent data (Guirhem et al., 2021; Lezama-Ochoa et al., 2019a; Lezama-Ochoa et al., 2019b; Lezama-Ochoa et al., 2020a; Lezama-Ochoa et al., 2020b; Putra et al., 2021). This highlights the clear overlap in distribution of fisheries operations with Spinetail devil ray distribution. Previous studies predicted high Chl-a concentration, presence of SST fronts and low sea surface height values akin to areas with high suitability (Lezama-Ochoa et al., 2019b, Lezama-Ochoa et al., 2020a; Guirhem et al., 2021; Putra et al., 2021). Similar to findings from Oceanic manta ray SDMs, these results indicate habitat preference for regions with upwelling systems, which are synonymous with high productivity.

Previous SDM studies suggest that Spinetail devil rays may inhabit waters that are further offshore (< 2000m), with high predicted suitability around the 200m isobath (Lezama-Ochoa et al., 2020a; Putra et al., 2022; Stevens et al., 2018). These findings hint at a potential trophic separation in preferred prey type or differing utilisation of bathymetric features (e.g., seamounts) (Lezama-Ochoa et al., 2020a; Stevens et al., 2018).

Despite evidence of seasonal migrations, there has been no study to date to investigate this in an SDM. Guirhem et al. (2012) explore interannual variability of presence using a GAM suggesting no annual trend of year effect in occurrences over the study period. However, data paucity issues continue to hamper the ability to model and understand how distributions may be changing over various spatial and temporal scales.

1.6.5 SDM for Oceanic manta rays

A commonality between previous SDM studies on Oceanic manta rays, is the prevalence of high concentrations of Chl-a in areas with predicted high suitability. Various methodologies (MaxEnt, Hacohen-Domené et al., 2017; GLM, Rohner et al., 2017; Ensemble (GLM, GAM, GBM, MaxEnt), Garzon et al., 2021; GAM, Farmer et al., 2022; MaxEnt, Putra et al., 2021), found this consistency, likely reflecting areas of high primary productivity and subsequent prey availability. These studies also predicted that suitability is highest in near-shore, shallow waters (< 50m) and along the continental shelf edge where strong thermal fronts are present (Farmer et al., 2022; Garzon et al., 2021; Hacohen-Domené et al., 2017; Putra et al., 2021; Rohner et al., 2017), unsurprising considering these habitats are often analogous with seasonal upwelling events that circulate colder, nutrient-rich waters to the surface and additional sources of nutrients from terrigenous sources (Carter et al., 2005), Due to the seasonality of upwelling events, these SDMs found that Oceanic manta rays' distributions also show seasonal patterns. On the east coast of the United States, in response to increases in SST during summer, there is a predicted range expansion to northern waters to exploit higher productivity in the colder waters (Farmer et al., 2022). By contrast, in the western Central Atlantic around the Caribbean and Mexico, the model predicted that during warmer months, there is a contraction of ranges and a subsequent expansion during winter months (Garzon et al., 2021). Although the response to warmer months varied between these two studies despite their proximity, both instances were linked to seasonal upwelling and subsequent fluctuations in productivity, highlighting the importance of productivity in determining Oceanic manta rays' distribution. It remains unclear how Oceanic manta ray distribution is changing over long-time scales and the investigation of these questions over finer spatial scales as most studies mentioned used a 4km spatial resolution (Hacohen-Domené et al., 2017; Garzon et al., 2021; Farmer et al., 2022).

Despite the high presumed importance of SST in directly and indirectly driving movement in large elasmobranchs (Wilson et al., 2001), previous SDM studies have found unclear relationships between habitat suitability and SST (Farmer et al., 2022; Rohner et al., 2013). For ectothermic elasmobranchs such as Oceanic manta rays, body temperature is directly dictated by environmental temperature. Physiological rates often scale with temperature, with performance increasing with temperature until a thermal optimum and then declining to lethal temperatures (Bernal et al., 2012; Neill & Stevens, 1974). Mobulid rays are known to bask at the surface for long periods of time presumably to recover and raise their body temperature following a deep dive into colder waters (Alexander, 2008). It is important to note that studies by Rohner et al. (2013) and Farmer et al. (2022) are based in the eastern coast of the North American continent, thus the reduced importance of SST despite high presumed relevance could be due to the lower variability in SST values closer to the equator. Further, the migratory nature of Oceanic manta rays are presumably movements between relatively warm waters to reduce the thermal range in which the animals move in to ensure energetics remain favourable. Thus, SDM studies that are restricted to a singular study site with intermittent occurrence of Oceanic manta rays during the year may find lower prevalence of SST due to the reduced ranges.

However, this ambiguous relationship could also be explained by the fact that the most productive areas in the marine context tends to be associated with colder water (Quillfeldt et al., 2015), with Chl-a and SST being inversely correlated (Nurdin et al., 2013). This inverse association exists because the ocean's waters are horizontally stratified and the underlying deep water is unable to be warmed through solar heating thus, is cooler than surface waters (Roels et al., 1979). When winds are sufficient and generate mixing, this results in upwelling, where cooler, nutrient-rich waters rise from the bottom (Nurdin et al., 2013). As a result, the surface layers are enriched with nutrient, and SST reduces, resulting in a complex balance between nutrients and SST, especially for ectotherms. Therefore, SST can indirectly drive elasmobranch distribution and could be producing an unclear signal in habitat suitability.

1.7 MODELLING METHOD

1.7.1 Decision Tree Model

Ecological data is complex, unbalanced and characterised with missing values and outliers that encompass the stochastic nature of the natural world. This makes it challenging for explanatory and statistical models to find meaningful patterns and predict to unsampled areas (De'ath & Fabricus, 2000). Further, these models are unable to incorporate relationships between variables that are non-linear and involve high-order interactions, which is a major limitation in an ecological context. A method that has been widely used in ecology to combat these limitations are tree-based models. Trees can explain the variation in a response variable in relation to multiple explanatory (or predictor) variables with response and explanatory variables varying from numeric (regression) or categorical (classification), which make them particularly advantageous (De'ath & Fabricus, 2000). The base mechanism of a tree stems from recursive binary splits defined by a simple rule based around an explanatory variable, with classification splits occurring based on categories and regression splits occurring based on values being greater than, less than or the same as a specific numeric range or given value of the explanatory variable. For example, if the simple rule was “sea surface temperature (SST) above or below 20°C”, observations will be split into two groups, one with observations of mobulids when the SST was below 20°C, and another group of observations for when SST was above 20°C (Fig 1.12).

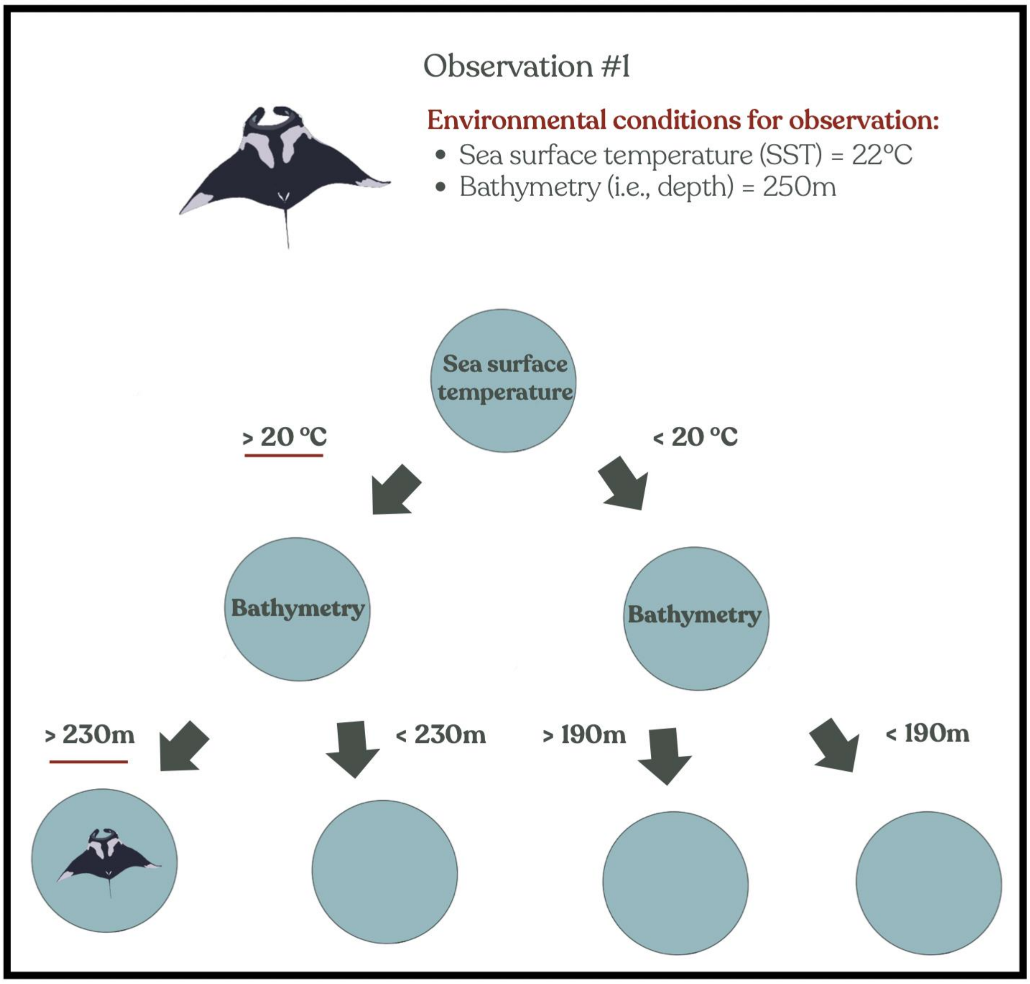

Figure 1.12 *Diagram illustrating an example of the mechanisms of a decision tree*

Decision trees can incorporate and model complex interactions in a simple manner and can handle missing values (De’ath, 2007; Friedman & Meulman, 2003). The hierarchical structure of a tree results in responses from one explanatory variable depending on responses higher up in the tree, so that interactions between multiple variables are included in the model automatically (Elith et al., 2008). This is an essential component of ecological modelling as the distribution of species is seldom driven by a single condition but an intricate mixture of various conditions.

Distribution and prediction are often dominated by few explanatory variables, and performance of many methods can degrade dramatically when large numbers of irrelevant variables are incorporated, impeding the predictive ability and application of the model (Friedman & Meulman, 2003). With trees, at each binary split only the variable that increases the homogeneity between the resultant groups is selected thus, the performance of the model is highly resistant to large numbers or extra irrelevant variables, removing the pressure of having to select the correct features. Therefore, trees are predictive tools that are easily interpreted and visualised in a two-dimensional graphical form (Friedman & Meulman, 2003).

Even so, small changes and adjustments in the data used to train the model can vastly change the series of splits, regarding the variable and the value at the split. Consequently, this results in a very different model, introducing uncertainty into the results, limiting interpretability, and reducing predictive performance (Elith et al., 2008; Hastie et al., 2001). Disadvantages associated with single decision tree models can be combated using multiple trees, for example, averaging across all trees (i.e., bagging) or sequentially adding trees to the residuals of the previous tree (i.e., boosting).

1.7.2 Boosted Regression Tree (BRT) Model

BRT uses boosting which is a sequential, stagewise procedure where a weak base learner is fitted with the data. At each iteration, a new tree is added sequentially on the residuals of the previous tree that best reduces the loss function – a measure that represents a loss in the predictive performance due to a flaw in the model (Elith et al., 2008; Hastie et al., 2001). The focus on the residuals (i.e., the variance not yet explained by the model) emphasises the observations that were poorly modelled or that were the hardest to predict and improves on the previous trees. Due to the stagewise nature of a BRT, trees are sequentially added to previous trees and existing trees are left unchanged, with the final model being a linear combination of many trees, reducing both bias and variance (Elith et al., 2008). For example, at the second step the tree is fitted with the residuals of the first tree. The second tree can contain different variables and values at the split nodes compared to the first and the model is updated to include two trees, residuals are calculated for the second tree, and so on (Fig 1.13).

Just as the simple decision tree model does, the split occurring at a point based on any given predictor variable is ultimately affected by any splits that occurred higher up in the tree, preserving any interactions between predictor variables, unlike methods such as GAM where an individual tree term is based on one predictor variable only where no interaction effects are considered (Leathwick et al., 2006). BRT is based on the principle that it is easier to find and average many weak learners than to find a single, highly accurate prediction rule (Schapire, 2003). Due to this forward and sequential procedure, BRT has high predictive performance and accuracy and is able to fit a wide variety of responses (e.g., Gaussian, Poisson, Binomial) (Elith et al., 2008).

In comparison, model-averaging methods (i.e., bagging) such that RF uses, constructs multiple independent trees using subsamples of the data with replacement, and the resultant model takes the average of all trees (Resinger et al., 2022). These models seek to find a single parsimonious model that best describes the relationship between the response and explanatory variables, where model results are an averaging of multiple iterations (Leathwick et al., 2006). Although model-averaging techniques reduces variance, models with smaller datasets and higher instability in predictions suffer from lack of interpretability of the results and increased bias (Iverson et al., 2004). For this reason and the ability for BRT models to deal with missing values, complex interactions especially on smaller datasets, BRT model was chosen for this thesis.

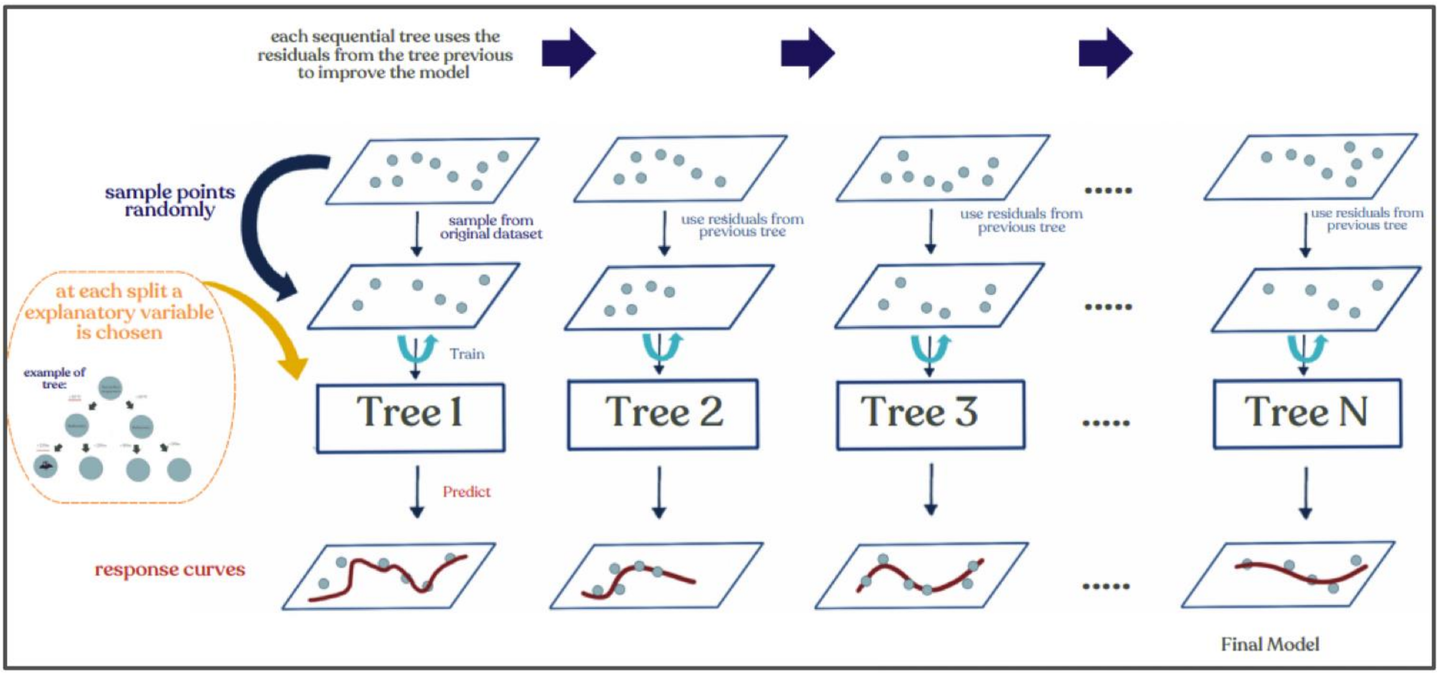

Figure 1.13 *Schematic diagram of the mechanisms behind the Boosted Regression Tree (BRT) model and the stagewise nature of the method.*

1.7.3 BRT model fitting

In BRT, trees are continuously added until eventually, all observations are fully explained by the model. However, this generally causes overfitting to the training data and a subsequent reduction in generality and limitation to applying the same model to unknown or unsampled areas (Friedman, 2001; Leathwick et al., 2006). This is particularly relevant for BRT models as trees can be continuously added sequentially until all variance in the training data is explained perfectly and the data is completely overfitted (Elith et al., 2008). Although the fitting of the model includes a pruning process whereby the number of trees is reduced at the end based on internal cross-validation (i.e., resampling method that tests model on withheld portion of data at each iteration) (Elith et al, 2008), there are additional steps that modellers can take.

To mitigate overfitting modellers can alter:

1. Learning rate

A value ranging from 0 to 1, and each iteration is scaled by this value, where smaller values (closer to zero) reduce the contribution of each tree added to the model, and larger values (closer to 1), increase the contribution (Elith et al., 2008). Learning rate is inversely proportional to another important model fitting parameter, the number of trees.

2. Number of trees

As the learning rate decreases and the relative weight of each tree decreases as a consequence, the number of trees increases. Elith et al. (2008) argues that a smaller learning rate and large number of trees are preferable. However, whether this is possible dependents on the time and computation resources available.

3. Tree complexity

The number of nodes in a tree and this directly impacts the number of trees required. For a given learning rate, if a highly complex tree is fitted, fewer trees are required to minimise the loss to the same extent (Elith et al., 2008). Therefore, if the number of trees were to stay static and tree complexity increases, the learning rate would have to decrease in response.

Thus, model fitting is the intricate balancing and assessments of trade-offs between learning rate, number of trees and tree complexity. A study by Elith et al. (2008) demonstrated that with small sample sizes with observations less than 250, the best model fitting metrics are to have simple trees (with tree complexity of 2 or 3) and a small enough learning rate to allow for at least 1000 trees to be fitted. This thesis will be using guidelines from Elith et al. (2008) in the model fitting process (see Chapter 2).

1.8 THESIS RATIONALE AND STRUCTURE

Observations of mobulid rays are largely restricted to the NE of the Te Ika-a-Māui North Island, characterised largely by the Tīkapa Moana Hauraki Gulf. However, mobulid rays within this region are exposed to a plethora of anthropogenic factors including ship strike and entanglement (Francis & Lyon, 2012) and bycatch (Duffy &

Abbott, 2003; Duffy et al., 2018; Francis & Jones, 2012; Francis & Lyon, 2012; Paulin et al., 1982). At present, the lack of understanding of their abundance and distribution within Aotearoa New Zealand waters is hampering the ability to effectively manage and protect populations (Duffy et al., 2018).

This research aims to use observational data collected from platforms of opportunity in conjunction with high-resolution environmental data to map the habitat suitability of Oceanic manta and Spinetail devil rays in the NE shelf of Aotearoa New Zealand and identify how this is changing over time. To address this aim, two models will be constructed: static model with long-term averages and a dynamic model that models habitat suitability on an annual timescale. Furthermore, two models are used to examine the difference in performance of a purely spatial model compared to a spatio-temporal model (Fig 1.14).

This thesis presents the first study of the distribution and habitat-use of Spinetail devil rays and Oceanic manta rays at a national scale in Aotearoa New Zealand. The overarching goal from these findings is to contribute information on habitat-use and distribution to conservation and management to ultimately decrease negative anthropogenic interactions.

Research Questions:

1. What environmental conditions do mobulids favour?
2. Where in the NE coast of the Te Ika-a-Māui North Island is the habitat suitability high and is there a hotspot?
3. How are the environmental conditions and areas of suitability different between Spinetail devil rays and Oceanic manta rays?
4. Does mobulid habitat suitability change over time?

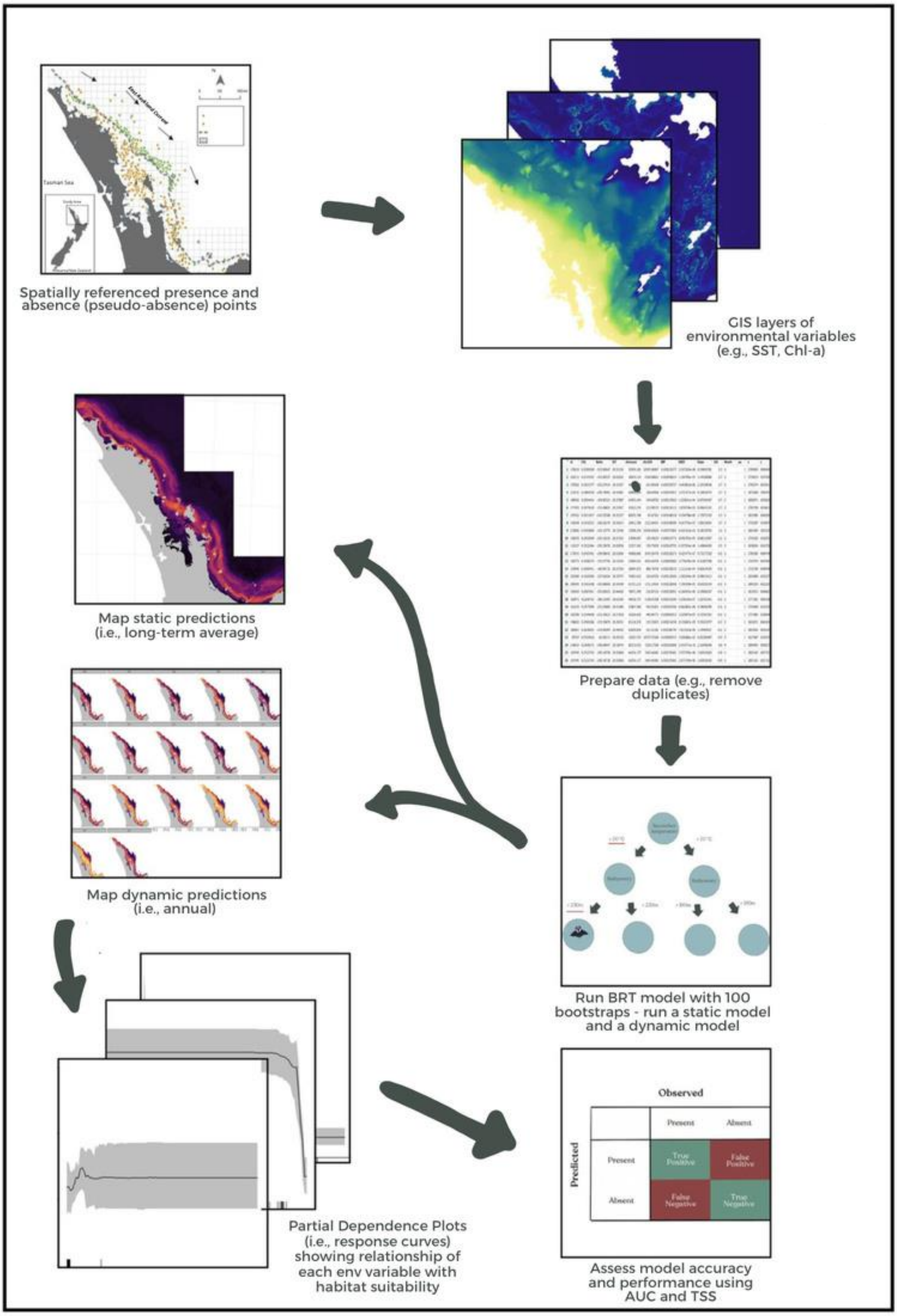

Figure 1.14 *Illustration of the modelling workflow used in this thesis.*

This thesis is comprised of three chapters as follows:

Chapter 1 (this chapter) contains background information on the study site and the introduction to the focal themes (i.e., distribution, habitat-use) comprised in this thesis. A global literature review on the habitat-use, distribution on Oceanic manta rays and Spinetail devi rays is followed by a national review of the same nature. Modelling methodology that will be used in this thesis is preliminarily introduced and discussed. The Chapter concludes with a review on current threats to both species and an overview on management and conservation strategies currently taking place.

Chapter 2 contains information on species records, environmental data and data processing protocols for all data sources. Model details including modelling fitting, the difference between the static and dynamic model and model evaluation metrics are explained in detail. Environmental variables important for the prediction for their distribution and maps illustrating the probability of occurrence are included. The Chapter concludes with a description of the results and a discussion of the results.

Chapter 3 concludes the thesis by summarising the findings from the two models for both species the limitations of this thesis are discussed. The significance of these findings are placed into the context of conservation and management in Aotearoa New Zealand and recommendations for future studies to build on this thesis are explored.

Chapter 2

Methods, Results and Discussion

Cover for chapter: *A survey trip with Manta Watch New Zealand in the Hauraki Gulf Marine Park (photo: Rika Ozaki)*

2.1 INTRODUCTION

Highly mobile marine animals are unevenly distributed in space and time (Hanski, 1999; Bucklin et al., 2010). The high mobility of these animals means that they can move between areas with highly favourable environmental conditions. However, the affinity for areas with high productivity result in interactions with fisheries and other human activities (Croll et al., 2012; Croll et al., 2015; McCauley et al., 2014) . Further, the high mobility creates challenges for conservation efforts particularly where distributions are not well understood.

Species distribution models (SDMs) are statistical methods that relate physiological or chorological (i.e., species location) data to ecogeographical (i.e., environmental, topographical, human, or purely spatial) variables to describe or predict a species' distribution and thus define their ecological niche (Franklin, 2010; Peterson et al., 2011; Silerro, 2011; Barbosa et al., 2012; Guisan et al., 2017; Sillero et al., 2021). SDMs have grown in popularity in conservation biology due to the ability to be projected to geographical space, visualising habitat suitability or the probability of species occurrence on a map (Acevedo et al., 2012; Guisan & Zimmerman, 2000; Hatten, 2014; Ørsted & Ørsted, 2019), especially in poorly sampled areas (Engler et al., 2004). Applications of SDMs include niche quantification (Austin et al., 1990; Breiner et al., 2017), testing ecological or evolutionary hypotheses (Leathwick 1998), predicting the effects of global change on biodiversity (Thomas et al., 2004; Thuiller et al., 2005), and estimating invasive species risk (Peterson & Vieglais, 2001; Petitpierre et al., 2012).

SDMs can be used to provide spatially explicit information on the distribution of the species' habitat such as the location(s), size, and quality of suitable habitat patches (Elith & Leathwick, 2009; Franklin, 2010; Sofaer et al., 2019). This is especially critical for species such as the Oceanic manta and Spinetail devil ray where SDMs can help to overcome the paucity of distributional data. In recent years, there has been critique of SDMs for disregarding the temporal variability in environmental variables which is argued to hamper the accuracy of the predictions (Franklin, 2010;

Robinson et al., 2011). The usage of long-term averages and subsequent assumptions of equilibrium may be causing potential underestimations of the real scale or extent of the species' ecological niche (Bateman et al., 2012; Perez-Navarro et al., 2020; Zimmermann et al., 2009). Despite substantial implications on the accuracy of the model, studies that account for temporal variability remain rare (Zimmermann et al., 2009; Niehaus et al., 2012; Hannah et al., 2014).

The NE shelf of the Te Ika-a-Māui North Island of Aotearoa New Zealand is characterised by a diverse range of environments that supports a plethora of biodiversity. It includes the country's most utilised marine environment; Tīkapa Moana Hauraki Gulf, with flows from of the EAUC bringing in tropical immigrants from northern, tropical waters, creates a unique environment that supports smaller schools of fish to large apex predators (O'Callaghan & Baker, 2002; Wiseman et al., 2011). Although the NE shelf is relatively well-studied compared to other regions in the country, mobulids are seldom studied and resulting lack of baseline information limits conservation efforts. Preliminary understanding of the distribution mobulids in the Tīkapa Moana Hauraki Gulf come from one-off observational accounts (Duffy & Abbott, 2003), behavioural observations (Duffy & Tindale, 2018) or investigations of post-release mortality from purse-seine vessels (Francis & Jones, 2016). Therefore, larger scale studies on the spatio-temporal distribution and environmental factors that describe these locations have not been previously assessed.

To understand the spatial and temporal distribution of both Oceanic manta rays and Spinetail devil rays in the northeastern shelf of the Te Ika-a-Māui North Island of Aotearoa New Zealand, I used species distribution modelling including accounting for temporal dynamics in environmental variables (Fig 2.1). The objectives of this chapter are to identify important variables or conditions that describe Oceanic manta ray and Spinetail devil ray distribution on the northeastern shelf of the Te Ika-a-Māui North Island of Aotearoa New Zealand using an SDM. Further utilising SDMs to make predictions on the habitat suitability of mobulid species and consequently, compare the difference in habitat suitability estimates using our annual approach (hereafter referred to as "dynamic") compared to the more commonly used 'static' approach of using long term environmental averages (hereafter referred to as "static") .

