Spatial Ecology and Foraging Behaviours of the Oceanic Manta Ray (*Mobula birostris*) in Aotearoa New Zealand

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Abstract

Understanding the movements and associated behaviours of animals is critical for facilitating informed conservation and management decisions. This is particularly important for species such as the globally endangered oceanic manta ray (*Mobula birostris*), which has a highly conservative life history and is therefore more vulnerable to population disturbances. Investigating the behaviours of highly mobile animals which spend most of their time underwater can be challenging. Satellite telemetry provides a valuable means of tracking movement, and collecting environmental data, facilitating the inference of behaviours and influences of environment variables on ecological processes. This thesis focuses on the fine-scale spatial ecology and foraging behaviours of oceanic manta rays during their seasonal presence in northeastern Aotearoa New Zealand. Seven individuals were tracked using high-resolution SPLASH10F satellite tags, which indicated broad variation in movements along the northeastern coast, with particular fidelity to Tīkapa Moana—Te Moananui-ā-Toi—the Hauraki Gulf. Throughout their range, manta rays displayed high fidelity to surface waters < 5 metres, with occasional deeper dives. I used Generalised Additive Models to investigate the environmental influences on behaviours inferred from horizontal movements, revealing that foraging was linked to clearer waters during the day and more turbid areas at night, suggesting a potential trade-off between increased visibility facilitating prey detection and discrimination, and foraging in areas with higher prey density. Deeper dives were more frequent at night, with depth of dives related to increased moon illumination. Manta rays occupied shallower waters around dusk and dawn, and at midday. Dives likely reflect a combination of searching, foraging, and navigational behaviours. These findings provide valuable baseline information on oceanic manta rays in New Zealand—a region where they are particularly understudied. Future research should attempt to integrate horizontal and vertical movements to further inform manta behaviours, and should aim to increase sample size, tagging a range of demographic groups across a longer time period. Incorporating prey distribution into modelling will increase understanding of how this species might respond to environmental stressors, informing conservation management, and ensuring this population can persist into the future.

Photo Credit: Manta Watch Aotearoa New Zealand

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Glossary and Abbreviations

(*In order of appearance)*

ENSO	El Niño Southern Oscillation
PTT	Platform Transmitter Terminal
GPS	Global positioning system
PATs	Pop-up archival tags
SPOTs	Smart position and temperature tags
PSATs	Pop-up satellite archival tags (hybrid tags)
chl-*a*	Chlorophyll-*a*
IUCN	International Union for Conservation of Nature
Te Whai Rahi	Te Reo Māori name for the oceanic manta ray
MWANZ	Manta Watch Aotearoa New Zealand
Gulf	Tīkapa Moana—Te Moananui-ā-Toi—the Hauraki Gulf
EAUC	East Auckland Current
ARS	Area-restricted search
GAM	General Additive Model
DW	Disc width
DVM	Diel vertical migration
rDVM	Reverse diel vertical migration
EEZ	Exclusive economic zone

Chapter 1

General Introduction

1.1 Movement ecology

Understanding how and why animals move, and how they might respond to future environmental changes, is critical for informing effective conservation and management practices (Nathan et al., 2008; Lisson et al., 2017; Hays et al., 2019; Armstrong et al., 2021). Movement ecology aims to understand the mechanisms and patterns of animal movement across varying temporal and spatial scales, driven by the heterogeneity of resources, environmental factors, physiological constraints, and social interactions (Nathan et al., 2008). At the largest scale, long-distance migratory movements take place between spatially separated resources and habitats. In the Serengeti, wildebeest (*Connochaetes taurinus*) migrate *en-masse,* accompanied by zebras (*Equus burchelli*) and Thomson's gazelles (*Gazella thomsoni*), in a predictable clockwise loop, moving between dry and wet season ranges (Torney et al., 2018). Fine-scale movements occur within localised regions and are often associated with daily behavioural patterns. Animals will adjust their movements throughout the day as they navigate their environment, in response to immediate environmental conditions and resource availability (Oleksyn et al., 2020; Zhao et al., 2020; Barras et al., 2021). For instance, the white-tailed deer (*Odocoileus virginianus*) will preferentially feed on patches of vegetation, selected based on factors like plant species composition, nutrient content, and accessibility (Webb et al., 2010). Throughout the day, these deer will adjust their grazing locations within a localised region in response to changes in sunlight, temperature, and the presence of predators. Across all scales, movement enables animals to fulfill their fundamental life history needs, including breeding and feeding (Shaw, 2016; Harris et al., 2021; Illán et al., 2022; Lassis et al., 2022).

1.1.1 Foraging ecology

Movement ecology is intrinsically linked to foraging ecology. The distribution and availability of food resources is a key driver of movement as all animals share a common goal of needing to eat to fulfill specific energetic requirements. However, foraging strategies are highly variable between and within species, selected to maximise resource gain while minimising energetic cost (Schoener, 1971; Lubitz et al., 2022). Environmental heterogeneity and stability drive diversification in foraging strategy. Whilst stable, homogenous habitats favour the evolution of specialist foragers with narrow diets; generalist strategists, which readily switch diet in response to locally available resources are typically selected for in more dynamic, variable conditions (Stephens & Krebs, 1986). Many animals will return to specific regions, or features, which are associated with high quality and predictable resource availability (Fagan et al., 2013). While site-fidelity is observed across both stable, and dynamic environments, it is particularly advantageous where resources are patchily distributed, but spatially and temporally predictable (Switzer, 1993). In some cases, strong site fidelity may cause animals to return to poor-quality habitats even when they are less profitable (Merkle et al., 2022). Animals can further enhance foraging opportunities through adapting navigation patterns, or the timing of movements, based on phenological variation in food resources, and local environmental conditions or prey encounters (Thorup et al., 2017; Abrahms et al., 2021).

1.2 Movement in the marine environment

The inherent complexity and inaccessibility of the marine environment presents a unique set of challenges for movement ecology research compared to terrestrial systems (Kressler et al., 2023). Unlike terrestrial landscapes, the marine environment is characterized by its three-dimensional space, where the complex interplay between dynamic oceanographic features such as sea surface temperature, winds, and ocean currents, along with stable features like bathymetry or seafloor structures, creates a highly spatiotemporally variable environment (Carr et al., 2003).

At the broadest scale, in the Pacific, El Niño Southern Oscillation (ENSO) drives basin-scale climatic fluctuations—characterised by interannual El Niño or La Niña phases. The El Niño phase is initiated by the weakening of the trade winds which causes warm water from the western Pacific to spread east. Whereas La Niña is the reverse of this, where strengthening trade winds move warm water westwards in the Pacific, causing the upwelling of cool, nutrient rich water off the coast of the Americas (Trenberth, 1997). These large-scale climatic fluctuations exert influences over a range of oceanographic features which vary between areas. At the regional scale, oceanographic currents cause seasonal and decadal shifts in productivity, which structure and support entire communities (Oviatt et al., 2015). Mesoscale eddies and submesoscale fronts create turbulence, drive nutrient fluxes, aggregate species, and provide habitats in pelagic waters (Scales et al., 2014; Lévy et al., 2018; Xiu et al., 2022). At even finer scales, daily tidal regimes and internal wave activity influence spatiotemporal habitat quality and resource distributions in many coastal areas (Embling et al., 2013; Kressler et al., 2023).

1.2.1 Prey patchiness, and prey-predator relationships

As a consequence of the highly dynamic and heterogeneous nature of the marine environment, prey distribution is often patchy and ephemeral (Grados et al., 2016; Wang, 2019; Seo et al., 2023). Patchiness of phytoplankton, the dominant primary producer in marine systems and the basis for most food webs, is one of the oldest and most well-known observations in oceanography (Bainbridge, 1957). This patchiness is expected to extend up the trophic chain, clustering predators near areas of high productivity. While coherence in the spatial distribution of predators and prey is commonly observed within terrestrial, freshwater, and benthic systems, in the pelagic marine environment, there is often a mismatch in temporal and spatial scales of predator-prey distribution (Jaquet & Whitehead, 1996; Godø et al., 2012; Benoit-Bird et al., 2013). Average biomass concentrations in marine systems are four orders of magnitude lower than in terrestrial systems (Benoit-Bird, 2024). Consequently, prey encounter rates are much lower and patches of prey therefore, are much more important. Indeed, a growing body of work indicates that marine predators will preferentially occupy fronts, eddies, and meanders, which concentrate and retain plankton creating high-quality prey patches (Cotté et al., 2007; Godø et al., 2012; Della Penna et al., 2015; Hernández-Hernández et al., 2020).

1.2.2 Foraging in the marine environment

To be successful within a highly heterogenous environment, predators must adopt foraging strategies that enable them to track and respond to variations in prey distributions and environmental conditions across time and space (Russell et al., 1992). Foraging strategies for marine species can vary inter- and intra-specifically (Austin et al., 2021; Schwarz et al., 2021). For some species, such as the large filter feeding whale shark (*Rhincodon typus*) and basking shark (*Cetorhinus maximus*), heavy reliance on dense zooplankton patches means that movements are closely tied to shifts in prey abundance. Humpback whales (*Megaptera novaeangliae*) migrate thousands of kilometres between polar feeding grounds, and tropical breeding grounds (Dawbin, 1966). However, other species may exhibit a more residential strategy, remaining in the same area year-round. Resident Bryde's whales (*Balaenoptera edeni bryde*i) in Aotearoa New Zealand exploit a wide range of seasonally available prey, including zooplankton and fishes (Izadi et al., 2022).

In the marine realm, movement occurs not only in the horizontal plane, but also vertically. It is important to consider movement along both these planes to gain a more comprehensive understanding of the ecological dynamics and intricate relationships that shape the marine environment (Andrzejaczek et al., 2022). Prey distribution and environmental conditions also vary vertically. For example, northern elephant seals (*Mirounga angustirostris*) *will* regularly dive to 400 to 600 metre depths to exploit high abundances of small fishes within the mesopelagic zone; they may also target larger demersal fish in benthic coastal regions (Adachi et al., 2021). Light attenuation drives vertical structuring of the pelagic zone. Below 200 metres, in the mesopelagic zone, minimal sunlight penetration requires animals foraging at these depths to possess enhanced visual senses or rely on other senses to find prey (Warrant & Locket, 2004; Naito et al., 2013; Adachi et al., 2022). Additionally, cold temperatures at depth will cause a reduction in metabolic rates (Steffensen, 2005). Some deep-diving species are endothermic, generating some degree of body heat, while others may exhibit behavioural thermoregulation, returning to warmer surface waters between dives to rewarm (Dickson & Graham, 2004; Thums et al., 2013).

Diel vertical migration is a widespread behavioural pattern in which organisms such as zooplankton and small fishes will spend time at depth, forming aggregations known as deep scattering layers. During dusk, these species migrate to shallow waters to feed on phytoplankton at the surface, descending again at the following dawn (Hays, 2003). These behaviours likely occur as a predator-avoidance strategy, providing refuge from visual predators while enabling the exploitation of phytoplankton near the surface (Lampert, 1989). These vertical migration patterns commonly drive vertical movement and foraging efforts of marine predators such as seals (Robinson et al., 2012), cetaceans (Todd et al., 2022), turtles (Fossette et al., 2010), and elasmobranchs (Sims et al., 2003). Alternatively, reverse diel vertical migration patterns allow predators to capitalise on vertically migrating prey species such as zooplankton (Andrzejaczek et al., 2021).

1.3 The ‘bio-logging’ revolution

Much of our understanding of animal behaviour comes from direct field observations (Altmann, 1974). However, the marine environment poses several challenges for this research, primarily due to the cryptic nature of many marine organisms, which often spend time at depth, and out of range of boat-based observations. These challenges are particularly pronounced for highly mobile and migratory species, that travel great distances across the open ocean throughout their lifetime. Over the last 50 years, the development and refinement of miniaturised animal-borne devices, also known as bio-loggers, have allowed researchers to passively and remotely log and relay data on an individual's physiology, environmental variables, and movement, revolutionising the field (Rutz & Hays, 2009; Hindell et al., 2020; Chung et al., 2021).

Satellite telemetry uses transmitters (Platform Transmitter Terminals/ PTTs) attached to animals and linked to networks of satellite receivers—either ARGOS (±5 km accuracy) or the Global Positioning System (GPS) satellite network (<1 km accuracy), to provide insight into the movements and behaviours of animals across space and time, even in remote and inaccessible locations (Lowther et al., 2015; Hofman et al., 2019; Watanabe & Papastamatiou, 2023). Satellite transmission cannot occur across the water-air interface, and therefore data cannot be transmitted when an animal is submerged. However, a broad range of satellite tags currently exist, which are designed with different modes of transmission to suit the specific needs of tracked species, including those which spend time at depth. Pop-up archival tags (PATs) log data over time, including vertical movements and light levels. This information is combined with known dawn and dusk times and the angle of the sun to calculate the approximate horizontal position of a tagged animal. Following the triggering of a timed-release mechanism, the tag will pop off the animal, and float to the surface where a summary of the archived data can be uploaded to satellites. While these tags often offer a more affordable option, there is large variability in the precision of these instruments; location estimates can be influenced by environmental variables, latitude, and time, regularly leading to errors of greater than 200 kilometres (Halpin et al., 2021). Therefore, these tags are designed to track broader scale movements of species which do not often come to the surface including tuna (*Thunnus thynnus*; Whitlock et al., 2022), marlins (*Kajikia audax*; Whitlock et al., 2022), some shark species (Ste-Marie et al., 2022), and eels (*Anguilla anguilla*; Verhelst et al., 2022). However, the accuracy of these tags is not good enough to provide insight into fine-scale movements. Smart position and temperature tags (SPOTs) use an antenna to transmit information, providing accurate horizontal position data to either the ARGOS or GPS satellite network. These tags contain an onboard computer, which can record various other parameters, including depth, temperature, and light level. As the antenna must break the surface to transmit, these tags are used for species which come to the surface regularly, such as air breathing mammals and reptiles (Cook et al., 2021; Citta et al., 2023), species which feed at the surface (Knochel et al., 2022; Spaet et al., 2022), and those which use the warmer shallower waters for thermoregulation (Elliott et al., 2022).

More recently, hybrid pop-up satellite archival tags (PSATs) have been developed, which are able to collect both horizontal and vertical movement data. These tags contain an antenna which will transmit data when it breaks the surface, but also log information—which can be retrieved following the release of a tag, at a finer-scale resolution than can be transmitted via satellite by PATs due to bandwidth constraints. These tags are particularly beneficial for tracking the movements of animals which spend less time at the surface producing limited satellite transmissions, as the physical recovery of PSATs provides the opportunity to retrieve the high-resolution archival data. SPLASH tags (Wildlife Computers) are one such example of these tags and are equipped with fastloc GPS technology which provide highly accurate GPS locations (precise to 20 metres), with fast location acquisition at the surface. These tags are commonly used to investigate fine scale vertical and horizontal movements of free-ranging marine animals (Fortune et al., 2020; Hart et al., 2021; Elliott et al., 2022).

Autonomous animal borne devices can be developed to concurrently collect physiological and environmental data alongside geolocation data. These devices can record information about sensory systems, heart rates, gastric activity, and muscular movements, providing detailed insight into tagged species such as physiological tolerances and behaviours (Whitford & Klimley, 2019). Environmental sensors provide *in situ* measurements of conditions such as temperature and salinity, providing valuable data for ecological studies and how these might influence behaviour. However there is also increasing interest in the use of animal-borne sensors for the purpose of providing fine-scale, environmental data, particularly for remote and inaccessible locations (McMahon et al., 2021). These sensors can measure physical oceanographic conditions such as temperature and salinity, contributing to our understanding of physical processes such as sea-ice formation, and ocean circulation dynamics (Charrassin et al., 2008; Mallett et al., 2018; Kokubun et al., 2021). When attached to seabirds, biologgers can also provide measurements of winds and currents at the air-sea interface (Yoda et al., 2014; Yonehara et al., 2016).

Advancements in biologging technology are complemented by the availability of satellite-based remote sensing. Satellites enable the large-scale, passive collection of fine-scale data on dynamic ocean conditions, such as sea surface temperature, ocean circulation, and the standing stock of primary producers (observed as chlorophyll-*a* (chl-*a*), estimated from satellite ocean colour) (Prabhakara et al., 1974; Neville & Gower, 1977; Goldstein et al., 1989). While the wide-ranging and often cryptic behaviours of these animals make them challenging to observe directly in the field, the integration of biologging with satellite derived remote sensing data facilitates research aimed at understanding their behaviours in relation to their dynamic ocean environment (Grémillet et al., 2022). When combined with increasingly available analytical and modelling methods, these data can be used to provide insights into the broader behavioural ecology of animals through the inference of distinct behavioural states, and examining the influence of environmental variables on movement metrics and patterns (e.g., Riekkola et al., 2019; Grainger et al., 2022).

1.4 Manta rays

Manta rays are large pelagic filter-feeding elasmobranchs from the family Mobulidae—a group which contains both manta rays and devil rays. There are currently two recognised species of manta rays—the oceanic manta ray *Mobula birostris* and the reef manta ray *Mobula alfredi* (Marshall et al., 2009). Previously these species were considered as one single species, M. birostris, until their reclassification in 2009, which confirmed the visually distinct *M. Alfredi* species and presented the possibility of a third manta species within the Gulf of Mexico—*Manta* sp. *cf. birostris* (Marshall et al., 2009). Comprehensive phylogenetic analyses later led to the reclassification of manta rays to the genus *Mobula* (White et al., 2018).

Following taxonomic revision separating manta rays into two separate species, much of the literature previously attributed to *M. birostris* has been reformed to now correctly describe the biology of *M. alfredi*. The more pelagic, migratory nature of the oceanic manta ray makes it much more challenging to study than the reef manta. Consequently, there is a lack of understanding regarding many of the fundamental aspects of the oceanic manta ray's biology and distribution.

1.4.1 Distribution and movements

Manta rays exhibit a wide-ranging distribution, found globally across temperate, subtropical, and tropical waters (Figure 1.1; Couturier et al., 2012). Reef manta rays inhabit tropical and subtropical productive coastal regions spanning the Indian and West Pacific Ocean. They are typically residential to shallow waters along continental coasts, reefs, or offshore islands, although regional and long-distance movements (<2400 kilometres) have been documented (Marshall et al., 2009; Couturier et al., 2012; Germanov & Marshall, 2014; Jaine et al., 2014). In contrast, oceanic manta rays have a broader, circumglobal distribution between 41° N and 40° S, where they tend to inhabit cooler, further offshore environments (Couturier et al., 2012). Oceanic manta rays are found in coastal regions, as well as near offshore islands, submarine ridges, and seamounts (Marshall et al., 2009). While some populations exhibit year-round residency patterns (Stewart et al., 2016a), seasonal shifts in presence may be indicative of migratory movements in other regions. In the Maldives, oceanic manta rays are typically only sighted throughout the months of March and April, coinciding with the transition between the northeast to southwest monsoon and the reversal of local current directions (Nicholson-Jack et al., 2021). Meanwhile, in New Zealand, satellite telemetry studies have provided evidence for a New Zealand—Fiji migration of greater than 1000 kilometres, taking place following the austral summer (Setyawan et al., 2021). It is plausible that seasonal migrations away from high latitudes are driven by thermal tolerances as manta rays seek refuge from cooling water temperatures. Distribution and movements of manta rays are also sensitive to climatic fluctuations, such as ENSO which is correlated to manta ray presence in certain regions of Mexico and Indonesia (Beale et al., 2019; Fonseca-Ponce et al., 2022; Cabral et al., 2023).

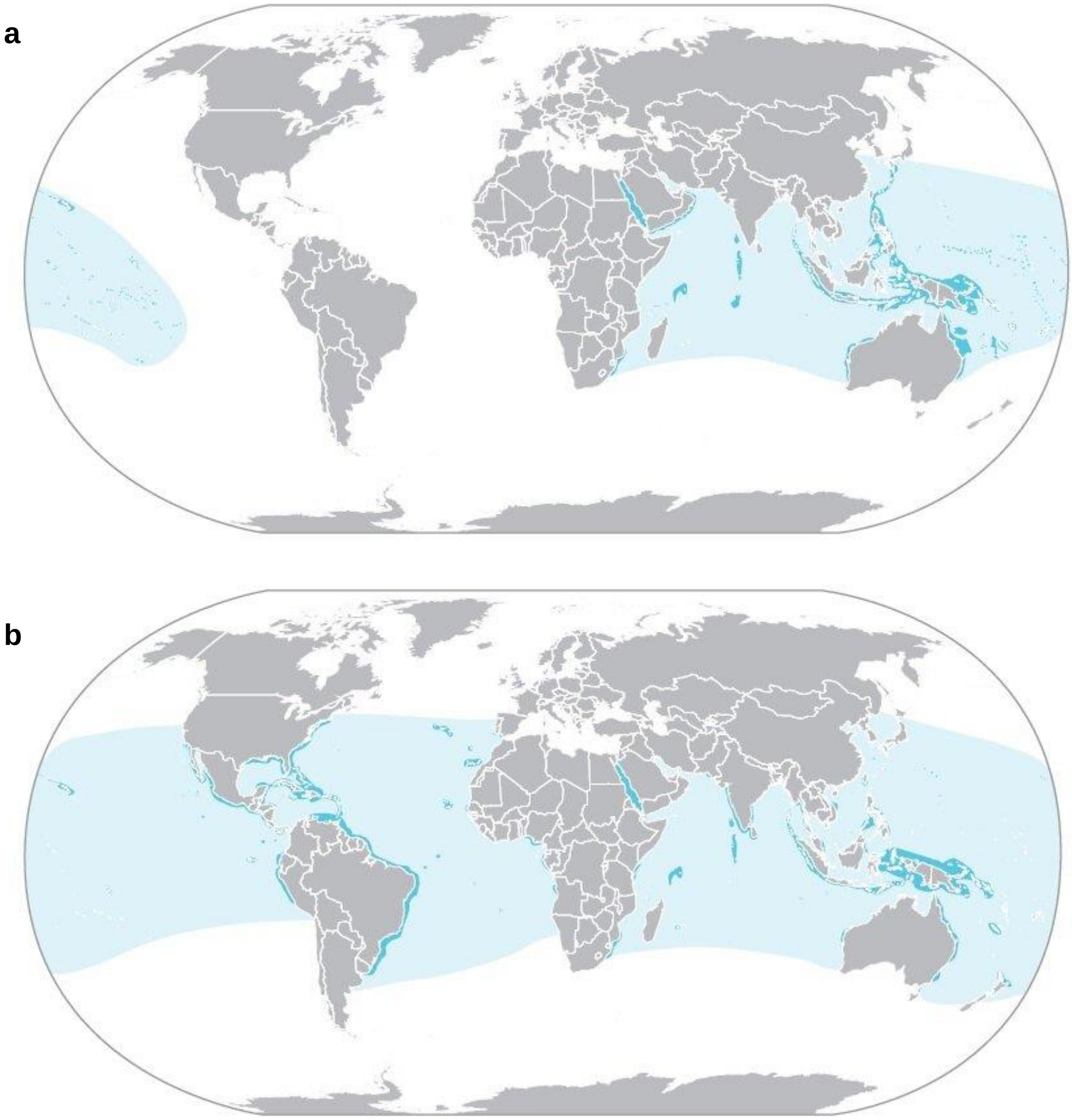

Figure 1.1 Global distribution of (a) the reef manta ray *Mobula alfredi* and (b) the oceanic manta ray *Mobula birostris*. Darker areas indicate confirmed range; lighter areas indicate expected range. Reproduced from Stevens et al. (2018a).

