# Movement Ecology, Population Dynamics, and Conservation of Reef Manta Rays (*Mobula alfredi*) in Raja Ampat, Indonesia

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# Abstract

Understanding the population dynamics, movement patterns, and habitat use of animals is critical to evaluate the effectiveness of management measures. However, investigating wide-ranging and highly migratory marine species is challenging. The global populations of reef manta ray *Mobula alfredi* have declined substantially primarily due to increased fishing pressures.

This thesis aimed to understand the population demographics, abundance, movement patterns, and conservation of reef manta rays in Raja Ampat, Indonesia. In brief, manta ray sightings between 2009 and 2019 from two marine protected areas (MPAs) in Raja Ampat: Dampier Strait and South East Misool were analysed using mark recapture modelling to investigate changes in demographic parameters. Management measures implemented in the region were reviewed to assess their potential impact on the manta ray populations. Drones were used to develop a novel method to measure the body size of reef manta rays, and to examine their maturity stage and other biological characteristics. I analysed telemetry data from five satellite and nine acoustic tags to understand residency patterns and habitat use of juvenile reef manta rays in the Wayag lagoon nursery. Finally, 114 acoustic tags and 11 satellite tags were examined using network analysis to explore whether reef manta rays form a metapopulation.

Reef manta ray populations in both MPAs demonstrated substantial increases over a decade of study, highlighting the efficacy of long-term implementation of management measures (primarily critical habitat protection and fisheries regulations) combined with the influence of the El Niño–Southern Oscillation. Reef manta rays measured from a drone provided accurate measurements, revealing clear evidence of sexual dimorphism between mature individuals; females were larger than males. Females started to mature at 324 cm disc width (DW) and males at 275 cm DW. Satellite tracked juveniles revealed limited home range sizes in Wayag lagoon, and acoustic tracked individuals demonstrated strong residency patterns and nearly continuous use of the lagoon, providing evidence to confirm Wayag lagoon as a nursery. Conversely, larger tagged individuals in Raja Ampat demonstrated wider home ranges and extended movements around the region. A network analysis based on passive acoustic tracking provided evidence supporting the likelihood that reef manta rays form a metapopulation.

While the global populations of reef manta rays show either declining trends or some stability, the reef manta rays in Raja Ampat have increased in abundance. This highlights that conserving large, long-lived, and highly migratory species is possible. My thesis has substantially improved our understanding of the differences in habitat use between reef manta rays based on their life stages. Juveniles use nursery areas, like in Wayag lagoon, for extended periods to improve survival in the early stages of their life. Furthermore, I have revealed three spatially discrete subpopulations that mostly likely form a metapopulation throughout Raja Ampat. I have also demonstrated the ability of small drones to collect accurate measurements of the body size of reef manta rays with limited or no impact on the animals. Future research should focus on other regions of importance to manta rays to ensure their conservation throughout Indonesia.

Dedicated to my mom, who used to pray for my successes,

but sadly, she passed away right before I started my PhD

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# Contents

# List of Figures

# List of Tables

# Chapter 1.

# General introduction

## 1.1. Movement ecology

The Earth provides abundant resources for millions of organisms that live on it. Animals living on land, freshwater or the ocean, are scattered discontinuously throughout many unique habitats. They move through often dynamic environments to secure resources critical to life functions (i.e., food, mates, shelter) that enable individuals to survive and thrive (Avgar et al., 2014). To survive, animals must be able to find sufficient resources (Kubelka et al., 2022) when distribution is typically affected by the heterogeneity of the environment at different spatial and temporal scales. The spatiotemporal distribution of resources along with other factors (e.g., seasonal presence and abundance of the resources, suitable habitats) are fundamental drivers of animal migration (Alerstam et al., 2003). Migration is associated with how animals adapt with the dynamics of these resources and consequently, it plays a major role in shaping the distribution and population dynamics (Johnson et al., 1992; Dingle & Drake, 2007). Alerstam et al. (2003) suggested a number of ecological and biogeographic drivers affecting migration, such as physical barriers, mortality, competition, body size, ability to navigate, and energetic costs.

Some species live in small and patchy habitats with little variability but sufficient essential resources supporting highly localised spatial distribution (Teitelbaum & Mueller, 2019). In contrast, there are species that migrate up to hundreds or thousands of kilometres away to fulfil several requirements to survive, for example humpback whales *Megaptera novaeangliae*, that migrate between tropical breeding grounds in Oceania and polar feeding grounds in the Southern Ocean (Riekkola et al., 2018) and Montagu's harrier *Circus pygargus* migrating between northern Europe in the summer and Sub-Saharan Africa in the winter (Trierweiler et al., 2014). There are also species with nomadic behaviours (Mueller & Fagan, 2008), where animals live in an environment with high variability, necessitating movements and disperse across large areas without seasonal patterns (e.g., Mongolian gazelles *Procapra gutturosa*, Arctic foxes *Vulpes lagopus*) (Mueller et al., 2008; Gravel et al., 2023).

No matter the scale, movement is one of fundamental features of most animals' lives, therefore, understanding how animals move in space and time is key topic in animal movement ecology. Nathan et al. (2008) introduced movement ecology as a paradigm for studying all aspects of animal movement, consisting of a) internal factors, describing animals' motivation to move, b) capacities to move and navigate, c) external factors, describing environmental conditions driving the movements, and d) the resulting spatiotemporal patterns of the movements. Studying the movement ecology of animals involves investigating resource selection, habitat use, distribution and dispersal of animals, as well as the dynamics of environmental drivers influencing animal movement. This is a complex field of research which has been made a little easier in recent years due to a range of emerging tools and technologies that can track the movements of both terrestrial and aquatic animals through their environment (Hussey et al., 2015; Kays et al., 2015; Lennox et al., 2017; Hellström et al., 2022).

## 1.2. Tracking technology informing movement ecology

The advancement of tracking technologies (i.e., integration of various sensors on the tags) and substantially large amount of movement data have been collected (Nathan et al., 2022), the use of "big data" approach could significantly improve our understanding of animal movement ecology and underlying processes that may not be able to be detected previously (Rodríguez et al., 2017; Grémillet et al., 2022; Nathan et al., 2022). Researchers have use electronic tags to track animals in both terrestrial and aquatic habitats using various technologies, such radio tracking, satellite tracking via Argos and Global Positioning Systems (GPS), and acoustic telemetry (Hussey et al., 2015; Kays et al., 2015; Lennox et al., 2017; Stewart et al., 2019; Matley et al., 2022; Moses et al., 2022). Furthermore, researchers have integrated several other sensors, such as accelerometer and animal borne cameras (Moll et al., 2007; Brown et al., 2013).

## 1.3. Population demography and dynamics

Understanding the population demographics (i.e., breeding success, survival rate, growth) of long-lived animals is challenging given long-term ecological and evolutionary processes (Clutton-Brock & Sheldon, 2010). In the ocean, it is even more difficult to study the demographics of large long-lived animals given a number of challenges, such as accessibility for animals that spend all or most of their time submerged, those that frequent the ocean depths, and/or migrate or move long distances (Lascelles et al., 2014). There are often logistical and financial issues undertaking long-term research in the marine environment due to the inaccessibility of many species, with the exception of those that have a life-stage requiring them to be on land, usually to reproduce (e.g., sea turtles, pinnipeds, seabirds, and sea otters). To investigate basic population dynamics such as births, deaths, immigration and emigration, researchers studying long-lived, wide-ranging animals typically require large datasets spanning multiple years. They also require an understanding of the environmental and ecological effects on these populations (Lindenmayer et al., 2012). Furthermore, Péron and Grémillet (2013) highlighted the importance of understanding the movements and distribution of these animals covering all age classes from juveniles to adults throughout their life histories. There are several large marine animals that vary in their dispersal patterns depending on age-class or reproductive status such as, wandering albatross *Diomedea exulans* (Weimerskirch et al., 2014), sperm whales *Physeter macrocephalus* (Lyrholm & Gyllensten, 1998), and some elasmobranchs (Phillips et al., 2021). This makes it challenging to ensure studies account for variation within and between sex and age-classes as well shifts in dispersal due to environmental changes (Niella et al., 2022; Pistorius et al., 2023).

For many years, researchers have used patterns of unique and/or permanent markings on individuals through photographic identification (photo-ID) to differentiate one individual from another. This technique has been commonly used to identify both terrestrial and aquatic animals, such as giraffes

(Lee et al., 2022), whales (Blount et al., 2022), sharks and rays (Marshall & Pierce, 2012), and sea turtles (Reisser et al., 2008). Genetic markers through DNA finger-printing and genomics are increasingly being used to identify individuals in a population but with the added benefit of determining the sex and relatedness of individuals (e.g., Ruzzante et al., 2019; Atkinson et al., 2021). These techniques are commonly used in mark-recapture population models to examine demographic parameters, such as population size and survival rate (Schwarz & Arnason, 1996). The emergence of new technologies, such as Unoccupied Aircraft Systems (often referred to as drones), passive acoustic monitoring and high-resolution satellite imagery are increasingly being refined for population distribution and abundance (Fretwell et al., 2014; Hodgson et al., 2018; McIntosh et al., 2018; Johnston, 2019; LaRue et al., 2021). Abundance estimates using distance sampling methods from aerial survey data is a well-established research approach (e.g., Buckland et al., 2005; Sollmann et al., 2016) but the potential that remotely sensed visual data can offer is changing the scales over which we can understand environmental factors affecting population dynamics (Elith & Leathwick, 2009; Putra et al., 2020; LaRue et al., 2021).

In the study of long-lived animals and their population dynamics, some of the key advantages of collecting long-term datasets include: 1) the ability to detect variation and changes affecting population processes, 2) demonstrating new insights into population dynamics, and 3) the potential to develop model systems allowing hypothesis testing using representative datasets (Reinke et al., 2019). Long-term telemetry studies on a variety of large marine animals in the Southern Ocean revealed areas of importance by species and season; information of value to managers developing marine protected areas (Hindell et al., 2020). Multiple years of satellite tracking revealed route fidelity during long-distance migration by some humpback whales, great white sharks *Carcharodon carcharias*, and northern elephant seals *Mirounga angustirostris* (Horton et al., 2017). Datasets consisting of a decade of tracking data combined with remote sensing revealed that long-term memory and resource tracking play an important role in the long-distance migration in blue whales *Balaenoptera musculus* and southern elephant seals *Mirounga leonina* (Rodríguez et al., 2017; Abrahms et al., 2021). Long-term studies inform our understanding of individual rates of growth to infer the age of unknown individuals, and the reproductive success of individuals and populations. This can be achieved by a variety of methods such as direct measurement often when the animal is captured for tagging (Casey & Natanson, 1992; Kessel et al., 2017), comparison to known size objects such as a person or vessel (Marshall et al., 2011; Kashiwagi, 2014; Burnett et al., 2019), paired-laser photogrammetry (Deakos, 2010), stereo-video system (Harvey et al., 2002), or aerial photogrammetry (Bierlich et al., 2021). Many of the aging techniques require dead animals (e.g., fish otoliths, Campana, 2005) or tooth extraction from living or dead animals (e.g., dolphins, Atkinson et al., 2021) but increasingly techniques such as epigenetics or telomeres (Haussmann & Vleck, 2002; Parrott & Bertucci, 2019) are being used to age living animals, and the development of these approaches were informed by long-term field data. It is important in demographic studies of long-lived species to know the reproductive age and reproductive success as this is key to population viability, especially with many of these species over-represented in endangered species lists.

## 1.4. Manta ray ecology

Manta rays, which belong to Mobulidae family and *Mobula* genus (White et al., 2017), consist of two species: the oceanic manta ray *M. birostris* and reef manta ray *M. alfredi*. They can be found circumglobally in tropical, subtropical, and temperate waters (Figure 1.1) (Marshall et al., 2020; Marshall et al., 2022). The distribution of reef manta rays, however, is limited to only in the Indo-Pacific regions. There have not been any verified or published records to date on the presence of this species in the Atlantic Ocean, including regions in the east side of American continent. Recently, Arauz et al. (2019) reported a sighting of reef manta rays in Cocos Islands, Costa Rica, confirming the easternmost sighting in the Pacific Ocean and west side of American continent.

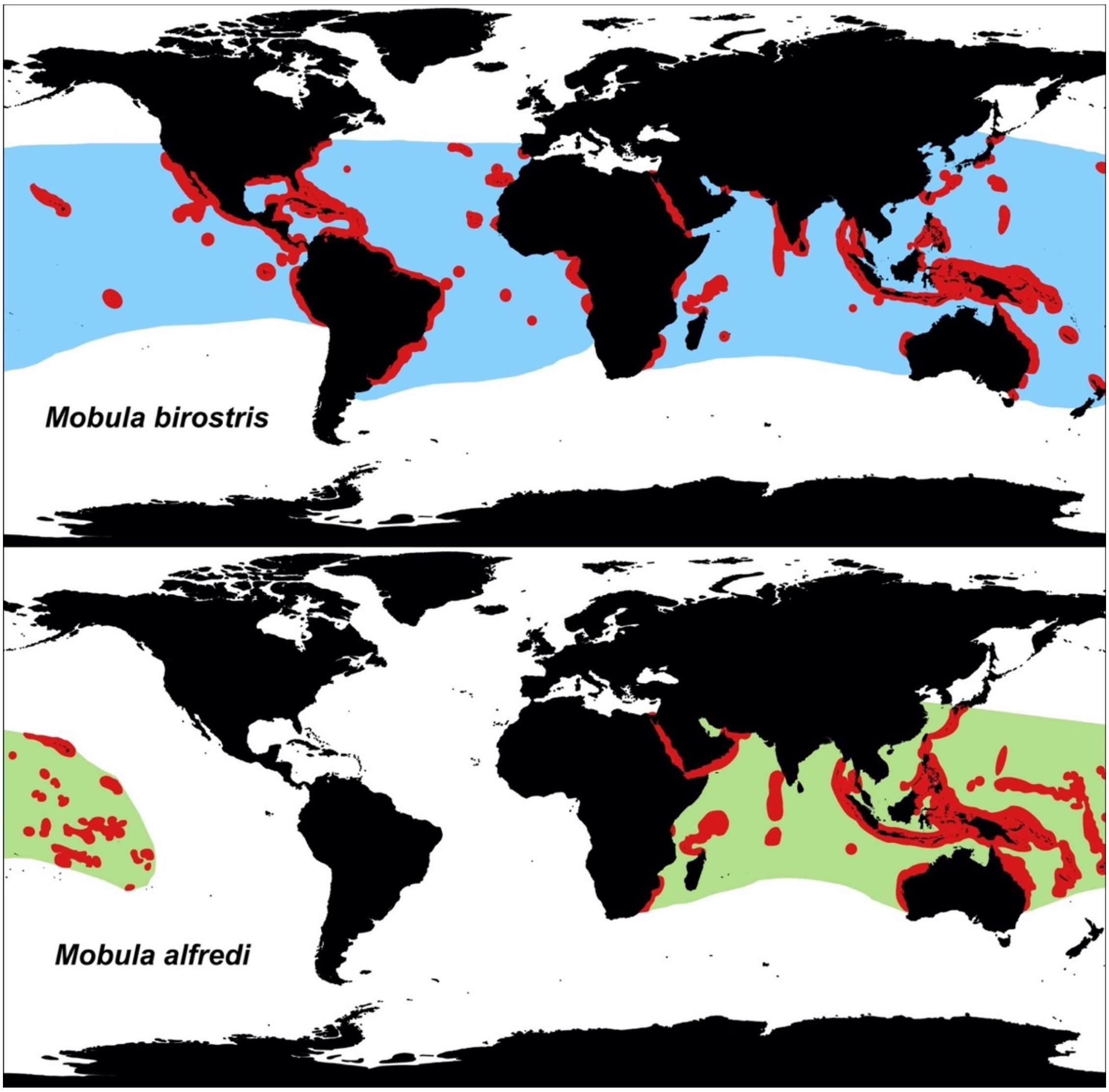

Figure 1.1. Global distribution of oceanic (top) and reef (bottom) manta rays. Red polygons represent areas where the species are extant, while the blue and green polygons represent areas the species are possibly extant. Modified from the IUCN.

Both manta ray species live in pelagic habitats with the oceanic manta ray is larger in body size and generally spends more time in the open ocean, while the reef manta ray is smaller and tends to inhabit more coastal waters, showing limited home range of local movements (Couturier et al., 2012). While showing larger home ranges than reef manta rays, the oceanic manta rays from three regions in the Indo-Pacific appeared to display restricted and no long-range movements (Stewart et al., 2016a). Both reef and oceanic manta rays are able to travel long distances up to 1,150 km and 1,500 km, respectively (Hearn et al., 2014; Armstrong et al., 2019).

Manta rays are filter feeders that feed mainly on zooplankton, krill, and small fishes by applying various feeding strategies such as surface feeding, cyclone feeding, somersault feeding, and bottom feeding (Couturier et al., 2012; Stevens, 2016; Stevens et al., 2018a; Gordon & Vierus, 2022). They will forage in a range of habitats, in channels, nearshore, and offshore waters and will move in response to environmental shifts in prey availability (Jaine et al., 2012; Weeks et al., 2015; Armstrong et al., 2016; Harris et al., 2021). Reef manta rays are usually solitary (Stevens, 2016), however, the attraction to prey means manta rays aggregate in the same area with tens to over one hundred animals often seen foraging in areas of productivity (Couturier et al., 2011; Stevens, 2016; Setyawan et al., 2020). As observed in most filter-feeding megafauna foraging on zooplankton (e.g., whale sharks *Rhincodon typus*, baleen whales), there is no evidence whether the feeding strategy in a large group indicates true cooperatively foraging or coordinated movements to avoid collisions between manta rays (Armstrong et al., 2021b).

Around the globe, both species of manta ray can occur within the same geographical regions either in microparapatry (both species were recorded within 2-100 km, but not at the same site) or microsympatry (co-occurrence was observed at the same dive sites) (Kashiwagi et al., 2011). They commonly frequent cleaning stations on shallow reef habitats to allow cleaner fish to clean their bodies from parasites (Homma, 1997). This behaviour occurs throughout their range and these sites are persistent over time with manta rays visiting them throughout their lives. Only few places where microsympatry was observed at cleaning stations, such as in the Hawaii, Mozambique, Marquesas Islands, Raja Ampat, and Philippines (Kashiwagi et al., 2011; Mourier, 2012; Carpentier et al., 2019; Setyawan et al., 2020; Rambahiniarison et al., 2022). Visiting cleaning stations can also provide other benefits, such as the opportunity for social interaction with other individuals (Stevens, 2016; Perryman et al., 2019). Courtship behaviours are also commonly observed at cleaning stations (Stevens et al., 2018b). Visiting cleaning stations, which are located in warmer shallow habitats, could help with metabolic and physiological processes, such as digestion, and especially gestation for females (Stevens, 2016). Habitat uses at cleaning stations by individual manta rays varied between sex, size, maturity stage. Female reef manta rays, especially adults, are more frequently sighted at cleaning sites and demonstrate a higher fidelity to these sites than males (Couturier et al., 2014; Stevens, 2016). Furthermore, Stevens (2016) found that at cleaning stations, adults were more frequently sighted than juveniles, and among juveniles, larger individuals were more likely to visit cleaning stations that smaller juvenile individuals.

In some regions, adult and young manta rays (e.g., newborns and juveniles) manta rays are often observed occupying separate habitats although individuals at different stages of maturity are observed at aggregation sites (e.g., cleaning stations, feeding sites) with different proportions of juveniles and adults (Stevens, 2016). Juvenile manta rays are more likely to occupy shallow and sheltered nursery areas during the early stage of their lives (Stewart et al., 2018b; Setyawan et al., 2020). Despite there is no evidence of females giving birth in nurseries, it is suggestive that females giving birth in nursery areas. For new-born and juvenile manta rays and other elasmobranch species, living in nurseries presumably provides protection from predation threats, easy access to sufficient resource (e.g., prey and cleaning stations), and social interactions and learning opportunities with conspecifics (e.g., on optimising feeding strategies) (Heupel et al., 2019). These places are rarely found and globally, there are few places that have been proposed as manta ray nurseries, such as those in Flower Garden Banks National Marine Sanctuary and southeastern Florida, United States of America (Childs, 2001; Stewart et al., 2018b; Pate & Marshall, 2020), the Maldives (Kitchen-Wheeler et al., 2011; Stevens, 2016), and Palmyra Atoll in central Pacific Ocean (McCauley et al., 2014).

### 1.4.1. Reef manta rays

The focus of my PhD research is on reef manta rays, which was designated as a unique species of oceanic manta ray in 2009 (Marshall et al., 2009). Several studies on the demographics, dynamics, and distribution of this species have been undertaken in populations from across their geographical range throughout tropical and subtropical regions in the Indo-Pacific, including Mozambique (Marshall et al., 2011; Carpenter et al., 2022), the Seychelles (Peel et al., 2019b), the Red Sea (Knochel et al., 2022), the Maldives (Kitchen-Wheeler, 2010; Stevens, 2016), the Philippines (Rambahiniarison et al., 2022), Indonesia (Germanov et al., 2019; Setyawan et al., 2020; Germanov et al., 2022), Australia (Couturier et al., 2011; Couturier et al., 2014; Armstrong et al., 2020a), New Caledonia (Lassauce, 2021), Japan (Kashiwagi, 2014), Hawaii (Clark, 2010; Deakos et al., 2011; Axworthy et al., 2019), and French Polynesia (Carpentier et al., 2019) (Figure 1.1).

This species is estimated to grow up to 5.5 m in wingspan (also referred to as the disc width - DW) (Marshall et al., 2009) with adults typically between 3.0 and 3.6 m DW (Deakos, 2010; Stevens, 2016). It is estimated that reef manta rays can live up to at least 50 years old based on a sighting of an adult male in 1982 (Couturier et al., 2014; Marquez, 2022). Males reach sexual maturity at 8-10 years of age, while females reach sexual maturity at 13-17 years of age (Stevens, 2016). Reproductive periodicity varies between one and seven years with biennial pregnancies are commonly observed in Mozambique, Hawaii, and Raja Ampat, although few individuals were observed pregnant in consecutive years (Marshall & Bennett, 2010; Deakos, 2012) up to four pregnancies in five consecutive years (Setyawan et al., 2020). On the other hand, reef manta rays in Japan gave birth every 3.6-3.9 years and, in the Maldives, every 7.3 years on average (Kashiwagi, 2014; Stevens, 2016). Difference in reproductive periodicity is likely affected by prey abundance that influenced fecundity. The gestation period in both wild and captivity was approximately one year (Stevens, 2016; Murakumo et al., 2020). Size at birth varies from 154–192 cm in disc width (DW) based on observations in Churaumi aquarium (Okinawa, Japan) (Murakumo et al., 2020). In the wild, the size of new-borns was estimated to be between 130–170 cm DW (Marshall & Bennett, 2010; Kashiwagi, 2014; Stevens, 2016).

While reef manta rays are distributed widely across the Indo-Pacific, this species tends to be coastal and occupy relatively shallow habitats around atolls and small island groups (Couturier et al., 2014). This species typically feed on zooplankton (Couturier et al., 2013), but sometimes they also target and feed on fish spawn (Hartup et al., 2013). A large aggregation of reef manta rays is often seen at feeding sites and cleaning stations around shallow coral reefs, channels, and lagoons (Stevens, 2016), to which this species showed strong fidelity, a tendency to return to previously occupied sites after being away for certain periods (Switzer, 1993). At local level, reef manta rays showed seasonal movements to visit highly productive areas for foraging (Anderson et al., 2011a; Harris et al., 2020). Moreover, this highly philopatric species is able to move long distance from hundreds to over a thousand kilometre (Armstrong et al., 2019; Andrzejaczek et al., 2020; Peel et al., 2020).

There is an increasing number of movement ecology studies aimed at understanding residency, spatial movement patterns (horizontally and/or vertically), and drivers affecting the movement of reef manta rays. Studies using passive acoustic telemetry showed that reef manta ray populations in many regions showed similar patterns of strong residency and affinity to aggregation sites (e.g., cleaning stations and feeding sites) (Clark, 2010; McCauley et al., 2014; Couturier et al., 2018; Peel et al., 2019b; Andrzejaczek et al., 2020; Venables et al., 2020; Knochel et al., 2022). At the same time, they also demonstrated highly localised movements between aggregation sites situated within few kilometres and regional movements between sites separated between tens to hundreds of kilometres (Jaine et al., 2014; Braun et al., 2015; Knochel et al., 2022). The use of satellite telemetry also showed restricted movements and home ranges of reef manta rays, such as those in the Red Sea, Western Australia, and New Caledonia (Kessel et al., 2017; Armstrong et al., 2020b; Lassauce, 2021).

Vertically, a recent study by Andrzejaczek et al. (2022) assessing the diving behaviours of reef manta rays in the Indo-Pacific using satellite telemetry revealed that this species typically spent their time in shallow waters up to 50 m depth, although deep dives (>200 m) were often recorded, including one that up to 672 m deep in New Caledonia (Lassauce et al., 2020). Furthermore, diel patterns in the diving behaviours of reef manta rays varied between regions, which is likely associated site-specific variation in the vertical distribution of prey (Andrzejaczek et al., 2022). In the Chagos archipelago, reef manta rays dived deeper during the day than night (Andrzejaczek et al., 2020), while in the Seychelles, they dived deeper during the night than day (Peel et al., 2019b).

The residency and movement patterns of reef manta rays were affected by a range of temporal and environmental factors, such as time of day, sea surface temperature, chlorophyll-*a*, tidal phase, monsoon, and moon phase. The reef manta ray presence at aggregation sites (e.g., cleaning stations and feeding sites) mostly occurred during the day and this pattern is consistent throughout the regions. The frequency of acoustic detections of reef manta rays was generally the highest during the new moon when the tidal range reached the highest (Peel et al., 2019b; Andrzejaczek et al., 2020). Foraging activities at feeding aggregation sites is affected by tidal phase, which can occur during ebb tide (Jaine et al., 2012; Armstrong et al., 2016) or high tide (Peel et al., 2019b). At larger temporal scale, the presence of reef manta rays at aggregation sites throughout the year varied between regions (Anderson et al., 2011a; Jaine et al., 2012; Peel et al., 2019b; Andrzejaczek et al., 2020; Peel et al., 2020; Harris & Stevens, 2021; Knochel et al., 2022), which appears to be associated with monsoon, sea surface temperature, and availability of prey (Anderson et al., 2011a; Armstrong et al., 2016; Couturier et al., 2018; Harris et al., 2020).

### 1.4.2. Reef manta rays in Indonesia

A recent study using reef manta ray tissue samples collected in the three main study regions suggests that overall, there is a low level of genetic diversity in Indonesia (Phardana et al., 2022). Furthermore, there is evidence that populations from Nusa Penida, Komodo, and Raja Ampat belong to a single population with shared haplotypes. Despite being suggested as a single population, there is no evidence of individual exchanges between the Raja Ampat population and both populations in Komodo and Nusa Penida, between which movements of reef manta rays were recorded (Germanov & Marshall, 2014). In comparison with reef manta ray populations in other countries, Phardana et al. (2022) provides evidence that two samples from Ningaloo Reef, Australia were genetically closely related with the reef manta ray populations in Indonesia, although no matches from photo-ID have been reported between the two countries.

Reef manta rays can be found throughout Indonesian waters (Figure 1.2), with known primary habitats distributed throughout three regions: Nusa Penida (Germanov et al., 2019), Komodo (Germanov et al., 2022), and Raja Ampat (Setyawan et al., 2020). Another aggregation site has been observed in Derawan Islands (East Kalimantan), but no studies have been done in these regions. Occasional sightings have been reported from Weh and Banyak Islands (Aceh), Lombok and Gili Islands (West Nusa Tenggara), Sumba and Rote (East Nusa Tenggara), Takabonerate Islands (South Sulawesi), Wakatobi Islands (Southeast Sulawesi), Lembeh Strait (North Sulawesi), Guraici Islands (North Halmahera), Fakfak (Southwest Papua), and Cenderawasih Bay (West Papua). Despite these numerous reports, the lack of research effort throughout most Indonesian waters means we do not know whether there are other established populations, migrants or vagrants, outside of the three primary areas where research has been undertaken.

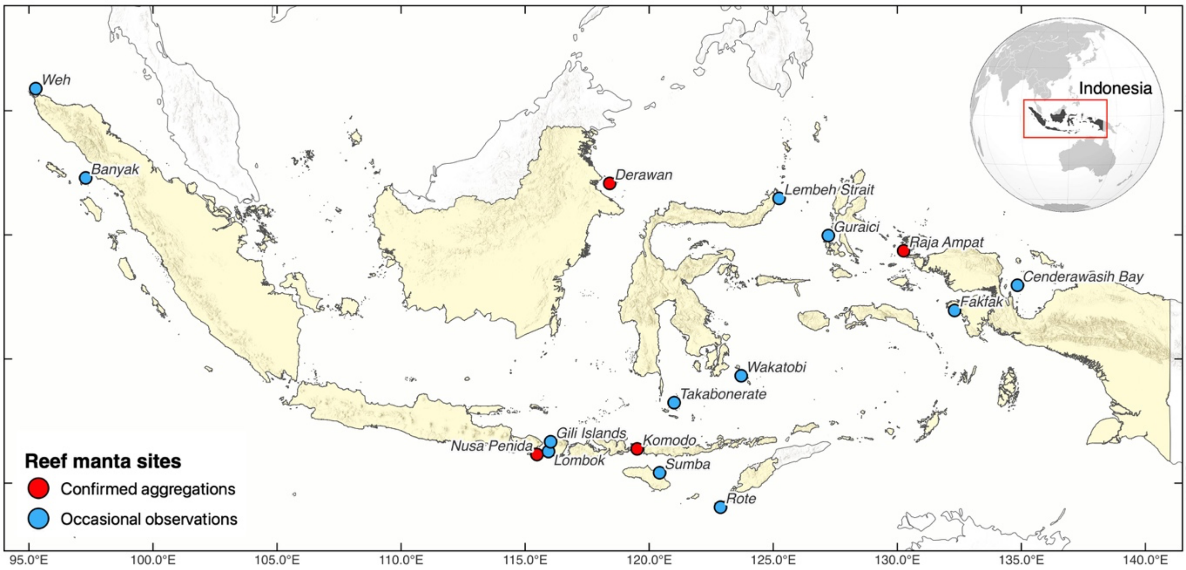

Figure 1.2. Reef manta ray sites consisting of confirmed aggregations (red) and occasional observations (blue) in Indonesia. The inset map shows the location of Indonesia in the Indo-Pacific region. Modified from the Indonesian Ministry of Marine Affairs and Fisheries (2015).

Comprehensive studies on reef manta rays are limited to Nusa Penida, Komodo, and Raja Ampat (Figure 1.2). Long-term monitoring using sightings data including photo-ID of the unique patterns of marks on the ventral side of individual manta rays, have identified hundreds to over a thousand reef manta rays Nusa Penida (n = 624) (Germanov et al., 2019), Komodo (n = 1,085) (Germanov et al., 2022), and Raja Ampat (n = 1,375) (Setyawan et al., 2020). As observed in other countries (e.g., Deakos et al., 2011; Couturier et al., 2014; Stevens, 2016), reef manta rays in the core regions in Indonesia are often seen in large aggregations of a few to tens of individuals. The largest recorded aggregation was up to 112 individuals at the Manta Ridge feeding area in Raja Ampat (Setyawan et al., 2020). These aggregations are typically associated with feeding events, but up to 25 animals can be found at a single cleaning station (Setyawan, pers. obs.), depending on the size of the cleaning sites. As observed elsewhere (Stewart et al., 2016a; Peel, 2019), cleaning stations and feeding sites are generally occupied by adults. Between sex, females overall are more likely to be sighted at cleaning stations than males (Setyawan et al., 2020), although variation in the sighting rates between sex also occurred (Germanov et al., 2019; Perryman et al., 2019). Despite mixing of individuals at different maturity stages was observed at aggregation sites, new-borns and juveniles tend to live in separate habitats like nursery areas which are located in more shallow, nearshore waters often in reef areas and lagoons. Several potential reef manta nursery areas have been identified in Nusa Penida (Germanov et al., 2019) and Raja Ampat (Setyawan et al., 2020), although further research is required to ensure these meet the criteria for a nursery area (Heupel et al., 2007).

Reef manta rays in Indonesia undertake short seasonal local migrations between aggregation sites situated in 40-150 km corridor habitats in Komodo (Dewar et al., 2008) and Raja Ampat (Setyawan et al., 2018). Despite the tendency to occupy coastal, shallow habitats, long distance movements of up to 450 km have been observed between Nusa Penida and Komodo (Germanov & Marshall, 2014), and there is evidence of interchange through low levels of geneflow between the well-studied regions (Phardana et al., 2022). A focus on adjacent areas where there have been occasional sightings of reef manta rays (Figure 1.2) will reveal a better understanding of population structuring in the reef manta rays in Indonesia. All of our understanding of this species is from horizontal movements within and between regions. To date, the reef manta ray vertical movements through use of the water column in Indonesian waters remains unknown. This is an important area for future research to determine drivers of distribution and habitat use, for example whether their feeding areas are depth dependent, or there are currents or depths that form barriers or conduits to dispersal.

## 1.5. Conservation of threatened species

In general, large, long-lived species are disproportionately represented in conservation management plans and protection measures (Ford et al., 2017; Lindsey et al., 2017) when the balance between humans and nature is disrupted (Treves & Santiago-Ávila, 2020). Large animals often face conflict with humans either directly through killing to mitigate immediate risks to human lives, or indirectly through competition for resources or other means; all of which threatens the survival of individual animals and potentially the viability of populations and species (Distefano, 2005; Woodroffe et al., 2005; König et al., 2020; Dulvy et al., 2021). These threats are many, including but not limited to coastal development, the introduction of invasive species, habitat loss and modification, climate change, bycatch, hunting, and unsustainable use of natural resources (e.g., overharvesting) (He et al., 2017; Dias et al., 2019). International collaborations involving multiple stakeholders, experts, knowledge holders and organisations can be a better approach to protect threatened species (Mason et al., 2020) which often requires a range of conservation actions from local (i.e., small ranged and endemic species), regional, to international levels (i.e., wide ranging and migratory species).

Understanding the movement ecology (e.g., home range, residency patterns) and population dynamics (e.g., growth rate, age at maturity) are important to inform the design of appropriate management and conservation strategies (Allen & Singh, 2016). However, researchers often do not have resources (e.g., time, financial support) to understand species of greatest conservation concern and are often reactive to mitigate risks rather than proactive in understanding their biology. One of the key questions in the field of movement ecology of long-lived species is how best to use existing movement data to proactively support conservation and management of species and habitats (Hays et al., 2016). A recent review summarised how movement data have contributed to conservation and management efforts to protect various taxa such as sea birds, sea turtles, and marine mammals (Hays et al., 2019). Importantly in this area, researchers are considering the importance of understanding human movement (e.g., Meekan et al., 2017) and the relationship Indigenous peoples have with ecosystems and species (McAllister et al., 2019; Molnár & Babai, 2021) when evaluating human relationships with other species and ecosystems.

### 1.5.1. Marine conservation and protection

Conserving marine ecosystems is challenging as the ocean is one continuous entity with many oceanic regions remote and inaccessible. Many marine megafauna, live in open ocean waters continuously throughout their lives (e.g., migratory whales) or for part of their lives (e.g., albatrosses), making research and monitoring logistically challenging and costly. This can hinder thorough investigation on the movements and distribution of marine organisms but in recent years this has become more accessible thanks to telemetry, remote sensing, big data, international collaborations, and data sharing (Harcourt et al., 2019; Grémillet et al., 2022). Hindell et al. (2020) provides a good example of how emerging technologies, data sharing, and international collaborations between scientists and organisations can be used to identify areas of ecological importance to marine megafauna and inform protection in the Southern Ocean. Queiroz et al. (2019) used a big data approach that combined the movements of satellite tracked sharks and global fishing fleets to show that internationally protected pelagic sharks were mostly at risk from fisheries. Similarly, access to large, global datasets has allowed understanding of potential risk of collision between large marine animals and vessel traffic (Pirotta et al., 2019; Schoeman et al., 2020; Womersley et al., 2022).

Nearly two-thirds of the ocean is unprotected as it falls outside of the territorial boundaries of the world's countries (Wright et al., 2018). Most of these areas, referred to as the high seas, are currently under pressure from various threats (i.e., resource exploitation, pollution, climate change) (Game et al., 2009). Mitigation of these threats is required to avoid further habitat degradation, promote recovery, ensure the sustainability of existing exploited habitats, and ensure protection for ecologically important regions.

Given the vast size of the ocean and the diversity of species to protect, collaborative approaches involving national and international parties and organisations are required.

At international levels, there are several initiatives to protect biodiversity. For example, the Convention on International Trade of Endangered Species (CITES) established in 1973, is an international agreement designed to ensure the protection of endangered flora and fauna from the threats of international trade. The Convention on Biological Diversity (CBD) is a multilateral treaty established in 1992 to conserve and ensure the sustainable use of biological diversity (Glowka et al., 1994). At national levels, many countries have also implemented national plans of action to protect certain species, such those conserving and managing sharks and rays (Pacoureau et al., 2023).

In addition to species protection, a common practice in marine conservation is protecting habitats or ecosystems through marine protected areas (MPAs) (Grorud-Colvert et al., 2021). A commonly used definition of an MPA is “a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long- term conservation of nature with associated ecosystem services and cultural values” (Dudley, 2008). MPAs have long been used tools to protect marine biodiversity and promote sustainable fisheries (Grorud-Colvert et al., 2021). Despite the often extensive processes required for designation and implementation, not all MPAs are effective at providing ecological and socio-economic benefits (Edgar et al., 2014).

Most MPAs are designed with static boundaries and are based on the abundance of species of conservation concern living in static habitats (e.g., coral reefs, mangroves) (Hooker et al., 2011). This approach does not adequately provide protection for large and wide-ranging species that are capable of migrating long distances from hundreds to thousands of kilometres like blue whales and leatherback turtles *Dermochelys coriacea* (Block et al., 2011; Möller et al., 2020). Despite this, many migratory marine species exhibit site fidelity for the key habitats and sometimes the migratory route taken (Lascelles et al., 2014). Threats to these species are not equal throughout their range, and therefore, spatial protection of these critical habitats could substantially reduce their mortality risk (Hooker et al., 2011). For migratory seabirds, threats to populations occurred both on land (e.g., at stopping sites), which are related to habitat degradation, predation, and human disturbance, and at sea, which mainly come from commercial fisheries (Croxall et al., 2012; Hua et al., 2015). In large and remote MPAs, the populations of highly migratory species with large home ranges might be at risk from illegal fishing practices (Jacoby et al., 2020), which highlights the importance of enforcement. Enforcement is more challenging when animals are in the high seas but there are remote sensing technologies such as Global Fishing Watch that may be effective managing some of these risks. Recently, the World Commission on Protected Areas (https://www.iucn.org/our-union/commissions/world-commission-protected-areas) was established by the IUCN to support the post-2020 Global Biodiversity Framework currently being negotiated through the CBD. The focus is on marine conservation initiatives through MPAs such as the 30 x 30 campaign to protect 30% of waters by 2030, designation of Important Marine Mammal Areas (Tetley et al., 2022) and the recently established Important Shark and Ray Areas that cover national and international waters.

## 1.6. Manta ray threats and conservation

Characterised by long lifespans, slow maturity, and low fecundity, manta rays are extremely vulnerable to overexploitation which may lead to local population extinction (Dulvy et al., 2014). The oceanic manta ray is listed as Endangered (EN) (Marshall et al., 2020), while the reef manta ray is listed as Vulnerable (VU) (Marshall et al., 2022) on the IUCN Red List of Threatened Species. The global populations of both species showed declining trends in their populations throughout their range and particularly rapidly in several regions due to fisheries pressure (Dulvy et al., 2021; Pacoureau et al., 2021; Sherman et al., 2023). They are mainly caught using gillnets, longlines, and harpoons in both targeted fisheries and as bycatch (Dewar, 2002; Fernando & Stewart, 2021). Manta rays are targeted for their gill plates, which are highly valuable on the international market and are used in (non-traditional) Chinese medicine (Heinrichs et al., 2011). Manta rays commonly aggregate in coastal areas with high productivity which makes them an easy target for fisheries (Couturier et al., 2012).

Despite the declining population trend, manta rays provide substantial economic benefits through manta ray watching and swim-with tourism (Anderson et al., 2011b). Several countries (e.g., Japan, Indonesia, the Maldives, Mozambique, Thailand, Australia, and Mexico) are top manta watching tourism destinations generating global revenue from this industry. It was estimated that globally, the direct economic impact of manta ray tourism was USD 140 million annually (O'Malley et al., 2013). Despite providing substantial economic benefits, manta tourism may have negative impacts on the animals if not properly managed. Potential impacts may come from interactions that may disturb or alter the natural behaviours of manta rays (Anderson et al., 2011b) and increased boat traffic around manta ray aggregation sites that may increase the rate of injury from vessel-strike (Stevens et al., 2018a).

### 1.6.1. Threats to manta rays in Indonesia

Indonesia is among the top shark and ray fishing nations (Dulvy et al., 2017). Lewis et al. (2015) reported there have been substantial declines in the number of mobulids (especially manta rays) landed in several sites in southern Indonesia, such as in Lamakera and Lamalera villages (East Nusa Tenggara). In these villages, manta rays were historically targeted using harpoons by artisanal fishers for local consumption and barters (Barnes, 2005). However, the increasing demands for manta ray gill plates in late 1990s and early 2000s from Chinese markets led to increased effort to catch them (Dewar, 2002). Threats to manta rays varied throughout Indonesian waters. While targeted fisheries were the main threat to their populations in East Nusa Tenggara, manta rays were commonly caught as bycatch by gillnet and longline fisheries (White et al., 2006). In Lembeh Strait (North Sulawesi), substantial effort in gillnet fisheries capture over 1,400 manta rays in only 10 months, which seems to lead to the eradication of the local manta ray population. In the study area for my PhD, Raja Ampat in West Papua (eastern Indonesia), the threats to manta rays were reduced with the introduction of a network of MPAs. I outline the development of these protection measures more fully in Chapter 2.

## 1.7. Thesis synopsis

In this PhD dissertation, I have the following objectives, 1) to review the long-term implementation of management and conservation measures in the Bird's Head Seascape, and then assess their potential impact on reef manta ray populations in Raja Ampat, West Papua, Indonesia; 2) to examine the demographics of reef manta ray populations in the Raja Ampat archipelago and investigate potential drivers affecting the population dynamics of this species; 3) to understand the life history parameters by measuring the body size of reef manta rays using drone photogrammetry; 4) to investigate the residency and horizontal movement patterns of reef manta rays; and finally 5) to investigate the metapopulation dynamics of reef manta rays in Raja Ampat.

Overall, this thesis contains seven chapters, with four of the five data chapters published in peer-reviewed journals. These are formatted in the same style throughout the thesis as required by University regulations. I provide a brief overview of each chapter below:

**Chapter 1**. I provide a general introduction about the field of movement ecology and population demographics. I also outline some of the challenges and approaches used in the protection and conservation of marine species, in particular large, long-lived species and their habitats, with a focus on manta rays.

**Chapter 2**. I review the process of implementing marine conservation plans and management measures in the Bird's Head Seascape (including the Raja Ampat archipelago). I then highlight the potential impacts of these measures on reef manta ray populations and ongoing challenges to protect this species in the region.

Published as: Setyawan, E., Erdmann, M.V., Gunadharma, N., Gunawan, T., Hasan, A.W., Izuan, M., Kasmidi, M., Lamatenggo, Y., Lewis, S.A., Maulana, N., Mambrasar, R., Mongdong, M., Nebore, A., Putra, M.I.H., Sianipar, A.B., Thebu, K., Tuharea, S., and Constantine, R. (2022a). A holistic approach to manta ray conservation in the Papuan Bird's Head Seascape: Resounding success, ongoing challenges. *Marine Policy* 137**,** 104953. https://doi.org/10.1016/j.marpol.2021.104953.

**Chapter 3**. I examine trends in reef manta ray abundance in the Raja Ampat archipelago over an 11-year period from 2009 to 2019. Using mark-recapture modelling and a long-term photo-ID data set, the main objective of this chapter was to estimate the key demographic parameters, population size, survival probabilities, per capita recruitment rates of reef manta rays in two large marine protected areas: Dampier Strait and South East Misool MPAs. These were the two locations with long-term photo-ID data datasets. I also investigated potential drivers affecting population-level changes on reef manta rays in the two MPAs.

Published as: Setyawan, E., Stevenson, B.C., Erdmann, M.V., Hasan, A.W., Sianipar, A.B., Mofu, I., Putra, M.I.H., Izuan, M., Ambafen, O., Fewster, R.M., Aldridge-Sutton, R., Mambrasar, R., and Constantine, R. (2022c). Population estimates of photo-identified individuals using a modified POPAN model reveal that Raja Ampat's reef manta rays are thriving. *Frontiers in Marine Science* 9**,** 1014791. https://doi.org/10.3389/fmars.2022.1014791.

**Chapter 4**. I explore the use of aerial photogrammetry to measure the body size of reef manta rays using small commercially available drones. In Raja Ampat, surface feeding is one of the most common feeding strategies observed. The reef manta rays swim against currents at the sea surface and open their mouths wide. This situation allows observation from the air using drones for a number of purposes including counting the number of individuals, observing their feeding behaviour, identifying individuals and their sex and maturity stage. In this chapter, I developed a novel and non-invasive method to accurately estimate the body size of reef manta rays through aerial photogrammetry using a small drone.

Published as: Setyawan, E., Stevenson, B.C., Izuan, M., Constantine, R., and Erdmann, M.V. (2022d). How big is that manta ray? A novel and non-invasive method for measuring reef manta rays using small drones. *Drones* 6(3)**,** 63. https://doi.org/10.3390/drones6030063.