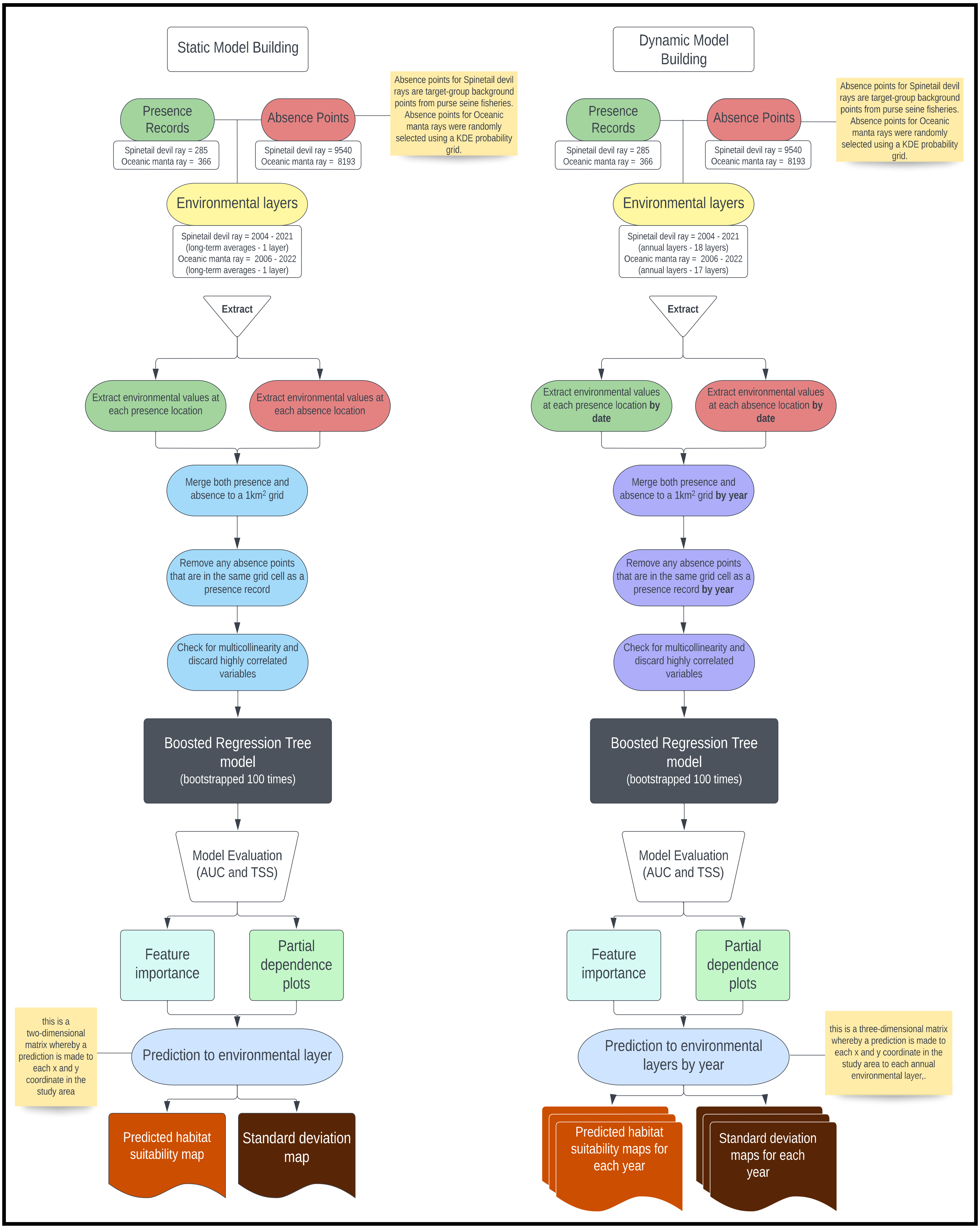

Figure 2.1 *Flowchart of the model flow and differences between processes between static and dynamic models.*

2.2 MATERIALS AND METHODS

2.2.1 Study area

The study area encompasses the northeastern (NE) continental shelf of the Te Ika-a-Māui North Island of Aotearoa New Zealand, including the Tīkapa Moana Hauraki Gulf Marine Park (≈ 33°–38°S; 172°–178°W; Fig 2.2). This region hosts low salinity, nutrient-rich waters that are bounded seaward by a warm, nutrient-poor, sub-tropical, south-eastward flowing current originating from the EAC and the Tasman Front, called the EAUC (Sharples et al., 1997; Stanton & Sutton, 2003; Zeldis et al., 2004). Terrigenous and riverine outputs to the shelf are relatively low with most of the nutrient supply coming from offshore, deep ocean sources during upwelling periods (Sharples et al., 1995; Sharples, 1997; Sharples & Greig, 1998; Zeldis et al., 2004) with additional nutrient supply from sediment remineralisation (Giles et al., 2007). The narrow continental shelf (< 40km wide) creates favourable conditions for upwelling making this region one of the most productive waters in the country (Bury et al., 2012; Gaskin, 2021). Wind stress and consequently, mixing of oceanic, shelf and Gulf waters in the NE shelf exhibits high seasonal and inter-annual variability (Chang et al., 2003). This has implications on light and nutrient availability and hence, primary productivity (Sharples et al., 1995; Sharples, 1997; Sharples & Greig, 1998; Zeldis et al., 2004). Within the year, late winter, spring, and late summer bringing prevailing westerly winds, driving upwelling conditions (Sharples & Greig, 1998; Zeldis et al., 2004). In late summer, there is a marked transition to easterly winds, making downwelling the dominant mode, evident in the low chlorophyll-a values across the whole shelf (Chang et al., 2003). Simultaneously, oligotrophic EAUC surface water intrudes shoreward, across the shelf, introducing warm, nutrient-poor waters to the mid- and outer shelf (Fig 2.3; Chang et al., 2003; Zeldis, 2004; Zeldis & Willis, 2015). Multiple studies have also uncovered not only the temporally dynamic nature of the NE shelf but the horizontally spatially variant nature. Nutrient and prey availability, water clarity (Gall & Zeldis, 2011), phytoplankton community assemblages (Chang et al., 2003; Zeldis et al., 2005) and degree of benthic mineralisation are factors that are seen to vary between coastal

Gulf waters and offshore shelf waters. The NE shelf consists of waters along various environmental gradients on distinct temporal and spatial scales makes it an environment unique to this region. For these reasons, this region is recognised for its biodiversity, with multiple studies describing the Gulf as important feeding and breeding grounds for many species including whales (Carroll et al., 2019; Constantine et al., 2015; Wiseman et al., 2011), dolphins (Dwyer et al., 2016; Hupman et al., 2015) and seabird (Borrelle et al., 2015; Dunphy et al., 2020; Heswall et al., 2022).

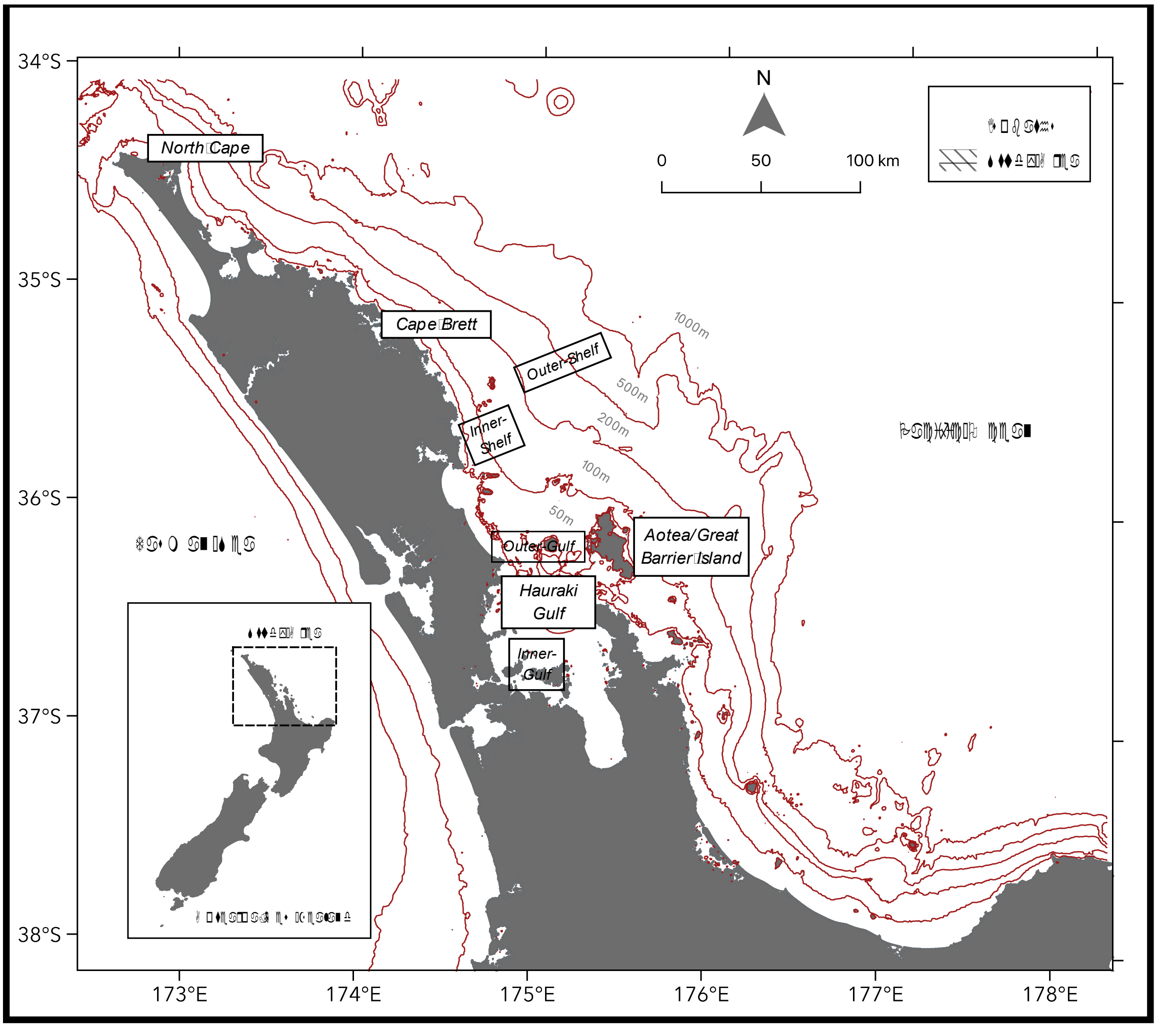

Figure 2.2 *Map of the northeastern shelf of the Te Ika-a-Māui North Island of Aotearoa New Zealand. The gridded lines indicate the extent of the study area, and the colourful labelled boxes are regions of the study area that are referred to in this thesis. Red lines are isobath.*

2.2.2 Data

2.2.2.1 Species Records

Spinetail devil ray records (n = 304) were obtained from the Ministry for Primary Industries (MPI) Centralised Observer Database (COD) for observer reported captures and Non-Fish Protected Species (NFPS) database where commercial captures were reported (replog 13952; obtained under a confidentiality deed between MPI and the University of Auckland; Fig 2.3). The records variously included geographic coordinates, date and time of capture, the length of the vessel and spanned 17 years (2004 – 2021). As there have been no dedicated sampling effort for Spinetail devil rays in Aotearoa New Zealand, all records were converted to presence records. Although there were 13 records (2017 – 2021) from citizen science sources (Manta Watch New Zealand), due to the difference in biases associated with the data from fisheries data (i.e., selection bias), the benefits to incorporating additional records was not deemed profitable in comparison to the added uncertainty and they were therefore removed. The final dataset included 285 locations that had no duplicates (i.e., unique locations).

Oceanic manta ray records (n = 340) were obtained from the Manta Watch New Zealand (MWNZ). MWNZ is a charitable organisation that dedicates research efforts and collects citizen science data with the aim to understand more about Oceanic manta rays in New Zealand. The collection of citizen science data involved mainly social media sources and now with a dedicated website, reporting sightings. The MWNZ research team are also involved in surveys over the summer months, especially since the purchase of a research vessel, and have dedicated effort within the Tīkapa Moana Hauraki Gulf. Citizen science records comprise sightings that have variable reliability however, MWNZ advocates for all sightings to be associated with a photograph or a video so individuals can be attributed to the correct species and prevent misidentification, especially due to the morphological and geographical similarities between Oceanic manta rays and Spinetail devil rays. The records included geographic coordinates, date and time of encounter and span 16 years (2006 – 2022). Although records were available through MPI, this was deliberately left out of the model due to the lack of evidence in the literature regarding Oceanic manta rays' presence as bycatch and the potential misidentification with Spinetail devil rays.

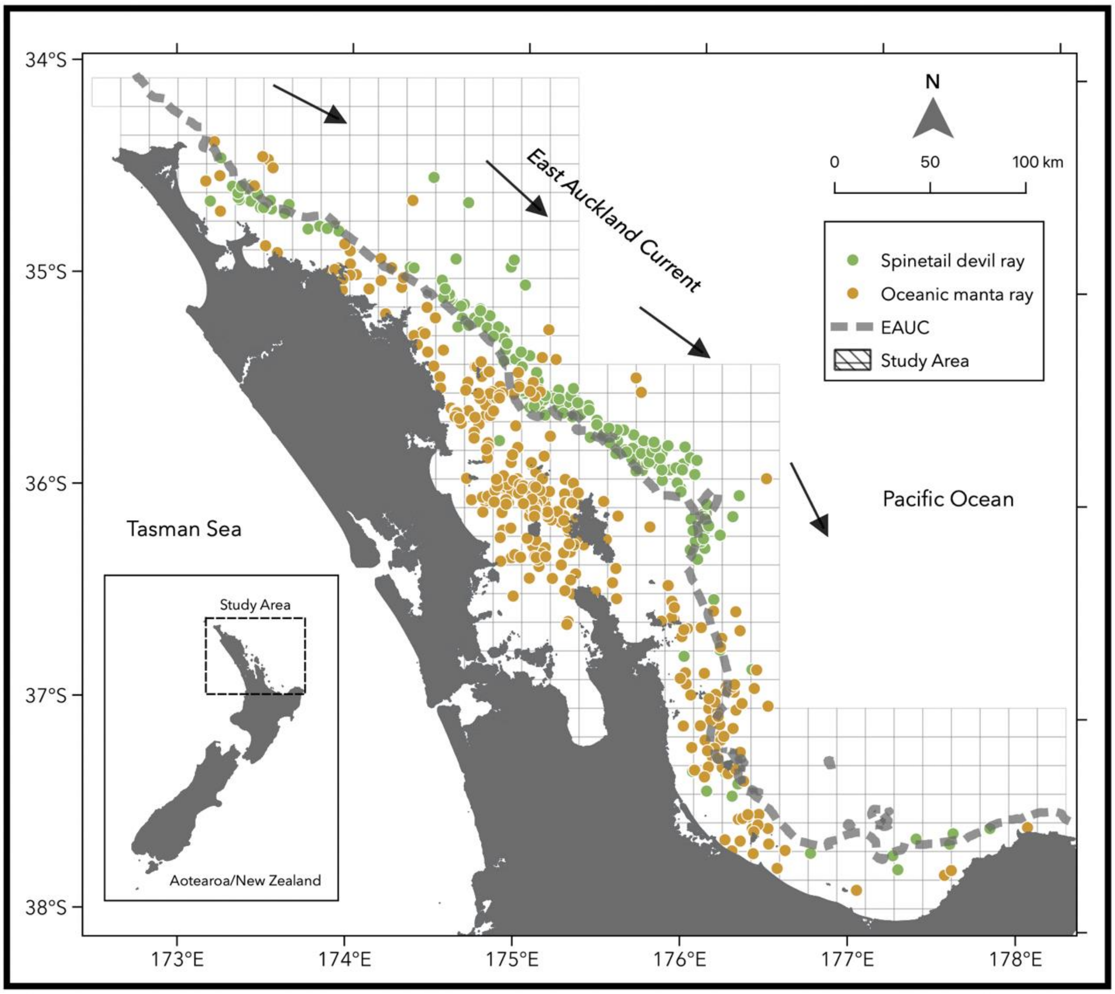

Figure 2.3 *Map with Spinetail devil ray presence records (green) and Oceanic manta ray records (orange). The 200m depth contour line (dashed line) indicates the shelf edge and approximate path of the subtropical East Auckland Current flowing southeastward. Study area is shown within the gridded box.*

For both species, there were a few locations on the western coast of the Te Ika-a-Māui North Island of Aotearoa New Zealand (Spinetail devil ray = 10; Oceanic manta ray = 3). However, these have been omitted from the study as this research is focussing on the habitat suitability of both species on the NE shelf of the Te Ika-a-Māui North Island.

This was deliberately done due to the increased research and sightings effort on the NE coast and the lack of research on mobulids and relatively unknown oceanography on the western coast of the country (Sutton & Bowen, 2011). The few points on the western coast if added, could be a potential cause of overestimation in the model. Further, the EAUC, a subtropical current split off at Otou North Cape (i.e., top of the country; Fig 2.2.) and travels down the eastern coast of the Te Ika-a-Māui North Island, contributing little flow to the west coast (Stevens et al., 2021). This current is thought to be an important source of subtropical water to the temperate waters of Aotearoa New Zealand, and an important driver of Oceanic manta ray and Spinetail devil ray distribution in the country (Duffy & Abbott, 2003; Lyons & Francis, 2012).

2.2.2.2 Absence/Pseudo-absence selection

Boosted regression trees (BRTs) require both presence and absence records to correlate environmental conditions where species are present and the difference in conditions where species are not. However, a limitation of using presence records from opportunistic data in comparison to dedicated survey records is the lack of real absence records (i.e., points where the species is known to be absent). Although the benefit of presence-absence modelling has been tested in the literature, presence-only modelling is also proven to be robust to sample selection bias when pseudo-absences used has the same associated bias (Phillips et al., 2009; Stephenson et al., 2021; Yackulic et al., 2013). Due to the different sources of data for Spinetail devil ray and Oceanic manta ray and subsequent differences in sample selection bias associated with each, separate absence selection techniques will be used.

I generated Spinetail devil ray absence points using a process called “target group background data” (Phillips et al., 2009) where observation points from a closely related or associated species is used from the same dataset as absence points (Yackulic et al., 2013). Due to the closely related nature of Spinetail devil rays’ distribution to purse-seine fisheries, all purse-seine catch locations from the Ministry for Primary Industries database (replog 14573; obtained under a confidentiality deed between MPI and the University of Auckland; Fig 2.4) from purse-seine vessels were used from the same period from 2004 to 2021. Purse-seine records from months that Spinetail devil ray was not present were discarded to ensure the same temporal scale as well. This will ensure that both presence and absence records are associated with the same sampling bias (Milanovich et al., 2010). Although this is not the same as a real absence nor does it guarantee the absence of a Spinetail devil ray, such locations are expected to be more likely to actual absences compared to absences that are randomly generated in the study area and has been shown to improve average performance of regression-based models (Phillips et al., 2009; Stephenson et al., 2020b). Due to these records being associated with the same bias and over the same temporal and spatial scale, these records in the literature are referred to as “absence records” and will be referred to as such in this thesis.

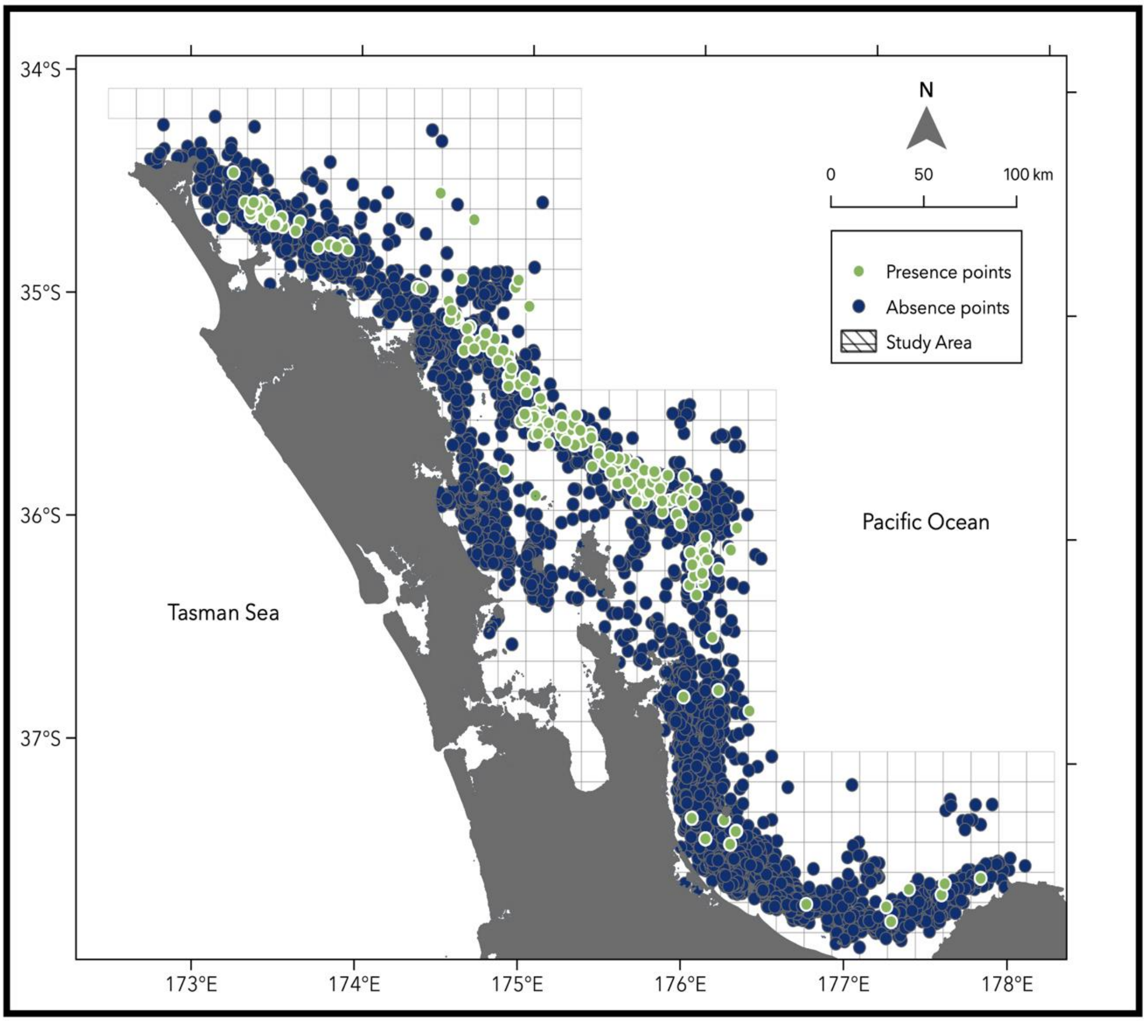

Figure 2.4 *Map of study area showing locations of absences (blue; purse-seine catches between 2004 and 2021) with presence records of Spinetail devil rays (green).*

In contrast, as Oceanic manta ray occurrence records were obtained from various sources (i.e., citizen scientist), there was not one source where a different species occurrence could be used as target group background data with the same associated sampling bias. Hence, a different method was used whereby to preferentially generate more background points in areas with more presence records, a two-dimensional kernel density estimate (KDE) was produced for all Oceanic manta ray presence records using a bandwidth of 100km. This bandwidth was selected after testing 400km, 100km and 50km, and was denoted as the best one due to the realistic environmental conditions that Oceanic manta rays could be in, but distinct enough that there are differential elements (see Appendix 2.1 for map of KDE probability grid). KDE estimates the underlying density of the data and produces a probability grid following the density pattern (Chen, 2017). Five thousand background points were sampled using the probability grid generated from the KDE according to the probability grid weights (i.e., where KDE was high, the probability of selecting as pseudo-absence was also high) (Fig 2.5; Georgian et al., 2019). Pseudo-absence selection using a KDE was chosen over traditional random selection due to the reduction of sampling bias and improvement in model performance that was seen in previous studies (Elith et al., 2010; Georgian et al., 2019; Finnuci et al., 2021). Due to the lack of absence records with the same bias for Oceanic manta rays, the absence records will be referred to as "pseudo-absences."

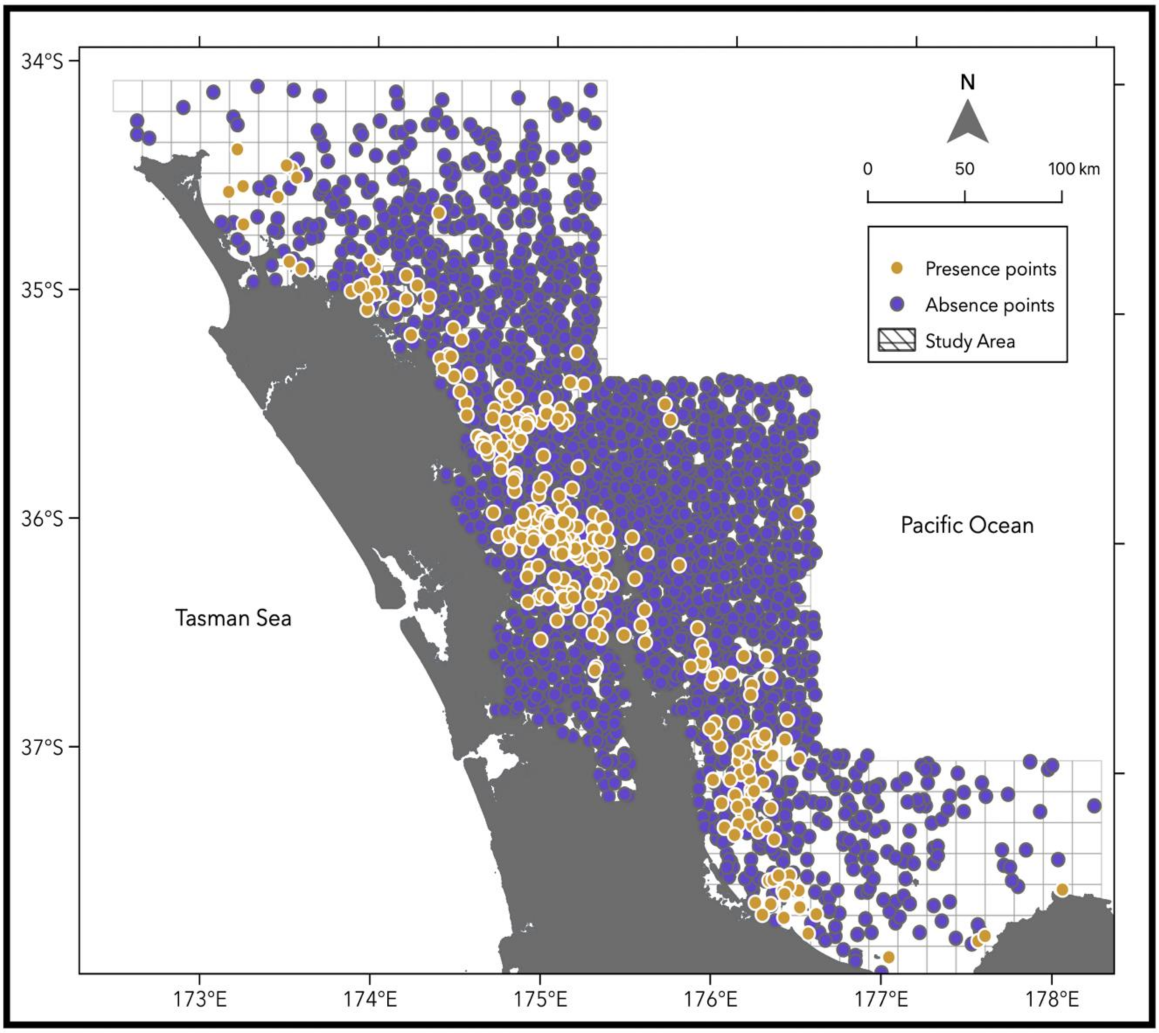

Figure 2.5 *Map of study area showing locations of pseudo-absences (purple; randomly generated based on KDE probability grid) with presence records of Oceanic manta rays (orange).*

2.2.2.3 Environmental predictor variables

Environmental predictor variables were chosen from previous work in the global literature on mobulids, based on which influenced their distribution and movement the most which is as follows: Chl-a, SST , SST and Chl-a gradients, bathymetry, distance to the 200m isobath, distance to coast, Slope of the seafloor, SOI, (Table 2.1). The main prey item for mobulid species is zooplankton, however, this could not be collected at locations matching the observations nor were there any available data sources with the temporal and spatial coverage appropriate for this study. However, satellite Chl-a concentrations are known to be a proxy of the biomass of phytoplankton present in surface waters and there is often high zooplankton biomass where there is high phytoplankton biomass, although a temporal lag (Flagg et al., 1994; Plourde & Runge, 1993). Chl-a and SST gradients are layers that represent productivity fronts and an estimation of mesozooplankton feeding habitats as well as important habitats for mobile marine animals (Scales et al., 2014), as fronts are known to persist long enough for this association (Druon et al., 2019). Therefore, despite the recognition of a temporal lag between phytoplankton and zooplankton blooms, Chl-a, Chl-a and SST gradients will be used as a proxy of local productivity within the model (Druon et al., 2019; Jaine et al., 2012), obtained from Stephenson et al. (2020a).

All predictor layers were collated and interpolated to a 1km grid to ensure the same resolution and the removal of missing values, especially for layers such as Chl-a in which cloud cover impacted the dataset. Bathymetry was obtained from the National Institute of Water and Atmosphere (NIWA) bathymetric dataset of the New Zealand region, cropped to the study area (Mitchell et al., 2012). Distance to the 200m isobath (km) was calculated in R Studio (v. 4.2.1.) and *st_distance* function from the *sf* package where the Euclidean distance between each centroid of each grid cell and a bathymetric buffer of 200-250m. The same methodology was used to calculate the closest distance between a centroid of a grid cell and land (obtained from Land Information New Zealand), distance to coast (km), as a proxy for the influence of coastal elements. Slope was calculated from the bathymetry layer using the Slope tool in ArcGIS and SOI, an index for ENSO was obtained from NOAA National Weather

Service Climate Prediction Centre (https://www.cpc.ncep.noaa.gov/) as standardised monthly values.

Table 2.1 *Environmental variables used in habitat suitability model.*

Abbreviation	Model type	Temporal Resolution	Spatial Resolution	Description	Units	Source
Bathy	Bathymetry	Static	250m	Sea bed depth around New Zealand. Interpolated from multi-beam sensors, single beam echo sounders, and satellite gravimetric inversion (Mitchell et al., 2012)	m	Mitchell et al. (2012)
Chl-a	Chlorophyll-A	Mean monthly	1km	A proxy for biomass of phytoplankton in the near-surface water column (to ~ 30m) as the most abundant form of chlorophyll in photosynthetic organisms. Blended from default open-ocean Chla values from MODIS-Aqua and coastal ChlA estimate [quasi-analytic algorithm (QAA), aph*(488)].	mg m^{-3}	Gall et al. (2022)
SST	Sea surface temperature	Mean monthly	1km	Blended from default SST product from SeaDas 7.2, OI-SST Ocean product (Reynolds et al., 2002), coastal MODIS-Aqua product (Gall et al., 2022).	°C	Gall et al. (2022)
SSTGRAD	Sea surface temperature gradient	Mean monthly	1km	Derived by computing the horizontal gradient of SST from the blended SST product from SeaDas 7.2, OI-SST Ocean product (Reynolds et al., 2002), coastal MODIS-Aqua product. Averaged to mean monthly layers over the study period.	°C	Stephenson et al. (2020a)

CHLGRAD	Chlorophyll-A gradient	Mean monthly	1km	Derived by computing the horizontal gradient of SST from the blended Chl-a product from MODIS-Aqua and coastal ChlA estimate [quasi-analytic algorithm (QAA), aph*(488)]. Gaussian smoothing function to remove potential sensor strips. Averaged to mean monthly layers over the study period.	mg m^{-3}	Stephenson et al. (2020a)
Slope	Slope of the seafloor	Static	250m	Rate of change of elevation from one cell to the next in degrees using the bathymetry dataset derived from Mitchell et al. (2012) and calculated using Calculate Slope in Spatial Analyst toolbox ArcGIS.	° (degrees)	Calculated from Mitchell et al. (2012)
SOI	Standardised Southern Oscillation Index	Monthly	non-spatial	Standardised Southern Oscillation Index calculated monthly as the observed sea level pressure difference between Tahiti and Darwin, Australia. It represents the difference in air pressure between the eastern and western equatorical Pacific and can indicate an El Niño event when values are negative, and a La Niña event when values are positive. The strength of each event is represented by the value itself, the larger the number, the higher the intensity of the conditions. SOI was retrieved from the National Centres of Environmental Information (NOAA) from https://www.ncei.noaa.gov/access/monitoring/enso/soi.	no units	National Centres of Environmental Information (NOAA)

For temporally dynamic variables, monthly mean estimates were derived from satellite images (MODIS-AQUA), obtained from NIWA-SCENZ (Gall et al., 2022) for each respective study period (Oceanic manta rays: 2006 to 2022; Spinetail devil rays: 2004 to 2021). Each monthly variable layer was averaged by year to create annual layers. When creating the annual layers, months where each species was not present in the occurrence data were removed (i.e., September, October, November) to ensure the model did not extrapolate into temporal ranges that mobulids were not known to be in Aotearoa New Zealand waters for. Although seasonality and impacts to distribution on mobulids within the year is proven to be an important point of research, the number of observations per month for each respective year for each species was not enough to model and was beyond the scope of this study. Hence, the model is mainly restricted to predicting habitat suitability in the warmer summer months (summer: December – February). However, due to the hypothesised migration that mobulids participate in, immigrating to New Zealand during summer, this may indicate that the model is incorporating the most important timeframe. In contrast, the static model did incorporate the same temporally dynamic variables however, these were long-term averages of the same variable over the study period length thus, assuming equilibrium in these attributes over that time.

Observations collected from both species did not exceed bathymetric depth of more than 2500m thus, a predictions for all environmental predictors were limited to this depth. This was to ensure that the model did not extrapolate beyond unsampled areas and predict presence in locations where individuals have not been confirmed yet which in turn reduces uncertainty in predictions.

Due to the stagewise nature of the selection of variables in BRT, there are no penalties for the number of predictors within the model or the order that the variables are inputted. Thus, the variables were chosen based on hypothesised biological importance on distribution and feasibility of obtaining data. However, multicollinearity between variables was examined where a value of over 0.9 was considered highly correlated.

2.2.3 Data Processing and Preparation

All Spinetail devil ray occurrence data was prepared to ensure that there were no duplicate records where an individual was recorded by commercial records as well as an observer on board. Further, records from both datasets with missing coordinates and an approximate date reference (month and year) were removed from the dataset. Both datasets were initially plotted to visually check the validity of points and points with positional errors (i.e., on land) were removed. After the data was cleaned, all records were reprojected from longitude and latitude coordinates (ESPG: 4326) to New Zealand Transverse Mercator (ESPG: 2193). This was to ensure that the projection of datapoints matched that of the environmental raster layers and when calculating distance metrics, Euclidean distance could be used using metres as the unit. All points were subsequently aggregated to a 1km^2 grid by specific year and any absence point within the same grid as a presence record was removed so there was no spatial overlap.