1.4.2 Behavioural ecology

Manta rays have been observed to form aggregations, which can range between just a couple of individuals to hundreds (Setyawan et al., 2020; Armstrong et al., 2021). These aggregations may form in response to social or environmental factors. For instance, female recruitment runs, or “mating trains” occur when multiple courting males pursue a single female in an attempts to mate with her (Yano et al., 1999; Marshall & Bennett, 2010b; Stevens et al., 2018b). Key aggregation sites are formed where repeated aggregations occur in response to predictable drivers. Cleaning stations are one such example, where manta rays aggregate to be cleaned by small cleaner fishes which feed on harmful ectoparasites and dead or diseased tissue (O'Shea et al., 2010; Barr & Abelson, 2019). These sites often serve multiple purposes; in addition to cleaning, aggregations of manta rays at cleaning stations may also facilitate courtship and mating behaviours (Stevens et al., 2018a). One of the most common drivers of aggregation is around areas with concentrated food resources (Harris et al., 2021). These aggregations may occur seasonally, in response to predictable pulses of resources, or opportunistically. In the Maldives, reef manta rays aggregate in groups of up to 150, to engage in 'cyclone' feeding strategies, where individuals will circle in an anticlockwise direction producing a vortex which concentrates zooplankton (Armstrong et al., 2021). Not all foraging aggregations, however, involve cooperative behaviours or interactions among individuals. In some cases, particularly for the oceanic manta rays, individuals may just gather in response to high abundances of food within a localised area (Palacios et al., 2023).

As a planktivorous filter-feeder, most observations of manta ray foraging behaviours occur in surface and sub-surface waters in areas of high zooplankton density (Armstrong et al., 2021). In oceanic manta rays, four distinct foraging modes have been observed: (i) straight feeding—where individuals will swim horizontally, completing feeding runs then turning 180° to feed along the same plane in the opposite direction; (ii) surface feeding—which is similar to straight feeding but the manta ray tilts its' head so their upper jaw is kept out of the water, capitalising on prey concentrated in the top few centimetres of the water column; (iii) somersault feeding—where individuals will perform a tight backwards somersault to take advantage of patches of prey; and (iv) sideways feeding—which is similar to straight feeding except the individual is rotated 90° from the typical horizontal position (Stevens, 2016). Additionally, reef manta rays will also engage in several different group foraging strategies—chain feeding, piggy-back feeding, cyclones, and bottom feeding (Stevens, 2016).

Surface zooplankton is generally considered to be the primary prey of manta ray species; however, several studies have indicated the additional contribution of mesopelagic prey to dietary intake, particularly in oceanic manta rays. Stomach content analyses of oceanic manta rays found that while *Euphausia* spp. comprised the majority of diet, there was also evidence of myctophid fishes and copepods (Rohner et al., 2017). Dietary contribution of mesopelagic prey is highly variable between populations and can also vary significantly between individuals of the same population. In Ecuador, muscle tissue δ^{13}C values indicated that the majority of dietary intake was of mesopelagic origin (Burgess et al., 2016). In the Philippines however, zooplankton was the largest contributor (Rohner et al., 2017). Stable isotope studies have indicated large intraspecific variation in δ^{13}C and δ^{15}N values, suggesting either a generalist diet or a subpopulation comprised of individual specialists (Burgess et al., 2016). An opportunistic observation from a submersible recorded footage of an oceanic manta ray somersault feeding on a dense aggregation of zooplankton (*Mysidae* spp., *Euphausiacea* spp., and *Calanoida* spp.) at between 130–140 metres depth, however mesopelagic prey also undergo diel vertical migration, and it is not yet known whether foraging on these species is most common at depth, closer to the surface during the night or both (Stewart et al., 2016b).

1.4.3 Manta ray conservation

Both the reef manta ray and the oceanic manta ray have a very conservative life history. In reef manta rays, females reach sexual maturity between 13 to 17 years of age, and males at eight to ten years (Stevens, 2016). Female oceanic manta rays are estimated to reach sexual maturity around 8.6 years, although there is often a delayed onset between maturity and pregnancy, where the first pregnancy may be delayed up to four years as a result of the high nutrient requirements of bearing a large foetus (Rambahiniarison et al., 2018). Manta rays also have the lowest intrinsic rates of population increase of any elasmobranchs (Dulvy et al., 2014). Reef manta rays give birth to one pup on average every four to five years, and this is assumed to be similar in oceanic manta rays (Marshall et al., 2022b), although it can be highly variable—in Indonesia, reef manta rays have been observed giving birth in consecutive years (Setyawan et al., 2020), but in contrast in the Maldives, reproductive periodicity is estimated at 7.3 years (Stevens, 2016). Consequently, manta ray populations are extremely susceptible to population disturbances.

Although global manta ray populations are not well understood, numerous studies have described the sharp decline in the sightings and landings of these species over time where fisheries have existed, such as in the Philippines, Indonesia, India, Sri Lanka, China, and Mexico, (Marshall et al., 2011; Lewis et al., 2015; Croll et al., 2016; Fernando & Stewart, 2021; Carpenter et al., 2023). While mobulids have been targeted by people for centuries, over the last 30 years fisheries have expanded in response to the increasing demand for gill rakers, which are traded internationally for their uses in Asian medicines (Heinrichs et al., 2011). Manta rays are also regularly caught as bycatch by both artisanal and industrial fisheries (Couturier et al., 2012). In regions where manta rays are legally protected, such as Australia, Japan, and the Maldives, sighting trends appear to be relatively stable, however there are concerns that habitat degradation and climate change induced shifts in prey-distribution may pose a future risk to manta ray populations (Marshall et al., 2022a). An additional threat to manta ray population viability is the lack of baseline information and fundamental ecological knowledge on this species. The concern for reef manta rays and oceanic manta rays has led to their current classifications as Vulnerable and Endangered respectively on the International Union for Conservation of Nature (IUCN) Red List, and their inclusion in the Convention on Migratory Species and the Convention on the International Trade in Endangered Species treaties (Marshall et al., 2022a; Marshall et al., 2022b).

1.4.4 Manta rays in New Zealand—Te Whai Rahi

New Zealand waters support a population of oceanic manta rays, representing the southernmost limits of their distribution. Here, they occur at least seasonally, and are commonly sighted off the coast of northern New Zealand throughout late austral spring (~November) to late austral autumn (~April). Species distribution modelling also suggests high habitat suitability around the west coast of the northern tip of Te Ika-a-Māui the North island and along the west coast, although there is a lack of observer presence in these regions to corroborate these predictions (Ozaki, 2023). Observations of courting behaviours, and heavily pregnant females suggest that New Zealand waters may potentially include a nursery habitat, although this is unconfirmed (L. Green, Manta Watch Aotearoa New Zealand, pers. comm). Manta rays in New Zealand have been protected under the Wildlife Act (1953) since 2011, however to date there have not been any comprehensive publications on their ecology in New Zealand waters. Consequently, oceanic manta rays are currently classified as Data Deficient under the New Zealand Threat Classification Scheme (Duffy et al., 2018). However, over recent years there has been a dedicated effort led by Manta Watch Aotearoa New Zealand (MWANZ; https://mantawatchnz.org/) Charitable Trust and colleagues. MWANZ aims to combine citizen science, collaborative research, and historic sightings data which has aided our understanding of this species in New Zealand. Photo-identification (photo-ID) records and satellite tagging methods provide insight into the broader scale movements of this species. In 2019, an oceanic manta ray named “Emmy” was tracked during her over-winter migration 1982 kilometres between New Zealand and Fiji. Photo-ID confirmed her return to New Zealand waters the following summer (Setyawan et al., 2021). However, there remains a significant research gap regarding the finer scale movements of manta rays in New Zealand.

1.5 Study site

Tīkapa Moana—Te Moananui-ā-Toi—the Hauraki Gulf (hereafter referred to as the Gulf), is a shallow semi-enclosed embayment located on the northeast coast of the North Island of New Zealand, near Tāmaki Makaurau Auckland (Figure 1.2). This region, alongside the Firth of Thames, and eastern coast of Te Tara-o-te-Ika-a-Māui the Coromandel Peninsula forms the Hauraki Gulf Marine Park (est. 2000)—an area designated for protection and preservation in recognition of its ecological, economic, social, and cultural value (Hauraki Gulf Marine Park Act, 2000). In the Gulf, prevailing westerly winds throughout autumn, winter, and spring, can drive the upwelling of cooler, nutrient rich waters (Sharples, 1997; Zeldis et al., 2004). The Gulf is influenced by the East Auckland Current (EAUC)—a subtropical western boundary current originating from the East Australian Current, which extends along the continental margin of the New Zealand northeastern continental slope, and drives hydrodynamics in this region (Stanton et al., 1997; Sharples & Greig, 1998). During late austral summer, dominant westerly winds give way to south easterly winds, promoting downwelling, and facilitating cross-shelf intrusions of the EAUC (Zeldis et al., 2004). This brings warm, subtropical waters to the Gulf, altering the composition of zooplankton and phytoplankton assemblages (Chang, 2003). This is one of the most productive ocean regions in New Zealand (Murphy et al., 2001), supporting an abundance of marine fauna diversity (Hauraki Gulf Forum, 2023) Warmer waters attract seasonally occurring tropical species, including the oceanic manta ray (Middleton et al., 2023; Ozaki, 2023).

Situated on the doorstep of Auckland, New Zealand's most populous city, the Gulf is highly accessible and a popular area for recreational water activities. Reports of manta rays in this region have significantly increased in recent years, attributed to enhanced public outreach and education efforts by MWANZ which actively encourages people to submit their photos and sighting information, contributing to the growing database (L. Green, MWANZ, pers. comm). A taonga (treasured) species to many New Zealanders, studying oceanic manta rays in New Zealand contributes to the global scientific knowledge of this species and aids conservation and management efforts, helping to ensure their long-term survival into the future.

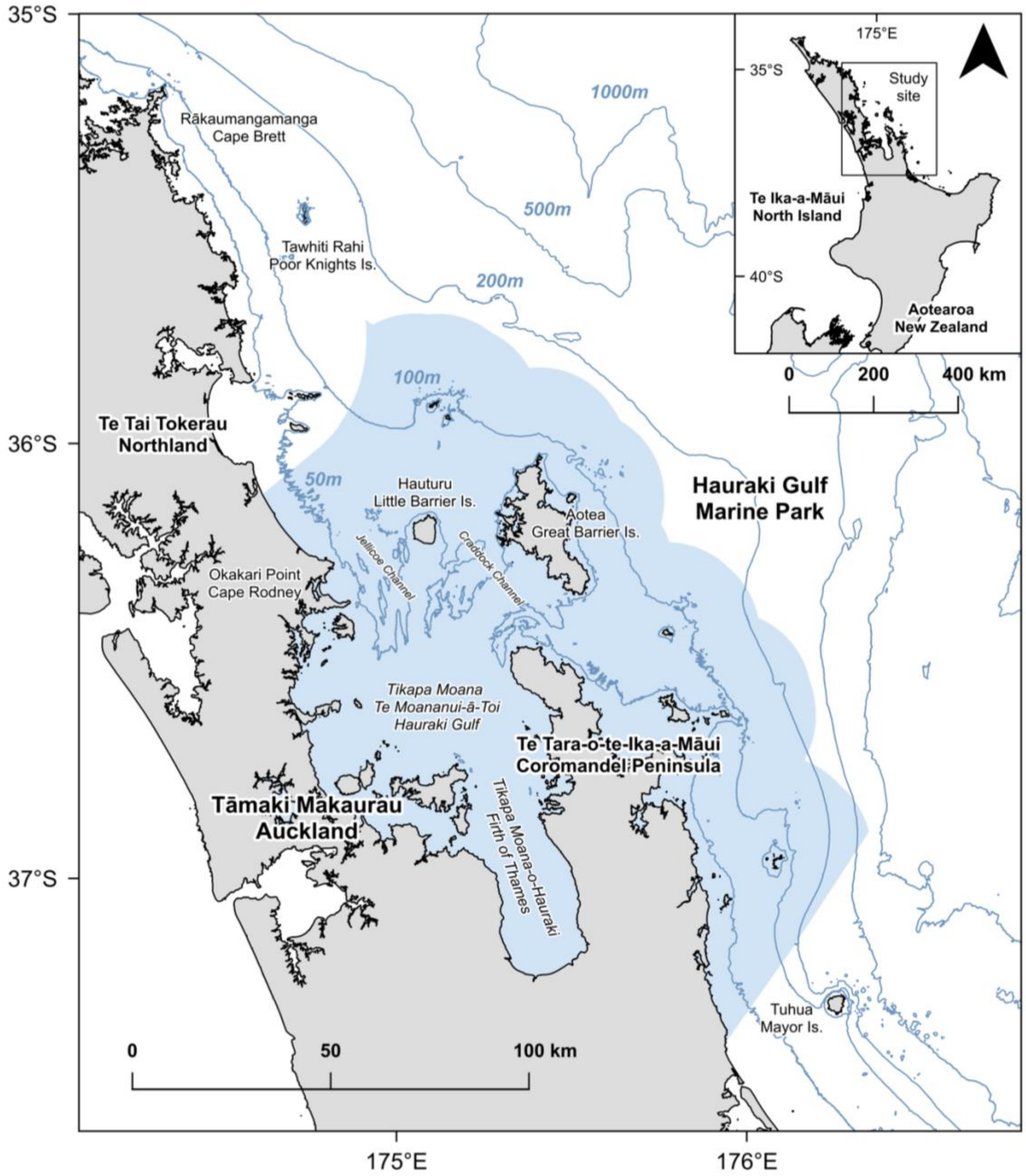

Figure 1.2 Map of the study site outlining the Hauraki Gulf Marine Park shaded in blue and key island groups/regions. Inset shows position in relation to the North Island of New Zealand. Isobath lines are shown in blue.

1.6 Thesis aims and objectives

My thesis aims to investigate the foraging ecology and spatial distribution of oceanic manta rays in New Zealand. Using satellite telemetry, I analyse both the horizontal and vertical movements of manta rays tagged within the Gulf, inferring patterns in movement and behaviour within northeastern New Zealand, as well as the influence of key environmental variables on these behavioural patterns. Ultimately, this research will provide valuable insight into the movement ecology of a data-deficient species within a key area of their distribution in northern New Zealand waters, information which can then be used to inform management and conservation actions.

This thesis is structured as follows:

Chapter 1 – General Introduction

Chapter 1 introduces the present study and provides a literature review on the movement ecology of animals, with a central focus on foraging behaviours. Here I describe challenges in studying movement within the marine realm, and how satellite telemetry can be used to assist research in this field. I also provide an overview of current knowledge of the oceanic manta ray globally, and within New Zealand.

Chapter 2 – Environmental drivers of fine-scale horizontal movement and behaviours of oceanic manta rays

Here I assess the fine-scale horizontal/surface movements of oceanic manta rays along the northeastern coast of New Zealand. Data from satellite tags are analysed to determine the behavioural states of individuals and how these are influenced by environmental variables.

Chapter 3 – Diving behaviour

Here I analyse the vertical movements and diving behaviours of oceanic manta rays along the northeastern coast of New Zealand. Data from satellite tags are analysed to identify patterns in vertical movements as well as how environmental variables influence diving behaviours.

Chapter 4 – General Discussion

This chapter summarises and discusses the overall findings within this thesis and provides future directions for further research.

Chapter 2

Environmental drivers of fine-scale horizontal movement and behaviours of oceanic manta rays

2.1 Introduction

How an animal interacts with its environment is shaped by the interplay between internal factors such as physiological constraints, and external cues such as social interactions, as well as the heterogeneity of environmental conditions and resources (Nathan et al., 2008). Understanding these drivers is a fundamental aspect of behavioural ecology, and is useful in predicting how populations respond to ecosystem variability, which in turn is important for effective conservation and management strategies (Fraser et al., 2018; Brownscombe et al., 2022; Lopes et al., 2023). Satellite telemetry and remote sensing technology provide opportunities to gain insights into the movement ecology of wide-ranging or cryptic marine species, allowing the continuous tracking of individuals across ocean basins, and inference of the relationship between movement and environmental conditions or resources (Harcourt et al., 2019; Hindell et al., 2020) This technology is being constantly improved, allowing increasingly higher resolution and accuracy of information to be gained, providing insight into behaviours and finer spatiotemporal resolutions.

The marine environment is characterised by its dynamic nature, driven by both static (e.g. bathymetry) and variable (e.g. sea surface temperature) features which contribute to the ephemeral and patchy nature of resources through space and time. Animals must engage in behaviours which fulfill their life history requirements, whilst navigating and responding to this environment. Migrations often occur across great distances, and are driven by responses to seasonal changes or the pursuit of key breeding and feeding grounds (Weng et al., 2007; Rizzo & Schulte, 2009). Aggregations form around common needs or shared resources, including social purposes such as breeding or for maintenance requirements like parasite removal near cleaning stations (Oliver et al., 2011; Dickson et al., 2022). Animals are expected to show strong behavioural responses to environmental conditions which may influence prey availability, varying their movements accordingly. Foraging animals may engage in area-restricted search (ARS)—a movement behaviour characterised by the switching between two distinct movement patterns. Focused exploitation is characterised by slower speeds and increased turning frequency within localised areas, typically attributed to foraging behaviours, whilst transiting behaviour involves faster, more directional movement during exploration between prey patches or other directional travel such as migration (Kareiva & Odell, 1987; Dorfman et al., 2022; Allegue et al., 2023).

The oceanic manta ray is a large, globally endangered species of planktivorous mobulid ray, distributed throughout tropical to subtropical regions, and occasionally occurring in warm temperate habitats (Armstrong et al., 2020; Marshall et al., 2022a). While some populations of oceanic manta rays appear residential, in other areas such as New Zealand this species is migratory, travelling thousands of kilometres over the austral winter to reside in warmer waters near Fiji, Tonga and the Cook Islands (Stewart et al., 2016a; Andrzejaczek et al., 2022; Gordon & Vierus, 2022). Seasonal, long-distance movements are often tied to the spatiotemporal availability of resources (Alerstam et al., 2003). The Gulf, located off the coast of Auckland, New Zealand is an internationally recognised marine biodiversity hotspot. The Gulf, and its adjacent waters support diverse year-round communities of large marine species such as sharks, cetaceans and seabirds (Rayner et al., 2015; Stephenson et al., 2023). Overwinter mixing and upwelling are the dominant circulation modes in the Gulf, contributing high levels of nitrate to the system and supporting some of the highest primary productivity levels seen in coastal regions of New Zealand (Sharples & Greig, 1998; Murphy et al., 2001; Chang, 2003). This heightened productivity, particularly within the Gulf, supports abundances of mesozooplankton, with copepods the dominant species (Jillett, 1971; Zeldis & Willis, 2015). Zooplankton communities in the region exhibit temperate-subtropical affiliations, displaying marked seasonal variation in zooplankton community structure (Jillett, 1971; Carroll et al., 2019). At the boundary of EAUC surface waters, a strong front separates blue, high salinity oceanic waters from green, low salinity waters of the inner shelf, driving distinct differences in zooplankton community composition (Sharples, 1997). The austral summer sees a shift towards prevailing easterly winds and downwelling, and the cross-shelf intrusion of subtropical waters from the EAUC (Sharples, 1997; Zeldis et al., 2004). Summer intrusions of subtropical EAUC waters have been associated with the immigration of oceanic species such as salps (*Thalia democratica* and *Salpa fusiformis*) (Zeldis & Willis, 2015). The presence of seasonally migratory species including false killer whales (*Pseudorca crassidens*), tropical fishes, marlins, and spinetail devil rays (*Mobula mobular*) aligns with warming temperatures from these EAUC intrusions (Sippel et al., 2007; Zaeschmar et al., 2013; Middleton et al., 2023; Ozaki, 2023). Sightings of manta rays in New Zealand also coincide with this increased influence of warmer waters associated with the EAUC (Ozaki, 2023), most commonly occurring along the northeastern coast of the North Island throughout the late austral spring to late austral autumn period.

Within the Gulf a few potential 'hotspots' (Figure 2.1) for manta rays have been identified based on the relatively consistent and numerous sightings recorded in these areas over the past five years (L. Green, MWANZ, pers. comm). In these areas, manta rays are often sighted somersault feeding on dense patches of zooplankton, including *Nyctiphanes australis,* particularly during the falling tides (L. Green, MWANZ, pers. comm)*.* Despite the potential to be an important foraging area for oceanic manta rays in this region, little is known about their movement patterns and associated foraging behaviours here.

In this chapter I use SPLASH10F satellite tags to investigate the fine-scale movements of oceanic manta rays around northeastern New Zealand. I then investigate potential environmental drivers of ARS (indicative of foraging) behaviours during these movements.

2.2 Methods

2.2.1 Study site

This study was carried out in the Hauraki Gulf Marine Park, located in the North Island of New Zealand, and the adjacent coastal shelf extending between 35.2°S to 37.4°S and 174°E to 176.5°E, encompassing Tuhua Mayor Island in the Bay of Plenty to the south, up to Rākaumangamanga Cape Brett at the entrance of Ipipiri the Bay of Islands (Figure 1.2). The southernmost boundary was determined by the furthest southward travel of manta rays tagged in this study. The northern limits were selected as a natural boundary before manta rays appeared to move away from the coast, likely beginning their offshore migrations—movement which is out of the scope of this research project. The Gulf is a shallow, semi-closed embayment (mostly within 100 metres depth), and follows a gently sloping topography towards the edge of the continental shelf (Manighetti & Carter, 1999). Within this region several potential hotspots for manta ray foraging have been suggested by MWANZ based on field observations and verified sightings from the general public (Figure 2.1).

2.2.2 Tagging procedures

Over the 2019 to 2023 period, 19 Wildlife Computers SPLASH (models SPLASH10F-321A and SPLASH10F-321E) satellite tags were deployed on oceanic manta rays within the Gulf during research expeditions led by MWANZ in collaboration with Conservation International Aotearoa, the University of Auckland Waipapa Taumata Rau, the Department of Conservation, Te Papa Atawhai and Tindale Marine Research Charitable Trust. Tags were attached to a tether and deployed by an experienced tagger using a hand spear, to allow the tag to be anchored into the rear dorsal surface of the animal in a controlled manner (Figure

2.2). To guide the tagger in the water to the manta ray, when possible, a drone was deployed to provide better visualisation, and followed the manta ray. The drone continued to follow the individual post tagging, to document any behavioural changes.

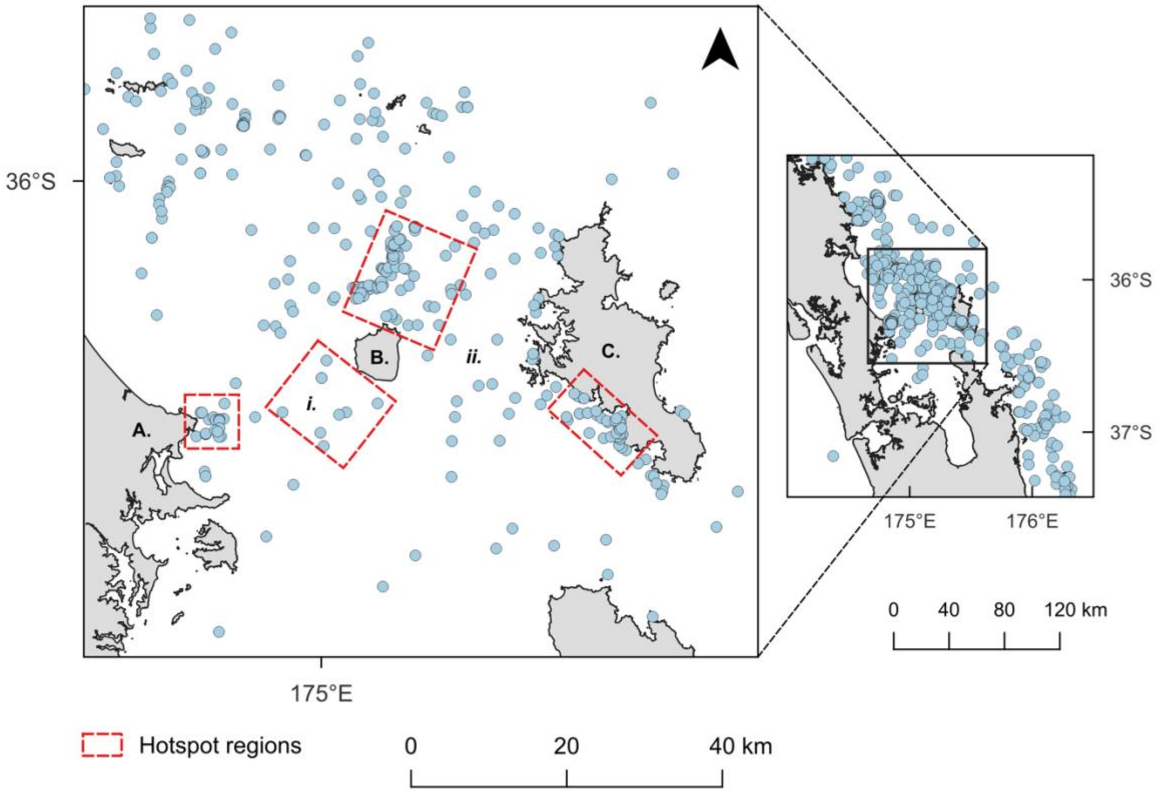

Figure 2.1 Map of suggested hotspots for manta ray foraging activity in northeastern Aotearoa New Zealand. Study area is depicted on the right. Significant landmarks from left to right: (A) Okakari Cape Rodney, (B) Hauturu Little Barrier, and (C) Aotea Great Barrier. Channels marked are (i) Jellicoe Channel and (ii) Cradock Channel. Each point (*n* = 604) represents a verified sighting of a manta ray from between 2001–2023. Red boxes denote putative hotspots based on field observations and verified sightings from the general public collected by Manta Watch Aotearoa New Zealand.