**Chapter 5**. I examine the residency patterns and horizontal movements of juvenile reef manta rays in a potential nursery area in Wayag lagoon, northwestern Raja Ampat. Using a multi-disciplinary approach including photo-ID, drones, passive acoustic telemetry, and satellite telemetry, this chapter conclusively confirms that Wayag lagoon is a reef manta ray nursery. Identifying key areas in the life cycle of reef manta rays is required to assist the conservation effort of this globally threatened species.

Published as: Setyawan, E., Erdmann, M.V., Mambrasar, R., Hasan, A.W., Sianipar, A.B., Constantine, R., Stevenson, B.C., and Jaine, F.R.A. (2022b). Residency and use of an important nursery habitat, Raja Ampat's Wayag Lagoon, by juvenile reef manta rays (*Mobula alfredi*). *Frontiers in Marine Science* 9. https://doi.org/10.3389/fmars.2022.815094.

**Chapter 6**. I investigate the spatial connectivity of reef manta rays throughout the Raja Ampat region. Using a five-year passive acoustic telemetry dataset from 2016 to 2021, I undertook a network analysis to reveal three spatially distinct subpopulations with very low levels of connectivity. These findings along with satellite telemetry data supported the hypothesis that the reef manta rays of Raja Ampat most likely form a metapopulation. Upon final submission of this dissertation, a revised version of Chapter 6 is in review.

Finally, **Chapter 7** consists of a general discussion of the research findings, its relevance to the conservation of reef manta rays in Raja Ampat and throughout Indonesia and suggest future research directions.

# Chapter 2.

# A holistic approach to manta ray conservation in the Papuan Bird's Head Seascape: Resounding success, ongoing challenges

## 2.1. Introduction

Global populations of sharks and rays, caught both in targeted fisheries and as bycatch, are in steep decline (Pacoureau et al., 2021), with approximately one-third of all shark and ray species now considered threatened with extinction (Dulvy et al., 2021). Manta and devil rays in the genus *Mobula* are no exception (Ward-Paige et al., 2013). Numerous studies have revealed sharp declines in their local populations, from Mozambique (Rohner et al., 2013; Marshall et al., 2020) to Sri Lanka (Fernando & Stewart, 2021), and from the Philippines (Acebes & Tull, 2016) to the Eastern Tropical Pacific (Croll et al., 2015). Mobulids are frequently caught as bycatch in net and longline fisheries in particular (Croll et al., 2015), and since at least the 1990s have been targeted for their gill rakers, which are sold as a non-traditional "medicine" in southern China and other parts of southeast Asia (Heinrichs et al., 2011). As a result of this fisheries pressure and their slow growth and low fecundity (Dulvy et al., 2014), reef manta rays (*M. alfredi*) are now listed as Vulnerable on the IUCN Red List (Marshall et al., 2022), while oceanic manta rays (*M. birostris*) have recently been listed as Endangered (Marshall et al., 2020).

Indonesia is representative of the global plight of elasmobranchs, and for over three decades it has led the world in fisheries landings of sharks and rays (Dharmadi et al., 2015; Prasetyo et al., 2021). Mobulids are frequently recorded as bycatch in Indonesia (White et al., 2006), while targeted harpoon fisheries are well known from the Savu Sea region and have seen steep declines in landings and even local extirpations over the past decade (Lewis et al., 2015). In Raja Ampat in the Papuan Bird's Head Seascape (BHS) in eastern Indonesia (Figure 2.1), there is no historical evidence of systematic exploitation of mobulids by local fisheries (Beale et al., 2019), though there are anecdotal reports of sporadic targeting of manta ray aggregations in northern Raja Ampat in the early 2000s by shark fishers from Sulawesi (Varkey et al., 2010). Local community members also report that manta rays were observed as bycatch when fishing boats from Sulawesi and Maluku using large drift nets occasionally operated in Raja Ampat in the 1990s and early 2000s (Mambrasar, pers. obs.).

Despite this occasional mortality from fisheries two decades' ago, manta ray populations in Raja Ampat are now fully protected and appear to be thriving (Setyawan et al., 2020). Oceanic manta rays (*Mobula birostris*) in the Raja Ampat archipelago are both relatively abundant (588 individuals recorded over six years) and are estimated to have high survival rates (Beale et al., 2019). The reef manta ray (*M. alfredi*) population in Raja Ampat is the largest reported from Indonesia (1,375 individuals recorded over 15 years), with evidence of an unusually high rate of pregnancies compared to other populations across the Indo-Pacific and at least four active nursery habitats (Setyawan et al., 2020). Additionally, a mark-recapture analysis of sightings data from 1,052 individual Raja Ampat reef manta rays from 2009-2019 revealed significant annual increases in estimated population size in both the Dampier Strait and South East Misool MPAs (Setyawan et al., 2022c). By comparison, the well-studied reef manta ray population in Mozambique, which has been targeted in subsistence fisheries (O'Malley et al., 2017) showed a decreasing trend in apparent survival over 15 years (2003–2018), suggesting high mortality linked to continuing pressure from targeted fisheries and insufficient conservation efforts to protect the population (Rohner et al., 2013; Venables, 2020).

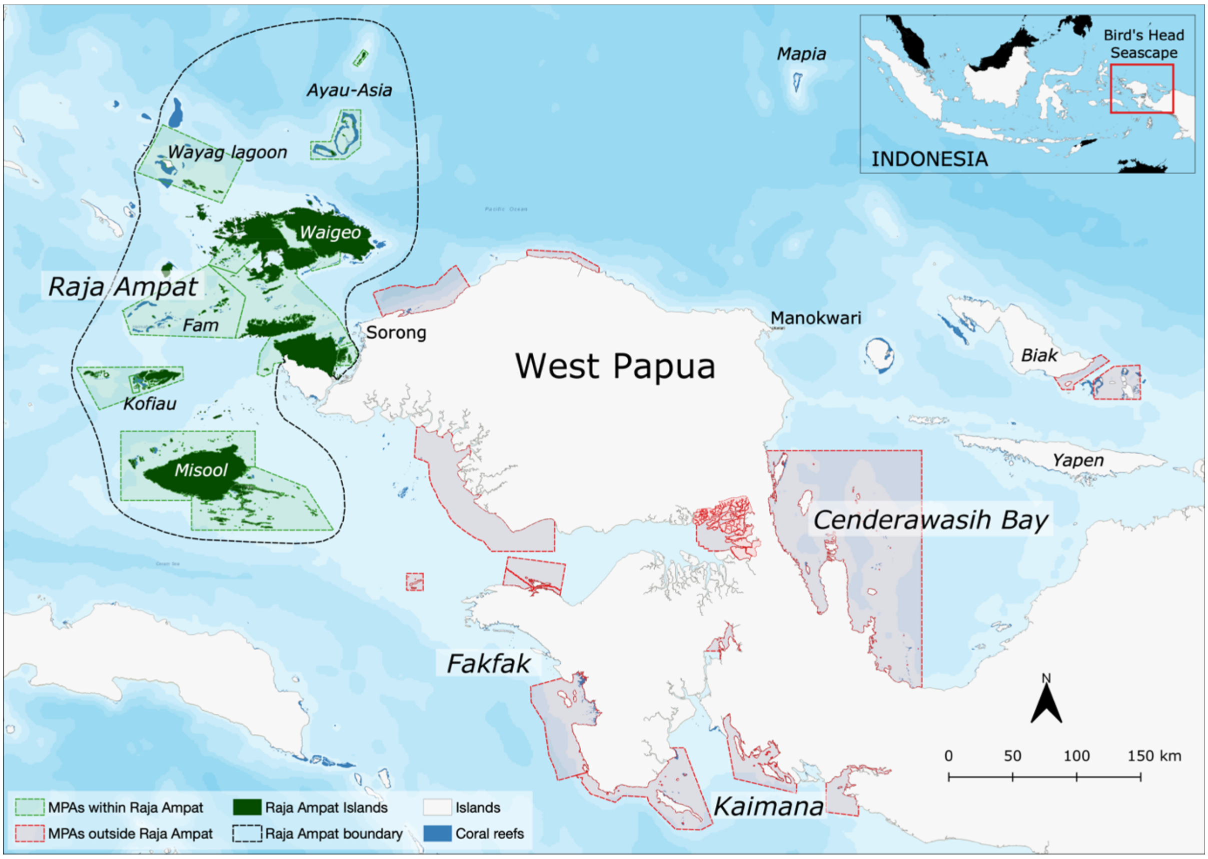

Figure 2.1. The Bird's Head Seascape in West Papua, Indonesia, with key coastal regencies and large islands labelled and the network of 26 individual marine protected areas (MPAs) denoted by polygons (green for those within Raja Ampat Regency, and red for those outside Raja Ampat Regency). The approximate boundary of Raja Ampat's administrative boundary is demarcated by a dashed line.

We posit that the comparatively optimistic outlook for manta rays in Raja Ampat is most likely a result of two decades' of intensive conservation efforts in the BHS (Mangubhai et al., 2012; Purwanto et al., 2021) by a dedicated stakeholder coalition comprised of local and national government agencies, traditional communities, local universities and local and international non-governmental organisations (NGOs) (Murphy et al., 2021). These efforts have not only protected the manta rays of Raja Ampat, but have moreover leveraged national level protection for manta rays (Indonesian Ministry of Marine Affairs and Fisheries, 2014) and other elasmobranchs (Indonesian Ministry of Marine Affairs and Fisheries, 2013; VanderWright et al., 2021) while inspiring other regencies (the secondary level of local government administration in Indonesia, one step below the level of province), including West Manggarai (Government of Manggarai Barat, 2013) and Berau (Government of Berau, 2019), to similarly protect manta rays in their waters.

In this paper we document the progressive development of a holistic approach to manta ray conservation in Raja Ampat, providing insights on the strategies used, in order that they might inform similar efforts towards elasmobranch conservation in other parts of Indonesia and across the developing tropics. We also highlight ongoing challenges that are currently being addressed to ensure that manta rays and other elasmobranch populations not only continue to grow in Raja Ampat but also begin to show signs of recovery in other regions of the BHS.

## 2.2. 2001-2011: A decade of MPA development in the BHS

While the traditional communities of West Papua have long practiced *sasi* – a traditional resource management technique utilizing spatiotemporal prohibitions on collection of certain marine species (usually invertebrates) as a means of allowing these exploited populations to recover (McLeod et al., 2009), "formal" (legislated) marine conservation in the BHS only began in the late 20th century with the designation of the 60,000 ha Raja Ampat Marine Wildlife Sanctuary in 1993 (see timeline in Figure 2.2). Soon thereafter, a marine rapid ecological assessment (MRAP) conducted by the Indonesian Institute of Sciences, University of Cenderawasih, and Conservation International (CI) in 2001 (McKenna et al., 2002) brought the world's attention to the Raja Ampat archipelago's superlative marine biodiversity. Results from a series of follow-on surveys throughout the BHS sponsored by CI and The Nature Conservancy (TNC) cemented the BHS' reputation as the global epicentre of coral reef biodiversity (Erdmann, 2011). Ongoing research has shown the BHS is home to over 600 species of hard coral (Veron et al., 2009), 14 species of cetacean (Ender et al., 2014; Cerchio et al., 2019), 1,876 species of reef fish (Allen & Erdmann, 2009), and both species of manta rays (Setyawan et al., 2020), making it Indonesia's top priority region for marine biodiversity conservation (Huffard et al., 2012a; Asaad et al., 2018).

The designation of Raja Ampat as a new regency in West Papua in 2003 provided an opportunity for its nascent government to craft a development plan that featured a strong focus on conservation and sustainability. To further guide this governmental vision, the traditional *adat* communities of Raja Ampat set forth the Tomolol Declaration in December 2003, calling for an end to the rampant illegal and destructive fishing practices being conducted by outside fishing boats in the regency's waters and demanding the government prioritise sustainable marine resource management to guarantee food security for local communities. Environmental NGOs (led by CI and TNC) and the State University of Papua worked closely with the Raja Ampat government and local communities to help realise this vision, which centred upon the development of a network of MPAs, collaboratively managed by the regency government and local communities, and designed to both protect marine biodiversity and ensure food security by serving as a focal point for sustainable fisheries and marine tourism development (Mangubhai et al., 2012).

## Timeline of key milestones in conservation and management of manta rays in the Bird's Head Seascape

**1993**
Ministry of Forestry designates the Raja Ampat Marine Wildlife Sanctuary as the first of Raja Ampat's MPAs

**2001**
Marine Rapid Assessment (MRAP) identifies Raja Ampat as global epicenter of marine biodiversity and top conservation priority

**2003**
Traditional (*adat*) communities of Raja Ampat issue the Tomolol Declaration expressing their solidarity in halting illegal and destructive fishing in Raja Ampat

**2006**
Traditional adat communities declare five new MPAs in Raja Ampat.

**2007**
Raja Ampat MPA network (seven MPAs) formally established through governmental regulations*

**2009**
Raja Ampat MPA zonation regulations forbid all forms of net-fishing and long-lines in MPAs

**2010**
Restriction on the use of destructive fishing gears and capture of sharks and manta rays in Raja Ampat to support sustainable fisheries and tourism

**2012**
Full protection of all sharks and rays in Raja Ampat waters

**2013**
CITES COP16 lists both species of manta rays on Appendix 2;

First Indonesian National Symposium on Conservation of Sharks and Rays

**2014**
Full protection of both species of manta rays in Indonesian territorial waters

**2016**
Development of Raja Ampat Manta Task Force ("POKJA MANTA");

Special tourism rules formulated for Wayag lagoon manta nursery area

**2017**
Manta Sandy ranger post and manta tourism protocol implemented

**2019**
Expansion of MPA network in Raja Ampat to include additional reef systems with known manta ray aggregations and nurseries

**2020**
Bird's Head Seascape MPA Network expands to include 26 MPAs totaling 5,229,782 ha, with over 90% of known manta ray sites included within these MPAs

* Governmental regulations issued by Raja Ampat government and the Indonesian Ministry of Marine Affairs and Fisheries

1. Regional Regulation 66/2007
2. Regional Law 27/2008
3. Regional Regulation 5/2009
4. Ministerial Decree 64/2009
5. Ministerial Decree 65/2009
6. Ministerial Decree 36/2014

Figure 2.2. Timeline of key milestones in conservation and management of manta rays in the Bird's Head Seascape, Indonesia.

MPAs were chosen as the initial primary conservation intervention by the Raja Ampat government, as they have long been proven to be an effective tool to protect benthic communities and increase the abundance and biomass of coral reef fish species both within and outside their boundaries (Gell & Roberts, 2003). They have also been shown to promote the recovery of large mobile species (e.g., reef sharks), especially in large MPAs (Edgar et al., 2014; Jaiteh et al., 2016). With this in mind, Indonesia's Ministry of Marine Affairs and Fisheries (MMAF) has for the past two decades prioritized the establishment of a representative national network of MPAs, and has moreover targeted protecting 10% of its marine area (32.5 million ha) as part of its commitment to the Convention on Biological Diversity's (CBD) Aichi Target 11 (Indonesian Ministry of National Development Planning, 2021).

In 2006, traditional *adat* leaders declared five new MPAs in Raja Ampat, including the Kawe, Dampier Strait, Mayalibit Bay, Kofiau-Boo Islands, and South East Misool MPAs. In 2007, the Ayau-Asia MPA was similarly declared, after which the full network of seven MPAs in Raja Ampat was then legally gazetted by the Raja Ampat government (Government of Raja Ampat, 2007, 2008, 2009; Indonesian Ministry of Marine Affairs and Fisheries, 2009b, 2009a) under new national legislation by the Indonesian Ministry of Marine Affairs and Fisheries (Government of Indonesia, 2004a, 2004b) that encouraged decentralised, local ownership and management of MPAs. Similar efforts were initiated in other regencies in the BHS, and by 2011 a network of 12 MPAs covering nearly 3.6 million hectares was established and under active co-management by local communities and the government (Mangubhai et al., 2012). At the time, ten of these were managed by the Regency governments of Raja Ampat and Kaimana, but in 2014 a new national law (Government of Indonesia, 2014) transferred the authority for managing these local MPAs to the provincial level. As a result, at the present time, 19 of the 26 MPAs in the BHS MPA network are managed collaboratively between the West Papua provincial government and local stakeholders, while the remaining seven are national level MPAs managed by the MMAF or the Ministry of Environment and Forestry.

Each of the MPAs in the Raja Ampat network is actively enforced by its own joint patrol team comprised of rangers recruited from local communities and either police or fisheries officers, generally targeting at least 3 patrols per week (Mangubhai et al., 2012; Purwanto et al., 2021). The patrol system is sustainably financed via the Raja Ampat MPA environmental services fee levied upon all domestic and international visitors, and is one of the primary reasons that the Raja Ampat MPA network fulfils nearly all of the criteria (except for having boundaries demarcated by buoys) for a blue rating ("managed optimally") in MMAF's E-KKP3K MPA Management Effectiveness Assessment (Pakiding et al., 2020).

Importantly, the siting of MPAs within Raja Ampat (and the broader BHS) was based upon a combination of traditional ecological knowledge and community marine tenure and socioeconomic considerations, combined with the results of a series of scientific studies investigating the ecology, oceanography and genetic connectivity of the BHS (Huffard et al., 2012b; Mangubhai et al., 2015). While manta rays were not a specific focus of research or conservation prior to 2011, local communities and tourism operators both considered them an important tourism asset in Raja Ampat, and known manta aggregation sites were explicitly included in MPAs (Mangubhai et al., 2012). Moreover, a participatory zonation planning process resulted in all forms of net fishing and long-lining being banned in Raja Ampat MPAs (Agostini et al., 2012). While these fishing gears were banned by local communities for sustainability reasons, this move was undoubtedly highly beneficial to Raja Ampat's manta ray populations. As mentioned previously, though manta rays were never consistently targeted by fisheries in Raja Ampat, the area was heavily fished for sharks (Jaiteh et al., 2016), with manta rays regularly caught as bycatch in shark gillnets and longlines (Varkey et al., 2010; Muhajir et al., 2012) and sometimes even used as bait on shark long-lines (Mambrasar, pers. comm).

## 2.3. An increasing focus on manta rays

By 2011, Raja Ampat's coral reefs were under active local management, with illegal and destructive fishing practices largely under control and marine tourism rapidly becoming the primary economic engine for Raja Ampat (Mangubhai et al., 2012). As the coalition of conservation stakeholders in Raja Ampat began to focus on fine-tuning conservation efforts, four separate but synergistic developments combined to greatly advance manta ray conservation, not only in Raja Ampat but nationally. First, a targeted campaign by Misool EcoResort, WildAid and Shark Savers convinced the Regent of Raja Ampat to announce his intention to make Raja Ampat a shark and ray sanctuary (Government of Raja Ampat, 2010) to increase tourism to the region. With the help of the CI and TNC Raja Ampat programs, this initiative was brought to the Raja Ampat parliament and leveraged into a Regency Law (Government of Raja Ampat, 2012) in 2012, strictly protecting all sharks and rays in Raja Ampat waters – the first of its kind in southeast Asia.

Also in 2011, the Indonesian Manta Project (and its related initiative, the Misool Manta Project, both affiliates of the Manta Trust) began collecting photo-identification images of Raja Ampat's reef and oceanic manta rays and launched a collaboration with CI, TNC and the Raja Ampat MPA Management Authority to investigate the natural history of manta rays in the region. These partners also worked with the Raja Ampat Department of Tourism and local marine tourism operators to encourage the implementation of a code of conduct for divers and snorkelers interacting with manta rays.

In 2013, two final developments of particular importance in the same timeframe included the publication of an analysis of the global economic impact of manta ray watching tourism, which revealed Indonesia to be the second most valuable manta tourism industry in the world (worth over US$15 million annually) (O'Malley et al., 2013), and the historic decision at the CITES CoP16 conference to list both species of manta ray (and six species of shark) on CITES Appendix II (CITES, 2013).

Buoyed by the successful campaign for the Raja Ampat shark and ray sanctuary, the BHS conservation coalition supported MMAF in hosting the first National Symposium on Shark and Ray Conservation in 2013, primarily as a vehicle to highlight the conservation vision of the Raja Ampat government and to encourage other regencies to also protect their elasmobranchs. The symposium was attended by about 80 participants and presided over by the Minister of Marine Affairs and Fisheries. At a pre-symposium press briefing, the Minister voiced concern about the implications of the recent CITES shark and ray listings, noting that while Indonesia was obliged as a signatory to CITES to uphold these new protections, there were sure to be negative economic impacts upon coastal fishing communities deriving incomes from elasmobranch fisheries.

VALUING MANTAS

Manta and mobula rays span the tropics of the world and are among the most captivating and charismatic of marine species. However, their survival is severly threatened by growing fisheries pressure driven by demand for the gill rakers that the animals use to filter feed.

MANTA ECONOMICS

$5 MILLION vs $140 MILLION

The estimated global value of the manta gill raker trade*

The expected global tourism value of manta rays*

DEADorALIVE?

<$500 vs $1,000,000

The estimated fisheries value of a single manta ray, **DEAD**

The estimated tourism value of a single manta ray over its lifetime, **ALIVE**

* O'Malley MP, Lee-Brooks K, Medd HB (2013) The Global Economic Impact of Manta Ray Watching Tourism. PLoS ONE 8(5): e65051. doi:10.1371/journal.pone.0065051

Photo: © Trond Larsen

Figure 2.3. "Mantanomics" poster produced in 2013 as part of a strategy to convince the Indonesian Minister of Marine Affairs and Fisheries of the strong economic argument in favour of protecting manta rays as valuable tourism assets.

When the coalition later presented the results of the manta tourism economic study, explained as a "mantanomics" argument that a single manta ray was worth less than $500 dead for its gill plates but over $1M alive as a tourism asset (Figure 2.3), the Minister commented that having such a strong economic argument provided clear justification for conservation action for manta rays. In his closing comments to the symposium, he instructed his Marine Conservation Directorate to convene a high-level shark and manta ray conservation working group to formulate and justify national level legislation to protect manta rays and to consider similar protections for the other CITES-listed sharks, particularly if there were economic justifications for doing so (Erdmann, 2013).

This working group met regularly for the second half of 2013, producing the academic justification document for the proposed legislation, and then drafting the manta protection regulation for consideration by the Minister. Importantly, the initiative was championed on social media by Indonesian television celebrity Riyanni Djangkaru and her "Save Sharks Indonesia" campaign (Erdmann, 2014a). In early 2014, the Minister signed a Regulation (Indonesian Ministry of Marine Affairs and Fisheries, 2014) fully protecting both species of manta rays in Indonesian territorial waters (Dharmadi et al., 2015), thus creating the world's largest manta ray sanctuary at nearly 6,000,000 km$^2$ (Erdmann, 2014a).

Over the course of two years, the world's largest shark and ray fishing nation had rapidly adopted and championed robust elasmobranch conservation initiatives. Importantly, whale sharks (*Rhincodon typus*) were also given full protected status (Indonesian Ministry of Marine Affairs and Fisheries, 2013) based also upon their tourism value, and other fisheries regulations quickly followed, providing varying levels of protection to thresher (*Alopias* spp.) and oceanic whitetip (*Carcharhinus longimanus*) sharks (Dharmadi et al., 2015). Indonesia's transition to a country with a significant elasmobranch conservation focus had begun, underscored by steadily increasing participation in the three successive national Symposiums on Sharks and Rays in 2015 (124 participants), 2018 (235 participants) and 2021 (776 online participants). Importantly, the 2015 symposium resulted in the signing of Indonesia's first National Plan of Action on Manta Ray Conservation for the period 2016–2020 (Indonesian Ministry of Marine Affairs and Fisheries, 2015).

## 2.4. A new threat: Tourism

Throughout this period of increasing manta ray protection, marine tourism grew rapidly in Raja Ampat, from a total of about 300 guests visiting the region via one resort and one liveaboard dive vessel in 2001 (Jones et al., 2011), to 28,952 guests accommodated by 11 resorts, over 50 homestays and more than 70 dive liveaboards in 2018 – with a nearly 3000% increase in visitor arrivals between 2007 and 2018 (Purwanto et al., 2021). Raja Ampat's manta rays had become a top attraction, and overcrowding and disturbance by divers at popular manta "cleaning stations" was a common concern voiced by both scientists and tourism operators (Setyawan et al., 2018). Reef manta rays routinely aggregate at specific coral colonies to be "cleaned" of their ectoparasites by a variety of reef fishes including the cleaner wrasse *Labroides dimidiatus*; these cleaning stations also provide opportunities for courtship and other social interactions between manta rays (Armstrong et al., 2021a). Importantly, while manta cleaning stations are often targeted by divers due to the reliability of manta sightings, the presence of large numbers of divers, as well as aggressive behaviours by divers such as approaching too closely to cleaning manta rays, has been shown conclusively to cause disruption to manta ray behaviour and often results in manta rays leaving and avoiding cleaning stations, which may decrease individual fitness (Murray et al., 2020).

In response to this new threat, in 2016 the Raja Ampat Tourism Department and MPA Management Authority jointly launched a Raja Ampat Manta Task Force (the “POKJA Manta”) comprised of representatives from communities, government, the tourism sector, NGOs and several manta ray researchers. The Task Force initially focused its efforts on implementing special management of the “Manta Sandy” dive site, an important manta ray cleaning station which at times had up to 9 boats and 50 divers crowding the site at once and clearly affecting the behaviour of the manta rays (Lawrence, 2018). In 2017, the Task Force built a ranger station at the dive site and hired and trained the “Manta Cadre”, a group of young manta conservationists from nearby villages that began strictly limiting the numbers of divers and snorkelers allowed on the site at a given time and enforcing the code of conduct for appropriate manta interactions (Kasmidi, 2017; Kasmidi & Gunadharma, 2017). Later, as ongoing surveys revealed the presence of manta nursery areas in Wayag Lagoon and other reef systems, the Task Force worked to formulate special rules to prevent disturbances to juvenile manta rays in the nurseries, including limiting boat speeds in these sensitive areas (Setyawan et al., 2020). While the impacts of these management interventions have not been quantified, dive operators in 2019 reported general satisfaction with the new regulations and an increase in the numbers of manta rays visiting the Manta Sandy cleaning station (Kasmidi, pers. obs.).

## 2.5. Further considerations and ongoing challenges

Over the past decade, communities around the BHS have continued to call for more MPAs, with the BHS MPA network now comprising 26 MPAs covering 5,229,782 hectares (Jones, 2021). Importantly, of the 127 sites in the BHS where regular manta ray sightings have been recorded, 91% (n = 115) of them are distributed within 13 of the BHS MPAs (Setyawan et al., 2020). Moreover, 68 of the 70 known manta ray cleaning and feeding aggregation sites and all four of the known manta nursery areas (Wayag lagoon, Ayau Besar lagoon, Hol Gam lagoon, and the Fam islands) are within MPAs (Setyawan et al., 2020). In a previous study, we have shown that all four nurseries fulfil the three criteria of elasmobranch nurseries proposed by Heupel et al. (2019), with (1) Young-of-the-Year (YoY) and juvenile reef manta rays (defined as individuals ≤ 2.0 m DW (disc width) and ≤ 2.4 m DW, respectively) more commonly encountered in the nursery areas than elsewhere in the BHS, (2) YoY and juvenile *M. alfredi* shown to remain in the nursery area for extended periods of up to 1.7 years; and (3) the nursery areas used repeatedly by YoY and juvenile *M. alfredi* across periods of 3-14 years (Setyawan et al., 2020).

Although both species of manta ray are capable of long distance movements in excess of 1000 km (Stewart et al., 2016a; Armstrong et al., 2019), a range of studies have shown that populations of both species across the Indo-Pacific demonstrate strong patterns of site fidelity (Stewart et al., 2016a; Andrzejaczek et al., 2020), and some authors have shown that even short distances of 20-50 km across deep water can serve as a barrier to reef manta ray movements in particular (Deakos et al., 2011; Peel et al., 2020). Previous movement studies in Raja Ampat have similarly shown that both *M. alfredi* and *M. birostris* show strong site fidelity to the region (Stewart et al., 2016a; Setyawan et al., 2018; Beale et al., 2019; Setyawan et al., 2020). While data on oceanic manta home ranges is lacking, the home range size of reef manta rays has been estimated as ranging from 64-2,457 km$^2$ (Kessel et al., 2017). With Raja Ampat MPAs ranging in size from 50-3,573 km$^2$ (and BHS MPAs up to 14,535 km$^2$) they are considered appropriately-sized for reef manta ray conservation (Setyawan et al., 2020).

Nonetheless, both reef and oceanic manta rays have been shown to occasionally move southwards from Raja Ampat into the Seram Sea and the waters of Fakfak and Kaimana regencies, and manta rays have been recorded from four of the 17 BHS MPAs outside of Raja Ampat Regency (Beale et al., 2019; Setyawan et al., 2020). However, extensive surveys in these areas have confirmed that manta ray populations in these areas are much smaller than in Raja Ampat (Setyawan et al., 2020). Unfortunately, net fishing (including with set and drifting gill nets and large net traps) is still practiced in much of the BHS, and given the frequency of manta ray bycatch recorded in net fisheries globally (Croll et al., 2015; Fernando & Stewart, 2021), it is likely the low numbers of manta rays found outside Raja Ampat is a direct consequence of these nets. Moreover, while targeted manta ray fisheries in the BHS are not generally known, there is one report of local communities opportunistically harpooning manta rays in southern Yapen Island in the eastern BHS (Indonesian Ministry of Marine Affairs and Fisheries, 2015).

With this in mind, the BHS conservation coalition is in ongoing discussions with the Kaimana and Fakfak regency governments and the West Papua provincial government to urge the implementation of net bans and possibly a province-wide shark and ray sanctuary in an attempt to expand protections for manta rays throughout the BHS in order to promote population recovery. Fortunately, the West Papua government has declared itself Indonesia's first "Conservation Province", and the provincial law which provides the substance of this declaration (Government of Papua Barat, 2019) includes strong justification for further protection for economically-important elasmobranchs. As with most conservation work globally, the COVID-19 pandemic has unfortunately slowed these efforts, but as the pandemic eases and tourism begins to recover in the BHS, we anticipate renewed interest in elasmobranch conservation, particularly in those regencies with strong "elasmotourism" potential.

Continued monitoring of manta ray populations in Raja Ampat and the broader BHS will be required to investigate the efficacy of the management and conservation measures described herein and is considered a priority by both governmental agencies (ranging from the Raja Ampat and Cenderawasih Bay MPA Management Authorities to the West Papua provincial government and MMAF's National MPA Management Authority in Kupang) and NGOs such as Conservation International and Thrive Conservation. Given the vast region to cover and the challenges in monitoring marine megafauna, tourists and tourism operators in the BHS will be called upon to continue assisting with the monitoring the manta ray populations through citizen science (Setyawan et al., 2020). The Raja Ampat MPA Management Authority in particular is currently developing an integrated system to improve the contribution of citizen science to manta ray monitoring, and also continues to collaborate with NGOs and Universities to actively survey and monitor Raja Ampat's manta ray populations. Moreover, the Authority has now requested the Raja Ampat Manta Task Force to develop additional manta tourism regulations for eight additional dive sites with manta ray cleaning stations.

## 2.6. Conclusions

Science-based management, well-enforced MPAs, and protection of aggregation sites and critical habitats (e.g., nursery areas) are each considered important to ensure the recovery of elasmobranch populations (Ward-Paige et al., 2012). The adoption of each of these components in a holistic approach to manta ray conservation and management by Raja Ampat government agencies has allowed manta populations in the archipelago to thrive. Importantly, this approach was not carefully formulated in an *a priori* fashion; rather, it developed organically. Beginning with the designation of an extensive network of MPAs managed collaboratively by local communities and government and supported by NGOs, academia and the private tourism sector, the initiative added fisheries gear restrictions, a shark and ray sanctuary, a national manta awareness campaign, national protection legislation and multistakeholder tourism management components as it developed. It made use of a carefully worded "mantanomics" argument in favour of manta conservation over fisheries exploitation, and it worked with Indonesian media celebrities to utilize the power of social media to garner public support and influence policymakers. As this manta conservation initiative gained momentum in Raja Ampat, it influenced other elasmobranch protections (Indonesian Ministry of Marine Affairs and Fisheries, 2013) and eventually leveraged other regencies in Indonesia (including West Manggarai and Berau) to follow suit in protecting their manta rays (Government of Manggarai Barat, 2013; Government of Berau, 2019). It launched the first National Symposium on Conservation of Sharks and Rays, which has grown into a triennial event with continuously increasing numbers of Indonesian elasmobranch conservationists and scientists participating. It has thus provided an important "ray of hope" for the future of not only manta rays but all elasmobranchs in the world's largest archipelagic nation.

# Chapter 3.

# Population estimates of photo-identified individuals using a modified POPAN model reveal that Raja Ampat's reef manta rays are thriving

## 3.1. Introduction

Understanding population dynamics, particularly abundance and growth, through demographic modelling is crucial in evaluating the effectiveness of management strategies for threatened marine species in marine protected areas (MPAs) (Beissinger & Westphal, 1998; Norris, 2004). MPAs have long been known to provide protection to sessile benthos (e.g., hard corals) and to increase the abundance and biomass of relatively sedentary fish and invertebrate species (e.g., snappers, groupers and lobsters) both within and outside their boundaries (Gell & Roberts, 2003; PISCO, 2007). Recently, MPAs have also been shown to promote the recovery of populations of large mobile species (e.g., reef sharks) particularly when the MPAs themselves are large (Knip et al., 2012; Edgar et al., 2014; Jaiteh et al., 2016; Speed et al., 2018). Nonetheless, in large and remote MPAs, where enforcement is costly and difficult, the populations of those species with large home ranges are potentially more exposed to illegal fishing activities (Graham et al., 2010; Jacoby et al., 2020).

Estimating the abundance of highly mobile and migratory marine megafauna can be challenging, as individuals are capable of traveling vast distances, often remain submerged, and commonly use different habitats on a seasonal basis (Carroll et al., 2013; Couturier et al., 2014; Armstrong et al., 2019). Given these challenges, investigating predictable aggregation sites regularly occupied by these species provides an excellent opportunity to estimate demographic parameters such as population abundance through mark-recapture studies (Dudgeon et al., 2008; Williams et al., 2011).

The reef manta ray *Mobula alfredi*, listed as Vulnerable (VU) (Marshall et al., 2022) on the IUCN Red List, is distributed throughout the Indo-Pacific around nearshore areas in tropical and subtropical regions (Marshall et al., 2009). At a regional scale, *M. alfredi* frequently demonstrates seasonal movement patterns (Jaine et al., 2014; Setyawan et al., 2018; Armstrong et al., 2020b; Harris et al., 2020). At a local scale, this philopatric species shows high site fidelity to key aggregation sites such as cleaning sites and feeding grounds (Dewar et al., 2008; Couturier et al., 2011; Setyawan et al., 2018; Peel et al., 2019b). The predictable presence of *M. alfredi* at known and accessible aggregation sites facilitates the compilation of photographic identification (photo-ID) databases (Marshall & Pierce, 2012; Stevens, 2016), similar to those used extensively for population studies of whale sharks (*Rhincodon* *typus*) and white sharks (*Carcharodon carcharias*) (Graham & Roberts, 2007; Towner et al., 2013; McKinney et al., 2017).

Photo-ID techniques have been used to study the population demographics of manta rays in many regions. This non-invasive technique uses the patterns of natural ventral markings that are unique to each individual (Marshall et al., 2011). These markings remain unchanged throughout the individual's life, or at least for periods of 30 years or more (Couturier et al., 2014). These characteristics have enabled long-term photo-ID data to be used extensively to examine life history traits and reproductive strategies, and determine the fecundity and age at maturity of *M. alfredi* (Stevens, 2016). Long-term photo-ID datasets have also been used to estimate *M. alfredi* population size and survival probabilities using mark-recapture models in several countries (Deakos et al., 2011; Kitchen-Wheeler et al., 2011; Marshall et al., 2011; Couturier et al., 2014; Peel, 2019; Venables, 2020).

The Raja Ampat archipelago in West Papua, Indonesia, harbours large populations of both *M. alfredi* and oceanic manta rays *M. birostris* (Setyawan et al., 2020). Although manta rays have been subject to targeted fisheries in several regions of Indonesia (Heinrichs et al., 2011; Lewis et al., 2015), historically, they have not been systematically targeted by local fisheries in Raja Ampat waters (Beale et al., 2019). Nonetheless, there are anecdotal reports of sporadic targeting of manta ray aggregations in the early 2000s by shark fishers in northern Raja Ampat (Varkey et al., 2010). Local fishers also reported that manta rays were frequently observed as bycatch when outsider fishing boats using large drift nets occasionally operated in Raja Ampat in the 1990s and early 2000s (Setyawan et al., 2022a). Importantly, Raja Ampat's manta rays have been protected since 2007, when the Raja Ampat local government and local stakeholders started to implement a series of conservation measures in the region that began with the implementation of a network of MPAs, progressed to the declaration of all of Raja Ampat's regency waters as Southeast Asia's first shark and ray sanctuary in 2012, and culminated with the Indonesian government granting full national-level protection to both species of manta ray in 2014 (Setyawan et al., 2022a). As a result, Raja Ampat's manta rays have enjoyed increasingly strict protections for over a decade. However, the impact of these management measures on *M. alfredi* in one of Indonesia's most popular manta diving tourism destinations (O'Malley et al., 2013) has not yet been formally assessed. Setyawan et al. (2020) provided a broad overview of the natural history and basic demographic features of the *M. alfredi* population in Raja Ampat; however, no analysis of population dynamics was conducted. The only study to date on manta ray population dynamics in Raja Ampat was focused on *M. birostris*. Using mark-recapture models, Beale et al. (2019) estimated high survival probabilities for both females and males in annual population surveys from 2011–2016. This research highlighted the impact of the 2015–2016 major El Niño Southern Oscillation (ENSO) event in significantly increasing *M. birostris* sightings in southern Raja Ampat at the time.

In a recent assessment, Pacoureau et al. (2021) reported the global abundance of 31 species of oceanic sharks and rays (including *M. alfredi* and *M. birostris*) declined by 71% over the past five decades, primarily due to an 18-fold increase in relative fishing pressure. Similarly, Rohner et al. (2013; 2017) reported dramatic declines in *M. alfredi* sightings in southern Mozambique (with a 98% decrease between 2003 and 2016), while numerous authors have noted that the life history characteristics of manta rays (including late maturation and extremely low fecundity) make them highly vulnerable to population decline (Ward-Paige et al., 2013; Dulvy et al., 2014; Croll et al., 2015). While anecdotal evidence and testimonies by local communities and marine tourism operators suggest that Raja Ampat's *M. alfredi* population has been spared such a fate (Setyawan et al., 2022a), the aim of this paper is to examine manta ray population trends in Raja Ampat in a quantitative manner. Here, we used open population mark-recapture models based on photo-ID sighting data of *M. alfredi* sourced from citizen science and active surveys by the authors to explicitly examine the potential impacts of manta ray conservation and management efforts in the extensive Raja Ampat MPA network. The use of sightings data contributed by the public through citizen science, integrated with those collected by researchers, has been shown to be accurate and robust in mark-recapture studies (Davies et al., 2012; Robinson et al., 2018), and have been used in studies involving a range of different species including whale sharks (Meekan et al., 2006; Holmberg et al., 2009; Magson et al., 2022), manta rays (Beale et al., 2019), and sperm whales (*Physeter macrocephalus*) (Boys et al., 2019).

Using a modified version of the POPAN model (Schwarz & Arnason, 1996), we aimed to estimate the annual population sizes, survival probabilities, sighting probabilities, and per capita recruitment rates of *M. alfredi* (sub)populations using 11 years of sightings data from the two MPAs in Raja Ampat with the highest manta ray survey effort: Dampier Strait and South East (SE) Misool. Importantly, Raja Ampat's *M. alfredi* population is best described as a metapopulation consisting of at least four (and up to seven) local subpopulations, including those in the Dampier Strait and SE Misool (Setyawan et al., 2020). While individuals have been recorded moving between Dampier Strait and SE Misool MPAs using both photo-ID and acoustic telemetry, such movements are rare (only 10 recorded in fifteen years' of survey effort (Setyawan et al., 2020)), leading us to fit separate POPAN models for these two subpopulations. In general, the subpopulation in SE Misool MPA is relatively isolated (over 160 km between the closest known manta ray aggregation sites in SE Misool and Dampier Strait and with deep water to the south of the SE Misool MPA). By comparison, the Dampier Strait subpopulation shows the strongest connections to other subpopulations in Raja Ampat based upon evidence of movement of individuals from photo-ID and acoustic telemetry data (Setyawan et al., 2018; 2020). Given the proximity of the Dampier Strait to other hypothesised subpopulations (12-20 km to the West Waigeo and Fam subpopulations, respectively) and the frequent observation in Dampier Strait of large seasonal feeding aggregations of up to 112 individuals (Setyawan et al., 2020), we expected a significant number of "transient" individuals pass through Dampier Strait and might not be recorded there again – a situation that violates one of the key assumptions of the standard POPAN model. Based upon this concern, we have also incorporated a transience parameter in modelling the Dampier Strait subpopulation (described further below in the POPAN methods section).

## 3.2. Material & Methods

### 3.2.1. Study area

The Raja Ampat Archipelago covers an area of ~6.7 million hectares and is situated on the northwestern tip of West Papua Province in eastern Indonesia (Figure 3.1). The region is protected by a network of nine MPAs (including Dampier Strait and SE Misool) that cover nearly 2 million hectares; this network is part of a larger network of 26 MPAs covering 5.2 million hectares of a region commonly referred to as the Bird's Head Seascape of West Papua (Mangubhai et al., 2012; Setyawan et al., 2022a). In Raja Ampat, *M. alfredi* sightings have been documented from at least 101 different sites within the archipelago (Setyawan et al., 2020), while ventral photo-IDs of *M. alfredi* were captured from 51 sites (Figure 3.1).

Figure 3.1. Map of the Raja Ampat Archipelago in West Papua, Indonesia, denoting both the network of nine MPAs (shaded green polygons) and the 51 sites from which *M. alfredi* photo-IDs have been collected (red dots with white outline).

## 3.2.2. Data collection

### 3.2.2.1. Photo-ID

We collected *M. alfredi* ventral identification photos or videos (Stevens, 2016; Stevens et al., 2018b) from three primary sources (active surveys by the authors, submissions from collaborating dive resorts and liveaboard vessels, and contributions from citizen scientists) and entered into the Raja Ampat *M. alfredi* photo-ID database using the protocols developed by Stevens (2016). We determined the sex of individual manta rays from the presence (male) or absence (female) of claspers. We further used the length and extent of calcification of the claspers and development of clasper glands to estimate maturity in males (Marshall & Bennett, 2010). We recorded the presence of mating scars or visible signs of pregnancy and used these as indicators of sexual maturity in females (Marshall & Bennett, 2010; Stevens, 2016).

As detailed in Setyawan et al. (2020), each *M. alfredi* sighting in the Raja Ampat database included photographs of the ventral surface of the individual and associated metadata including date, time, location, estimated size (wingspan), sex, notes on maturity, and a number of other variables not pertinent to the present study. Sightings data contributed by citizen scientists consisted of photo-ID images, date and time, and location. We (ES and MI) manually matched all photo-ID images from each *M. alfredi* sighting, including those from collaborators and citizen scientists to the Raja Ampat *M. alfredi* identification catalogue. We then recorded either as a resighted individual or assigned a new unique identification code if sighted for the first time.

Here we used *M. alfredi* sightings data from only two MPAs (SE Misool and Dampier Strait) (Figure 3.1), where the collection of photo-ID data was the most consistent and where the most *M. alfredi* sightings data were recorded (Setyawan et al., 2020). Furthermore, we restricted our modelling to sightings data collected only from 2009–2019, due to the small amount of data available before 2009 (Appendix A Figure A.1). These 2009–2019 data from SE Misool and Dampier Strait MPAs were from 27 of the 51 sites in Raja Ampat from which *M. alfredi* ventral ID photos were recorded. Here we used the same *M. alfredi* sightings data reported in Setyawan et al. (2020), together with additional historical sightings data collected subsequently from professional underwater photographers.

## 3.2.3. POPAN models for Dampier Strait and SE Misool

### 3.2.3.1. Overview

First described by Schwarz and Arnason (1996), POPAN is an open population capture-recapture model capable of estimating population size, and how it changes, over a number of sampling occasions. The parameters directly estimated by a POPAN model are $M$, the superpopulation size of individuals available for sighting on at least one occasion; $p$, sighting probability; $\phi$, apparent survival probability; and $p_e$, the entry probability (i.e., the expected proportion of the $M$ individuals that are first available for sighting on any given occasion). Estimates of these parameters are used to derive estimates of the expected population size for each occasion, denoted $E(N_t)$ for occasion $t$. See Appendix B for further details.

Under the simplest POPAN model, sighting probabilities, survival probabilities, and entry probabilities are assumed to be constant over time. Alternatively, POPAN models allow us to estimate how these demographic parameters change between occasions, either by modelling how they relate to occasion-level covariates or by estimating a separate parameter for each occasion. They also allow us to estimate separate parameters and expected population sizes for males and females, choosing to either share parameters across sexes or estimate them separately. We denote $p_t$, $\phi_t$, and $p_{e,t}$ as the parameters for occasion $t$, noting that we require one fewer $\phi$ parameter than the number of occasions, because $\phi_t$ denotes the probability of survival between one occasion and the next, and the number of intervals between occasions is one fewer than the number of occasions.

Standard POPAN models require us to assume that sighting and survival probabilities are the same for all individuals within the same occasion. Because survey effort varied between Dampier Strait and SE Misool, we expected sighting probabilities for individuals typically resident at each location to be different. Differing environmental conditions may also induce spatial variation in survival. We therefore analysed sighting data from Dampier Strait and SE Misool separately, allowing us to estimate different model parameters (including population size) at each location. We considered each year to be an occasion, and so the data required by our model is a capture history for each detected individual, indicating the years in which each individual was detected.

### 3.2.3.2. Goodness-of-fit

We assessed goodness-of-fit for standard POPAN models using the suite of tests implemented in the R package R2ucare (Gimenez et al., 2018). Tests applied included an overall test for goodness-of-fit and TEST 3.SR that is often interpreted as a test for transience.