For all observations, environmental values at each spatial point (for static model), and at each spatial and temporal point (for dynamic model) was extracted from the environmental predictor variable layers. The use of remotely sensed satellite data from ocean colour is associated with missing values when cloudy days persist, thus, to remove this likelihood of happening, dynamic environmental layers were used at a monthly resolution instead of finer temporal scales (i.e., daily).

It is important to note that records are highly likely to be spatially and temporally biased; for Spinetail devil ray records, to locations and timeframes where purse seine vessels are present, and for Oceanic manta rays, to locations and timeframes frequented by people, often in the summer in coastal areas. For these reasons, absence/pseudo-absence selection must be done carefully as without this, differences between locations of presence and absence may just be a manifestation of these biases, and not true differences in environmental conditions. Additional biases that need to be accounted for also include detection bias; that is, the observer's ability to detect the animal which can be impacted by the sea state, bad weather, low visibility conditions and surfacing-diving behaviour, or failure to observe despite presence (Kanaji et al., 2011). This is especially relevant in this context due to the lack of surface-breathing requirements for mobulids and subsequent reduction in the ability to spot an individual. Morphological similarities between the two species and historical misidentification also indicate that the data may be subject to further biases. These biases will be accounted for within the modelling framework through absence/pseudo-absence selection (see Section 2.2.2.3. Absence/Pseudo-absence selection).

2.2.4 Habitat Suitability Modelling

2.2.4.1 BRT model fitting (i.e., regularisation)

In all SDMs, model fitting must be done with caution to maximise the ability of the model to make accurate predictions by balancing complexity and generality. Overfitting a model, i.e., fitting data too closely to the training data, can cause the model to misleadingly perform well on training data but lack the generality to accurately predict to unseen testing data (Friedman, 2001). On the other hand, when the model is overly simple and general, there is not enough complexity to identify important patterns, leading to the reduction in predictive accuracy (i.e., underfitting) (Friedman, 2001). Regularisation methods attempt to balance generality, complexity and predictive performance (Friedman, 2002; Hastie et al., 2001).

A regularisation method used in BRTs to avoid overfitting involves manipulating the learning rate, also known as “shrinkage” (Copas, 1983). A learning rate is a value that ranges from 0 to 1. Each tree is scaled by this value, where smaller values (closer to zero) reduce the contribution of each tree added to the model, and larger values (closer to 1), increase this contribution (Friedman, 2001). Learning rate is inversely proportional to another important model fitting parameter, the number of trees. As the learning rate decreases and the relative weight of each tree decreases consequently, the number of trees increases. The final term that is involved in the regularisation of BRT is tree complexity; the number of nodes in a tree and this directly impacts the number of trees required. For a given learning rate, if a highly complex tree is fitted, fewer trees are required to minimise the loss to the same extent (Elith et al., 2008). Therefore, if the number of trees were to stay static and tree complexity increases, the learning rate would have to decrease in response. Thus, regularisation is the intricate balancing and assessment of trade-offs between learning rate, number of trees and tree complexity. A study by Elith et al. (2008) found that with small sample sizes with observations less than 250, there was no advantage to increasing tree complexity on predictive performance and the best model fitting metrics are to have simple trees (with tree complexity of 2 or 3) and a small enough learning rate to allow for at least 1000 trees to be fitted.

The data was fit to a BRT in R version 4.2.1 (R Core Team, 2022) using the *dismo* package (Hijmans et al., 2017) to model the presence/absence of mobulid with a *bernoulli* error distribution with the response variable being the presence (positive observation) of a mobulid in a grid cell. Based on the recommendation by Elith et al. (2008) where smaller sample sizes are best modelled with simple trees and a slow learning rate, both static and dynamic models used a learning rate of 0.001 and a tree complexity of 2. This was a learning rate that allowed for at least 1000 trees to be fitted at each iteration and a tree complexity that was simple enough where computing energy and time was not limited.

Each static and dynamic BRT model was bootstrapped 100 times, in that at each iteration, a random “training” sample was extracted from the full occurrence dataset with replacement. The same number of absences/pseudo-absences was also sampled from the full dataset and these presence and absence/pseudo-absence records were then used in the model. Presence records that were not selected at random at each iteration was combined with a random sample of absence/pseudo-absences and set aside for independent assessment of model performance, called evaluation data. At each iteration, geographic predictions were made to a 1km grid using environmental predictor variables and at the end, predictions were averaged for each grid for the final prediction. As this BRT model used absence/pseudo-absences and not true absences that incorporate nuances of “sightability” or “catchability”, we refer to our outputs as habitat suitability, rather than the probability of occurrence (Anderson et al., 2016;). Final outputs of the data were the habitat suitability maps and maps showing the degree of uncertainty (measured as the standard deviation of the mean habitat suitability index calculated from 100 bootstrap layers).

2.2.4.2 Static to Dynamic Model

The temporally explicit dynamic model and long-term static model have inherent differences in the methods involving aggregation of records and environmental variables, predictions and outputs of the model (Table 2.2). For the dynamic model, to incorporate time, an additional variable was added which denoted the year that the observation was made for the occurrence and absence data, as well as the environmental predictor data. Further, geographical predictions were made to a three-dimensional matrix where each slice of two-dimensional matrix was a different year and each column was a new bootstrap iteration, out of the 100 done. Predictions were then averaged for every bootstrap iteration, keeping the slices intact so that in the end each year had geographic predictions to a 1km grid. In this way, the model was constructed with the nuance of time and presence was predicted for each specific year. It is important to note that although “Year” is incorporated into the model, this is a singular number denoted the year and is a spatially invariant variable (i.e., not linked to spatial processes). Environmental predictors in the model vary over space and time and the model estimates how it changes over time using “Year” as a differentiating factor between these timeframes. However, high feature importance for “Year” does not mean that in that specific year, there was higher habitat suitability. Instead, “Year” is a latent variable where the model estimates a relationship of habitat suitability however, as it is unmeasured, the differences cannot be attributed to a specific variable. Thus, the higher contribution of “Year” in the model indicates the higher degree of variability over time that is not attributed to the environmental variables included in the model.

Table 2.2 *Differences in methodology and outputs between static and dynamic models.*

Difference	Static	Dynamic
Aggregation	Presence and absence points are aggregated to a 1km² grid regardless of different occurrence times.	Presence and absence points are aggregated to a 1km² grid based on the year of occurrence.
Environmental Variables	Dynamic environmental variables (e.g., Chlorophyll-A) are averaged over the entire study period to a singular layer.	Dynamic environmental variables are averaged from monthly estimates to annual layers.
Prediction	No reference to time. Predictions are made to a single environmental layer that is a long-term average of the entire study period (Spinetail devil rays: 2004 to 2021; Oceanic manta rays: 2006 to 2022).	Model is constructed by each individual year and predictions are made to environmental layers for the corresponding year.
Output	One map for habitat suitability over entire study period and one map for standard deviations from bootstrapped predictions.	One predicted habitat suitability map for each year from the study period and a map of standard deviations from bootstrapped predictions for each year (Spinetail devil rays: 18 maps; Oceanic manta rays: 17 maps).

2.2.4.3 Interpreting the model

One of the most important characteristics of decision trees that BRT forfeits is interpretability. BRT models are constructed of hundreds and thousands of trees and especially when working with pseudo-absences, this can make it difficult to understand outputs of the model. Thus, BRT outputs must be handled and understood in different ways and various methods are used to achieve this. Key ingredients in interpretability are understanding what variables were important to prediction (feature importance), and how these variables are affecting the response variable (using partial dependence plots, Friedman & Meulman, 2003).

2.2.4.4 Variable contribution

As discussed above (Section 2.2.2.3), although models are fit with several explanatory variables, often, only few have a substantial influence on the response variable, in this case the habitat suitability for Spinetail devil rays and Oceanic manta rays. Due to the characteristic of BRT models ignoring irrelevant variables when fitting trees, the number of times a variable is selected at each binary split is recorded and weighted by the squared improvement of the model as a result of the split, averaged over all trees then scaled so cumulatively all contributions add up to 100 (Friedman & Meulman, 2003). Through this, relative contribution to the model is examined and ensures easy interpretation which variables contributed to prediction the most. An example is outlined below in Figure 2.6 where Griffen et al. (2021) examine habitat selection of multiple shark species – the example outlines two species from their analysis: nurse sharks (turquoise) and tiger sharks (gold). Through simple visualisation, readers can see that nurse sharks and tiger sharks have very similar habitat preferences with depth and distance to land contributing significantly to their distributions. Variable contribution can be simply visualised in this way to aid with interpretation, even for those that are not well-versed with BRT.

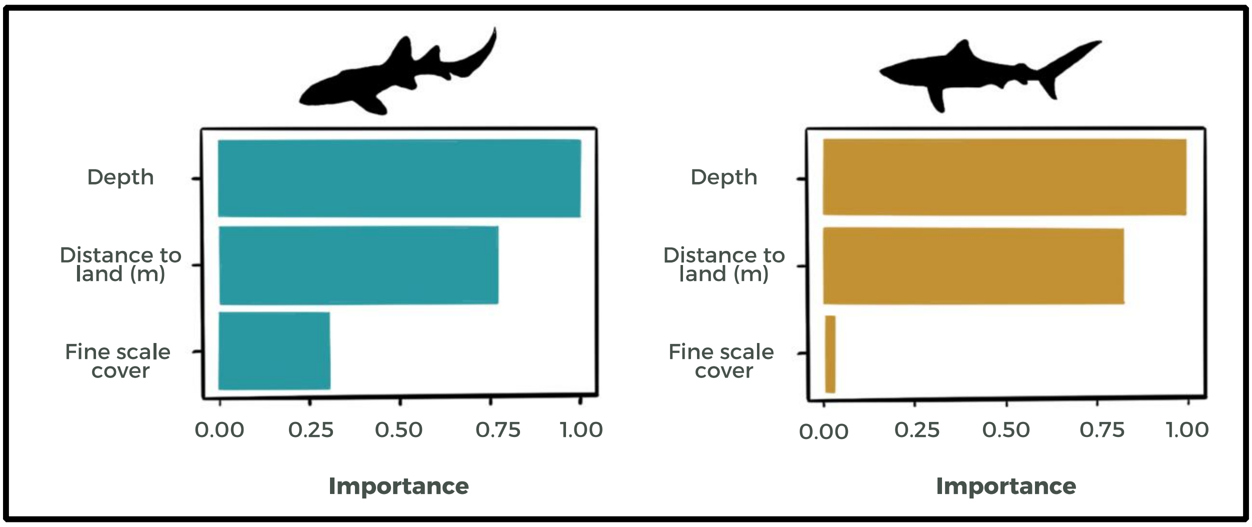

Figure 2.6 *Example of variable contribution plots adapted from Griffen et al. (2021) of nurse sharks (turqoise) and tiger sharks (gold).*

2.2.4.5 Partial dependence plots

After most relevant variables are identified, the next step is to assess how these variables affect the response variable. Partial dependence plots are graphical representations of these relationships. The function of a predicted explanatory variable is plotted against each value of the response, holding all other explanatory variables at their average value and essentially, conditioned out to examine how a single variable affects the response (De'ath, 2007; Friedman, 2001).

For example, a partial dependence plot illustrated below shows the relationship between habitat suitability and SST (Fig 2.7). The plot shows habitat suitability on the y-axis, with habitat suitability being just under 0.4 at 10 °C compared to over 0.6 at 20 °C. The increase in habitat suitability with increasing SST can easily tell the reader that this species must prefer warmer waters. Confidence intervals can be visually represented by an envelope (Fig 2.7) or lines on the plot, describing the uncertainty in predictions of the relationship between the habitat suitability at a given value. Graphically, the curvilinear nature of the BRT model can be seen where explanatory variables with high relative contribution have a more complex and curvilinear gradient. This is because as it is selected as the splitter more often, and splitting occurs at different values, small steps are added to the graph (step size dependent on the learning rate) at different values of the explanatory variable (Elith et al., 2008). This is by no means a comprehensive nor perfect representation of how each explanatory variable impacts the response especially if there are highly correlated variables, high interaction effects however, it gives a good basis for interpretation and clues (Friedman, 2001; Friedman & Meulman, 2003).

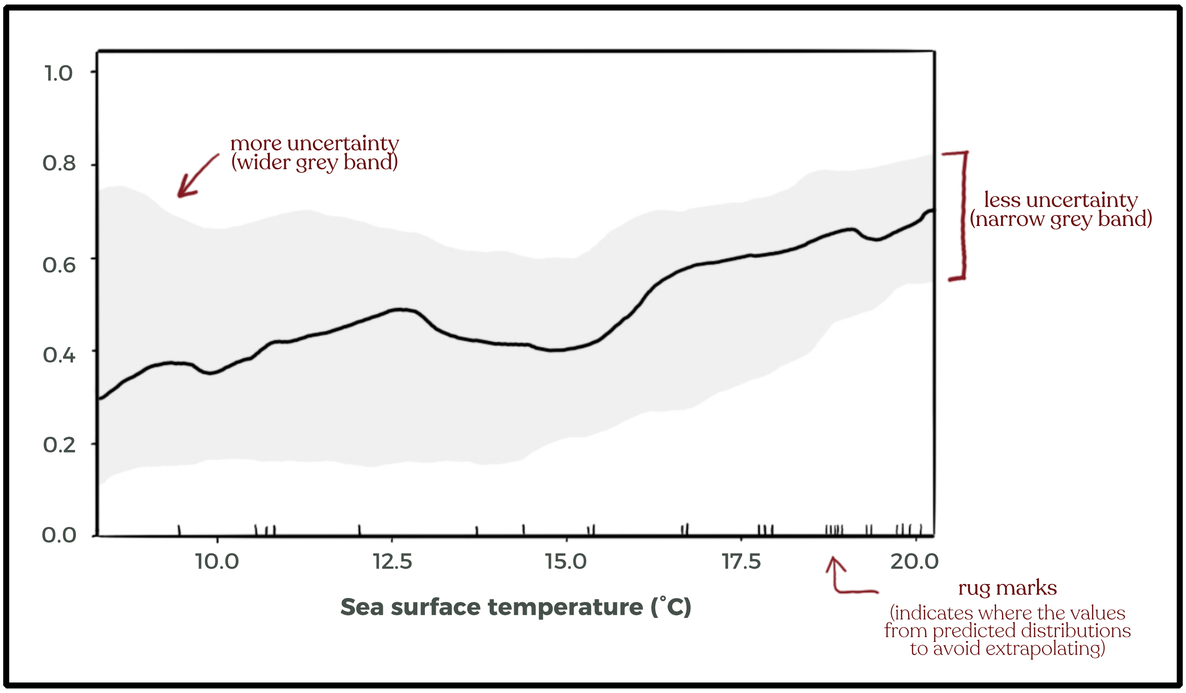

Figure 2.7 *Example of a partial dependence plot describing the relationship between SST and habitat suitability, while holding all other variables at their mean. The y-axis represents habitat suitability from 0 to 1 on a probability scale.*

2.2.4.6 Model evaluation

The need for a process or metric to evaluate model performance is widely acknowledged as it can help to determine the application of the model, identify areas that need to be improved or help to compare various modelling methodologies (Allouche et al., 2006; Barry & Elith, 2006; Guisan & Thuiller, 2005). There is a plethora of statistical tests of model fit and comparison with existing knowledge to address this need (Elith & Leathwick, 2009).

When the response variable is categorical (i.e., presence/absence), confusion matrices are made to evaluate the performance of a model (Redfern et al., 2006). A confusion matrix is constructed when comparing model predictions to withheld or independent data and records the number of true positives (i.e., model predicts presence and test data confirms this is true); false positives (i.e., model predicts presence but test data shows absence); false negative (i.e., model predicts absence but test data shows presence); true negative (i.e., model predicts absence and test data confirms this is true) (Fig 2.8; Allouche et al., 2006; Pearson, 2010). However, predictions of a model are usually expressed between 0 and 1 hence, a threshold must be chosen whereby any value above it will be classified as a presence, and below as absence (Redfern et al., 2006). Selection of a threshold is critical to the context and application of a study as selection of a low threshold will result in many presences, while a high threshold will result in few presences (Pearce & Ferrier, 2000). This threshold is often viewed as arbitrary and introduces an added complication to interpretation (Redfern et al., 2006). However, arguments against this state that practical applications of SDMs in conservation planning require dichotomous presence-absence maps and predictions therefore, predictive accuracy should be evaluated based on a threshold-dependent metric (Allouche et al., 2016). Thus, this study will use two quantitative performance metrics: Area under the curve (AUC) (threshold-independent) and True Skill Statistic (TSS) (threshold-dependent).

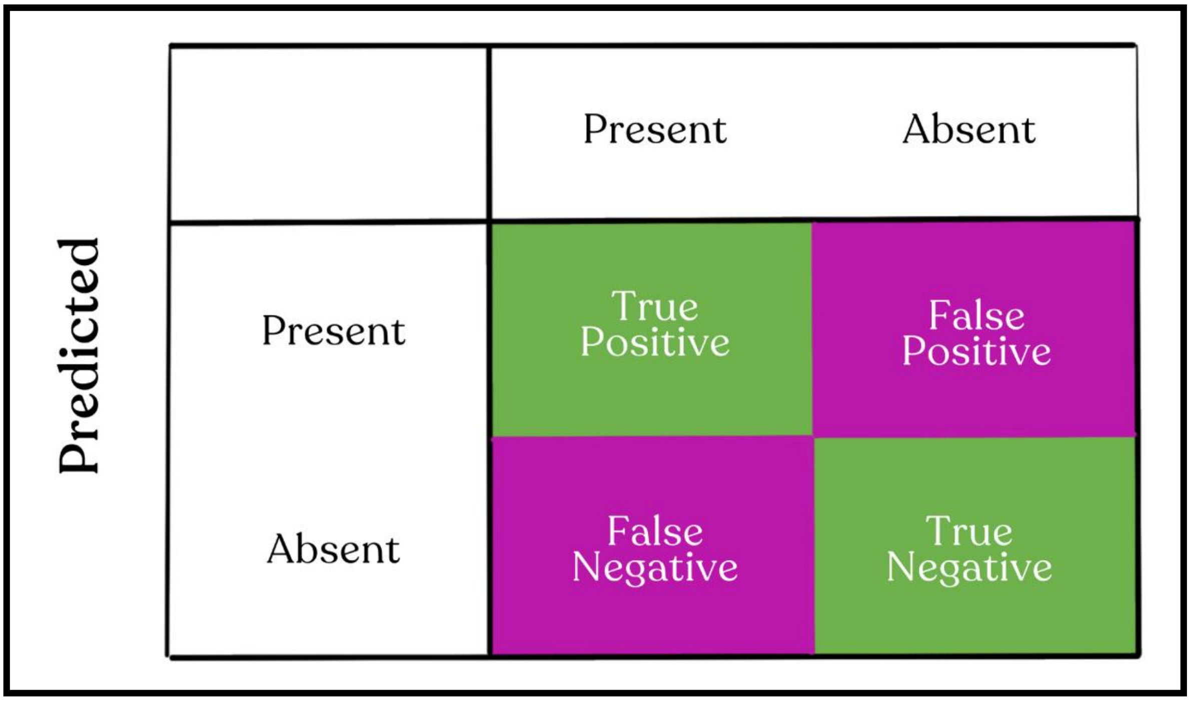

Figure 2.8 *Confusion matrix showing true positives (i.e., model predicts presence and test data confirms this is true); false positives (i.e., model predicts presence, but test data shows absence); false negative (i.e., model predicts absence but test data shows presence); true negative (i.e., model predicts absence and test data confirms this is true).*

AUC is a common metric used in SDM literature and measures the ability of a model to distinguish areas where the species is present, to those where they are absent

(Hanley & McNeil, 1982). This is useful as it gives modellers an idea of how good the model is at correctly identifying important areas as habitat for a given species (Elith et al., 2006). TSS is also gaining popularity within presence-absence models compares the number of correctly predicted presences minus those predictions that were attributed to random guessing to hypothetical set of perfect predictions (Allouche et al., 2006).

Both AUC and TSS deal with concepts of sensitivity, specificity, threshold, and confusion matrix. A threshold determines an arbitrary value between 0 and 1 that predicts the species as present if their HSI is above the threshold and absent if not (Pearson et al., 2010), sensitivity is the proportion of observed presences that are correctly classified whereas, specificity is the proportion of observed absences that are correctly classified (Allouche et al., 2006).

AUC scores are derived from a ROC curve that plots sensitivity against '1 – specificity' across a range of possible thresholds and describes the area under this curve (Allouche et al., 2006; Pearson, 2010), to classify scores into confusion matrices, producing sensitivity and specificity values for each (Allouche et al., 2006). Specificity is subtracted from 1 to ensure that when plotting, specificity and sensitvitiy change in the same direction in response the varying thresholds (Pearce & Ferrier, 2000). AUC scores range from 0 to 1 with 0.5 indicating that that model performance is equal to random chance, a score of 0.7 indicating good performance and a score above 0.8 indicating excellent model performance (Elith et al., 2006; Komac et al., 2016). TSS is an alternative metric to AUC and is a threshold-dependent measure of predictive accuracy and has the advantage of not being affected by the size of the validation dataset (Allouche et al., 2006). In contrast to AUC, TTS ranges from -1 to +1 where a score of +1 means perfect agreement between the distribution of observed presence and predicted presence whereas, a score of -1 indicates no better than random chance. A score greater than 0.6 is considered good to excellent (Allouche et al., 2006; Komac et al., 2016). Hence, due to the advantages of both metrics and their differences related to threshold, both measures were used in the evaluation of predictive accuracy. Further, a point of consensus between many studies is that no single method should be used alone to assess model accuracy

(Allouche et al., 2006; Fielding & Bell, 1997; Franklin, 2010), justifying the use of both metrics.

2.2.4.7 Measures of Uncertainty

Models are assigned a challenging task of summarising complex ecological and distributional patterns with reduced set of predictor variables and observations, hence, will inevitably produce mismatches between predicted and actual distributions (Barry & Elith, 2006). Therefore, it is important to recognise this within the evaluation stage of the model and to consider model uncertainty. This is especially crucial when considering the use of SDMs in decision-making for conservation planning and biosecurity (Elith & Leathwick, 2009).

As the model within this study exclusively deals with prediction, evaluation must test predictive ability/performance and this often includes data resampling (i.e., splitting samples, bootstrapping) or more rarely, independent datasets (Elith & Leathwick, 2009). This is when the model is assessed based on how well the model predicts the withheld data, called evaluation data (also known as 'test data') (i.e., data not used to train the model) (Boyce et al., 2002; Elith et al., 2006, Pearson, 2010). Although there are cases where predictive accuracy is measured by how well the model predicts to training data (data used to develop model), this creates opportunities for the model to be unknowingly overfit, reducing the ability to predict to evaluation data and hence, limiting real-life applications of the model (Araújo et al., 2005; Pearson, 2010). Ideally, the evaluation dataset would consist of observations that are independent however, given the small sample sizes of both mobulid species in the study, this is not possible. Therefore, bootstrapping was used where 100 models are built and at each iteration, the original observed presences were sampled randomly with replacement (i.e., same observation can be chosen more than once) and the same number of absences were also randomly sampled with replacement (Pearson, 2010). For each model, the observed presences that were not randomly sampled and the same number of absences were set aside evaluation data to assess the model at each iteration (i.e., AUC and TSS).

In addition, a spatial measure of uncertainty was generated by calculating the standard deviation from all bootstrapped models where larger values are indicative of higher uncertainty in the prediction and lower values indicate higher certainty. This is the projected spatially to understand at which locations were predictions more uncertain than others.

Predictions were not made beyond the range of the original training data used to develop the model. Extrapolation can be inherently risky without observed presences to confirm the actual occurrence of a species and violates several statistical and ecological assumptions of SDMs thus, is not recommended especially without independent data to evaluate the accuracy of predictions (Elith & Leathwick, 2009; Pearson, 2010). An example of extrapolation can be seen from a hypothetical SDM that is developed for a species where the occurrences' temperature ranges from 10-20°C and the model is used to predict occurrence in a different region where temperatures exceed 25°C (Pearson et al., 2010). The model has no prior information on occurrences in that thermal range and therefore, predictions may be useful to explore but careful interpretation and a clear acknowledgement of extrapolation must be done. Hence, using a prediction horizon, no extrapolations are made to ensure the reduction of any preventable sources of uncertainty.

2.2.4.8 Uncertainty discounting

Due to data paucity issues, especially in offshore waters, despite predictions in certain areas showing high habitat suitability, these predictions may be associated with high uncertainty. Thus, interpreting these locations as 'hotspots' or ecologically important will be associated with substantial error. Hence, a method called uncertainty discounting was used to weight the predictions at each pixel by a degree of error. The predictions were weighted with a high α (i.e., horizon of uncertainty), indicating that although habitat suitability will decrease, these values will be associated with low uncertainty (Moilanen et al., 2006; Stephenson et al., 2021). High robustness is required, thus, a high α value is also required. For this study, an α value of 1.0 was chosen (representing maximum uncertainty of one standard deviation), and this higher value implies that higher targets must be achieved reliably. This ensures that areas with high habitat suitability and high standard deviations are penalised and the higher the standard deviation, the larger the prediction is discounted by.

2.3 RESULTS

2.3.1 Spinetail devil ray

2.3.1.1 Spinetail devil ray records

Records that were included in the model (n = 285) were all obtained from the Ministry for Primary Industries. Most Spinetail devil ray records (89%; n = 253) occurred in summer months (Dec – Feb) and the final model was constructed to only represent their distribution at these times. The most recent occurrence record was on March 23rd, 2021, where an individual was captured as bycatch in a purse-seine net targeting skipjack tuna. Although some occurrence records (56%; n = 159) included the number of individual rays caught, the rest of the data had the weight (in kg) or both values were missing. Whilst this could have given insight into abundance of Spinetail devil rays in the NE shelf, due to the difficulty associated with converting weight to count (or vice versa) without accurate information on the weight of an individual ray especially with potential sexual dimorphism, this thesis only deals with a habitat suitability model with occurrence data.

2.3.1.2 Model performance

Model performance was measured through AUC and TSS and these indices indicate that this model was useful in predicting Spinetail devil ray habitat suitability using long-term averages (AUC: 0.90 and TSS: 0.78; AUC above 0.7 and TSS above 0.5; Table 2.3). Similarly, the dynamic model using annual averages also performed well (AUC: 0.91 and TSS: 0.73; Table 2.3). The similarity between the indices for the two models indicates that although some years in the dynamic model had very few occurrence records, this did not seem to hinder the performance of the model. Further, the low and consistent standard deviations of both indices suggests that both models are performing consistently across the 100 bootstrap samples. Model fits for the dynamic and static model between training data and evaluation or quite consistent across both metrics as well, and in both cases the model fit for evaluation data being slightly lower than the training data, as expected. However, the similarity between the evaluation and training data model fits suggests that both models were not overfitted to the training data and performed well.

Table 2.3 *AUC and TSS values both on training and evaluation (testing) data is shown for both static and dynamic models for Spinetail devil rays.*

Study period	Model type	AUC (training data)	AUC (evaluation data)	TSS (training data)	TSS (evaluation data)
2004 - 2021 (Spinetail Devil Ray)	Static	0.94 ± 0.01	0.89 ± 0.03	0.92 ± 0.01	0.75 ± 0.03
	Dynamic	0.93 ± 0.01	0.90 ± 0.03	0.91 ± 0.02	0.74 ± 0.04

2.3.1.3 Variable contribution

The static model suggests that habitat suitability for Spinetail devil rays is highest in shallower waters in around 150m to 500m depth that has moderately high Chl-a concentrations (Fig 2.9). There was strong evidence that habitat suitability was higher where strong El Niño conditions were present (negative SOI value) in gently sloping areas away from the coast. Environmental variables that were frequently important in all models was bathymetry (46.1%), Chl-a concentration (18.5%), SOI (ENSO index) (9.3%) and distance to coast (8.1%) (Fig 2.10). Interestingly, habitat suitability of Spinetail devil rays over the study period did not seem to be influenced by fluctuations in sea surface temperature or the distance from the 200m isobath. All variables were chosen to be incorporated in the final model, after checking for multicollinearity using a Pearson's correlation test. No variables were highly correlated (for BRT models, > 0.9), thus, all variables were included in the final model (see correlation matrix of key variables in Appendix 2.2).