Satellite tags were programmed to collect location data consisting of Fastloc GPS and ARGOS locations, ambient temperature, and depth. For the tags deployed in 2022 and 2023, Fastloc GPS data were collected every five and six seconds. For tags deployed in 2021 (i.e., PTT #197235), Fastloc GPS data were collected every 60 minutes. The archived data consisting of ambient temperature and depth were collected every second for tags deployed in 2022 and 2023, and every 10 seconds for those deployed in 2021. Note that for all tags, transmission was limited to periods when the antenna was above the surface. Tags were programmed to detach after a set time. If possible, tags were retrieved; however, due to the highly mobile and pelagic nature of this species, tag detachment was not always local and thus, retrieval was not always achievable. All tagging and drone procedures were conducted following guidelines under permits issued by the Department of Conservation (96119-FAU) to Lydia Green, MWANZ and the University of Auckland Animal Ethics Committee (AEC23490) to Rochelle Constantine, University of Auckland.

Seven of the 18 tags were analysed as they had sufficient (15 or more locations) data of movements within the study area and/ or met *post-hoc* filtering criteria. Although all 11 tags not used here were able to transmit some data, eight of these tags produced fewer than 15 locations total, and the other three which did transmit sufficient data moved north after tagging, outside of the study boundary. Analysis of the tag data was conducted using R version 4.3.2. (R Core Team, 2023). Packages used for analysis were: *aniMotum* (Jonsen et al., 2023), *pathroutr* (London, 2021), *mgcv* (Wood, 2015), *gratia* (Simpson, 2024), and *suncalc* (Thieurmel & Elmarhraoui, 2022). Data were filtered to remove unlikely data points based on the residuals (GPS location quality indicator. Based on LocSolve algorithm used to estimate the animals location; Wildlife Computers) and the time error (estimate of instrument clock error based on snapshot time and downloaded RINEX files). Filtered horizontal data were visually evaluated using QGIS version 3.3.2 (QGIS, 2023), and data points on land removed (*n* = 1). Data were then subset to remove movements following each individual's exit from the study boundaries. There were a total of 434 GPS locations remaining following cleaning and filtering. The original directions for this chapter included the collection of additional drone footage for focal-follows of individuals, with the intention of creating an ethogram. However, after auditing all the footage (*n* = 415; 8 hours) there were insufficient data for analysis.

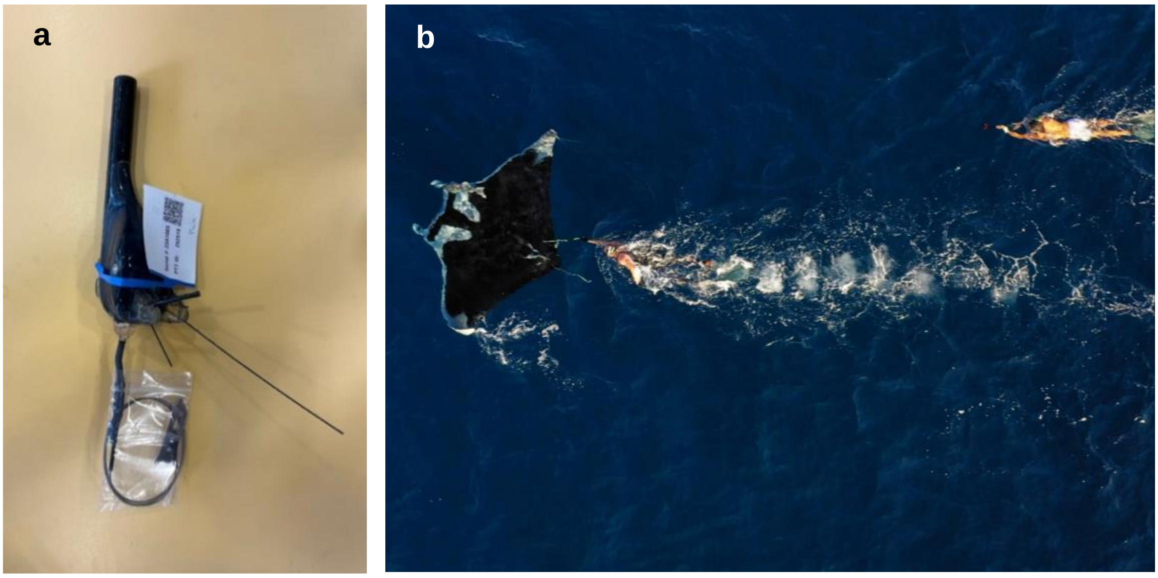

Figure 2.2 (a) SPLASH10F tag (b) Oceanic manta ray being tagged with a SPLASH10F tag attached to a hand spear. Support person to the right of frame. Source: Edy Setyawan

2.2.3 *State space modelling*

To regularise time-steps between raw (Argos) locations for further behavioural analysis a time-varying move persistence (mp) state space model was fitted to the data using the *fit_ssm* function from the R package *aniMotum* (Jonsen et al., 2023). In this model movements are random, with correlation in direction and magnitude that varies in time (Jonsen et al., 2023). This model was selected as it simultaneously estimates true locations and move persistence values and therefore is robust to data gaps seen in the data, and which are common among species which undergo long periods underwater. Tracks were fitted with a six-hour time step, selected to provide insight into the fine-scale drivers of movement, whilst considering the limited number of locations for some tracks in order to avoid overfitting. Move persistence (γ_t) was then estimated from the rerouted tracks using the *fit_mpm* function with the joint move persistence model (jmpm). While the *aniMotum* package includes a wrapper function to reroute predicted tracks off land, the complexity of the near shore environment, involving several islands and peninsula areas meant that this had to be done manually, using the *pathroutr* package (London, 2021). Tracks were re-routed off land using a one-kilometre buffer. This package identifies and removes locations on land, rerouting tracks around barriers based on the shortest path through a visibility graph network (London, 2021).

Data were mapped in QGIS (v.3.32.3 – Lima). High use areas by manta rays were identified using the integrated Heatmap (Kernel Density Estimation) symbology function, with 20 kilometres entered as the radius, and maximum value automatically selected.

2.2.4 Connecting behavioural states to environmental variables

Environmental conditions and oceanographic processes drive many behaviours in animals. In line with current research on the foraging behaviours and habitat use of other large marine planktivorous species (Rohner et al., 2013; Curtis et al., 2014), the following environmental variables were identified for analysis as potentially important drivers of manta ray movement (Table 2.1).

The influence of these variables was analysed using a General Additive Model (GAM; see Table 2.1 for variables included in the final model), fitted to regularised GPS locations from the satellite tags using the R package *mgcv* (Wood, 2015), and visualised using R package *gratia* (Simpson, 2024). Many studies designate behavioural modes based on move persistence values. For instance, Jonsen et al., (2018) uses a threshold of 0.75, where high move persistence (i.e., transiting behaviours) occur when $\gamma_t > 0.75$, while low move persistence (i.e., ARS behaviours) occur when $\gamma_t < 0.25$. Variations on these thresholds occur. Bailey et al., (2012) uses a threshold of use 0.5 γ_t to categorise the behaviours of leatherback turtles (*Dermochelys coriacea*). Other work commonly classifies movemenets Between 0.25–0.75 γ_t as undefined, with insufficient information to distinguish between behaviours (Jonsen et al., 2007). These methods have been broadly applied to a range of animal movement studies including humpback whales (Andrews-Goff et al., 2018), white sharks (*Carcharodon carcharias*; Franks et al., 2021), turtles (*Eretmochelys imbricata*; Marshall et al., 2020), and reef manta rays (Harris, 2019). However, I argue that using this threshold may bias the results. Manta rays are obligate ram ventilators and as such must be continuously moving.

Therefore, it is probable that movements would follow different patterns from species such as humpback whales and turtles. Instead, I decided to use a continuous response variable (move persistence γ_t 0–1) for the GAM. This choice results in a continuous 0–1 response variable described using a beta regression family (in contrast with other studies using binomial responses), selected based on the results of a Cullen and Frey analysis (R package *fitdistrplus*; Delignette-Muller & Dutang, 2015). While 0 and 1 are legitimate observations, to keep the log likelihood bounded, data at these values are reset to be just within 0–1 using the eps (epsilon) argument for numerical stability during optimisation procedures (Wood, 2015).

The formula used for the GAM is as follows:

```
gam(1- γt ~
      s(wind_direction, bs = 'cc', k = 6) +
      s(wind_speed, k = 6) +
      s(kd490, k = 6) +
      s(bathy, k = 6) +
      s(sst, k = 6) +
      s(sunaltitude, k = 6) OR s(moonfraction, k = 6+
      factor(tide_category) +
      factor(id ) +
      factor(sex ) +
     data = gam_df,
     method = "REML",
     family = betar (link = "logit", eps=0.0000000001))
```

The response variable in this GAM was modelled as 1-γ_t, as the aim of this investigation is to focus on predictors of low move persistence, as an indicator of foraging behaviour, rather than on transiting behaviours. Data were split into two separate models—one for observations taken at night (*n* = 225), and one for the day (*n* = 499). In the day model, the altitude of the sun was also included, as a proxy for daylight. In the night model, the illuminated fraction of the moon was included as a proxy for moonlight intensity.

Pearson correlation coefficient testing indicated a high level of correlation (0.95) between wind speed and max hourly gust variables, and therefore max hourly gust was omitted from the final GAM. There was also a high correlation (0.88) between chl-*a* and kd490, which are both estimated using similar ocean colour-based approaches and related to the number of particles in seawater. While chl-*a* is the most commonly used parameter for monitoring phytoplankton biomass and productivity, kd490 is generally used to indicate the total organic and inorganic matter held in the water column. In coastal regions, like the study site in this research, the presence of coloured-dissolved organic matter may introduce bias into chl-*a* values, potentially indicating substances beyond phytoplankton (Dierssen, 2010). Therefore, kd490 was selected for the final analysis. Correlation was also observed between kd490 and bathymetry (0.52), however both variables were ultimately included in the GAM analysis as they have been described in the literature to have distinct roles in driving movement and foraging dynamics of pelagic elasmobranchs, and are of interest for directing field surveys (Lauria et al., 2015; Copping et al., 2018; De Wysiecki et al., 2022; Saltzman & White, 2023). It is important to note, the influence of cloud cover on satellite based remote sensed variables. Consequently 54% data were missing for kd490, and 50% for sea surface temperature.

2.2.5 Hotspot regions

In addition to being included in the overall GAM analysis, locations identified as being inside putative hotspot areas were analysed using additional, separate GAMs to see whether there were any differences in environmental drivers of ARS behaviours within each hotspot.

Table 2.1 Environmental variables investigated for influence on oceanic manta ray foraging behaviour. Variables in bold were included in the final GAM model.

Variable	Temporal resolution	Spatial resolution	Description	Source
Bathymetry (Outside of Hauraki gulf; m)	—	15”	2023 continuous global terrain model produced using gridded bathymetric data augmented to the SRTM15+ base grid. Bathymetric data sets are developed by the four Seabed 2030 Regional Centers and largely based on multibeam data.	GEBCO Compilation Group (2023) GEBCO 2023 Grid
Bathymetry (Within Hauraki Gulf; m)	—	20 m	Combination of multibeam, single beam acoustic surveys (offshore) and Light Detection and Ranging (LiDAR; nearshore) measurements compiled by MetOcean for Waikato Regional Council and Auckland Council.	Sarah Gardiner, MetOcean Auckland Council Waikato Regional Council
Chlorophyll-*a* (mg/m^3)	Daily	300 m	Mass concentration of chlorophyll-*a* (L3) in sea water, derived from ocean colour.	Copernicus (2016)
Kd490 (m^{-1})	Daily	4 km	Diffuse attenuation coefficient of light at 490 nm.	Same as Kd490
Period (Night/Day)	—	—	Time of day is identified based on times of Sunrise (top edge of the sun appears on the horizon) and Sunset (sun disappears below the horizon, evening civil twilight starts). Extracted using the *getSunlightTimes* function.	*Suncalc R Package*
Solar Altitude (°)	Based on the precision of the location	Based on the precision of location	Sun altitude above the horizon in radians, e.g. 0 at the horizon and 90° at the zenith (overhead).	*Suncalc R Package*
Tide (Rising/Falling/Slack)	Minute	50 km	High tide times extracted from the NIWA Tide Forecaster Model. Slack tide is identified as the period within 30 min on either side of high tide.	NIWA Tide Forecaster Model
Wind direction (°T)	Hourly	Measured from the nearest wind station	The direction the wind is blowing from, measured over the 10 minutes preceding the observation time and in degrees clockwise from Geographic North.	Meteorological Service of New Zealand Ltd (Metservice)
Wind max hourly gust (ms^{-1})	Hourly	Measured from the nearest wind station	The maximum wind gust recorded during the hour preceding the observation time.	Metservice
Wind speed (ms^{-1})	Hourly	Measured from the nearest wind station	The average wind speed recorded during the 10 minutes preceding the observation time.	Metservice

2.3 Results

2.3.1 Horizontal movements

Of 18 SPLASH tags (Appendix 1) successfully deployed on manta rays, seven were selected for analysis following cleaning and filtering of the data (Table 2.2). The seven tagged individuals ranged in size from an estimated 3.6–4.8 m disc width (DW; length from wingtip to wingtip) and comprised three adult females (two which were visually estimated as mid-pregnancy), and four males (three adults, one sub-adult). The combined tags provide 434 GPS locations (mean = 62 ± 34.1 SD) collected from transmission periods ranging between 9 to 83 days (mean = 27 ± 18.5 SD), across 2021 to 2023. All locations were from the months January to March. Tracks reveal individual variation in movement throughout the outer regions of the Gulf and beyond (Figure 2.3a). While all three females remained north of 36.3° S latitude, in line with Okakari Cape Rodney, the four males travelled further south than this, travelling south-east around the Coromandel Peninsula, with PTT#238016 reaching the southern movement extent near Tuhua Mayor Island at -36.36° S latitude. The pregnant manta rays did not display any substantial differences in movement patterns compared to the other female. All tags except PTT# 197235 and PTT# 238016, were tracked moving north along the coastline, past the study boundaries. PTT# 238016 initially travelled north, exhibiting significant movement near Tawhiti Rahi the Poor Knights Islands for a duration of 11 days (26th January 2023 to 5th March 2023), before returning south to the Gulf. PTT# 197235 remained in a relatively small area between Te Hauturu-o-Toi Little Barrier Island and Aotea Great Barrier Island throughout the entire tracked movement period (5th February 2021 to 8th March 2021; 31 days; Figure 2.3a). These two tags detached within the study boundary and were able to be recovered. Movements were mostly constrained within the 200 m bathymetric contour (Figure 2.3a). Kernel density analysis indicates a potential hotspot region in the Cradock Channel, situated between Hauturu and Aotea (Figure 2.3b).

Table 2.2 Summary of deployment and characteristics of the seven individuals used for analysis. *Platform Transmitting Terminal

Manta PTT*# Name	Deployment date	# Days programmed for or date of programmed release	Days transmitted	# Locations after data cleaned	Sex	Estimated size (Disc width; cm)	Notes
197235 Camille	03-Feb-2021	180	34	29	Female	520	Tag recovered
204511 Nate	10-Jan-2022	90	81	88	Subadult male	360	
238014 Pukukino	22-Jan-2023	03-Mar-2023	40	42	Female	440	Mid-pregnancy
238015 Kawa	22-Jan-2023	96	33	32	Male	420	
238016 Motairehe	22-Jan-2023	03-Mar-2023	21	112	Male	425	Tag recovered
238018 Anna	22-Jan-2023	03-Mar-2023	40	39	Female	440	Mid-pregnancy
238019 Rehua	22-Jan-2023	96	76	92	Male	420	

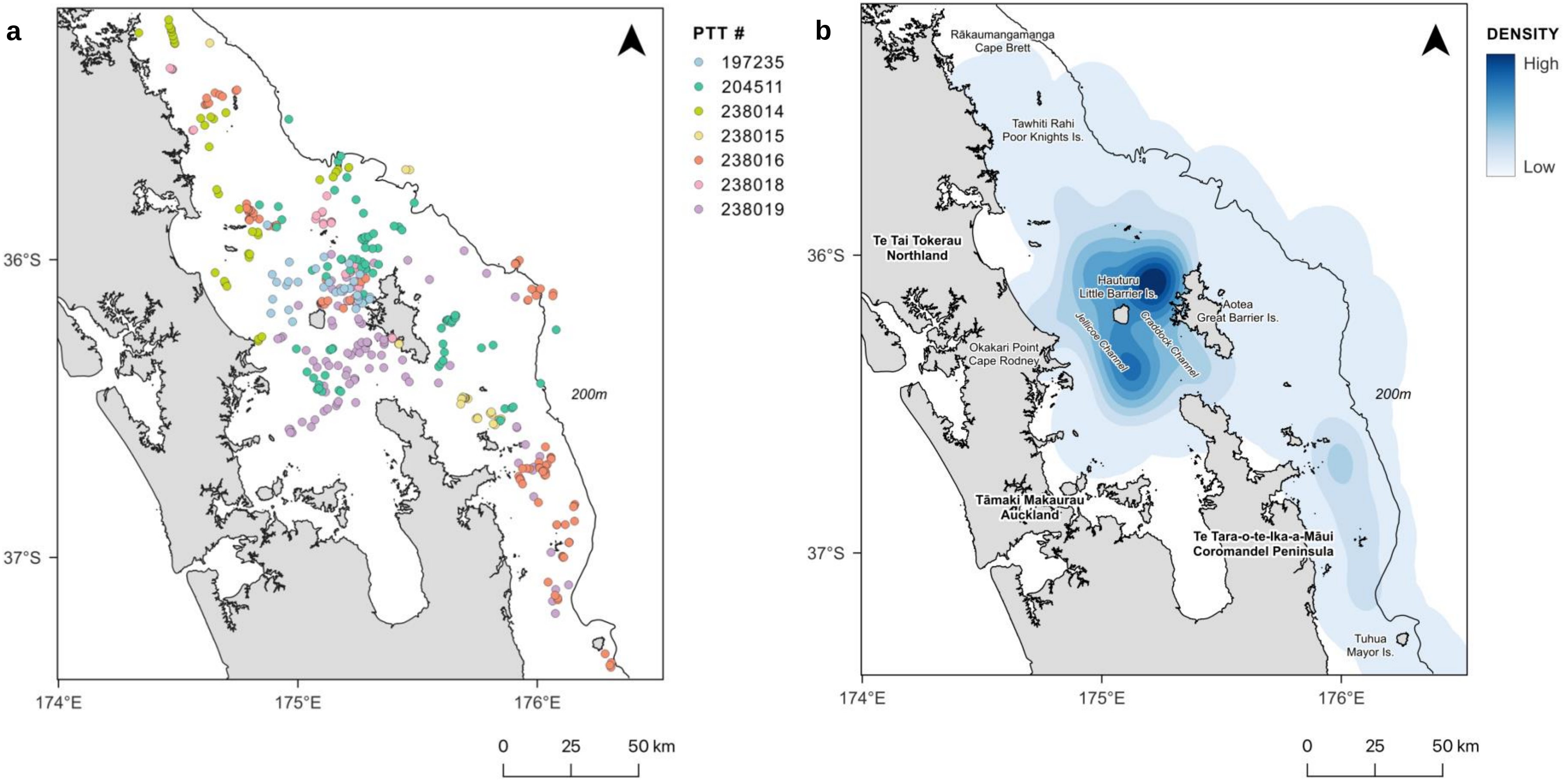

Figure 2.3 Cleaned tracks of seven oceanic manta rays tagged with SPLASH10F tags in the Hauraki Gulf, New Zealand. (a) indicates fast-loc GPS positions (accuracy < 20 m). (b) Location heatmap for 434 locations where darker blue areas indicate higher kernel densities. PTT# 197235, PTT# 238014* and PTT# 238018* are females, PTT# 204511, PTT# 238015, PTT# 238016 and PTT# 238019 are males. **Indicates pregnant manta rays*

2.3.2 State space modelling & move persistence

For all manta data combined, move persistence estimates indicate that ARS behaviours (indicated by areas of low move persistence) occurred throughout the study area (Figure 2.4). Movements outside of the HGMP were generally more persistent (indicative of travelling) with transiting movements separated by localised areas of low move persistence (indicative of ARS behaviours, including foraging). The *aniMotum* package was unable to calculate move persistence for PTT# 238015, suspected as a consequence of the animals' sporadic movements, including large data gaps relative to the prediction interval. Hereafter this tag is removed from analysis.

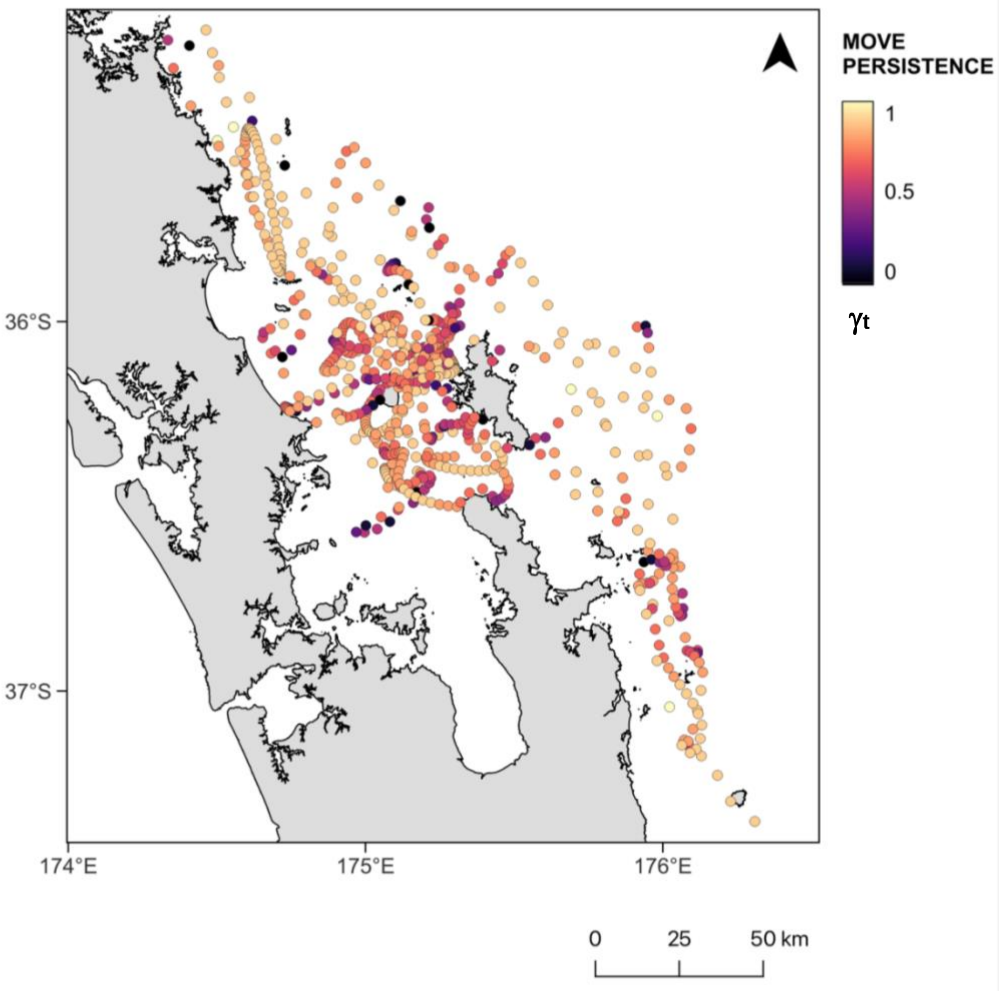

Figure 2.4 Inferred move persistence (γ_t) from six-hour regularised GPS tracks of oceanic manta rays. Higher values represent areas of faster, more directional movement; lower values represent slower, more tortuous movement.