### 3.2.3.3. POPAN models with transience

As mentioned above, we considered transience is a likely scenario in the Dampier Strait *M. alfredi* subpopulation. The presence of transient individuals violates the assumption of constant survival probability required by standard POPAN models: transient individuals are only available for a single occasion before they permanently emigrate, thus, upon recruitment, they have apparent survival probabilities of zero. See Pradel et al. (1997) and Genovart and Pradel (2019) for the treatment of transience effects in capture-recapture models, although their focus is on models that estimate survival and recruitment only; here we focused on models that additionally estimate abundance.

We developed an extension to the standard POPAN model to accommodate transient individuals. Technical details of our new model are available in the Appendix B. We used a two-component discrete mixture to model survival probabilities (similar to "Parameterisation B" proposed by Genovart and Pradel (2019)), which introduces a new parameter, $\gamma_t$, the probability that an individual recruited on occasion $t$ is a transient. Newly-recruited individuals have apparent survival probabilities of zero with probability $\gamma_t$, and the usual apparent survival probability of $\phi_t$ with probability $1 - \gamma_t$. By considering transience a latent state, our model does not require us to determine which individuals are transients and which are not.

### 3.2.3.4. POPAN models with per capita recruitment

We made one further modification to the standard POPAN model. Typically, recruitment is estimated using the parameter $p_{e,t}$, the expected proportion of the $M$ individuals in the superpopulation that are recruited on occasion $t$. Under a null-model specification for recruitment, the same number of individuals is expected to be recruited each year, regardless of the underlying population size.

However, it is common for population dynamics models to link recruitment to the size of the population, because larger populations have the capacity to recruit more individuals (Snider & Brimlow, 2013). We included this feature by reparameterising the POPAN model to directly estimate per capita recruitment, denoted $\psi_t$ for occasion $t$, rather than the probabilities of entry, $p_{e,t}$, so that the expected number of new recruits in year $t + 1$ is given by $\psi_t N_t$. One advantage of our specification over the standard POPAN model is that per capita recruitment rates are more easily interpreted and are more biologically relevant than probabilities of entry. See Appendix B for further details, including how to calculate the usual probabilities of entry from our model as derived parameters.

### 3.2.3.5. Incorporating covariates

We considered the effects of an environmental covariate, the bimonthly Multivariate ENSO Index (MEI), on apparent survival, per capita recruitment, and sighting probabilities. We used the bimonthly MEI obtained from the NOAA Physical Sciences Laboratory (https://psl.noaa.gov/enso/mei/) to represent environmental conditions in the region. High positive values (>0.5) of the bimonthly MEI denote El Niño events, while low negative values (<-0.5) denote La Niña events (Appendix A Figure A.2). We then averaged the bimonthly MEI into annual indices to be consistent with the annual values of demographic parameters.

### 3.2.3.6. Candidate models

We first fitted models without transience and considered eight different model specifications (Table 3.1) for the sighting probabilities, survival probabilities, and per capita recruitment rates. We used a log link function to model per capita recruitment rates, and logit link functions for sighting and survival probabilities. With eight possible specifications for each of the three parameters, we obtained a total of 512 total candidate models. We did not consider models including effects of both time and MEI, because the parameters of such a model are not identifiable.

In the event that goodness-of-fit tests provided evidence for lack-of-fit, and in particular indicated the presence of transient individuals, we then additionally considered the same 512 model specifications, but also accommodated the effects of transience using our new model. We considered models that have a different transience probability for the first year of the study, then a constant transience probability for the remaining years. In the first year of our study, all individuals present are considered newly available for sighting, including those that were recruited that year (a mixture of transients and non-transients) and those that were recruited in previous years (all of which must be non-transients, because transients do not survive from one year to the next). On later occasions, only the mixture of transients and non-transients recruited that year are newly available for sighting, thus we expected a higher proportion of these new individuals to be transients compared to the first occasion.

Table 3.1. Description of model specifications for the sighting probabilities, survival probabilities, and per capita recruitment rates of *M. alfredi* subpopulations in Dampier Strait and SE Misool MPAs.

| No. | Model specification | Description |
|---|---|---|
| 1 | Intercept only | The parameter was constant for all years and the same for both sexes. |
| 2 | MEI only | After applying a link function, the parameter varied over time according to a linear relationship with MEI. |
| 3 | Time only | The parameter varied freely for each occasion but was the same for both sexes. This specification required estimating a separate sighting probability parameter for each occasion |
| 4 | Sex only | The parameter was constant over time, but different for each sex. |
| 5 | MEI and sex (additive) | After applying a link function, the parameter varied over time according to a linear relationship with MEI, and also with a constant difference between sexes. |
| 6 | MEI and sex (interaction) | After applying a link function, the parameter varied over time according to a linear relationship with MEI, with a different linear effect of MEI for each sex |
| 7 | Time and sex (additive) | The parameter varied freely for each occasion with a constant difference between sexes, so that the effect of time was the same for both sexes. |
| 8 | Time and sex (interaction) | The parameter varied freely for each occasion, with separate effects of time estimated for each sex. |

### 3.2.3.7. Model selection and model averaging

We used AIC to assess the degree to which each model is supported by the data, or QAIC if goodness-of-fit tests indicated the presence of overdispersion (Cooch & White, 2001). In the event that (Q)AIC did not identify a single model with considerably more support than all others, we calculated model-averaged estimates using the bootstrap approach recommended by Buckland et al. (2001).

Under this procedure, we selected a final candidate set of models within 10 (Q)AIC units of the model with the highest support (i.e., lowest (Q)AIC value). For each of 1,000 bootstrap iterations, we resampled *n* capture histories with replacement, where *n* is the number of capture histories in the original data. To each new data set, we fitted all the final candidate models. We retained estimates from the model with highest (Q)AIC support from each iteration. We then calculated the model-averaged point estimates by taking the mean of these retained estimates across the bootstrap resamples. Furthermore, we obtained 95% confidence interval (CI) limits from the 2.5th (lower CI limit) and 97.5th percentiles (upper CI limit) of these retained point estimates.

We also used the bootstrap procedure for hypothesis testing. We conducted hypothesis tests comparing males and females in terms of population size, survival probability, per capita recruitment rate, and sighting probability. For each, the null hypothesis was no difference between the sexes. We also tested for changes in these parameters over time. Again, each null hypothesis tested was for no difference between two specified occasions. To calculate a p-value, we obtained the proportion of estimates retained across the 1,000 bootstrap iterations that were in the tail of the distribution beyond the hypothesised value and multiplied this proportion by 2 for a two-sided test.

We conducted all analyses of goodness-of-fit, model fitting, model selection, model averaging, and hypothesis testing using custom code written in R version 4.1.2 (R Core Team, 2021), available in GitHub (https://github.com/b-steve/manta-popan).

### 3.2.3.8. Environmental variables

We examined two environmental variables, sea surface temperature (SST) and chlorophyll-*a* (chl-*a*) concentration to characterize the occurrence of El Niño events in the study area, as ENSO is a known contributor to the interannual variability of surface chl-*a* concentration and SST (Setiawan et al., 2020). We obtained annual SST Level 3 data between 2009 and 2019 from Moderate Resolution Imaging Spectroradiometer (MODIS) (https://oceancolor.gsfc.nasa.gov/) and plotted these using QGIS 3.22.3 (QGIS.org, 2021). Similarly, we used seasonal SST and chl-*a* distribution to examine the distribution changes of these variables every quarter between 2014 and 2016. The spatial resolution of both SST and chl-*a* was 4 km x 4 km.

## 3.3. Results

### 3.3.1. Population demographics and pregnancy rates

A total of 1,041 unique *M. alfredi* individuals were identified from 3,759 sightings recorded over 11 years of observations (2009–2019) in both Dampier Strait and SE Misool MPAs. Of these, more sightings were recorded in Dampier Strait (n = 2,580 sightings) than in SE Misool (n = 1,179 sightings). Despite this, the number of unique individuals identified was slightly higher in SE Misool (n = 536) than in Dampier Strait (n = 515), with 10 individuals recorded in both MPAs. Of these, 256 individuals (47.8%) in SE Misool and 332 individuals (64.5%) in Dampier Strait were resighted at least once.

The proportion of pregnant *M. alfredi* that were sighted and resighted in Dampier Strait, SE Misool, and both MPAs combined fluctuated over time from 2009–2019 (Figure 3.2). In Dampier Strait, the percentage of pregnant *M. alfredi* ranged from 0–26.9% (mean ± SD = 12.8 ± 8.7%). In SE Misool, the percentage of pregnant *M. alfredi* ranged from 3.2–41.4% (mean ± SD = 23.9 ± 12.9%) with high pregnancy rates in 2011 and 2015–2016. The lowest percentage of pregnancies were recorded in 2016 (Dampier Strait) and 2017 (SE Misool). Combining pregnancy rates in both MPAs, the rate declined after a peak in 2011 before rising sharply to the highest rate (35.1%) in 2016.

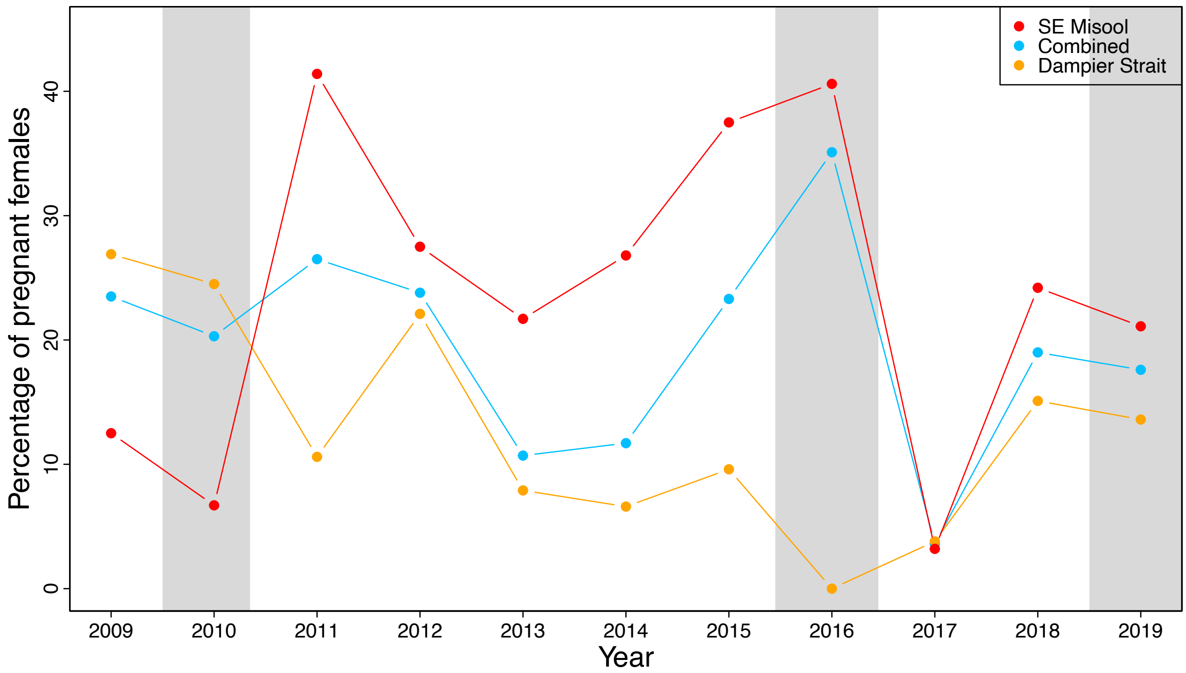

Figure 3.2. The percentage of pregnant *M. alfredi* relative to the total number of females in South East (SE) Misool (in red), Dampier Strait (in orange), and both MPAs (in blue) combined in 2009–2019. Grey shading represents three different El Niño events based on MEI.

### 3.3.2. Goodness-of-fit (GOF) tests

The GOF tests on capture history data showed contrasting results between SE Misool and Dampier Strait. The overall test was not significant ($\chi^2_{70}$ = 65.462, p = 0.631) for SE Misool, but was significant ($\chi^2_{69}$ = 187.003, p < 0.001) for Dampier Strait. Further tests for Dampier Strait showed that TEST 3.SR for females was significant ($\chi^2_{9}$ = 46.682, p < 0.001, z = 5.339), and likewise TEST 3.SR for males was significant ($\chi^2_{9}$ = 30.482, p < 0.001, z = 3.357), which can be explained by the presence of transient individuals (Genovart & Pradel, 2019). This provided evidence of lack-of-fit for a standard POPAN model, which is unsurprising given that we expected the presence of transient individuals in Dampier Strait.

### 3.3.3. Population modelling

We considered models that accommodate transients for Dampier Strait MPA because the GOF tests indicated that the standard POPAN models did not fit well. Model selection did not clearly identify a single combination of covariates that was best supported by the data. For each location, we retained models with an AIC/QAIC value within 10 units of the model with the highest AIC/QAIC support, resulting a total of 33 best-fitting models for Dampier Strait and 32 best-fitting models for SE Misool. Nevertheless, all retained models estimated similar increasing population trajectories for both MPAs, with variations in several years over the study period (Appendix A Figure A.3 & A.4).

In Dampier Strait, the annual estimated population sizes varied slightly amongst all best models (Appendix A Figure A.3). Several models showed a steady increase during the study period; some showed a considerable increase in 2010–2012 followed by a slight drop in 2016. Several other models showed two declines in the estimated population size in 2011, before a sharp increase in 2012–2014, despite an overall increasing trend over time. In comparison, the population sizes in SE Misool were relatively stable or increased steadily over the study period (Appendix A Figure A.4). Most models demonstrated substantial increases in 2016–2017 following the relatively stable rise in 2010–2015. Because the data did not clearly support one model over the others, we used a model-averaging procedure to calculate final estimates (Buckland et al., 2001). In the following three subsections, we report estimates obtained from the model averaging procedure described in subsection 2.3.7 (Model selection and model averaging) using the following format: point estimate (lower 95% CI limit, upper 95% CI limit).

### 3.3.4. Estimated population size

The total estimated population of females and males showed an increasing trend throughout the survey both in Dampier Strait (Figure 3.3A & 3.3B) and SE Misool (Figure 3.4A & 3.4B). In Dampier Strait, due to high uncertainty in the estimated population size in 2009 (which was likely caused by the low survey effort in that year), we did not include the estimates from 2009 when examining the population changes over time. Over the period 2010–2019, the estimated total population size increased significantly ($p = 0.018$) from 226 (161, 283) to 317 (280, 355), with a difference of 90 (18, 179) individuals over the decade. Although the percentage change in population size between years varied throughout the study, the estimated overall increase between 2010 and 2019 is the same as we would observe from a population with a compound growth of 3.9% (0.7, 8.6) per annum. A particularly steep rise occurred between 2011 and 2014, with a significant ($p = 0.012$) increase of 58 (7, 135) individuals and a compound annual growth of 8.1% (0.9, 20.5). The highest rate of change was estimated between 2013 and 2014, during which the population increased significantly ($p = 0.006$) at a rate of 11.8% (0.94, 39.3) in one year. Between sexes, there was no significant difference ($p = 0.968$) in the compound annual growth between males (4.0%; 0.7, 8.7) and females (3.9%; 0.2, 8.8) in 2010–2019. Furthermore, the mean population size of females (137 individuals; 125, 151) was not significantly ($p = 0.264$) larger than that of males (130 individuals; 114, 148), with a mean expected female to male ratio of 1.06:1 (0.96:1, 1.24:1) (Figure 3.3F).

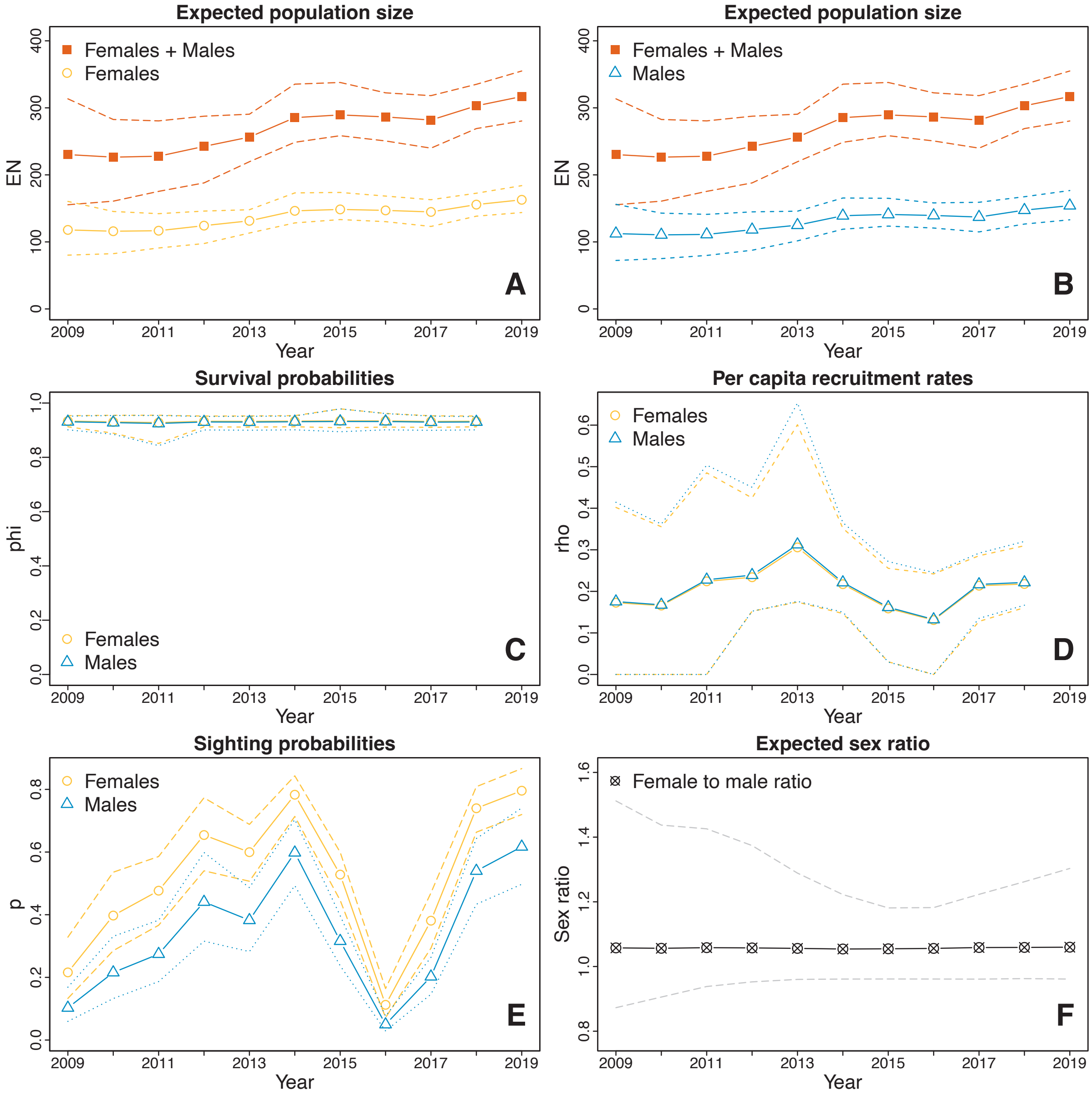

Figure 3.3. Estimates (solid lines) and CIs (dotted and dashed lines) derived from model averaging procedures for the *M. alfredi* subpopulation in the Dampier Strait MPA. (A & B) The estimated expected population sizes of females and males relative to the estimated expected overall population sizes of both sexes combined; (C) Survival probabilities of females and males; (D) Per capita recruitment rates of males and females; (E) Sighting probabilities of females and males; and (F) Expected female to male ratio. The orange lines represent female estimates, blue lines represent male estimates, and red lines represent total estimates of females and males. Black and grey lines represent sex ratio estimates (female to male). Dotted lines represent upper and lower confidence intervals.

In SE Misool, due to high uncertainty in the estimated population size in 2019, we did not include the estimates from 2019 when examining the population changes over time. Over the period 2009–2018, the estimated total (female and male) population size increased significantly ($p = 0.008$) from 210 (137, 308) to 511 (393, 618), with an estimated difference of 300 (139, 427) individuals over a decade. Despite variation in the percentage change in population size between years throughout the study, the estimated overall change during this period is the same as we would observe from a population with a compound annual growth of 10.7% (4.3, 16.1). A steep rise occurred between 2015 and 2017, during which the estimated population size increased significantly ($p = 0.034$) from 327 (253, 418) to 474 (390,

575) in just two years, with an estimated difference of 147 (5, 277) individuals and a compound annual growth of 21.1% (0.6, 41.8). In 2015–2017, the compound annual growth of females (30.8%, 13.7, 47.4) was higher than that of males (5.7%, -26.3, 62.4). In 2016, in particular, the estimated female population size increased at the highest rate (41.5%; 15.0, 71.7). Additionally, the estimated mean population size of females was significantly ($p < 0.001$) larger than that of males, with a difference of 111 (70, 149) individuals and a mean expected female to male ratio of 2.01:1 (1:48:1, 2.59:1) (Figure 3.4F).

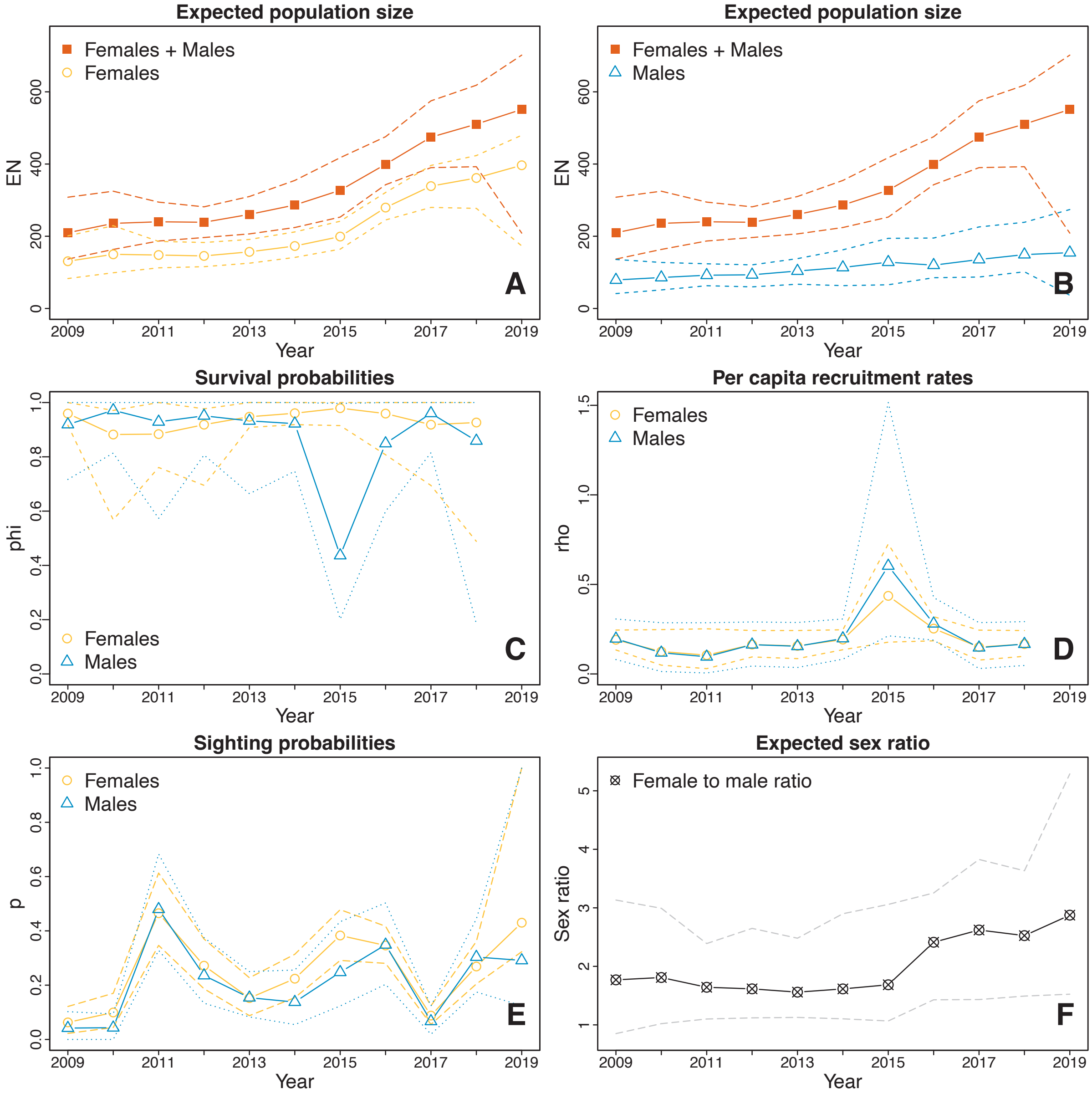

Figure 3.4. Estimates (solid lines) and CIs (dotted and dashed lines) derived from model averaging procedures for the *M. alfredi* subpopulation in the SE Misool MPA. (A & B) The estimated expected population sizes of females and males relative to the estimated expected overall population sizes of both sexes combined; (C) Survival probabilities of females and males; (D) Per capita recruitment rates of males and females; (E) Sighting probabilities of females and males; and (F) Expected female to male ratio. The orange lines represent female estimates, blue lines represent male estimates, and red lines represent total estimates of females and males. Black and grey lines represent sex ratio estimates (female to male). Dotted lines represent upper and lower confidence intervals.

### 3.3.5. Survival probabilities and per capita recruitment rates

The estimated apparent survival probabilities in both MPAs showed no significant differences between years or sexes. In Dampier Strait, the estimated survival probabilities were similar across all years and the difference between sexes was not significant (Figure 3.3C). The estimated mean apparent survival probability was 0.93 (0.91, 0.95) for females and 0.93 (0.90, 0.95) for males with no significant difference between the sexes ($p = 0.940$). In SE Misool, the estimated mean apparent survival probability for females (0.93; 0.87, 0.97) was higher than that of males (0.87; 0.76, 0.94), however, the difference was also not significant ($p = 0.216$) (Figure 3.4C). The estimated apparent survival probability for males decreased to 0.44 (0.20, 1.00) in 2015, however, the drop was not significant as seen from the wide CI.

The estimated per capita recruitment rates in both MPAs were typically around 0.20 for both sexes (Figure 3.3D & 3.4D). There were no significant differences between years or sexes. In Dampier Strait, the estimated mean per capita recruitment rate for females was slightly higher than that of males, but the difference was not significant ($p = 0.959$). In SE Misool, the sharp increases in per capita recruitment rates in 2015 were not significant given the wide CIs.

### 3.3.6. Sighting and transient probabilities

The estimates of sighting probabilities in Dampier Strait (Figure 3.3E) overall were higher than those in SE Misool (Figure 3.4E). For both MPAs, the estimated sighting probabilities varied depending on sex and years. In Dampier Strait, the estimated mean sighting probabilities of females $\hat{p}^f = 0.52$ (0.47, 0.57) was significantly ($p < 0.001$) higher than that of males $\hat{p}^m = 0.34$ (0.28, 0.38). The sighting probabilities showed a similar trend over time, with general increase from 2009 to 2014, reaching the lowest probability in 2016 and rising again in the following years. In SE Misool, the estimated mean sighting probability of females $\hat{p}^f = 0.25$ (0.21, 0.31) was slightly higher than that of males $\hat{p}^m = 0.21$ (0.16, 0.30), but the difference was not significant ($p = 0.294$). A significant dip was estimated in 2017 for both sexes.

Transient probabilities were only estimated for Dampier Strait MPA following the GOF test results. As per the Methods subsection *POPAN models with transience*, we estimated a constant transience probability across all occasions, aside from the first occasion (2009), for which we estimated a separate probability. The estimated transience probability for the first occasion was 0.10 (0.00, 0.30) and was 0.49 (0.32, 0.63) for the remaining occasions.

## 3.4. Discussion

Over a decade during the study period, the estimates of the population size of *M. alfredi* in both the Dampier Strait and SE Misool MPAs showed increasing trends, with slightly different growth patterns between populations. In Dampier Strait, the population exhibited a significant growth in size, particularly between 2011 and 2014. In comparison, the population in SE Misool was estimated to have increased substantially after 2015. The increased estimated population size in both MPAs over a decade suggests that these are robust findings. Setyawan et al. (2020) reported a higher proportion of pregnant females in Raja Ampat than in other studied populations of *M. alfredi* across the Indo-Pacific. Despite several studies reporting biennial or longer reproductive periodicities (Marshall & Bennett, 2010; Deakos et al., 2011; Stevens, 2016), a total of 16 female *M. alfredi* in Raja Ampat were recorded with annual reproductive periodicity, including one exceptional individual which had four consecutive-year pregnancies and a total of five pregnancies confirmed in seven years. Setyawan et al. (2020; 2022b) reported four *M. alfredi* nurseries in Raja Ampat, and 65 young-of-the-year (YoY) were identified between 2011 and 2019, a number that surpasses other published studies (Marshall & Bennett, 2010; Couturier et al., 2014; Stevens, 2016; Germanov et al., 2019; 2022). These findings all support the suggestions of our models that *M. alfredi* (sub)populations are growing in both Raja Ampat MPAs studied here, with high fecundity and per capita recruitment rates. Importantly, the overall rates of annual population increase estimated in our study (3.9% in Dampier Strait and 10.7% in SE Misool) match well with the theoretical rates of increase calculated by previous authors. Dulvy et al. (2014) calculated the maximum intrinsic rate of population increase ($r_{max}$) of manta rays, with the median $r_{max}$ of 0.116 per year (notably, one of the lowest $r_{max}$ of 106 species of sharks and rays examined), while Ward-Paige et al. (2013) estimated an intrinsic rate of population increase of *M. alfredi* of 5% per year.

The 2016–2017 increase in estimated population size in SE Misool, which was largely driven by females, is likely associated with favourable environmental conditions in Raja Ampat, particularly in the southern region. This coincides with the occurrence of an intense El Niño event between May 2015 and May 2016, as indicated by high positive MEI values (Appendix A Figure A.2). Beale et al. (2019) showed that El Niño conditions lead to a drop in SST and an increase in wind-driven vertical mixing in SE Misool, which in turn leads to a shallowing of the thermocline and apparent increases in plankton density. With this in mind, we posit that the intense El Niño likely enhanced the environmental conditions for feeding for *M. alfredi* and therefore attracted migrants into the study area from neighbouring regions or unmonitored areas in SE Misool. This can be seen from the spikes in the per capita recruitment rates estimated for both females and males in SE Misool in 2015 (Figure 3.4D). Among all 32 best models in SE Misool, the per capita recruitment rates in 29 models and survival probabilities in 18 models varied depending on MEI (Appendix A Table A.2). Similarly, among the 33 best models in Dampier Strait, the per capita recruitment rates in 14 models and the survival probabilities in 19 models varied depending on MEI (Appendix A Table A.1). Given the small number of YoY and juveniles observed in the study area, it is possible that the high per capita recruitment rates in this period may not reflect YoY individuals entering the existing study populations but are rather indicative of the immigration of adult or subadult individuals, as observed for *M. birostris* during the extreme El Niño event in 2015–2016 (Beale et al., 2019). The sharp spike of estimated per capita recruitment rates in 2015 led to the substantial increase in the estimated population size in 2016. This increase, however, only occurred with female *M. alfredi* mainly due to the drop in male survival probability regardless of the high per capita recruitment rates. One possibility is that in 2015 several males in the population left the SE Misool study area, but at the same time males immigrated from neighbouring regions outside the study area. However, our estimates of per capita recruitment rate and survival probability for males in 2015 are imprecise, as indicated by their wide CIs, and so care should be taken when interpreting patterns in these estimates.

The 2015–2016 El Niño also likely led to the increase in sighting probabilities in SE Misool (Figure 3.4E). This extreme El Niño, combined with the southeast monsoon at a regional scale, generated upwelling-induced cooler SSTs, and high chl-*a* concentrations. These were indicative of higher-than-normal productivity (Gordon, 2005; Setiawan et al., 2020), especially in the third and last quarter of 2015 (Appendix A Figure A.6 & A.7). Chl-*a* concentrations were positively correlated with the number of *M. alfredi* sighted (Jaine et al., 2012; Harris et al., 2020) and the high number of sightings is most likely due to increases in zooplankton density, attracting foraging aggregations (Weeks et al., 2015).

In comparison to the SE Misool population, the extreme 2015–2016 El Niño likely affected the *M. alfredi* in Dampier Strait differently. In this region, the sighting probabilities for both females and males were estimated to drop significantly in 2015 and were lowest in 2016 (Figure 3.3E), despite the high and stable apparent survival probabilities for both sexes. Moreover, the per capita recruitment was also estimated to be declining after reaching a peak in 2013 and was lowest in 2016 for both sexes. In 2015–2016, the relatively low sighting probabilities and per capita recruitment rates in Dampier Strait were likely driven by fewer individuals sighted due to temporary emigration to areas of high productivity to maximise foraging activities, possibly to west Waigeo Island. Setyawan et al. (2018) found that *M. alfredi* tracked using passive acoustic telemetry moved seasonally between Dampier Strait and areas in the west of Waigeo. During the second half of 2015, the west Waigeo region and southwestern Raja Ampat waters were substantially cooler than in the Dampier Strait (Figure 3.1; Appendix A Figure A.6). During this time period, which coincided with the southeast monsoon and the extreme El Niño event, considerably fewer acoustic tagged *M. alfredi* were detected by the receiver at Manta Ridge in Dampier Strait compared to the same period in the previous year, and there were more detections on receivers located at Yefnabi Kecil and Eagle Rock in west Waigeo region, situated less than 70 km from Manta Ridge (Setyawan et al., 2018) (Figure 3.1).

The cooler waters and higher productivity measured in SE Misool during El Niño events likely resulted in highly abundant prey for *M. alfredi* during these periods. Based on our field observations, these periods of increased prey availability also seem to have caused more frequent and larger *M. alfredi* aggregations, leading to increases in the opportunities for mating (Setyawan et al., 2020). We hypothesise that increased pregnancy rates, in particular those in SE Misool in 2011 and 2015–2016, were likely caused by the El Niño events leading to greater foraging opportunities, better body condition and more mating opportunities in the cooler waters (Appendix A Figure A.5 & A.6). This is supported by per capita recruitment rates and apparent survival probabilities in SE Misool that are strongly linked with MEI (Appendix A Table A.2). In the same region and period, Beale et al. (2019) reported a significant increase in *M. birostris* sightings as a result of the favourable feeding conditions created by the ENSO event.

The high pregnancy rates occurred during and/or shortly after the El Niño events, with an elevated number of YoY individuals expected to enter the population approximately 1–2 years thereafter. However, only small numbers of juveniles were observed in the Dampier Strait and SE Misool, the majority of which were newly identified sub-adults or adults >2.4 m disc width (DW) (Setyawan et al., 2020). This apparent lack of YoY individuals in the study areas following periods of high pregnancy rates is perhaps not surprising. As observed in other countries (Couturier et al., 2014; Stevens, 2016; Peel, 2019), primary *M. alfredi* feeding and cleaning sites such as those in Dampier Strait and SE Misool tend to be dominated by adults, while YoY and juvenile individuals are generally believed to occupy nursery areas, where they are assumed to have a reduced risk of predation, until they are large enough to join adult aggregations (Marshall & Bennett, 2010; Heupel et al., 2019). With this in mind, we hypothesise that the expected high number of YoY manta rays following these periods of high pregnancy rates were most probably born and remained in nursery areas adjacent to Dampier Strait and SE Misool. For example, many juveniles <2.4 m DW have been observed in Yefnabi Kecil (Figure 3.1) in West Waigeo (Setyawan et al., 2022d), while three other nursery habitats have been identified in areas adjacent to the Dampier Strait, with juvenile residency periods up to 28 months (Setyawan et al., 2020). Despite being further away from Dampier Strait and SE Misool, the best studied manta ray nursery in Raja Ampat, the Wayag lagoon nursery (Setyawan et al., 2022b), may also have hosted a number of the YoY expected after the high pregnancy rates seen during El Niño events. Indeed, Setyawan et al. (2020) also documented the movement of a YoY first identified in the Wayag lagoon nursery as a 1.8 m DW male and then resighted six years later as a 2.6 m DW young adult male in SE Misool, 296 km south of the nursery.

As the 2015–2016 El Niño event ceased, the environmental conditions changed and a La Niña event ensued from mid 2016 until early 2018, indicated by negative MEI values in that time period. This may be associated with decreases in the sighting probabilities in 2017 and gradual declines in per capita recruitment rates between 2016 and 2017 in SE Misool, slightly slowing the rate of increase of the population towards the end of the study period. In Dampier Strait, the situation was reversed, where the per capita recruitment rates and also the sighting probabilities increased in 2017 and 2018. During the La Niña event, the surface waters in southern (around Misool) and western Raja Ampat (West Waigeo) were relatively warmer and less productive (Setiawan et al., 2020), and hence less favourable to manta ray feeding. A decrease in the amount of food might lead to two different possible scenarios. First, fewer individuals immigrated to the study area in SE Misool from neighbouring regions, therefore the per capita recruitment rates declined. At the same period, more individuals immigrated into the study area in the Dampier Strait from neighbouring regions in western Raja Ampat. Second, Chapman et al. (2012) highlights that partial migration is extremely common in fishes, in which some individuals in the population are residents and some are migratory. Andrzejaczek et al. (2020) suggested that *M. alfredi* may be partial migrants, from which we might conclude that resident individuals in SE Misool and West Waigeo stayed and exploited deeper water to forage, while migratory individuals left these areas to forage in more productive areas around Raja Ampat, including the Dampier Strait.

The high apparent survival probabilities of non-transient female and male *M. alfredi* in both MPAs implies a relatively low rate of individual mortality, or a low rate of permanent emigration from the core study areas, or likely a combination of both. The low rates of mortality and permanent emigration are reflected in the high frequency of resighting, with several individuals sighted regularly over periods of more than ten years. Setyawan et al. (2020) reported that 46% of the *M. alfredi* identified were resighted at least once after they were first sighted, with some individuals resighted up to 13 years later. High apparent survival was also reported from eastern Australia (Couturier et al., 2014) and Hawaii (Deakos et al., 2011), where *M. alfredi* showed strong site fidelity to aggregation sites and targeted fisheries were absent. By comparison, *M. alfredi* in Mozambique were targeted in subsistence fisheries (O'Malley et al., 2017), and the population showed a decreasing trend in annual estimated apparent survival from 0.76 to 0.65 over 15 years (2003–2018), suggesting high mortality associated with continuing pressure from targeted fisheries and insufficient conservation efforts to protect the population (Rohner et al., 2013; Venables, 2020). Increasing fishing pressure is responsible for major global declines in oceanic shark and ray populations in the last five decades (Dulvy et al., 2021; Pacoureau et al., 2021). *M. alfredi* is a long-lived and late-maturing species that only becomes sexually mature at 11 (males) and 15 years (females) of age (Stevens, 2016); therefore, a high survival probability over a long period of time is required to ensure that populations persist and continue to thrive (Kanive et al., 2015).

Overall, the estimated sighting probabilities were higher in Dampier Strait than in SE Misool, which likely reflects the higher survey effort and substantially larger amount of sightings data collected in Dampier Strait than in SE Misool. The estimated sighting probabilities for females were in general higher than those for males, in particular in Dampier Strait. This is likely because most *M. alfredi* sightings collected in both MPAs were from cleaning sites, and females, especially adults, visit cleaning sites more frequently than males (Couturier et al., 2014; Stevens, 2016; Perryman et al., 2019). Indeed, the majority of the 20 most-sighted individuals in Raja Ampat were females (Setyawan et al., 2020).

Using TEST 3.SR, we found evidence to suggest that new individuals sighted for the first time had a lower probability of being resighted in comparison with individuals that had been sighted previously, and the presence of transient individuals is one explanation for this effect (Genovart & Pradel, 2019). Using our model, we estimated that approximately half of individuals (0.49; 95% CI: 0.32, 0.63) recruited to the population in Dampier Strait were transients. Transience might be higher in wide-ranging species capable of travelling long distances (Armstrong et al., 2019) and in large aggregations (Setyawan et al., 2020), thereby increasing the challenge of photo-identifying all individuals. Future studies using long-term photo-ID and incorporating photos from other regions may reveal the transient individuals as permanent or temporary migrants (Hupman et al., 2018). Our modification of the standard POPAN model by incorporating per capita recruitment and transience parameters represents an important advance in mark-recapture modelling that should prove useful when examining other manta ray populations and other highly migratory species that are likely to have a significant percentage of transient individuals.

Science-based management, MPA enforcement, and protection of aggregation sites and critical habitats (e.g., nursery areas) are each considered critical to ensure the recovery of elasmobranch populations (Ward-Paige et al., 2013). The adoption of each of these components in a holistic approach to manta ray conservation and management by the Raja Ampat MPA Management Authority likely helps explain the significant population increase reported in our study (Setyawan et al., 2022a). These management measures were responsible for effectively forcing shark fishers to relocate to areas outside Raja Ampat or change their livelihoods (Jaiteh et al., 2016). While limited shark fishing (and the resulting potential for manta ray bycatch) undoubtedly still occurs in the more remote and unpatrolled areas outside of Raja Ampat's MPA boundaries, almost all known manta ray aggregation sites and all known nurseries are located within the actively-patrolled MPA network – suggesting that Raja Ampat's *M. alfredi* are indeed well-protected (Setyawan et al., 2020). By contrast, the reef regions in closest proximity to Raja Ampat (including Halmahera to the west and Seram to the south) both host local populations of manta rays, but they are currently not protected by MPAs. *M. alfredi* in Raja Ampat exhibit a strong pattern of residency, likely due to the year-round presence of reliable and abundant food sources precluding any need to risk crossing the deep-water barriers to these adjacent islands and reef systems (Setyawan et al., 2018; 2020). As such, while occasional movements to unprotected reef areas are certainly possible, we suggest that the current MPA network and associated manta ray protection measures in Raja Ampat (Setyawan et al., 2022a) are seemingly sufficient to ensure this population is both protected and in fact actively growing. Viewed in the context of the Pacoureau et al. (2021) report of a major global decline in oceanic shark and ray populations (including *M. alfredi*) over the last five decades, primarily due to increasing fishing pressure, the reverse situation in Raja Ampat provides a reason for optimism when a holistic approach is adopted for elasmobranch conservation initiatives. This study also underlines the importance of long-term monitoring to evaluate the effectiveness of conservation management measures on *M. alfredi* populations.

## 3.5. Conclusions

We found strong evidence that the populations of *M. alfredi* in both the Dampier Strait and SE Misool MPAs in the Raja Ampat archipelago have increased significantly over our decade-long study period. Our results suggest that the series of conservation and management measures implemented in Raja Ampat since 2007 (Setyawan et al., 2022a), including the creation and enforcement of a large-scale network of nine MPAs, the designation of Southeast Asia's first shark and ray sanctuary, a national manta ray protection regulation, and the formulation of gear restrictions and manta tourism regulations in Raja Ampat MPAs, have substantially reduced fisheries-related pressures on the *M. alfredi* populations there. Coupled with El Niño–Southern Oscillation events that are strongly associated with increased per capita recruitment rates and high apparent survival probabilities, all these factors have enabled the *M. alfredi* (sub)populations in the Dampier Strait and SE Misool MPAs to thrive. Finally, we made substantial advances in the use of POPAN models to estimate the population size of large migratory species like manta rays by incorporating transience and per capita recruitment parameters.

# Chapter 4.

# How big is that manta ray? A novel method to measure the size of *Mobula alfredi* using small drones in Raja Ampat, Indonesia

## 4.1. Introduction

Body size is a life history parameter used to provide insights into key aspects of a species' and individual's biology, including maturity stage, reproductive status, the demographics of a population, and environmental and habitat conditions to which individuals are exposed (Perryman & Lynn, 1993; Christiansen et al., 2016; Rogers et al., 2017; Gray et al., 2019). Given this, obtaining accurate measurements of animal body size is crucial for the conservation and management of most animal species (Gray et al., 2019). Measuring the morphometric features of large animals, which can be difficult or dangerous to approach, can be problematic (Perryman & Lynn, 1993; Deakos, 2010). Most methods require close contact with or restraint of the animals, which has the potential to impact negatively upon these individuals (Gaudioso et al., 2014). Photogrammetry, a non-invasive approach, allows us to accurately obtain measurements of large animals without physical contact (Schenk, 2005; Gray et al., 2019). Photogrammetry has been used to estimate the length, body weight, and other size measurements of a wide variety of animal species, from sheep to sharks to dolphins (Bräger et al., 1999; Jeffreys et al., 2013; Menesatti et al., 2014).

The reef manta ray (*Mobula alfredi*) is listed as Vulnerable on the IUCN Red List of Threatened Species, primarily due to fisheries exploitation (both as a target and as bycatch) of this slow breeding species (Marshall et al., 2022). Comprehensive information on the body size and size at maturity of manta rays is important to understand their life history and to design effective conservation management strategies (Stevens, 2016; Rambahiniarison et al., 2018). To date, three methods have been commonly used to measure the body size of free-swimming manta rays, including visual estimation (Stevens, 2016), paired laser photogrammetry (Deakos, 2010), and estimation using paired stereo video camera systems (Peel et al., 2019b).

Of these three techniques, underwater visual estimation is the most commonly-used method to record the size of *M. alfredi*; typically, disc width (DW, defined by Notarbartolo Di Sciara (1987) as the greatest dimension between the outermost tips of the pectoral fins) is estimated based on known lengths of divers or snorkelers directly above, below, or next to the manta rays (Marshall & Bennett, 2010; Stevens, 2016). Despite the ease and practicality of this approach, visual size estimation can generate significant biases and inconsistencies in size estimates (Sequeira et al., 2016).