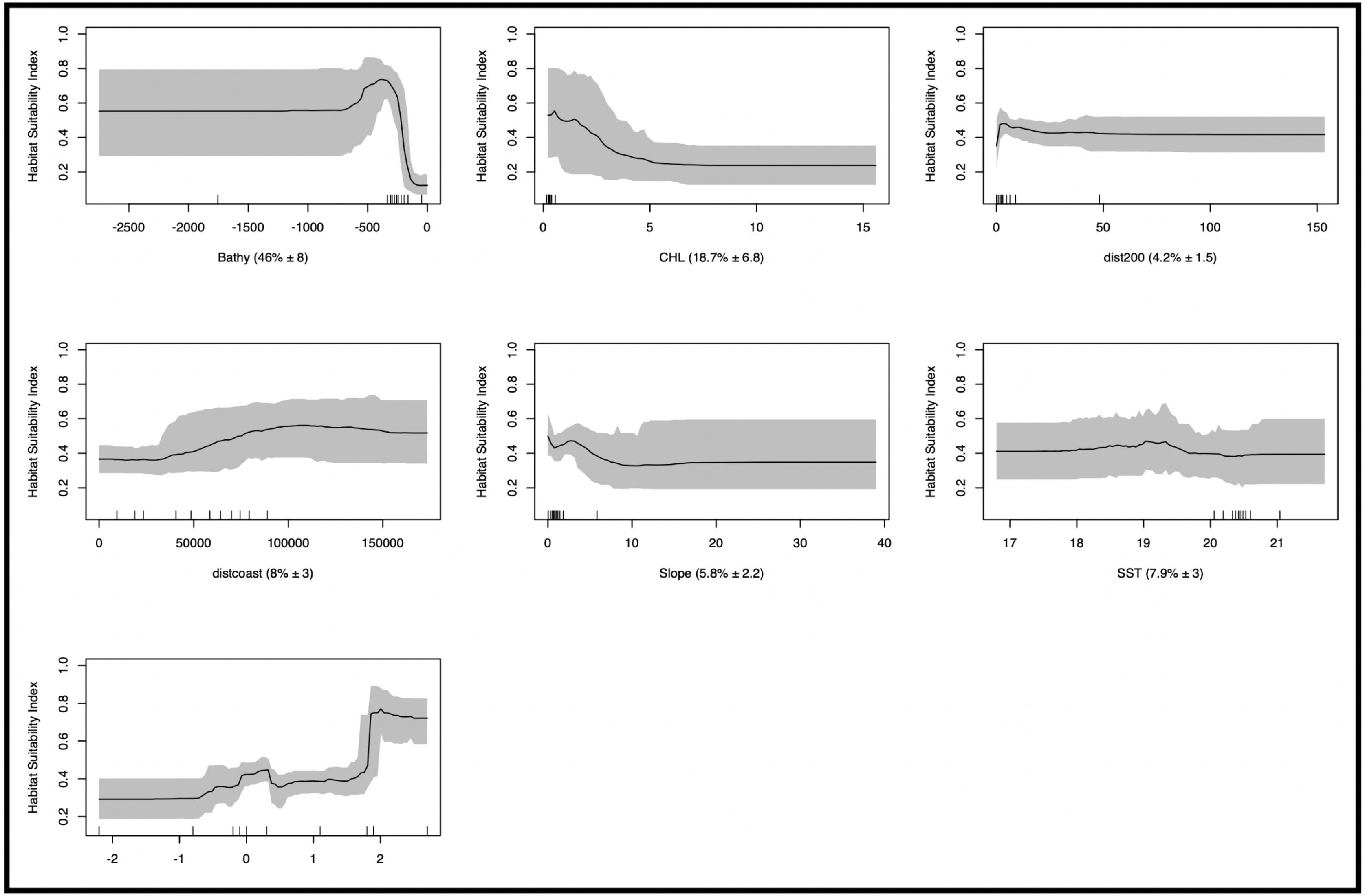

Figure 2.9 *Partial dependence plots for the static Spinetail devil ray model. The plot shows the relationship between the habitat suitability of Spinetail devil rays against the gradient of a given environmental variable, while holding all other variables at a constant. The grey envelope represents the uncertainty in these predictions, with a wider envelope indicating higher uncertainty at these ranges.*

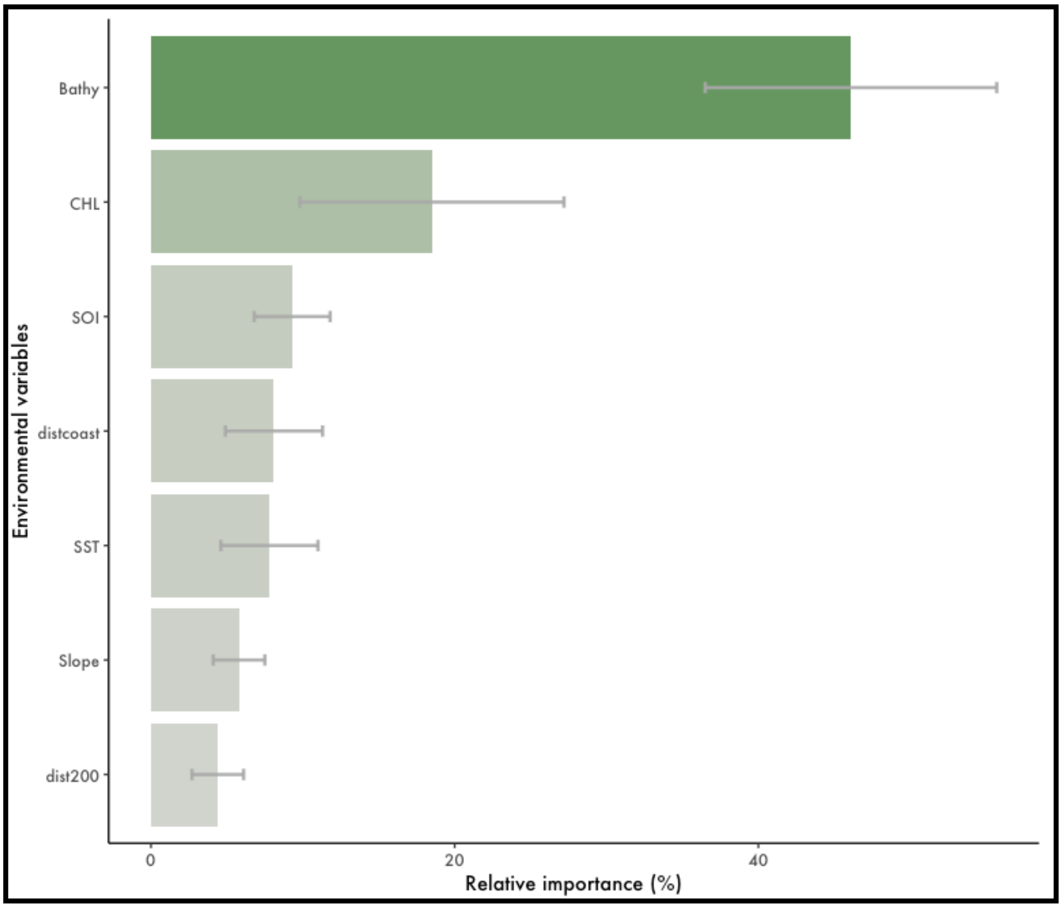

Figure 2.10 *Variable contribution for static Spinetail devil ray model. Green bars indicate variable contribution while grey lines depict the error associated with the contribution value. Larger and darker green bars indicate higher relative importance while smaller and lighter green bars are indicative of low relative importance to habitat suitability.*

Like the static model, the dynamic model suggests high habitat suitability in the same depth range away from the coast. However, in this model there is strong evidence that habitat suitability is higher in warmer waters that have low turbidity (Fig 2.11). High Chl-a values continue to support areas with high habitat suitability especially in gently sloping areas around the 200m isobath (Fig 2.11). There is an unclear relationship between SST and Chl-a gradients and habitat suitability however, there is a decreasing habitat suitability trends as SST and TSS increase but an increase where Chl-a gradient is more pronounced (Fig 2.11). The most influential environmental variables in the dynamic model were bathymetry (42.3%), Year (16.2%) and distance to coast (8.9%) (Fig 2.12). Year 2022 shows the highest habitat suitability based on Year and this indicates that with an increase that cannot be attributed to other environmental variables, and this represents a part of the model that is unexplained (Fig 2.11). Thus, “Year” represents 16.2% of the changes in habitat suitability that are happening over time that are not explained by the environmental variables included in the model – this could include variables such as survey effort or prey density (zooplankton specific). Like the static model, no variables were highly correlated (for BRT models, > 0.9), thus, all variables were included in the final model (see correlation matrix of key variables in Appendix 2.3).

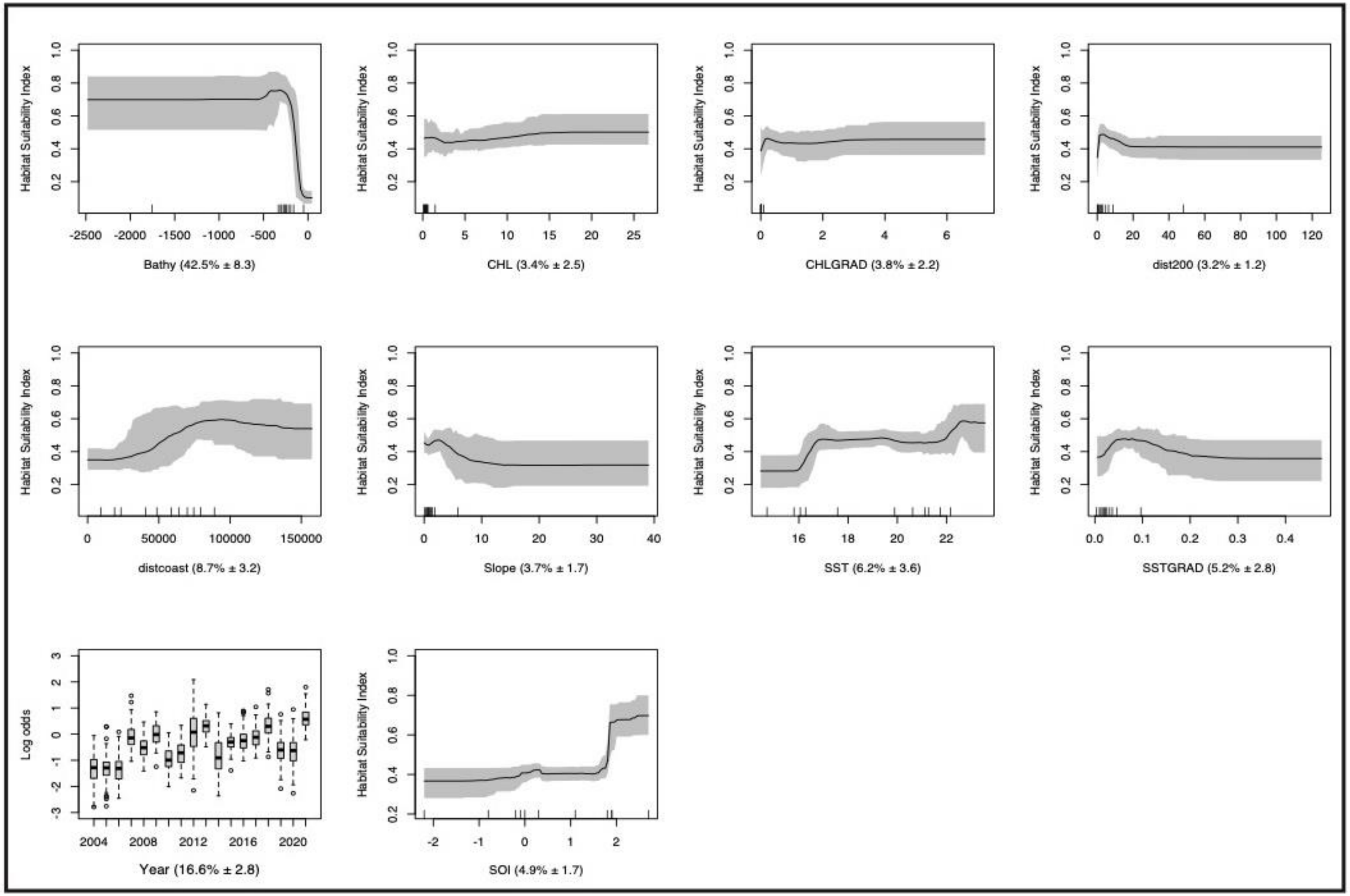

Figure 2.11 Partial dependence plots for the dynamic Spinetail devil ray model. The plot shows the relationship between the habitat suitability of Spinetail devil rays against the gradient of a given environmental variable, while holding all other variables at a constant. The grey envelope represents the uncertainty in these predictions, with a wider envelope indicating higher uncertainty at these ranges. Note that "Year" denotes a latent variable that is not linked to any spatial processes. It represents variability in predicted habitat suitability over the years that is not captured by the environmental variables in the model.

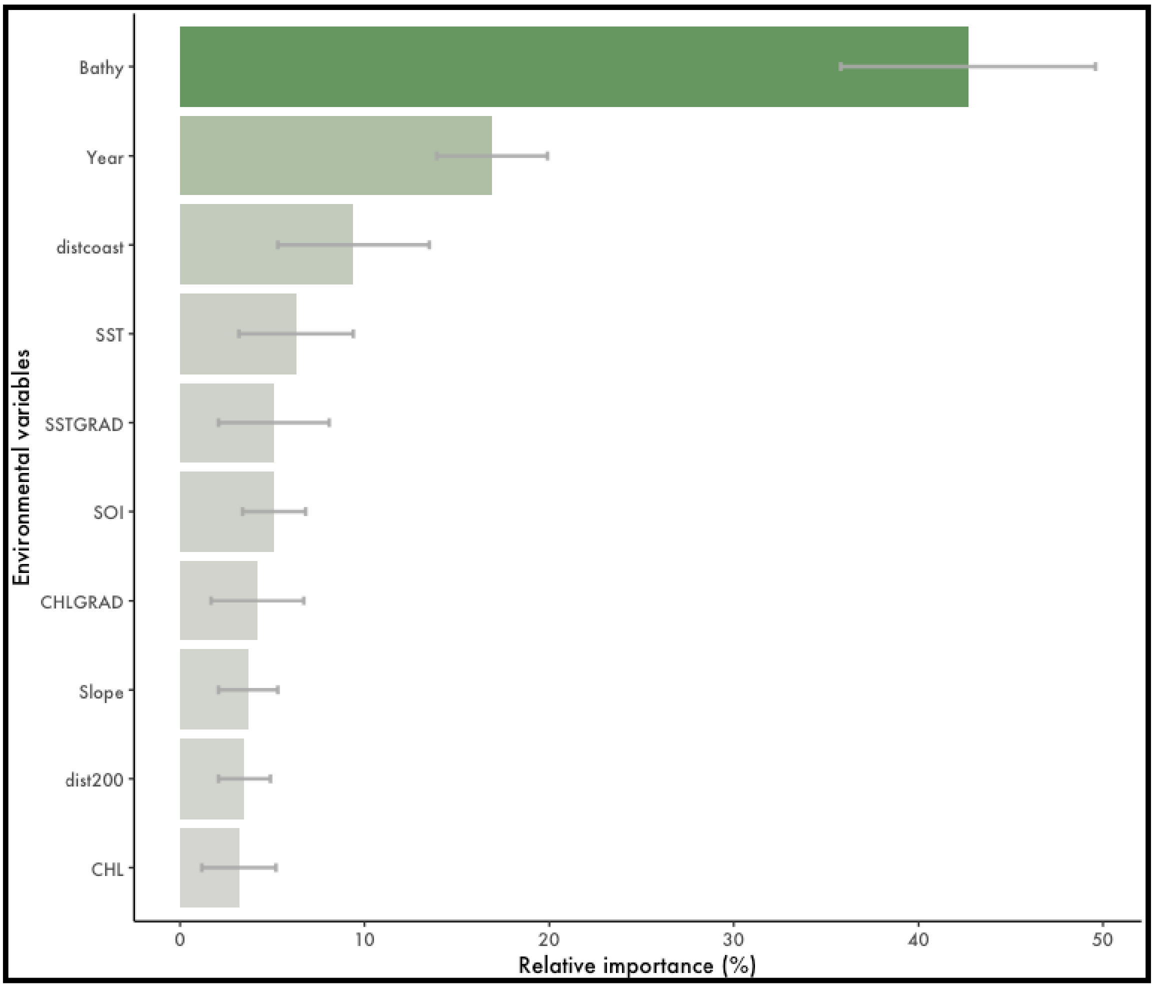

Figure 2.12 *Variable contribution for dynamic Spinetail devil ray model. Green bars indicate variable contribution while grey lines depict the error associated with the contribution value. Larger and darker green bars indicate higher relative importance while smaller and lighter green bars are indicative of low relative importance to habitat suitability*

2.3.1.4 Predicted habitat suitability

Static model

Areas of high habitat suitability predicted from the static model for Spinetail devil rays in Aotearoa New Zealand occurred along the continental slope, especially along the 200m depth contour line around the Te Ika-a-Māui North Island (Fig 2.13a). Predictive maps indicated that the highest habitat suitability is seen past Aotea Great Barrier Island along the continental shelf at the 200m line. This area is also predicted with moderate certainty (SD < 0.2; Fig 2.13b). The inner Tīkapa Moana Hauraki Gulf and coastal areas have extremely low habitat suitability values. These coastal areas are predicted with high certainty (SD < 0.05) and indicative of the preference for offshore waters. Another pocket of high habitat suitability is seen off the coast of the northern tip of the country, past Otou North Cape which is past the 200m line and adjacent to an area with very low habitat suitability. However, within the spatial coverage of the species, areas with moderate to high uncertainty (SD > 0.2) were most offshore waters, past the 200m contour line especially further south in Te Moana a Toi-te-Huatahi Bay of Plenty and further north, off the coast of Rākaumangamanga Cape Brett (Fig 2.13b).

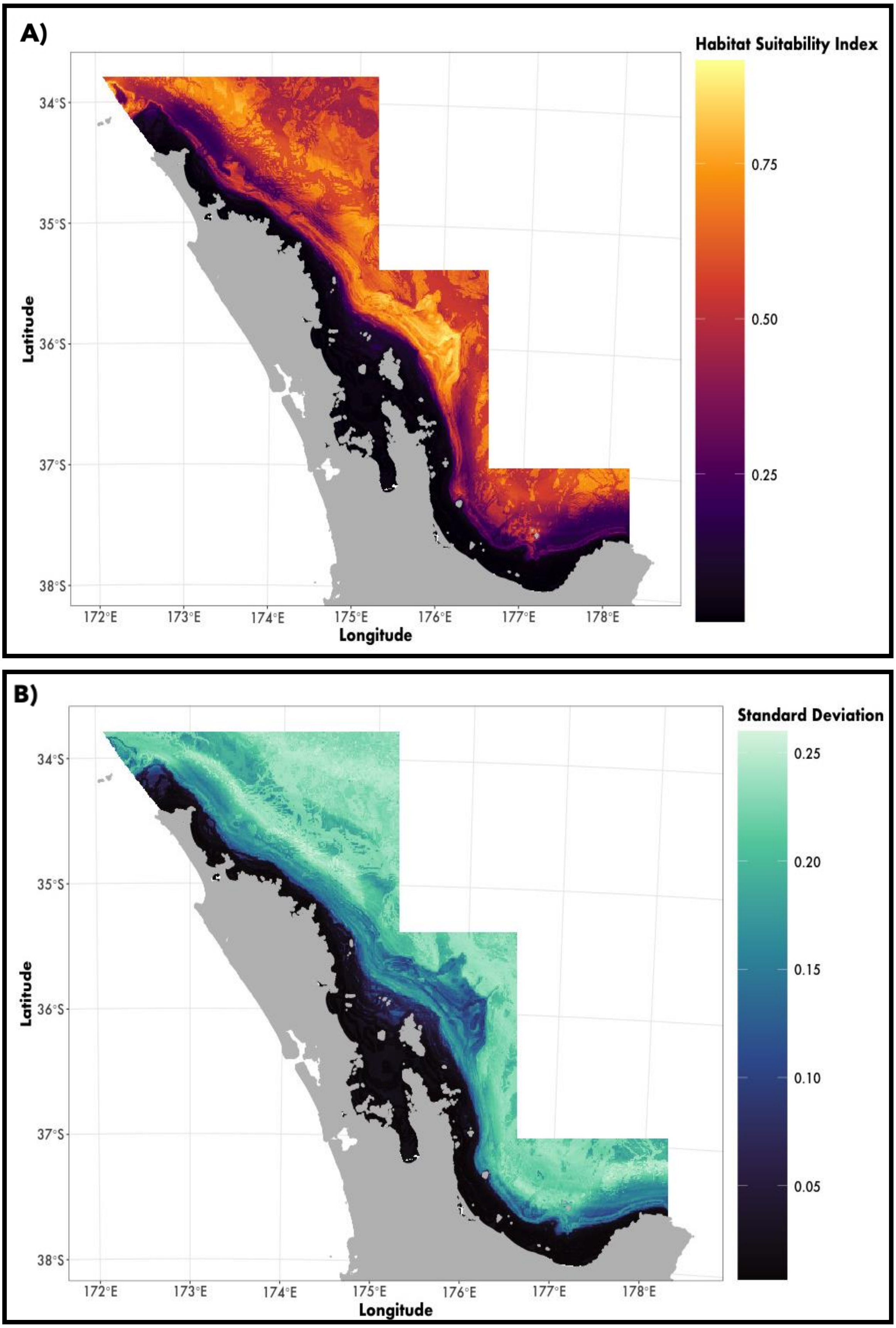

Figure 2.13 A) *Predicted habitat suitability index (HSI) of Spinetail devil rays in the northeastern shelf of the Te Ika-a-Māui North Island, New Zealand for each year between 2004 and 2021 using 100 bootstrapped temporally explicit (dynamic) BRT model.* ***B)*** *Standard deviation of predicted HS of Spinetail devil rays for every year of the study period (2004-2021) calculated from the 100 bootstraps of the model. Higher values in lighter blue indicate higher degree of uncertainty in predictions.*

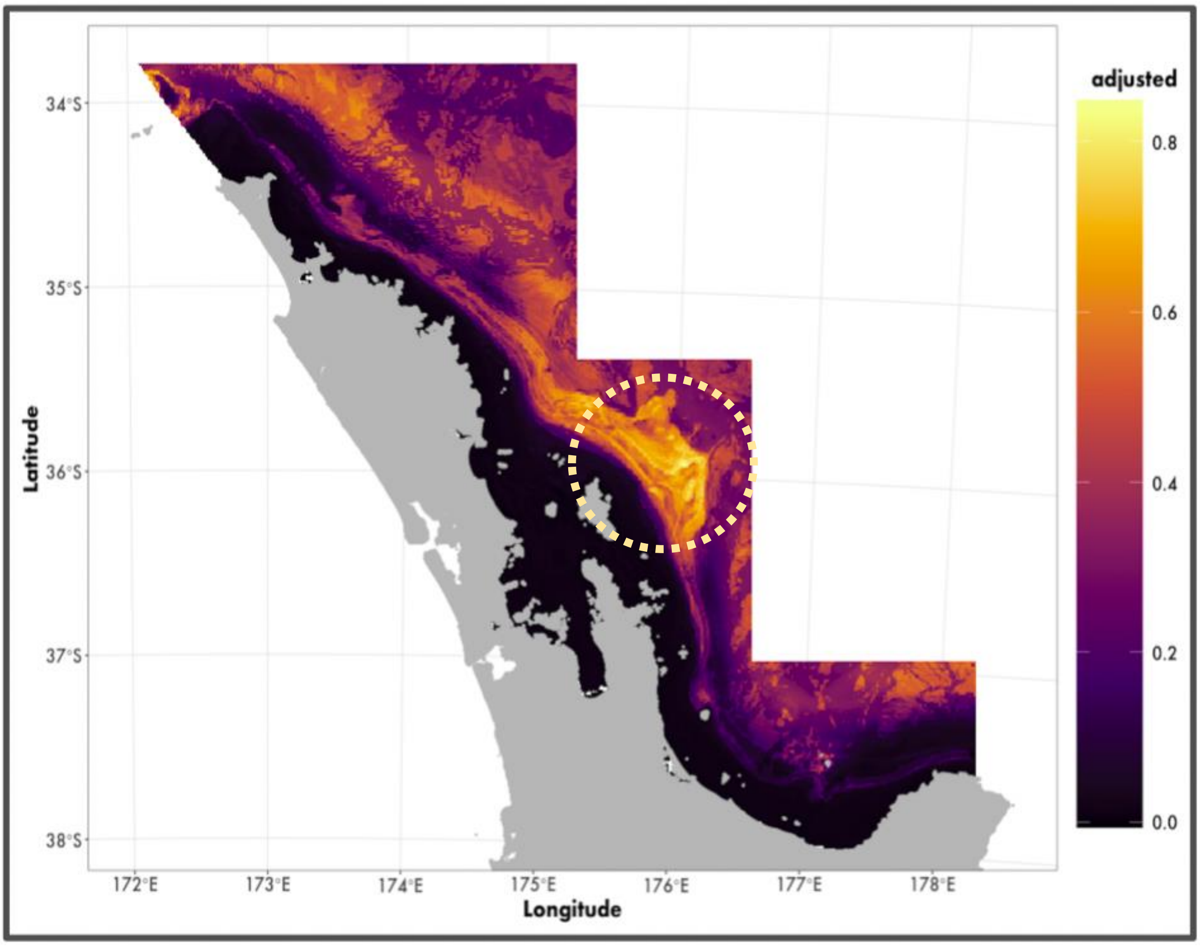

Figure 2.14 *Predicted habitat suitability index of Spinetail devil rays in northeastern shelf of the Te Ika-a-Māui North Island of New Zealand from 2004 to 2021, weighted by degree of error following Moilanen et al. (2006) and Stephenson et al. (2020b). Calculated by multiplying standard deviation with a value representing horizontal uncertainty then subtracting original predications with this value – called uncertainty discounting. Yellow dashed circle representing potential hotspot in outer shelf.*

Due to the few observations further offshore, although these areas show high habitat suitability, it is also associated with high uncertainty (Fig 2.13b). Hence, a method called uncertainty discounting was used to weight the predictions at each pixel by a degree of error. This ensures that areas with high habitat suitability and high standard deviations are penalised and the higher the standard deviation, the larger the prediction is discounted by. Compared to the prediction map (Fig 2.13a), the uncertainty discounted map shows that the highest habitat suitability is solely found at the outer shelf by the Tīkapa Moana Hauraki Gulf, tracing the contour of the 200m isobath, and extending further offshore towards the 500m isobath (Fig 2.14).

Dynamic model

In contrast to the static model, the dynamic model suggests greater areas of high habitat suitability (Fig 2.15). The most consistent predictions for habitat suitability remains within the inner- and outer Gulf and borders the coastal areas along the edge of the country, where low habitat values are predicted with high certainty for all years (SD < 0.05) (Fig 2.16). Areas of high habitat suitability extend further offshore especially far off the coast of Rākaumangamanga Cape Brett which is also predicted with moderate certainty (SD > 0.15). Over the study period, there is no substantial change in habitat suitability. The distribution of habitat suitability remains consistent and the only fluctuating differences between the years is the intensity or degree of habitat suitability and whether the area moves marginally further inshore. Years of higher habitat suitability are 2005, 2007, 2009, 2011, 2013, 2017, 2019 and 2021. Years where the areas of high suitability appear to move slightly inshore are 2007, 2009, 2011, 2013, 2017, 2019 and 2021. Areas of high uncertainty (SD > 0.2) appear to be further south by Te Moana a Toi-te-Huatahi Bay of Plenty, off the coast of the Otou North Cape. Although the static model predicted high habitat suitability along the 200m contour line, due to the high values elsewhere, this area does not seem to be especially favourable from year to year (Fig 2.15). The distribution of uncertainty remains consistent throughout the years and similar to habitat suitability, the degree of uncertainty is the only observed changes over the study period.

Similarly to the static model, habitat suitability predictions were adjusted by the standard deviation to assess whether predictions would change consistent after being weighted by uncertainty (Fig 2.17). When accounting for uncertainty, predictions reflect that of the static model more and the high habitat suitability predictions along the 200m isobath along the outer shelf is highlighted along the whole continental shelf. Offshore areas that were predicted with high index values now show low adjusted values, indicating that the calculations accounted for the high uncertainty in this area in an appropriate manner (Fig 2.17). However, similar to the original predictions (Fig 2.15), there seems to be little variation between years, with no evidence of a long-term shift in distribution of Spinetail devil rays over the study period (Fig 2.17). Further, inter-annual variations seem to manifest in the increase/decrease in habitat suitability along the shelf-edge or the increase of suitability further offshore (especially notable in 2004, 2006, 2010, and 2020).

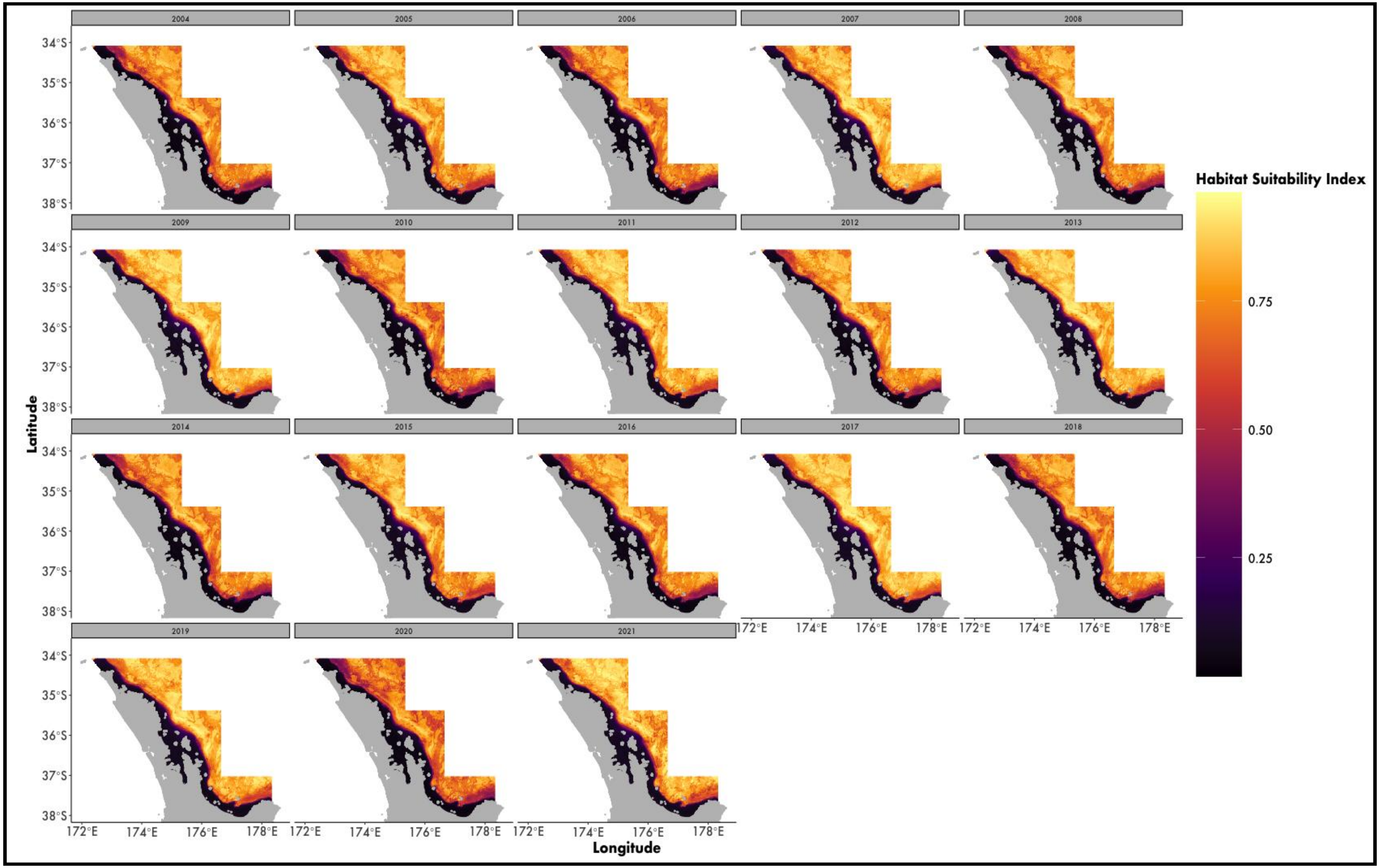

Figure 2.15 *Predicted habitat suitability index (HSI) of Spinetail devil rays in the northeastern shelf of Te Ika-a-Māui North Island, Aotearoa New Zealand for each year between 2004 and 2021 using 100 bootstrapped temporally explicit (dynamic) BRT model. Yellow areas indicate higher habitat suitability, and darker colours are indicative of lower suitability.*

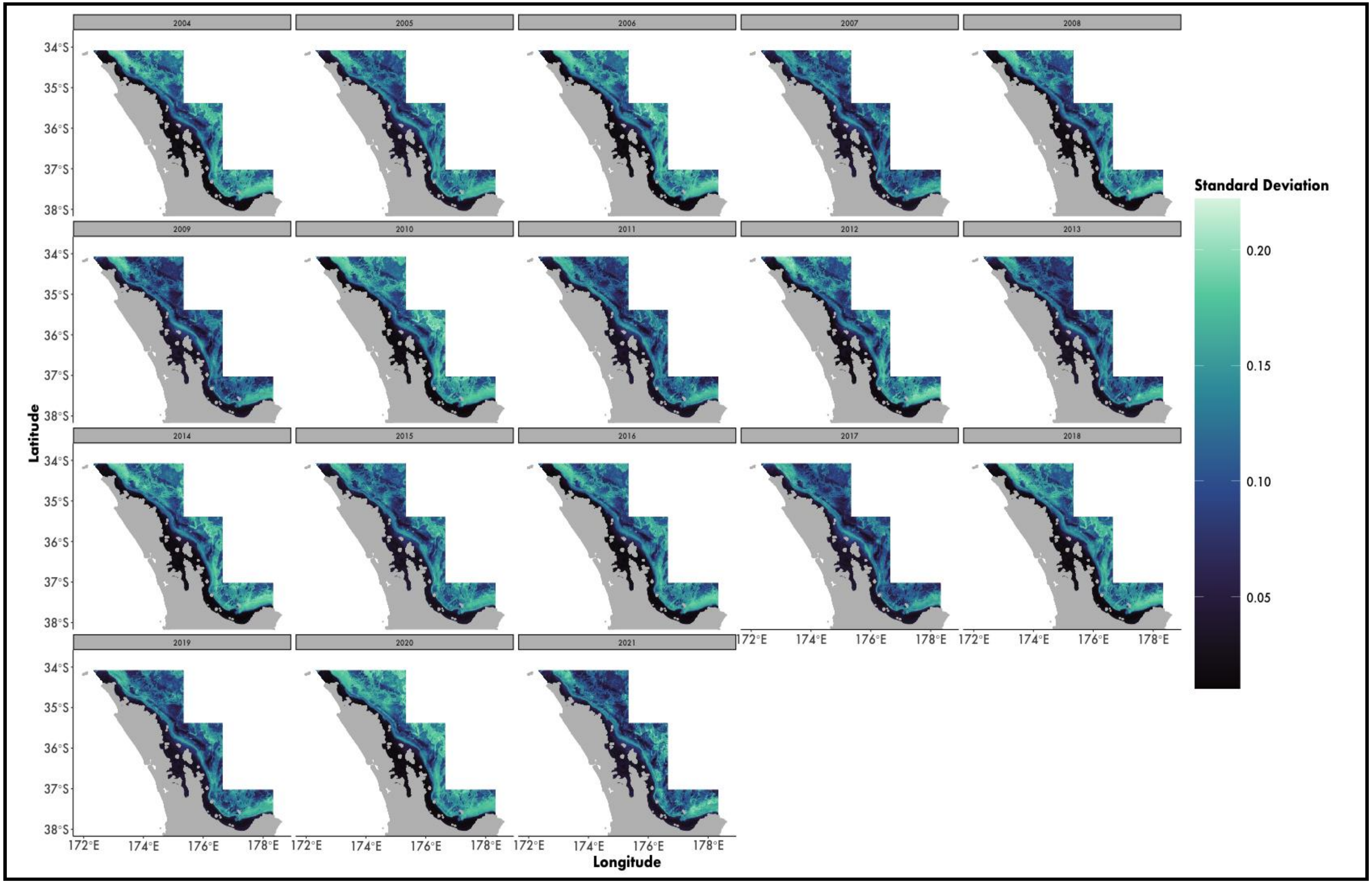

Figure 2.16 *Standard deviation of predicted HS of Spinetail devil rays for every year of the study period (2004-2021) calculated from the 100 bootstraps of the model. Higher values indicated by lighter blue represent higher degree of uncertainty in predictions.*