2.3.3 Generalised Additive Model

Environmental variables investigated in the daytime GAM accounted for 47% of deviance observed in move persistence (Figure 2.5). Kd490 was the most important predictor of ARS behaviour ($p < 0.001$). Manta rays were more likely to engage in ARS behaviours when in areas of lower kd490 (higher water clarity). ARS behaviours also increased during easterly winds ($p < 0.05$; Figure 2.5). The day model also suggests the significance of rising tides for predicting foraging behaviour ($p < 0.05$). For night movements, the GAM was able to explain 59.5% of deviance (Figure 2.6). While kd490 was also the most important predictor of ARS behaviour during night movements ($p < 0.001$), this pattern is the reverse of what is seen during the day—manta rays were more likely to forage in areas of decreased water clarity at night. The night model also suggests significance of slack tides for predicting foraging behaviour ($p < 0.05$). Across both models, there was also a large amount of variation between different individuals. PTT# 238018 spent a significantly greater proportion of time foraging compared to other individuals (Figure 2.5; Figure 2.6).

2.3.4 Hotspot analysis

Sample size was limited for each hotspot region—from west to east the hotspots contained the following number of locations (2 locations, 1 individual; 23 locations, 2 individuals; 38 locations. 4 individuals; 6 locations, 2 individuals; Figure 2.1). Additionally, as some locations were missing data due to cloud cover, there were not enough data for reliable GAM analyses.

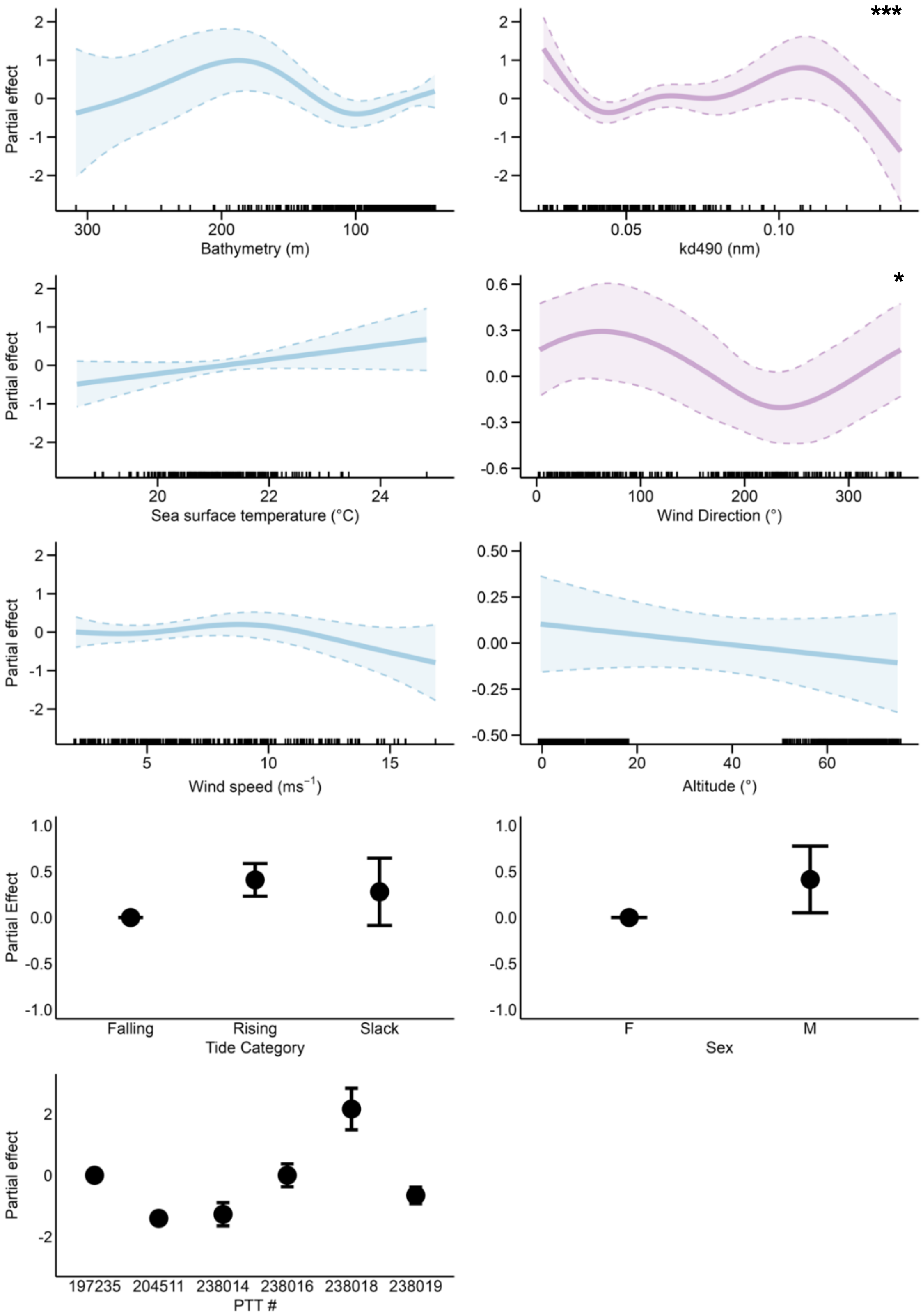

Figure 2.5 GAM smooth and parametric terms of environmental predictors of oceanic manta ray ARS behaviour during the day. Solid lines and circles represent estimates, while shaded areas represent estimated standard errors and bars. Purple smooth terms indicate significant drivers (*** $p < 0.001$; * $p < 0.05$). Note, to aid visualisation the Y-axes scales differ between terms.

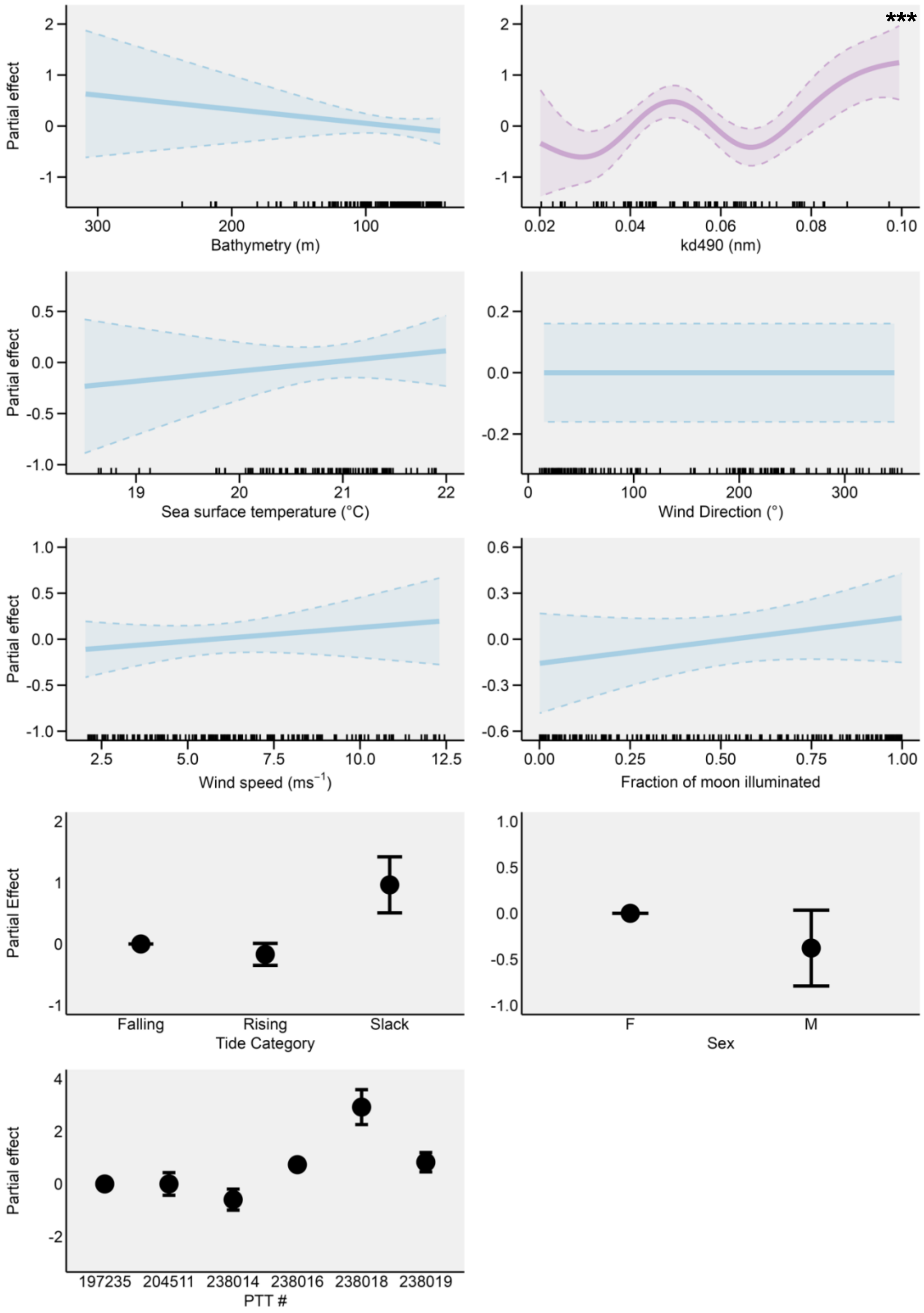

Figure 2.6 GAM smooth and parametric terms of environmental predictors of oceanic manta ray ARS behaviour at night. Solid lines and circles represent estimates, while shaded areas represent estimated standard errors and bars. Purple smooth terms indicate significant drivers (*** $p < 0.001$) Note, to aid visualisation the Y-axes scales differ between terms.

2.4 Discussion

This thesis represents the first fine-scale telemetry study of oceanic manta rays in New Zealand waters—filling a gap in our understanding of the patterns of movements and foraging ecology of this species, which is understudied and data-deficient, especially in the western Pacific. Given the scarcity of telemetry studies on elasmobranchs in New Zealand, these findings not only add to our knowledge of manta rays but also offer potential insights applicable for other species.

2.4.1 Movements and behaviours of manta rays in New Zealand

Satellite tags revealed broad scale movements of the seven individuals tagged within the Gulf, throughout the outer Gulf region with variation among individual movements along the northeastern coast. This is in line with current understandings of the distribution of manta rays in New Zealand, based on photo-ID and encounter records (Ozaki, 2023). All satellite tag data were collected between January to March, after which the tag was either released, or the tagged individuals travelled north out of the study area. As the focus of my study was on fine-scale habitat use, I constrained my study area to the broader highly productive Gulf waters that support other large marine species (Whitehead et al., 2019; Ozaki, 2023; Stephenson et al., 2023). Visual inspection of the manta rays' movement patterns outside of study boundaries indicated that these individuals transited north off the coast of New Zealand, likely remaining in warmer south Pacific waters over winter. PTT# 204511 was tracked all the way to southern Tonga. These findings support seasonal offshore migration patterns evidenced in photo-ID studies and unpublished broad scale satellite tagging data, which have demonstrated connectivity between New Zealand and the Tonga and Fiji island groups in the South Pacific (Setyawan et al., 2021). Seasonal occurrence of manta rays in New Zealand is also supported by the lack of sightings throughout the austral winter (Ozaki, 2023).

Seasonality in manta ray presence has been documented in a number of places, including parts of Revillagigedo National Park and Bahía de Banderas in Mexico, and the Maldives and is likely linked to seasonal temperature variability and productivity flux (Nicholson-Jack et al., 2021; Cabral et al., 2023; Domínguez-Sánchez et al., 2023). In subtropical Brazil, presence of oceanic manta rays occurs during the austral winter, coinciding with the emergence of a highly productive coastal front (Luiz et al., 2009).

Manta ray movements in northeastern New Zealand were predominantly confined within the 200-metre depth contour, coinciding with the EAUC. These findings align with those of Ozaki (2023), who also observed the significance of the 200-metre isobath acting as a demarcation line separating the spatial distributions of oceanic manta rays, and spinetail devil rays which aggregate around this isobar, and of which this isobar represents the inshore extent of presence. Therefore, my results support the concept of trophic separation amongst mobulid species in New Zealand. Trophic separation is a common feature among elasmobranch communities whereby feeding on differentiated prey reduces interspecific competition (Afonso et al., 2022). Whilst trophic separation is not observed between these species in other regions, (Sampson et al., 2010; Rohner et al., 2017; Stewart et al., 2017; Rambahiniarison et al., 2018), it does occur between other mobulid species. In Raja Ampat, West Papua, Indonesia, feeding aggregations of longhorned pygmy devil ray (*Mobula eregodoo*) are observed only in the southern region of Misool, whereas feeding aggregations of the shorthorned pygmy devil ray (*Mobula kuhlii*) have only been observed in northern Raja Ampat (M. Erdmann; E. Setyawan, Conservation International, pers. comms). Large-filter feeding species require a certain prey density to be reached for foraging to be energetically profitable (Nelson & Eckert, 2007; Armstrong et al., 2016). Patchy distribution of high-density prey sources means individuals are more likely to converge and forage in these patches leading to trophic overlap. However, as previously discussed, the northeastern coast of New Zealand is highly productive. Therefore, high-density prey patches may be abundant enough that individuals do not need to all feed together. Ozaki (2023) suggests that trophic separation in New Zealand may also be a consequence of differences in energetic requirements or prey preference—oceanic manta rays (max DW = 7 m; Compagno, 1999) are substantially larger than spinetail devil rays (max DW = 3.5 m; Notarbartolo di Sciara et al., 2020) and have much greater energy requirements (Rohner et al., 2017). However, further studies are needed to determine whether these species are targeting different prey species.

GPS tracks indicated potential sex-based movement differences, with males, travelling further south than females within the Gulf, and also transiting south-east around the Coromandel Peninsula, although there were no differences seen in foraging behaviours. Sex-based differences in movement and space use has been well documented in elasmobranchs, driven by competitive exclusion, sexual dimorphism, differences in reproductive needs, or in fitness (Phillips et al., 2021). In reef manta rays, sex biased individual variation in fine-scale movement patterns has been observed in Hawaii with females tending to display more residential movement patterns, while males display greater mobility and explore new areas more frequently (Axworthy et al., 2019). It has also been suggested that female reef manta rays may use cleaning stations more often than males (Stevens, 2016). Cleaning stations are recognised as important habitats for reef and oceanic manta rays, as well as other elasmobranch species. Cleaning sites facilitate interspecific interactions with cleaner fish species, which are critical for reducing parasite load and maintaining fish health (O’Shea et al., 2010; Jaine et al., 2012; Barr & Abelson, 2019). However, the presence of cleaning stations has not yet been confirmed for New Zealand waters. Sample size for this study was limited, and so further research is needed to confirm this pattern in sex-based movements.

As a part of the initial concept for this thesis, I investigated MWANZs drone-footage, tracking and observing surface behaviours of manta rays. While there were insufficient data to develop an ethogram, it was clear that when oceanic manta rays were near the surface, they were often engaging in foraging behaviours. As GPS locations can only be transmitted at the surface, which occurs in manta rays particularly during somersault feeding (Stevens, 2016), GPS locations likely represent areas where foraging is occurring.. While manta rays have been observed in the Gulf feeding on *Nyctiphanes* spp., other targeted prey is unknown (L. Green, MWANZ, pers. comm.). Zooplankton aggregations in the Gulf are targeted by a number of higher trophic level species, including the large, resident filter feeding Bryde’s whales (Carroll et al., 2019).

During field surveys, drone footage has occasionally captured Bryde's whales feeding alongside manta rays, suggesting that manta rays likely target some of the same species as Bryde's whales. Bryde's whales are generalist filter-feeders which target euphausids including *Nyctiphanes*, copepods, salps, and schooling fishes (Carroll et al., 2019). Similar dietary patterns are observed in studies of oceanic manta rays, where euphausiids comprise the majority of diet, alongside varying contributions of copepods and small fishes (Burgess, 2017; Rohner et al., 2017; Bessey et al., 2019). Salps, despite their low nutritional value, are an important zooplankton prey important for other species in the Gulf including Bryde's whales (Carroll et al., 2019), snapper (*Pagrus auratus*; Godfriaux, 1969) and several seabird species (Rayner et al., 2021). While mobulid rays are often seen feeding around gelatinous zooplankton such as salps, it is unknown whether they are targeted. Gelatinous taxa are digested quickly, and therefore are often underrepresented in stomach contents analyses. However, in reef manta rays, gelatinous taxa, including salps, chaetognaths and eggs were also underrepresented in plankton tow samples taken during foraging, compared to samples collected during non-foraging periods (Armstrong et al., 2021).

Inference of move persistence from the regularised tracks indicated that foraging and transiting occurred throughout the study site. Patterns in move persistence were characterised by small, localised areas of foraging, separated by periods of transiting behaviour that are in line with what would be expected from an animal engaging in ARS behaviour.

2.4.2 Environmental drivers of foraging behaviours

The most significant predictor of the foraging behaviour of oceanic manta rays in northeastern New Zealand was kd490. However, the observed patterns revealed a contrasting trend depending on the time of day. During daylight hours, manta rays tended to exhibit foraging behaviours in clearer waters, whereas at night, they displayed a preference for more turbid waters.

Kd490 is a measure of the rate at which light at 490 nm (blue–green) is attenuated with depth. This parameter is influenced by various optical properties, such as the absorption coefficient and scattering coefficient (Lei et al., 2020), which are determined by the concentrations of total suspended matter, coloured dissolved organic matter, and algal concentrations present in the water column (Shi & Wang, 2010). In the open ocean, scattering is primarily due to phytoplankton concentrations, however this relationship becomes more complex in coastal regions such as the study site of this thesis, where terrestrial inputs and coastal runoff introduce greater levels of particulate matter into the water column (Wang et al., 2009; Dierssen, 2010; Shi et al., 2011). Therefore, areas with higher kd490 values may represent areas of enhanced productivity, or more coastal regions where higher proportions of sediment in the water column.

The movement patterns of planktivorous megafauna are closely linked to the distribution of prey aggregations (Rohner et al., 2013; Armstrong et al., 2016; Guzman et al., 2022). In areas of decreased water clarity, often associated with enhanced primary productivity these species may display increased presence and foraging activity (Curtis et al., 2014; Hacohen-Domené et al., 2015; Weeks et al., 2015). In contrast, in Isla de la Plata, off the coast of mainland Ecuador, increased water clarity has previously been linked to increased presence, as well as more frequent cleaning interactions of oceanic manta rays (Burgess, 2017). However, so far, no research has focused on the impact of water clarity on the foraging behaviours in this species. Many elasmobranch species are observed to be visual predators, relying on visual cues for finding and acquiring food resources (Jordan et al., 2013). Increased water clarity is related to increased visibility, facilitating prey discrimination and foraging efforts (Reinero et al., 2022). Although the role of vision for foraging has not been comprehensively studied in manta rays, this species does possess a large optic tectum and telencephalon compared to other elasmobranchs, and in captivity has been observed to respond to visual food stimuli (Ari, 2008; Ari & Correia, 2008). Therefore, it is reasonable to suggest that preferences of oceanic manta rays for foraging in clearer waters during the daytime may facilitate visual predation. However, at night, where visual cues are less important, manta rays may instead favour areas with increased prey availability at the surface. The choice to forage in more turbid regions at night could also signify a shift in distribution towards shallower, coastal areas. In the Hawaiian Islands, micronekton assemblages migrate closer to the shore at night to exploit nearshore zooplankton food resources (Benoit-Bird et al., 2008). However, if this were the case, we would expect to observe an increase in shallow-water foraging activity at night, which is not supported by the results of the GAM model. It's worth noting that the sample size for this study was relatively small, and further investigation is warranted, as more movement data is collected from ongoing tracking studies.

During the day, foraging activity was also correlated with north-easterly winds. During summer in the Gulf, prevailing northerly and northeasterly winds drive intrusions of oceanic water south through Jellicoe Channel (Greig, 1990; Zeldis et al., 2004), and contribute to sediment transport through Cradock Channel (Manighetti & Carter, 1999). These intrusions of warmer, oligotrophic EAUC waters create favourable conditions for oceanic manta rays, allowing them to inhabit warmer waters while capitalising on the higher productivity within the Gulf.

The influence of tides varied between day and night models, with manta rays more likely to forage in the rising tide during the day, and during the slack tide at night. To my knowledge, no work has examined the impact of tides on the distribution of zooplankton within this study region. However, studies conducted in other regions demonstrate how tidal currents can influence zooplankton distributions, forming dense aggregations which can be exploited by planktivorous megafauna (Alldredge & Hamner, 1980; Sims, 2008; Armstrong et al., 2016). To understand how tidal currents drive the observed patterns in manta ray foraging behaviour, it is necessary to measure how zooplankton aggregations are modulated by tidal currents within the complex bathymetry of the Gulf.

Despite being considered one of the primary drivers of fish movement patterns, linked to foraging behaviours of many fish and elasmobranch species, sea surface temperature was not significant in this analysis (Schlaff et al., 2014). However, the range of temperatures experienced throughout the tracking periods was limited, with 95% of observations between 18.9°C and 22.7°C reflecting the manta's presence during the later spring to early autumn seasons associated with the warm

EAUC. Manta rays are ectothermic, and therefore rely on external temperatures to regulate their internal bodily temperature. Seasonal patterns of occurrence of manta rays means that it is likely that presence of this species within New Zealand waters is dictated by sea surface temperature, however it does not appear to influence foraging behaviour (Ozaki, 2023). While no significant long-term warming trends have been recorded for northeastern New Zealand, Shears and Bowen (2017) demonstrate a long-term shift in seasonality, with sea surface temperatures staying warm later into the year, but declining over the October to December period. This shift is reflected in the redistribution of Bryde's whales and common dolphins (*Delphinus delphis*) in the Gulf towards the outer Gulf and Coromandel Peninsula, which occurs during warmer conditions (Colbert, 2019). A much greater range of temperature is experienced with vertical movements, and so temperature at depth may have a more significant influence on the spatial ecology of manta rays. This relationship between temperature and movement will be examined further in Chapter 3 which focused on the diving behaviours of manta rays.

2.4.3 Increased foraging by a pregnant female

GAM results also revealed increased foraging behaviour by PTT# 238018, a ~440 cm DW female suspected to be mid-pregnancy at the time of tagging. Delayed onset between maturity and first pregnancy, large size at birth (~200 cm), and long gestation periods suggests that pregnancy is very energetically demanding for oceanic manta rays, requiring high levels of maternal input (Rambahiniarison et al., 2018). Therefore, higher proportions of time spent foraging may reflect greater energetic requirements. However, these patterns were not seen in the other pregnant female which was tagged (PTT# 197235), indicating the necessity for a larger sample size to determine whether these behaviours are consistent across populations.