In an attempt to improve upon the accuracy of the visual estimation approach, Deakos (2010) and Couturier et al. (2014) utilized paired laser photogrammetry to measure the body size of *M. alfredi* in Hawaii and eastern Australia, respectively. Two laser pointers were mounted on an aluminum plate parallel to each other and at a measured distance apart from one another, with a video or still camera mounted midway between the two pointers. The laser pointers project two light points, which are a known distance apart (either 50 cm (Couturier et al., 2014) or 60 cm (Deakos, 2010)) onto the manta ray, thereby allowing an extrapolation of the manta ray's size using readily available photo processing software (Deakos, 2010).

More recently, a paired stereo-video camera system has been used to measure *M. alfredi* in the Seychelles (Peel et al., 2019b). This technique utilizes a pair of video cameras mounted on a bar at a measured distance apart, allowing overlap of the cameras' field of view (Letessier et al., 2015). Resulting paired images of each manta ray are processed with a custom software that allows calculation of the size of the animal; this technique has been proven to estimate the length of fishes more accurately than the visual estimation technique (Harvey et al., 2002), and has recently been used to accurately measure whale sharks *Rhincodon typus* (Sequeira et al., 2016) and oceanic whitetip reef sharks *Carcharhinus longimanus* (Delacy et al., 2017). While the aforementioned methods have been used with increasing accuracy to measure the body size of *M. alfredi*, all three methods require a diver or snorkeler to be in the water with the manta rays to visually estimate their size or operate the camera setups, which can be time-consuming and costly and potentially lead to negative behavioral responses from the manta rays being measured (Murray et al., 2020).

Importantly, many authors attempting to measure the body size of manta rays have expressed concern over the use of the disc width (DW) dimension, noting that it can be difficult to reliably measure the maximum distance between the fully-extended wing tips for a variety of reasons - ranging from the challenge of photographing free-swimming manta rays at exactly the moment of maximum extension of the pectoral fins (Francis, 2006; Marshall et al., 2008; Deakos, 2010) to issues with preserved specimens that have been stored with the wings in a curled fashion that prevents straight-line measure (Notarbartolo Di Sciara, 1987). Nonetheless, DW remains the standard measure of body size for all rays in the Order Myliobatiformes, including manta rays in the Family Mobulidae (Last et al., 2016). Because of the fragility and common breakage of the elongated tails, measures of total or standard length (TL or SL) common for most other fishes are considered unreliable in these rays, with DW being the largest reliable dimension to measure (Notarbartolo Di Sciara, 1987). Because of the difficulties of measuring DW in live manta rays especially, previous authors have suggested measuring disc length (DL, defined by Notarbartolo Di Sciara (1987) as the dimension measured from the midpoint of the rostral margin to the free rear tip of the pectoral fin; Figure 4.1) as a more easily and accurately measured dimension of size, from which DW can then be readily calculated using a regression formula (e.g., Deakos (2010)).

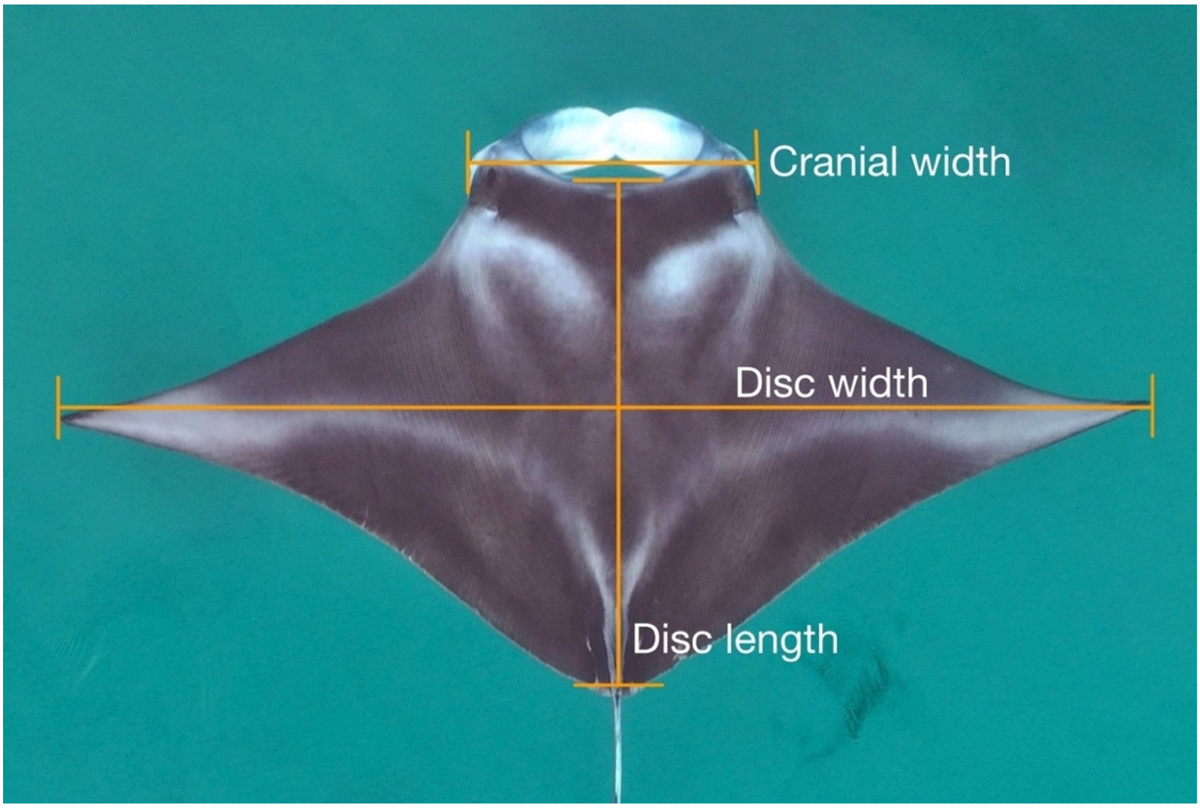

Figure 4.1. Three dimensions (Disc width – DW, Disc length – DL, and Cranial width – CW) of *M. alfredi* measured during image processing and measurements, as defined by Notarbartolo Di Sciara (1987).

Drones are an emerging technology that are increasingly affordable and easy to operate and have been used extensively for a wide variety of marine research purposes (Torres et al., 2018; Johnston, 2019; Lyons et al., 2019; Schofield et al., 2019; Landeo-Yauri et al., 2020). We believe drones have tremendous potential to address some of the difficulties in measuring body size in manta rays with little or no disruptive interaction with the observed animals. Measurements generated using drones through photogrammetry, however, are imperfect and subject to errors and uncertainties resulting from various factors including altitude reading, image quality, and the position of objects in the water (Dawson et al., 2017; Christiansen et al., 2018; Burnett et al., 2019). Given these concerns, statistical methods for analyzing drone-based measurements are required to assess these errors if they are non-negligible (Bierlich et al., 2021).

Taking the above into account, we report here the development of a novel method using small, commercially available drones to measure body size of surface-feeding *M. alfredi* in Raja Ampat, West Papua, Indonesia. Specifically, we employed aerial photogrammetry techniques, including a floating polyvinyl chloride (PVC) pipe of known length as a reference scale, to measure three morphometric dimensions of *M. alfredi*: the aforementioned disc width DW and disc length DL, as well as cranial width CW (defined by Notarbartolo Di Sciara (1987) as the maximal dorsal width between antorbital processes). We developed a hierarchical multivariate model for several purposes, including to estimate the true value of measurements of these three dimensions from replicate drone measurements, to examine correlations between these three dimensions, and to predict the notoriously difficult-to-measure DW from the drone measurements of other dimensions (CW and DL) (Figure 4.1), while also dealing with imperfect drone measurements associated with errors and uncertainties. The “true value” of a given measurement is defined as “the actual value that would be obtained with perfect measuring instruments and without committing any error of any type in collecting primary data” (Eurostat, 2002). Finally, we report upon our initial efforts to use drones to determine the sex and maturity status of surface-feeding *M. alfredi*.

## 4.2. Material & Methods

### 4.2.1. Study area

This study was undertaken in the Raja Ampat Archipelago, West Papua, eastern Indonesia (Figure 4.2). This region covers ~4.5 million ha and is home to large populations of both *M. alfredi* and oceanic manta rays (*M. birostris*) (Beale et al., 2019; Setyawan et al., 2020) that have been fully protected in this region since 2012 (Setyawan et al., 2022a). The surveys were conducted in five areas of Raja Ampat: Wayag lagoon, Yefnabi Kecil fringing reef, the Fam islands, Hol Gam bay, and the patch reefs east of Arborek island (Dampier Strait) (Figure 4.2). These five areas are all well-protected from significant wave action and frequently host adult and/or juvenile *M. alfredi* surface feeding or cruising in calm water conditions that are ideal for drone photogrammetry (Setyawan et al., 2018; Setyawan et al., 2020).

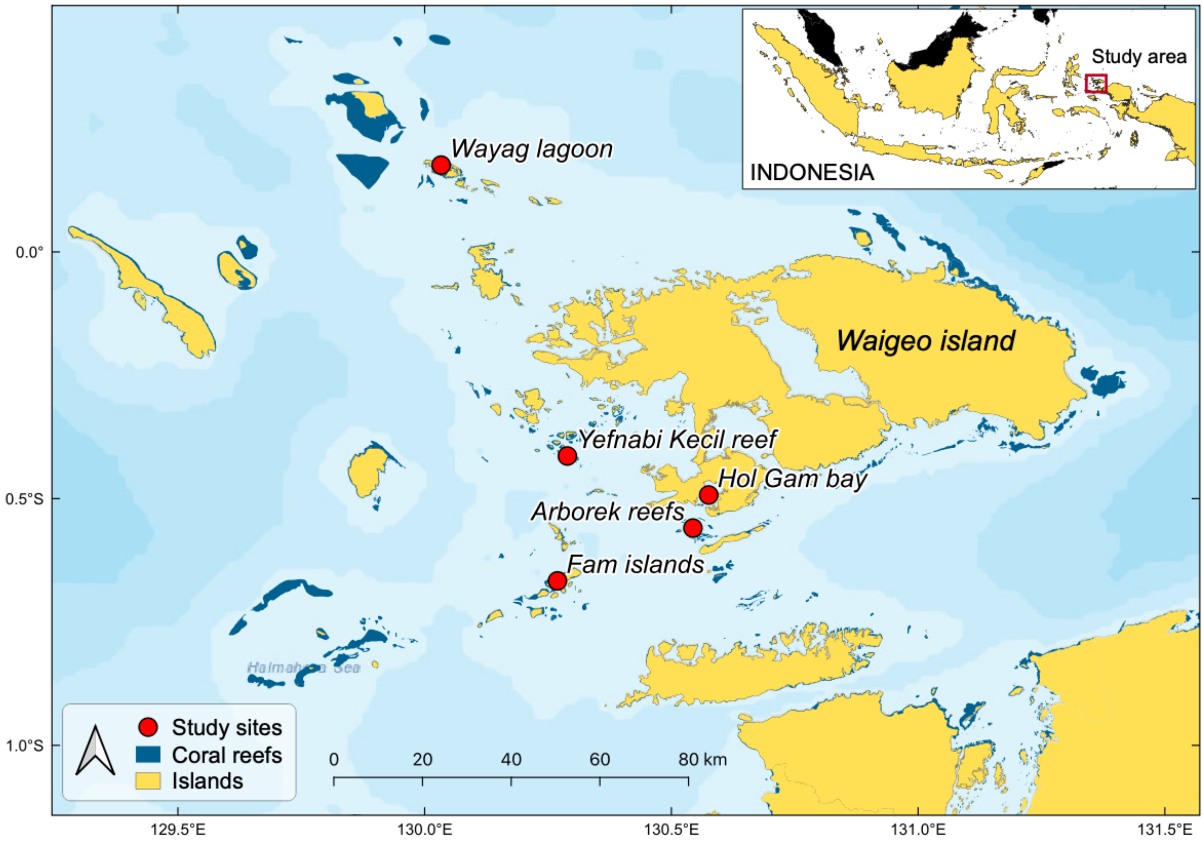

Figure 4.2. Study sites (red dots) in northern Raja Ampat archipelago, West Papua, Indonesia.

### 4.2.2. Data collection

Aerial video footage of *M. alfredi* was taken using small, commercially available DJI Mavic 2 Pro drones during boat surveys in January–February 2020 and May–August 2021. The drone was hand-launched from a boat, and then positioned at an altitude of 5–15 m above *M. alfredi* that were feeding or cruising on the surface. The drone camera was tilted to 90° vertically to take high resolution 4K video footage of the *M. alfredi* with a reference scale comprised of a 2-m floating PVC pipe placed in the water in the vicinity of the animals. Video clips were generally 15–60 seconds long, with the camera recording for those periods when the manta ray(s) were at the surface with the reference pipe included in the field of view (Figure 4.3).

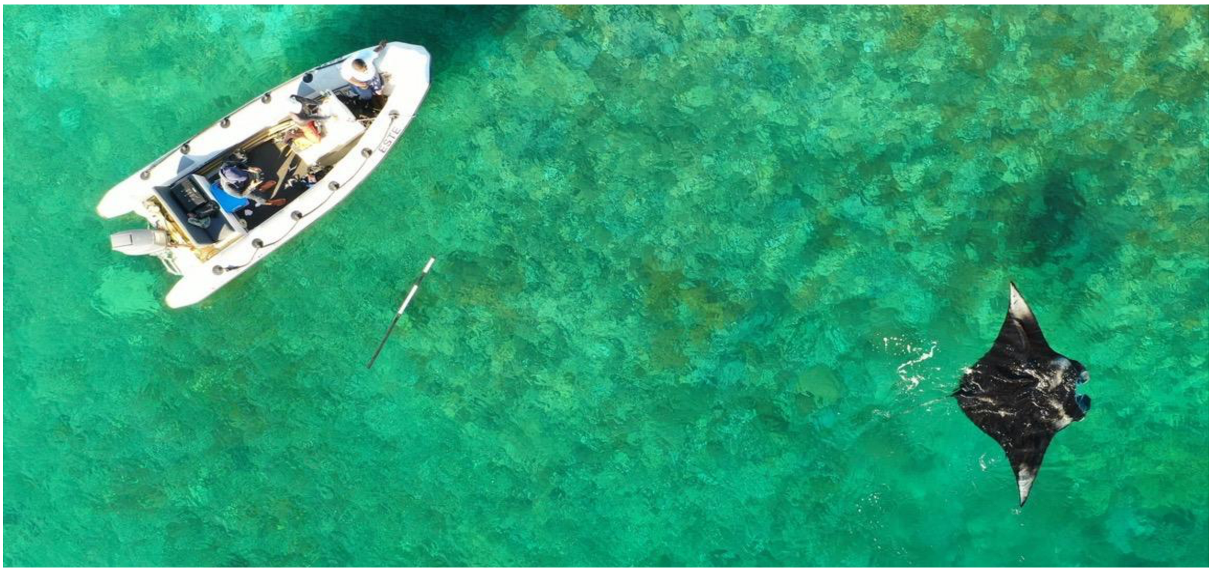

Figure 4.3. A surface-feeding mature female *M. alfredi* and the 2-m floating black and white PVC reference pipe as observed from a drone (research boat also visible in frame).

### 4.2.3. Image processing and measurements

The footage taken was extracted using Final Cut Pro software to obtain multiple still images of each manta ray at those moments when its pectoral fins were fully extended (to allow for accurate measurement of DW; see Figure 4.1). We only included manta rays in our analysis for which we were able to extract and measure at least two separate “wing spread” still images. The measurements were undertaken using the open-source software Tracker (https://physlets.org/tracker/) (Brown et al., 2021). The dimensions of each *M. alfredi*, including the DW, DL, and CW were measured to 1 cm resolution (Figure 4.1). The three dimensions were measured simultaneously from each image, and this procedure was then repeated 2-10 times for the same individual using each of the appropriate frames showing full pectoral fin extension extracted from the footage.

### 4.2.4. Demographic parameters

In addition to the morphometric dimensions of *M. alfredi*, we opportunistically recorded key demographic parameters of the measured individuals, specifically sex and evidence of maturity. The sex of a manta ray is typically determined in ventral view by divers or snorkelers, with the presence of claspers indicating a male and a cloaca indicating a female (Stevens, 2016). Males are considered mature when their claspers are enlarged and calcified and extend posteriorly beyond the pelvic fins (Deakos, 2010), a morphological feature that is readily observed from a dorsal view (Figure 4.4; (Setyawan et al., 2020)). While the cloaca of a female manta ray is not visible in dorsal view, the mating scars on the left-wing, a clear sign of a mature female (Stevens, 2016), are clearly visible (Figure 4.4; (Setyawan et al., 2020)). For each animal measured, we recorded if they were mature using the criteria above. Manta rays with neither visible claspers nor mating scars were recorded as unsexed individuals.

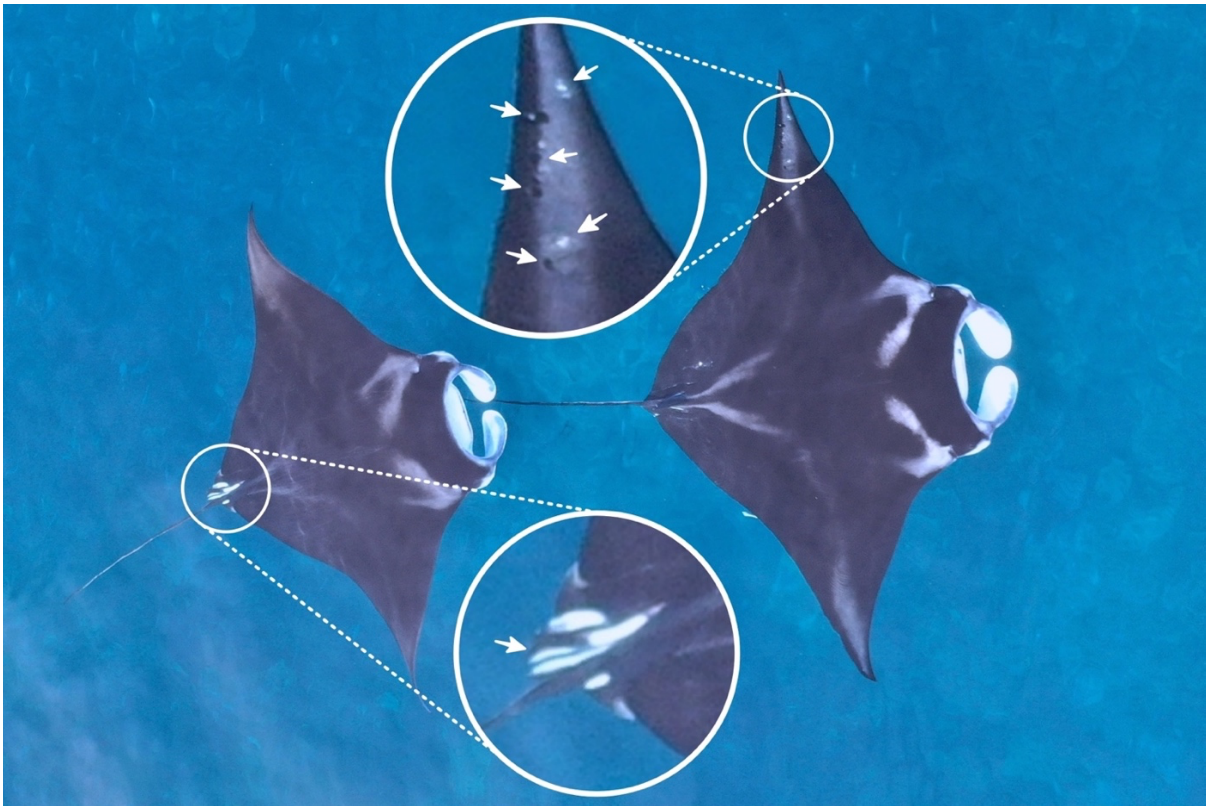

Figure 4.4. A mature chevron male *M. alfredi* (left) with claspers (white coloration) extended beyond pelvic fins and a mature chevron female (right) with mating scars (black and white marks) on her left wing.

### 4.2.5. Statistical analysis

We used a multivariate mixed-effects model (alternatively known as a multivariate hierarchical model) to analyse our data, which we describe in detail in Appendix C. See Bolker et al. (2009) and Zuur et al. (2009) for overviews of mixed-effects models in ecology. Such models are commonly used when multiple observations are taken from each individual, and when the goal is to estimate the distribution of random effects across individuals, as well as the variance between observations from the same individual.

In our case, we have multiple photographs (or multiple still images extracted from footage) taken from each individual manta ray. Our random effects are the unobserved, true morphometric measurements of the individuals, and so we estimate the distribution of true morphometric measurements across manta rays in the population. Additionally, observed measurements will vary between different photographs of the same individual due to measurement error. Note that here we define measurement error to be the unobserved difference between a single measurement from a photograph and the true measurement of the manta ray. Repeated measurements from different photographs of the same manta ray allow us to estimate the variance of measurement errors without observing the true manta ray measurements. One important assumption required by our model is that the drone measurements are unbiased: although they will not be exactly correct due to measurement error, on average they are equal to the true measurement.

One additional distinction between our model and a standard mixed-effects model is that ours is multivariate: we measure three different dimensions from each photograph, so we estimate correlations between the true measurements in addition to the distributions of each individual dimension in the population. All analyses were conducted using R (Ihaka & Gentleman, 1996), with the code and data included in the Supplementary Data available in https://www.mdpi.com/article/10.3390/drones6030063/s1.

We fitted two models to our data. First, we analyzed all manta rays as a single group, estimating parameters for the population as a whole. Second, we fitted a model to analyze data from only the sexually mature individuals. We estimated separate parameters for the distributions of males' and females' morphometric dimensions, but assumed the measurement error parameters were the same for both groups.

## 4.3. Results

### 4.3.1. Measurement summary, accuracy, and precision

A total of 86 individual *M. alfredi* were measured using drones from five areas: Arborek reefs (n = 53 individuals), Hol Gam bay (n = 6), Fam (n = 11), Yefnabi Kecil reef (n = 14), and Wayag lagoon (n = 2). These individuals consisted of 30 sexually mature males, eight sexually mature females, and 48 unsexed individuals. A total of 507 measurements of the three dimensions (DW, DL, and CW) were undertaken from all individuals. We fitted our model to examine population level parameters for all manta rays combined and to estimate the true measurements of these three dimensions for all individuals (summarized in Appendix C Table C.1). Among all individuals, the smallest animal was an unsexed individual estimated at 206.8 cm DW (95% CI: 204.9–208.6), while the largest was a female estimated at 375.6 cm DW (95% CI: 373.2–378.0).

Additionally, we estimated the population level parameters for sexually mature individuals separately for each sex. Although we fitted our model to three groups (mature males; mature females; and unsexed individuals, presumably immature individuals), we are primarily interested in comparisons between sexually mature males and females, so we only present these results here for brevity. The model estimated that the mean DW of sexually mature males (290.1 cm, 95% CI: 286.9–293.4) was smaller than that of sexually mature females (353.4 cm, 95% CI: 343.7–363.1). The population standard deviations of the three dimensions for sexually mature males, moreover, were smaller than those for sexually mature females (Table 4.1).

The probability density of drone measurement error showed high accuracy for each dimension, with an estimated standard deviation (SD) of 1.13 cm for CW (95% CI: 1.06–1.21), 1.69 cm for DL (95% CI: 1.58–1.80), and 2.16 cm for DW (95% CI: 2.01–2.30) (Table 4.1, Figure 4.5). These estimated standard deviations are very small relative to the estimated means of these dimensions for the population of all manta rays (0.75% as large for DW; 1.30% for DL; and 1.52% for CW).

Table 4.1. Estimates of model parameters, including standard errors (SE), and 95% confidence intervals (CIs) for all individual manta rays combined and for sexually mature males and females separately.

| Demographic group | Model parameters | Estimates | Standard Error (SE) | 95% CIs | |
|---|---|---|---|---|---|
| | | | | Lower | Upper |
| All manta rays combined (n = 86) | $\boldsymbol{\mu}_{\mathrm{DW}}$ | 286.5 | 4.87 | 277.0 | 296.1 |
| | $\boldsymbol{\mu}_{\mathrm{DL}}$ | 129.8 | 2.54 | 124.8 | 134.7 |
| | $\boldsymbol{\mu}_{\mathrm{CW}}$ | 74.3 | 1.37 | 71.6 | 77.0 |
| | $\boldsymbol{\sigma}_{\mathrm{DW}}$ | 45.1 | 3.44 | 38.4 | 51.9 |
| | $\boldsymbol{\sigma}_{\mathrm{DL}}$ | 23.5 | 1.79 | 20.0 | 27.0 |
| | $\boldsymbol{\sigma}_{\mathrm{CW}}$ | 12.7 | 0.97 | 10.8 | 14.6 |
| | $\boldsymbol{\rho}_{\mathrm{DW,DL}}$ | 0.99 | 0.003 | 0.982 | 0.993 |
| | $\boldsymbol{\rho}_{\mathrm{DW,CW}}$ | 0.99 | 0.003 | 0.980 | 0.991 |
| | $\boldsymbol{\rho}_{\mathrm{DL,CW}}$ | 0.98 | 0.004 | 0.977 | 0.991 |
| | $\boldsymbol{\psi}_{\mathrm{DW}}$ | 2.16 | 0.07 | 2.01 | 2.30 |
| | $\boldsymbol{\psi}_{\mathrm{DL}}$ | 1.69 | 0.06 | 1.58 | 1.80 |
| | $\boldsymbol{\psi}_{\mathrm{CW}}$ | 1.13 | 0.04 | 1.06 | 1.21 |
| Sexually mature males (n = 30) | $\boldsymbol{\mu}_{\mathrm{DW}}$ | 290.1 | 1.7 | 286.9 | 293.4 |
| | $\boldsymbol{\mu}_{\mathrm{DL}}$ | 131.1 | 0.9 | 129.3 | 132.8 |
| | $\boldsymbol{\mu}_{\mathrm{CW}}$ | 75.2 | 0.4 | 74.4 | 76.1 |
| | $\boldsymbol{\sigma}_{\mathrm{DW}}$ | 9.0 | 1.2 | 6.7 | 11.3 |
| | $\boldsymbol{\sigma}_{\mathrm{DL}}$ | 4.8 | 0.6 | 3.5 | 6.0 |
| | $\boldsymbol{\sigma}_{\mathrm{CW}}$ | 2.4 | 0.3 | 1.8 | 3.0 |
| Sexually mature females (n = 8) | $\boldsymbol{\mu}_{\mathrm{DW}}$ | 353.4 | 4.9 | 343.7 | 363.1 |
| | $\boldsymbol{\mu}_{\mathrm{DL}}$ | 167.3 | 3.1 | 161.2 | 173.3 |
| | $\boldsymbol{\mu}_{\mathrm{CW}}$ | 93.5 | 1.7 | 90.1 | 96.9 |
| | $\boldsymbol{\sigma}_{\mathrm{DW}}$ | 13.9 | 3.5 | 7.1 | 20.8 |
| | $\boldsymbol{\sigma}_{\mathrm{DL}}$ | 8.7 | 2.2 | 4.4 | 13.0 |
| | $\boldsymbol{\sigma}_{\mathrm{CW}}$ | 4.8 | 1.2 | 2.4 | 7.2 |

The model parameters consisted of population mean ($\boldsymbol{\mu}$) for the dimensions for each demographic group, population standard deviations ($\boldsymbol{\sigma}$) for the dimensions for each demographic group, population correlation between two dimensions ($\boldsymbol{\rho}$) for each demographic group, and standard deviation of measurement error ($\boldsymbol{\psi}$) for each dimension. DW = disc width, DL = disc length, and CW = cranial width.

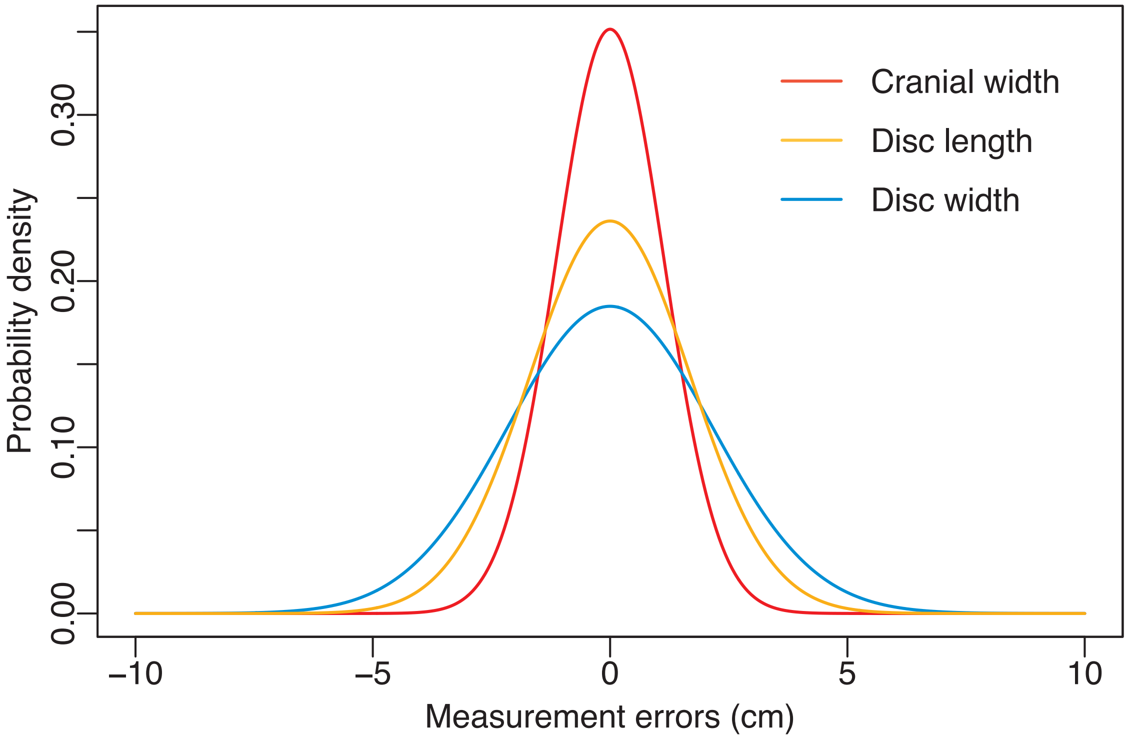

Figure 4.5. Probability density of drone measurement errors for each dimension (DW, DL, and CW).

## 4.3.2. Relationships between measured dimensions

Each pairing of DW, DL, and CW for all individual *M. alfredi* measured using drones and estimated using our model in this study was strongly linearly correlated, with estimated coefficients of correlation ranging between 0.98 and 0.99 (Table 4.1, Figure 4.6). The correlation between DW and DL was the highest of the dimension pairings with 0.99 (95% CI: 0.982–0.993), though the correlation between DW and CW was nearly identical at 0.99 (95% CI: 0.980–0.991).

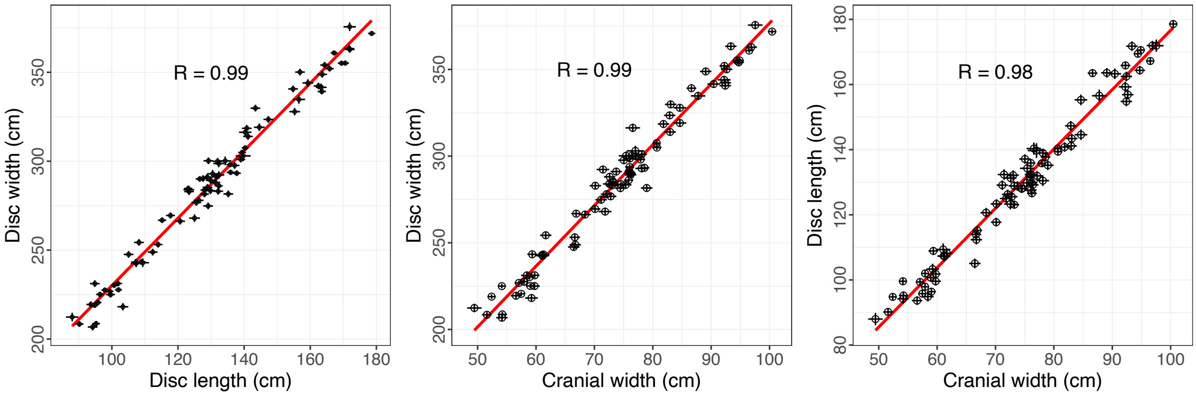

Figure 4.6. Correlation between each pairing of disc width (DW), disc length (DL), and cranial width (CW) for all individual *M. alfredi* measured using drones and estimated using our model. Black circles represent estimated measurements of each manta ray; horizontal and vertical lines crossing the circles represent the confidence intervals of estimated true measurements of each individual.

We also calculated estimated ratios of the various dimensions for each individual (DW:DL, referred to as “Disc Ratio” or DR by Deakos (2010), as well as DW:CW and CW:DL) using their estimated sizes from our model. We fitted a linear model, using these estimated ratios as the response variable and the estimated DW as the explanatory variable. For this secondary analysis, we assume that our estimated ratios and DW measurements have negligible errors. We deemed this assumption was met given the very narrow 95% CIs of the estimated true measurements from our hierarchical multivariate model (Appendix C Table C.1). The linear model showed a clear negative correlation between each ratio and DW (Figure 4.7). DW explained about 37% of variation in DW:DL ratio, but it only explained about 14% of variation in DW:CW ratio. Taken together, these negative correlations suggest that *M. alfredi* have a faster rate of growth in the DL dimension than in the DW or CW dimensions, becoming relatively more slender as they grow longer – commonly described as negative allometric growth (Riedel et al., 2007). Moreover, our results suggest that the growth rate of CW is faster than that of DW.

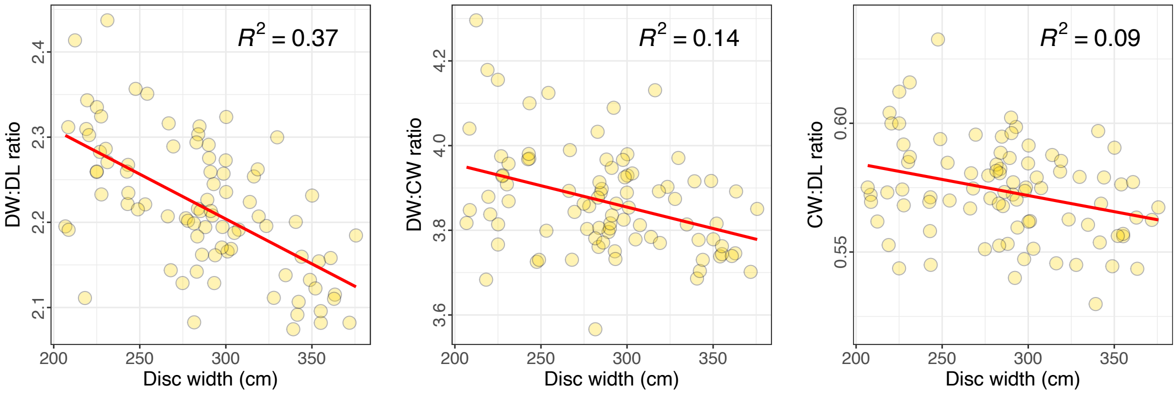

Figure 4.7. Correlations between DW and DW:DL, DW:CW, and CW:DL ratios of *M. alfredi* measured using drones.

### 4.3.3. Using the model to predict unmeasured DW from other measured dimensions

Given the strong linear relationships between dimensions of *M. alfredi*, our models allow the prediction of unmeasured dimensions from other measured dimensions. Here we provide an example of predicting the otherwise difficult-to-measure DW for 13 different individuals using drone-based measurements of either CW alone or DL and CW from these individuals (Figure 4.8). The 95% confidence intervals of predicted DWs based on CW measurements alone were wider than those based on drone-based measurements of both CW and DL, indicating DW is most accurately predicted for a given individual using a model that incorporates measurements of both CW and DL.

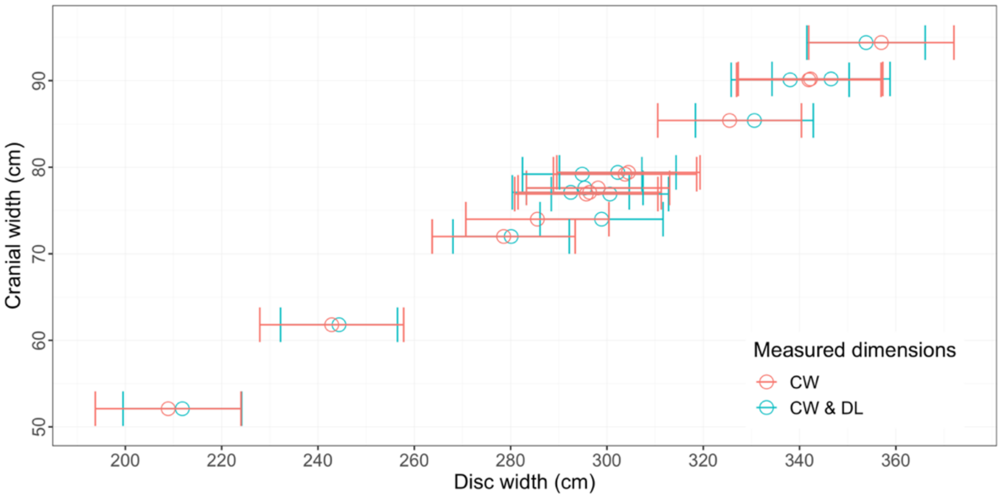

Figure 4.8. The estimated true measurements of DW predicted using a single drone measurement of CW (red) and drone measurements of both CW and DL (blue) with 95% confidence intervals shown from 13 individuals measured from drones.

### 4.3.4. Size at maturity and evidence of sexual dimorphism

Forty-five percent (39 of 86) of the individual *M. alfredi* measured displayed visible signs of maturity observable from our drones. We estimated that the smallest male with claspers visibly extending posteriorly beyond the pelvic fins was 274.8 cm DW (95% CI: 272.9–276.7), while the smallest female with visible mating scars was 323.5 cm DW (95% CI: 321.6–325.4) (Appendix C Table C.1). By contrast, we estimated that the largest sexually mature male was 316.3 cm DW (95% CI: 313.9–318.7), and the largest sexually mature female was 371.8 cm DW (95% CI: 370.4–373.2).

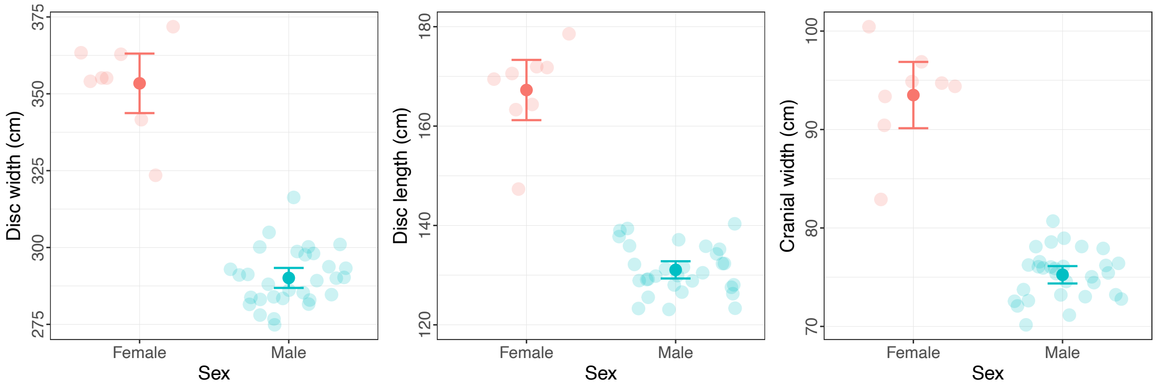

Figure 4.9. Estimated mean DW (in cm) with 95% confidence intervals of sexually mature female (n = 8; solid red circle with CI) and male (n = 30; solid blue circle with CI) *M. alfredi* measured using drones and estimated by our model. The transparent circles represent the estimated true measurements of DW of each individual, color coded by sex.

The three morphometric dimensions taken for the 30 mature males and eight mature females showed no overlap in any of the measurements, with the smallest mature female recorded having larger dimensions than the largest male (Appendix C Table C.1, Figure 4.9). Using the most common measurement of body size in manta rays, the mean DW of sexually mature females (353.4 cm; 95% CI: 343.7–363.1) was significantly ($p < 0.001$) larger than that of sexually mature males (290.1 cm; 95% CI: 286.8–293.4) estimated in our study (Table 4.1).

## 4.4. Discussion

Drones have been increasingly commonly used in elasmobranch research in the last few years to study the abundance, habitat use, fine-scale movements, feeding and social behaviors of various shark and ray species (Butcher et al., 2021; Oleksyn et al., 2021a) including manta rays (Pate & Marshall, 2020; Setyawan et al., 2020). Here, we show that it is possible to reliably measure the size of manta rays using small, commercially available drones, and have developed a model for use in other studies. Paired with visual signs of sexual maturity from drone images, we were able to advance our understanding of the population demographics of *M. alfredi* in Raja Ampat. Recently, Oleksyn et al. (2021b) published the first study using drones to measure body size of an elasmobranch, the short-tailed stingray, *Bathytoshia brevicaudata*. Our study is the first to our knowledge to describe a method for measuring the body size of manta rays using drones. Our methodology differs significantly from that utilized by Oleksyn et al. (2021b) and other studies using drones to measure whales (Durban et al., 2016; Dawson et al., 2017; Christiansen et al., 2018; Burnett et al., 2019). Morphometric measurements in each of those studies were calculated using the known size of the drone's camera sensor (i.e., width in pixels) and the altitude reported by the drone at the time the image was recorded, with drone altitude derived from onboard barometric or laser altimeters. However, barometric altitude measurements from drones are known to have poor accuracy due to sensitivity to rapid changes in air pressure unassociated with the changes in drone altitude, such as wind gusts or other atmospheric conditions (Sabatini & Genovese, 2014). In our study, we used small drones (the same used by Oleksyn et al. (2021b)) equipped with low-cost sensors that are reported to have severe issues of drift and delay in their barometric altitude readings (Wei et al., 2016). To avoid the measurement error related to this uncertainty, we used a known length object as a scale within the same frame to measure the size of manta rays. This is similar to the approach of Christiansen et al. (2016), who used a research vessel as a scale to measure humpback whales *Megaptera novaeangliae*, utilizing this scale photograph to convert relative measurement (in pixels) obtained from different photographs into absolute measurements (in cm). However, instead of using different still images as a scale photograph, we use the same photograph with a floating PVC pipe as a reference scale to measure the manta ray body size. This approach provides more robust measurements, particularly when using low-cost drones with high uncertainty in altitude readings.

Nonetheless, even when using objects of known size as a reference, drone photogrammetry is subject to uncertainties resulting from image processing and variations in body size between individuals in a population (Durban et al., 2016; Burnett et al., 2019). While dealing with these sources of uncertainty, our model accurately estimated the measurements of animals in our study. Similar to our method, Bierlich et al. (2021) developed a Bayesian model to predict drone morphometric measurements of whales while considering various uncertainties. Both that model and ours have the ability to estimate the predictive distribution of a measurement, instead of a single value, providing more robust information about individuals and populations. The ability to predict population-level morphological relationships and predict unmeasured dimensions of marine animals based on parameter estimates derived from a model is an important advancement in the use of photogrammetry. Importantly, our method is able to estimate an expected value of any dimension using any combination of the other dimensions based on coefficients calculated by a single fitted model. Our model can accommodate any number of dimensions of interest, and is therefore widely applicable to a variety of studies.

While the most commonly used methods for estimating or measuring the dimensions of manta rays require divers/observers to be in the water (Deakos, 2010; Stevens, 2016; Peel et al., 2019b), our method offers an alternative non-invasive approach requiring no in-water interaction and having minimal or no impact on the animals. The only impact observed using our method was related to the floating PVC pipe. Most of the time, the manta rays showed no reaction towards the pipe floating near them, particularly when it remained outside of the animals swimming path while they were feeding. The manta rays displayed some minor, short-term avoidance behavior when the pipe floated directly into their swimming path, in which case they would either submerge beneath the pipe and then resurface as the pipe passed over them, or swim laterally around the pipe and then rejoin the feeding behavior.

### 4.4.1. Accuracy and measurement methods

Drone measurements on surface feeding or cruising *M. alfredi* were highly accurate and precise. The estimated standard deviation of measurement error using our approach was less than 2.2 cm for each of the dimensions, which is extremely small relative to the true measurements. The precision of our measurements of manta ray dimensions was higher than that derived from paired laser photogrammetry in Hawaii, which is promising as researchers endeavor to improve measurement accuracy (Deakos, 2010). Importantly, the precision of our drone measurement was comparable to work on southern right whales *Eubalaena australis* using a larger DJI Inspire 1 Pro equipped with LIDAR to measure altitude (Dawson et al., 2017). It is encouraging that data we collected with the smaller, more affordable Mavic Pro drone has provided reliable results.

Of the three dimensions we measured, CW was the most accurate, while the measurements of DW were the least accurate. The larger variability in DW measurements is likely due to the difficulty of capturing images of manta rays at exactly the moment of maximum extension of the pectoral fins when swimming – a difficulty also discussed by Deakos (2010) when using paired laser photogrammetry in Hawaii. Burnett et al. (2019) suggest that errors in measurement with aerial photogrammetry of marine animals in general may come from a combination of various factors, including inaccurate readings of relative altitude by the drone, animal body flex, and animal bodies that are partially submerged in the water. In our study, we did not utilize altitude readings, and we only took video measurements when the manta rays were clearly surface feeding or cruising in calm water conditions. Body flex, however, is another means of describing the difficulty of capturing the manta ray with maximum wing extension, and is one of the main reasons that Francis (2006) suggested that DW has more measurement errors than other dimensions and should be replaced by DL as the primary measurement used for describing body size in mobulid rays. While our drone measurements indicated that DW had the smallest standard deviation relative to the mean body size, CW and DL are easier to measure in practice, with CW being the most accurate. As such, we suggest that CW should be considered as a primary metric in describing manta ray body size when using a drone, considering that these measurements can be established accurately using our model. We acknowledge that standard scientific convention most commonly uses

DW in describing manta ray body size, in which case our model offers the ability to accurately predict DW from measurements of either CW or DL (or preferably, both). Importantly, this approach of using CW or DL to calculate DW can be applied not only to drone measurements, but also to the aforementioned in-water estimation/measurement methodologies for manta rays.