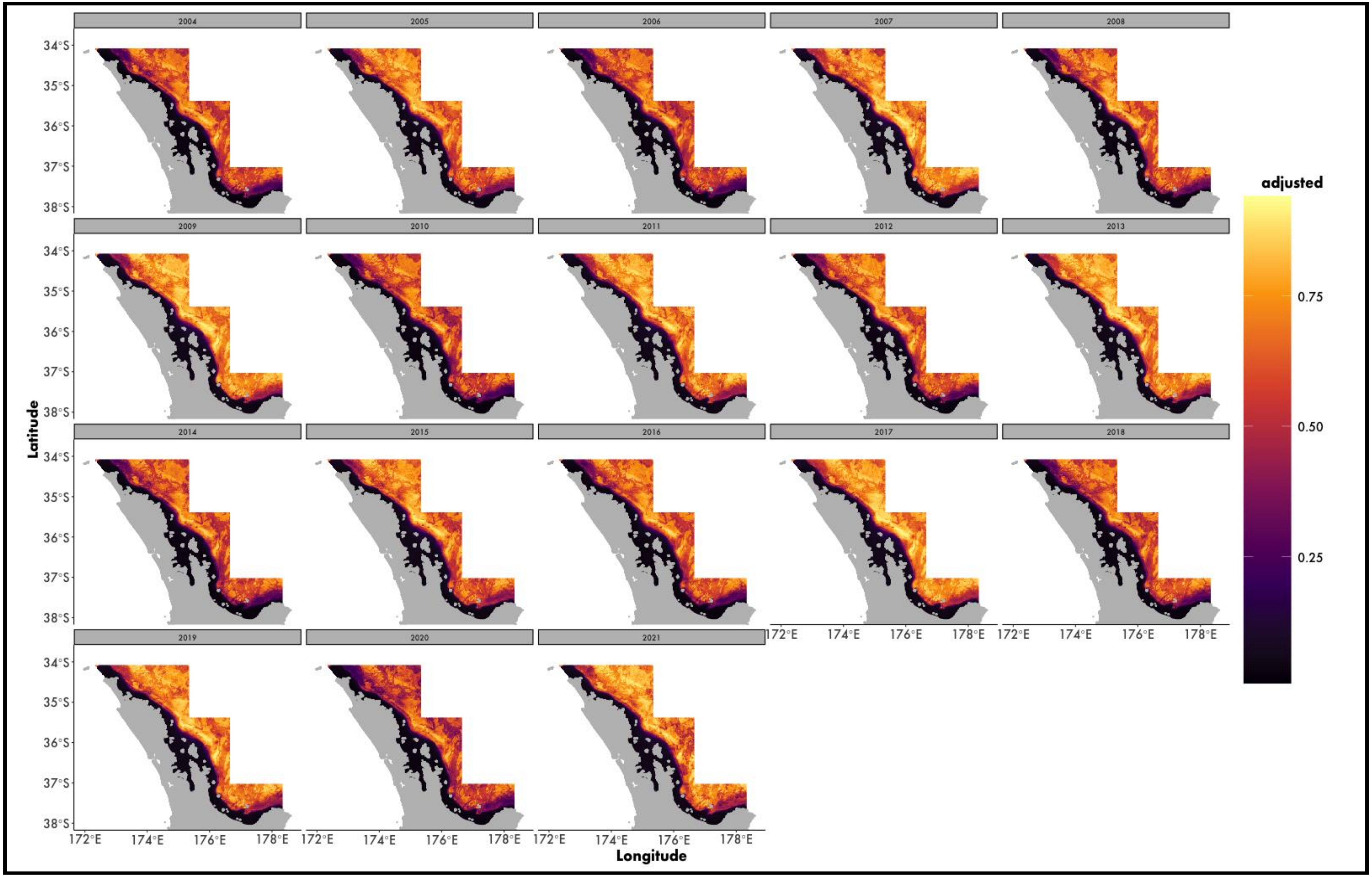

Figure 2.17 *Predicted habitat suitability index of Spinetail devil rays in northeastern shelf of the Te Ika-a-Māui North Island of AotearoaNew Zealand for every year of the study period from 2004 to 2021, weighted by degree of error following Moilanen et al. (2006) and Stephenson et al. (2020b). Calculated by multiplying standard deviation with a value representing horizontal uncertainty then subtracting original predications with this value – called uncertainty discounting.*

2.3.2 Oceanic manta ray

2.3.2.1 Oceanic manta ray records

The final records that were incorporated in the model (n = 366) were all obtained from Manta Watch New Zealand's database (MWNZ; https://mantawatchnz.org/). Oceanic manta rays were observed in all months of the year except July, August and October, but most records (89%; n = 327) were in the summer (Dec-Feb). However, the model was fitted to incorporate all months that Oceanic manta rays were observed in regardless of the number of sightings, thus, depicting a larger part of the year instead of a purely summer model. The most recent observation was February 23rd in 2022. Unlike the data obtained from the Ministry for Primary Industries, the only information available was geographical coordinates, possibly reflecting the limitation of citizen science data to provide further information on sex and size.

2.3.2.2 Model performance

Based on AUC and TSS indices, model performance for both static (AUC: 0.73 and TSS: 0.49; Table 2.4) and dynamic (AUC: 0.90 and TSS: 0.77; Table 2.4) are deemed useful in in predicting Oceanic manta ray habitat suitability. Interestingly the dynamic model, despite presumed issues with few occurrence records in some years, performed better than the static model. Although this could be indicative of issues associated with pseudo-absence selection, the high model performance of the dynamic model suggests that this is probably not the case. Further, although the model performance for the static model is less than that of the dynamic, the AUC value is above 0.7, and the TSS value close to the arbitrary 0.5 threshold for usefulness, thus, the model can be deduced to be useful in predictions and better than random chance. The low standard deviations across all indices and models are indicative of a consistent model across all 100 bootstraps. The similarity in model fits between training and evaluation data suggest that the model is not overfitted and the evaluation data lower than that of the training, is consistent with what is expected.

Table 2.4 *AUC and TSS values both on training and evaluation (testing) data is shown for both static and dynamic models for Oceanic manta rays.*

Study period	Model type	AUC (training data)	AUC (evaluation data)	TSS (training data)	TSS (evaluation data)
2006 - 2022 (Oceanic manta Ray)	Static	0.86 ± 0.01	0.73 ± 0.04	0.79 ± 0.01	0.49 ± 0.03
	Dynamic	0.95 ± 0.01	0.90 ± 0.03	0.93 ± 0.01	0.77 ± 0.04

2.3.2.3 Variable contribution

The static model suggests that habitat suitability for Oceanic manta rays is higher in areas with high Chl-a concentrations, lower SST values in shallower waters close to the coast in comparison with Spinetail devil rays (Fig 2.18). Although the impacts of seasonality and ENSO would have been insightful and useful to understand, the use of pseudo-absences and the random generation of “Year” and “Month” to each point meant that the interpretation of such Month and ENSO variables would have been difficult with no real relationship to analyse. Environmental variables that were frequently important in all models were Chl-a (22.6%), SST (19.5%), bathymetry (18.4%) and slope (18.2%) (Fig 2.19). Unlike the static Spinetail devil ray model where a singular variable dominated variable contribution, five variables were almost all equally important in the habitat suitability, with only one variable (distance to 200m isobath) relatively unimportant (Fig 2.19). All variables were chosen to be incorporated in the final model, after checking for multicollinearity using a Pearson’s correlation test. No variables were highly correlated (for BRT models, > 0.9), thus, all variables were included in the final model. The correlation matrix of key variables is shown in the Appendix 2.3.

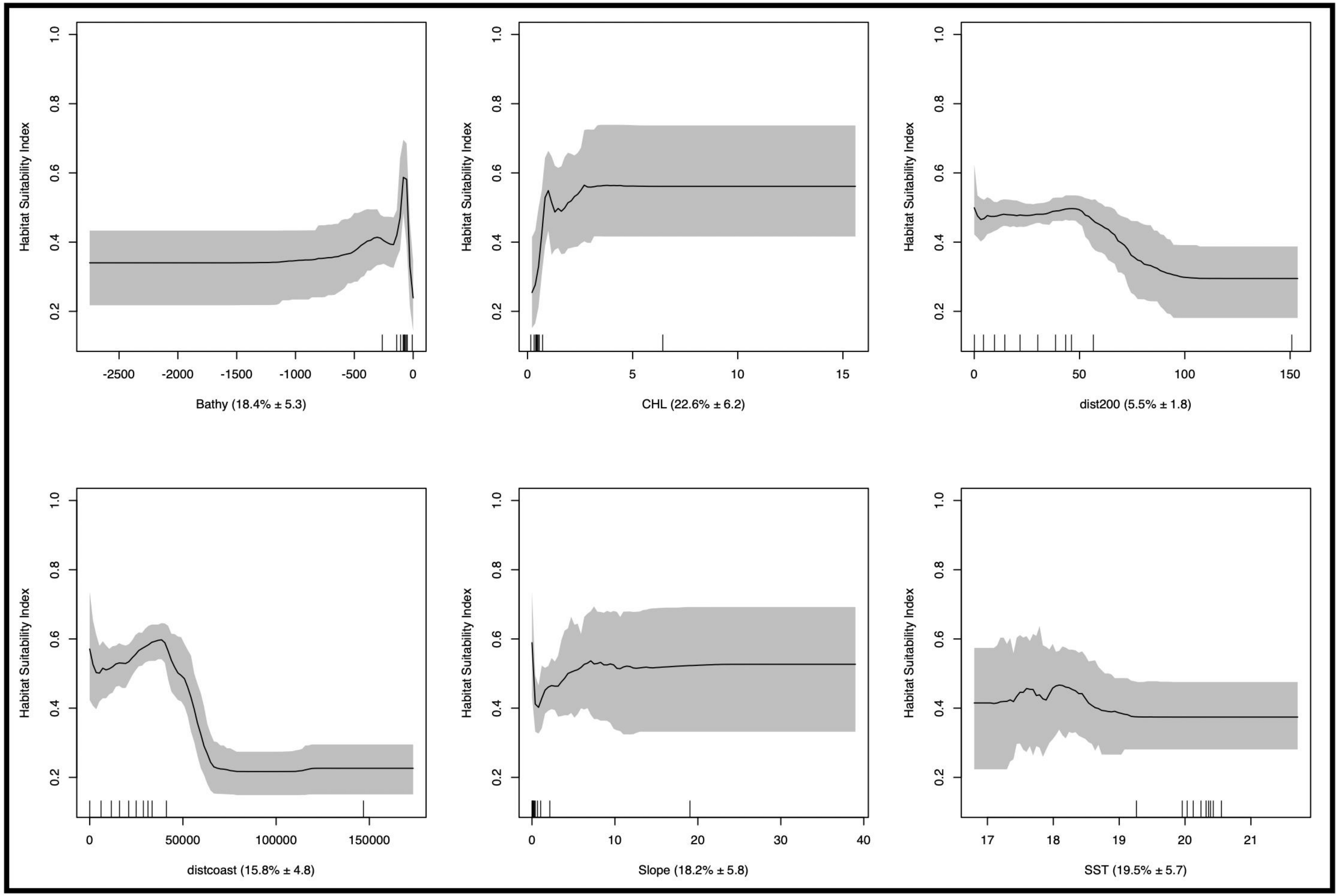

Figure 2.18 *Partial dependence plots for the static Oceanic manta ray model. The plot shows the relationship between the habitat suitability of Oceanic manta rays against the gradient of a given environmental variable, while holding all other variables at a constant. The grey envelope represents the uncertainty in these predictions, with a wider envelope indicating higher uncertainty at these ranges.*

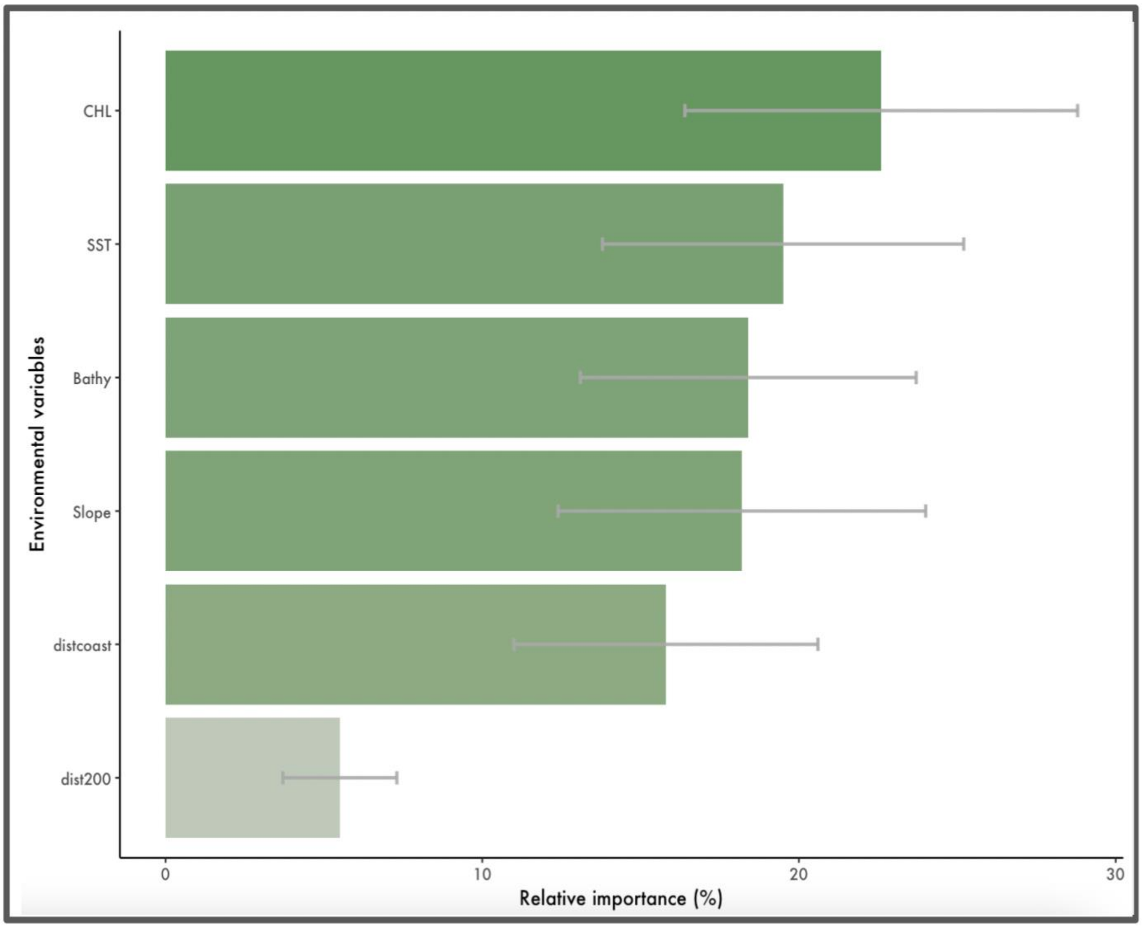

Figure 2.19 *Variable contribution for static Oceanic manta ray model. Green bars indicate variable contribution while grey lines depict the error associated with the contribution value. Larger and darker green bars indicate higher relative importance while smaller and lighter green bars are indicative of low relative importance to habitat suitability.*

By contrast, the dynamic model suggests high habitat suitability in areas with high SST values and moderate Chl-a concentrations (Fig 2.20). As expected, the static variables such as bathymetry, distance to coast parameters are remain the same in the dynamic model. Dynamic variables such as Chl-a and SST gradient indicate that habitat suitability is high in areas with a high SST gradient, perhaps indicative of frontal activity, and moderately low Chl-a gradient values (Fig 2.20). The most prevalent variables within the dynamic model were Year (48.7%), distance to coast (9.7%) and SST (8.8%) (Fig 2.21). Further, the extremely high importance of the "Year" suggests that variations in environmental or ecological variables over time, that are not captured or incorporated into the model are a large contributor to Oceanic manta ray habitat suitability. These variables are attributed to increasing the habitat suitability of Oceanic manta rays within the NE shelf over time, with suitability increasing exponentially and an eventual peak in 2021 and 2022. Similar to the static model, no variables were highly correlated after being tested with the

Pearson’s correlation test; thus, all variables were included in the final model for further analysis (see Appendix 2.3 for correlation matrix of key variables).

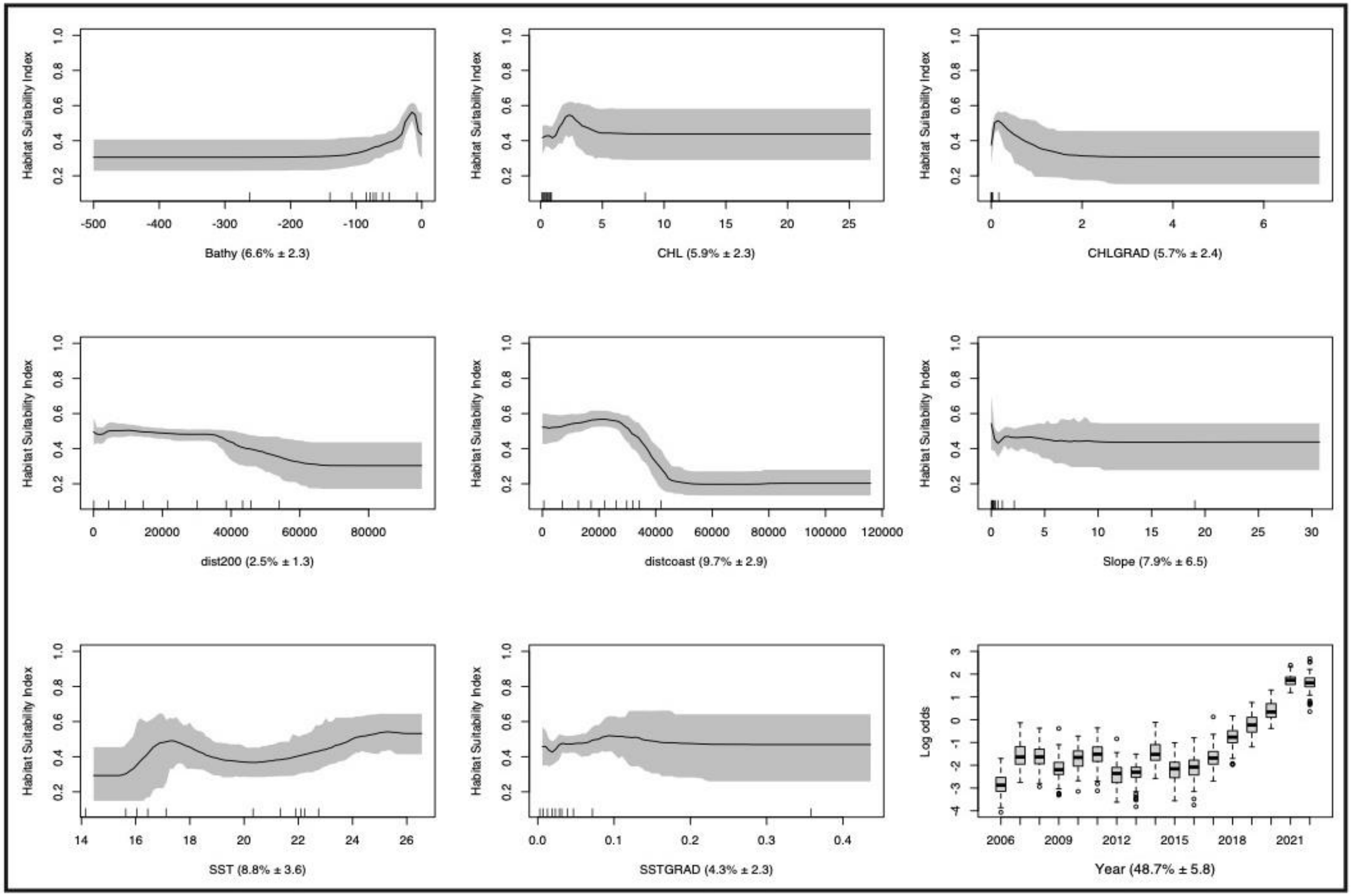

Figure 2.20 *Partial dependence plots for the dynamic Oceanic manta model. The plot shows the relationship between the habitat suitability of Oceanic manta rays against the gradient of a given environmental variable, while holding all other variables at a constant. The grey envelope represents the uncertainty in these predictions, with a wider envelope indicating higher uncertainty at these ranges. Note that "Year" denotes a latent variable that is not linked to any spatial processes. It represents variability in predicted habitat suitability over the years that is not captured by the environmental variables in the model.*

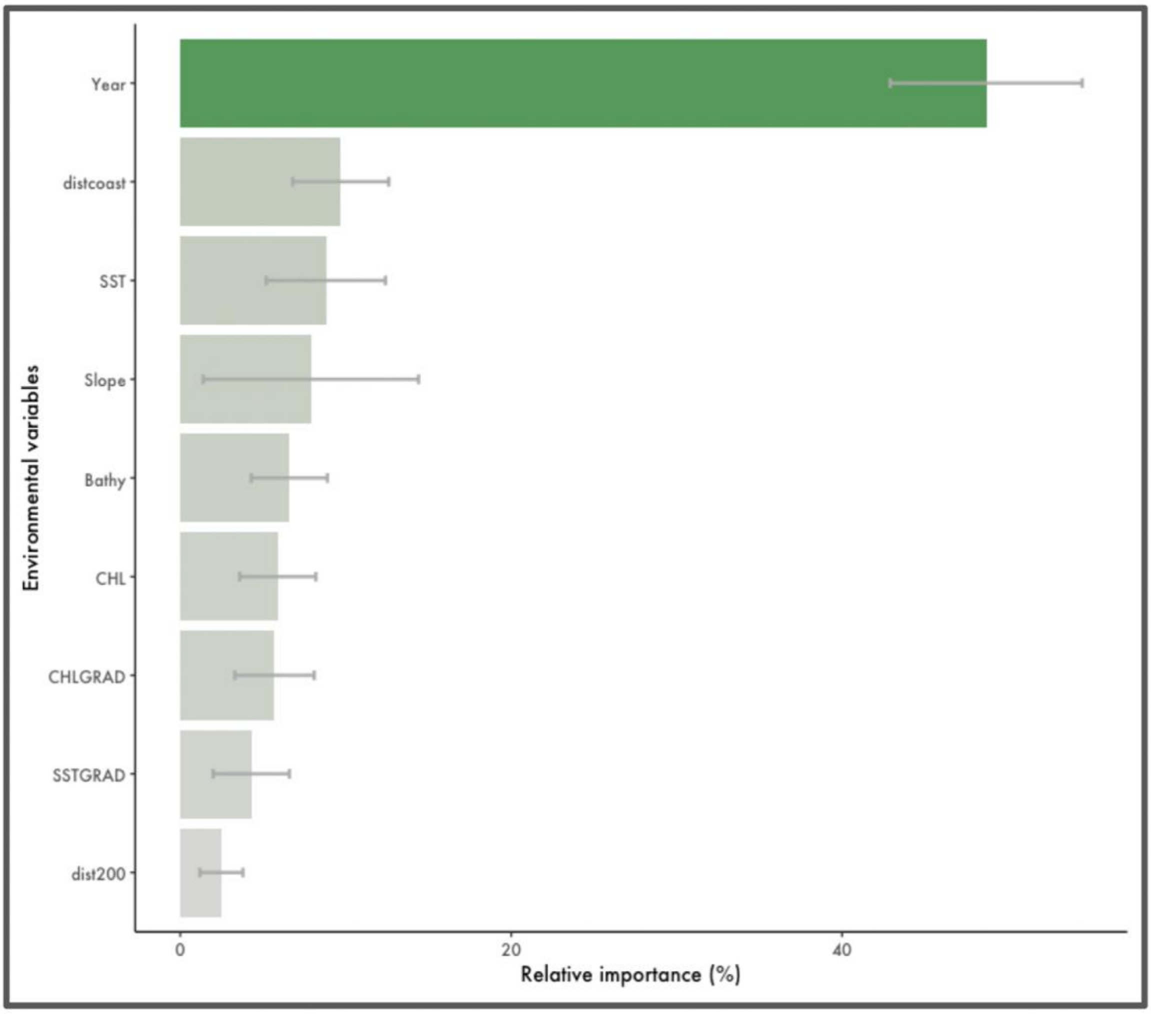

Figure 2.21 *Variable contribution for dynamic Oceanic devil ray model. Green bars indicate variable contribution while grey lines depict the error associated with the contribution value. Larger and darker green bars indicate higher relative importance while smaller and lighter green bars are indicative of low relative importance to habitat suitability.*

2.3.2.4 Predicted habitat suitability

Static model

The static model for Oceanic manta rays suggests that areas of high habitat suitability are coastal areas, starting from Otou North Cape, down the eastern coastline to the East Cape (Fig 2.22a). In comparison to the Spinetail devil ray static model where the 200m isobath marked the inshore extent of high suitability areas, for Oceanic manta rays, this contour line depicts the offshore extent of their predicted high habitat suitability (Fig 2.22a). In particular, an area with high suitability is located within the Tīkapa Moana Hauraki Gulf, in the Cradock Channel between Aotea Great Barrier Island and Te Hauturu-o-Toi Little Barrier Island, as well as the Jellicoe Channel between Te Hauturu-o-Toi Little Barrier Island and Rākaumangamanga Cape Brett (Fig 2.22a). Offshore waters past the 200m isobath are predicted by the model to be areas of extremely low habitat suitability (HSI < 0.2; Fig 2.22b). Inshore coastal waters that show high habitat suitability are predicted with the highest uncertainty, however, even then the model predictions seem to be associated with relatively low uncertainty (SD < 0.2) in comparison with the Spinetail devil ray model output.

The relatively high certainty in predictions can be seen in Figure 2.23 where prediction values have been discounted by the degree of error (in this case, standard deviation at each cell). Like Spinetail devil ray models, the predictions were weighted with a high α (i.e., horizon of uncertainty), indicating that although habitat suitability will decrease, these values will be associated with low uncertainty (Moilanen et al., 2006). High habitat suitability remains close to the coast all down the eastern coastline, with a decrease of values further off the coast compared to the original map. Areas of the highest suitability remain just at the coast, within the Tīkapa Moana Hauraki Gulf through the Jellicoe and Cradock Channel and coastal Te Moana a Toi-te-Huatahi Bay of Plenty (Fig 2.23).