2.4.4 Long term climatic influence on spatial ecology

While it is evident that local and daily variability in environmental conditions can influence the distribution and behaviours of oceanic manta rays in New Zealand, it is also important to acknowledge the impacts of long-term climatic patterns such as the ENSO cycle, which govern interannual variability in these conditions. Manta ray populations are highly sensitive to large scale climate variability, which influences physical conditions, and prey availability (Beale et al., 2019; Cabral et al., 2023; Domínguez-Sánchez et al., 2023). In Bahía de Banderas, Mexico, El Niño is associated with warmer, less productive waters, causing manta rays to migrate away from the region (Domínguez-Sánchez et al., 2023). However, in New Zealand the opposite occurs, and La Niña is associated with those conditions (Greig et al., 1988; Kidson & Renwick, 2002). We suggest that while foraging behaviour is not influenced by sea surface temperature, occurrence in New Zealand is likely associated with warming waters. Therefore, warmer temperatures associated with La Niña may promote longer periods of residency here. Under La Niña conditions easterly winds become more prevalent. While conditions are overall less productive, in some areas such as on the leeward side of Aotea, these easterly winds promote strong upwelling (Black et al., 2000). Indeed, the 2011 La Niña event saw increased abundance of Bryde’s whales in the area (Dwyer et al., 2016), and this is the location of our hotspot for manta ray occurrence. Warming sea surface temperatures have also been linked to a shift in the spatial distribution of Bryde’s whales from the inner Gulf towards the outer Gulf also preferred by the manta rays (Colbert, 2019). Since all tracking data for the present study were collected during a La Niña, as 2024 sees the transition to an El Niño system it is important to continue tagging manta rays to see how differing climate regimes might influence population dynamics, behaviours, and habitat use in New Zealand.

2.4.5 Hotspots of manta ray distribution and foraging

Due to limited sample size, I was unable to conduct separate analyses for putative hotspot areas. The tracking data indicated a potential hotspot region at the northern end of the Cradock Channel, situated between Hauturu and Aotea, coinciding with one of the hotspot areas suggested by the MWANZ team and Ozaki (2023). This area has also been found to be an important habitat for common dolphins and Bryde’s whales (Dwyer et al., 2016). The Cradock channel is one of three channels which connects the inner Gulf to the Pacific Ocean and is characterised by strong tidal currents of oceanic waters, high frontal probability and diverse zooplankton communities (Black et al., 2000; Carroll et al., 2019; Lhériau-Nice & Penna, 2024). Rocky reefs and kelp forests are prevalent throughout the channel, distributed amongst complex topography which features a ridge running through the middle of the channel, and several pinnacles. Horn Rock (36.255° S, 175.190° E) is one notable rocky outcrop located in the channel and is well-known to recreational fishers and divers as a site of highly biodiverse aggregations of fishes (Putland et al., 2017). Cleaning stations are often found on prominent portions of structurally complex reefs which offer shelter and habitat for cleaner fish species, such as are found in the Cradock Channel (Hay et al., 2004). It is likely that the high productivity of Cradock Channel makes it an important feeding area for oceanic manta rays, however potentially this area could also serve as a cleaning station.

While there was no evidence of increased foraging or presence of manta rays within hotspots located in Jellicoe Channel or on the southwest coast of Aotea, these areas have been found to be important habitats for other species. The hotspot on the southwest coast of Aotea appears to be particularly crucial for Bryde’s whales and bottlenose dolphins (*Tursiops truncatus*; Dwyer et al., 2016; Stephenson et al., 2023). Additionally, eddies situated either side of the Cape Rodney contribute to further upwelling and vertical mixing (Hume et al., 1997; Black et al., 2000). Although this study did not find evidence of these areas being significant hotspots, sample size was small for this study. Further surveying and tagging should be done to examine the influence of environmental variables specific to these regions.

When conducting surveys, it's important to take into account observer bias. Instead of focusing observer effort on specific areas (i.e., hotspots), survey effort should cover broad regions across all time periods. Systematic transect surveys are a valuable tool to reduce observational bias and assess different potential areas. Restrictions to nearshore waters and the restricted field of view as a consequence of constrained height above sea level can pose logistical challenges for small-boat surveys. However, aerial surveys have proven successful in the Gulf for analysing the abundance and distribution of large marine species (Hamilton et al., 2023; Stephenson et al., 2023). Surveys typically take place during clear, calm conditions, as it becomes difficult to spot manta rays when it is choppy. Drones, which are used for photo-ID and to film manta ray behaviours, are unable to fly during windy or rainy weather. As a consequence, occurrence and behaviours of manta rays during poorer weather conditions may be underrepresented.

This chapter reveals the broad distribution and individual variability of the movements of oceanic manta rays along the coast of northeastern New Zealand, during their seasonal presence throughout summer to early autumn. Environmental drivers of foraging behaviours were explored, with manta rays exhibiting distinct preferences depending on the time of day. Most significantly, manta rays used clearer waters during the day, and more turbid areas at night, potentially indicating a trade-off between visual foraging cues, and foraging in more productive areas where visibility is decreased. I also identify a hotspot in foraging activity within Cradock Channel, which warrants further investigation as it has the potential to serve as a cleaning station habitat. This work highlights the need for further surveying efforts and satellite telemetry studies, collecting data across a broad range of variables including different demographic classes of manta rays, times of day, and across longer timescales.

Chapter 3

Patterns in diving behaviour and vertical profiles of oceanic manta rays

3.1 Introduction

When studying the movement ecology of marine animals, it is important to recognise the three-dimensional nature of their environment. In the ocean, environmental conditions and resource distribution vary with depth, as well as horizontally. Vertical movements throughout the water column enable marine animals to navigate and respond to their surroundings, facilitating fundamental behaviours such as foraging, predator avoidance, and reproduction (Hooker & Baird, 2001; Andrzejaczek et al., 2022; Braun et al., 2022).

For large marine predators, diving behaviours are most commonly associated with foraging activity. Diel vertical migrations are a widespread phenomenon observed throughout the ocean, where organisms transition from deeper waters during the daytime to shallower waters at night (Lampert, 1989). While for zooplankton and small fishes this movement pattern serves as a strategy to avoid visual predators while feeding on surface plankton, these migration patterns extend beyond primary consumers, propagating up the food chain as predators engage in diel, or reverse diel vertical movements to capitalise on concentrated prey at the surface, or increase encounters with migrating prey (Hooker & Baird, 2001; Hays, 2003). Alongside diurnal patterns in vertical habitat use, many marine predators will also undergo infrequent, deep dives to mesopelagic and bathypelagic depths. While foraging at these depths has been confirmed (Watwood et al., 2006; Adachi et al., 2021; Watanabe et al., 2021; Braun et al., 2023), it is suggested that in some species deep dives may have other purposes. For instance, elasmobranchs may dive to take advantage of stronger geomagnetic fields, and topographic features found at deeper depths, which can provide navigational cues for long distance movements and homing behaviours (Braun et al., 2022). Both deep and shallow dives can serve as an efficient mode of travel, where animals will take advantage of their negative buoyancy to glide during descent and expend minimal effort, actively swimming during ascent (Gleiss et al., 2011; Andrzejaczek et al., 2020b). This also facilitates periods of rest which is an important function for all large marine animals.

Vertical movements expose animals to rapid changes in environmental conditions due to the far greater variability in physical parameters such as light availability, dissolved oxygen, and temperature experienced when moving through the water column compared to movement over the same distance horizontally (Kramer, 1987; Warrant & Locket, 2004; Favilla & Costa, 2020). Often these conditions will impose depth limits, with organisms adjusting their behaviour in response to varying conditions to remain within their optimal range. Ectothermic fishes and reptiles for example, will often spend prolonged periods near the surface or out of the water to rewarm following deep dives to cooler waters (Dawson et al., 1977; Thums et al., 2013; Watanabe et al., 2021). In contrast, in warmer areas animals may remain in deeper waters to reduce body temperatures (Teo et al., 2007; Okuyama et al., 2021).

Many elasmobranchs spend the majority of their life subsurface, yet, while studies on horizontal movement are widespread, and associated behaviours and drivers discussed over a range of scales, research on vertical movements remains comparatively limited (Andrzejaczek et al., 2022). Incorporating knowledge of vertical movement has been enlightening for informing conservation management decisions. Bycatch is currently one of the greatest threats for sharks and rays and is closely intertwined with vertical distribution. Blue sharks (*Prionace glauca*), for instance, dominate bycatch compositions in longline fisheries across the Atlantic and Pacific Ocean (Oliver et al., 2015). In the Adriatic Sea, these sharks display diel vertical movement patterns, with a tendency to occupy shallower waters during the night. This behaviour leads to increased overlap with longline hooks during night-time operations, resulting in higher catch rates, and this is particularly pronounced in September (Hinrichs et al., 2021; Vedor et al., 2021). Therefore, deploying surface longlines in September only during daylight hours may reduce blue shark bycatch (Hinrichs et al., 2021). Using horizontal movements alone cannot provide an accurate assessment of fisheries bycatch risk (Murua et al., 2021)

While studies focusing on the vertical movement of oceanic manta rays are limited, they reveal patterns of high occupation of surface waters (~5–10 metres), punctuated by occasional deep dives (Andrzejaczek et al., 2021; Andrzejaczek et al., 2022). These patterns are variable—in the Revillagigedo Archipelago, Mexico, diving activity of manta rays undergoes a seasonal shift from surface waters to 100-150 metre depth. Opportunistic observations indicate that foraging occurs at these depths (Stewart et al., 2016b). Reverse diel movement patterns allow manta rays to exploit vertically migrating zooplankton, however as elasmobranchs, cold temperatures at depth are expected to pose a thermoregulatory challenge, requiring regular surfacing intervals to rewarm (Andrzejaczek et al., 2021).

Oceanic manta rays occur seasonally in New Zealand waters from at least the late austral spring (~November) to late austral autumn (~May). They are most commonly sighted along the northeastern coast of the North Island, and particularly in the Gulf—a highly productive shallow embayment, located off the coast of Auckland City (Murphy et al., 2001; Ozaki, 2023). While opportunistic sightings of manta rays, and satellite telemetry results from Chapter 3 reveal high occupancy of the surface waters of the Gulf and adjacent waters, we currently do not know much about their subsurface behaviours, and whether they follow similar patterns to those observed in other regions. This chapter represents the first investigation into the vertical movement of manta rays in this specific region and aims to provide insight into associated behaviours at depth.

3.2 Methods

3.2.1 Tag data

See section 2.2.1. for detailed description of the attachment procedures and of the study site.

All seven SPLASH10F tags described in Chapter 2 were used to analyse general patterns in the vertical habitat use of oceanic manta rays in northeastern New Zealand. The data for these tags were subset based on the previously described GPS tracks, to only assess diving behaviours within the study regions (Figure 2.3). The two recovered tags (PTT# 197235 and PTT# 238016) provide a full dataset of high temporal resolution (10 seconds and one second respectively), including the external temperature recorded throughout the dives. In contrast, the other six tags provide a summarised account of diving behaviours at a lower resolution due to bandwidth constraints.

3.2.2 Vertical habitat use

For analysis of time spent at depth, the data for the seven tags were regularised to the broadest temporal resolution transmitted (5 min; see Table 3.1 in results section for resolution of tags) and classified into one of four groups for depth (0–5 m, 5–50 m, 50–100 m, 100–250 m) based on the literature and initial visual analysis of the vertical movement Using R version 4.3.2. I calculated the percentage of overall time which was spent in each of these depth bins. To assess whether there was a diurnal effect on diving behaviour each record was categorised as day (sunrise to sunset) or night (sunset to sunrise) using the *suncalc* package in R (Thieurmel & Elmarhraoui, 2022). I then assessed whether the time of day had any influence on diving behaviours, by comparing the average frequency of dives performed each hour.

3.2.3 Dive profile analysis

While all seven tags were used for analysis of general trends in time at depth, and diel dive patterns, unrecovered tag data resolution was determined to be insufficient for conducting further analysis of behavioural modes and exploring environmental influences on diving metrics. Therefore, detailed analysis of behavioural modes will focus solely on the two recovered tags. Dive profiles were visualised and analysed using the *diveMove* package in R (Luque, 2024), which separates vertical movement into individual dives, and calculates dive statistics. Dives were defined as beginning from a depth of 10 metres, to avoid classifying surface behaviours such as foraging somersaults, as dives. Based on a preliminary literature review e.g. (Seminoff et al., 2006; Elliott et al., 2022), dive profiles were defined and assigned to each dive (Figure 3.1).

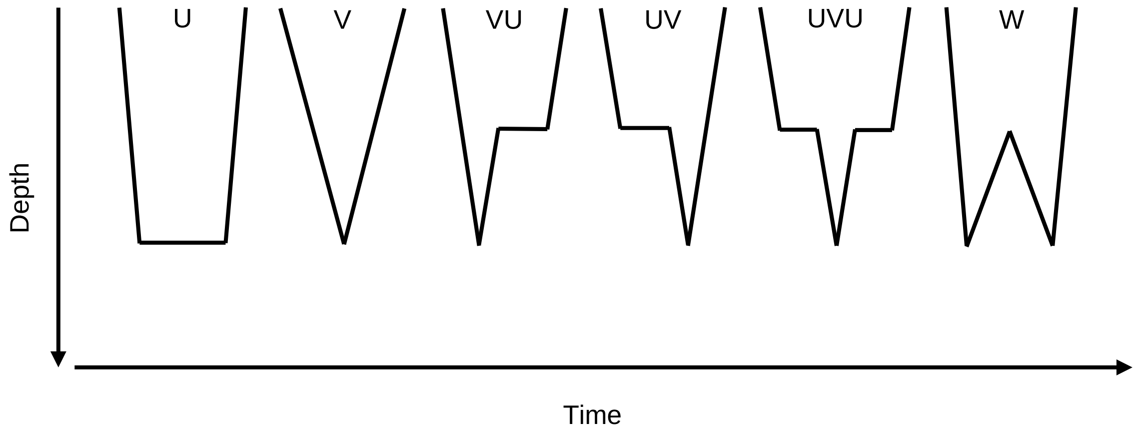

Figure 3.1 Dive profiles identified in this study. Not pictured = Short dives (S), which are characterised by being less than 30 s long, but which can assume different shapes.

Patterns in dive behaviour can be used to infer specific behavioural modes from remotely sensed data if direct observations are unavailable. Classification of dive profiles typically follows one of two approaches: manual classification, where dives are assigned visually, but can be subject to observer bias, or statistical methods such as hierarchal cluster analyses and hidden Markov models (Schreer et al., 1998; Bagniewska et al., 2013; Lemieux Lefebvre et al., 2018), which group dives automatically. While statistical methods are preferable for large datasets, they may miss parts of dives and require manual training (Thums et al., 2008). Two fundamental dive types—U-shaped and V-shaped dives, are described across a range of taxa including pinnipeds (Le Boeuf & Naito, 2022), cetaceans (Ishii et al., 2017), turtles (Seminoff et al., 2006), seabirds (Cox et al., 2016), and elasmobranchs (Elliott et al., 2022).

U-shaped dives are typically attributed to foraging behaviours. These dives are characterised by distinct descent, bottom, and ascent phases, with the prolonged bottom period at a relatively stable depth likely indicating foraging on aggregations of prey (Figure 3.1). Longer bottom durations increase the likelihood of prey encounters, and have been found to be positively correlated with food intake in some species (Carroll et al., 2014; Heaslip et al., 2014; Viviant et al., 2014). V-shaped dives, with little to no bottom phase can be indicative of travelling, searching, or navigational behaviours (Figure 3.1).

Diving metrics such as pitch angle and the speed of ascent or descent may help differentiate between different behavioural modes associated with dives (Gleiss et al., 2011; Andrzejaczek et al., 2020b). For example rapid ascents and descents through the water column may indicate searching behaviours, as they increase the probability of detecting olfactory cues that propagate horizontally through the water due to vertical stratification of layers with different densities (Gregg & Briscoe, 1979; Carey et al., 1990). In comparison, gliding transitory behaviours will have slower descent speeds relative to ascents (Weihs, 1973; Gleiss et al., 2019).

W-shaped dives also indicate searching behaviours, as animals swim up and through the water column, crossing through depth layers, potentially for enhanced detection of olfactory cues (Queiroz et al., 2017; Elliott et al., 2022). W-shaped dives are defined as involving between two to four undulations during the bottom phase, with depth change during this phase >10% of maximum dive depth. During dives individuals may exhibit a combination of these behavioural modes, where V-shaped movements are indicative of search behaviours and U-shaped movements are associated with finding and exploiting resources. In this study we have identified three key combinations of these profiles—VU, UV, and UVU dives (Figure 3.1). Dives that did not match any of the defined profiles were classified as "other." U, VU, UV, and UVU shaped dives are indicative of foraging behaviours, while V and W dives may suggest active search or pursuit of pelagic prey or searching behaviours. (Seminoff et al., 2006; Elliott et al., 2022).

3.2.4 GAM analysis of environmental influences on diving metrics

In this chapter I focus on the influence of variables which have been previously observed to be influential on manta ray diving metrics: solar altitude and time of the day, moon illumination, and temperature.

Time of day provides insight into diel movement patterns. Oceanic manta rays have been described to follow reverse diel migration patterns, remaining deeper during the night and ascending to shallower depths during the day (Andrzejaczek et al., 2021). During the night these ascents are often influenced by lunar illumination levels (Alldredge & King, 1980; Last et al., 2016). During the full moon, zooplankton will tend to stay deeper in the water column to avoid predators which rely on visual cues for foraging and increase foraging activity during increased moonlight intensity. (Hernández-León et al., 2001). Many predators which prey on these vertical migrators will adjust movements accordingly (Fallows et al., 2016; Shaff & Baird, 2021; Meyers, 2023). For observations during the day solar altitude were used as a proxy for light availability. Moon illumination and solar altitude were calculated for the start of each dive descent using the *suncalc* package in RStudio, which does not account for cloud cover that might reduce light availability (Thieurmel & Elmarhraoui, 2022).

To examine the influence of environmental variables on diving behaviour, I selected four diving metrics calculated from the previous *diveMove* analysis which were not strongly correlated with one another. These descriptors were mean bottom depth (mean depth during the bottom phase of the dive; m), max depth (m), total dive time (s), and post dive duration (the time spent at the surface following the dive; s). These variables were analysed using separate GAMs for each individual, as well as separating night and day observations. While night observations looked at the influence of moon illumination, dives conducted during the day will instead be analysed using solar altitude. The models will be fitted using the tw family, based on the tweedie family but which includes estimation of the power parameter (p) during fitting (Wood, 2015). The power parameter determines the specific tweedie subfamily which is used; Different values of p correspond to different distributions for example Poisson (p = 1) and gamma (p = 2). The tweedie family is used to deal with data which exhibit characteristics such as being zero-inflated, heteroscedastic, or are highly skewed which suits the diving data as it is highly skewed to short, shallow dives (Tweedie, 1984).

3.3 Results

3.3.1 Tag deployment

Resolution of the data which was able to be recovered varied between five minutes, to one second (Table 3.1). Not all dives were transmitted, there are some periods where no dive data are available. Gaps in data occurs randomly but may be exacerbated by rough water conditions where the antennae may not be out of the water for sufficient periods to transmit data.

Table 3.1 Summary of deployment of seven SPLASH10F satellite tags on oceanic manta rays. Recovered tags provide full archival set, including external temperature, while non-recovered tags provide a summary of diving behaviours, at a lower temporal resolution.

Manta PTT#	Temporal resolution of vertical data	Days tracked	Recovered
197235	10 s	34	Yes
204511	5 min	31	No
238014	15 s	22	No
238015	5 min	11	No
238016	1 s	20	Yes
238018	1 min 15 s	9	No
238019	5 min	72	No

3.3.2 Vertical habitat use

Looking at the general patterns observed for all seven tags, vertical habitat use was heavily skewed to the top five metres (Figure 3.2), with PTT# 238016 the only individual to record depths of greater than 200 metres (maximum depth of 210.5 metres). Comparisons of the timing of these dives to the closest GPS location in Chapter 2 (Figure 2.3a) indicates that these deep dives occurred approximately 50 km east of northern Aotea. Manta rays displayed significant patterns of reverse diel vertical movements (Mann-Whitney U test $p < 0.001$; Figure 3.2) spending a greater proportion of time in surface waters in the day (0–5 m; 65.4% compared to 46.2%) and undertaking more deep dives during the night-time. The average temperature recorded by PTT# 197235 was 21.13 °C ± 0.45 SD (range:14.4 °C–23.7 °C) and for PTT# 238016 this was 20.89 °C ± 1.09 SD (range:13.7 °C–27.5 °C). Warmer temperatures were measured near the surface and declined with depth (Figure 3.3).

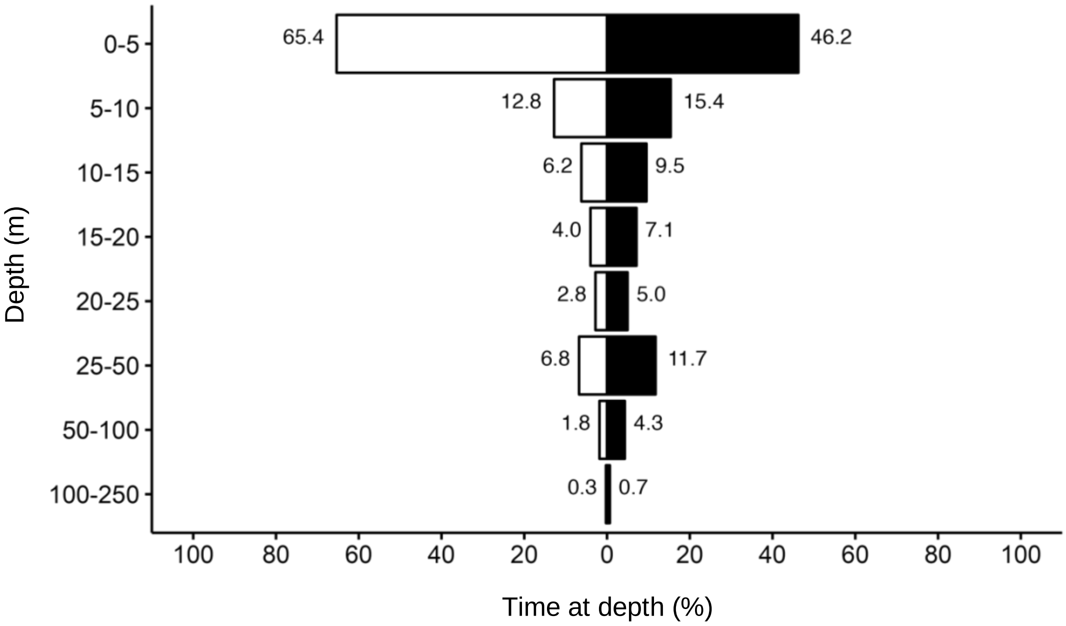

Figure 3.2 Proportion of time at depth for seven satellite tagged oceanic manta rays in northeastern New Zealand. White bars indicate vertical habitat use during the day; black bars indicate vertical habitat use during the night. Analysis for figures calculates percentage based on the total recorded movements, excluding periods where data were not transmitted.