### 4.4.2. Allometric growth, size at maturity and sexual dimorphism

One of the more unexpected findings of our study was the negative allometric growth. Deakos (2010) previously reported that *M. alfredi* show isometric growth, which is unusual in fishes, but our data show that *M. alfredi* in Raja Ampat become relatively more slender (as measured by either DW or CW) as they grow longer, reflecting clear negative allometric growth (Riedel et al., 2007). Of the three morphometric dimensions we consider, each has different growth rates. DL has the fastest growth rate, followed by CW, with DW experiencing the slowest rate of growth of the three dimensions. Nonetheless, despite the differences in growth rates, each pairing of dimensions shows a very strong linear correlation across the range of body sizes we measured, thereby conveniently allowing the calculation of one unmeasured dimension from the other measured dimensions.

While our sample size of 86 individual *M. alfredi* is not large enough to confidently describe demographic parameters of the large Raja Ampat population (Setyawan et al., 2020), we were nonetheless able to record some valuable observations that are worth comparing to the *M. alfredi* from across their Indo-Pacific distribution. The largest animal estimated in our study was a 375.6 cm DW female, which is similar to other studies e.g., Hawaii, the Maldives, and the Seychelles using different techniques (Deakos, 2010; Stevens, 2016; Peel et al., 2019b).

Adult or sexually mature male and female *M. alfredi* were determined by morphological features (Marshall & Bennett, 2010; Stevens, 2016) observed in the drone imagery when surface-feeding. We estimated that the smallest sexually mature male was 274.8 cm DW (95% CI: 272.9–276.7), while the smallest sexually mature female was 323.5 cm DW (95% CI: 321.6–325.4). These findings are consistent with studies from Hawaii (Deakos, 2010) and the Maldives (Stevens, 2016). In the Maldives, males were estimated to reach maturity at approximately 270–280 cm DW and females at approximately 320–330 cm DW (Stevens, 2016). In Japan, however, they are considerably larger, with females estimated to mature at 380–400 cm DW and males at 280–300 cm DW (Kashiwagi, 2014).

We found strong evidence of sexual dimorphism in body size of *M. alfredi*, with adult females larger than adult males in all three morphometric dimensions we measured. This finding is similar to those in several other regions (Deakos, 2010; Kashiwagi et al., 2010; Marshall & Bennett, 2010; Stevens, 2016). This is likely related to female *M. alfredi* requiring a larger body to gestate the large, precocial pups (Cortés, 2000; Hussey et al., 2010).

### 4.4.3. Limitations of the methodology

Despite its utility, we nonetheless recognize some important limitations of our method. First, it is only useful for measuring manta rays that are surface-feeding or cruising at the surface in calm water conditions. While this limits its utility, our experience in using drones to observe *M. alfredi* throughout Indonesia, Papua New Guinea, and New Caledonia and *M. birostris* in New Zealand suggests that these conditions are met at least part of the time in each of these areas, such that the methodology should be broadly applicable.

A more important limitation of the methodology is that the measurements collected cannot necessarily be attributed to individuals that are tracked over time in the manner that the other in-water methods of measurement are able to do. *M. alfredi* have uniquely identifiable ventral spot patterns that enable the collection of photographic images, which can be collated in a database and allow the tracking of individuals over time (Marshall & Pierce, 2012; Stevens, 2016; Setyawan et al., 2020). In the studies using visual estimation, paired laser photogrammetry or estimation with paired stereo video cameras to measure the size of *M. alfredi*, a key advantage is that these methods include the linking of the measurements taken with a photo-ID image of the manta ray. This in turn allows the researchers to make repeated measures of the same individuals and thereby calculate growth rates. We note, however, that it is often possible to link drone measurements to an individual if the manta ray being measured performs somersault feeding near the surface, which allows excellent identification images to be taken (Setyawan et al., 2020) at the same time as measurements are collected. Somersault feeding is particularly common in our experience with juvenile *M. alfredi* in nursery areas in Raja Ampat (Setyawan et al., 2020) and with *M. birostris* feeding offshore of New Zealand (Setyawan et al., 2021), and may very well be common in other localities depending on oceanographic conditions and planktonic prey behaviors.

Finally, while our drone-based methodology did allow for collection of opportunistic observations on sex and maturity status of individuals being measured, we are not able to reliably determine this for all manta rays encountered. It is impossible to determine the sex of a juvenile manta ray from a drone unless the individual happens to be somersault feeding (Setyawan et al., 2020). For sexually mature males, we are able to very reliably identify the claspers extending beyond the pelvic fins using drone photogrammetry, which will allow us to produce highly accurate estimates of size at maturity for males in a given population.

Maturity in females, however, has proven much more difficult to reliably measure with drones. Using Steven’s (Stevens, 2016) estimate of size at maturity for Maldivian female *M. alfredi* of 320–330 cm DW (from the most comprehensive study yet published on *M. alfredi* demographic characteristics), we observed 17 individuals that were over 330 cm DW and did not show extended claspers in the dorsal view – and thus can reasonably be assumed to be adult females. However, we only observed mating scars from a dorsal view on 41% of these individuals. Importantly, seven of the ten large females on which we did not observe mating scars were melanistic individuals; the lack of white shading on the dorsal wing tips (compare to Figure 4.4 for a normal “chevron” colored female) of these melanistic females makes it much more difficult to see any evidence of mating scars (Setyawan pers. obs.). The remaining three large chevron-colored females with no visible dorsal mating scars either had not previously mated, only showed mating scars ventrally, or had healed their mating scars to the point they could not be recognized. Whatever the reason, it is clear that drone photogrammetry is limited in its ability to identify females and sexual maturity in females, except when these females perform somersault feeding and allow a ventral view of their cloaca and pectoral fins.

## 4.5. Conclusions

We have demonstrated conclusively the value of using small, commercially available drones to accurately measure the body size of surface-feeding or cruising *M. alfredi* with minimal or no impact on the animals. The three morphometric dimensions of *M. alfredi* measured from drones in this study (DW, DL, and CW) were strongly linearly correlated, allowing us to develop models that can predict an unmeasured or less accurately measured dimension (such as DW) using drone measurements of CW, DL, or preferably both. We also showed that drones can be used to determine sexually mature individuals, a key demographic parameter useful for conservation management (Stevens, 2016). Finally, we found evidence of sexual dimorphism in body size (with females significantly larger than males) and negative allometric growth (with growth rates for DL > CW > DW).

Although our method can only be used on surface-feeding or cruising manta rays in relatively calm waters, if the individual is somersault feeding at the time of measurement we can also individually identify the animal and more accurately assign sex to females that are difficult to identify from the dorsal view. Importantly, our drone-based methodology is beneficial in providing an accurate "snapshot" of the size distribution of *M. alfredi* aggregations, and in reliably determining size for mature male individuals. Moreover, our robust models for calculating DW from either CW or DL measures (or, more accurately, both) should be equally useful for in-water measurement techniques including paired laser photogrammetry and estimation by paired stereo video cameras.

In the future, this novel method can be used to identify *M. alfredi* critical habitats, such as nursery areas, by determining the size distribution of neonates and juveniles occupying the nursery. In combination with photographic identification, this method can be used to accurately estimate the growth rate of manta rays. Importantly, given the simplicity of the data collection and functionality of the data analysis, this method is easily replicable to measure the body size of manta ray populations in other countries and possibly that of other marine megafauna species that spend time at the surface.

# Chapter 5.

# Residency and use of an important nursery habitat, Raja Ampat's Wayag lagoon, by juvenile reef manta rays (*Mobula alfredi*)

## 5.1. Introduction

Although nursery areas have been identified for a variety of elasmobranch species (Heupel et al., 2019), few studies have specifically examined the benefits of nursery areas for newborn and juvenile elasmobranchs, such as improved fitness and increased survival. Many elasmobranch species, including manta rays and other mobulid rays (*Mobula* spp.), use shallow and sheltered habitats like lagoons as nursery areas for newborns (Heupel et al., 2007; Stewart et al., 2018b). Reef lagoons provide several benefits for juvenile elasmobranchs, such as calm sea conditions, protection from large predators, reliable food availability, and opportunities for social interaction with conspecifics (Guttridge et al., 2011; Jacoby et al., 2012b; McCauley et al., 2014; Rojas et al., 2014; Heupel et al., 2019). Occupying sheltered nursery areas may also contribute to higher chances of newborn survival by enabling individuals to grow in a safe environment and become better equipped to later escape predators and find diffuse prey (Branstetter, 1990).

In the last five decades, global populations of oceanic sharks and rays, including the reef manta ray *Mobula alfredi*, have declined significantly (Pacoureau et al., 2021). To promote the recovery and persistence of manta ray populations, Stewart et al. (2018a) highlighted the importance of identifying critical habitats, including pupping and nursery areas, as an urgent priority to support conservation management efforts. While the majority of literature on the spatial ecology of *M. alfredi* has focused primarily on large or sexually mature individuals, with juveniles included opportunistically (Jaine et al., 2014; Braun et al., 2015; Kessel et al., 2017; Couturier et al., 2018; Peel et al., 2019b; Lassauce et al., 2020; Peel et al., 2020; Venables et al., 2020), the ecology and ontogeny of juvenile *M. alfredi* remain understudied. Information on juvenile movements, residency, and habitat use in nursery areas is urgently required to inform the planning and management of existing marine protected areas (MPAs), specifically to develop the most appropriate strategies and regulations to safeguard this vulnerable species (Stewart et al., 2018a).

Several locations around the globe have been proposed as manta ray nurseries. The Flower Garden Banks National Marine Sanctuary in the northwestern Gulf of Mexico has been suggested as a nursery habitat for Caribbean manta rays *M. cf. birostris* (Childs, 2001; Stewart et al., 2018b). Similarly, Pate and Marshall (2020) suggested a coastal region of southeastern Florida may also function as a nursery for that species. Additionally, several potential nursery areas for *M. alfredi* have been suggested in the

Maldives (Kitchen-Wheeler et al., 2011; Stevens, 2016), Palmyra Atoll (McCauley et al., 2014) and Nusa Penida in southern Indonesia (Germanov et al., 2019).

In the Raja Ampat archipelago of West Papua, Indonesia, four areas have also been identified as potential *M. alfredi* nurseries (Setyawan et al., 2020), based upon the three criteria proposed by Heupel et al. (2007) to define elasmobranch nurseries. These criteria, as applied to *M. alfredi*, include (1) Young-of-the-Year (YoY) and juvenile animals are more commonly encountered in the nursery area than in other areas; (2) YoY and juveniles remain in the nursery area for extended periods; and (3) the nursery area is used repeatedly by YoY and juveniles across years.

Of the four proposed *M. alfredi* nursery areas in Raja Ampat, the Wayag Lagoon has been the focus of the most intense research efforts. Based upon surveys in the Wayag lagoon between 2013-2019, Setyawan et al. (2020) provided evidence that the area fulfils Criteria (1) and (3) of Heupel et al. (2007) in functioning as a *M. alfredi* nursery. Specifically, those authors showed that YoY and juvenile animals (defined as individuals ≤2.0 m DW and ≤2.4 m DW (Peel et al., 2019b), respectively) are more commonly observed within the Wayag lagoon than in the general population. YoY and juvenile *M. alfredi* comprise 47.6% and 95.2% of individuals recorded from Wayag lagoon, compared to only 4.7% and 11.1% of the 4,052 sightings recorded for the entire Raja Ampat population. Moreover, they reported that YoY and juvenile *M. alfredi* were observed on all 26 surveys conducted over the seven-year period, confirming Criterion (3) that the nursery is used repeatedly across years.

As noted by Heupel et al. (2019), assessing Criterion (2) of their elasmobranch nursery definition (residency within the nursery for extended periods) is best conducted using acoustic or satellite telemetry. Preliminary results of a pilot study using a Wildlife Computers SPOT5 satellite tag showed a YoY *M. alfredi* remained in and near the Wayag lagoon continuously for 6.5 months (Setyawan, Unpubl. Data). Here, we expand upon that study to assess Criterion (2) of the elasmobranch nursery definition using a combination of photo-identification (photo-ID), satellite telemetry, and passive acoustic telemetry to further describe the movement patterns and residency of juvenile *M. alfredi* in and around the Wayag lagoon. For the purposes of this study, we use the definition proposed by Chapman et al. (2015) that residency represents a nearly continuous occupancy by an individual in a restricted area for an extended period of time. Finally, we describe the home-range and habitat use patterns of the tracked juvenile *M. alfredi* in relation to the Wayag lagoon nursery area.

## 5.2. Materials & Methods

### 5.2.1. Study area

The Raja Ampat archipelago in West Papua, Indonesia, is home to large populations of both *M. alfredi* and oceanic manta ray (*M. birostris*) that appear to be in a healthy state with high survival rates and reproductive periodicity (Beale et al., 2019; Setyawan et al., 2020). Both species have been fully protected in this region since the Raja Ampat government designated the entire archipelago as Southeast Asia’s first shark and ray sanctuary in 2012 (Dharmadi et al., 2015; Setyawan et al., 2022a). Wayag (S 0.172995°, E 130.035316°), located in the northwest of the Raja Ampat archipelago (Figure

5.1), is an island comprised of mountainous limestone karst. It is part of the SAP (*Suaka Alam Perairan* – marine reserve) Waigeo Barat MPA, established in 2011 and covering an area of 1,550 km$^2$ (Mangubhai et al., 2012). The Wayag lagoon covers an area of ca. 14 km$^2$ and has been identified as a potential *M. alfredi* nursery area (Erdmann, 2014b; Setyawan et al., 2020).

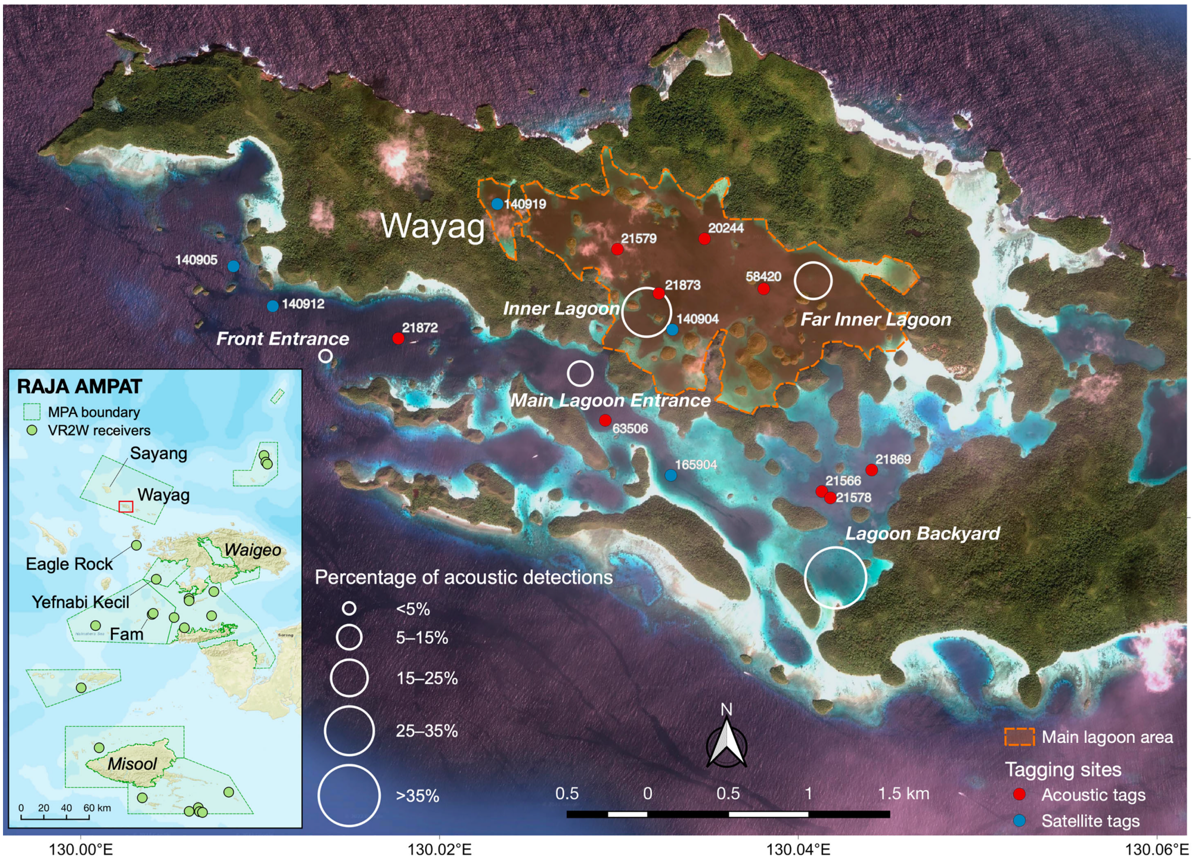

Figure 5.1. The Raja Ampat, West Papua, Indonesia region (inset) and Wayag lagoon denoted in the red box. Green points on the inset map depict the location of acoustic receivers deployed throughout the Raja Ampat archipelago. White circles on the main map indicate the location of the passive acoustic telemetry array deployed in the study area to monitor juvenile *M. alfredi* residency and habitat use. The size of circles indicates the proportion of tagged *M. alfredi* acoustic detections recorded by each receiver throughout the study period. Red and blue points on the main map indicated the deployment locations of all transmitters.

## 5.2.2. Data collection

### 5.2.2.1. Photo-identification

Between January 2013 and May 2021, surveys were undertaken every three to six months in Wayag. In all these surveys, we collected photo-ID images of *M. alfredi* in the Wayag lagoon via 1) underwater surveys by free diving and deploying GoPro camera traps at cleaning stations, and 2) starting in 2019, opportunistic aerial surveys of somersault-feeding manta rays using drones (Setyawan et al., 2020; 2022d). Individuals were identified using the unique spot patterns on their ventral side (Marshall & Pierce, 2012; Stevens et al., 2018b) and visually matched to catalogued individuals in the “Bird’s Head Seascape *M. alfredi* Photo-ID Database” (Setyawan et al., 2020) to determine whether each juvenile was a newly-sighted individual or a resighting. For each photo-ID, we recorded date, time, location, sex, colour morph, and estimated disc width (DW) to the nearest 10 cm (Setyawan et al., 2020). The DW of juvenile *M. alfredi* was also measured opportunistically to the nearest 1 cm using a novel photogrammetry method using drones (Setyawan et al. (2022d). The sex of each individual was determined through observation of claspers on males and lack thereof for females (Marshall & Bennett, 2010; Stevens, 2016).

### 5.2.2.2. Transmitter deployments

We equipped five juvenile *M. alfredi* with SPLASH10-F-321A satellite transmitters (Wildlife Computers, Redmond, USA) in the Wayag lagoon in 2015 (n = 3) and 2017 (n = 2) (Table 5.1, Figure 5.1). Additionally, nine juvenile *M. alfredi* were tagged using V16-5H acoustic transmitters (Innovasea, Halifax, CA) operating at 69 kHz frequency and transmitting pings randomly every 60–130 s. The transmitters were deployed in Wayag lagoon (Figure 5.1) over four different periods: May 2019 (n = 2), October 2019 (n = 2), January 2020 (n = 2), and May 2021 (n = 3) (Table 5.2), following Setyawan et al. (2018). Briefly, each transmitter was attached to a titanium dart via a 25 cm (satellite tags) or 12 cm (acoustic tags) stainless steel tether coated with heat shrink tubing. Both satellite and acoustic transmitters were coated with non-toxic silicone based Propspeed™ ablative coating to prevent fouling of the transmitters and antennae. Transmitters were deployed while free diving using a pole spear to insert the titanium dart tip into the dorsum of the ray in the muscle band between the right pectoral fin and the body cavity. Prior to tagging, we also collected identification photographs of each juvenile and sexed them, whenever possible.

Table 5.1. Summary details for juvenile *M. alfredi* satellite tracked in Wayag lagoon in 2015 and 2017.

| **PTT ID** | **ID #140905** | **ID #140912** | **ID #140919** | **ID #140904** | **ID #165904** |
|---|---|---|---|---|---|
| Sex | F | U | U | F | F |
| Est. DW (cm) | 230 | 190 | 200 | 220 | 210 |
| Tagging date | 28 Jan 2015 | 28 Jan 2015 | 24 Feb 2015 | 22 Feb 2017 | 22 Feb 2017 |
| Release date | 11 Feb 2015 | 09 Apr 2015 | 13 Apr 2015 | 03 Apr 2017 | 18 Mar 2017 |
| Tracking period (days) | 12 | 69 | 45 | 38 | 22 |
| Min. dist. travelled (km) | 185.6 | 630.9 | 164.3 | 135.6 | 115 |
| Daily mean min. dist. (km) | 15.5 | 9.1 | 3.7 | 3.6 | 5.2 |
| 50% UD (km$^2$) | 181.8 | 2.0 | 18.3 | 43.5 | 1.1 |
| 95% UD (km$^2$) | 1,195.4 | 12.8 | 120.7 | 311.9 | 5.3 |

Note: Sex = M (male), F (female) and U (unknown). Est. DW = estimated disc width. The tracking period represents the number of days between the transmitter deployment and release date. Min. dist. travelled = minimum distance travelled (straight line including over land) by the tagged juveniles during the deployment period (km). Daily mean min. dist = mean minimum distance travelled per day (km). Core activity space (50% UD) and the extent of activity space (95% UD) calculations for each tagged juveniles are based on Continuous Time Movement Modelling. All UDs are expressed in km$^2$.

Table 5.2. Summary details for the nine juvenile *M. alfredi* tracked within the Wayag lagoon using passive acoustic telemetry.

| **Transmitter ID** | **ID #21873** | **ID #21872** | **ID #21566** | **ID #21578** | **ID #20244** | **ID #21869** | **ID #21579** | **ID #58420** | **ID #63506** |
|---|---|---|---|---|---|---|---|---|---|
| Sex | U | F | F | U | F | U | U | U | M |
| Est. DW (cm) | 180 | 190 | 200 | 170 | 180 | 180 | 190 | 200 | 190 |
| Tagging date | 17 May 2019 | 18 May 2019 | 18 Oct 2019 | 18 Oct 2019 | 12 Jan 2020 | 12 Jan 2020 | 11 May 2021 | 12 May 2021 | 25 May 2021 |
| Last date detected | 13 Sep 2019 | 30 Jul 2020 | 25 Mar 2020 | 09 Jun 2020 | 07 Aug 2020 | 04 Jul 2020 | 16 Sep 2021 | 20 Jul 2021 | 12 Sep 2021 |
| No. receivers | 1(1) | 5(5) | 5(5) | 5(5) | 5(5) | 5(5) | 5(5) | 5(5) | 5(5) |
| Total detections | 2,066 | 20,357 | 8,661 | 12,249 | 23,722 | 4,772 | 13,872 | 5,527 | 6,257 |
| Days detected | 52 | 327 | 106 | 185 | 126 | 91 | 125 | 64 | 108 |
| Tracking duration (days) | 119 | 439 | 159 | 235 | 208 | 174 | 128 | 69 | 110 |
| Residency Index (%) | 43.7 | 74.5 | 66.7 | 78.7 | 60.6 | 52.3 | 97.7 | 92.8 | 98.2 |
| Mean visitation duration (min) | 56.1 | 46.9 | 72.5 | 50 | 96.9 | 46.4 | 90.7 | 56.6 | 48.9 |
| No. visitations | 119 | 1,694 | 418 | 994 | 669 | 452 | 603 | 395 | 430 |
| No. movements | NA | 976 | 183 | 568 | 375 | 280 | 333 | 233 | 186 |
| Max. consecutive detection days | 25 | 118 | 82 | 112 | 79 | 75 | 119 | 69 | 107 |

Residency index, visitations and movements as defined in section 2.3.2 on acoustic telemetry data analysis. Further explanations of metrics in the first column as follows: Est. DW: estimated disc width; No. receivers: total number of receivers at which each individual registered detections. Number in bracket represents the number of receivers deployed in the array; Total detections: total number of acoustic detections recorded for each individual; Days detected: total number of detection days; Tracking duration: total number of days between transmitter deployment and last date of detection; No. visitations: total number of visitations recorded for each individual; Mean visitation duration: mean time spent within detection range of a receiver; No. movements: total number of movements recorded between receivers; Max. consecutive days: maximum number consecutive days a tagged individual was detected by receivers.

The SPLASH10-F-321A satellite transmitters were programmed to remain attached for 180 days to collect Fastloc GPS locations every hour with a maximum of 24 locations per day. Upon surfacing, the SPLASH10-F-321A satellite tags transmitted location data, including both ARGOS and Fastloc GPS locations. For subsequent analyses, we only report on GPS positions based on their higher accuracy for estimating home range and fine-scale habitat use patterns (Dujon et al., 2014; Thomson et al., 2017). Additionally, the satellite transmitters were programmed to record and archive dive-depth, light levels, and ambient sea temperature. In this study, however, we only focused on horizontal movements and therefore don't report on these other data.

#### 5.2.2.3. Acoustic receiver deployments

To record detections transmitted by the V16-5H acoustic transmitters, we deployed Innovasea VR2W-69 kHz acoustic receivers at five sites, approximately 550-1900 m apart, inside the Wayag lagoon (Figure 5.1). The receivers were deployed at depths ranging from 8–26 m, and they were securely cable-tied to buoyed moorings that were directly attached to the substrate using galvanised chain anchors and ropes, with each receiver approximately 1.5 m above the surrounding substrate (Setyawan et al., 2018). Four of the receivers were deployed in areas where juvenile *M. alfredi* had been previously observed feeding or cleaning (Setyawan, Unpubl. Data), while the "Front Entrance" (Figure 5.1) receiver was strategically placed to record any manta rays leaving the lagoon through the main channel connecting the lagoon to the deeper waters outside of Wayag. One receiver ("Main Lagoon Entrance") was deployed in May 2019, while the other four were deployed in January 2020, for a period of 325–460 days (Table 5.3). At the same time, a larger array of 23 VR2W-69 kHz acoustic receivers were deployed throughout the Raja Ampat archipelago. These receivers were part of a broader study on manta rays and were located 35 (Eagle Rock) to 280 km (Misool) away from the Wayag lagoon receivers (Figure 5.1).

Importantly, the detection range of each acoustic receiver can vary dramatically depending upon ambient noise levels, receiver biofouling, and environmental conditions, and has been estimated to vary between ~0–800 m (Heupel et al., 2008; Kessel et al., 2014; Huveneers et al., 2016). Receivers were serviced and downloaded every 3-6 months when our team was on site, and thus biofouling did not impact receiver performance. In order to quantify the detection range of the receivers in our array, a basic range test was conducted at the "Lagoon Backyard" receiver (Figure 5.1). Limited time and resources prevented us from undertaking a rigorous range test at all receiver sites. The range test was undertaken by deploying a fixed delay transmitter for one hour during the day at each of the following distances from the receiver: 0, 100, 150, 175, 200, 300, and 400 m. The tag was secured at 2 m depth by a rope attached to an anchor and buoy. The shallow (<8 m), sandy bottom location in the vicinity of that receiver was most likely to restrict detection range and hence this receiver was considered to be the "worst case scenario" and a conservative estimate for range detection for the five receivers in the array (Babin et al., 2019). No detections were recorded by this receiver from the fixed delay transmitter placed further than 150 m from the receiver. This test indicated reliable detection when a transmitter was within ~150 m of the receiver, which is similar to the detection range estimated in a study using the same types of receivers and transmitters in other areas of Raja Ampat (Setyawan et al., 2018).

Table 5.3. Summary of acoustic receiver deployments within the Wayag lagoon, Raja Ampat.

| **Receiver ID** | **VR2W-123685** | **VR2W-135749** | **VR2W-128687** | **VR2W-123682** | **VR2W-123681** |
|---|---|---|---|---|---|
| Receiver station | Main Lagoon Entrance | Front Entrance | Far Inner Lagoon | Inner Lagoon | Lagoon Backyard |
| Deployment date | 16 May 2019 | 11 Jan 2020 | 11 Jan 2020 | 12 Jan 2020 | 12 Jan 2020 |
| Recovery date | 29 May 2021* | 16 Sep 2021 | 16 Sep 2021 | 16 Sep 2021 | 16 Sep 2021 |
| No. transmitters detected | 9(9) | 8(8) | 8(8) | 8(8) | 8(8) |
| Total detections | 12,364 | 1,792 | 17,196 | 27,412 | 38,719 |
| No. detection days | 370 | 171 | 302 | 320 | 248 |
| Tracking period (days)** | 460 | 325 | 337 | 336 | 336 |
| Detection Index (%)** | 80.4 | 52.6 | 89.6 | 95.2 | 73.8 |
| No. visitations | 1,628 | 216 | 1,098 | 2,001 | 831 |
| Mean visitation duration (min) | 30.3 | 28.5 | 65.6 | 60.2 | 123 |

Further explanations of metrics in the first column as follows: No. transmitters detected: Total number of transmitters that were detected by the receiver. Number in bracket represents total number of active transmitters when the receiver was deployed; No. detection days: total number of detection days; No. visitations: total number of visitations recorded by each receiver from tagged juveniles. * The battery in the receiver at the Main Lagoon Entrance site was exhausted on 29 May 2021 and stopped recording on that day, despite being recovered on the same date as other receivers. ** Tracking period and Detection Index were calculated by excluding the period during which there were no active transmitters in the Wayag lagoon (275 days, from 8 August 2020 and 10 May 2021). Station locations reported in Figure 5.1.

One undeployed acoustic transmitter (#21839), that accidently fell off and was not able to be recovered, was continuously detected by the receiver at MLE from 16–29 May 2021 (the receiver battery was exhausted and therefore the receiver stopped recording on 29 May 2021). We used the detection data from this lost ‘sentinel tag’ to assess the temporal variation of detections recorded by a receiver throughout the 24-hour cycle, as well as to examine receiver ability to detect a transmitter when the tagged juveniles were absent from areas where receivers had been deployed (Couturier et al., 2018).

## 5.2.3. Data analyses

### 5.2.3.1. Satellite telemetry data analysis

Each SPLASH10-F-321A satellite transmitter was equipped with a Fastloc GPS receiver that takes a “snapshot” of the radio signals produced by all GPS satellites orbiting above the transmitter at any given time the manta ray is on the surface and the transmitter’s GPS antenna exposed to the air. Each snapshot was compressed onboard the transmitter and the data were transmitted to the Wildlife Computers Data Portal via the ARGOS satellite network. GPS location datasets were initially processed using the Wildlife Computers’ Fastloc GPS Processor as described in the “Location Processing (GPE3 & Fastloc GPS)” in the Wildlife Computers Data Portal User Guide (v.202007). GPS locations were further processed in Movebank (https://www.movebank.org) in order to allow us to manually remove outliers based on a maximum plausible swimming speed of 2 m/s. Furthermore, any GPS locations situated on land and further than 70 m inland from shore, based upon the accuracy of Fastloc GPS locations (Dujon et al., 2014), were also removed. These processed and filtered data were then used to track the patterns and scale of movements of juvenile *M. alfredi*.

Given the small scale and very fractioned landscape in Wayag, we did not restrict movement tracks to preclude movement over land masses. We calculated the minimum distance (including crossing land) travelled by the tagged juveniles using the ‘move’ package (Kranstauber et al., 2021) in R version 4.1.2 (R Core Team, 2021). To estimate core activity space (50% UD) and the extent of activity space (95% UD), we fitted an optimally weighted Autocorrelated Kernel Density Estimator (AKDE) (Fleming et al., 2018) on the filtered GPS locations using the ‘ctmm’ R package (Calabrese et al., 2016). The optimally weighted AKDE takes into account the autocorrelation of GPS locations obtained from satellite-tagged individuals and the highly irregular nature of location data collection in the marine environment (which, if ignored, typically leads to underestimation of home range size), and has been demonstrated to be applicable for *M. alfredi* satellite tag data (Fleming et al., 2018).

Despite the satellite transmitters being programmed to collect GPS locations every hour, the resulting GPS data were obtained irregularly, with time difference between subsequent GPS locations across tagged individuals ranging from 2.2–11.0 hours (mean ± SD: 6.2 ± 4.4 hours) due to the unpredictable nature of manta ray surfacing behaviour. Given the irregularity of the available GPS location data, we fitted a state-space model on the GPS location data to estimate the most likely movement tracks for each individual using the ‘foieGras’ R package (Jonsen & Patterson, 2020). We applied correlated random walks with a six-hour time step to produce estimated locations every six hours. We used the move persistence index between estimated locations to characterise the likely behaviours of the tagged individuals during the tracking period (Jonsen et al., 2019). The move persistence index, which captures autocorrelation in both movement speed and direction, ranges between 0 and 1, with a low index suggestive of correlated random walks or Area Restricted Search (ARS) behaviour, and higher index values indicative of uncorrelated movement steps or likely transiting behaviour (Jonsen et al., 2019).

### 5.2.3.2. Acoustic telemetry data analysis

Acoustic detection data were recorded as a timestamped log of transmitter IDs detected by each of the five receivers. We used a two-sample t-test to compare the hourly mean number of acoustic detections between daytime (06:00–18:00) and night-time (18:00–06:00). To examine residency of the tagged juveniles, we used the ‘VTrack’ R package and its Animal Tracking Toolbox (Campbell et al., 2012; Udyawer et al., 2018). A residency index (RI) (Couturier et al., 2018; Andrzejaczek et al., 2020; Venables et al., 2020) was calculated for each tagged juvenile using the following formula:

$$\boldsymbol{RI = \frac{No. of\ days\ a\ transmitter\ was\ detected\ by\ acoustic\ receiver\ array}{No. days\ between\ tagging\ date\ and\ last\ detection}\, x\ 100}$$

We used a linear model to examine the correlation between tracking period and RI. In addition to RI for each tagged individual, we calculated a Detection Index (DI) for each acoustic receiver in the array using the following formula:

$$\boldsymbol{DI = \frac{No. of\ days\ recording\ detections}{No. days\ between\ first\ deployment\ and\ last\ detection}\ x\ 100}$$

We also examined the number and duration of visitations at receiver stations. A visitation represents a period when a tagged juvenile was detected continuously by a receiver. It begins when a transmitter is detected by a given receiver and terminates if either the transmitter is not detected again by that receiver within 60 mins or if the transmitter is detected by another receiver (Setyawan et al., 2018). In addition to visitations, we also calculated the number of movements of these juveniles between receivers. Overall, data were visualised using ‘gpplot2’ R package (Wickham, 2016), while the number of movements were visualised using the circular layout in the ‘circlize’ R package (Gu et al., 2014).

## 5.3. Results

### 5.3.1. Juvenile reef manta ray sightings

Juvenile *M. alfredi* were observed at multiple sites within the Wayag lagoon. Most sightings occurred when individuals were somersault feeding near the surface, and some when they visited cleaning stations. A total of 34 individuals were photo-identified from 47 sightings between May 2013–May 2021. Twelve of these (35.2%) were female, 11 (32.4%) were male, and 11 (32.4%) were of unknown sex. Nine of the 34 juveniles (26.5%) were resighted at least once within the Wayag lagoon (Figure 5.2); five were resighted once and the other four were resighted twice over periods ranging from 1–648 days (~1.7 years), with six of the nine individuals recording sighting spans in excess of 320 days (Appendix D Table D.1). None of the remaining 24 photographically identified juveniles from the lagoon have been resighted to date as part of regular visits to the site every three to six months. The size of the 34 juveniles ranged between DW of 150–240 cm at first sighting (mean ± SD: 199 ± 19 cm), with 18 individuals with a DW ≤200 cm at first sighting and thereby considered as YoY (Setyawan et al., 2020) (Appendix D Table D.2). The DW of two unidentified juveniles measured using drones were 218 cm (95% CI: 216–220) and 219 cm (95% CI: 218–221). Several of the YoY *M. alfredi* recorded in the Wayag lagoon appeared to be true newborns, as evidenced by their small size (estimated 150–180 cm DW), unmistakably “clean” and unmarked appearance with no scratches evident (Marshall & Bennett, 2010), and obvious “creases” between pectoral fins and body cavity, presumably from the folding of the fins over the body while *in utero* (Marshall et al., 2008).

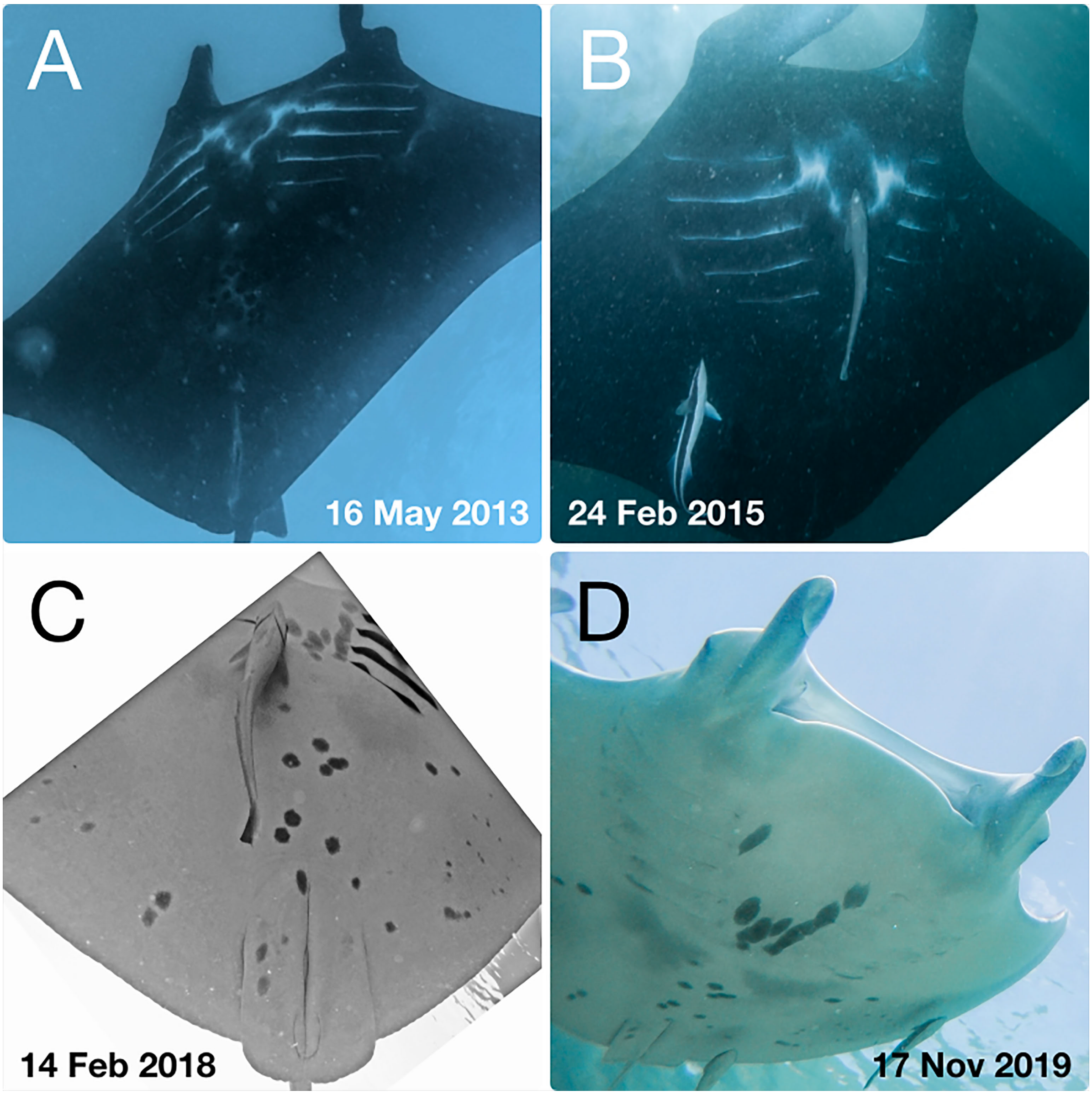

Figure 5.2. Example of resighted juvenile *M. alfredi* RA-MA-1322 (A and B) and RA-MA-0525 (C and D) within the Wayag lagoon, Raja Ampat.

## 5.3.2. Movements and regional habitat use as revealed by satellite telemetry

### 5.3.2.1. Core and the extent of activity space

The tracking duration across all five juvenile *M. alfredi*, three females and two of unknown sex (Table 5.1), ranged from 12–69 days (mean ± SD: 37 ± 22 days) between January 2015 and April 2017. The filtering procedure resulted in the removal of 15 (1.25%) out of 1,199 Fastloc GPS locations. The minimum straight-line distance travelled, including over land (a result of the complex geography of the lagoon), ranged from 115.0–630.9 km (mean ± SE: 246 ± 96.9 km), with mean daily distances travelled ranging from 3.6–15.5 km (mean ± SE: 7.4 ± 2.25 km).

Despite occasional excursions to areas outside the Wayag lagoon and the MPA boundary (Figure 5.3, Appendix D Figure D.3), the majority of satellite-tracked juveniles demonstrated narrow and restricted core activity space (50% UD) located within the Wayag lagoon or near Wayag Island (Figure 5.4). The 50% UD core activity space ranged from 1.1–181.8 km$^2$, while the extent of activity space (95% UD) was 5.3–1,195.4 km$^2$. The size of the 95% UD varied between individuals, from just outside Wayag lagoon to areas up to ~45 km away from the lagoon. The smallest 50% and 95% UDs were registered by ID #165904 (1.1 km$^2$ and 5.3 km$^2$), while ID #140905 exhibited the largest (181.8 km$^2$ and 1,195.4 km$^2$) (Table 5.1) with 50% UD (mean ± SD: 49.3 ± 76.0 km$^2$) and 95% UD (mean ± SD: 329.2 ± 499.8 km$^2$) across all tracked individuals.

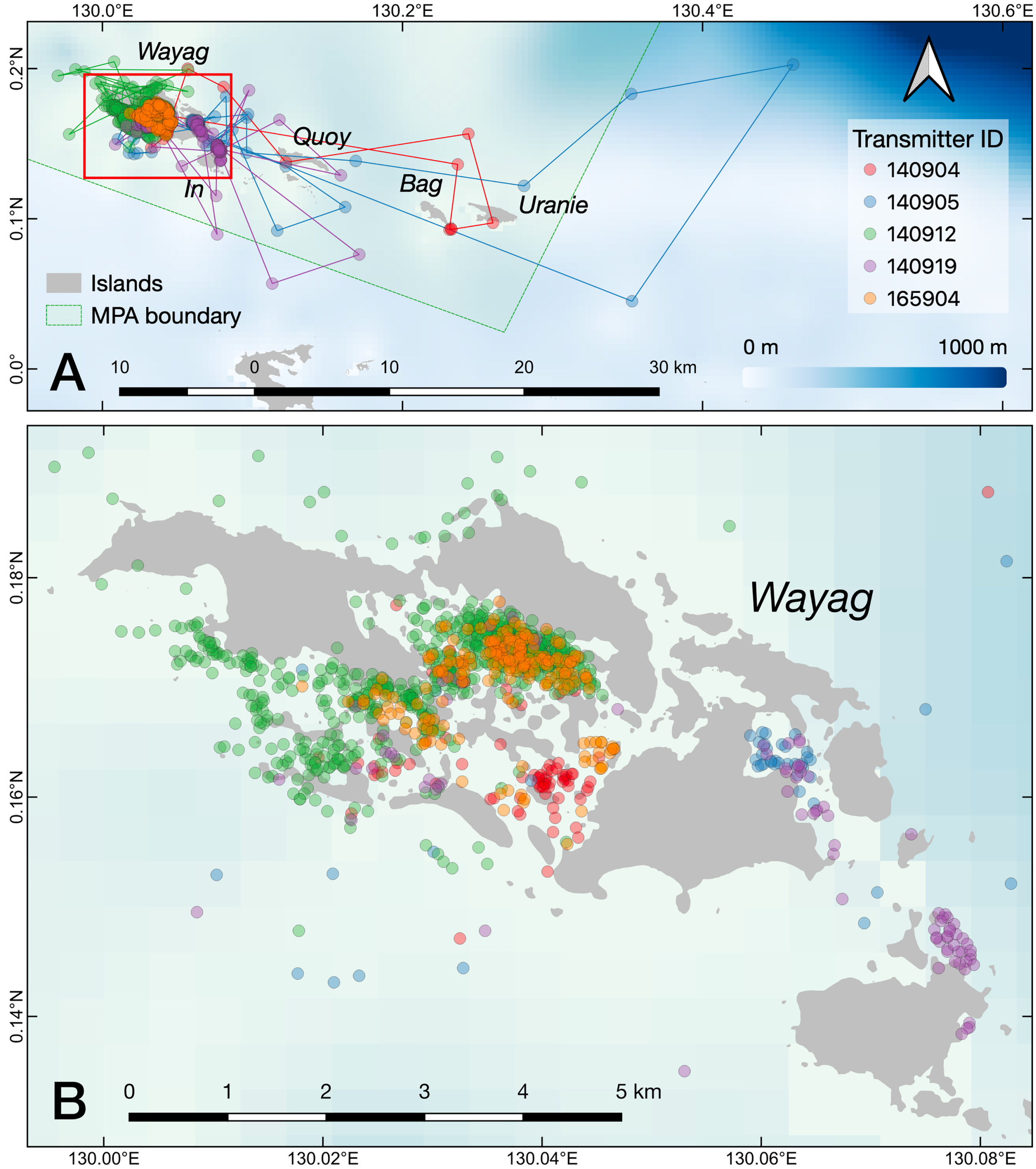

Figure 5.3. The raw movement tracks (lines) derived from GPS locations (dots) recorded by the satellite transmitters on the five tagged juvenile *M. alfredi*. (A) the SAP Waigeo Barat MPA with names of the islands; (B) a close up of the Wayag lagoon.