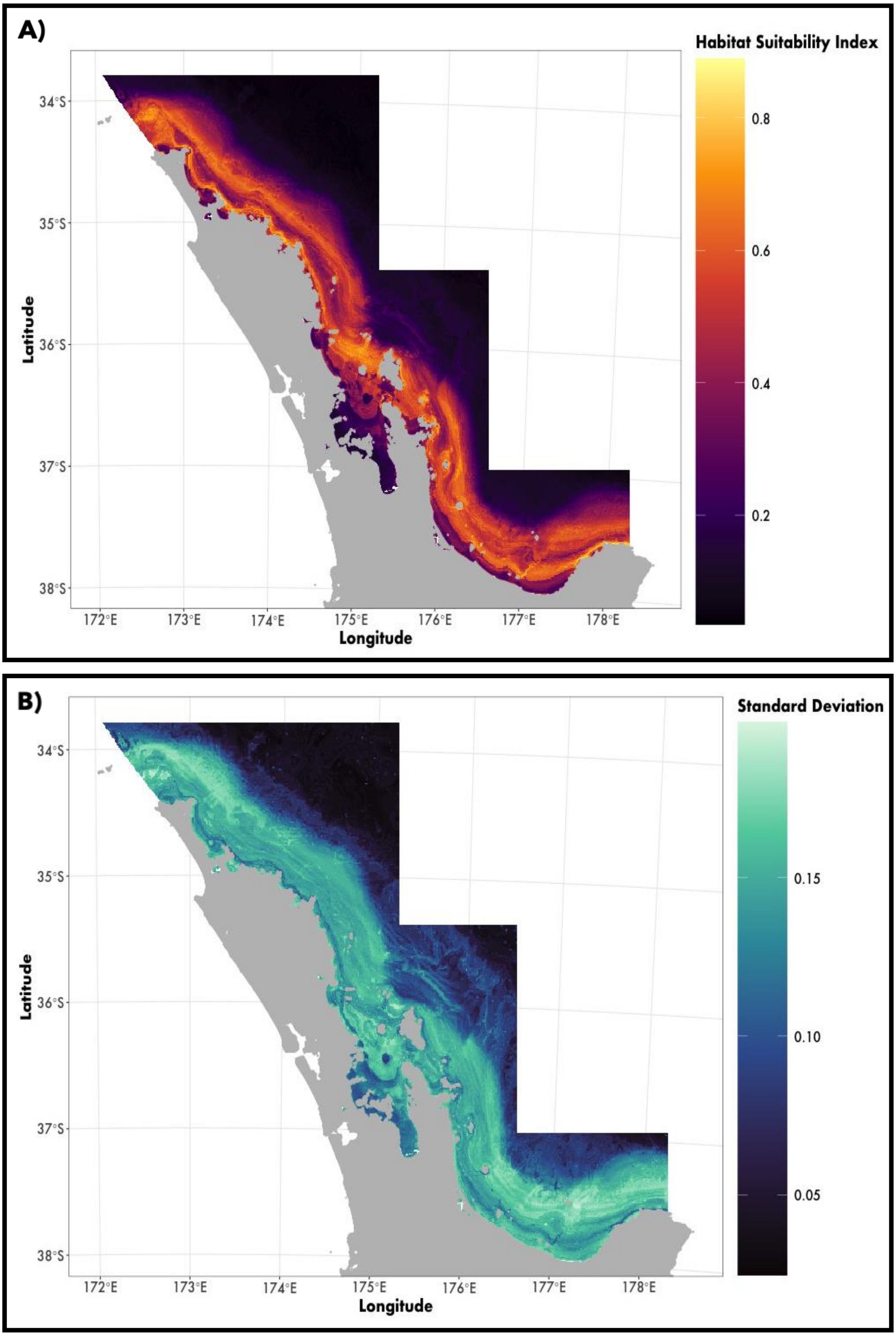

Figure 2.22 A) *Predicted habitat suitability index (HSI) of Oceanic manta rays in the northeastern shelf of the Te Ika-a-Māui North Island, Aotearoa New Zealand for each year between 2006 and 2022 using 100 bootstrapped temporally explicit (dynamic) BRT model.* ***B)*** *Standard deviation of predicted HS of Oceanic manta rays for every year of the study period (2006-2022) calculated from the 100 bootstraps of the model. Higher values indicate higher degree of uncertainty in predictions.*

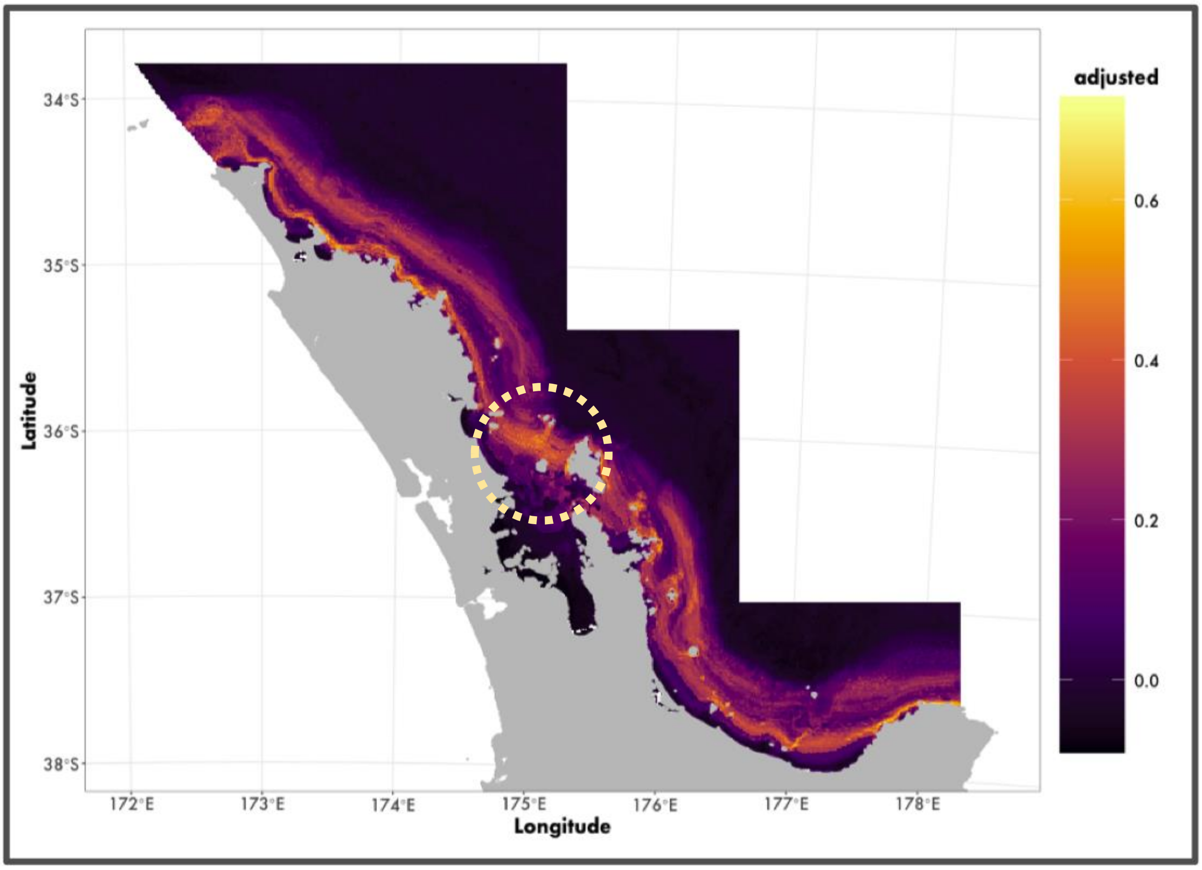

Figure 2.23 *Predicted habitat suitability index of Oceanic manta rays in northeastern shelf of the Te Ika-a-Māui North Island of Aotearoa New Zealand from 2006 to 2022, weighted by degree of error following Moilanen et al. (2006) and Stephenson et al. (2020). Calculated by multiplying standard deviation with a value representing horizontal uncertainty then subtracting original predications with this value – called uncertainty discounting. Yellow dashed circle represents potential hotspot area in the Jellicoe and Cradock Channel.*

Dynamic model

The dynamic model predicts coastal, inshore waters down the eastern coastline as areas with high habitat suitability, similar to the static model. Interestingly, a clear difference between each year of the study period can be seen in the maps (Fig 2.24). It is evident through the comparison of the maps that 2015, 2017, 2019, 2021 are years with the highest habitat suitability, denoted by the higher incidence of yellow within the maps. Further, out of these years 2019 and 2021 seem to be particularly predicted with high habitat suitability. These differences between the years cannot be due to pseudo-absence points, as the same 10,000 points were duplicated for every year, before subtracting duplicates. These years with high habitat suitability are also predicted with high certainty (SD < 0.2; Fig 2.25), and Figure 2.26 where uncertainty in predictions is accounted for. Similar to the Spinetail devil ray dynamic model, although there are differences between years in the degree of suitability, there seems to be no evidence of a shift in distribution, whether that be short-term in response to interannual variability, or a long-term shift in response to shifting environmental conditions due to climate change. We note that due to the use of pseudo-absence records that were randomly generated within a KDE probability grid and not based on biological information, that the inclusion of SOI, could not be included in this model. The inclusion of SOI could have given insight into the relationship with ENSO events however, such inclusion would have resulted in relationships that were no better than random.

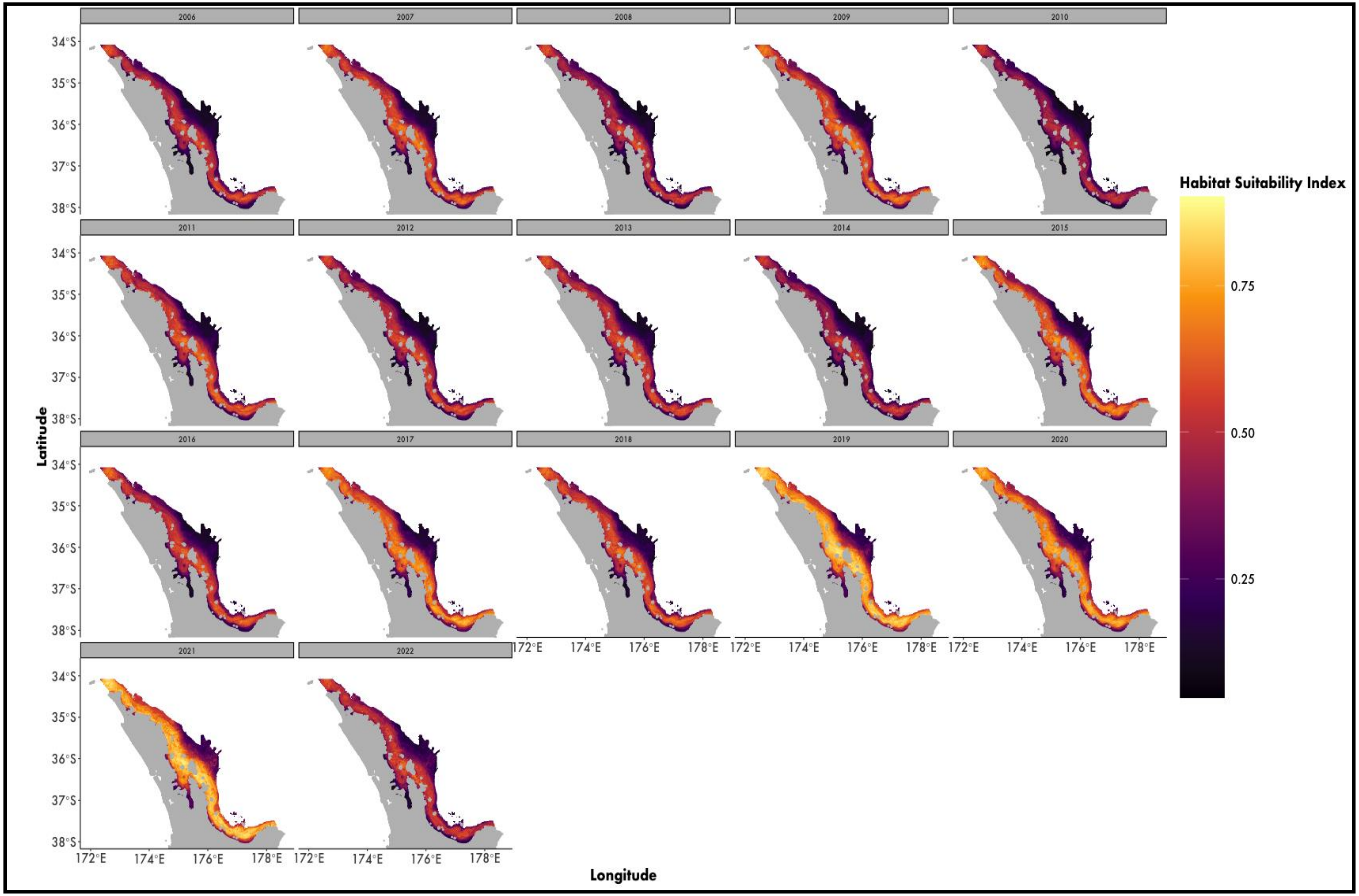

Figure 2.24 *Predicted habitat suitability index (HSI) of Oceanic manta rays in the northeastern shelf of the Te Ika-a-Māui North Island, Aotearoa New Zealand for each year between 2006 and 2022 using 100 bootstrapped temporally explicit (dynamic) BRT model. Yellow areas indicate higher habitat suitability, and darker colours are indicative of lower suitability.*

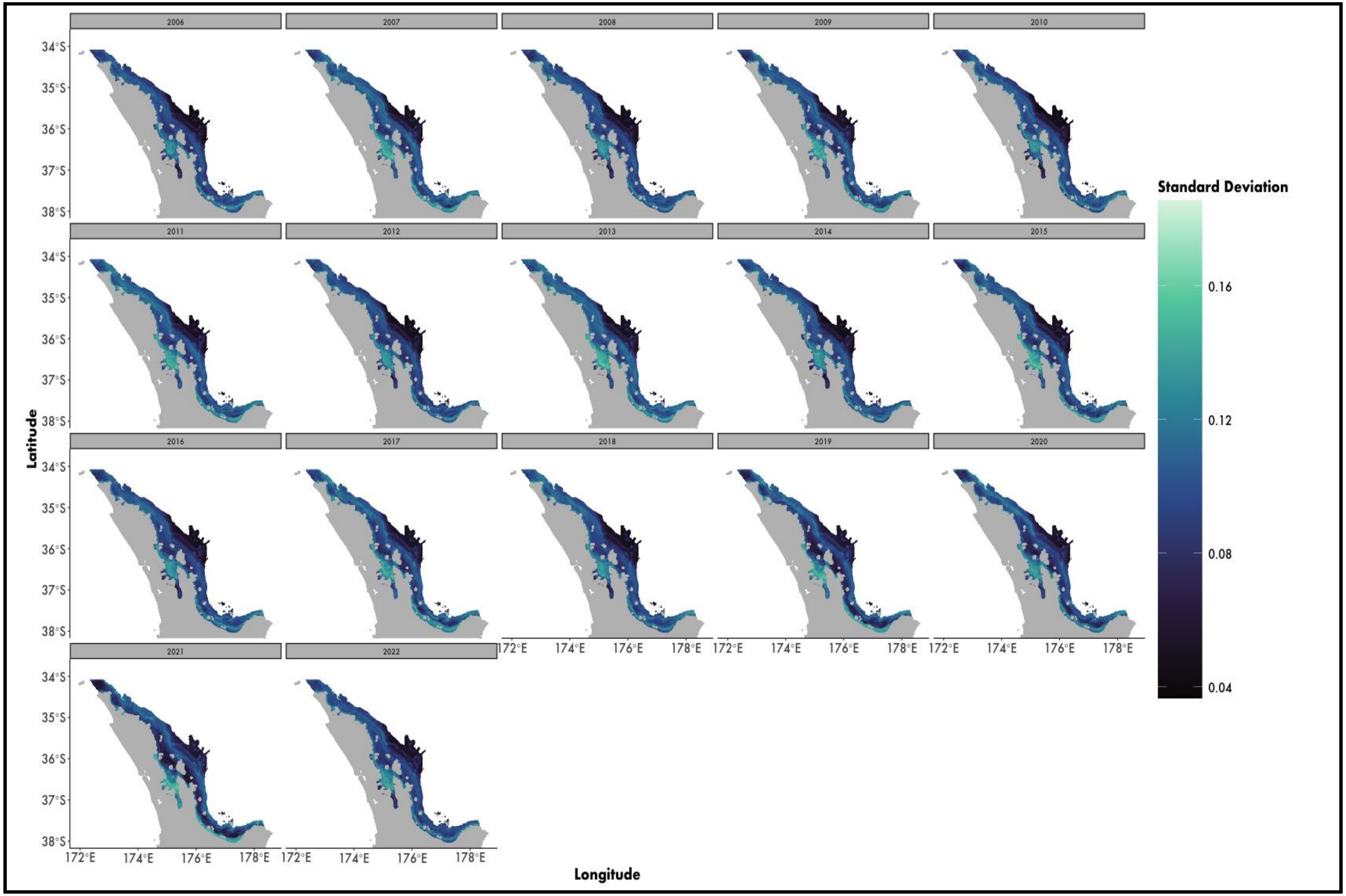

Figure 2.25 *Standard deviation of predicted HS of Oceanic manta rays for every year of the study period (2006-2022) calculated from the 100 bootstraps of the model. Higher values indicated by lighter blue represent higher degree of uncertainty in predictions.*

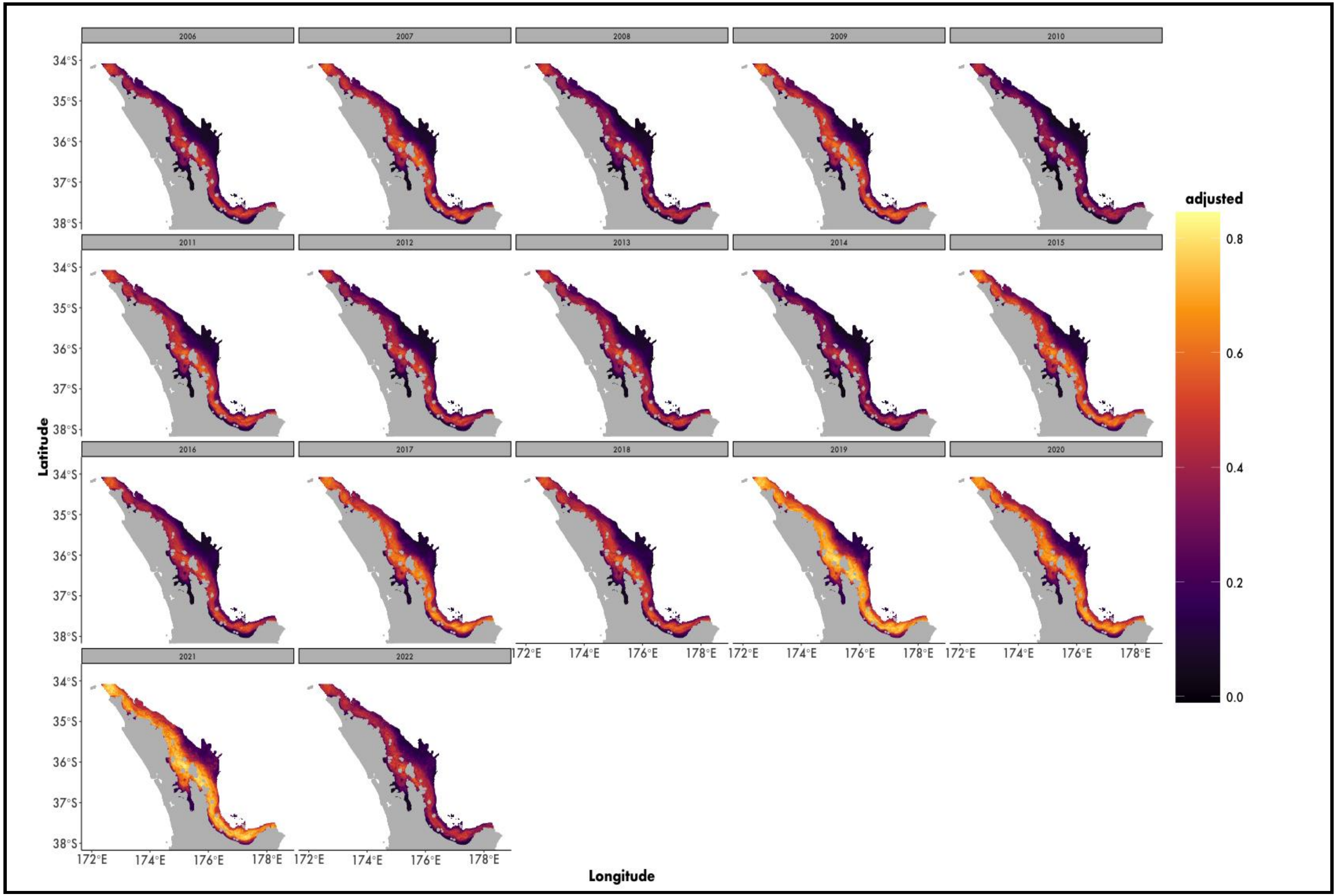

Figure 2.26 *Predicted habitat suitability index of Oceanic manta rays in northeastern shelf of the Te Ika-a-Māui North Island of AotearoaNew Zealand for every year of the study period from 2006 to 2022, weighted by degree of error following Moilanen et al. (2006) and Stephenson et al. (2020b). Calculated by multiplying standard deviation with a value representing horizontal uncertainty then subtracting original predications with this value – called uncertainty discounting.*

2.4 DISCUSSION

This chapter discusses the first SDM for mobulids in Aotearoa New Zealand. The results from the models and predictive mapping contribute to the current understanding of mobulids in terms of their habitat selection and distribution in the NE continental shelf of the Te Ika-a-Māui North Island. The current advances in the SDM literature indicate a movement towards explicitly incorporating time within models to agccount for the dynamic nature of marine environments and the organisms that live within it. The findings from this model reflect a contribution to this by comparing a long-term average model (static) and an annual model (dynamic). The most frequently influential variables across both species were distance to coast, bathymetry, and Chl-a concentration.

2.4.1 Spinetail devil ray habitat selection

The static model results suggests that habitat suitability for Spinetail devil rays is along the outer shelf of the Tīkapa Moana Hauraki Gulf with high Chl-a concentrations. Bathymetry was the highest contributor to habitat suitability with the highest values found between 150 and 500m for both static and dynamic models. The high prevalence of distance to coast suggests that although coastlines show favourable conditions, waters further offshore seem to be important. Habitat suitability peaks at 100km from the coastline probably around the continental shelf where individuals can access deep water prey. Multiple studies have found that devil rays are one of the deepest diving elasmobranchs with evidence of individuals reaching depths of over 1000m in Aotearoa New Zealand waters (Francis & Jones, 2016). Diving to these depths is presumably to exploit vertically migrating prey that move to deeper depths during the day; a response to avoid visually reliant predators (Hays, 2003; Zaret & Suffern, 1976). This behaviour is seen in other large filter feeders such as megamouth sharks (Nelson et al., 1997), whale sharks (Wilson et al., 2006), and basking sharks (Sims et al., 2005), and presents a significant advantage especially where nutrient-rich waters lie beneath the overlying euphotic waters

(Chang et al., 2003). This deep-diving behaviour is more likely to occur in deeper waters explaining the importance of bathymetry and distance from coast. This is supported by the high influence of Chl-a, a proxy for primary production, in the static model. Habitat suitability models and similar pelagic filter feeders' distributional drivers, suggests that it is highly likely that their distribution in the NE shelf is intimately linked with the locations of prey and subsequently, seasonal upwelling systems (Celona, 2004; Lezama-Ochoa et al., 2019b).

2.4.1.1 Prey availability

The common main prey item for Spinetail devil rays globally is euphausiids (also known as 'krill') (Rohner et al., 2017; Sampson et al., 2010; Shirlamaine et al., 2018), a crustacean that is known to occur in large swarms and exhibit diel vertical migration; migrating to deeper waters during the day and returning to the surface at night (Rohner et al., 2017; Tattersall, 1924). The high reliance on euphausiids is highlighted in multiple studies where authors found over 90% of Spinetail devil rays' total diet contain a specific euphausiid species (Fortuna et al., 2014; Rohner et al., 2017; Sampson et al., 2010; Shirlamaine et al., 2018). Although euphausiid species differs between studies, the highly specialised diet of Spinetail devil rays is consistent between them all. The sole euphausiid species within coastal and shelf waters in New Zealand is *Nyctiphanes australis* (Lagos et al., 2022), thus it is likely that Spinetail devil rays are associated with this species. The tendency for *N. australis* to aggregate in large swarms (Mauchline, 1980), makes it an accessible prey for large filter feeders such as Spinetail devil rays, where it is likely that prey aggregations must exceed a certain abundance threshold for energetics of feeding to be favourable (Bone & Moore, 2008; Parker & Boeseman, 1954).

The highest habitat suitability in both static and dynamic models is the Tīkapa Moana Hauraki Gulf shelf waters, which can be explained by the known high abundance *N. australis* in this region. Within the Tīkapa Moana Hauraki Gulf, abundance of *N. australis* peaks during January and February (Jillet, 1971). This during the late summer months also explains the relationship that shows a high preference for high Chl-a abundance, but a decreasing HSI (habitat suitability index) as Chl-a values increase in the static model. In late summer, little phytoplankton biomass (Chl-a) is found in shelf surface waters, with higher values found at outer- and inner Gulf sites due to downwelling favourable conditions (i.e., easterly winds). (Chang et al., 2003; Gall & Zeldis, 2011; Zeldis et al., 2004). The discrepancy in Chl-a concentrations between Gulf and shelf waters is likely the difference in terrigenous nutrient loading from nearby continental material and river inputs (Wollast, 2003). If Spinetail devil rays are thought to be linked to areas of high productivity and prey abundance, this begs the question of why their distribution is concentrated on the shelf, where productivity seems to be lower than that of the inner- and outer Gulf. This is probably highly correlated with the location of *N. australis*, who occur along the continental shelf edge rather than residing inshore (Jillet, 1971). This shelf species is known to take extensive migrations to depth during the day to exploit mesopelagic prey in deep scattering layers and avoid predation at the surface (Jillet, 1971). An explanation could be that *N. australis* forage not only on phytoplankton but are omnivorous, known to feed on copepods and other zooplankton assemblages thus, are likely to exhibit temporal and spatial lags in distribution relative to Chl-a (Ritz et al., 1990). Hence, the low Chl-a influence may be attributed to time lags and the inability for Chl-a to serve as a proxy for *N. australis* distribution and abundance.

An attempt to include zooplankton (i.e., *N. australis*) was made by incorporating Chl-a gradient in the dynamic model. Chl-gradient represents productivity of fronts known to attract and aggregate higher trophic level predators (Scales et al., 2014; Woodson & Litvin, 2015), and is often a better indicator of upwelling systems and zooplankton occurrence (Druon et al., 2021). This was included in the model in conjunction with SST gradients, indicative of areas with mixing of warm, nutrient-poor, and cold, nutrient-rich waters and are significantly related to upwelling intensity (Vazquez-Cuervo et al., 2017). Further, industrialised fisheries are known to target persistent fronts (Hartog et al., 2011; Podestá et al., 1993) thus, given the high interaction between Spinetail devil rays and fisheries, theoretically is an important variable. However, despite the presumed association, a significant relationship between habitat suitability and Chl-a and SST gradients was not found. Most likely, the temporal scale that the data were analysed at, and the model was run, was problematic. Productivity fronts are known to be active over periods of weeks and months, not a full year (Druon et al., 2021). The aggregation of the data to annual layers, although only incorporating months that Spinetail devil rays were present (i.e., spring and summer), this may have resulted in the loss of temporally finer patterns within gradient layers, that annual aggregation may have smoothed over. Further, productivity fronts detected from Chl-a and SST gradients are calculated from satellites thus, can only capture fronts at or near the surface. Therefore, despite an attempt to capture *N. australis* distribution, this was done unsuccessfully and requires investigation using finer temporal scales.

Chl-a included in this model was restricted to surface Chl-a values derived from satellite ocean colour measurements, thus, is unlikely to capture productivity in deeper layers. Due to the NE shelf exhibiting a deep Chl-a/biomass maxima during spring and summer months, this may have caused mismatches in Chl-a concentrations (Chiswell et al., 2022). Although in-situ measurements capture deep Chl-a maxima better, these measurements are often sparse and logistically challenging. Perhaps an investigation into potentially combining these two data sources (Chiswell et al., 2022) to capture a fuller image of Chl-a in the whole water column would be beneficial.

2.4.1.2 Role of the continental shelf edge

The affinity for both Spinetail devil rays and *N. australis* species to aggregate along the continental shelf edge at around 200m at depth (Jillet, 1971; Blackburn, 1980; Gómez, 1995) is consistent with both the static and dynamic model which show high habitat suitability along the continental shelf edge, around 100km from the coast. This interrelationship between the two species is exhibited in accounts of Spinetail devil rays' being more present at the surface during night, likely foraging at depth during the day (Francis & Jones, 2016; Irigoien et al., 2014), possible due to their retia mirabilia (i.e., brain heater), despite being ectothermic (Thorrold et al., 2014). This is a necessary adaptation considering the significantly colder water at depths below 200m and the subsequent reduction in metabolic rates (Bernel et al., 2012).

Although distance to coast was a prevalent variable and the preference for areas around the 200m isobath is known for Spinetail devil rays in relation to foraging (Putra et al., 2020), a significant relationship between distance to 200m and habitat suitability could not be detected. This may be explained by a hypothesis by Rohner et al. (2017) that Spinetail devil rays go through cycles of starvations and feeding events, and individuals within the dataset may have not been observed during feeding events, especially as Spinetail devil rays are often at depth during the day.

2.4.1.3 Relationship with SST

Ectothermic organisms' internal body temperature matches the ambient water temperature closely (Brill et al., 1994) which means that these organisms experience large fluctuations in temperature (Bernel et al., 2012). The limited relationship between SST and HSI within the static model could potentially be due to a failure to account for the temporally dynamic nature of SST, in that it changes rapidly over hourly and daily resolutions. An 18-year long-term average may not have successfully captured the nuances in the SST and HSI relationship due to this. By contrast, the dynamic model captures a response profile of increasing SST associated with increasing HSI, which is what was expected from previous studies (e.g., Canese et al., 2011). However, the relative contribution of SST is lower than that of the static model. Despite attempting to address the dynamic nature of SST by using an annual model, perhaps the temporal resolution chosen was too broad to capture finer intricacies of the relationship. Alternatively, the limit of occurrence records and hence the model to summer months could be reducing the thermal ranges that Spinetail devil rays experience consequently reducing the influence of SST on HSI.

The relationship between SST and HSI in the model may have been captured through the lack of presence records further south than the Te Moana a Toi Bay of Plenty, despite equal survey effort in areas south (Langley, 2019) and the seasonal patterns in occurrence records. The southern limit of the records is likely to represent a thermal limit, with this region coinciding with the East Cape; the southern extent of the EAUC (Santana et al., 2021). SST in the NE shelf during summer months is around 20 °C whereas southern waters can get as low as 13 °C (Garner, 1969). The seasonal occurrence in the NE shelf with no occurrences during winter months may also represent a temporal thermal limit as during winter in the NE shelf SST drops to around 15 °C (Garner, 1969). These patterns must be related to a condition separate to prey availability as *N, australis* is present in areas further south such as Cook Strait, Kaikoura (Mehl, 1969), Marlborough Sounds, Wellington Harbour and Otago, throughout the year (Bartle, 1976). This supports the hypothesis that Spinetail devil rays are limited by colder SST, especially in the south and in winter where influences from Subantartic flows result in substantial declines in SST (Garner, 1969). Bryde's whales (*Balaenoptera edeni*), large filter-feeders known to feed on euphausiids (Wiseman, 2008), have year-round occurrence within Aotearoa New Zealand waters (Wiseman et al., 2011). Although both species may have similar requirements, the lack of endothermy (i.e., warm-blooded) for Spinetail devil rays may attribute largely to the seasonal departure from Aotearoa New Zealand waters. Thus, Spinetail devil rays appear to be temporally and spatially localised in response to SST.

SST may also indirectly influence the distribution of Spinetail devil rays by directly impacting their prey. Studies on *N. australis* have found that reduction in abundance is a result of intrusions of subtropical waters and the subsequent decline of nutrients and thus, phytoplankton (Ritz et al., 1990; Young et al., 1993). Therefore, the intrusion of the EAUC in the Tīkapa Moana Hauraki Gulf over shelf waters in late summer must lead to a reduction in the availability of *N. australis*. This explains the lack of Spinetail devil rays occurrence records in late summer to early autumn (March-April), despite warmer SST around the NE shelf than in early summer months (Paul, 1968).

Spinetail devil rays likely migrate to Aotearoa New Zealand waters during summer months when intrusions of the EAUC increase SST to their thermal range and allow them to capitalise on the abundant *N. australis* resource in the shelf waters. The eventual departure during late summer to autumn is likely triggered by the shoreward intrusion of the EAUC causing the reduction of prey abundance and the colder SSTs further south restricting them from further exploiting this resource.

2.4.1.4 Potential impacts of ENSO

With temporally dynamic elements that alter environmental conditions such as El Niño Southern Oscillation (ENSO) and climate change, the dynamic model is an important step towards attempting to understand how Spinetail devil rays' distribution may have changed in response to these drivers in the past.

For Spinetail devil rays, a significant distributional shift cannot be detected and visually the changes between the years seems to be limited to changes in the intensity and extent of areas of high habitat suitability. However, the strongly positive SOI values, indicative of the La Niña phase, is a relatively high component. The higher habitat suitability associated with positive SOI values in the static and dynamic model are indicative of La Niña conditions, which are associated with increased easterly winds, warmer than usual SST, downwelling conditions and thus, reduced productivity (Willis et al., 2007). Due to previous studies suggesting that upwelling regions was a strong predictor in Spinetail devil ray occurrence, this finding is contradictory.

However, a positive relationship between HSI and La Niña might be an artifact of elevated SST that La Niña conditions bring which might fit better within Spinetail devil rays' thermal tolerance. Further, warmer waters may allow Spinetail devil rays to reside in Aotearoa New Zealand waters for a longer period, increasing overlap and possible interactions with fisheries and hence, occurrence records.

Despite this hypothesis, it is clear that this relationship is highly nuanced and may be a fine balancing act between SST and productivity. Although warmer SST that La Niña conditions elicit may suit Spinetail devil rays better, increasing easterly winds cause a decrease in productivity and especially relevant to this species, reduction in *N. australis*. This was shown in the summer of 1988/89 where a strong La Niña event caused increased intrusion of subtropical waters, leading to the depletion of *N. australis* and subsequent collapse of the jack mackerel (*Trachurus declivis*) fishery in Tasmania (Harris et al., 1991; Young et al., 1993). However, skipjack tuna, a species that's distribution is tightly interwoven with Spinetail devil rays' distribution and feed mainly on *N. australis*, is seen to increase in abundance in New Zealand waters during La Niña events (Langley, 2019).

It is clear that more analysis into the reasonings behind this discrepancy and more data collected in El Niño years and normal years is required to understand the association between ENSO and Spinetail devil rays as the study years were dominated by La Niña years.

2.4.2 Oceanic manta ray habitat selection

Shallow, near-shore regions that have moderate to high sloping seafloor appear to be indicative of areas with high habitat suitability for Oceanic manta rays in this study. Habitat suitability peaked around 50km from the coastline at depths of around 100m, suggesting that Oceanic manta rays in the NE coast utilise coastal regions close to the land-sea interface, with highest suitability occurring within the Tīkapa Moana Hauraki Gulf. These results are analogous with previous studies on manta ray habitat preference in shallow, near-shore regions (Couturier et al., 2013; Hacohen-Domené et al., 2017; Putra & Mustika, 2020).

2.4.2.1 Near-shore coastal regions

The Gulf and shelf regions exhibit differing oceanographic conditions largely due to the intrusion of the EAUC shoreward as far as the 150m isobath, which creates a physical boundary between these two regions (Zeldis & Willis, 2015). Consequently, the lower salinity, nutrient-rich shelf and Gulf waters, support higher primary productivity, greater abundance, and diversity in zooplankton assemblages with reduced seasonal fluctuations (Chang et al., 2003; Zeldis & Willis, 2015). Increased productivity in coastal waters is likely captured by the high importance of Chl-a in the static model, with Oceanic manta rays being more prevalent in areas with higher Chl-a concentrations. The prevalence of Oceanic manta rays at outer Gulf areas where there may be potential mixing of coastal and offshore waters may explain the positive relationship of suitability with SST gradients. The importance of fronts for

Oceanic manta (Graham et al., 2012; Luiz et al., 2009) are known to use areas with high productivity (Acha et al., 2004; Franks, 1992; Le Fèvre, 1986) as are similar filter-feeders such as whale sharks (Wilson et al., 2002).