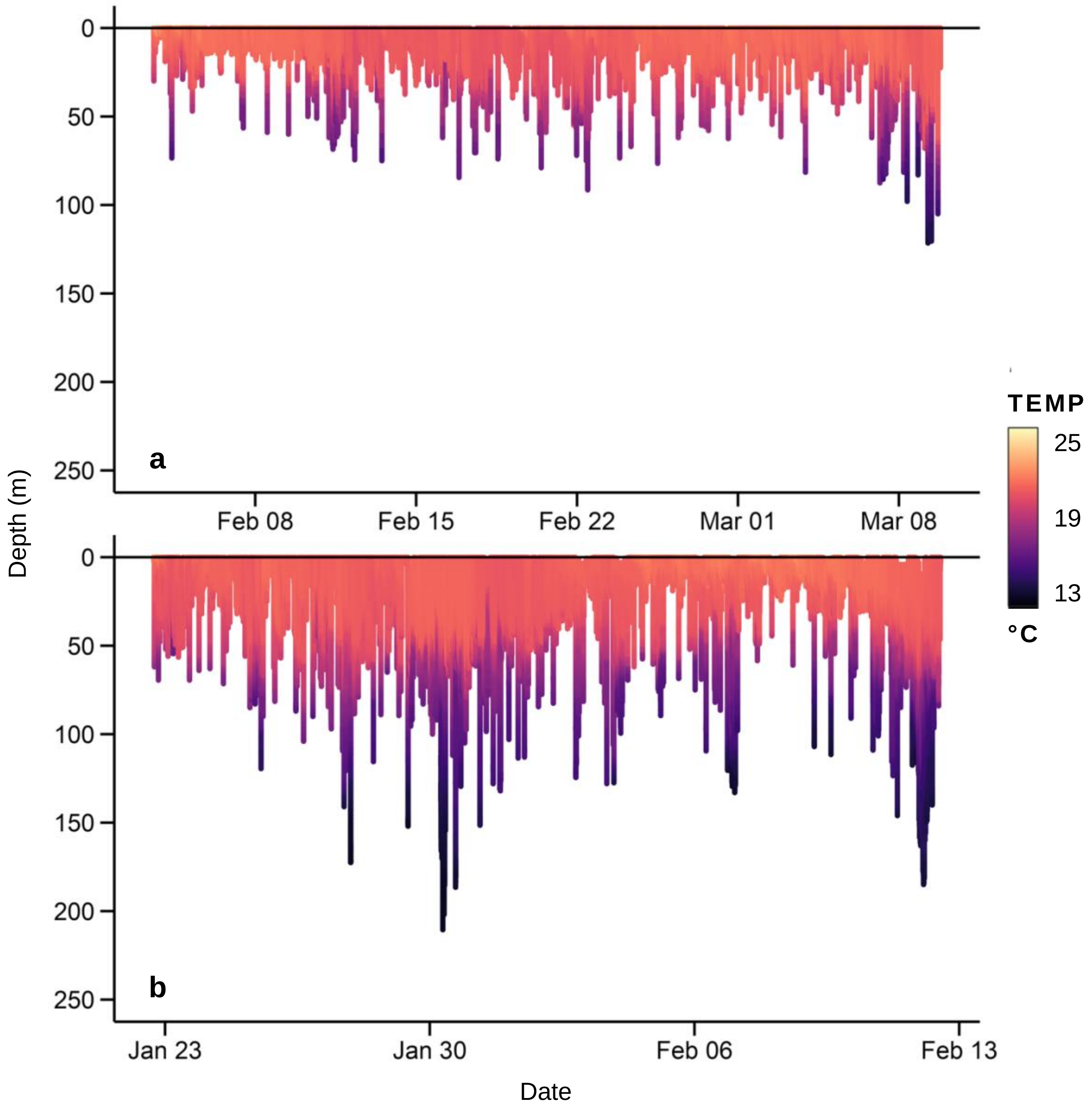

Figure 3.3 Time-series of vertical movement from recovered archival data for two oceanic manta rays (a) PTT# 197235 (mean depth = 4.35 m ± 9.9 SD) and (b) PTT# 238016 (mean depth = 12.33 m ± 19.2 SD). Colour scale starts from 13°C and saturates at 25°C for visual clarity (267 points > 25°C; maximum temperature = 27.5 °C).

3.3.3 Dive profiles and diving behaviours

Dive profile analysis revealed that the majority of dives were short and shallow, lasting less than 30 seconds. However, dives involving foraging (PTT# 197235 *n* = 374; PTT# 238016 *n* = 752) and searching associated movements (PTT# 197235 *n* = 996; PTT# 238016 *n* = 960) occurred throughout the tracked period (Table 3.2).

Dives that could not be classified as one of the defined profiles often exhibited a complex combination of movements such as numerous oscillatory movements or several U-shaped dives at depth, separated by periods spent in shallower (but still deeper than 10 m) waters. There were no significant differences found in the ascent or descent speeds for U and V shaped dives (not shown).

Table 3.2 Classification of dives performed by oceanic manta rays into distinct dive profiles and associated behaviours.

	Number of dives								
	Foraging				Searching				
PTT #	U	VU	UV	UVU	V	W	Short	Other	**Total**
197235	245	79	46	4	865	131	469	4	**1843**
238016	515	91	120	26	681	279	4976	101	**6789**

3.3.4 Influence of environmental variables on diving metrics

Maximum depth

Across both individuals, during night and day dives, maximum depth was correlated with colder minimum temperatures ($p < 0.001$; Figures 3.4a–3.7a). While there was no relationship between maximum dive depth and sun altitude for PTT# 197235 (Figure 3.4a), for PTT# 238016, maximum dive depth was the shallowest when the sun was at the horizon, and when it was directly overhead ($p < 0.001$; Figure 3.5a). Manta rays also tended to dive deeper when there was greater moon illumination ($p < 0.001$; Figures 3.6a, 3.7a).

Mean bottom depth

Relationships between the environmental variables and the mean bottom depth followed the same patterns described in maximum depth. Mean bottom depth was correlated with colder minimum temperatures ($p < 0.001$; Figures 3.4b–3.7b) and increased moon illumination ($p < 0.001$; Figures 3.6b, 3.7b). For PTT# 238016, mean bottom depth was deeper when the sun was directly overhead, around midday (Figure 3.5b).

Dive duration

Across both individuals, day and night dives declined in length with warmer water temperatures, becoming much shorter at temperatures warmer than 20°C ($p < 0.001$; Figures 3.4c–3.7c). Dives were shorter when the sun was at maximum altitude ($p < 0.01$; 3.4c, 3.5c), and for PTT# 238016 were also shorter during the full moon ($p < 0.001$; 3.7c).

Post dive duration

The models examining post-dive duration were only able to account for less than 10% of the deviance suggesting that this metric is driven by variables which have not been considered in this analysis (not shown).

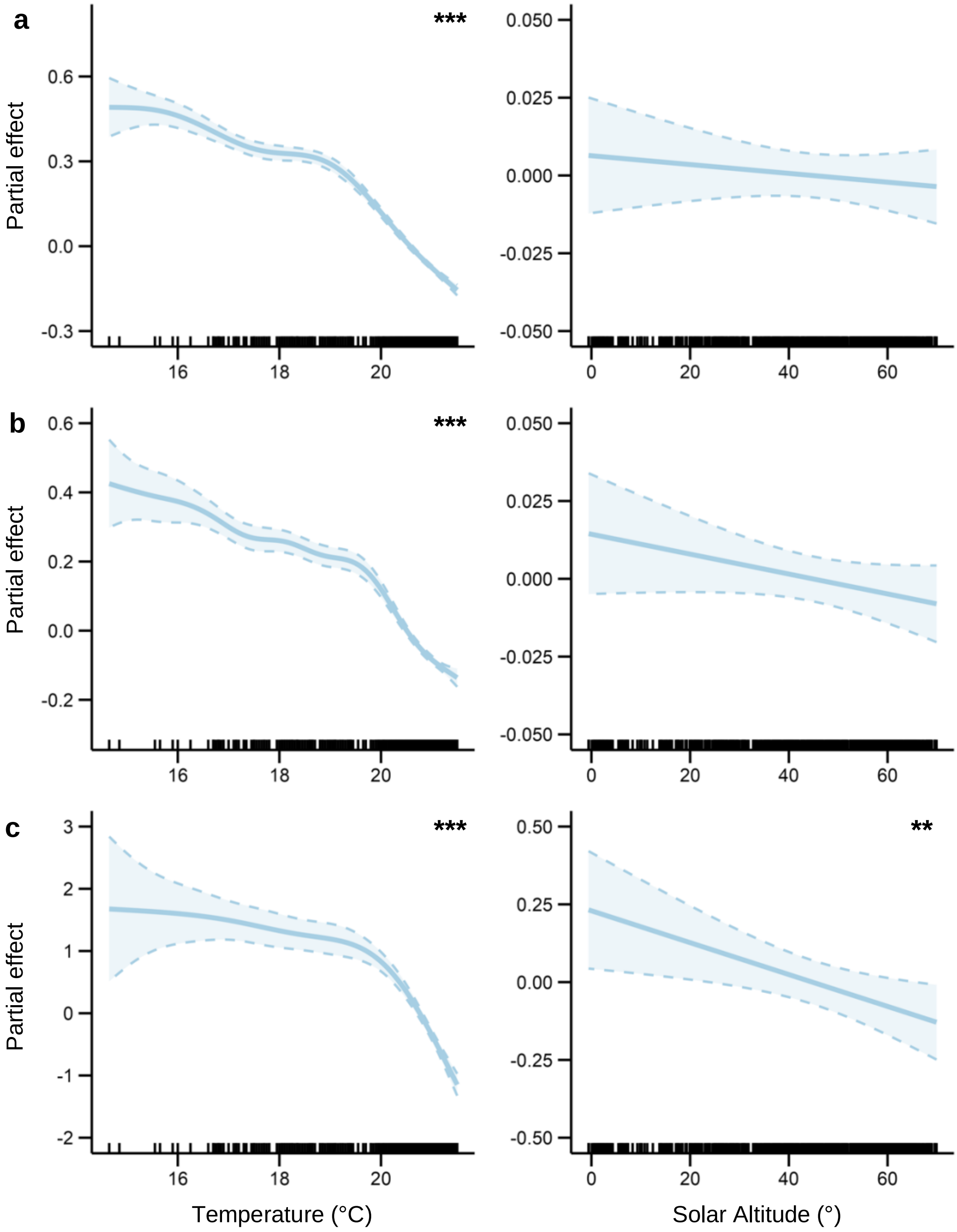

Figure 3.4 Environmental influences on daytime dives by oceanic manta ray PTT# 197235. Modelled as the partial effects of smoothed terms looking at the influence of the minimum temperature (°C), and solar altitude (°), on (a) maximum depth (b) average bottom depth, and (c) dive duration. Deviance explained by the models was 72.5%, 69%, and 33.2% respectively. Significance of terms is indicated as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$). Note, to aid visualisation the Y-axes scales differ between terms.

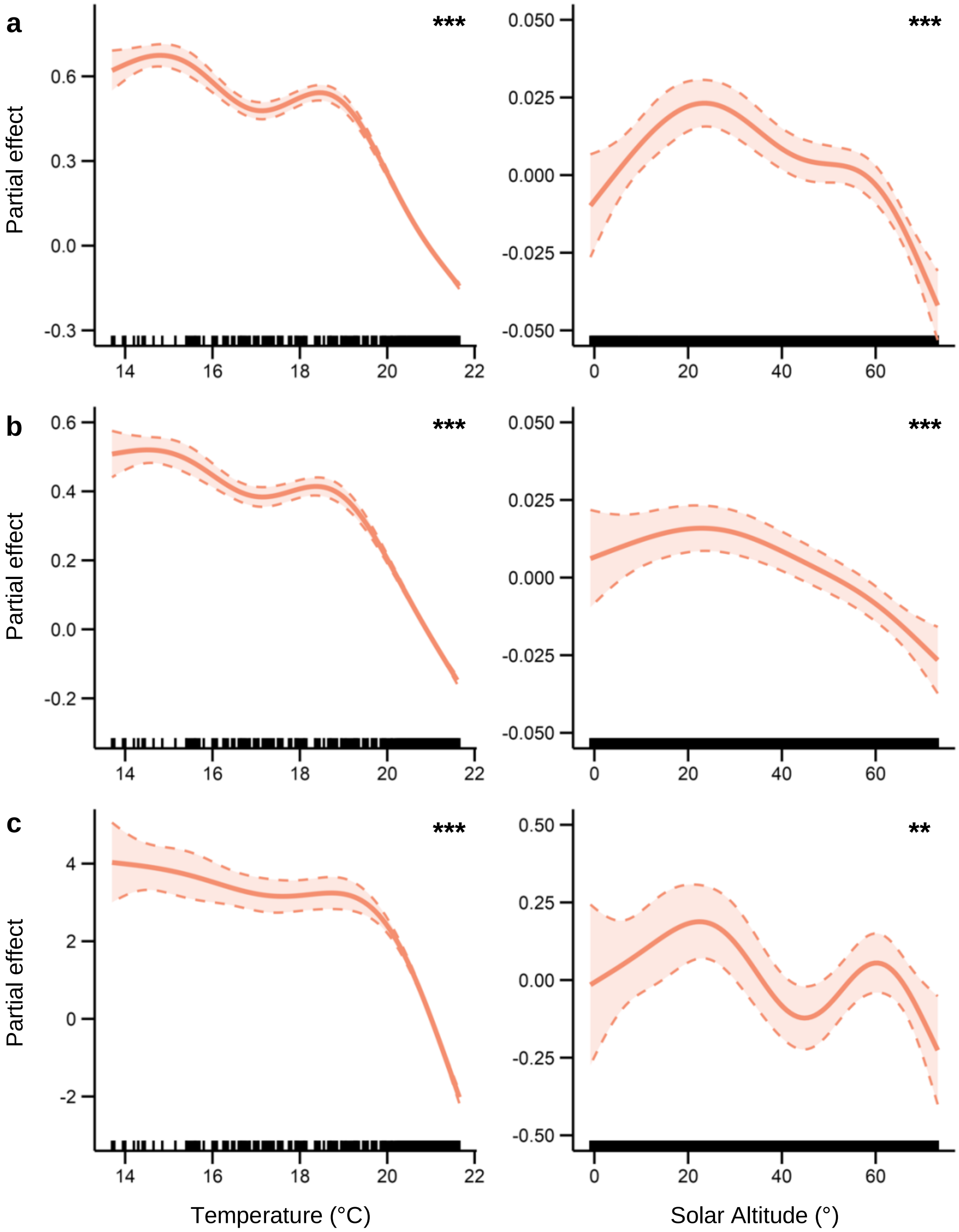

Figure 3.5 Environmental influences on daytime dives by oceanic manta ray PTT# 238016. Modelled as the partial effects of smoothed terms looking at the influence of the minimum temperature (°C), and solar altitude (°), on (a) maximum depth (b) average bottom depth, and (c) dive duration. Deviance explained by the models was 61.8%, 61.2%, and 34.6% respectively. Significance of terms is indicated as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$). Note, to aid visualisation the Y-axes scales differ between terms.

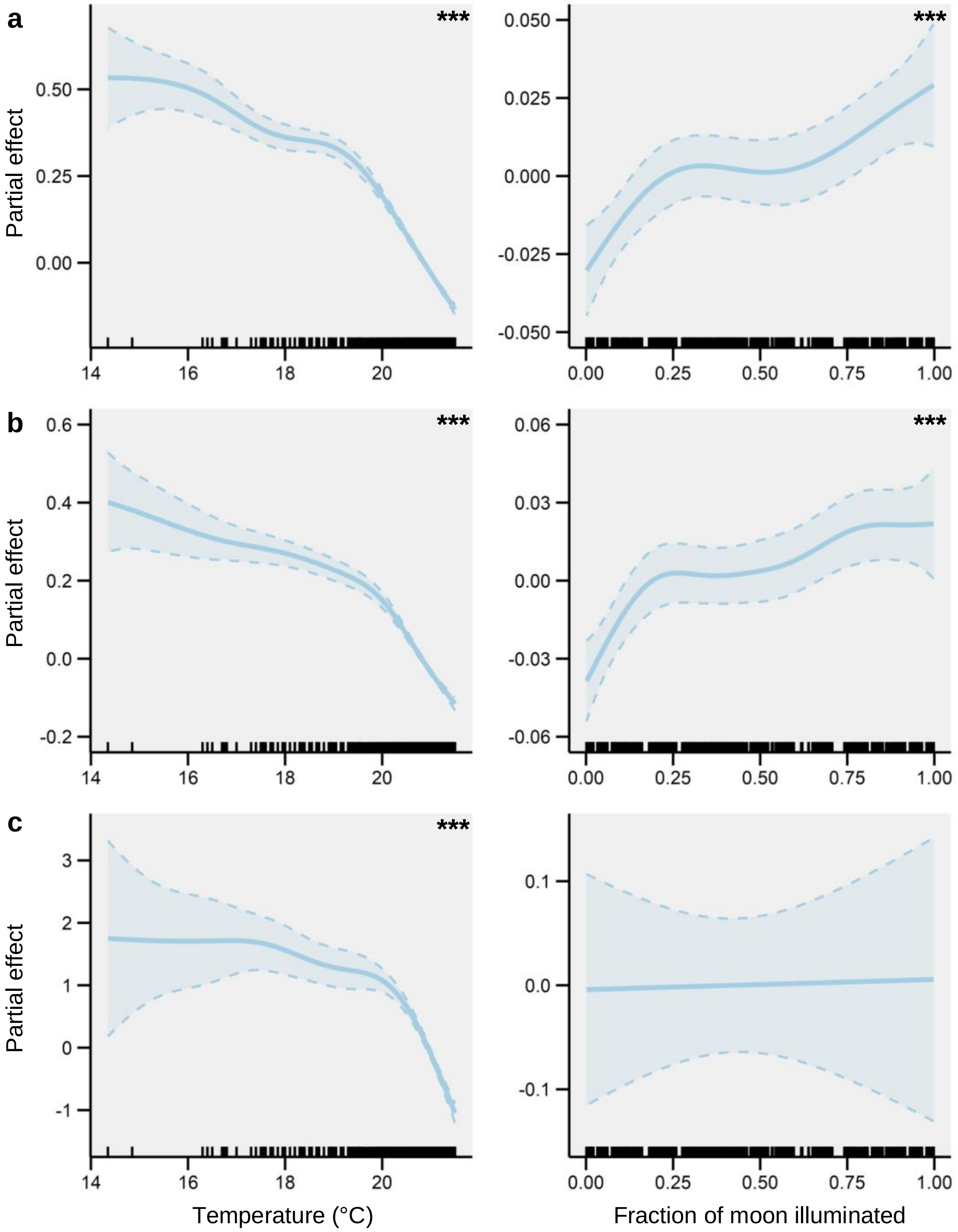

Figure 3.6 Environmental influences on night dives by oceanic manta ray PTT# 197235. Modelled as the partial effects of smoothed terms looking at the influence of the minimum temperature (°C), and moon illumination on (a) maximum depth (b) average bottom depth, and (c) dive duration. Deviance explained by the models was 59.6%, 55.9%, and 23.1% respectively. Significance of terms is indicated as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$). Note, to aid visualisation the Y-axes scales differ between terms.

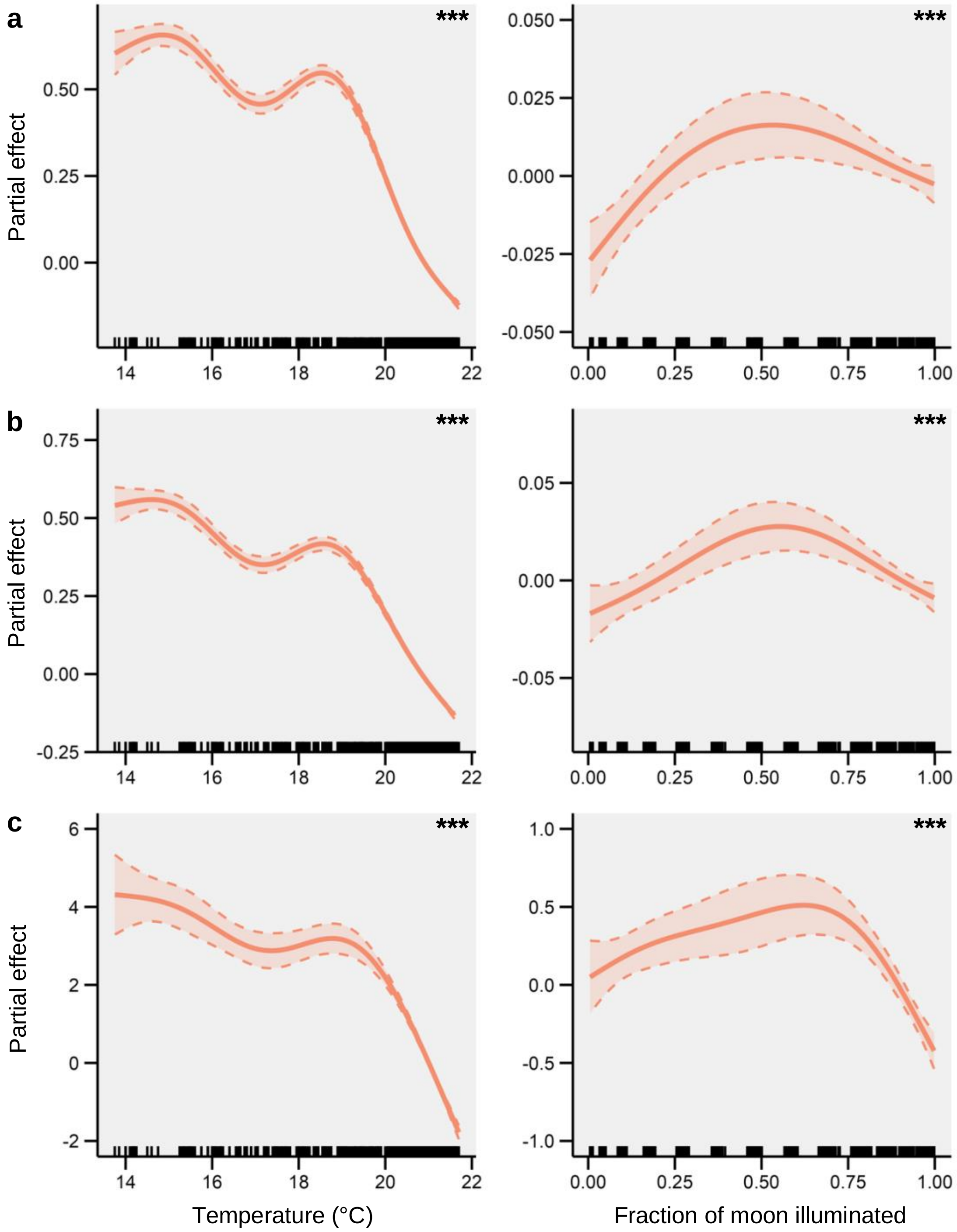

Figure 3.7 Environmental influences on night dives by oceanic manta ray PTT# 238016. Modelled as the partial effects of smoothed terms looking at the influence of the minimum temperature (°C), and moon illumination on (a) maximum depth (b) average bottom depth, and (c) dive duration. Deviance explained by the models was 70.8%, 73.1%, and 39.1% respectively. Significance of terms is indicated as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$). Note, to aid visualisation the Y-axes scales differ between terms.

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3.4 Discussion

Most of our current understanding of oceanic manta rays in New Zealand is derived from brief and opportunistic observations taken at the surface (Duffy & Abbott, 2003; Ozaki, 2023). This thesis represents the first on the diving behaviours of oceanic manta rays in temperate waters, specifically in New Zealand and contributes to the global understanding of this species' subsurface ecology.

3.4.1 Vertical habitat use

Oceanic manta rays displayed high fidelity to surface waters (< 5 metres) along the northeastern coast, occasionally diving to deeper waters. These patterns were observed for all manta rays except PTT# 238015, which spent more time at depth, particularly around 25–50 metres (Appendix 2d). Patterns of high surface occupancy have been documented in other studies looking at the vertical habitat use of this species in the tropical East Atlantic (Andrzejaczek et al., 2021; Andrzejaczek et al., 2022). It is important to note that the Gulf, which formed most of the manta rays' ranges in the study area (Figure 2.3), is a relatively shallow area with most of their time spent in waters less than 80 metres deep.