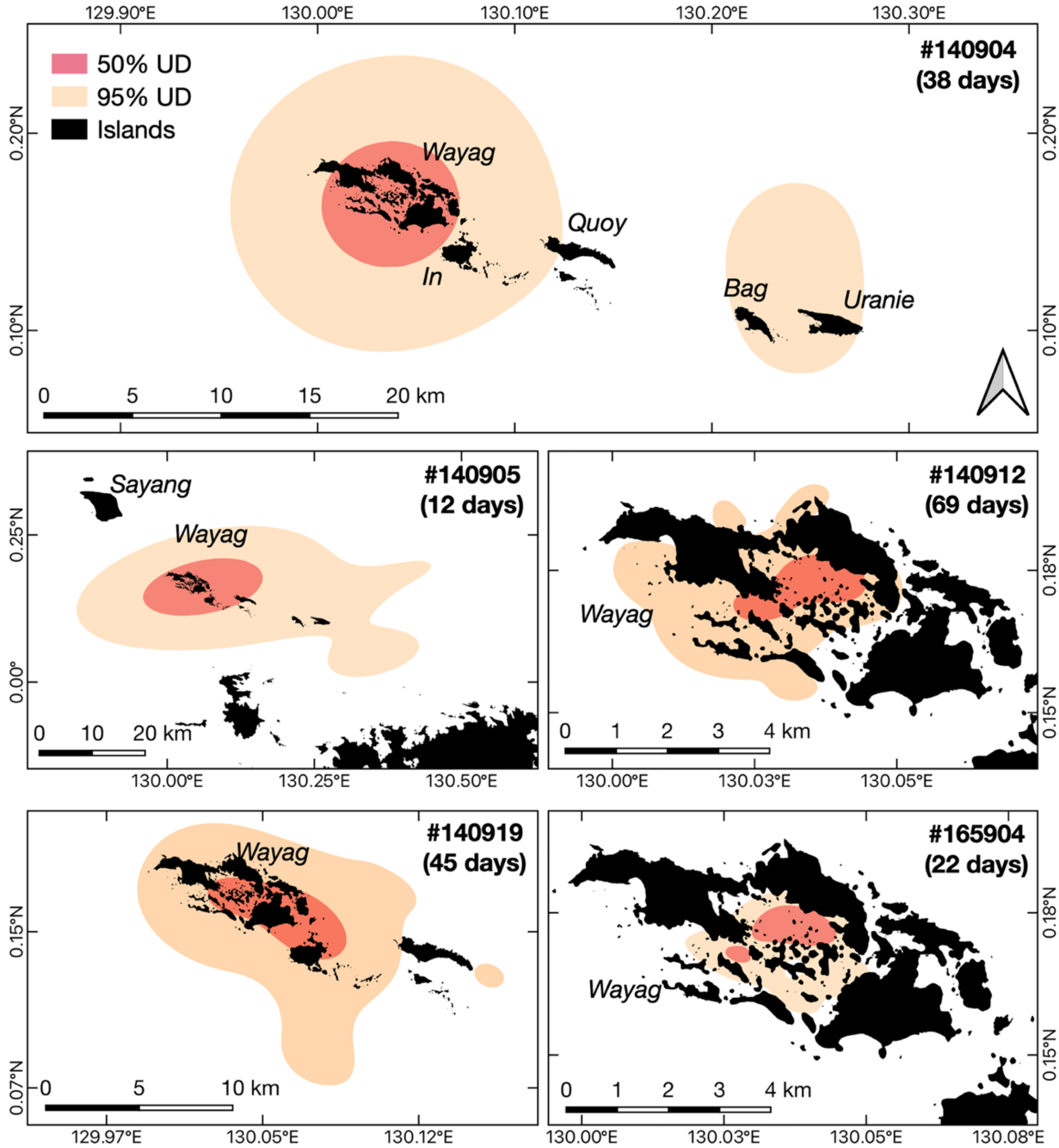

Figure 5.4. Core activity space and the extent of activity space for each of the five juvenile *M. alfredi* satellite tracked around Wayag, Raja Ampat. The red polygons (50% UD) and the orange polygons (95% UD) denote the smallest estimated core activity space and the extent of activity space, respectively, where the tagged juveniles were expected to spend their time during the tracking period.

### 5.3.2.2. Regional movements and residency within the Wayag lagoon

The estimated movement tracks derived from the state-space model suggested that all of the tagged *M. alfredi* spent the majority of their time within the Wayag lagoon, where they were tagged, or in waters adjacent to Wayag (Figure 5.5A). When in or around the Wayag lagoon, all tagged individuals displayed less persistent and directed movements in their localised tracks, suggesting affinity to this area (Figure 5.5B). Individuals occasionally made excursions to other areas around the small islands to the east and just outside of the Wayag lagoon. Three juveniles (ID #140904, #140905, and #140919) exhibited movements likely indicative of transiting behaviour, with more directed and faster movements as shown by higher move persistence index values for estimated locations outside of the Wayag lagoon (Figure 5.5B). Two individuals (ID #140905 and #140919) also travelled to areas outside the MPA boundary. While traveling outside of Wayag, ID #140905 also displayed low move persistence values in Wayag. ID #140912 spent all of its time within 5 km of the Wayag lagoon and showed low move persistence values during the 69-day tracking period.

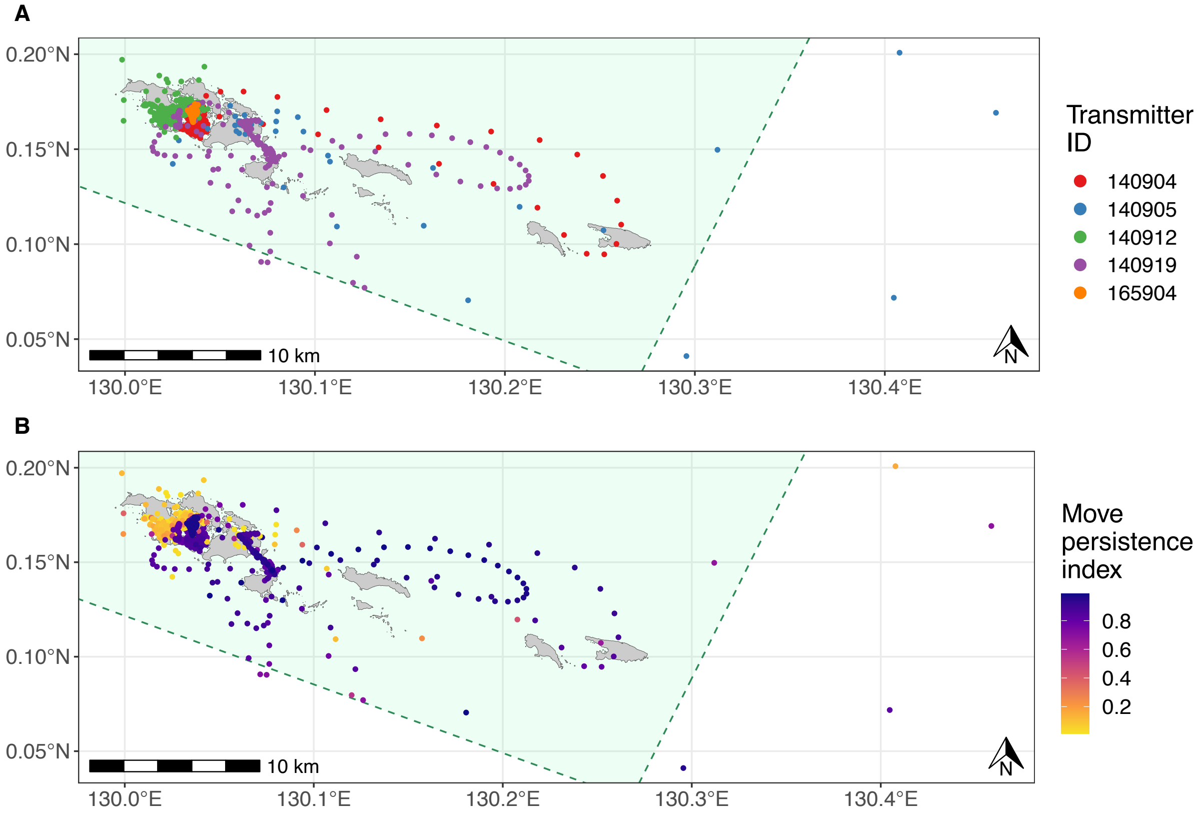

Figure 5.5. Movement tracks for the five satellite-tracked juvenile *M. alfredi* estimated using state-space models with six-hour time steps. (A) Most likely track for each tagged individual; (B) Move persistence behavioural indices for all estimated *M. alfredi* positions. The green polygons in both panels denote SAP Waigeo Barat MPA boundary and the grey polygons represent islands.

### 5.3.3. Residency and fine-scale habitat use within the Wayag lagoon as revealed by acoustic telemetry

Between May 2019–September 2021, nine juvenile *M. alfredi* (size-range = 170–200 DW) were tracked via passive acoustic telemetry (Table 5.2). Individuals were tracked for periods of 69–439 days (mean ± SD: 182 ± 109 days), with a total of 97,483 detections recorded across the five monitored receiver sites within the Wayag lagoon. Nearly a quarter (23,722 detections; 24.3%) of these detections were registered from ID #20244. The maximum number of consecutive detection days ranged between 25 (ID #21873) and 119 days (ID #21579) (mean ± SD: 87 ± 30 days). Excluding ID #21873 that was only detected by one receiver, the maximum number of consecutive days ranged from 69–119 days (mean ± SD: 95 ± 21 days). In addition, a total of 11,728 detections were recorded from the ‘sentinel tag’ by the ‘Main Lagoon Entrance’ receiver from 16–29 May 2021. Across 24-hour periods, the hourly mean number of detections of the sentinel tag was relatively constant (Appendix D Figure D.1). During that period, the mean detection rate at night-time (35.6 detections/hour) was slightly higher than that at daytime (35.3 detections/hour), and the difference (0.38 detections/hour) was not significant (two-sample t-test, $p = 0.285$).

### 5.3.3.1. Detection pattern and residency

Detection patterns for the nine tagged *M. alfredi* varied between sites. The receiver deployed at Lagoon Backyard (Figure 5.1) recorded the most detections (38,719; 39.7% of all detections) with Front Entrance recording the fewest detections (1,792; 1.8%) (Table 5.3). The receiver at Main Lagoon Entrance, deployed in May 2019, detected all nine tagged individuals while the other receivers, deployed in January 2020, detected all eight available transmitters (as the first transmitter deployed, ID #21873, was no longer active in the lagoon at the time these four receivers were deployed). Importantly, none of the acoustically tagged *M. alfredi* were recorded by an extensive array of 23 receivers deployed within the broader Raja Ampat region (Figure 5.1).

The Detection Index (DI) calculated for acoustic receivers deployed in Wayag lagoon similarly varied between receiver sites. The Front Entrance receiver accounted for the lowest DI of all receivers (56.2%) (Table 5.3). DIs at receivers inside the main lagoon of Wayag (i.e., the Inner Lagoon and Far Inner Lagoon receivers) were higher than 89% for both receivers, and overall larger than those outside the main lagoon. This suggests that the tagged juveniles were more detectable within the main lagoon, especially around the two receivers, than outside of the main lagoon on a daily basis.

Residency behaviour varied slightly among the nine tagged individuals yet indicated high residency of the tagged rays to the Wayag lagoon. The RI of each tagged juvenile, particularly the eight individuals detected by all five receivers, ranged between 52.3–98.2% (mean ± SD: 77.7 ± 17.4%). The single individual detected by only one receiver accounted for a smaller RI of 43.7%. A linear model showed that even though the tracking period was negatively correlated ($R^2 = 0.13$) with the RI of eight individuals, this correlation was not significant ($p = 0.38$). On average, juvenile *M. alfredi* spent between 46.4–96.9 mins around a given acoustic receiver for each recorded visitation (Table 5.2). Detectability of individuals varied between sites, with the Inner Lagoon receiver recording the highest number of visitations (2,001), and the Front Entrance receiver recording the lowest (216; Table 5.3). Despite recording the second highest number of visitations, the mean duration of these visitations at the Main Lagoon Entrance receiver was relatively low (30 mins) compared to other sites further into the Wayag lagoon, where the mean duration was over one hour for the Inner Lagoon and Far Inner Lagoon receivers, and up to two hours at the Lagoon Backyard receiver.

Overall, the longest continuous visitation was recorded at the Lagoon Backyard receiver, where ID #20244 remained continuously for 16.6 h (Figure 5.6), followed by ID #21579 remaining within the detection range of the Inner Lagoon receiver for 10.6 h. At the other receiver sites, the maximum visitation durations were less than half of that in Lagoon Backyard, with Front Entrance receiver recording the same individual for 3.6 h, Main Lagoon Entrance receiver for 7.8 h, and Far Inner Lagoon receiver for 8.3 h.

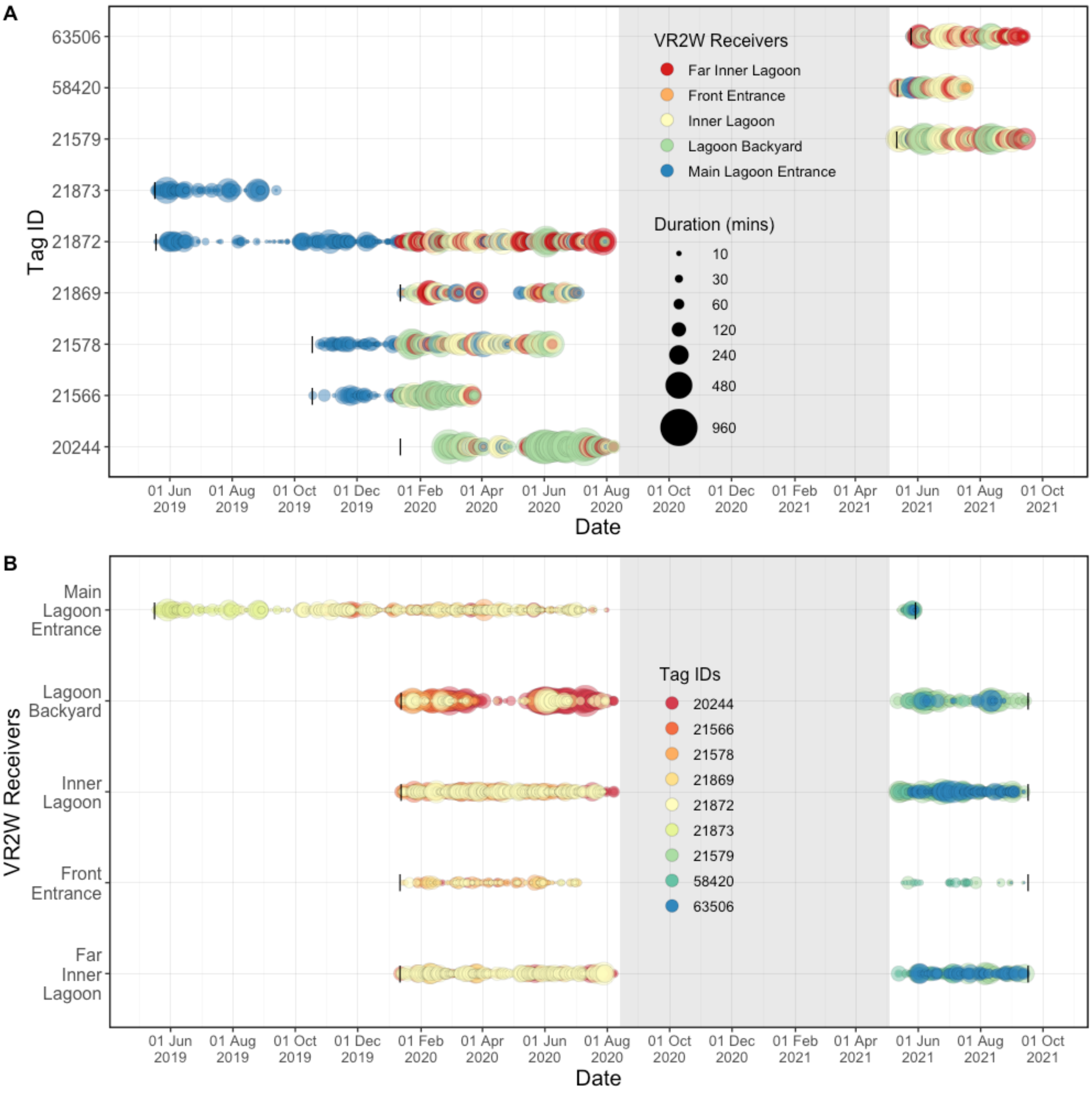

Figure 5.6. Acoustic detections recorded over time for each tagged juvenile *M. alfredi* at each receiver deployed in the Wayag lagoon between May 2019–September 2021. The size of the bubbles indicates (A) the duration of visitations recorded by each receiver for each individual; and (B) the duration of visitations recorded for each individual at each receiver site. The grey shaded areas denote the period during which there were no active acoustic transmitters on manta rays in the lagoon, yet the receivers were still deployed in the lagoon. Black vertical lines in Panel A represent deployment dates of each transmitter, while black vertical lines in Panel B represent deployment and recovery dates of each receiver.

Within the lagoon, the tagged juveniles moved numerous times between receivers, ranging from 183–976 movements per individual (mean ± SD: 392 ± 267 movements), with a total of 3,134 movements recorded. No movement was recorded from ID #21873, as only a single receiver was deployed in Wayag during its period of detection (Table 5.2). Movements recorded between receivers were variable and were generally made between nearby receivers (Figure 5.7). For example, of the 357 movements starting from the Lagoon Backyard receiver, 41% ended at the Main Lagoon Entrance, 33% at the Inner Lagoon, and 21% at the Far Inner Lagoon receiver.

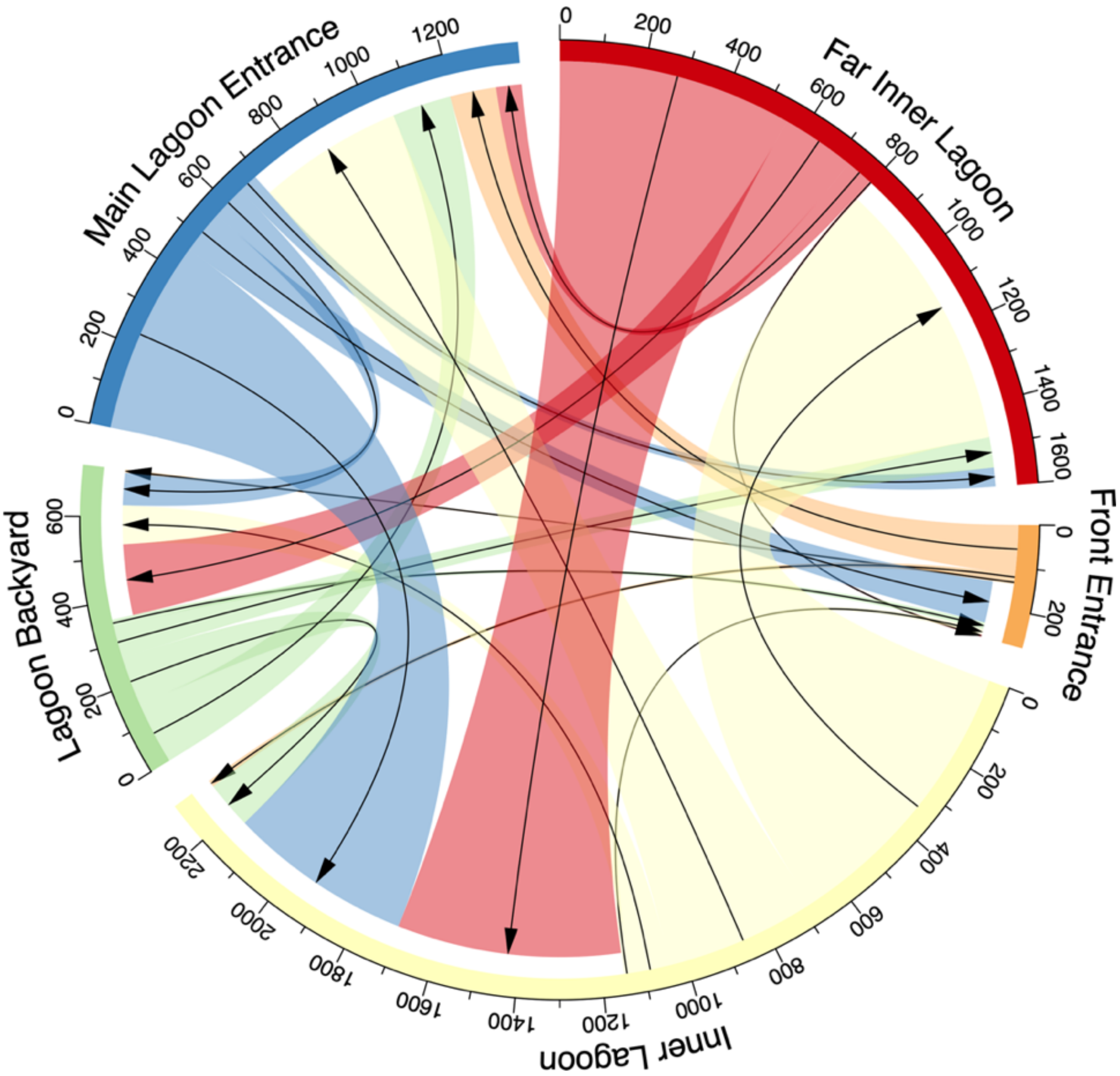

Figure 5.7. Connectivity plot presenting the number of movements of acoustically tagged juvenile *M. alfredi* between receivers in the Wayag lagoon. The arrows show the direction of movement from one receiver to another, and the colour-coded receiver location names are outside the circle.

### 5.3.3.2. Seasonality and periodicity in visitation

The five acoustic receivers deployed within the Wayag lagoon recorded transmitter detections more or less continuously after their initial deployment (Figure 5.6B). However, some of the juveniles were not detected by any receiver in the array in several instances, suggesting that they may have left the lagoon for brief periods, or at least remained in areas of the lagoon where they were not detectable (Appendix D Figure D.2). For example, ID #21869 disappeared from the array in late March 2020 for 40 days before being detected again in early May 2020 (Figure 5.6A).

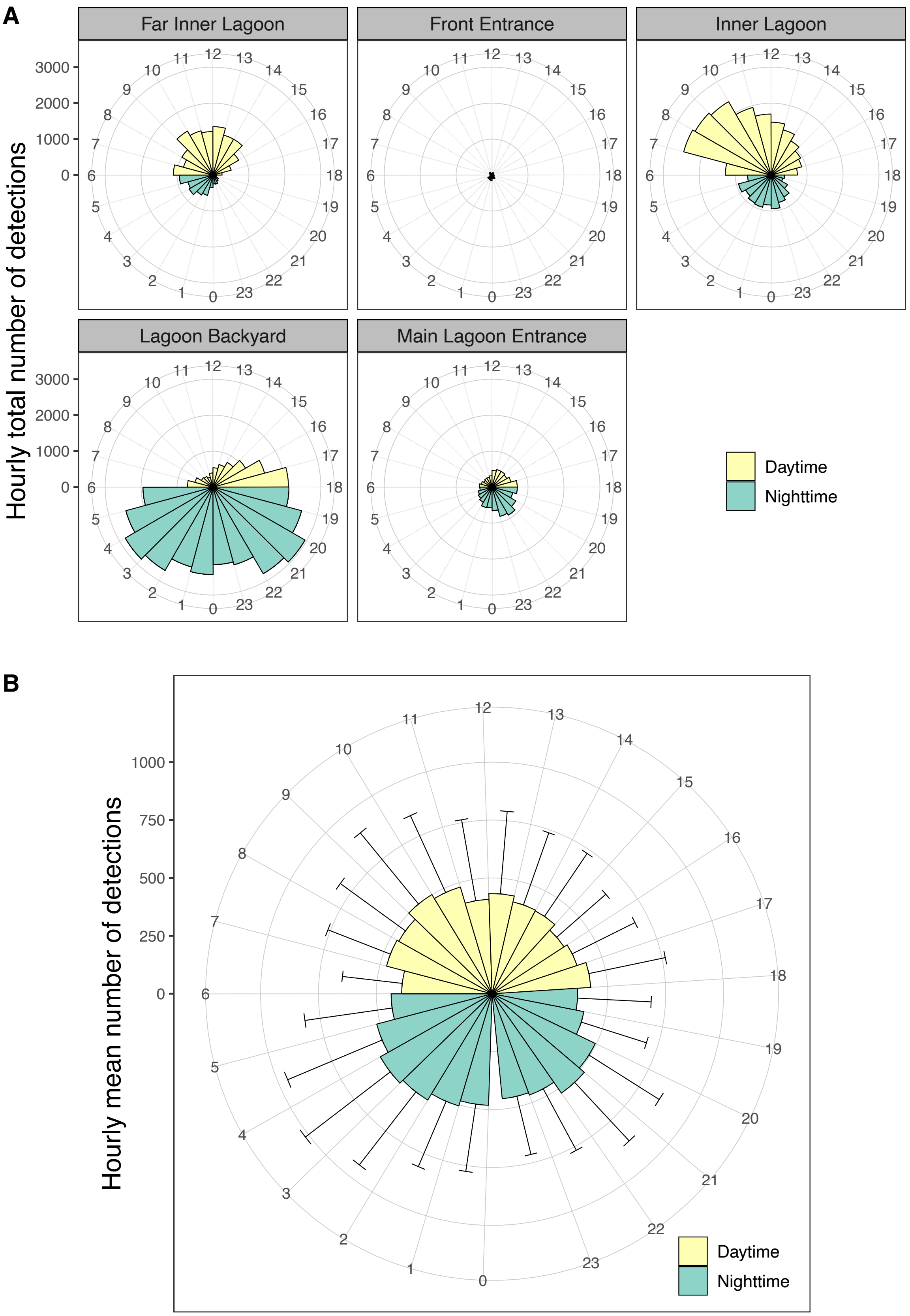

Figure 5.8. (A) Hourly total number of acoustic detections for 24 h (0–23) in the Wayag lagoon between 17 May 2019 and 16 September 2021 recorded by each receiver, and (B) Hourly average number of detections for all tagged juveniles with error bars showing the variability across individuals. As Wayag is less than 20 km north of the equator, daylight hours are more or less constant throughout the year and denoted here as 06:00 to 18:00.

During the same period, considerable gaps in detection of all tagged individuals were also observed at Lagoon Backyard (though detections were continuous through this time at the other four receivers). Importantly, the six transmitters deployed on juveniles in May and October 2019 and January 2020 all disappeared from the array by early August 2020 (Figure 5.6). Of these, two (ID #21873 & #21566) were detected for periods of four and six months, respectively, while the other four transmitters all disappeared from the array between early June 2020 and early August 2020 (Figure 5.6B). No detections occurred on the array between August 2020 and May 2021, until the final deployment of three transmitters in early May 2021. All receivers then continued to record detections until 16 September 2021, when they were downloaded for the final time for this study. Unfortunately, the Main Lagoon Entrance receiver's battery inexplicably ceased to function on 29 May 2021 (despite having been replaced with a new battery in early May at the time of transmitter deployment).

Overall, the mean hourly number of acoustic detections recorded by all receivers combined was significantly different (two-sample t-test, $p = 0.01$) between daytime (mean ± SD: 3,817 ± 343 detections) and night-time (mean ± SD: 4,307 ± 494 detections). The juveniles displayed a striking contrast in spatial use of the Wayag lagoon between day and night (Figure 5.8A). While the Inner Lagoon and Far Inner Lagoon receivers recorded the majority of their detections during daylight hours, the Lagoon Backyard and Main Lagoon Entrance receivers recorded most of their detections during night-time (detections at the Front Entrance receiver were too few to discern a pattern). Every tagged individual was detected by receivers throughout the 24 h diel cycle, with variations in daytime and night-time occupancy among individuals at each hour of the day (Figure 5.8B).

## 5.4. Discussion

Using multiple investigative techniques, this study provides compelling evidence that fulfils Criterion (2) for elasmobranch nursery areas as proposed by Heupel et al. (2007); i.e., demonstrated residency by juveniles within the proposed nursery area for extended periods. We reveal juvenile *M. alfredi* tend to remain within or briefly leave and return to the Wayag lagoon for extended periods, with only short excursions outside of the study area. Some of the photo-identified juveniles were resighted within the Wayag lagoon up to 1.7 years after their first observation, while satellite and passive acoustic telemetry data revealed restricted movements and near-continuous use of the lagoon for extended periods of up to ~14.5 months. Previously, Setyawan et al. (2020) showed conclusively that the Wayag lagoon fulfils Heupel et al. (2007)'s elasmobranch nursery Criteria (1) and (3); i.e., YoY and juvenile *M. alfredi* are more commonly encountered in the Wayag lagoon than in other areas and that the lagoon is used repeatedly by YoY and juveniles across years. Taken together, these studies present the most robust assessment to date of a *M. alfredi* nursery and show conclusively that juveniles use Wayag lagoon in northwestern Raja Ampat as a nursery.

The body size distribution of *M. alfredi* observed in the Wayag lagoon obtained from visual estimation and drone measurements suggests that the Wayag lagoon not only serves as a primary nursery area used by newborn or YoY individuals, but also serves as a secondary nursery area (Bass, 1978) based on the presence of juveniles sized ≤2.4 m DW (Setyawan et al., 2020). Primary and secondary nurseries occur in the same areas for a number of elasmobranch species (Simpfendorfer & Milward, 1993), and have been identified in several tropical marine regions (Yokota & Lessa, 2006; Palacios et al., 2021). We suggest that the Wayag lagoon may also act as a pupping ground. Despite the general dearth of adult manta ray sightings in the lagoon, since the start of our monitoring program in 2013, three near-term pregnant female *M. alfredi* have been observed in Wayag, in particular in the channel between the Front Entrance and Main Lagoon Entrance receivers (Setyawan et al., 2020). A pregnant female acoustically tagged in the Dampier Strait region of Raja Ampat (Figure 5.1) was detected several months later (close to her estimated time of parturition) by a receiver in the Wayag lagoon (Setyawan et al., 2018). Additionally, the estimated sizes of several YoY *M. alfredi* that appeared to be newborns, are equal to the smallest reported birth size of *M. alfredi* by Murakumo et al. (2020). Furthermore, the obvious "creases" observed on these individuals, where their pectoral fins would have been dorsally folded over their body cavity within the mother's uterus, were much like those shown by Marshall et al. (2008) for a late-term *M. alfredi* foetus in Mozambique.

Whilst all of the satellite-tracked juveniles exhibited sustained and restricted movements inside the Wayag lagoon area, occasional excursions to adjacent areas were also recorded. Individuals equipped with acoustic transmitters occasionally went undetected for a period of weeks by the acoustic receiver array inside Wayag lagoon, particularly from the end of March to early May. We hypothesise that these excursions outside of the nursery area were likely associated with maximising foraging activities in nearby highly productive waters to the east of Wayag at the end of the northwest monsoon. A mature male *M. alfredi* satellite tagged in Eagle Rock (Figure 5.1) in Feb 2015 transmitted a substantial number of GPS locations from areas between Quoy and Uranie islands (Figure 5.3) in March-April 2015 (Setyawan, Unpubl. Data), which might indicate that these locations were associated with extensive surface foraging activities. Additionally, it is possible that the acoustically tagged juveniles that disappeared between the end of March and early May from the array in Wayag visited nearby Sayang and Piai islands, approximately 15 km to the northwest (Figure 5.1). Juvenile *M. alfredi* are frequently sighted foraging at the surface along the south coasts of Sayang and Piai islands around March–April (Ferdiel Ballamu pers. comm.) during the transitional period between the northwest and southeast monsoon. These excursions may be evidence of the juvenile manta rays' exploratory behaviours and developing their foraging behaviours including searching for prey in a more open ocean environment – a necessity for young elasmobranchs like basking sharks (*Cetorhinus maximus*), which have lower prey encounter success rates than adults (Sims et al., 2006). Such behaviour is reported in a number of ocean-going taxa; for instance, Grecian et al. (2018) found differences in foraging proficiency between mature and immature gannets (*Morus bassanus*), while younger individuals of narwhals (*Monodon monoceros*) demonstrated different movement patterns from older individuals, likely associated with increased exploratory behaviours and less developed foraging proficiency (Laidre et al., 2004).

Though *M. alfredi* are capable of travelling up to several hundred kilometres to visit seasonally-productive sites (Anderson et al., 2011a; Couturier et al., 2014; Jaine et al., 2014), the 14 satellite or acoustically-tagged individuals in this study showed high residency to the Wayag lagoon, with a maximum movement of 47 km to the east of the lagoon. None of the acoustically-tagged individuals were detected within the an array of 23 acoustic receivers placed at all known *M. alfredi* aggregation sites in the Raja Ampat archipelago (Figure 5.1), including at the heavily-visited cleaning and feeding aggregation site Eagle Rock, just 36 km to the south of the Wayag lagoon (Setyawan et al., 2018).

Despite several movements to areas outside the Wayag lagoon, the tagged juveniles repeatedly returned to and showed a strong residency to the study site. Three of five satellite-tagged juveniles exhibited the extent of activity space (95% UD) that extended less than 10 km from the Wayag lagoon (Figure 5.4). Notably, the core activity space (50% UD) of all satellite-tagged juveniles mainly encompassed the Wayag lagoon and nearby areas within a 5 km radius. The largest 50% and 95% UDs identified in our study encompassed 182 and 1,195 km$^2$, respectively. These are much smaller than those of a juvenile male in the Red Sea, with 50% and 95% UDs of 414 and 2,457 km$^2$ (Kessel et al., 2017). It is important to note that the activity space estimated in our study was restricted to short periods of satellite tracking (12–69 days), therefore it might realistically be larger than what is currently estimated. We also note that satellite tagged juveniles in our study were mostly females, therefore we were unable to explore sex-linked nuances in the spatial movements of juveniles, though maturity is a more relevant factor than sex when identifying nurseries.

The restricted activity space and low move persistence recorded for satellite-tracked individuals in the vicinity of the Wayag lagoon suggest strong residency within this site. This residency may be driven by the safe habitat for juveniles or could also reflect the reliable availability of prey in this area. For manta rays, which rely on finding large quantities of diffuse zooplankton prey in a dynamic pelagic ocean, sheltered coral reef lagoons may supply reliable and sustained quantities of prey to support the energetic needs of juveniles. Numerous studies have documented large *M. alfredi* foraging aggregations at isolated coral reefs where local tidal dynamics act to concentrate zooplankton prey (Jaine et al., 2012; Weeks et al., 2015; Armstrong et al., 2016), including inside the lagoons of coral reef atolls (Papastamatiou et al., 2012; Armstrong et al., 2021b). Within the Wayag lagoon, juvenile *M. alfredi* are frequently observed using surface and somersault feeding strategies (Setyawan et al., 2020) similar to other lagoon habitats (McCauley et al., 2014; Stevens, 2016). We did not investigate the taxonomic composition or biomass of the planktonic prey targeted by feeding juvenile manta rays in the Wayag lagoon, though this certainly represents an important future field of study.

Acoustic telemetry detections of the tagged juvenile *M. alfredi*, in particular eight individuals that were detected by all receivers, indicated high residency indices (RI: 52–98%) at the monitored sites within the Wayag lagoon. Such residency levels are substantially higher than that of individuals (mostly adults) tagged during a previous acoustic tagging study in northern Raja Ampat (RI: 21%) (Setyawan et al., 2018). Similarly, acoustically-tagged juvenile *M. alfredi* in the Amirantes, Seychelles, also showed a higher residency than adults around key habitats (Peel et al., 2019b). In the Red Sea, the residency of small (<2.5 m DW, likely juvenile) *M. alfredi* was also relatively high at 65% (Braun et al., 2015). Lower residency levels (15–40%) of acoustically-tagged animals have been reported from other populations (Clark, 2010; Couturier et al., 2018; Andrzejaczek et al., 2020; Venables et al., 2020), presumably because the studies tagged adult individuals. It is also possible that our RI may have been affected by the design of our acoustic tracking array. In addition to age-class (Chapman et al., 2015; Peel et al., 2019b), the number of receivers, their position and the design of the acoustic array are important considerations (Espinoza et al., 2016; Peel et al., 2019b). This artefact of array design is demonstrated by the fact that the lowest RI in our study (43.7%) was registered by ID #21873 when there was only one receiver deployed in the lagoon at the beginning of the study period.

Passive acoustic monitoring of tagged juvenile *M. alfredi* revealed individual and temporal variability in fine-scale (<4 km) space use and site occupancy within the Wayag lagoon. The nine acoustically tracked individuals exhibited strong site affinity, with high residency times around acoustic receivers and frequent, repeated visits to the sites. The maximum consecutive days of acoustic detections by tagged juveniles of up to 119 days (~4 months), with an average of 95 days (~3 months) of maximum consecutive detection days for tagged juveniles detected by five receivers, clearly indicate that these sites provide important habitat in Wayag lagoon. The long-term residency of juvenile *M. alfredi* in Wayag lagoon has been documented through individual photo-ID, with some juveniles resighted on several occasions over a 21-month period, as well as by passive acoustic telemetry revealing quasi-continuous occupancy in the nursery for over 14 months. Globally, it is still unclear how long juvenile reef manta rays use a nursery area, and at what age or size they decide to leave the nursery. In another proposed *M. alfredi* nursery area located in Fam, Raja Ampat (approximately 100 km to the south of Wayag), three juveniles were visually resighted after 26 months, and one resighted after 28 months, still present in the nursery (Setyawan et al., 2020); however, it is unknown whether these individuals had left the area during this time. We provide here the first documented continuous occupancy of juvenile manta rays in a nursery area. Coupled with multi-year presence of the juveniles, their continuous occupancy highlights the importance of this nursery area for their early-stage development. Further studies are required to better understand the ecological function of nursery areas in contributing to recruitment into adult populations of *M. alfredi*. Setyawan et al. (2020) documented one such recruitment; a juvenile *M. alfredi*, first sighted in Wayag lagoon as a 180 cm DW YoY male in November 2013, was resighted six years later as a 260 cm DW adult in the South East Misool MPA in southern Raja Ampat, 296 km to the south. Other valuable lines of future investigation include examining the social interactions and bonds created between newborns and juveniles within nurseries and their persistence over time, as well as investigating the "carrying capacity" of the area to serve as a nursery for newborn and juvenile *M. alfredi*, given the small size of the Wayag lagoon.

Passive acoustic tracking in Wayag lagoon yielded similar proportions of juvenile detections between day (47%) and night (53%), though the number of night-time detections was significantly higher than during the day. This is in sharp contrast with similar studies conducted in several other sites in Indonesia (Dewar et al., 2008; Setyawan et al., 2018) and other countries (Clark, 2010; Couturier et al., 2018; Peel et al., 2019b; Andrzejaczek et al., 2020; Venables et al., 2020), in which the numbers of acoustic detections of adult or subadult *M. alfredi* were significantly lower during the night than during the daytime. Most of these studies reported that manta rays would visit and occupy receiver sites mainly during the day for foraging and cleaning, but at night, tagged individuals would disappear from the tracking arrays, presumably moving to offshore or deeper waters to feed on vertically migrating deep scattering layers or emerging benthic zooplankton (Clark, 2010; Couturier et al., 2013; Braun et al., 2014). This doesn't appear to be the case in Wayag, where the juveniles were detected in the lagoon throughout both day and night. Furthermore, the distinct variations in the daytime and night-time detections between those receivers inside main lagoon area, that are surrounded by deep water, and Lagoon Backyard, located in shallow water, highlight a potentially interesting distinction in habitat use by juveniles in nursery areas. McCauley et al. (2014) observed that *M. alfredi* in a sheltered lagoon in Palmyra Atoll continuously used large areas of the lagoon and spent more time at greater depth during the day than at night. Further research into the vertical movements of *M. alfredi* in and outside of the Wayag lagoon using satellite telemetry will help understand the diel diving behaviour of juveniles.

In contrast to the main lagoon area (Figure 5.1) that was used extensively by juvenile *M. alfredi* during the day, the shallow Lagoon Backyard site was primarily visited around dusk and at night, often for extensive periods up to 16 hours. In most other acoustic telemetry studies conducted in reef environments and published in the literature, it is indeed possible that biological noise emanating from the reef at night may have prevented some detections to be recorded by the receivers (Kessel et al., 2014). However, data from the sentinel tag detected at the Main Lagoon Entrance receiver showed no obvious reduction in tag detectability based on time of day, suggesting continuous ability of the receiver to detect transmitters in the absence of tagged juveniles. Therefore, the distinctive diel pattern in visitation at the receivers in Wayag lagoon was likely due to actual juvenile visitations rather than being an artefact of detection range. Sheltered, shallower sites can act as ideal night-time habitats by providing safety from potential predators (Wetherbee et al., 2007; Guttridge et al., 2012) and a potential suitable supply of demersal zooplankton emerging from the shallow seabed (Alldredge & King, 1977; Ohlhorst, 1982). In southern Mozambique, acoustically tagged *M. alfredi* visited a feeding site mostly at night (Venables et al., 2020), though it is unclear whether they were foraging around the receiver at this site. At Palmyra Atoll in the Line Islands, Papastamatiou et al. (2012) recorded high nocturnal area-restricted search behaviour associated with high zooplankton prey patches at specific sites inside a coral reef lagoon. It is possible that juvenile *M. alfredi* in Wayag use the Lagoon Backyard site for the same reason. Further research into the night-time behaviour of *M. alfredi* at this site, potentially using active acoustic tracking, may help ascertain the drivers of the observed high nocturnal residency times in this shallow area of the Wayag lagoon.

Importantly, the findings of this study have been shared with the Raja Ampat MPA Management Authority and have already been used to redesign and improve conservation and management measures for manta ray protection in the SAP Waigeo Barat MPA. Our findings have contributed to the designation of manta rays as one of the primary conservation targets for this MPA due to the importance of the Wayag lagoon as a manta ray nursery. Given the status of manta rays as a conservation target, stricter protection must now be implemented in Wayag; therefore, some areas within the main lagoon of Wayag have recently been designated as a “core conservation zone” with strictly restricted access. The areas outside of this core zone remain designated as tourism zones, where visitors, but no fishing, is allowed. The MPA Management Authority is currently working on finalising the legislation for both the revised zonation system and the management plan for SAP Waigeo Barat MPA, which will include important regulations (e.g., boat speed limits of less than 5 knots inside the main lagoon and the areas around Lagoon Backyard, as well as stipulated mooring areas for liveaboards far from known manta sites) to ensure the nursery function of the Wayag lagoon is not compromised.

## 5.5. Conclusions

This study shows conclusively that the Wayag lagoon in Raja Ampat archipelago serves as a nursery for newborn and juvenile *M. alfredi* and provides the most robust assessments to date of a *M. alfredi* nursery. It also provides key information on the residency and fine-scale habitat use of *M. alfredi* in this nursery area. These important findings have been used to underpin the formulation of management strategies to specifically protect the Wayag lagoon and its function as a manta ray nursery. Safeguarding this nursery could ultimately be instrumental for the survival and recovery of *M. alfredi* populations in the region.

# Chapter 6.

# Spatial connectivity of reef manta rays across the Raja Ampat archipelago, Indonesia

## 6.1. Introduction

Effective spatial management and conservation of wild fauna requires a robust understanding of the structure and movement connectivity of populations (Crowder & Norse, 2008). For example, identifying the degree of space use overlap between two populations of a same species can provide insights into their reproductive ecology, shared use of key habitats or food resources, or important migratory corridors (e.g., Warren et al., 2020; Emmons et al., 2021; Simpson et al., 2021), from which tailored management strategies can be drawn. An emerging concept transferred from terrestrial ecosystem research to the marine environment is that of a 'metapopulation' (Grimm et al., 2003). A metapopulation is defined as a set of discrete subpopulations of the same species inhabiting the same general geographical region, between which individuals move through migration and dispersal (Akçakaya et al., 2007). Two key assumptions that separate a metapopulation from a single panmictic population are that 1) subpopulations are geographically discrete, and that 2) the mixing of individuals between subpopulations is less than that within them (Akçakaya et al., 2007). In marine environment, the metapopulation concept is now commonly used particularly for coral reef fish communities that occupy spatially distinct coral reef habitats and for other marine organisms that have limited larval dispersal (Kritzer & Sale, 2010). For marine megafauna, the metapopulation concept has been considered less relevant due to the ability of these wide-ranging animals to migrate large distances and the extensive home ranges they are generally assumed to occupy (Kritzer & Sale, 2006). Nevertheless, many marine populations of conservation concern appear to have a metapopulation structure driven by juvenile dispersal and adult migration (e.g., sharks, sea turtles) (Encalada et al., 1998; Crowder & Figueira, 2006; Sandoval-Castillo & Beheregaray, 2015).

The globally vulnerable reef manta ray *Mobula alfredi* is widely distributed throughout nearshore pelagic waters of the tropical and subtropical Indo-Pacific (e.g., Couturier et al., 2012; Marshall et al., 2022). This highly mobile species is known to exhibit strong site affinity and high residency in isolated parts of its range, such as oceanic island chains (Deakos et al., 2011; Carpentier et al., 2019). The species is also capable of undertaking long distance movements to areas located several hundred (Couturier et al., 2011; Germanov & Marshall, 2014; Jaine et al., 2014; Setyawan et al., 2020) to over 1,000 kilometres away (Armstrong et al., 2019), and therefore the metapopulation concept has not generally been considered relevant to this species. However, recent genetic studies have revealed that some fine scale genetic differentiation between nearby *M. alfredi* populations is possible. For example, Lassauce et al. (2022) found strong evidence of genetic structure between *M. alfredi* sampled from three different cleaning station aggregation sites located 110-335 km apart in New Caledonia. Similarly, two genetically distinct *M. alfredi* subpopulations were recently identified in Hawai'i between oceanic islands located only 150 km apart yet separated by waters over 2,000 m deep (Whitney et al., 2023). No matches had previously been identified between photographically identified individuals from these two subpopulations, supporting the idea of distinct subpopulations with no connectivity between the nearby islands (Deakos et al., 2011). These findings highlight the importance of delineating population structure and distinct 'management units' for *M. alfredi* to enable effective management and conservation (Stewart et al., 2018a).