Although coastal regions are analogous with higher productivity due to influx of additional nutrients from terrigenous, riverine, and anthropogenic sources (Carter et al., 2005; Chang et al., 2003; Mann and Laier, 1991), the reason why Tīkapa Moana Hauraki Gulf coastal areas are of particular importance could be due to the role of nutrient regeneration.

Late summer in the Hauraki gulf (Jan to Feb) is associated with prevalent easterlies and downwelling favourable conditions, resulting in strong stratification and the depletion of nutrients (Zeldis, 2004). Despite a reduction in productivity, Oceanic manta ray sightings in this study were disproportionately higher from these late summer months, especially February. This could be explained by the potential role of alternative sources of nutrients Giles et al. (2007) demonstrated that due to the shallow nature of the Gulf, nutrients released through benthic remineralisation were able to sustain productivity in late summer. This may explain the longer duration that Oceanic manta rays are observed in the NE coast in comparison to Spinetail devil rays. Although Chl-a was the most influential variable on the long-term distribution of Oceanic manta rays, due to Chl-a values being derived from satellite sources that are not representative of deeper Chl-a values, the interrelationship is likely underestimated. For Oceanic manta rays that occur within the Gulf where benthic remineralisation processes are responsible for 10-13% of the primary productivity (Giles et al., 2007), underestimations may be exacerbated. Consequently, the ambiguous relationship between Chl-a and distribution in the dynamic model may be explained by this as well. For example, specific years with particularly high deep Chl-a blooms (e.g., spring 1999, autumn 2000; Gall & Zeldis, 2011), would be unaccounted for. Deep Chl-a blooms appear to be especially relevant to Oceanic manta rays due to the well-documented depth utilisation during foraging, and the exploitation of demersal and mesopelagic prey sources (Burgess, 2017; Couturier et al., 2013; Fonseca-Ponce et al., 2022).

2.4.2.2 Relationship with SST

Oceanic manta rays are ectotherms; thus, SST is likely to directly influence physiologically and energetically favourable areas, and thus, migration and aggregation (Couturier et al., 2012; Graham et al., 2012). Further, prey availability, namely zooplankton abundance is demonstrated to be correlated with SST (Richardson, 2008; Wilson et al., 2003) hence, SST is likely to influence Oceanic manta ray distribution indirectly as well. Therefore, it is unsurprising that SST is one of the most important drivers of distribution for both static and dynamic models. The relationships predicted differ for both models. The static model suggests that habitat suitability is higher in colder waters, with a clear peak just above 18 °C. In contrast, the dynamic model shows increasing suitability to around 17 °C, a slight reduction before a peak at 26 °C is reached.

Higher habitat suitability in colder waters is consistent with high prevalence of coastal waters, as these areas are associated with upwelling systems and the absence of warmer EAUC waters. However, the increase in suitability with increased SST in the dynamic model is also unsurprising as observations have found a correlation between aggregation sites and warmer waters (Burgess, 2017). A potential discrepancy between the two is that the higher suitability in colder waters is associated with a higher degree of uncertainty in comparison to that of the association with warmer waters. Therefore, this may be associated with fewer presence records available at lower temperature ranges, resulting in extrapolation and subsequent uncertainty. Furthermore, long-term averages tend to correspond colder waters with high productivity but in finer temporal scales, the relationship between SST and productivity is likely to be more nuanced, dependent on factors such as the source of water (i.e., deep, riverine, terrigenous). Regardless, Oceanic manta rays are known to capitalise on mesopelagic prey at depths where temperatures are substantially colder than surface waters (Burgess, 2017), highlighting their ability to withstand colder SST, especially a prevalent behaviour while foraging. This species is thought to have a more complex and developed rete mirabilia than that described for Spinetail devil rays (Schweitzer & Notarbartolo di Sciara, 1986) and is a potential adaptation to the larger mouth of the Oceanic manta ray that when feeding and taking in large volumes of water, leads to greater cooling of the brain (Alexander, 2008). Cranial adaptations allow the maintenance a constant thermal temperature for the brain (Alexander, 2008), a hypothesised adaptation to expand thermal ranges (Block & Finnerty, 1994). The large, black dorsal surface allows individuals to recover at the surface, building up heat stores and thus, metabolic rate, allowing them to stay at depth for longer (Alexander, 2008; Cossins, 2012). Therefore, I hypothesise that both relationships in both models are true – colder SST represents increased prey availability (and this relationship dominates long term averages) however, surface waters need to be warm enough to allow for thermal recovery before or after undertaking vertical migrations (and this relationship emerges when finer scale analyses are performed).

2.4.2.3 Jellicoe and Cradock Channel

Manta rays are known to aggregate in areas of high productivity (Anderson et al., 2011; Compagno & Last, 1999; Couturier et al., 2011; Dewar et al., 2008; Homma et al., 1999; Luiz et al., 2009). These aggregations often happen at cleaning stations (i.e., reefs where cleanerfish remove ectoparasites from body), although a greater association is observed with Reef manta rays (Anderson et al., 2011; Homma et al., 1999; Marshall, 2009).

High habitat suitability found in both static and dynamic models in the Jellicoe and Cradock Channel provide insight into a potential aggregation site in Aotearoa New Zealand waters. The Cradock Channel separates Te Hauturu-o-Toi Little Barrier Island and Aotea Great Barrier Island with the underwater topography resembling an underwater saddle (Department of Conservation & Fisheries New Zealand, 2021). Reef systems exist in the middle of the channel with high sloping exhibited from depths ranging from 20 to 60m and high nutrient levels in surface waters (Sharples, 1997). The prevalence of moderate to high sloping in coastal regions such as the Cradock Channel are ubiquitous with the majority of manta ray aggregation sites or cleaning stations (Dewar et al., 2008; Jaine et al., 2012) as it can be indicative of complex features at the seabed including pinnacles and oceanic islands (Marshall et al., 2009; Stewart et al., 2016a). Aggregations physical features or areas of complex topography are common in migratory pelagic species (Holland & Grubbs, 2007; Morato et al., 2008; Tsukamoto, 2006;) and provide conditions with increased nutrient availability (Genin et al., 1986; Lueck & Mudge, 1997) and could be providing a sheltered environment and subsequent reduction in energy expenditure against tides and currents (Genin, 2004; Morato et al., 2009), especially in the Jellicoe and Cradock Channel which is characterised by strong tidal currents (Black et al., 2000; Department of Conservation & Fisheries New Zealand, 2021). Therefore, it could present suitable locations for mating, feeding, nursery grounds for migratory pelagic species (Morato et al., 2010), which may be particularly true for the Cradock Channel as it is already an important habitat for Bryde's whales and bottlenose dolphins (Dwyer, 2014).

The Jellicoe Channel is located between Leigh Harbour (mainland) and Te Hauturu-o-Toi Little Barrier Island. This channel resembles a U-shape and is around 30km wide with the maximum depth just over 50m (Sharples, 1997). Similar to the Cradock Channel, strong tidal currents (Hume et al., 2000) are prevalent with high degrees of sloping are present, for example, depth dropping from 20m to 50m in less than 8km (Sharples, 1997). Although both Jellicoe and Cradock Channels act as the "northern entrance" to the Gulf (Black et al., 2000), previous studies have found that intrusions of the EAUC are higher in the surface waters of the Jellicoe Channel during summer months (Chang et al., 2008; Sharples, 1997). Thus, the Jellicoe Channel is an important region where offshore water (high salinity, low nutrient-levels) mixes with coastal water (low salinity, high nutrient-levels), resulting in high Chl-a values at this thermal boundary (Sharples, 1997). Due to the high productivity associated with the Jellicoe Channel, it is no surprise that high habitat suitability for Oceanic manta rays was predicted here.

2.4.2.4 Variance in the dynamic model

The dynamic model demonstrates that almost 50% of the variance in habitat suitability between years is unquantified by the model. Due to data availability issues, important variables identified from previous studies could not be incorporated into this model. In particular, the distribution and movement of Oceanic manta rays seems to be strongly linked to moon phases and tidal currents (Dewar et al., 2008). Vertically migrating organisms such as zooplankton appear to migrate to deeper waters during a full moon resulting in reduced foraging and decreased occurrences during these times, compared to half and new moon phases (Blaxter, 1974; Hernández-León et al., 2001; Rohner et al., 2013). As this study was based on citizen science data for Oceanic manta rays, sightings were likely to be collected during the day when the influence of moon phase and zooplankton migration in response was relatively low. Therefore, moon phase was left out of the study. If night sightings were included in the model, moon phase may become important.

Strong tidal currents as well as greater tidal ranges has seen an increase in foraging for Oceanic manta rays, due to greater water column mixing (Dewar et al., 2008; Fonseca-Ponce et al., 2022). Similar to moon phases, this was left out of the study as well due to citizen science records missing the time of observation. Tides are temporally dynamic and can change rapidly thus, including it in the model by randomly assigning a time would have resulted in misled interpretation. If incorporation of sightings with time were to occur, this would be an important variable to include. However, the importance of the Jellicoe and Cradock Channel – both of which are characterised by strong tidal currents, may highlight this important association despite the exclusion of this variable from the model.

A variable that is likely attributed to most of the unexplained variance between the study years is ENSO. The primary source of interannual variability is ENSO (Chavez et al., 1999; Feely et al., 1987) and previous studies have demonstrated a clear relationship between Oceanic manta rays' distribution and ENSO phase (Burgess, 2017; Fonseca-Ponce et al., 2022; Lea & Rosenblatt, 2000; White et al., 2015). Overall, La Niña (eastern Pacific) events resulted in greater sightings and activity (Burgess, 2017; Fonseca-Ponce et al., 2022; White et al., 2015) and during a strong El Niño event (eastern Pacific), a poleward shift away from warmer waters was seen for several elasmobranch species, including Oceanic manta rays (Lea & Rosenblatt, 2000). I note that these studies were all based in the eastern Pacific, and where Aotearoa New Zealand is in the western Pacific, where El Niño is associated with cooler SST and the opposite for La Niña conditions. Unfortunately, the model could not be run with SOI as the “Year” for each absence record was randomly generated and thus, interpretation of results of the impact of SOI on habitat suitability would have been no better than random. However, based on the strong relationships found in previous studies, the potential of this relationship cannot be dismissed, and this could explain the large variance in Year, that was not seen in the Spinetail devil ray model. Therefore, further investigations using a more sophisticated absence methodology (i.e., target background points, real absence records) will allow for a greater understanding of the environmental drivers behind Oceanic manta rays over time.

2.4.3 Evidence of trophic separation

The clear segregation in areas with high habitat suitability for Oceanic manta rays and Spinetail devil rays is a possible hint to trophic separation. The 200m isobath line acts as a clear demarcation line between the two distributions, with Spinetail devil rays the line representing their inshore extent, and with Oceanic manta rays, their offshore extent. As filter feeders with morphological similarities, both species will likely have similar habitat requirements and preferences, and thus, similar prey (Stewart et al., 2017). Trophic separation between those of the same species is usually to limit this competition for the same resources (Rohner et al., 2017).

Furthermore, this separation may be due to the difference in size between Spinetail devil ray and Oceanic manta ray and corresponding dissimilar energetic requirements. Typically, with teleost fish, the size of their mouth gape dictates the maximum size of prey they can target and thus prey items may differ between species (Scharf et al., 2000; Stewart et al., 2017). However, with filter feeders where their mouth gape is incomparably larger than their prey, the same conclusions may not apply.

Previous studies have found that regardless of body size, mobulid species have been shown to overlap distributions (Notarbartolo di Sciara, 1988; Sampson et al., 2010; Stewart et al., 2017), with overlap increasing with depletion of resources (Stewart et al., 2017). This refers back to the filter feeders' energetics where prey density must exceed a threshold (Armstrong et al., 2016) and in the wake of reducing prey availability, there is likely to be a limited number of prey patches that meets these requirements, hence greater trophic overlap. By contrast, in the productive waters of the NE coast with only two mobulid species, there is likely to be reduced convergence and individuals are likely able to feed on preferred zooplankton prey, increasing trophic separation.

Although Stewart et al. (2017) argues that in filter feeders, body size is highly unlikely to impact trophic separation, in this case, the relatively larger size of the Oceanic manta ray and hence, increased caloric requirements, are probable elements of trophic separation in the NE coast. Oceanic manta rays are unlikely to meet their caloric needs if individuals primarily consumed one prey type with earlier studies demonstrating that their stomach can hold up to 5kg of prey (Rohner et al., 2017).

Further, the coastal waters support a higher variety of zooplankton biomass, with high egg, larval and adult copepod abundances during spring and summer months within the gulf (Zeldis & Willis, 2015), known prey items of Oceanic manta rays (Rohner et al., 2017).

With increasing SST due to climate change, exacerbated by frequent La Niña events, this interspecific relationship is likely to change. Based on previous studies in oligotrophic, warm waters, it is likely that prey will be available at lower densities, with a patchier distribution. This will reduce prey patches that exceed energetic thresholds, resulting in the convergence of prey sources and the subsequent increase in trophic overlap.

2.5 LIMITATIONS OF THE STUDY

2.5.1 Limitations of fishery-based data

Spinetail devil ray occurrence records were all obtained from fishery-based data. Despite the plethora of strengths associated using this data especially with a species that faces data paucity issues, it is also critical to identify the limitations. The first major concern with this data is the potential spatial and temporal bias or unequal sampling in that fisheries tend to preferentially go to areas that have high densities of their target species, driven by economic factors rather than a random and equal sampling footprint (Karp et al., 2023). Therefore, the evident trophic separation between Spinetail devil rays and Oceanic manta rays could be a manifestation of fisheries preference to occur in offshore waters and out of protected habitats (i.e., marine reserves). However, through examination of the absence records that were also obtained from fisheries purse-seine records, it can clearly be seen that purse-seine vessel operate further inshore (Fig 2.4). Purse-seine records can be seen all along the eastern coastline (Fig 2.4), even within the Jellicoe and Cradock Channel where Oceanic manta rays were predicted to have the highest suitability. Thus, trophic separation in Aotearoa New Zealand is likely not due to differing data collection methods. It should be noted that purse-seine fisheries may also exhibit a temporal bias, with skipjack tuna fisheries (i.e., fisheries that is most associated with Spinetail devil rays) mainly operational between January and March (Langley, 2019). Although occurrences drop dramatically in March, it cannot be dismissed that the seasonality of presence could be due to this temporal bias. There is no doubt that conducting surveys throughout the year will result in greater ecological insight in terms of habitat use in Aotearoa New Zealand however, given physiologically and energetic restraints, it is likely that this spring/summer model was able to capture much of their temporal range in Aotearoa New Zealand.

The second concern is associated with potential misidentification of Spinetail devil rays with Oceanic manta rays. This accurate species level identification is critical for identifying the correct habitat use and distribution of a species and could adversely impact results. Ongoing review of identifications, photographs to confirm identification, observer training on morphological differences that are easy to spot from the surface are principle to effective mobulid conservation. Spinetail devil ray data was obtained from MPI from two different databases, COD and NFPS. COD is a database comprised of data from an observer on board that is completely independent from fisheries whereas NFPS are reported catches from commercial fishers (Fisheries New Zealand, 2022). Although data from COD is checked for errors and species are verified before published, data from NFPS is not independently verified and thus, may be subject to species misidentification (Fisheries New Zealand, 2022). Detection bias related to difficulty observing an animal due to turbid waters or deep diving behaviours can also increase misidentification (Fortuna et al., 2014; Torreblanca et al., 2019). However, due to the lack of confirmed captures of Oceanic manta rays in Aotearoa New Zealand waters and lack of observations of other mobulid species (Ford et al., 2015, 2018; Jones & Francis, 2012; Paulin et al., 1982), the issue of misidentification is likely to be minimal. In contrast, detection bias may be a larger issue as Spinetail devil rays tend to dive deeper and spend less time at the surface during the day than at night (i.e., when purse-seine vessels are active) (Francis & Jones, 2016). Although the time spent at depth is relatively low, likely due to physiological restraints, daytime data collection may be underestimating Spinetail devil ray occurrence in Aotearoa New Zealand waters.

2.5.2 Limitations of citizen science data

It is important to address that although the use of data from platforms of opportunity create avenues for greater data collection with reduced logistical and financial costs (Torreblanca et al., 2019), there are also associated limitations. One of the main limitations especially relevant to mobulid species is the potential misidentification of the species (Francis, 1999; Pearson et al., 2010). Citizen scientists unlike scientists who survey with intent to encounter mobulids, have potentially less information and resources to correctly identify an individual, especially due to the morphological similarities between Spinetail devil rays and Oceanic manta rays. This is exacerbated by the lack of incentive for observers to correctly identify species (Francis, 1999) and associated difficulty to spot key morphological features when surface waters are turbid (i.e., detection bias) (Fortuna et al., 2014; Torreblanca et al., 2019). Detection bias occurs when observers are unable to detect animals due to their deeper diving behaviours or failure to detect an animal at the surface due to various reasons such as turbidity (Marsh & Sinclair, 1989) or in the absence of feeding activity (i.e., somersault feeding) where there is a lack of disturbance at the surface, it can be difficult to identify an animal just below the surface. However, unlike Spinetail devil rays, Oceanic manta rays are known to spend more time at the surface during the day (Andrzejaczek et al., 2021; Andrzejaczek et al., 2022), thus, detection bias due to deep diving behaviours may not be as much of a factor. Nonetheless, it is important to interpret the data with caution as a lack of presence does not necessarily indicate the lack of the animal but could just be the lack of observation (Torreblanca et al., 2019).

Opportunistic data is also associated with selection bias, where encounters usually occur in environments that are easier to access or have social and/or economic significance (i.e., tourism destinations) (Pearson et al., 2010). This can result in substantially biased data towards coastal areas, and reduced sightings in remote areas, such as offshore and deep ocean regions (Robinson et al., 2011). Although this study attempting to reduce this bias through the selection of appropriate pseudo-absences and the creation of a prediction horizon to reduce extrapolation, it is important to address that due to the deep diving capabilities of Oceanic manta rays and pelagic nature, these habitats may be equally as important as coastal regions. This study demonstrated that for Oceanic manta rays, near-shore, coastal regions are especially important in terms of suitability however, the selection bias of encounters in these relatively easily accessed areas may be responsible for this association. Therefore, despite previous studies in other regions also find high suitability in regions with the same environmental conditions, this possibility cannot be dismissed without systematic surveys (Fiedler et al., 2018). Opportunistic data potentially represents a biased and small fraction of the true distribution of animals (Praca et al., 2009) given that this study is the first attempt to map the distribution of mobulids in Aotearoa New Zealand waters, baseline information and understanding of the species has improved, fulfilling the aim of the study. Future studies will focus on robust sampling effort and fieldwork to assist with the results from the model (see section 3.4).

There is no doubt that the increased sophistication of smart-phone technology has changed the power that citizen scientists hold. This means that ecologically valuable data can be collected in near real-time, with increased confidence in identification as a result of increased camera resolution (Cranswick et al., 2022). This may be particularly useful to look at ways distributions may overlap with human activities, where citizen scientists are probable to be most active (Cranswick et al., 2022). Therefore, future studies may look at ways to combine this data in meaningful ways to maximise data available for ecological insight into fine-scale movements and distribution especially into the impacts of human activities.

2.5.3 Limitations of environmental layers

In this study, biotic interactions such as prey availability were included in the model through variables such as Chl-a and gradient layers but the lack of explicit inclusion (Wisz et al., 2013) prevented the model from capturing the full realised niche of both mobulid species. Temporal lags associated with phytoplankton and zooplankton abundance are also known limitations associated with Chl-a and this study used Chl-a and SST gradients to attempt to capture this. However, these fronts are active over temporal resolutions of weeks to months (Druon et al., 2019) instead of annual scales thus, the aggregation of monthly layers into annual layers likely led to the disappearance of much of these important patterns. The use of satellite and remotely sensed environmental data, although in high resolution, were unable to capture subsurface processes (Valavanis et al., 2008) such as deep Chl-a maxima that is evident in NE shelf waters (Chiswell et al., 2022). Although satellite Chl-a measurements have allowed for low-cost and wide spatial and temporal coverage, globally, satellite Chl-a values only represent one-fifth of the total Chl-a content within the euphotic zone (Morel & Berthon, 1989).

Satellite Chl-a measurements not only serve as a proxy for phytoplankton abundance but is a proxy for water clarity as well. Thus, interannual and seasonal fluctuations in Chl-a values may not reflect phytoplankton abundance but instead changes in water clarity related to river discharge or mixing related to wet seasons (Le et al., 2013). Although riverine discharge into the shelf is relatively low in the NE shelf with most nutrient sources coming from offshore waters (~65%) (Zeldis & Smith, 1999), there are no measures to quantify the degree into which coastal Chl-a values are being under- or overestimated due to this.

Mobulids distribution is largely dictated by areas where foraging energetics are favourable (Armstrong et al., 2016; Bone & Moore, 2008; Parker & Boeseman) therefore, the limitation associated with being unable to capture prey availability is a likely cause of under- or overestimation of suitability in certain regions. Further, mobulid distributions are likely sensitive to changes in abundance and distribution of their prey (Hays et al., 2005), and with the unprecedented unpredictability associated with climate change, mobulids' distributions are predicted to change (Richardson, 2008). It is critical to investigate methods to capture prey to accurately predict how mobulid distributions may change into the future with greater certainty.

2.5.4 Modelling limitations

2.5.4.1 Dynamic SDM

This study attempted to address the equilibrium assumption (Guisan & Thuiller, 2005), whereby static models neglect the dynamism in space and time between environmental conditions and species distribution (Skov & Svenning, 2004) and assume stable and unchanging niches (Guisan et al., 2017; Pearman et al., 2008). An annual model was compared to a static model to investigate whether a dynamic model, albeit even on a larger temporal scale such as year, would be able to capture differences in distribution over time. However, due to the migratory nature of mobulid rays in other parts of the world and potential migration to Aotearoa New Zealand during summer months, the limited temporal variability in dynamic environmental variables during these restricted months may have reduced the capability of this study capture their full niche. However, given the demand for future climate scenarios (Coumou & Rahmstorf, 2012) and the error associated with basing forecasts on long-term averages (Niehaus et al., 2012), the importance of annual models will likely substantially increase. Furthermore, the lack of distributional shifts within the dynamic model may also be attributed to the low number of occurrence records in some years, especially in the earlier years as awareness of the presence of both mobulids species was relatively low. The increase of systematic survey and subsequent occurrence records will ensure the entire environmental range of mobulids is captured, especially in areas such as the West Coast of the Te Ika-a-Māui North Island where intermittent sightings are present however, survey effort is lacking.

Despite the importance of the inclusion of temporal dynamism, studies that incorporate this interannual variability are generally rare (Zimmerman et al., 2009). Although occurrence data was limited to mostly spring and summer months, with future climate scenarios predicting increasing temperatures and subsequent shifts of species poleward, there is immense unpredictability in how the distributions of mobulids will change going forward. This study was limited to a largely summer-time model and the investigation of seasonal suitability was rendered relatively unnecessary. Still, as climatic variables tip towards the extreme and animals move southward, the potential increase in time of residency in Aotearoa New Zealand waters might subsequently increase as well. Greater portion of the year spent in Aotearoa New Zealand waters might elicit the necessary investigation of habitat suitability with a finer temporal scale (i.e., seasonal), to correctly characterise the species geographical distribution and prevent the loss of predictive power (Perez-Navarro et al., 2021).

2.5.4.2 Absence records

Presence-only modelling refers to models that incorporate data that has not been collected through systematic surveys and a major implication to this is that proper absence records are lacking (Yackulic et al., 2012). However, Phillips et al. (2009) demonstrated that these models can be robust to selection bias if the pseudo-absences selected are associated with the same bias. For Spinetail devil rays, fisheries record from all purse-seine vessels within the same region, study years and months were used so the associated bias was consistent (i.e., target-group background data, Phillips et al., 2009). Due to this, the records could be referred to as absence records and the model perform well indicated by the high AUC and TSS scores. By contrast, Oceanic manta ray data was collected by citizen scientists which are highly variable in quality and the lack of associated species with this species meant that target-group background data could not be used. To reflect the selection bias of the data, random points were selected based on a KDE probability grid of the occurrence records, called pseudo-absences. Although this has been shown to reduce selection bias and increase predictive accuracy (Elith et al., 2010; Fitzpatrick et al., 2013; Georgian et al., 2019; Finnuci et al., 2021), pseudo absences, are less informative than true absences.

For Oceanic manta rays, despite the relatively high performance and 'usefulness', the performance is within the constraints of presence-only modelling. Presence-only models are more likely to deliver higher incidences of false positives (i.e., mobulid is predicted to be present at a location but is absent) rather than the opposite (Stephenson et al., 2021; Vierod et al., 2014). For the application of conservation management of endangered mobulids, false positives are considered better as the implications for underestimating their habitat could result in the continuation of harmful interactions (i.e., fisheries) that contributed to their depletion. However, in conservation the trade-offs between economic loss must be considered as well thus, for potential fishery closures, false positives or overestimations of their habitat is likely to have negative implications (Stephenson et al., 2021).

To avoid limitations associated with presence-only modelling, for Oceanic manta rays, survey effort data and real absence records must be obtained (Stephenson et al., 2021). For Spinetail devil rays, although absence records were more reliable as they were associated with the same bias, the collection of presence and absence points that are removed from fisheries dependency will confirm whether these habitat suitability patterns are a manifestation of commercial fisheries interest or real distributions. Given the aim of this study for conservation applications, systematic surveys, and subsequent collection of observed absence records for both species is necessary to confirm and support these results to avoid negative ramifications to relevant stakeholders.

Chapter 3

General Discussion and Conclusion

Cover for chapter: *Photo taken during a survey trip with Manta Watch New Zealand in the Hauraki Gulf Marine Park (photo: Rika Ozaki)*

3.1 GENERAL SUMMARY OF FINDINGS

Spinetail devil rays were distributed in areas around the continental shelf, especially around the outer shelf region by the Tīkapa Moana Hauraki Gulf, with the 200-depth contour line demarcating their inshore extent. Their affinity for areas further offshore, at depths of 150-500m indicated that vertical depth utilisation may be an important criterion for habitat selection and was indicative of foraging at depth. The dynamic model revealed that temporal and spatial patterns were generally quite consistent across the study years with slight variations in the value of suitability were visible but no evidence of a short- or long-term shift in distribution could be seen.

The ambiguous relationship with Chl-a is supportive of their high suitability around the outer shelf, where lower values of Chl-a have been reported compared to the inner- and outer Hauraki Gulf regions. Despite filter feeders' affinity towards areas with high Chl-a concentrations, the lack of this could be due to a proposed interrelationship between Spinetail devil rays and *N. australis*, the most abundant euphausiid species in Aotearoa New Zealand coastal waters. *N. australis* occur around the outer shelf and Spinetail devil ray prevalence to this location could be attributed to a highly specialised diet of this species.

Although no annual patterns were identified, there is 16.2% of change in habitat suitability over the study period that is not explained by the model – this is attributed to variables that are not included in the model such as survey effort, or changes over time in dynamic variables such as SST that are not captured in the environmental data due to factors such as resolution. However, this unexplained variance is substantially less than that of the Oceanic manta rays, possibly attributed to the inclusion of SOI. Both static and dynamic model suggested that habitat suitability is higher during La Niña years, especially stronger events. Although productivity declines during La Niña events, the increase in SST may allow Spinetail devil rays to reside in Aotearoa New Zealand for longer, compared to El Niño events, increasing the time available for interaction events with fisheries vessels. It is important to address that during the study years, La Niña events have been the majority thus, survey effort is required in El Niño years to ensure this relationship is not due to a sampling bias.

Oceanic manta rays were predicted to have the highest habitat suitability near-shore, all along the eastern coastline, especially in the Tīkapa Moana Hauraki Gulf within the Jellicoe and Cradock Channel. Although seasonality could not be assessed, the records at face-value suggested that Oceanic manta rays may occur mostly during late summer months and reside in Aotearoa New Zealand waters for longer than Spinetail devil rays. Predicted habitat preferences suggested areas with high Chl-a concentrations with moderate to high sloping, analogous with regions within the Gulf. The inconsistent relationship in SST across the static and dynamic model may be indicative of the complex relationship between the trade-offs of being an ectotherm that requires warmer waters for increased metabolic rate, but the colder waters representing areas with higher productivity and prey availability. Spatial and temporal patterns over the study period seem to be relatively consistent like Spinetail devil rays however, there is a clear increase in suitability in 2017, 2019, 2020 and 2021.

The lack of a gradual long-term shift and evidence of interannual variability, suggest that ENSO or other interannual modes may be influencing their distribution. The exclusion of ENSO from the model due to the use of random pseudo-absences could explain the reason for 48.7% of variance in habitat suitability over time that is unexplained by the model. The high importance of Chl-a and SST for both models and the tight coupling between ENSO and these variables suggest that Oceanic manta rays' distribution could be intimately linked with the ENSO phases. Nevertheless, habitat suitability appears to be increasing over time according to this spatially latent variable thus, requires more attention and further investigation.

Although mobulid species appear to be similar in habitat requirements, the findings from this study provide evidence for the contrary. The different relationships between the environmental variables and the clear separation in predicted distributions with the 200m isobath acting as a demarcation line, provide strong support for probable trophic separation in the northeast shelf. There is a clear separation in habitat utilisation, potentially linked to their preferred prey or energetic requirements (i.e., larger caloric requirements for Oceanic manta rays).

3.2 SIGNIFICANCE AND CONTRIBUTION OF RESEARCH FINDINGS

3.2.1 Implications of this study

The protection of species and conservation planning processes often require spatially explicit information regarding their distribution, habitat use and abundance and subsequent information on the quality of these habitats (Akçakaya, 2000; Franklin, 2010). This thesis presented the investigation of habitat suitability within the NE shelf of the Te Ika-a-Māui North Island of Aotearoa New Zealand, using a BRT model. Predictive maps over this study region for mobulid species were created for the first time and provided the initial conditions of suitable habitats and the environmental conditions that are responsible for driving this suitability.

Species distributions tend to shift spatially in response to specific changes in environmental conditions (Melo-Merino et al., 2020) thus, by uncovering the conditions that are suitable for both species, their distribution can be understood and predicted for future scenarios where changes in these conditions are expected. Due to these expected shifts, this thesis examined habitat suitability over time on an annual scale to investigate whether shifts were already occurring. Dynamic models for both species indicated that habitat suitability increased over time which could be attributed to increasing SST, and a greater portion of the year that rests within their thermal range. Fine-scale environmental data was used within the BRT models and revealed high habitat suitability for both species around the Tīkapa Moana Hauraki Gulf region, highlighting the importance of this area.

The identification of a hotspot for Spinetail devil rays on the outer shelf, past the Tīkapa Moana Hauraki Gulf is indicative of their high prevalence as bycatch. High suitability occurs just beyond the boundary of the Tīkapa Moana Hauraki Gulf Marine Park (Figure 2.14, 2.17) and beyond MPA or areas with robust protection. This is evidenced by Spinetail devil rays being one of the most captured protected fishes (Francis & Lyon, 2012) especially around the 200m contour by skipjack tuna purse seine fisheries (Francis & Jones, 2012). Conservative life history traits coupled with the lack of protection and the predominant diet for skipjack tuna to also be *N. australis* in Aotearoa New Zealand waters (Ministry for Primary Industries, n.d.), explains their high prevalence as bycatch. Currently, the predictive maps from this study suggest that Spinetail devil rays are not being adequately protected within Aotearoa New Zealand waters, and the NE shelf of the Te Ika-a-Māui North Island in particular. Therefore, these maps and findings presented in this thesis provide reliable distributional information to support conservation initiatives to reduce the occurrence of Spinetail devil rays as bycatch. This aligns with the Conservation Services Programme Protected Marine Fishes Medium-Term Research Plan by the Department of Conservation which outlines the high priority of research related to Spinetail devil rays' overlap with fisheries, factors influencing bycatch (e.g., vessel size) and habitat preferences (Department of Conservation, 2021). Due to the high mortality after being released from purse-seine nets and the high risk and consequence score from qualitive assessments of the risk of commercial fishing (Ford et al., 2015, 2018), further investigations of this hotspot with survey (e.g., boats, aerial) or satellite tags is likely to increase understanding of these elusive animals.