In my study, manta rays spent significantly less time at the surface during the night compared to the day, indicating patterns of reverse diel vertical migration (rDVM). Although they still primarily occupied the first five meters of the water column at night, there was an increase in the frequency of deeper dives (Appendix 2). Both DVM and rDVM patterns have been described for planktivorous elasmobranchs reflecting the close correlations between the movements of these species and prey distribution (Nelson et al., 1997; Braun et al., 2014; Andrzejaczek et al., 2022). In oceanic manta rays, rDVM have been documented off the coast of northern Peru (Andrzejaczek et al., 2021). Many species exhibit plasticity in these patterns, as individuals adjust their foraging patterns to track the movements of prey. For instance, basking sharks around the United Kingdom exhibited DVM when in deeper, well-stratified waters, aligning with the migration of zooplankton from deep scattering layers to the surface. However in shallower inner shelf regions, the same sharks exhibited rDVM, hypothesised to be a response to rDVM patterns exhibited by prey in the area (Sims et al., 2005). Similarly, whale sharks in the Gulf of Mexico demonstrate rDVM patterns when in shallower, coastal areas, yet in offshore regions, they remain almost continuously at the surface during the night (Tyminski et al., 2015). Reef manta rays exhibit DVM patterns in the Chagos Archipelago and Palmyra Atoll (McCauley et al., 2014; Andrzejaczek et al., 2020a), rDVM patterns in the Red Sea and the Seychelles (Braun et al., 2014; Peel et al., 2020), and in some areas do not display any significant DVM patterns at all (Andrzejaczek et al., 2022).

While diel patterns are generally linked to the diel vertical migration patterns of zooplankton prey from deep scattering layers to surface waters, it is important to note that the formation of deep scattering layers occurs between 200–1000 m (Aksnes et al., 2017). In this study, the deepest waters which manta rays ventured into were at the edge of the continental shelf, around 200 metres deep (observed in one individual across two separate dives; See Figure 2.3 for the horizontal distribution of this individual and its proximity to the 200 metre isobath), and the majority of their time was spent in even shallower waters. The relatively shallow topography of the Gulf and northeastern continental shelf is unlikely to support the formation of deep scattering layers or vertical migration patterns. Instead manta rays may be targeting benthic or demersal zooplankton which emerge from shallow coastal habitats at night (Alldredge & King, 1985; Andrzejaczek et al., 2021). Demersal plankton has been identified as an important component of the diet of reef manta rays in Australia (Couturier et al., 2013), with emergence becoming more pronounced during summer and with the full moon (Jacoby & Greenwood, 1989). Although the presence of emergent demersal plankton has not been studied in the Gulf, this phenomenon could also explain the increased dawn and dusk foraging activity reported in common dolphins in the region (Putland et al., 2017). It is possible that during their migrations, when transiting through offshore regions with deep scattering layers, oceanic manta rays may exhibit typical diel vertical migration patterns, as it could be more profitable in such environments.

The opportunistic recovery of archival tags provided high resolution data on the diving behaviours of two manta rays, indicating wide variation between individuals.

In Chapter 2 I detailed the horizontal movements of the manta rays, where PTT# 238016 travelled broadly along the northeastern coast from Mayor Island to the Poor Knights Islands, whilst the movements of PTT# 197235 were restricted within a relatively small area between Cape Rodney and Aotea (Figure 2.3a). Looking at the vertical movement of these two individuals PTT# 197235 remained in much shallower waters than PTT# 238016. The substantial differences observed in both the horizontal and vertical movement patterns of these two individuals highlights the importance of tagging more individuals to gain an understanding of any patterns across the general population.

Throughout the tracked period, PTT# 197235 made frequent dives between 50 to 100 meters. Given the general location of this individual within the inner Gulf, as inferred from horizontal movements, these dives are likely to be at, or near to the seafloor. Similarly, horizontal movements for PTT# 238016 indicated that the individual only briefly ventured into waters deeper than 210 metres (Figure 2.3a). The maximum bathymetric depth inferred for this individual from the state space model was 230 metres. Therefore, these dives were also most likely demersal. This suggests that manta rays tend to dive close to the seafloor throughout the study site, regardless of depth.

In other regions, diving to the seafloor can be a means of predator avoidance. Observations, and bite marks provide evidence for predatory attacks from killer whales (*Orcinus orca*) and white sharks on manta rays in other regions including the Galápagos Islands, Mozambique, Hawai'i and Australia (Alava & Merlen, 2009; Marshall & Bennett, 2010a; Deakos et al., 2011; McGregor et al., 2019; Strike et al., 2022). Although distribution of manta rays overlaps with these species in New Zealand, there is no evidence to date which suggests manta rays are interacting with these predators even though large pelagic sharks and killer whales are found in the area (Stephenson et al., 2023).

Diving to the seafloor may be for navigational purposes. Several species of teleosts (Formicki et al., 2019; Naisbett-Jones & Lohmann, 2022), elasmobranchs (Meyer et al., 2005; Newton & Kajiura, 2020; Keller et al., 2021), and sea turtles (Benhamou et al., 2011; Brothers & Lohmann, 2015) have the capacity to use the

Earth's magnetic field for navigation, and it is suggested that diving to the seafloor may enable these species to exploit the increased intensity of the geomagnetic field found at greater depths (Braun et al., 2022). Southern bluefin tuna (*Thunnus maccoyii*) display spike dives that are precisely timed to align with the peak in intensity of the Earth's magnetic field during sunset and sunrise (Willis et al., 2009). Much more research is needed in this area to confirm this hypothesis. While magnetoreception is documented in several elasmobranch species, it has not yet been confirmed in manta rays. Additionally, these studies have primarily focused on deeper waters, and it remains unclear whether dives to 50 metres will offer the same navigational cues. In addition to magnetic cues, other factors found at depth such as topographic landmarks and electric fields may also aid in navigation (Braun et al., 2022).

3.4.2 Environmental influences on diving behaviour

In Chapter 2, I examined the role of temperature as a driver of horizontal movements and behaviour. Despite being one of the most prominent variables studied in the literature for its' influence on movements and foraging across a wide range of taxa (e.g. Byrne et al., 2019; Riaz et al., 2021; Ransome et al., 2024), sea surface temperature did not show a significant impact on the foraging behaviours of oceanic manta rays in this study. Given the relatively stable sea surface temperature throughout the tracked period, I proposed that the influence of temperature might be more significant for vertical movements, due to the rapid decline in temperature with depth. As expected, deeper dives were correlated with colder temperatures (Figures 3.4 to 3.7), and vertical movements of manta rays exposed them to greater variability in temperature, from a minimum of 13.7°C to maximum 27.5°C. However, temperature did not appear to place an upper limit on dive depth or duration and was a poor predictor of post-dive duration. This finding was unexpected, as I had hypothesised that manta rays may need to spend basking time at the surface following cold, deep dives, for thermoregulation. Oceanic manta rays in other ocean regions dive much deeper than was recorded in this study, experiencing far colder temperatures. During their migrations from New Zealand to the Pacific Islands, age data have recorded dives of up to 1376 metres depth, encountering temperatures as low as 3.9 °C (Setyawan et al., 2021).

While manta rays are classified as ectotherms, the presence of well-developed cranial retia mirabilia may be evidence for a counter-current heat-exchange system which would allow warmth to be transmitted to the brain (Alexander, 1996). This adaptation may allow these animals to tolerate colder temperatures during dives. In the Chilean devil ray (*Mobula tarapacana*), the maintenance of brain activity and visual acuity during deep dives is proposed as evidence for foraging at depth (Thorrold et al., 2014). Therefore, it is likely that the temperatures of New Zealand waters are not cold enough to require rewarming. Given that manta rays spent the majority of their time at the surface, often engaging in foraging behaviours, factors such as surface prey availability likely exert a greater influence on the amount of time spent at the surface between dives.

While moon illumination was not identified as a significant driver of horizontal foraging behaviours, it was found to be significant in predicting vertical movements—manta rays remained in shallower waters during decreased moonlight illumination (Figures 3.6a, b; Figures 3.7a, b). While the new moon phase is often linked to increased abundances of zooplankton in the surface waters (Gliwicz, 1986; Asha et al., 2016; Amin & Alangavan, 2022), this phenomenon is likely a result of diel vertical migration, which, as discussed earlier, is unlikely to occur in the shallow northeastern New Zealand environment. However, the new moon phase has also been linked to the decreased emergence of demersal zooplankton in Puerto Rico, Australia, and in the Gulf of California (Alldredge & King, 1980; Jacoby & Greenwood, 1989; Ríos-Jara, 2005). If manta rays are targeting demersal species, it may not be energetically profitable for manta rays to dive during the new moon, instead they may opt to forage on surface zooplankton. Interestingly, for PTT# 238016, dives were shorter during the full moon, as well as during the new moon (Figure 3.7c). While there is a substantial difference in lunar illumination during these phases, it is important to note that they coincide with the periods of the greatest tidal range and associated increases in tidal intensity. In other regions such as Indonesia, (Dewar et al., 2008) and Australia (Jaine et al., 2012), reef manta rays exhibit increased foraging activity and presence during these periods to take advantage of tidal current driven aggregations of prey. However this is not always the case—in Bahia de Banderas oceanic manta ray occurrence was highest during intermediate moon phases (Domínguez-Sánchez et al., 2023).

Solar angle was selected as a proxy for light availability during the day as a comparison to moonlight illumination, which indicates light availability at night. While solar angle was not significant in driving maximum or average bottom depth for PTT# 197235 (Figures 3.4a, b), this individual did complete dives of longer duration when the sun was at its peak, around an altitude of 90° (Figure 3.4c). The relationship with solar altitude was more complex for PTT# 238016. Dives tended to be shallower and shorter when the sun was at its peak, but also when the sun was near the horizon, at lower angles of altitude (Figure 3.5). Light intensity declines with reduced angles of sun elevation (Allen et al., 2006; Spitschan et al., 2016; Storrie et al., 2022). Therefore, when the sun is at lower angles, decreased light availability reduces visibility. Conversely, when the sun is at its peak, light intensity and therefore visibility will be the greatest. Observed patterns may indicate a combination of factors including the distribution and accessibility of prey, as well as overall visibility however, further studies are needed to address these relationships.

In mid-February 2023, tropical cyclone Gabrielle passed along the northeastern coast of New Zealand, causing heavy rainfall, strong winds and storm surge (Noll, 2023). By midnight on the 13th February the cyclone was centred above Aotea, coinciding with the general location of PTT #238019 (Figure 2.3a). While there was a gap in the dive record from 3pm on the previous day till 8am on the 13th, visual analysis indicated that PTT# 238019 moved to deeper waters mostly > 20 m (Appendix 3g), with no surfacing recorded between 10:20am till around 1:30pm. Responses to storm events are highly variable—often animals will leave the area and move out to deeper waters (Udyawer et al., 2013; Crowe et al., 2020; Gutowsky et al., 2021) or dive to greater depths as was exhibited by PTT# 238019, and other species including hawksbill turtles (*Eretmochelys imbricata*; Matley et al., 2019) and porbeagle sharks (*Lamna nasus*; Wang et al., 2020) likely taking refuge from violent surf and variable salinity due to heavy rainfall.

3.4.3 Dive profile analysis for oceanic manta rays

Manta rays displayed both V-shaped and U-shaped dives throughout their tracked period, indicating that diving is multipurpose, involving searching, foraging, and navigation behaviours. There was no significant difference found between ascent and descent velocities to indicate gliding behaviours. However, from visual observation of the data there were several patterns in diving which were grouped into the V-shaped dive category. While many of the dives clearly displayed gradual descents followed by a rapid ascent, there were also many dives where both the ascent and descent were rapid.

Assigning dive profiles to 2D diving movement has been used across taxa to infer behavioural modes (Lesage et al., 1999; Seminoff et al., 2006; Elliott et al., 2022). However, manual classifications are highly subjective, and can be subject to observer bias. The geometry of a dive type is influenced by the maximum depth achieved. For instance, dives may involve similar bottom durations but different maximum depths. If this dive is shallow, it will be characterised as a U-shaped dive, whereas if it is deeper, it is more likely to be characterised as a V-shaped dive, as the profiles work off the relative proportions of dive time spent during these different phases. While the majority of studies using these methods focus on deeper oceanic habitats, this study was conducted in the relatively shallow environment. Dives were often shallow and short, less than 30 seconds long, which were difficult to attribute to the pre-defined dive profiles in the literature. While these could have been excluded from the study, these dives likely still reflect important aspects of oceanic manta ray habitat use and behaviour. Shallow dives have been associated with increased rates of horizontal movement in seals, owing to decreased drag at the surface (Lesage et al., 1999). However, observations of manta rays at the surface suggest that these shallow dives may be reflective of prey-searching behaviours (E. Setyawan, Conservation International, pers. comm.).

Other studies have used statistical methods to characterise dive profiles, which are particularly useful when working with large datasets which would otherwise be highly time consuming to classify manually. Dive metrics, including mean and maximum depth, velocity, and duration of ascent, descent, and bottom phases, are extracted and analysed using techniques such as statistical clustering, principal components analyses, hidden Markov modelling, or machine learning algorithms (Schreer et al., 1998; Godard et al., 2020). However, when data for this study was inspected through the *diveMove* package, many of the identified points for the onset of bottom time and ascent phases were found to be incorrect. Additionally, comparisons of subjective and statistical methods in inferring diving behaviours for gray whales (*Eschrichtius robustus*) indicated that statistical techniques may miss subtle differences in dive geometry which may represent behavioural differences. Therefore, these statistical methods would still require manual inspection of each dive, which was not feasible in this study due to time constraints. Given the potential for errors and bias associated with these methods, it is important to obtain subsurface observations to validate these findings. ‘Crittercams’ have been successfully deployed on both reef and oceanic manta rays in Mexico and the Maldives, revealing foraging on zooplankton aggregations at the thermocline (Stewart et al., 2019; Pelletier et al., 2023). In reef manta rays, they provided evidence of social behaviours, and interactions with spinetail devil rays which were previously unknown (Pelletier et al., 2023). As revealed in Chapter 2, both the oceanic manta ray and the spinetail devil ray occur in New Zealand waters, with a clear distinction in habitat use at the 200 metres depth contour. These methods could provide insight into whether competitive interactions occur at this boundary, potentially contributing to trophic separation. Additionally, they will allow behavioural inferences and suggestions from my study to be validated.

This chapter provides novel insights into the subsurface movements and behaviours of oceanic manta rays in northeastern New Zealand. Vertical habitat use was consistent with findings from other regions—manta rays displayed a preference for surface waters (< 5 metres) with occasional deeper dives, and reverse diel vertical movement patterns. I suggest that these dives may be for navigational purposes or targeting emerging demersal zooplankton. This work highlights the need for further research on the influences of environmental variables such as temperature and lunar illumination on manta ray behaviour and proposes the use of advanced techniques like 'Crittercams' to validate behavioural inferences.

Chapter 4

General Discussion

4.1 Thesis aims and overview

The overarching aim of my thesis was to investigate the spatial ecology and diving behaviours of oceanic manta rays in northeastern New Zealand. While oceanic manta rays are poorly studied globally, this is particularly true for temperate regions. At the limits of their geographical distribution, manta rays are subject to different environmental conditions compared to their tropical and subtropical populations. Seasonally cooler temperatures likely drive important aspects of ecology, such as the migratory behaviour observed in oceanic manta rays in New Zealand over the during the broader summer to autumn (Setyawan et al., 2021). In comparison, populations inhabiting tropical and sub-tropical waters, where colder temperatures are not a limiting factor, tend to be more residential (Stewart et al., 2016a). The Gulf, where manta rays spend the majority of their time is particularly unique, as it is relatively shallow (~80 m) in comparison to the deeper habitats of other populations. Understanding the spatial ecology of these animals in northeastern New Zealand provides valuable insights into how this species responds to different environmental conditions which is important for predictions of future distributions.

The characteristics of an ecological system are scale dependent, with the scale of investigation determining the observable ecological processes and patterns (Wiens, 1989). Effective management and conservation action should integrate broad scale and fine scale knowledge to ensure a comprehensive understanding of species' ecology, allowing for the development of strategies which can address overarching global threats, as well as localised challenges (Chaplin-Kramer et al., 2021). In New Zealand, this research is still in its early stages with initial work on manta rays focused on broad-scale movements such as migration paths, patterns of seasonal occurrence, and long-term drivers of habitat suitability (M. Erdmann., unpub; Ozaki, 2023). My thesis is the first to investigate the fine-scale movements, examining associated behaviours, and localised environmental drivers of movements in the Gulf—a core habitat for oceanic manta rays in New Zealand waters, and in adjacent areas along the northeastern coast of the North Island (L. Green, MWANZ, pers. comm).

In Chapter 2, tracks obtained from satellite tags revealed wide variation in the movements of seven oceanic manta rays along the northeastern coast from Mayor Island in the Bay of Plenty, up to Te Tai Tokerau Northland (Figure 2.3a). Near-surface foraging behaviours were strongly correlated to water clarity, with manta rays exhibiting a preference for clearer waters during the day and more turbid areas at night. I suggest that this adaptive behaviour may be linked to increased visibility in clearer waters, which facilitates visual predation. However, at night, when visual cues are less important, manta rays may select for areas with higher productivity. Manta rays foraged throughout their range in New Zealand, with a particular hotspot noted in the Cradock Channel—a potentially important foraging site which could additionally serve as a cleaning station.

Chapter 3 focused on the vertical movements of manta rays in the Gulf region, to investigate their behaviours throughout the water column. Here, I found high occupation of the surface waters (< 5 metres), with occasional deeper dives occurring throughout the day, but which were more frequent at night. During periods of decreased moonlight illumination, manta rays were more likely to remain in shallower waters at night. Additionally, during the day, dives of PTT# 238016 were shallower and shorter around dusk and dawn, as well as during midday. Water temperatures experienced in New Zealand during the summer to early autumn period did not appear to constrain dives. Dives likely represent a combination of foraging, travelling and navigational functions. While the Gulf appears to be too shallow to support vertical migrations of nocturnal prey as seen in deeper water, I suggest that deeper dives at night could be targeting emerging demersal zooplankton.

4.2 The environment influences life

Life is inextricably linked to the environment. Every aspect of an organisms' existence, from physiological processes to its movements, is shaped by interactions with, and responses to its surroundings. As seen in my study, environmental conditions such as water clarity, tides, and light availability can influence both horizontal and vertical movements, driving behaviours, with ultimate consequences for fitness and survival of these animals. With climate change continuing to affect the marine environment, it is important to understand how animals respond to environmental variables to predict how their movement patterns and behaviours may be affected in the future.

Prior to 2022, the presence of oceanic manta rays in the Gulf was gathered from photo records and satellite tracking. This informed the development of my research project, and it was anticipated that manta rays would remain in the Gulf over the summer-autumn months with tags deployed in January 2023 programmed to detach in early March allowing the research team to retrieve the archival SPLASH10F tags. The intention was that the tags would detach while the manta rays were still in or near the Gulf, so that the high-resolution archival data could be recovered. However, in early 2023 tagged manta rays travelled north sooner than expected, suspected to be a response to two closely timed severe weather events associated with a strong La Niña. On January 27th 2023, a highly localised convective weather system delivered unprecedented rainfall in northeastern New Zealand, with many areas experiencing rainfall anomalies of over 500% (Macara, 2023; NIWA, 2023). Not long after this event, between February 13th–14th tropical cyclone Gabrielle passed just offshore, once again bringing extreme rainfall, winds, and storm surges to the Northland, Auckland, Waikato, and Bay of Plenty regions (Noll, 2023). The occurrence of this cyclone over Aotea was likely linked to the deeper vertical distribution exhibited by one tagged manta ray which was in the area. Heavy rain events and storm events exacerbate terrestrial sedimentation input and resuspend benthic sediments, increasing local water turbidity (Boxberg et al., 2020; Zweifler et al., 2021). Chapter 2 indicated that during the day, manta rays exhibited a preference for increased water clarity. Therefore, movements north and offshore may indicate an avoidance strategy away from waters with high concentrations suspended sediment. Typically, environmental conditions in the Gulf are relatively stable during periods of manta ray occurrence. These sudden and extreme weather phenomena likely disrupted the typical environmental stability of the region, and we suggest that this may have prompted the manta rays to commence their northern migration early. Manta rays could have a preference for stable environmental conditions which may also lead to reliable aggregations of zooplankton prey patches, driving the seasonal presence of manta rays. Globally, aggregations of oceanic manta rays can be highly predictable in upwelling areas with consistent or seasonal biological productivity (Stewart et al., 2016a; Stewart et al., 2016b; Harty et al., 2022). Given current global warming trends, it is projected that we will see an increase in the frequency and intensity of storm events, including tropical and extratropical cyclones (Lee et al., 2023). Warming temperatures have been linked to shifts in the distribution of other zooplankton foragers within the Gulf, such as Bryde’s whales (Colbert, 2019). Shifts in the distribution of manta rays has unknown ecosystem consequences not only for New Zealand, but also for those regions which they travel to overwinter.

4.3 The ‘missing link’

Throughout this study, I focus on how environmental conditions influence the movement and foraging behaviours of manta rays. Central to many of these discussions are the inferences made regarding how the environment shapes the distribution and abundances of zooplankton communities, and subsequently, how these influences are reflected in manta rays. However, there is a lack of data to corroborate this—a common ‘missing link’ in marine ecological studies and valuable when included (e.g. Stephenson et al., 2023). Research tends to focus on predators rather than prey. As filter feeders, it is highly likely that including prey dynamics will produce better predictions of foraging behaviours and of both horizontal and vertical movement patterns. However, it can be difficult to gather data on prey species. In the Gulf there have only been a few studies to look at the composition and general distributions of zooplankton, and these have not looked at how the environment influences zooplankton population dynamics (Zeldis & Willis, 2015; Carroll et al., 2019). Additionally, we still do not know the preferred prey for manta rays in New Zealand. Stable isotope and fatty acid analyses are non-lethal methods which have had success in elucidating their diet in other populations (Burgess et al., 2016; Stewart et al., 2017; Burgess et al., 2018). Simpler methods could even involve the collecting of *in-situ* zooplankton samples during field surveys to identify potential prey (Armstrong et al., 2016; Armstrong et al., 2021). In Guam, video recordings have been successful in documenting reef manta rays targeting the gamete clouds of spawning fish (Hartup et al., 2013). Manta rays require very high food intakes in order to meet energetic requirements (Rohner et al., 2017). In other areas, diets need to be supplemented with mesopelagic food sources. While foraging in northeastern New Zealand appears to mainly target surface zooplankton, if zooplankton communities change it is possible we will see oceanic manta rays rely more on mesopelagic food sources found out deeper. This may result in greater overlap with spinetail devil rays, which current inhabit deeper waters to 200 metres depth (Ozaki, 2023).

To date, the only species confirmed as prey for oceanic manta rays in New Zealand is *N. australis* (L. Green, MWANZ, pers. comm.). *N. australis* are highly sensitive to environmental change, particularly warming sea surface temperatures, which are associated with declining food availability and lifetime egg production numbers (Lagos, 2022). Additionally, *N. australis* quickly depletes its energy reserves to maintain metabolic activity when exposed to warmer and lighter conditions (Lagos, 2022). With projected warming trends, this may have significant implications for *N. australis* populations, and consequently for predators which target this species. More research is needed to determine whether oceanic manta rays display much diet plasticity in New Zealand, and whether they are targeting and other species, to predict how they might be affected if N. *australis* populations do decline or shift to cooler regions.

It is important to know what species manta rays are feeding on so that we can predict how potential prey may be impacted by changing environmental conditions, as demonstrated for Bryde's whales in the Gulf (Colbert, 2019). In the Gulf, prey availability is a strong year-round predictor for the distribution of several shark and cetacean species, so this may also hold true for oceanic manta rays (Stephenson et al., 2023). Incorporation of prey availability has also been successful in informing habitat suitability modelling of basking sharks throughout the wider New Zealand exclusive economic zone (EEZ) (Finucci et al., 2021).