The Raja Ampat archipelago, eastern Indonesia, is home to at least 1,375 individual *M. alfredi*, with numbers documented to be increasing over the past decade (Chapter 3). The species has been fully protected in the region since 2012 and essentially managed by the Raja Ampat Marine Protected Area Management Authority as a single and homogeneous population (Chapter 2). Throughout the 6.7 million ha of the archipelago, the species is distributed unevenly and exhibits high residency and strong affinity to numerous cleaning station and feeding aggregation sites (Setyawan et al., 2020). Individual *M. alfredi* have also been reported to seasonally migrate between some aggregation sites located along a 130 km corridor through Dampier Strait and West Waigeo (Setyawan et al., 2018). Setyawan et al. (2020) hypothesised that *M. alfredi* in Raja Ampat might form a metapopulation comprised of seven spatially distinct subpopulations inhabiting island groups or regions located 25–125 km apart and separated by waters 800–1,400 m deep (Figure 6.1). Each of these island groups or regions, namely Ayau, Wayag Islands, West Waigeo, Dampier Strait, Fam & Bambu, Kofiau & Boo, and Misool, is hypothesised to have its own *M. alfredi* subpopulation, between which limited exchange of individuals occurs. A deeper understanding of connectivity between these hypothesised subpopulations is necessary to support this theory and improve the effectiveness of conservation management strategies for this vulnerable species in the region.

Metapopulations in the marine environment exhibit limited demographic connectivity between local populations (subpopulations) (Kritzer & Sale, 2006), which can be inferred from the movements of individuals between these subpopulations (Lowe & Allendorf, 2010). Various approaches have been used to assess demographic connectivity in marine environments, including visual observations (i.e., photographic identification), mark recapture, as well as acoustic and satellite telemetry (Kool et al., 2013; Lédée et al., 2021). Passive acoustic telemetry, consisting of acoustic transmitters and a stationary network of acoustic receivers deployed at strategic locations, is a powerful tool to inform the presence, residency and habitat use of acoustically tagged animals at these sites and detect movements over a range of spatial scales and for extended periods of time (Heupel et al., 2006; Brodie et al., 2018; 2018). Multi-year use of passive acoustic telemetry has enabled tracking the regional movements of highly migratory species, including *M. alfredi* at their aggregation sites in several regions across the Indo-Pacific (Dewar et al., 2008; Couturier et al., 2018; Setyawan et al., 2018; Peel et al., 2019b; Venables et al., 2020).

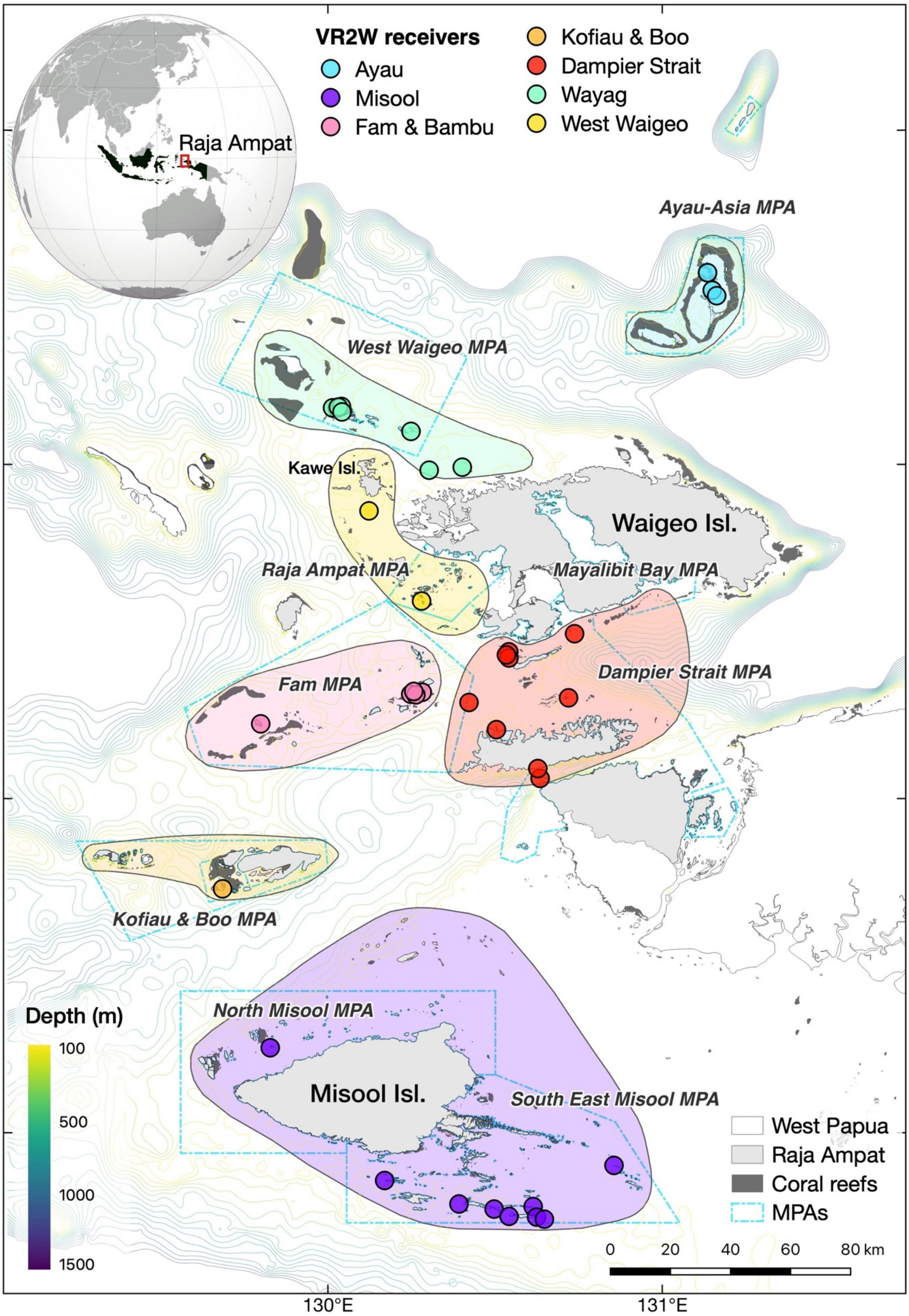

Figure 6.1. Map of acoustic receivers (coloured circles) deployed in Raja Ampat archipelago. Coloured polygons with solid lines depict approximate boundary of island groups (regions) inhabited by hypothesised *M. alfredi* subpopulations. Different colours of each polygon and circle represent different subpopulations. Polygons with blue dash-dotted lines depict the Raja Ampat MPA network. Contours show bathymetry throughout the study region.

Passive acoustic telemetry has increasingly been used in combination with network analysis in behavioural and movement ecology studies (Jacoby & Freeman, 2016). The inherent structure of acoustic telemetry data suits the application of network analysis to elucidate the directionality and frequency of movements between sites monitored, with nodes typically denoting acoustic receiver stations and edges representing the movements of tagged animals between receiver stations (Lédée et al., 2015; Mourier et al., 2018). These combined approaches have been successfully used to reveal population structure, habitat use and connectivity of marine species, including manta rays and other elasmobranchs, at regional to continental scales and over long periods (Mourier et al., 2012; Brodie et al., 2018; Casselberry et al., 2020; Jacoby et al., 2020; Friess et al., 2021; Lédée et al., 2021; Perryman et al., 2022).

While passive acoustic telemetry allows for long-term tracking of marine animals over multiple years and the potential to estimate their home range (Udyawer et al., 2018), the movements of acoustically tagged individuals can only be monitored within the detection range of acoustic receiver stations (Heupel et al., 2018). As such, the ability to monitor the full range of movements of the individuals in a population and to estimate their home range is strictly limited by the number of receivers in the array and their spatial extent – with strong potential to significantly underestimate the extent of their movements and home range if the acoustic receiver array is not sufficiently large. By comparison, satellite telemetry allows to track movements of marine animals in a manner that is not dependent upon the size and extent of an acoustic receiver array (Hussey et al., 2015). Combining passive acoustic telemetry and satellite telemetry therefore provides an opportunity to track the movements of marine animals over multiple spatial scales (Meyer et al., 2010; Hussey et al., 2015).

Here, we examined the spatial connectivity and population structure of manta rays in Raja Ampat using acoustic and satellite telemetry approaches. We first conducted a network analysis of five years of acoustic telemetry data derived from an array of 34 receivers deployed across the seven regions of interest to identify connectivity patterns as well as key migratory corridors and habitats. A subsequent home range analysis of 11 satellite tracks from *M. alfredi* tagged within different MPAs in Raja Ampat was performed to further assess the extent of their activity space.

## 6.2. Material & Methods

### 6.2.1. Study area

The Raja Ampat archipelago (0.711°S, 130.407°E) in the Bird's Head Seascape (BHS), northwestern Papua, is home to Indonesia's largest populations of reef *Mobula alfredi* (Setyawan et al., 2020) and oceanic *M. birostris* manta rays (Beale et al., 2019). Over 70 manta ray aggregation sites are distributed throughout the archipelago, protected by a network of nine marine protected areas (MPAs) that cover a large geographical region of nearly 2 million ha (Setyawan et al., 2020) (Figure 6.1). Here, both manta ray species have been fully protected since the Raja Ampat regency government designated the entire archipelago as Southeast Asia's first shark and ray sanctuary in 2012 (Dharmadi et al., 2015; Chapter 2).

The Raja Ampat archipelago is characterised by complex coastlines and bathymetry with shallow shelf (<200 m depth) and deep channels (800-1400 m). The deep channels naturally isolate several groups of islands such as Misool in the south, Kofiau and Boo island group in the west, and the Ayau atolls in the north of the archipelago (Figure 6.1). Primary productivity in the Raja Ampat archipelago is affected by upwellings, occurring during the southeast monsoon in several regions including the Dampier Strait, Bougainville Strait (in the northwest of Waigeo Island), and southeast Misool (Mangubhai et al., 2012; Setiawan et al., 2020).

## 6.2.2. Data collection

### 6.2.2.1. Transmitter deployments

We deployed V16-5H acoustic transmitters (Innovasea, Halifax, CA) operating at 69 kHz frequency and transmitting pings randomly every 60–130 sec on 117 individual *M. alfredi* throughout the study region. All acoustically tagged *M. alfredi* were subadults and adults larger than 2.4 m disc width. The transmitters were deployed in five different phases between February 2016 and February 2020 (Appendix E Table E.1) in the seven regions representing the hypothesised *M. alfredi* subpopulations across the Raja Ampat archipelago. Additionally, we note that the number of the acoustic transmitters deployed in each region was not equal (Appendix E Figure E.1) due to logistical issues to undertake fieldwork in this remote region.

We also equipped 11 *M. alfredi* with SPLASH10-F-321A satellite tags (Wildlife Computers, Redmond, USA) (Table 6.2), which were programmed to remain attached for 59–180 days on the tagged animals. These tags were deployed between October 2014 and May 2022 in all of the seven regions of interest, except Wayag and the Fam & Bambu (Table 6.2). Similar to acoustic transmitters, the number of satellite tags deployed was not equal in each region. The satellite tags collected both Argos location and Fastloc GPS location data upon surfacing, but for subsequent analysis, we only analysed positions obtained via Fastloc GPS due to their higher accuracy (Dujon et al., 2014). The preparation (i.e., coating, tether length) and deployment of all acoustic transmitters and satellite tags followed established procedures used in similar studies in Raja Ampat (Setyawan et al., 2018; Chapter 5).

### 6.2.2.2. Acoustic receiver deployments

To document the presence of acoustically tagged animals at the sites of interest, we deployed an array of 34 VR2W-69 kHz acoustic receivers (Innovasea, Canada) across Raja Ampat archipelago (Figure 6.1) between February 2016 and September 2021. These acoustic receivers were deployed in regions inhabited by the seven hypothesised *M. alfredi* subpopulations (Setyawan et al., 2020): Ayau, Wayag, West Waigeo, Dampier Strait, Fam & Bambu, Kofiau & Boo, and Misool. They were strategically placed at or near *M. alfredi* feeding and cleaning sites or other known aggregation sites in order to optimise data collection (Setyawan et al., 2018).

The acoustic receiver array in each region varied from one to nine receivers (Figure 6.1). The deployment periods of these acoustic receivers also varied (Appendix E Figure E.2) due to several factors, including theft or damage of a number of receivers; unfortunately, the logistical difficulty of monitoring and replacing any stolen or damaged receivers in the remote Raja Ampat archipelago led to some significant data gaps at some receivers. Given the difference in the number of aggregation sites identified in each region as well as logistical and financial constraints, the acoustic receiver array in each of these regions was not equally dense (Figure 6.1).

## 6.2.3. Data analyses

### 6.2.3.1. Passive acoustic telemetry data

Detection data from passive acoustic telemetry receivers were extracted from the VUE software and recorded as a timestamped log of transmitter IDs detected by acoustic receivers at 34 stations deployed across the study region (Figure 6.1). Detections from all tagged *M. alfredi* recorded by acoustic receivers including single detection due to the highly mobile nature of manta rays (Appendix E Figure E.3). The resulting data consisted of transmitter IDs, timestamps of detections, receiver metadata (e.g., geographic coordinates, station category), and transmitter metadata (tagging time and location). The movement data were formatted using the ‘VTrack’ package (Campbell et al., 2012) in the R environment (R Core Team, 2021).

### 6.2.3.2. Network analyses

Movement networks were constructed to assess spatial connectivity of *M. alfredi* between receiver stations deployed throughout Raja Ampat. Additional movement networks were generated to explore the movement and dispersal patterns of *M. alfredi* tagged in each region. Each movement network consisted of nodes representing receiver stations, and edges denoting the number *M. alfredi* movements recorded between these receiver stations. Edges were weighted based on the proportion of movements recorded during the tracking period. All movement networks were constructed and plotted in both geographic coordinate and multidimensional scale layouts using the ‘igraph’ package (Csardi & Nepusz, 2006).

To understand the structure of movement networks, each network was measured for its network-level metrics and node-level metrics. Network-level metrics were measured to understand the patterns of connectivity between all nodes and edges in the network (Rayfield et al., 2011). These metrics consisted of eight measures, including 1) the number of all nodes within the network, 2) the number of nodes within regions where tagging occurred, 3) the number of connected nodes, 4) the number of edges between two nodes, 5) the number of *M. alfredi* movements between two nodes, 6) edge density, 7) average path length (APL) and 8) diameter (Table 6.2). The edge density represents the proportion of existing edges out of a total number of possible edges in the network (Brodie et al., 2018), while APL shows the mean length of the shortest path connecting all nodes in the network (Rayfield et al., 2011). Finally, diameter represents the longest path between any pair of nodes within the network, indicating the network size (Urban & Keitt, 2001).

At node level, centrality measures (node-level metrics), which were determined from the level of connectivity between nodes either directly or indirectly via other nodes, were calculated for each network to describe the relative importance of a node (i.e., manta ray aggregation site) and the influence of nodes have on the overall structure of each movement network (Jacoby et al., 2012a). In this study, we calculated six centrality measures, including in-degree, out-degree, degree centrality, betweenness, closeness, and eigenvector (Table 6.1). In-degree and out-degree represent the number of neighbours for each node with incoming and outgoing edges respectively (Urban et al., 2009). Degree centrality shows the number of all edges connected to a node, which is the sum of in-degree and out-degree (Newman, 2018). Betweenness demonstrates the number of shortest paths crossing through a node, which indicates how much a receiver station was involved in the movements of *M. alfredi* (Minor & Urban, 2007). Closeness calculates average distance from a node to other nodes, showing how central the position of a node is within the network. Eigenvector shows how important a node is within a network by considering the degree centrality of other nodes connected to this node (Newman, 2018).

To determine if the space use of *M. alfredi* within the acoustic receiver array in Raja Ampat occurred in a non-random manner, the network was tested for non-random movements of acoustically tagged animals using edge permutation (Jacoby et al., 2012a). A network with community structure typically has longer APL than a random network with the same number of nodes and edges (Pattanayak et al., 2022). The null hypothesis was that each node in the observed network had the same probability to be connected to other nodes through movements of *M. alfredi* despite its distance to another, therefore, the observed network would have a similar APL with a random network. The edge permutation was performed based on observed movements between nodes in the network with 10,000 bootstrap iterations. Edges from the observed network were shuffled randomly, and then new networks were generated using the same degree distribution as the observed network using *degree.sequence.game* function from the 'igraph' package (Csardi & Nepusz, 2006). Following this, the distribution of APL values obtained from these newly permuted networks was then compared with the APL of the observed network. A $p$-value was then calculated based on a one-tailed test to examine if the probability of the observed APL falling within the distribution of APL values from the permuted networks.

Following this non-random test, we used a community detection algorithm based on modularity (Newman, 2006) to identify community structure within the acoustic receiver array network and determine clusters consisting of densely connected nodes (acoustic receiver stations) with fewer connectivity across clusters (Newman, 2004b). A positive value of modularity indicates the possible presence of community structure within the network, and a modularity of 0.3 or larger suggests a good division within the network to generate clusters (Newman, 2004a, 2006). The analysis was undertaken using *cluster_optimal* function in the 'igraph' package by including edge weights representing the number of *M. alfredi* movements within pairs of nodes (acoustic receiver stations) (Csardi & Nepusz, 2006). Finally, to assess differences in movement patterns between females and males *M. alfredi*, the total movements made between pairs of receiver stations and the mean direct distance travelled by the acoustically tagged manta rays were examined. A Shapiro-Wilk normality test was used to test if the data were normally distributed, before applying an unpaired two samples Wilcoxon test to determine if there were any differences between females and males in each of two measures. All statistical significances for hypothesis tests were reported based on Muff et al. (2021).

### 6.2.3.3. Home range analysis

The GPS position data obtained from the satellite tags were processed following the procedure detailed in Chapter 5. The resulting GPS locations were then analysed to estimate the home range of the satellite-tracked *M. alfredi*. An optimally weighted Autocorrelated Kernel Density Estimator (AKDE) (Fleming et al., 2018) was fitted to these processed GPS positions using the 'ctmm' R package (Calabrese et al., 2016) to estimate the extent of activity space (95% Utilisation Distribution – UD). AKDE has been proven to better predict home range than other conventional home range estimators that did not consider autocorrelation during estimation (Fleming et al., 2015). It has also been previously applied to satellite tracking data from *M. alfredi* (Fleming et al., 2018; Setyawan et al., 2022b) which was characterised by irregularity in data collection due to the unpredictable nature of the surfacing behaviour of this species. The area of 95% UD of each individual was then calculated in km$^2$ by excluding the area of any islands included within the UD.

## 6.3. Results

### 6.3.1. Passive acoustic tracking

Passive acoustic tracking of *M. alfredi* in the Raja Ampat archipelago was conducted between February 2016 and September 2021. Of the 117 transmitters deployed, only 94 tagged individuals (80%) were detected at least once by the 34 receivers in the array (Appendix E Table E.1, Figure E.3). Of these 94 individuals, 72 were detected by two or more receiver stations. Movements between receiver stations were then examined for these 72 *M. alfredi* (44 females, 27 males, and one unsexed individual).

A total of 1,094 movements were recorded (Table 6.1), consisting of 777 movements by females, 315 movements by males, and two movements by the unsexed individual. On average, females (mean ± SD = 18 ± 28 movements) moved more frequently than males (mean ± SD = 12 ± 22 movements), but the mean direct distance travelled by the females (mean ± SD = 23.3 ± 16.3 km) was shorter than that by the males (mean ± SD = 38.8 ± 48.5 km). Additionally, the maximum straight-line distance travelled by females (70.7 km) was much shorter than that by males (252.0 km).

A Shapiro-Wilk normality test suggested that the total movement data were not normally distributed ($p < 0.001$) for both sexes. Furthermore, an unpaired two samples Wilcoxon test suggested there was no evidence ($p = 0.116$) of the difference in the total movements made by females (median: 8 movements) and males (median: 4 movements) (Appendix E Figure E.4). In terms of mean direct distance travelled by tagged *M. alfredi*, a Shapiro-Wilk normality test also suggested that the data were not normally distributed for both females ($p = 0.011$) and males ($p < 0.001$) given $p >$ 0.05. Despite the median of mean direct distance travelled per movement made by males (23.5 km) being larger than that of female *M. alfredi* (19.3 km), an unpaired two samples Wilcoxon test suggested there was no evidence ($p =$ 0.255) that the medians were different between sexes (Appendix E Figure E.4).

### 6.3.2. Movements between acoustic receiver stations

The movement network of 72 *M. alfredi* tagged throughout the Raja Ampat archipelago was constructed from 34 nodes (receiver stations) and 131 edges (Figure 6.2), consisting of a total of 1,094 movements between these nodes (Table 6.1). All these nodes were connected, except for two receiver stations at North Misool in Misool and Uranie in Wayag. At the regional level, stations within the Misool regional receiver array seemed to be closely connected with each other and frequent movements were recorded primarily by receivers at Magic Mountain, Eagle's Nest, and Southwest Batbitim. Similar to Misool, three receiver stations in Ayau were closely connected and grouped together, with frequent movements of *M. alfredi* between two receivers at a cleaning station and a feeding ground. On the other hand, the receiver stations in central Raja Ampat (Dampier Strait, Fam, and West Waigeo) were all connected with the others at various degrees of movements. The only receiver station in Kofiau was quite isolated from other receiver stations in the network and was only connected with the Wai receiver station (Dampier Strait). Furthermore, three receiver stations in Wayag region were connected with both receiver stations in the West Waigeo region and with the acoustic receiver at Magic Mountain in Misool.

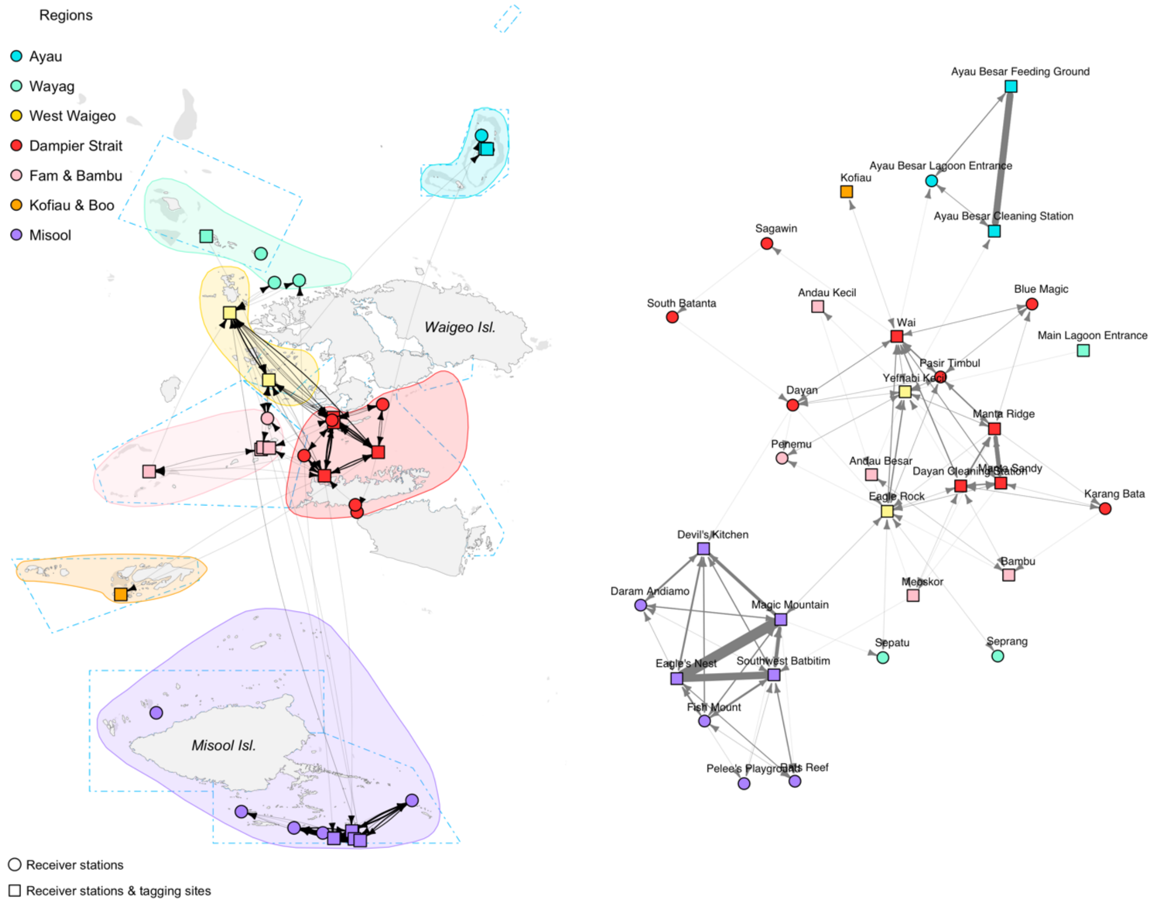

Figure 6.2. Movement networks of acoustically tracked *M. alfredi* in Raja Ampat archipelago between February 2016 and September 2021 displayed using a geographic coordinates (left panel) and multidimensional scaling layout (right panel). Nodes (coloured circles and squares) symbolise either receiver stations or both tagging sites and receiver stations. Edges (grey lines) represent the movements of *M. alfredi* between the nodes. Arrows indicate the direction of movements. The thickness of the edges represents frequency of movements between nodes (the thicker the lines, the more frequent movements occurred between two connected nodes). Blue polygons with blue dash-dotted lines depict the Raja Ampat MPA network.

The majority (92.5%) of the 1,094 movements occurred between receiver stations within each regional receiver arrays, especially in Misool, Ayau, and Dampier Strait, where receivers in these regions were geographically located close to each other (Appendix E Table E.2). In Misool, four receiver stations (Magic Mountain, Eagle's Nest, Southwest Batbitim, Devil's Kitchen) contributing to 41% of total movements were located within a maximum of 11.8 km from one another. In Ayau, two receiver stations in Ayau (Ayau Besar Cleaning Station and Ayau Besar Feeding Ground), which are located 930 m apart, contributed to 11% of total movements. In Dampier Strait, two receiver stations (Manta Ridge and Manta Sandy) were located 2.2 km apart and contributed to 7% of total movements.

Of the 34 receiver stations in the network (Figure 6.2), eight showed degree centrality that was higher than the 75th percentile (11.75) of all receiver stations (Appendix E Table E.3). These receiver stations are distributed within the Dampier Strait (i.e., Wai, Dayan Cleaning Station, Manta Ridge), West Waigeo (i.e., Eagle Rock, Yefnabi Kecil), and Misool (i.e., Magic Mountain, Southwest Batbitim, Eagle's Nest,) regional receiver arrays. Moreover, most of these receiver stations had higher values of Betweenness, Closeness, and Eigenvector, which emphasised the relative importance of these receiver stations compared to others in Raja Ampat receiver array network. Eagle Rock and Wai recorded the highest degree centrality values, and Eagle Rock had substantially higher Betweenness value than all other receiver stations, which indicates that Eagle Rock was connected to many other receiver stations and highly influential in the regional movements of *M. alfredi*.

Table 6.1. Network-level metrics of centrality for the observed *M. alfredi* movements in Raja Ampat between February 2016 and September 2021. N nodes (in network) = the total number of nodes in the network; N nodes (in each tagging region) = the number of nodes in the tagging region; N nodes connected = the total number of nodes in Raja Ampat network that are connected by edge(s); N edges = the total number of edges connecting two nodes in the network; N movement = the total number of movements made by individuals tagged in each respective tagging region; Tagging regions = the regions where the acoustic transmitters were deployed.

| **Network metrics** | **Raja Ampat (receiver station level)** | **Movement networks based on tagging regions** | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | **Ayau** | **Dampier Strait** | **Fam & Bambu** | **Kofiau & Boo** | **Misool** | **Wayag** | **West Waigeo** |
| N nodes (in Raja Ampat) | 34 | 34 | 34 | 34 | 34 | 34 | 34 | 34 |
| N nodes (in tagging region) | N/A | 3 | 10 | 5 | 1 | 9 | 4 | 2 |
| N nodes connected (in Raja Ampat) | 32 | 3 | 22 | 5 | 2 | 10 | 2 | 9 |
| N edges | 131 | 6 | 74 | 6 | 2 | 43 | 1 | 20 |
| N movements | 1,094 | 46 | 288 | 7 | 2 | 625 | 1 | 125 |
| Edge density | 0.117 | 0.005 | 0.066 | 0.005 | 0.002 | 0.038 | 0.001 | 0.018 |
| Average path length | 2.71 | 1 | 2.73 | 1.83 | 1 | 1.51 | 1 | 1.98 |
| Diameter | 6 | 1 | 6 | 4 | 1 | 3 | 1 | 4 |

### 6.3.3. Detecting structure in movement network

A non-random test suggested there was strong evidence ($p < 0.001$) that the APL of the observed network (2.708) was higher than that we would expect from random networks (Appendix E Figure E.5), suggesting that the movements of acoustically tracked *M. alfredi* were non-random and there is a structure within the movement network. An analysis using a community detection algorithm on 32 of 34 nodes resulted in a positive modularity score of 0.558, which indicates the presence of structure in the network. Two nodes (receiver stations in Uranie and North Misool) were removed from this analysis as they were disconnected from other nodes. The 32 nodes were grouped into three different clusters representing different regions, consisting of Ayau, Misool, and central Raja Ampat (Figure 6.3). The cluster in Ayau consisted of all three receiver stations, and similarly, all receiver stations in Misool, were classified into one tight cluster. Interestingly, all receiver stations deployed in Wayag, West Waigeo, Fam & Bambu, Dampier Strait, and Kofiau & Boo were classified into a large single cluster.

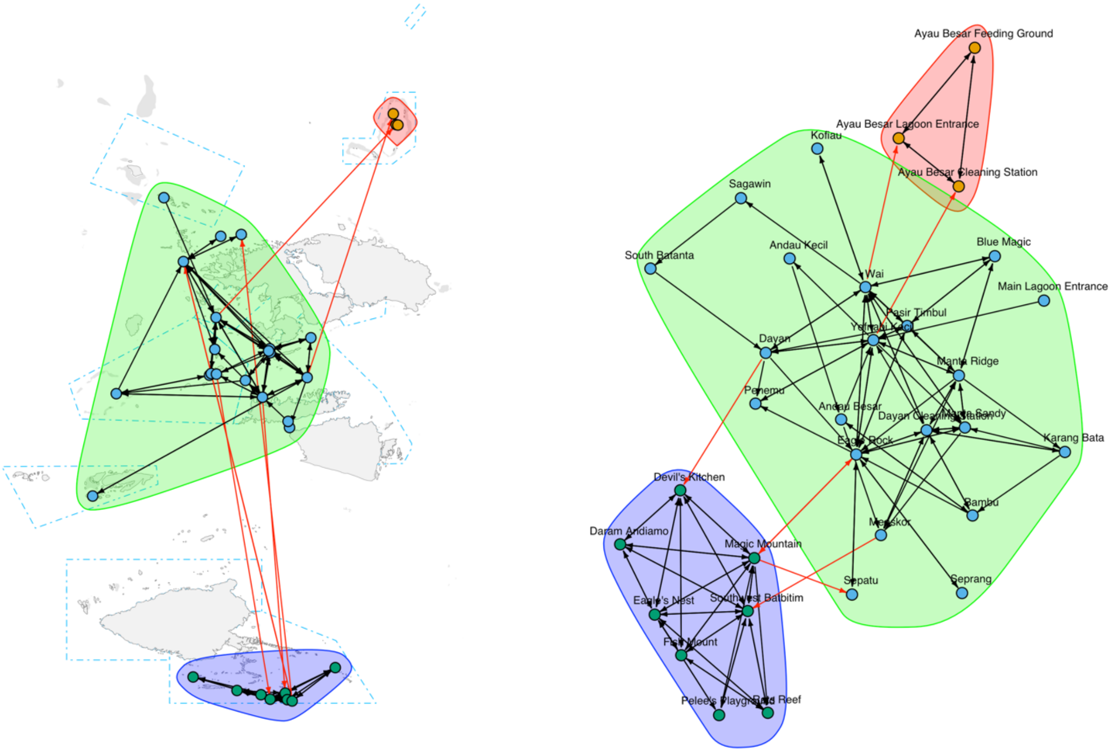

Figure 6.3. Movement network of *M. alfredi* in the Raja Ampat archipelago showing cluster-based community structure displayed using geographic coordinates (left panel) and a multidimensional scaling layout (right panel). Nodes (coloured circles) symbolise acoustic receiver stations. Edges represent the movements of *M. alfredi* between the nodes. Black arrows indicate the direction of movements within the clusters, while red arrows represent movements between the clusters. The thickness of the edges represents frequency of movements between nodes (the thicker the lines, the more frequent movements occurred between two connected nodes). The colours of nodes and clusters represent different *M. alfredi* subpopulations identified by the analysis. Blue polygons with blue dash-dotted lines depict the Raja Ampat MPA network.

## 6.3.4. Movements of *M. alfredi* acoustically tagged in each region

Of 36 individuals tagged in Dampier Strait, 29 were detected by at least two receiver stations (Appendix E Table E.1) resulting in 288 movements between receiver stations (Table 6.1). The movement network for *M. alfredi* tagged in Dampier Strait region showed high connectivity between four receiver stations where tagging occurred: Manta Ridge, Manta Sandy, Wai, and Dayan Cleaning Station (Figure 6.4).

These receiver stations also acted as hubs connecting Dampier Strait with these other regional receiver arrays in Fam & Bambu, West Waigeo, Misool, and Ayau (Appendix E Table E.2). The edge density for movement network of individuals tagged in Dampier Strait was the highest of all movement networks based on tagging region, suggesting substantially more frequent local movements within the Dampier Strait regional receiver array (Table 6.1).

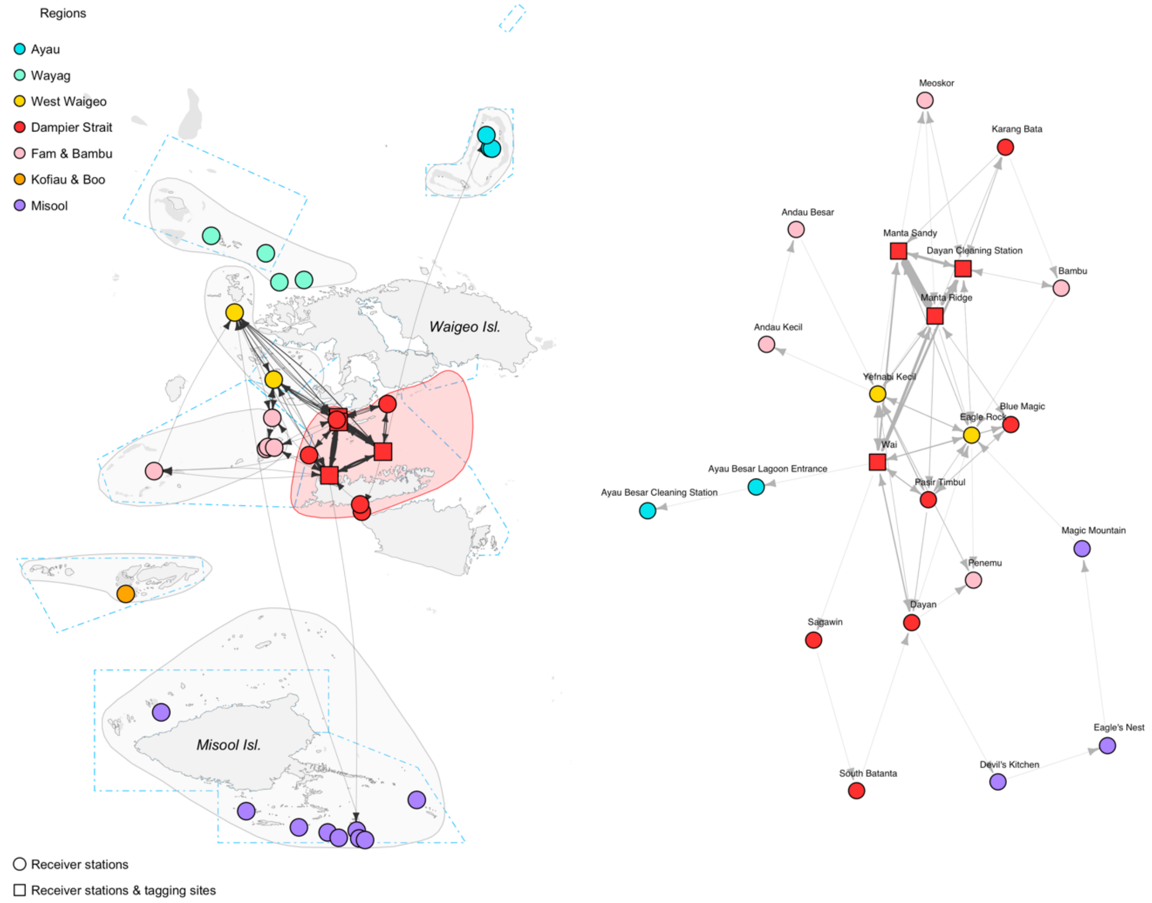

Figure 6.4. Movement networks of *M. alfredi* acoustically tagged in the Dampier Strait region between February 2016 and May 2021. Geographic coordinate layout (left panel). Multidimensional scale layout (right panel).

The 28 *M. alfredi* acoustically tagged in the West Waigeo region contributed to 125 movements, including those to two neighbouring regions (Dampier Strait and Wayag) and to the Ayau region (Table 6.1, Figure 6.5). Interestingly, most movements recorded in the Ayau region were mostly from an individual tagged in Yefnabi Kecil. Several movements were also recorded between the only two receiver stations in West Waigeo (Eagle Rock and Yefnabi Kecil).

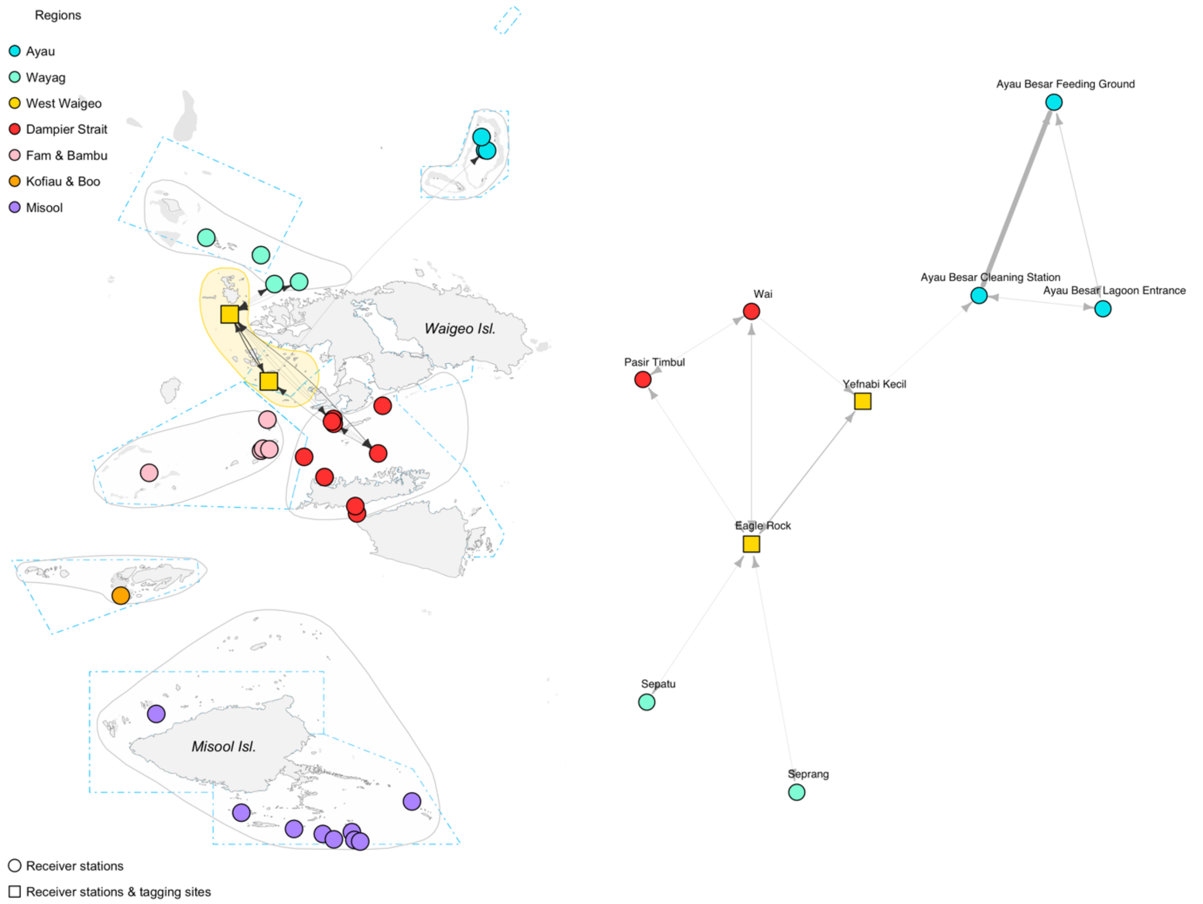

Figure 6.5. Movement networks of *M. alfredi* acoustically tagged in the West Waigeo region between February 2016 and May 2021. Geographic coordinate layout (left panel). Multidimensional scale layout (right panel).

The movement network of *M. alfredi* tagged in Misool was constructed from 10 connected nodes, mainly from the Misool regional receiver array (Figure 6.6). Of 28 tagged *M. alfredi*, 24 were detected by two or more receiver stations, resulting in 625 movements (57% of total movements) that were recorded mainly within the Misool regional receiver array (Table 6.1). Two movements were detected between Magic Mountain in Misool and Eagle Rock in West Waigeo, which are located ~240 km apart. Another relatively long-distance movement was recorded from Magic Mountain to Sepatu in the Wayag region, located ~275 km away.

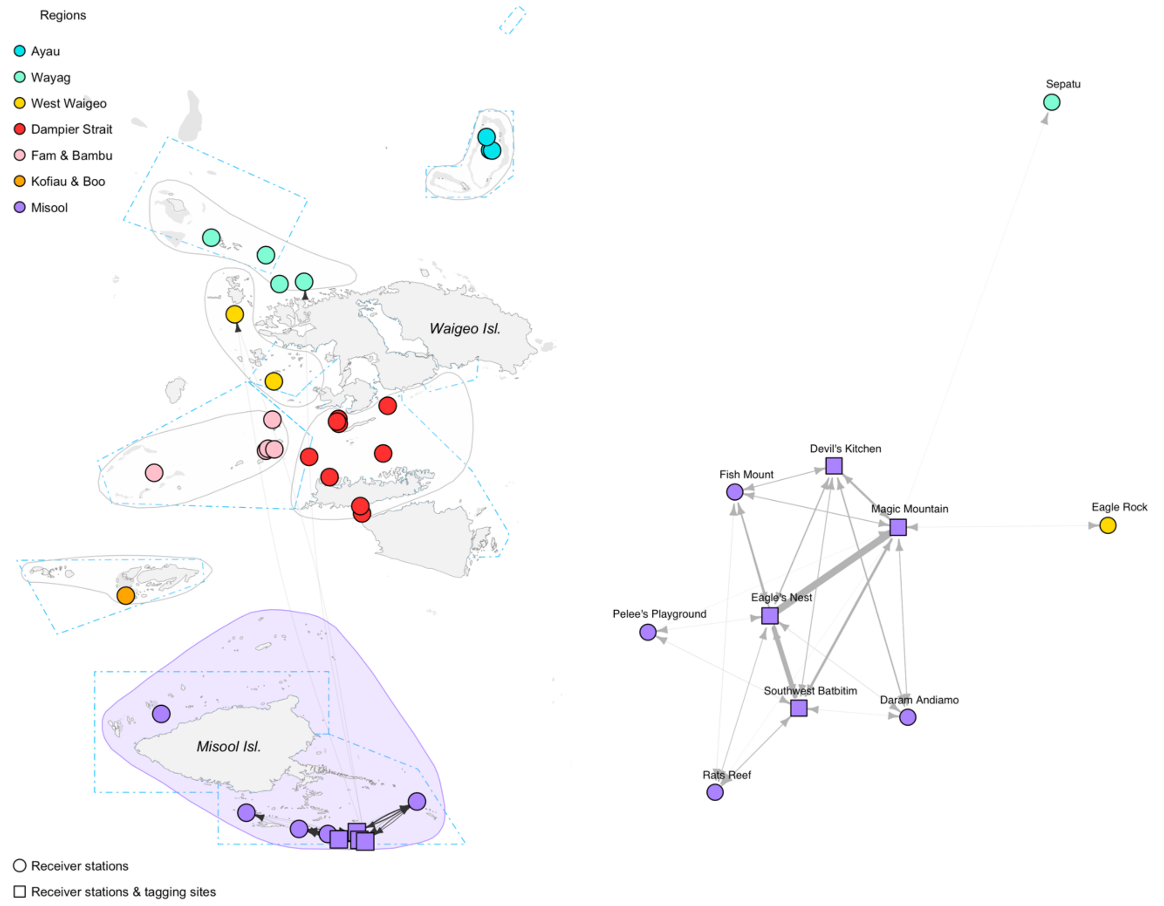

Figure 6.6. Movement networks of *M. alfredi* tagged in the Misool region between February 2016 and May 2021. Geographic coordinate layout (left panel). Multidimensional scale layout (right panel).