Oceanic manta ray hotspot was identified through the predictive maps, as the Jellicoe and Cradock Channel. Due to the coastal and near-shore nature of the habitat requirements predicted for this species, their distribution lies within the Tīkapa Moana Hauraki Gulf Marine Park. In response to declining biodiversity and health of the Gulf, *Sea Change Tai Timu Tai Pari* is a marine spatial plan with the sole purpose of restoring the health, social and economic wellbeing of the region (Department of Conservation & Fisheries New Zealand, 2021). Although no MPAs are in place yet, due to a previous study combining survey effort and SDMs within the Tīkapa Moana Hauraki Gulf to investigate distribution and habitat use of cetaceans, the Cradock Channel was identified as a critical hotspot for both Bryde's whales and bottlenose dolphins (Dwyer, 2014). Through this identification and coupled with species richness assessments, *Sea Change* has proposed a 152km^2 protected area in the Cradock Channel (Department of Conservation & Fisheries New Zealand, 2021 Despite a central focus of this proposed MPA on benthic protection, the restriction of dredging and trawling will no doubt benefit Oceanic manta rays through increased visibility and disturbance.

The Jellicoe Channel was also identified as a hotspot however, this region remains unprotected with no proposed MPAs. However, the previous study by Dwyer (2014) demonstrates the influence that distributional studies can have on policy and driving the implementation of protected areas. Therefore, the identification of the Jellicoe Channel can serve as a recommendation to *Sea Change* for a protected area, especially due to the alignment with their aim of creating a network of MPAs in the Tīkapa Moana Hauraki Gulf. A potential protected area in this channel can serve as an extension of the Cape Rodney Okakiri Point Reserve and Goat Island Reserve to increase protection of critical species, namely the Oceanic manta ray.

3.2.2 Dynamic Marine Protected Areas

Although protected areas that are proposed or implemented above can be an important tool for conservation (Lubchenco et al., 2003), to date, there is little evidence of the efficacy of these contemporary protected areas on mobile marine species (Game et al., 2009; White et al., 2015). The lack of efficacy is largely related to the static nature of these parks, neglecting the dynamic nature of marine systems and the animals the inhabit them.

The conversation has turned to dynamic MPAs that have mobile boundaries and can follow the movement of highly mobile species or dynamic systems (e.g., fronts, eddies) and account for seasonality, migration, or distributional shifts due to interannual variability or climate change (Bakker, 2022; Maxwell, 2015; Reynolds et al., 2017; Schofield et al., 2013). Although enforcement is a barrier, these issues are indifferent to stationary MPAs and the increasing presence of digital technologies (e.g., drones, marine tags, machine learning algorithms, on-board cameras; electronic monitoring) are tools that can be utilised in this space (Bakker, 2022; Maxwell et al., 2015; Rohde et al., 2020). As the ocean become increasingly unpredictable and dynamic (Dunn et al., 2017; Bakker, 2022), efficacy of static conservation strategies that are based in terrestrial management (Carr et al., 2003; Duck, 2012) is becoming obsolete. Further questions around the social and economic consequences of a MPA that restricted activity, set up to protect a certain species no longer contains that species (Cashion et al., 2020).

In response to the cost to relevant stakeholders associated with establishing MPAs, Maxwell et al. (2015) found that 34.2% to 82% less space was needed for a dynamic MPA compared to a traditional MPA, leaving more area available for human activities (Dunn et al., 2011). An example of a dynamic MPA is demonstrated by Howell et al. (2008) through the creation of TurtleWatch, a product that maps the near real-time areas where loggerhead turtles are likely to be based on SST preferences, to minimise interactions with longline fisheries. Due to the success of this product in identifying areas where turtle bycatch was likely to occur, it was extended to multispecies habitat use with the inclusion of leatherback sea turtles (Howell et al., 2015). The Tīkapa Moana Hauraki Gulf Marine Park is not only a biologically significant area, but an area with immense recreational and commercial fishery presence (Stevens et al., 2021). It is important to address that sustainability extends towards social and economic realms, and the compliance of such MPAs without this consideration is unlikely to be successful. Thus, dynamic MPAs are a likely solution that maximises environmental, social and economic wellbeing and sustainability by reducing area usage, increasing more space for human activities and the minimisation of fisheries interaction (especially for Spinetail devil rays).

3.3 FUTURE RESEARCH

This study serves as the first attempt to understand the potential habitat use and distribution of mobulids in Aotearoa New Zealand. The use of opportunistic data and

SDMs provided a low-cost option to provide baseline information on mobulids and bring awareness to potential distribution shifts over time. However, we note that SDMs could never replace dedicated and ongoing fieldwork or survey effort (Guisan & Thuiller, 2005). Further, SDMs must be continuously updated with the most recent data available, and the ecological rationality of modelled responses and predictions must be investigated (Burgman et al., 2005) especially if used in a conservation management context.

There are a few elements that should be investigated further to build on the findings from this thesis. In terms of facilitating the SDM work done in this thesis, it should be supplemented with systematic surveys either on a boat, plane or using satellite telemetry and track the finer scale horizontal and vertical habitat use of both species (Cabral et al., 2023). Surveys will allow for future models to be run with reliable observed absences and presence records.

Further, as filter feeders, mobulids' distribution and movement are likely to be inextricably linked to that of their specific prey. In this thesis, due to the availability of data only Chl-a and gradient files could be included however, there is no doubt that including specific prey distributions such as *N. australis* for Spinetail devil rays will lead to a better characterisation of their potential distribution. This could involve the collection of prey samples during mobulid surveys. There are also a couple of regions that have intermittent sightings of mobulids but a lack of survey effort, including the Te Moana a Toi-te-Huatahi Bay of Plenty and the West Coast of the Te Ika-a-Māui North Island. Increasing survey effort in these areas will ultimately lead to a better quantification of the full environmental range that mobulids utilise in Aotearoa New Zealand waters and may eventually lead to estimations of abundance and population dynamics.

As ectotherms and filter feeders, mobulids will likely be impacted by climate change and interannual variability such as ENSO (Richardson, 2008). Although ENSO was shown to influence the distribution of Spinetail devil rays, the lack of better absence records for Oceanic manta rays meant that this relationship could not be investigated further. Collection of data and running SDMs at finer temporal and spatial scales will likely to reveal interannual patterns better. Further, the collection of long-term data across broader scales (i.e., not limited to the NE coast) will be necessary to better understand habitat-use in Aotearoa New Zealand waters how this is changing over time and space in response to climate change and interannual variability.

Additionally, a larger dataset than is presented in this thesis is necessary to examine environmental and biological relationships on finer spatial and temporal scales, with more certainty. Systematic surveys can be undertaken and supplemented by satellite tagging to investigate the validity of hotspots that are suggested in this thesis and to examine the plausibility of foraging or nursing grounds in Aotearoa New Zealand waters. Given the evidence of courting behaviour for both species, heavily pregnant Oceanic manta rays (Lydia Green pers. comm) and near-term embryos collected for Spinetail devil rays, there is immense potential for the presence of a breeding or nursery ground and site fidelity. The loss of mobulids from global and Aotearoa New Zealand waters are largely unknown however, due to these animals constantly filtering water and sampling the environment, they are recognised as ecosystem indicators (Boldrocchi et al., 2023; Fossi et al., 2014). Similar to whales, mobulids may have an important ecological role as concentrated food drop to the deep (Higgs et al., 2014) delivering organic matter from the surface to the deeper ocean. There has previously been an oversight into the vulnerability of mobulids to anthropogenic impacts and the how their absence may impact coastal ecosystems and communities. But through increased awareness, data collection and collaboration, the re-population and conservation of mobulids is possible, seen through the increased sighting frequency in Hawaii since legal protection in 2009 (Ward-Paige et al., 2013) and the significant increase in abundance in Raja Ampat, as a result of a series of conservation measures and protection since 2007, a shark and ray sanctuary in 2012 and the Indonesian government declaring full national-level protection in 2014 (Setyawan et al., 2022a; Setyawan et al., 2022b).

3.4 CONCLUDING STATEMENT

In conclusion, the NE coast of the Te Ika-a-Māui North Island of Aotearoa New Zealand hosts a multitude of environments that are suitable for mobulids, with a clear preference for waters around the Tīkapa Moana Hauraki Gulf Marine Park. Though this study, several important hotspots and environmental drivers of habitat suitability have been identified with a purely spatial and a spatio-temporal approach. Future challenge lies with initiating/starting survey effort as well as the increased awareness for fisheries and boat users across the country, not just limited to the NE coast. The ill-understood nature of mobulid rays in Aotearoa New Zealand and globally highlights the necessary funding, effort and attention that is required to ensure their conservation and protection in the wake of current and future threats. This research has demonstrated the successful application of SDMs to species with limited observations and identified critical areas that require further investigation. The consistency between the results and previous studies suggest that these predictive maps can be useful in conservation initiatives and future planning. Further, this study highlights the need for increased survey effort across the entire year with collection of long-term datasets in future SDMs for better predictions across finer temporal scales and to avoid constraints associated with using pseudo-absences. Increased data availability and understanding of processes that drive mobulid distribution and habitat use will ultimately lead to increased robustness in their protection and conservation now and into the future.

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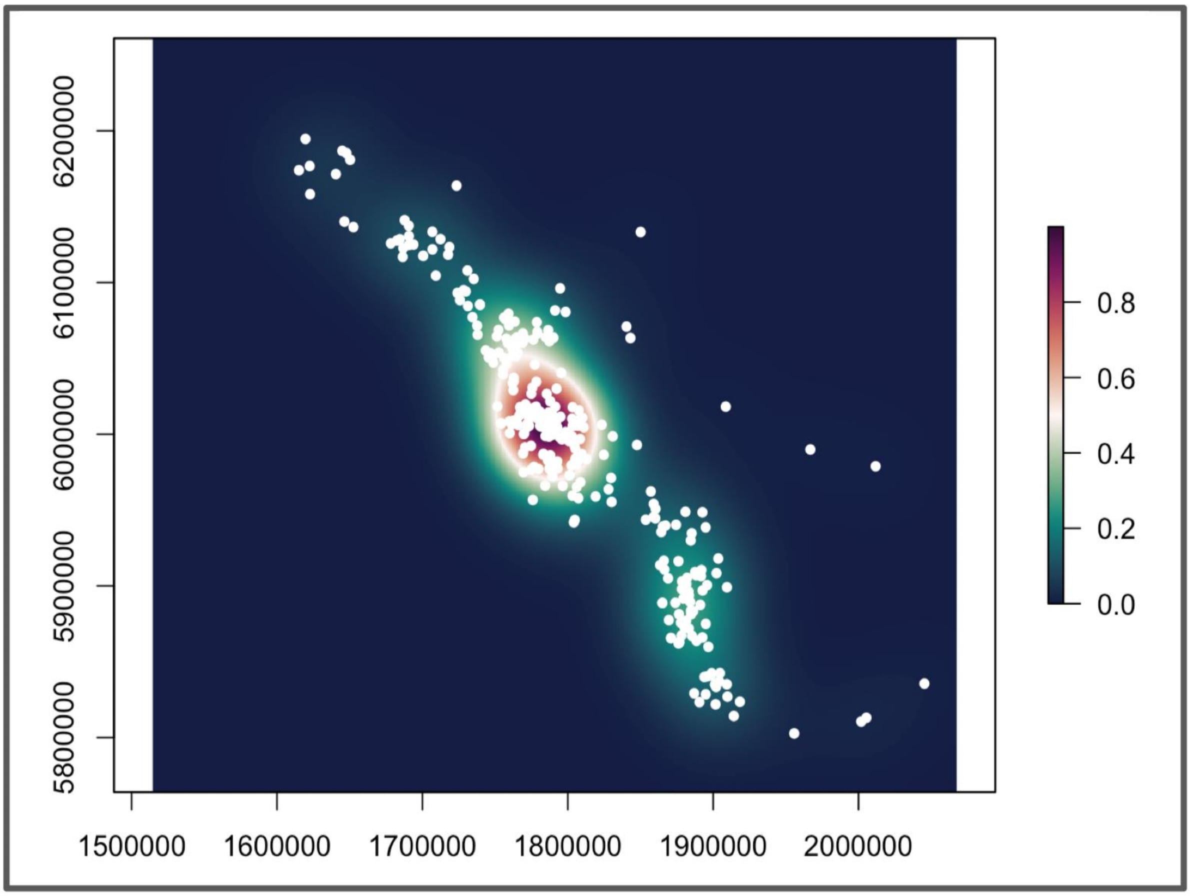
APPENDICES

Appendix 2.1

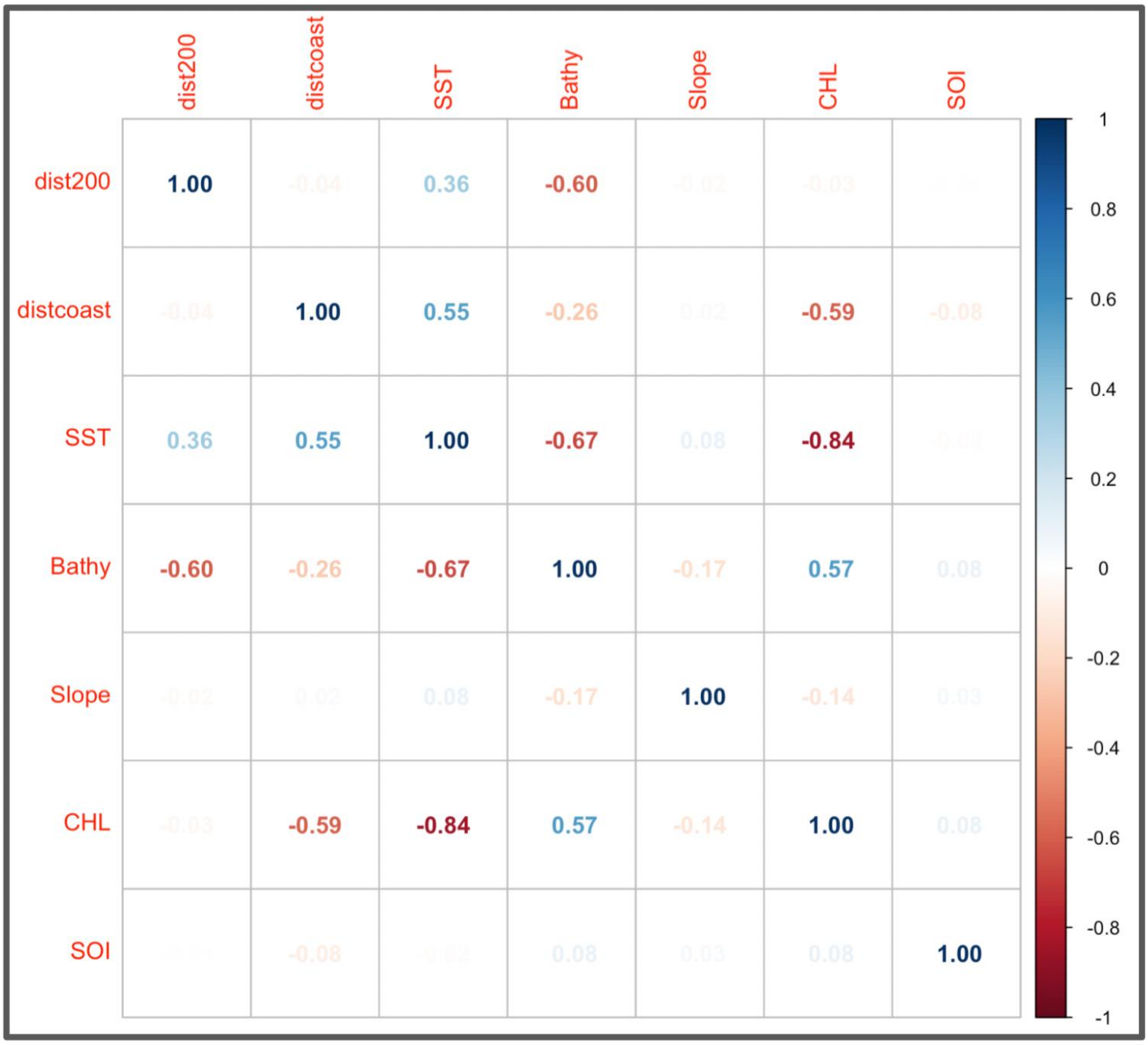
Map of KDE probability grid from Oceanic manta ray presence points (white dots), shown in ESPG: 9191. Pseudo-absence points are sampled from this probability grid. The higher values indicate that pseudo-absences will be sampled from here proportionately more than the lower values, according to the probability grid.



Appendix 2.2

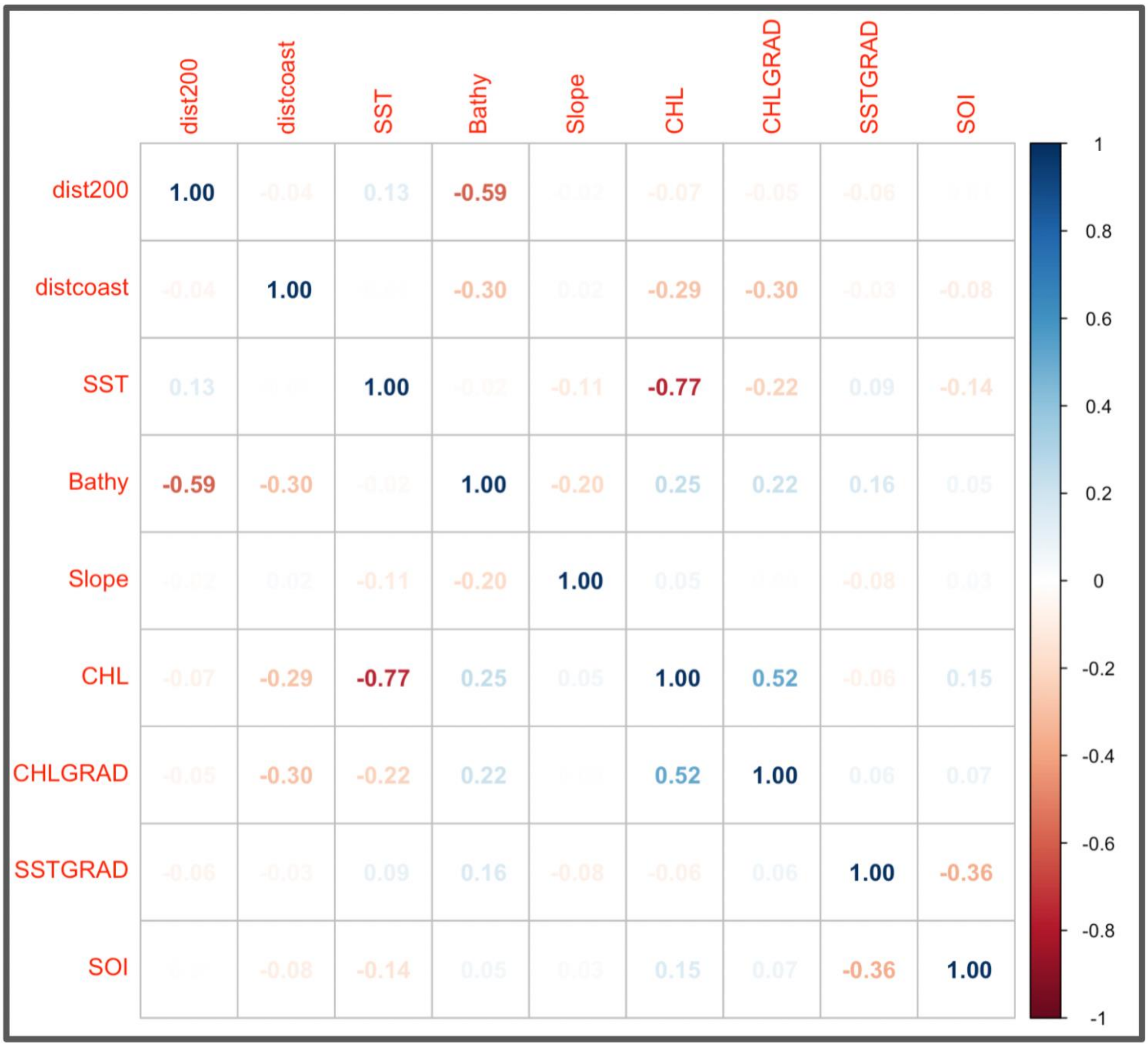
Correlation matrix shown for key variables for Spinetail devil rays – (a) static model, (b) dynamic model. Numbers are correlation coefficients, and the colour corresponds with positive correlation (red) and negative correlation (blue) with the degree of correlation indicated by the darkness of the colour. For BRT models, 0.9 is considered high correlation thus, all variables were included in the final model.

(a)



	dist200	distcoast	SST	Bathy	Slope	CHL	SOI
dist200	1.00	-0.04	0.36	-0.60	-0.02	-0.03	[illegible]
distcoast	-0.04	1.00	0.55	-0.26	0.02	-0.59	-0.08
SST	0.36	0.55	1.00	-0.67	0.08	-0.84	-0.02
Bathy	-0.60	-0.26	-0.67	1.00	-0.17	0.57	0.08
Slope	-0.02	0.02	0.08	-0.17	1.00	-0.14	0.03
CHL	-0.03	-0.59	-0.84	0.57	-0.14	1.00	0.08
SOI	[illegible]	-0.08	-0.02	0.08	0.03	0.08	1.00

(b)

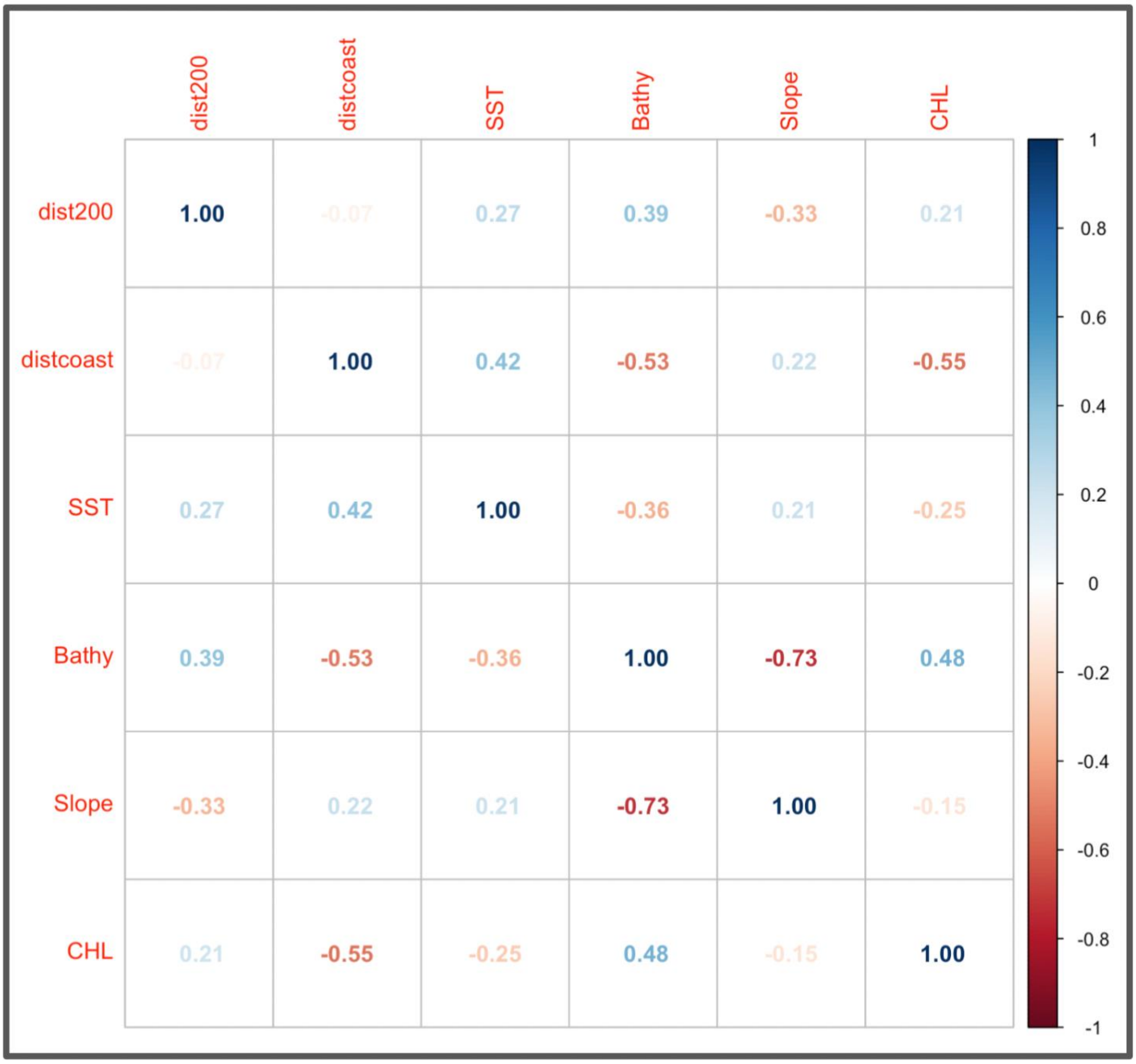


	dist200	distcoast	SST	Bathy	Slope	CHL	CHLGRAD	SSTGRAD	SOI
dist200	1.00	-0.04	0.13	-0.59	-0.02	-0.07	-0.05	-0.06	[illegible]
distcoast	-0.04	1.00	[illegible]	-0.30	0.02	-0.29	-0.30	-0.03	-0.08
SST	0.13	[illegible]	1.00	-0.02	-0.11	-0.77	-0.22	0.09	-0.14
Bathy	-0.59	-0.30	-0.02	1.00	-0.20	0.25	0.22	0.16	0.05
Slope	-0.02	0.02	-0.11	-0.20	1.00	0.05	[illegible]	-0.08	0.03
CHL	-0.07	-0.29	-0.77	0.25	0.05	1.00	0.52	-0.06	0.15
CHLGRAD	-0.05	-0.30	-0.22	0.22	[illegible]	0.52	1.00	0.06	0.07
SSTGRAD	-0.06	-0.03	0.09	0.16	-0.08	-0.06	0.06	1.00	-0.36
SOI	[illegible]	-0.08	-0.14	0.05	0.03	0.15	0.07	-0.36	1.00

Appendix 2.3

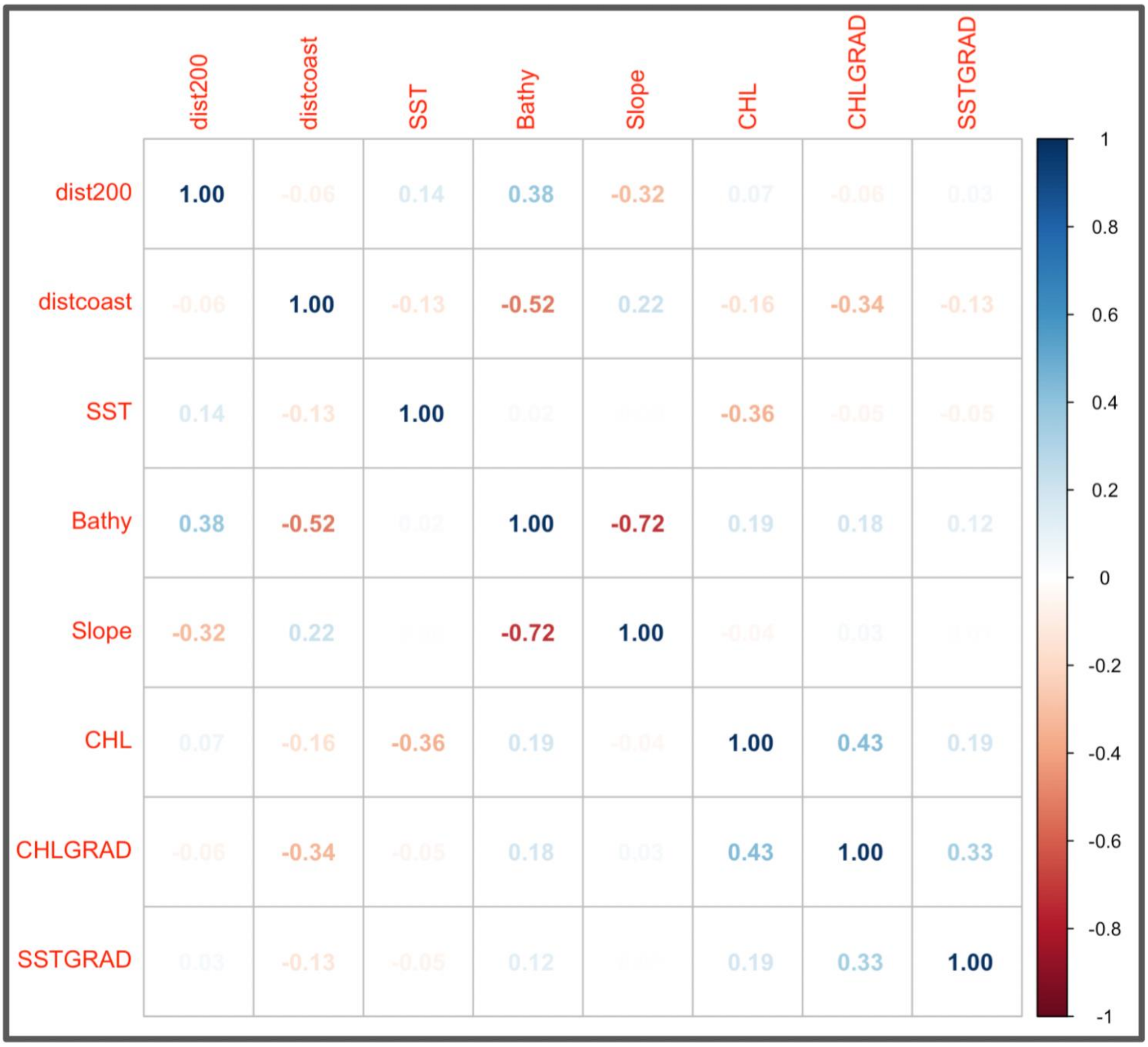
Correlation matrix shown for key variables for Oceanic manta rays – (a) static model, (b) dynamic model. Numbers are correlation coefficients, and the colour corresponds with positive correlation (red) and negative correlation (blue) with the degree of correlation indicated by the darkness of the colour. For BRT models, 0.9 is considered high correlation thus, all variables were included in the final model.

(a)



	dist200	distcoast	SST	Bathy	Slope	CHL
dist200	1.00	-0.07	0.27	0.39	-0.33	0.21
distcoast	-0.07	1.00	0.42	-0.53	0.22	-0.55
SST	0.27	0.42	1.00	-0.36	0.21	-0.25
Bathy	0.39	-0.53	-0.36	1.00	-0.73	0.48
Slope	-0.33	0.22	0.21	-0.73	1.00	-0.15
CHL	0.21	-0.55	-0.25	0.48	-0.15	1.00

(b)



	dist200	distcoast	SST	Bathy	Slope	CHL	CHLGRAD	SSTGRAD
dist200	1.00	-0.06	0.14	0.38	-0.32	0.07	-0.06	0.03
distcoast	-0.06	1.00	-0.13	-0.52	0.22	-0.16	-0.34	-0.13
SST	0.14	-0.13	1.00	0.02	[illegible]	-0.36	-0.05	-0.05
Bathy	0.38	-0.52	0.02	1.00	-0.72	0.19	0.18	0.12
Slope	-0.32	0.22	[illegible]	-0.72	1.00	-0.04	0.03	[illegible]
CHL	0.07	-0.16	-0.36	0.19	-0.04	1.00	0.43	0.19
CHLGRAD	-0.06	-0.34	-0.05	0.18	0.03	0.43	1.00	0.33
SSTGRAD	0.03	-0.13	-0.05	0.12	[illegible]	0.19	0.33	1.00