4.5 Connecting horizontal and vertical movements

Many marine animals move in three-dimensional space; individuals are moving simultaneously on the horizontal plane as well as the vertical plane. Despite this, most spatial ecology studies, including my thesis, tend to assess these movements separately in two-dimensions as they are typically recorded at different temporal resolutions. As I have detailed, horizontal movements are typically assessed using state-space models, where areas of low move persistence are assumed to represent foraging behaviours and areas of high move persistence are assumed to represent transiting behaviours. Similarly, vertical studies often aim to identify behavioural modes from dive profiles, or by using modelling such as multi-state hidden Markov models which characterise behavioural states and transitions between subsequent states based on dive metrics (Quick et al., 2017; Van Beest et al., 2019; Grainger et al., 2022). It is expected that there should be overlap in the spatiotemporal occurrence of foraging behaviours between horizontal and vertical movements. While this has been confirmed for some species of turtles and pinnipeds (Jonsen et al., 2007; Ramasco et al., 2015; Planque et al., 2020), interpretations of the horizontal movements of animals does not necessarily align with vertical behaviours (Bestley et al., 2015; Andrzejaczek et al., 2019). Riaz et al. (2021) demonstrated a disconnect between the putative foraging hotspots of Adélie penguins (*Pygoscelis* adeliae) identified from horizontal studies, and vertical foraging effort. They found that dive activity was more pronounced during periods of high move persistence, which is generally considered to inficate transitory behaviours. Incorporation of vertical depth components can also benefit inferences of behavioural modes. In white sharks three substates were identified within ARS behaviours—ARS-Shallow, ARS-Midrange, and ARS-Deep, facilitating more accurate behavioural analyses (Aquino-Baleytó et al., 2021).

Integrating horizontal and vertical movements can provide additional information for assessing drivers of behaviour. In Chapter 3 I discussed how some dives were likely performed close to, or at the seabed based on the bathymetry of the area. By integrating horizontal movements with dive activity, or the use of short-term high resolution archival tags it would be possible to accurately match dive depth to the sea floor depth. Therefore, we could determine the proximity to the sea floor, which may be indicative of bottom feeding (Stevens, 2016) or for navigation as has been described in other elasmobranchs (Keller et al., 2021; Braun et al., 2022). Additionally, this would enable the identification of geographic hotspots in diving activity, which could reveal important subsurface areas for manta rays such as cleaning stations or deep reefs which should be considered for protection.

4.6 Other behaviours

In this study we have primarily focused on the foraging and transiting behaviours of oceanic manta rays, due to the ability to discern these from two-dimensional movement patterns. However, oceanic manta rays have been documented to engage in a range of behaviours not investigated in this thesis. Opportunistic sightings have confirmed that courtship behaviours occur in New Zealand (L. Green, MWANZ, pers. comm.). While these observations were from surface behaviours, midwater courtship is more commonly documented for reef manta rays (Stevens et al., 2018b). The mating process of manta rays involved seven distinct stages (1) initiation, (2) endurance, (3) evasion, (4) precopulatory positioning, (5) copulation, (6) post-copulatory holding, and (7) separation. During this process, females have observed to engage in high speed, evasive flips, turns, and somersaults which are mimicked by male followers (Deakos et al., 2011; Stevens et al., 2018b).

Throughout this thesis I briefly mentioned the potential for cleaning stations in New Zealand—stable areas which are commonly associated with seamounts and rocky reefs where manta rays aggregate to be cleaned by small cleaner fishes feeding harmful ectoparasites and dead or diseased tissue (O'Shea et al., 2010; Barr & Abelson, 2019). While these are important habitats for other manta ray populations (O'Shea et al., 2010; Ashe, 2016; Barr & Abelson, 2019; Thibaut, 2022), it is possible that they are not necessary during temporary visitations to more temperate New Zealand waters in which species richness and rates of parasite accumulation are decreased compared to lower-latitudes (Torchin et al., 2002). Oceanic manta rays in New Zealand are also frequently sighted is association with remoras (L. Green, MWANZ pers obs). Remoras (*Remora* spp.) will often form close long-term associations with manta rays, feeding on ectoparasites for a range of benefits such as protection (Nicholson-Jack et al., 2021). The presence of cleaning stations have been confirmed in the temperate Azores, which are close to the northern limits for oceanic manta ray distributions (Narvaez et al., 2015). When visiting cleaning stations, manta rays will tend to hover above reefs while being cleaned (Germanov et al., 2019).

These additional behaviours, characterised by either high tortuosity during courtship, or minimal movement during resting or cleaning behaviours would likely have been categorised as ARS behaviours based on the methods of this study. Camera tags would enable the observation of these behaviours if they do New Zealand waters, providing a better understanding of how manta rays utilise their time in New Zealand.

4.7 Future research directions and concluding remarks

In New Zealand, oceanic manta rays are classified as data deficient, requiring more baseline information for a formal threat analysis (Duffy et al., 2018). This lack of data not only hampers conservation and management actions, but also means that conservation efforts may focus more on species which have been classified as endangered. My research is part of a larger project led by Manta Watch New Zealand which also includes a description of the species' population dynamics. While my thesis provides some baseline data for future research, I recognise that the work is limited by a small sample size making it difficult to make population level inferences. To address this limitation, future efforts should aim to deploy more satellite tags, targeting a diverse demographic range including males, females, pregnant animals, and individuals of different ages. Often behavioural patterns will vary between these groups (Bansemer & Bennett, 2009; Ferreira et al., 2018; Axworthy et al., 2019; Perryman et al., 2022). It is therefore important to understand these differences so environmental management actions can adequately protect all individuals within the population, throughout their lifetimes. Additionally, tags should be deployed over a broad temporal scale, including early summer, around November and December when the manta rays first begin to arrive in the Gulf. Deployments should cover various climatic conditions, such as El Niño events which were not covered in this thesis. Climatic variations can significantly influence the behaviour and movements of manta rays (Beale et al., 2019; Setyawan et al., 2022; Cabral et al., 2023), and so studying them across these different conditions can provide valuable insights into adaptive strategies, and further inform predictions on how the manta rays will respond to future environmental change. To ground truth inferences made on behaviours , researchers should deploy high resolution data tags and/or camera tags to collect short-term information about subsurface behaviours (Parrish et al., 2000; Rudd et al., 2021; Ryan et al., 2022).

In New Zealand, manta rays are protected under the Wildlife Act 1953; it is illegal to hunt, kill or harm manta rays within the New Zealand EEZ. To date, there has been one confirmed interaction between oceanic manta rays and fisheries in New Zealand, where in January 2021, one individual became entangled with the hook from a surface longline fisheries which was targeting swordfish (*Xiphias gladius*) over deep water (> 1000 metres) between the eastern Coromandel Peninsula and Bay of Plenty region (Finucci et al., 2022). This report indicates that overlap between fisheries operations and manta rays does occur in New Zealand, and given the conservative life history of manta rays and therefore low resilience to fishing pressures it is crucial to have a better understanding of the spatial distribution of this species and how distribution might change in the future in order to manage for and mitigate further fisheries interactions (Marshall et al., 2022b).

It is equally important to study what prey species manta rays are feeding on, so that we can understand how these species will be influenced by environmental variables, and subsequently how this will impact manta ray distributions. Establishing baseline information on prey composition and abundance will also enable ongoing monitoring to detect any shifts or changes in prey preferences over time. Such shifts can provide valuable insights into broader ecosystem changes and dynamics. For instance, between 2011 to 2020 Bryde's whales in the Gulf shifted from a primarily fish-based to predominantly zooplankton-based, likely reflecting to changes to prey availability in the region (Gostischa et al., 2021). By tracking such shifts in prey preferences over time, we can better understand the underlying drivers and implications for manta ray populations and their habitats, and this will also provide an inference as to the overall health of the ecosystem.

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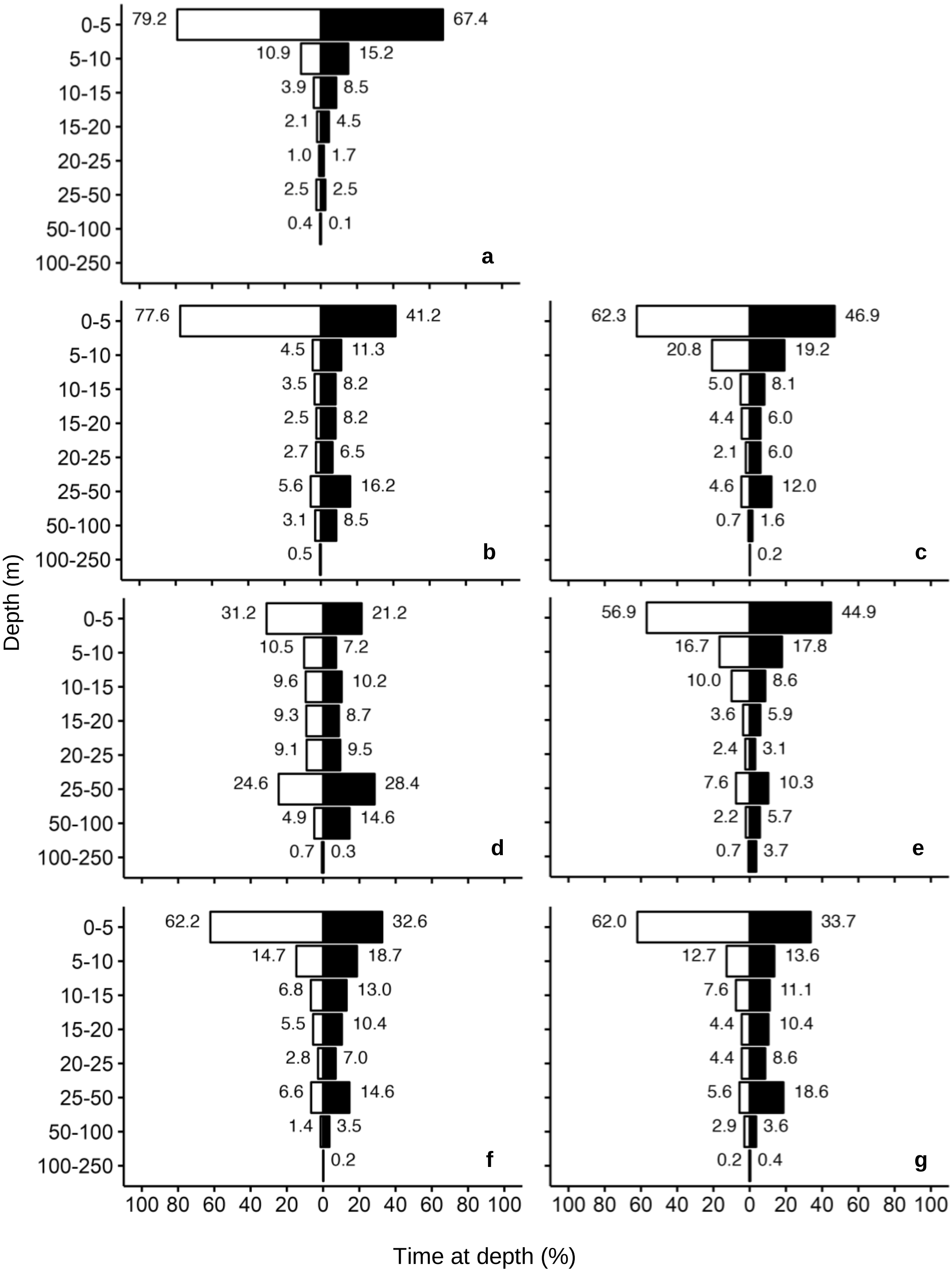
Appendices

Appendix 1 Oceanic manta rays tagged with SPLASH tags in New Zealand. Bolded entries indicate individuals with sufficient movement data in the study area to be selected for analysis. Tag duration indicates the time from deployment to release. * Indicates pregnant manta rays.

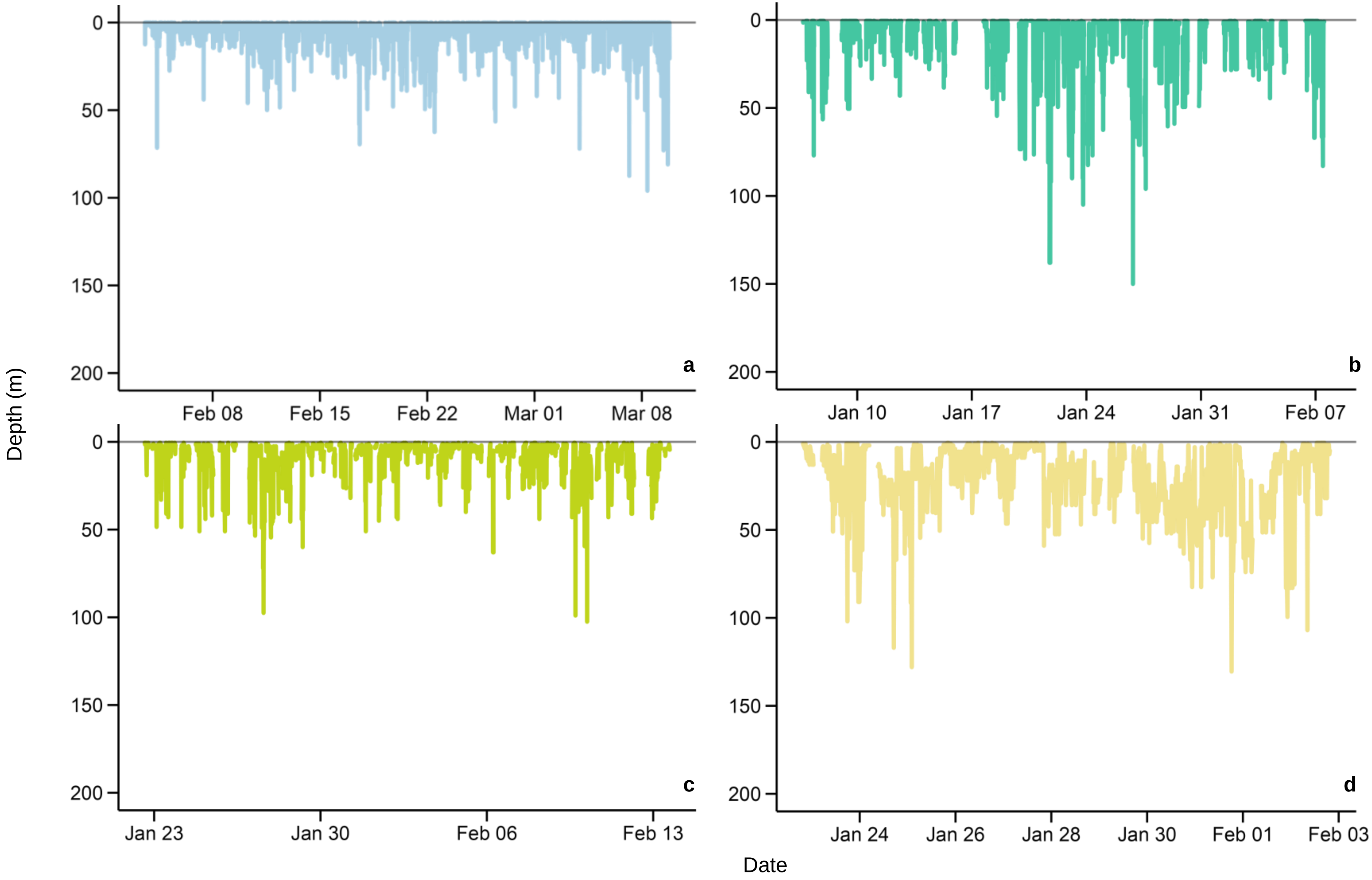
			Tag Deployment					
Tag type	PTT Number	Manta ID	Date / Time	Latitude. ºS	Longitude. ºE	Release date	Tag duration	Total Fast-GPS locs
SPLASH10F-321A	177766	Scott	05 Mar 2019 17:45	-35.013056	174.029167	17 Mar 2019 05:00	11d 11h 15m	11
SPLASH10F-321A	177767	Emmy	06 Mar 2019 17:50	-35.086944	173.948889	13 May 2019 19:00	68d 1h 10m	30
SPLASH10F-321A	177768	2019	20 Feb 2021 14:40	-36.320556	175.265556	16 Apr 2021 11:00	54d 20h 20m	33
SPLASH10F-321A	177769	Kathlyn (NZ-MB-0077)	20 Feb 2022 14:06	-35.993056	174.919167			4
SPLASH10F-321A	**197235**	**Camille (NZ-MB-0023)**	**03 Feb 2021 13:58**	**-36.305833**	**175.191111**	**11 Mar 2021 18:15**	**36d 4h 17m**	**40**
SPLASH10F-321A	197236	Baz	03 Feb 2021 16:52	-36.171111	175.242778	09 Mar 2021 23:00	34d 6h 8m	16
SPLASH10F-321A	197237	Charlotte/Vilkin (NZ-MB-0027)	03 Feb 2021 18:52	-36.1625	175.233611			0
SPLASH10F-321A	201382	Daniel Roozen/Harry (NZ-MB-0039)	21 Feb 2021 17:12	-36.04915	175.05563	28 Mar 2021 22:00	35d 4h 48m	7

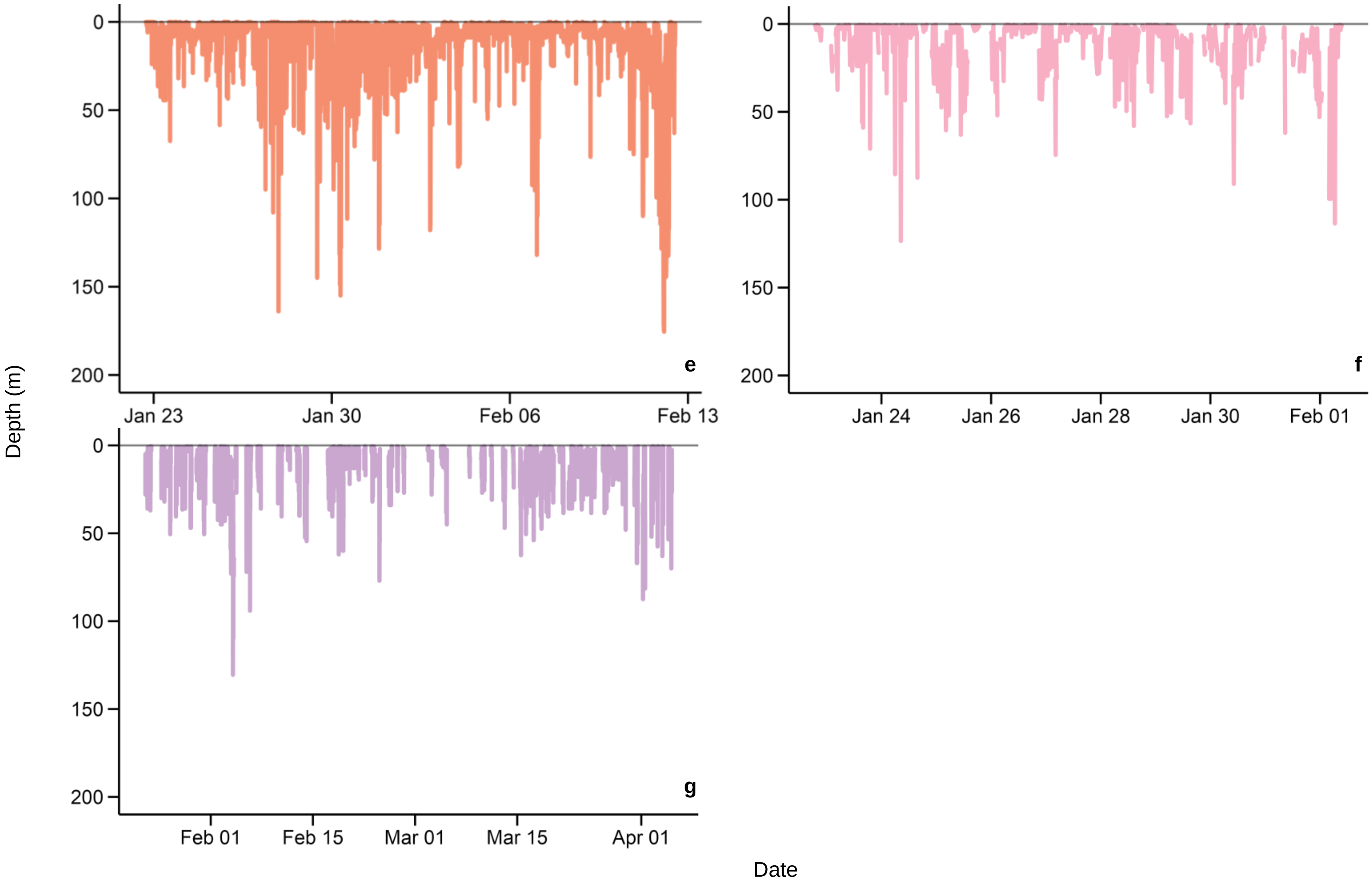
SPLASH10F-321A	**204511**	**Nate (NZ-MB-0055)**	**10 Jan 2022 17:15**	**-36.0315**	**175.12769**	**03 Apr 2022 16:00**	**82d 22h 45m**	**215**
SPLASH10F-321E	215016	Kat (NZ-MB-0065)	17 Feb 2022 16:27	-36.078611	174.926944	19 May 2022 03:00	90d 10h 33m	145
SPLASH10F-321E	226828	Myra (NZ-MB-0066)	17 Feb 2022 16:42	-36.128333	174.885278	11 May 2022 03:00	82d 10h 18m	40
SPLASH10F-321E	235905	Live Ocean	23 Feb 2023 19:00	-36.06929	175.10691			5
SPLASH10F-321E	**238014***	**Pukukino (NZ-MB-0109)**	**22 Jan 2023 14:30**	**-36.365556**	**174.888889**	**04 Mar 2023 07:00**	**41d 16h 30m**	**130**
SPLASH10F-321E	**238015**	**Kawa (NZ-MB-0114)**	**22 Jan 2023 19:40**	**-36.500556**	**175.508333**	**26 Feb 2023 04:00**	**34d 8h 20m**	**49**
SPLASH10F-321E	**238016**	**Motairehe (NZ-MB-0110)**	**22 Jan 2023 17:05**	**-36.369167**	**175.181667**	**13 Feb 2023 12:00**	**21d 18h 55m**	**116**
SPLASH10F-321E	**238018***	**Anna (NZ-MB-0111)**	**22 Jan 2023 18:40**	**-36.316389**	**175.508333**	**04 Mar 2023 07:00**	**40d 12h 20m**	**104**
SPLASH10F-321E	**238019**	**Rehua (NZ-MB-0113)**	**22 Jan 2023 19:00**	**-36.385833**	**175.488333**	**09 Apr 2023 20:00**	**77d 1h**	**111**

Appendix 2 Individual proportion of time at depth for seven tagged oceanic manta rays in northeastern New Zealand.(a) PTT# 197235 (b) PTT# 204511 (c) PTT# 238014 (d) PTT# 238015 (e) PTT# 238016 (f) PTT# 238018 (g) PTT# 238019. White bars indicate vertical habitat use during the day while black bars indicate vertical habitat use during the night. Analysis for figure calculates percentage based on the total recorded movements, excluding periods where data was not transmitted.



Appendix 3 Time series of tagged oceanic manta rays (a) PTT# 197235 (b) PTT# 204511 (c) PTT# 238014 (d) PTT# 238015 (e) PTT# 238016 (f) PTT# 238018 (g) PTT#238019




Depth (m)
0
50
100
150
200
e
Jan 23
Jan 30
Feb 06
Feb 13
0
50
100
150
200
f
Jan 24
Jan 26
Jan 28
Jan 30
Feb 01
0
50
100
150
200
g
Feb 01
Feb 15
Mar 01
Mar 15
Apr 01
Date