Of the 13 individuals tagged using acoustic transmitters in the Fam & Bambu region, only three were detected by two or more receiver stations. Several movements were detected by receiver stations within the Fam & Bambu regional receiver array, including those between Bambu and Andau Besar (Figure 6.7). One receiver station (Meoskor) acted as a hub connecting Fam & Bambu manta rays with those in the Misool region via the Southwest Batbitim receiver station, ~175 km away to the south. In the Wayag region, an individual tagged at the Main Lagoon Entrance moved to Yefnabi Kecil. Movements were also detected between receiver stations in the Kofiau and Wai from the same individual tagged in Kofiau. Interestingly, the movements of individuals tagged in Ayau were only recorded by the three Ayau receiver stations.

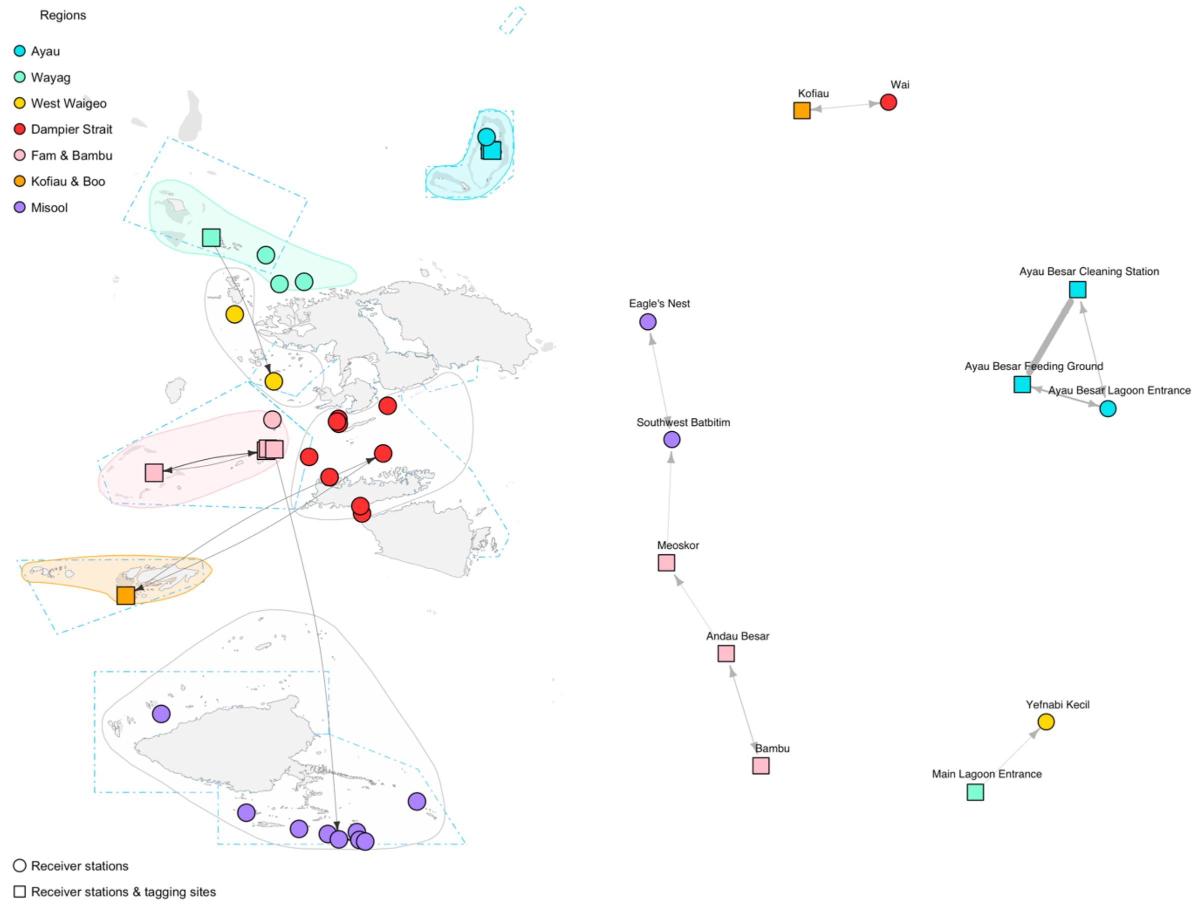

Figure 6.7. Movement networks of *M. alfredi* acoustically tagged in four regions (Ayau, Wayag, Fam & Bambu, and Kofiau & Boo) between February 2016 and May 2021. Geographic coordinate layout (left panel). Multidimensional scale layout (right panel).

## 6.3.5. Home ranges of satellite tracked *M. alfredi*

The 11 satellite-tagged *M. alfredi* were tracked for 20–117 days (mean ± SD = 62 ± 31) (Table 6.2, Appendix E Figure E.6). A total of 1,600 GPS locations were obtained and 11 were subsequently filtered out using a speed filter with a maximum plausible speed of 2 m/s or showed extremely high (outlier) residual values derived from the Wildlife Computers LocSolve GPS processor version 3.0.625. Optimally-weighted AKDE fitted to the resulting GPS locations showed that the estimated extent of activity space (95% UD) varied between individuals, ranging from 108 km$^2$ for an individual tagged in Ayau to 43,105 km$^2$ (mean ± SD = 5,472 ± 12,529) for an individual tagged in Misool.

The home range of an individual tagged in the Dampier Strait overlapped with those of two individuals tagged in West Waigeo (Figure 6.8). Moreover, the individuals tagged at Eagle Rock (West Waigeo) showed extended home ranges to several areas in Wayag and the northwest and north of Waigeo Island. Eagle Rock is located outside of the Raja Ampat MPA network and the home ranges of *M. alfredi* tagged at Eagle Rock were mostly located in this unprotected region.

Table 6.2. Deployment summary for 11 *M. alfredi* satellite tracked in Raja Ampat between 2014 and 2022. Sex = M (male) and F (female); Est. DW = the estimated disc width of satellite tagged *M. alfredi*. The tracking period (days) represents the number of days between the transmitter deployment date and transmitter release date; we make a distinction between the programmed tracking period and the actual tracking period, as all tags released prematurely. The estimated extent of activity space (95% UD) for each satellite tagged *M. alfredi* are based on optimally weighted AKDE (excluding land) and are expressed in km$^2$.

| PTT ID | Sex | Est. DW (cm) | Life stage | Tagging site | Tagging region | Transmitter deployment date | Transmitter release date | Programmed tracking period (days) | Actual tracking period (days) | 95% UD (km$^2$) |
|---|---|---|---|---|---|---|---|---|---|---|
| 140899 | F | 360 | adult | Eagle Rock | West Waigeo | 20-Oct-2014 | 16-Dec-2014 | 59 | 56 | 2,197 |
| 140902 | F | 320 | adult | Eagle Rock | West Waigeo | 20-Oct-2014 | 17-Dec-2014 | 59 | 57 | 1,176 |
| 140909 | F | 370 | adult | Eagle Rock | West Waigeo | 22-Feb-2015 | 12-Jun-2015 | 180 | 110 | 2,052 |
| 142780 | F | 330 | adult | Manta Sandy | Dampier Strait | 21-Jan-2015 | 19-May-2015 | 180 | 117 | 1,383 |
| 149141 | F | 370 | adult | Magic Mountain | Misool | 16-Jun-2015 | 22-Jul-2015 | 180 | 36 | 43,105 |
| 174992 | F | 260 | subadult | Ayau Besar lagoon | Ayau | 12-Dec-2018 | 08-Feb-2019 | 180 | 58 | 108 |
| 214961 | F | 320 | adult | Dayan | Dampier Strait | 28-Apr-2021 | 18-May-2021 | 120 | 20 | 1,003 |
| 214962 | F | 350 | adult | Yefnabi Kecil | West Waigeo | 10-May-2021 | 01-Aug-2021 | 90 | 82 | 2,605 |
| 214964 | M | 280 | adult | Dayan | Dampier Strait | 28-Apr-2021 | 02-Jul-2021 | 90 | 65 | 4,202 |
| 226829 | F | 330 | adult | Southwest Batbitim | Misool | 10-Jun-2022 | 19-Jul-2022 | 120 | 38 | 1,720 |
| 226830 | M | 280 | adult | Gebe Besar | Kofiau & Boo | 18-May-2022 | 27-Jun-2022 | 120 | 40 | 638 |

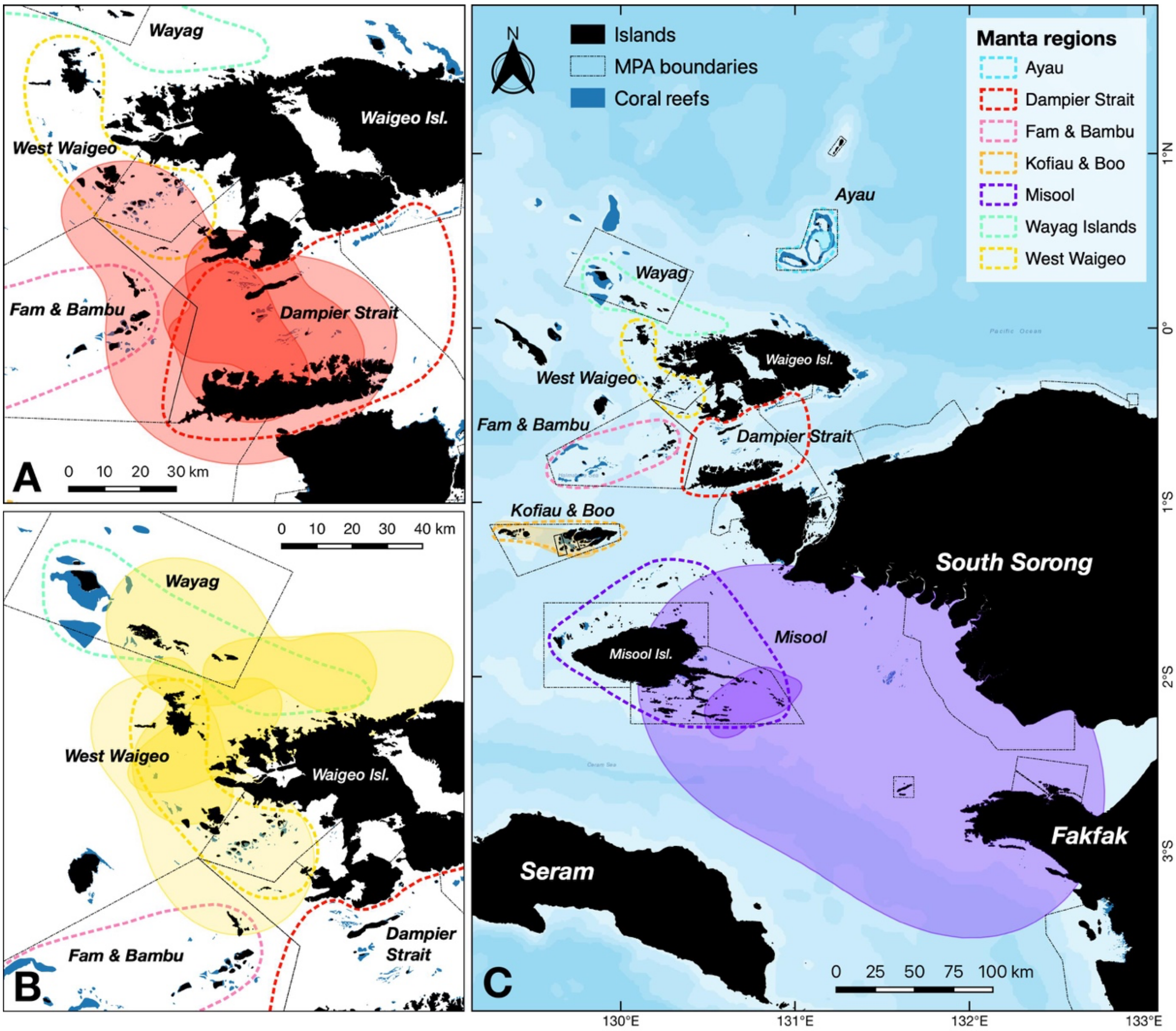

Figure 6.8. The extent of activity space (95% UD) of 11 *M. alfredi* satellite-tracked in Raja Ampat in 2014–2021 overlaid on the boundaries of the Raja Ampat MPA network (dash-dotted lined polygons) and regions occupied by the hypothesised subpopulations (regions denoted by coloured dashed lines). The colours of each estimated home range correspond to regions where the *M. alfredi* were initially tagged. The home range of *M. alfredi* tagged in (A) Dampier Strait, (B) West Waigeo, and (C) and Ayau, Kofiau & Boo, and Misool regions.

In contrast to the home ranges of *M. alfredi* tagged in central Raja Ampat, some individuals showed limited home ranges within and around the regions they were tagged in, such as those in Ayau, Kofiau, and Misool, that did not overlap with other manta regions in Raja Ampat. Over 58 days of tagging, the *M. alfredi* individual tagged in Ayau showed a restricted home range within the Ayau Besar lagoon where it was tagged. On the other hand, the home range of an individual tagged in Kofiau included two island groups in this region: Kofiau and Boo islands. In the southernmost region of Raja Ampat, one of two individuals tagged in Misool interestingly showed a substantially large home range which extended to regions outside of the SE Misool MPA and indeed beyond the Raja Ampat archipelago to the South Sorong and Fakfak coastlines (Figure 6.8).

## 6.4. Discussion

### 6.4.1. *M. alfredi* metapopulation and movements between subpopulations

Using multiple investigative techniques, this study provides further evidence that *M. alfredi* in the Raja Ampat archipelago form a metapopulation, consisting of three distinct subpopulations inhabiting the Ayau, Misool, and central Raja Ampat regions. Network analysis of an extensive acoustic telemetry dataset revealed that these subpopulations are geographically discrete and showed limited movements between these regions. These fulfilled the two key requirements of Akçakaya et al. (2007)'s metapopulation definition, including a) the subpopulations are geographically discrete, and b) the mixing of individuals between the subpopulations is less than that within them. Previously, Setyawan et al. (2020) subdivided the central Raja Ampat region into five separate hypothesised subpopulations: Kofiau & Boo and four subpopulation in northwestern Raja Ampat (Dampier Strait, West Waigeo, Fam & Bambu, and Wayag). Despite this, using a significantly expanded acoustic telemetry dataset, here we suggest these five hypothesised subpopulations show enough mixing to warrant their merging into a single large subpopulation.

Although the community detection algorithm suggested that the subpopulation in Kofiau & Boo island group should be merged with others into a single large subpopulation in central Raja Ampat, the only connectivity between Kofiau & Boo was from two movements by a single animal between the receiver station in Kofiau and the receiver station in Wai (Dampier Strait). After frequent detections by the receivers in Kofiau between 2016 and 2017, this individual was last detected in April 2017. The inclusion of Kofiau & Boo into the larger subpopulation in northwestern Raja Ampat by the community detection algorithm, which now formed the subpopulation in central Raja Ampat, is likely caused by the fact that there was only one acoustic receiver deployed in the Kofiau & Boo region. While the single receiver station allowed us to understand the movements of a single animal, it obviously did not allow for observation of localised movements within the region. However, geographic isolation (further discussed below) and the limited home range of satellite tagged *M. alfredi* from Kofiau (Figure 6.8) provides support for further data collection and future consideration of Kofiau & Boo as a separate subpopulation from the subpopulations in northwestern Raja Ampat.

The network analysis demonstrated frequent movements and high connectivity between acoustic receiver stations within the suggested subpopulations (except for that in Kofiau that only had one receiver station), but limited movements and low connectivity among them. Individuals in Ayau and Misool exhibited frequent localised movements between receiver stations within their respective regional arrays, while showing little connectivity with the other subpopulations in northwestern Raja Ampat. In contrast, substantial connectivity, and frequent local and regional movements between receiver stations (aggregation sites) were observed from Setyawan et al. (2020) previously hypothesised subpopulations. This suggests that *M. alfredi* in northwestern Raja Ampat are in fact panmictic and should be considered as a single large subpopulation. Setyawan et al. (2020) recorded frequent movements of photo-identified individuals between cleaning stations and feeding aggregation sites in Dampier Strait, Fam Islands, and West Waigeo. Some of these aggregation sites located between Dampier Strait and Wayag Islands are part of the seasonal migration corridor used by acoustically tracked *M. alfredi* (Setyawan et al., 2018). Furthermore, as suggested by Setyawan et al. (2020) and now presented here, the satellite tracking of large individuals exhibited some degree of overlap in the home ranges of *M. alfredi* tagged in Dampier Strait and West Waigeo regions but no overlap with the home range of those tagged in other regions (Kofiau & Boo, Ayau, and Misool).

The high degree of movements recorded within the large subpopulation in northwestern Raja Ampat is likely affected by the close proximity (50–120 km) of the island groups between Dampier Strait and Wayag Islands allowing *M. alfredi* to seasonally migrate and move locally between feeding and cleaning aggregation sites along this corridor habitat (Setyawan et al., 2018; Setyawan et al., 2020). This, therefore, allows them to maximise energy intake from foraging in areas of high productivity and at the same time saving energy by only traveling to relatively short distances. Similarly, *M. alfredi* at the Komodo Islands, central Indonesia, seasonally move between north and south aggregation sites along a ~40 km corridor (Dewar et al., 2008). The relatively shallow bathymetry in Raja Ampat's northwestern region also allows the mobility of the species. Dampier Strait–Fam–West Waigeo regions lay on the shallow shelf between 50–100 m depth, while Wayag and its neighbouring island chain are located on a slightly deeper shelf of 150 m deep. This is much shallower than *M. alfredi*'s known deepest dive (672 m) (Lassauce et al., 2020).

Despite the species' ability to migrate to seasonally highly productive areas located several hundreds of kilometres away (Anderson et al., 2011a; Couturier et al., 2014; Jaine et al., 2014; Harris et al., 2020), the acoustically and satellite tagged *M. alfredi* in Ayau, Kofiau & Boo, and Misool regions showed occasional long-distance movements and relatively restricted home ranges. This is likely caused by several factors, including natural barriers (i.e., deep water; island and coastal formation), prey density, and habitat use. Ayau, Kofiau & Boo, and Misool regions are surrounded by deep water separating these remote regions from the shallow shelf around the coast of Waigeo Island (Figure 6.1). Some studies suggested that deep waters, which imply high risk of exposure to large predators when crossing these, become the primary barrier to movements and long-distance migration of *M. alfredi* (Clark, 2010; Kitchen-Wheeler et al., 2011; Carpentier et al., 2019). Deep water (2,000 m depth) may be responsible for the limited connectivity between the subpopulations of *M. alfredi* located 150 km apart in Hawaii (Deakos et al., 2011) and between two cleaning station sites in the north east of New Caledonia (Lassauce et al., 2022). Ayau is the most isolated region in the Raja Ampat archipelago and is separated by a ~25 km span of 1,400 m deep water from the north coast of Waigeo Island. Similarly, the Kofiau & Boo island group is separated from Dampier Strait to the northeast by water depths of 900 m and from Fam & Bambu by water depths of 500 m between the island groups. Moreover, no movements were recorded between Kofiau & Boo and Misool despite being only 50 km apart. The 800-900 m deep channel between Kofiau & Boo and Misool likely serves as a barrier to movements of *M. alfredi* between these regions, and is an area known for frequent observations of pods of orca (*Orcinus orca*), a known predator of manta rays (Mangubhai et al., 2012). Several *M. alfredi* movements recorded from Misool to the central and northwest Raja Ampat region are likely using the relatively shallow shelf (mostly no deeper than 60 m with one 300 m trough in the Sagawin Strait) between Misool and Dampier Strait

(~160 km apart) (Setyawan et al., 2020). These shallow waters allow some individuals to travel relatively long distances.

The estimated home ranges (95% UD) of the satellite tagged *M. alfredi* were substantially larger than that of juveniles tagged in Wayag lagoon, northwest Raja Ampat (Chapter 5). Only one individual (#174992), tagged in Ayau Besar lagoon (Figure 6.8), had a relatively smaller home range than these juveniles. In comparison, the home range of a juvenile male in the Red Sea (Kessel et al., 2017) was larger (95% UD of 2,457 km$^2$) than that of some adults satellite tagged in our study. Despite this, it is important to note that *M. alfredi* home ranges in our study were estimated from short periods of satellite tracking ranging from 20–117 days; therefore, it is possible that the home range is likely to be much larger than the current estimation. Although having the largest estimated home range in our study, the female #174992 moved to areas only ~170 km to the southeast of Magic Mountain (Misool region), where it was satellite tagged. This distance is shorter than two acoustic tagged individuals from Magic Mountain that were detected by two receiver stations in northwest Waigeo, located approximately 240-260 km to the north (Figure 6.6), and is even shorter than a photo-identified male that moved from Wayag lagoon to Misool (296 km apart) (Setyawan et al., 2020).

Variation in long-distance movements and extended home range suggests that *M. alfredi* may be partial migrants (Chapman et al., 2012). Geographically, this variation is likely caused by coastal and island formation. The island chain of Lesser Sunda Islands allow some *M. alfredi* to migrate between aggregation sites in Nusa Penida and Komodo (Germanov & Marshall, 2014) situated approximately 400 km apart. The continuous coastal environment in eastern Australia facilitates juvenile *M. alfredi* to move as far as 1,150 km without crossing deep water (Armstrong et al., 2019). Despite this, individual *M. alfredi* that are partial migrants might undertake occasional long-distance dispersal in search of food, moving over deep water and acting as transient individuals visiting an area for a short period. A female *M. alfredi* recorded in Cocos Island, Costa Rica, was likely to have migrated to this site after crossing extensive deep water (Arauz et al., 2019), noting that the nearest confirmed sighting location was nearly 6,000 km away in the Marquesas Islands (Mourier, 2012). This situation does not seem to be the case in Raja Ampat; reliable and sufficient food sources likely eliminate the need for long-distance migration from even the isolated subpopulations, especially Misool and Ayau. Peel et al. (2020) suggested that island formation comprising of atolls or small island groups that are surrounded by or in the vicinity of deep waters often generates zooplankton accumulation, and therefore, offers abundant food resources. This factor likely contributes to the strong residency of *M. alfredi* in Ayau and Misool (and potentially Kofiau), and their limited connectivity with the large panmictic subpopulation around Waigeo Island in northwestern Raja Ampat.

Our findings suggest there is fine scale metapopulation structure on *M. alfredi* in Raja Ampat consisting of spatially distinct subpopulations with occasional movements across regions and potential large-scale dispersal and partially migrant individuals. Looking at other manta and devil ray species or populations in other regions that are much more data poor, considering the influence of partial migrants and occasional large-scale dispersal is particularly important when understanding metapopulation dynamics and interpreting patterns in population structure. These partial migrants may obscure genetic structure if they reproduce in distant regions and create gene flow among otherwise largely distinct subpopulations.

### 6.4.2. Key aggregation sites and habitats of *M. alfredi*

Node-level metrics derived from the movement network revealed eight receiver stations (Appendix E Table E.3) that were well connected with others and had high degree centrality. A site with high degree centrality indicates strong site fidelity by wide ranging species to this site (Jacoby et al., 2012a). Each of these eight receiver stations are located in close proximity to manta cleaning stations. This indicates that these aggregation sites, which are distributed in the Dampier Strait, West Waigeo, and Misool, play a central role as hubs for the spatial movements and migration of *M. alfredi* in Raja Ampat. Some of these cleaning stations are also used as feeding sites (i.e., Eagle Rock and Yefnabi Kecil in West Waigeo, and Wai and Manta Ridge in Dampier Strait), and have been identified through passive acoustic telemetry and photo-ID as key habitats providing essential services for *M. alfredi* both locally and regionally (Setyawan et al., 2018; Setyawan et al., 2020; Perryman et al., 2022).

All the nodes playing central roles in the *M. alfredi* movement network are well protected within the Raja Ampat MPA network (Setyawan et al., 2020), except for Eagle Rock, which was identified as a critical node in the *M. alfredi* movement network (Appendix E Table E.3). Given this, Eagle Rock should be urgently considered for inclusion into the Raja Ampat MPA network. It might be worthwhile to assess the impact of habitat loss through removal analysis (e.g., removing a central node like Eagle Rock from a network) on the stability of the movement network (Jacoby et al., 2012a; Chapter 2).

Cleaning stations play several crucial roles in the life cycle of manta rays, including serving as the venue for a number of important biological processes (e.g., removing parasites from their skin) and social interactions with other manta rays (Stevens, 2016; Perryman et al., 2019). Visiting cleaning stations that are located at shallow, warm habitat is also likely to physiologically benefit manta rays by increasing metabolic, digestive, and gestation rates (Hight & Lowe, 2007; Jirik & Lowe, 2012). Cleaning stations, normally situated not far from feeding sites, are favoured locations where *M. alfredi* tend to return to and/or remain near for extended periods (Stevens, 2016). Over 70 feeding aggregation sites and cleaning stations distributed across Raja Ampat waters (Setyawan et al., 2020) support *M. alfredi* philopatric behaviour and seasonal movements influenced by monsoonal prey availability (Dewar et al., 2008; Setyawan et al., 2018; Harris et al., 2020).

Satellite tracking of *M. alfredi* tagged at Eagle Rock (West Waigeo) revealed potential feeding areas located in remote areas in the northwest and north of Waigeo Island (Figure 6.8). These individuals also showed extended movements and home range covering areas currently unprotected within Raja Ampat's existing MPA network (Chapter 2). Similarly, *M. alfredi* tagged in Misool showed extensive home ranges to areas outside of MPAs and the boundary of Raja Ampat regency. While the majority of manta ray aggregation sites in Raja Ampat are protected within MPAs (Setyawan et al., 2020), this finding highlights the potential risk of exposure to net fishing in commercial fisheries that are still commonly practiced in the Bird's Head Seascape outside of the MPA network (Chapter 2). Globally, manta rays have frequently been caught as bycatch in commercial fisheries using nets (Croll et al., 2015; Fernando & Stewart, 2021).

### 6.4.3. Applications of acoustic telemetry, network analysis, and satellite telemetry

Our combined approach using passive acoustic telemetry and spatial network analysis has allowed for further investigation on the directionality of movements and the degree of movements between a pair of connected nodes (receiver stations) (Jacoby & Freeman, 2016; Mourier et al., 2018). These are not possible if we only used a passive acoustic telemetry approach without spatial network analysis. Understanding directionality provides more compelling evidence for identifying receiver stations important in *M. alfredi* migration and movement patterns in Raja Ampat, in addition to residency patterns at aggregation sites.

Our study allows for examination of the differences in spatial movements between female and male *M. alfredi*. Despite females having a higher median of total movements (between receiver stations) but a lower median of mean direct distance travelled between node pairs than males, there was no evidence of the effect of sex on the movements of 72 acoustically tagged *M. alfredi*. Other studies also found that there were no significant differences in the average daily distances travelled by males and females (Peel et al., 2019b; Venables et al., 2020). Sex did not appear to be a key factor in long distance movements of *M. alfredi* in another study in Indonesia (Germanov & Marshall, 2014), as the four individuals travelling further than 450 km in this study were comprised of two females and two males.

The identification of important habitats of *M. alfredi* in Raja Ampat and neighbouring regions that were previously unknown (i.e., the north of Waigeo Island and the South Sorong and Fakfak regions to the southeast of Raja Ampat) suggest the power of satellite telemetry (Jaine et al., 2014; Kessel et al., 2017; Armstrong et al., 2020b; Chapter 5) as compared to two other common approaches for studying manta rays: a) passive acoustic telemetry, that is highly dependent upon the configuration of the acoustic receiver array (Setyawan et al., 2018; Peel et al., 2019b; Andrzejaczek et al., 2020; Venables et al., 2020) and b) photographic identification, whose results are strongly influenced by survey effort (Stevens, 2016; Beale et al., 2019).

### 6.4.4. Limitations of our experimental design

Some results from our study underlined important limitations when using passive acoustic and satellite telemetry to investigate *M. alfredi* metapopulation structure and connectivity between subpopulations. There are several aspects that should be considered during analyses and interpretation of the results. First, the number of *M. alfredi* tagged using acoustic transmitters in each region and the period of acoustic tracking might be insufficient to make inferences at a population level. Andrzejaczek et al. (2020) highlighted variations in the residency and regional movements of *M. alfredi*, therefore a small number of acoustic transmitters deployed in a region may not represent the overall movement trend of the subpopulation. Lédée et al. (2021) suggested that there is a threshold in the number of acoustic tagged individuals to make inference at a population level, and the minimum sample size is species-specific depending on various factor (e.g., species behaviour) (Brodie et al., 2018). While we did not conduct removal analysis to calculate minimum sample size needed (Lédée et al., 2021), the movements of *M. alfredi* tagged in Dampier Strait and West Waigeo conformed well to results presented by Setyawan et al. (2018). Second, the number of acoustic receivers and acoustic receiver configuration (i.e., number and distance) in each region strongly influenced the results. Our study found that the movements of *M. alfredi* between receiver stations were more frequent between those located in closer proximity to each other, as seen with the Dampier Strait, Misool, and Ayau regional acoustic receiver arrays. This is similar to findings by Perryman et al. (2022) using smaller acoustic receiver arrays around Manta Ridge, Manta Sandy, and Wai in Dampier Strait. Logistical and financial constraints prevented us from having equally dense acoustic receiver arrays in all regions with some regions like Kofiau & Boo island group, Fam, and Ayau having only one to four receiver stations per region. The single receiver station in Kofiau & Boo did not allow for observation of local movements within the region. Despite this, our satellite tagging data (Figure 6.8) helped provide further evidence of *M. alfredi* movements and home ranges to further corroborate the potential for a metapopulation. An array of three acoustic receivers in Ayau seemed to reliably record local movements within the region and capture movements from other subpopulations and further helped examine the population structure of *M. alfredi* in Raja Ampat. Third, locations where the receivers were deployed, and limitation of acoustic telemetry technology might impact the outcome of movement network analysis. Tracking the movements and residency of acoustic tagged individuals is limited within the detection range of acoustic receivers (Heupel et al., 2018), which vary depending on various factors identified by Kessel et al. (2014). To optimise detections, we placed the acoustic receivers strategically within 150 m of *M. alfredi* feeding and cleaning sites considering reliable acoustic detections from range tests conducted in previous study using the same acoustic receiver and transmitter specification (Setyawan et al., 2018; Chapter 3).

### 6.4.5. Future research

Several recent genetic studies have found evidence of significant population structure in *M. alfredi* populations in oceanic island archipelagos, adding further weight to the utility of the metapopulation concept in describing *M. alfredi* population dynamics. In New Caledonia, Lassauce et al. (2022) found genetic differentiation between three local populations at cleaning station aggregation sites of *M. alfredi* located only 110 to 335 km apart. Whilst one of these aggregation sites was separated by a 2,000 m deep channel from the two other sites, the other two were connected through shallow water and continuous coastal habitats and do not have any obvious barriers to movement between them. In Hawaii, genetic structure was found between *M. alfredi* populations from two aggregation sites located only 150 km apart but separated by 2,000 m deep water (Whitney et al., 2023). In the Eastern Tropical Pacific, a genetic study also found two different populations of oceanic manta rays (*M. birostris*) in the Galapagos Islands and island groups off the coast of Ecuador located ~1,000 km apart (Rojas López et al., 2022). Based on these recent findings, a detailed genetic study in the Raja Ampat archipelago seems warranted and would provide further insights on possible genetic differentiation between the *M. alfredi* subpopulations in Raja Ampat. Finally, we are planning further satellite telemetry work in Raja Ampat, specifically targeting *M. alfredi* inhabiting the more remote regions of the archipelago including Kofiau & Boo island group, Misool, the Bambu Islands, Wayag, and Ayau. This will allow us to better understand the home ranges of individuals from these subpopulations and also to determine if they frequently leave the boundaries of the Raja Ampat MPA network (a potential management concern). This could potentially provide further evidence of connectivity between these remote subpopulations with other subpopulations in Raja Ampat archipelago.

## 6.5. Conclusions

Our study provides further evidence that *M. alfredi* in the Raja Ampat archipelago is likely to be a metapopulation, as previously hypothesised by Setyawan et al. (2020). We have identified three subpopulations inhabiting the Ayau, Misool, and northwestern Raja Ampat regions, that exhibit high site fidelity and affinity to aggregation sites (cleaning stations and feeding sites). Although we recommend future genetic analysis to reveal whether the *M. alfredi* in Raja Ampat form a true metapopulation. Our enhanced acoustic receiver array combined with network analysis and satellite telemetry provided further evidence of the connectivity of *M. alfredi* subpopulations in Raja Ampat. We revealed key aggregation sites that are highly connected and influential in the local and regional movements of *M. alfredi*. These sites provide essential services for the long-term viability of this philopatric species. Our study also revealed important habitats that are unprotected and situated outside of the Raja Ampat MPA boundary, highlighting the importance of protecting these critical sites to maintain the stability of the *M. alfredi* movement network in the region.

# Chapter 7.

# General discussion

My research presented here has contributed to the global knowledge about the demographics, abundance, and conservation biology of manta rays, in particular the reef manta rays. In Chapter 2, I reviewed the suite of conservation and management measures that were implemented over a 15-year period in Raja Ampat and the broader Bird's Head Seascape and the potential impact of these measures on manta ray populations in the region. In Chapter 3, using long term photo-ID datasets and modified open population mark recapture models, I estimated that the abundance of reef manta rays in the Dampier Strait and South East Misool MPAs increased significantly over a decade of study from 2009 to 2019. In Chapter 4, I pioneered a novel and non-invasive method to accurately measure the body size of reef manta rays using a small drones, providing new insights into the morphometrics of this species. In Chapter 5, using multiple investigative approaches including a long-term photo-ID dataset, drones, satellite telemetry, and acoustic telemetry, I provided strong evidence to confirm the presence of a reef manta ray nursery area in Raja Ampat's Wayag lagoon. This was the most comprehensive description to date of a manta ray nursery in this vast area. Finally, in Chapter 6, using passive acoustic tracking and network analysis coupled with satellite telemetry, I provided further evidence that the Raja Ampat region is likely to host a metapopulation of reef manta rays, as I showed three spatially distinct subpopulations with limited exchange of individuals between them. Future telemetry and genetic work will provide a greater resolution on whether the reef manta rays in Raja Ampat form a true metapopulation. Below I discuss some of the main research findings and put them in the context of conservation initiatives, the development of new research approaches and future directions.

## 7.1. Bucking the trend: increasing reef manta ray populations

Over the last 50 years, many reef manta ray populations throughout the species' range have declined in abundance primarily due to increasing pressures from targeted captures and bycatch in fisheries. Conservative life history traits (i.e., long lifespan, late maturation, and low fecundity) make them vulnerable to population decline (Ward-Paige et al., 2013; Dulvy et al., 2014; Croll et al., 2015). Subsequently, the species is listed as VU (vulnerable) in the IUCN Red List of Threatened Species (Pacoureau et al., 2021; Marshall et al., 2022). While the reef manta ray populations throughout the species' range are typically declining (Venables, 2020) or stable (Deakos et al., 2011; Couturier et al., 2014; Stevens, 2016), my research focused on areas where I had sufficient photo-ID data - two large MPAs in Raja Ampat - revealing an increase in abundance over a decade (see Chapter 3).

These findings showed that conservation actions to protect large, long-lived, wide ranging, and highly migratory species can be effective. There were two key drivers in the population recovery of reef manta rays in Raja Ampat: 1) management interventions that enabled manta rays to survive and thrive (see Chapter 2), and 2) favourable environmental conditions (ENSO events) during which they improved their body condition leading to high fecundity and recruitment (see Chapter 3). Management actions were implemented with two main objectives: 1) to reduce and minimise threats for manta rays, which was done through fisheries regulations; and 2) to protect manta ray critical habitats (i.e., cleaning stations and feeding areas). In many regions, bycatch in gillnet and longline fishing gear has been the main threat for manta and devil rays (Croll et al., 2015; Fernando & Stewart, 2021). Restriction on the use of fishing gear contributed to the decrease in manta ray mortality rates. The MPAs in Raja Ampat were first developed in 2007 with restriction on the use of nets within MPAs. The importance and benefits of long-term implementation of fisheries management actions on wildlife population recovery have also been observed in other marine megafauna, such as other elasmobranchs (Pacoureau et al., 2023) and cetaceans (Peter et al., 2003; Noad et al., 2019). In addition, well enforced MPAs allow effective protection of cleaning stations and feeding areas to ensure critical ecological and biological functions of manta rays (Stevens, 2016). MPAs, especially those that are large, old, well-enforced (Edgar et al., 2014) and are part of a MPA network (Martín et al., 2020), play a crucial role in the increased abundance of reef manta rays in Raja Ampat. For highly philopatric species, that tend to return to the same site and/or remain in certain areas for extended period, area-based protection is crucial. Many reef manta ray aggregation sites are located within the Dampier Strait and South East Misool MPAs (Setyawan et al., 2020). Both are older than a decade (developed in 2007), larger than 300,000 hectares, and well enforced by the management authority (Mangubhai et al., 2012). While reef manta rays are highly migratory and wide-ranging, they spend a considerable amount of time in coastal areas and demonstrate high dependency, strong site fidelity, and frequent local movements between cleaning stations and feeding areas located at coral reefs, which are well-protected within the Raja Ampat MPA network. My research in Raja Ampat shows a ray of hope for the recovery of the globally declining populations of reef manta rays. The suite of management approaches (see Chapter 2) can be adopted in other regions throughout Indonesia, and other regions where manta ray populations are well established and/or under threat.

Moving forward, it is important to continue monitoring the reef manta ray populations in Raja Ampat, especially those with long-term data. The MPA management authority and organisations actively involved in the research and conservation of manta rays should continue to monitor regularly surveyed aggregation sites, such as Dampier Strait and South East Misool. Annual surveys should be conducted, and mark recapture estimates should be undertaken every five years to allow monitoring and evaluation. Long-term sighting records and photo-ID data allows further investigation into the biology and ecology of reef manta rays, as well as the effects of potential stressors (e.g., impacts of climate change), naturally occurring processed (e.g., ENSO events), and the efficacy of any other management measures.

The concerted effort to undertake regular surveys undoubtedly faces some challenges, such as financial and logistical issues, especially with most areas being remote and difficult to access. In recent years, there has been growing attention and interest from tourists to participate in research through citizen science (Cusick et al., 2020; Kelly et al., 2020). When done well, citizen science can play an important role in addressing the financial and logistical constraints in the photo-ID data collection. A few tourism operators running liveaboard vessels and/or resorts have been actively contributing to the photo-ID data collections in the Raja Ampat region. With more than one hundred liveaboard vessels and land-based dive operators (e.g., resorts and local homestays) and thousands of tourists visiting Raja Ampat for diving (including with manta rays), a more concerted effort could made to ensure the obligatory contribution of photo-ID images and associated data from all operators as a part of an operating permit in Raja Ampat region.

While it is important to continue data collection in areas that have been regularly monitored, survey efforts should be expanded to areas where manta ray aggregations have been reported, but have less survey effort primarily due to inaccessibility (e.g., Kofiau, Eagle Rock and northwest Waigeo, and Ayau). Contributions from citizen scientists, especially from liveaboard vessels that can reach remote areas could help collect photo-ID data. It would also be worthwhile expanding research and survey efforts to areas adjacent to the well-studied sites (i.e., Dampier Strait and South East Misool), such as Fakfak, Halmahera, and Cenderawasih Bay where manta rays are reported and occasionally sighted, or around the established populations (e.g., Nusa Penida and Komodo) in Nusa Tenggara, such as Sumba, Rote, Lombok (see Figure 1.1). It would take considerable time and effort to survey these remote areas and collect a robust dataset, but the use of innovative approaches such as environmental DNA (eDNA) may be a useful initial survey approach. The use of eDNA combined with local knowledge detected the presence of large-tooth sawfish *Pristis pristis* in Australia (Simpfendorfer et al., 2016) and revealed the spatiotemporal presence of endangered scalloped hammerhead sharks *Sphyrna lewini* in Guam (Budd et al., 2023). This emerging and potentially efficient method could be used to monitor the presence of manta rays in regions where there are occasional sightings, and importantly alleviate some of the financial and logistical constraints with identifying key habitats requiring more concentrated research effort.

In addition to eDNA, it would be valuable to further examine the genetic differentiation and connectivity between the well-established populations and areas where reef manta rays have been occasionally sighted. Using mtDNA markers, Phardana et al. (2022) showed evidence that reef manta rays from Nusa Penida, Komodo, and Raja Ampat are a single population, despite being separated by distances of 450 km (Nusa Penida and Komodo) and 1,500 km (Komodo and Raja Ampat), over island chains and deep waters. In Mozambique and South Africa, no genetic structure was detected using SNPs from reef manta rays sampled from aggregation sites separated by 100 km (within Mozambique) and up to 1,300 km along the coastline between the two countries (Venables et al., 2021). In contrast, using similar approach, Lassauce et al. (2022) detected genetic structure between three reef manta ray populations located within up to 335 km apart. Similarly, Whitney et al. (2023) found genetic structure between two reef manta ray populations separated by 150 km of deep water in Hawaii. Following the findings by Phardana et al. (2022), further research into the genetic structure between the three main populations of reef manta rays in Indonesia might worthwhile to understand finer-scale connectivity within and between populations.

## 7.2. New findings about reef manta ray population ecology

One of the key challenges in manta ray research is identifying nurseries, which is one of priorities supporting the effectiveness of conservation actions for this globally threatened species (Stewart et al., 2018a). Heupel et al. (2007) proposed three criteria that should be fulfilled for an area to be identified as shark and ray nursery, which include: 1) newborn and juvenile sharks and rays are more commonly observed in this area than other areas; 2) these newborns and juveniles tend to remain in or return to this area for extended periods; and 3) newborns and juveniles use this area repeatedly across years. Addressing each of these criteria requires a combination of different approaches, such as regular surveys, mark recapture, passive acoustic telemetry, and satellite telemetry (Heupel et al., 2019).

Following initial findings in my earlier research (Setyawan et al., 2020), I used multidisciplinary approaches including photo-ID, drones, satellite telemetry, and passive acoustic telemetry during my PhD research to conclusively confirm that Wayag lagoon in northern Raja Ampat is a reef manta ray nursery. Chapter 5 shows that despite using small sample size (five satellite-tagged and nine acoustic-tagged juveniles), there was value in a multidisciplinary approach over the eight-year study-period. Photo-ID and drone imagery addressed the Heupel et al. (2007's)'s Criteria 1 and 3, while satellite and passive acoustic telemetry addressed Criteria 2 and Criteria 3.

Ultimately, Chapter 5 provides essential knowledge about the horizontal movements and residency patterns of juvenile reef manta rays in a nursery habitat, which has not been described thoroughly in the manta ray literature. I note that continuous effort is required to monitor newborn and juvenile reef manta rays in Wayag lagoon. Little is known about the movement ecology and life history traits of juvenile manta rays and the role that nurseries play for these individuals (Stewart et al., 2018a). I consider Wayag lagoon an excellent area to improve our knowledge on this species' juvenile period of life given year-round and long-term occupancy of this nursery area.

To support the conservation of reef manta rays throughout their life cycle, we need more of these critical areas in Raja Ampat and beyond to be identified and protected. Further research using similar multidisciplinary approaches (see Chapter 5) are required to conclusively identify other reef manta ray nurseries in Raja Ampat, such as those in the Fam Islands, Hol Gam, and Ayau lagoon, as suggested by Setyawan et al. (2020). Nursery areas play a critical role in increasing the survival rates of newborns and juveniles (Heupel et al., 2019), therefore, it is critical to protect these areas to ensure recruitment into the adult population. Globally, only a few manta ray nursery areas have been proposed, and therefore, further research effort is required to provide stronger evidence to confirm and designate protection for these areas.

The discovery of nursery areas attracts public attention in particular when they are relatively accessible for tourism. Increasing tourism and boat activities make newborn and juvenile manta rays more vulnerable to over-crowding, boat strikes, and noise pollution (Anderson et al., 2011b; Wilson et al., 2022). A clear, well-designed, and enforceable tourism management plan for nursery areas should include two main objectives: 1) protecting newborn and juvenile manta rays as well as habitat quality; and 2) ensuring the sustainability of manta ray tourism in the area. For tourism management in the

Wayag lagoon nursery area, I would recommend the development of a strict code of conduct (CoC) including the following measures: 1) limiting the number of boats, including liveaboard vessels entering the lagoon; 2) designating specific mooring area for vessels to minimise impacts from fuel and oil leaks and grey water discharge (Carreño & Lloret, 2021); 3) allowing a limited number of snorkelling approaches during in-water-interactions with manta rays. Strictly implementing a CoC for in-water interactions can manage negative impacts on manta ray behaviours as a result of misconduct, such as chasing and approaching manta rays from the front (Murray et al., 2020); 4) designate specific key manta habitats where tourism activities are restricted. To further identify these areas, a more extensive acoustic receiver array is required to obtain information on the fine-scale movements of new-born and juvenile manta rays within Wayag lagoon.

Another new insight presented in Chapter 6 is that the reef manta rays in Raja Ampat consist of several subpopulations living in spatially distinct regions. From a management perspective, these findings highlight the importance of considering each of these subpopulations as different management units with some connectivity, instead of a single management unit. To further confirm the degree of connectivity between these subpopulations, it would be worthwhile to examine the fine-scale genetic structure using similar approaches as Lassauce et al. (2022) in New Caledonia and Whitney et al. (2023) in Hawaii. This could also be used to identify the genetic origins and connectivity between juvenile reef manta rays living in nurseries and adult populations. More specifically, it would be useful to further understand the connectivity between nurseries and habitats dominated by adults, including aspects such as parentage analysis (Jones & Ardren, 2003), whether there are nursery areas specifically used by the same females, and the degree of relatedness between individuals on nursery grounds.

## 7.3. Methodological advancements

One of the greatest challenges for my research was analysing imperfect data. In Chapter 3, I only used reef manta sighting datasets from two locations: the Dampier Strait and South East Misool MPAs, although I had sightings data from other MPAs across the Raja Ampat region. However, these data were collected only occasionally as regular surveys were difficult to undertake given the challenges with access to such remote places. Furthermore, despite data collections from 2003 to 2019, I only used data from 2009 to 2019 as there was insufficient data collected prior to 2009. Nonetheless, the dataset spanning more than a decade allowed the investigation of population level changes in abundance for two regions (Dampier Strait and South East Misool) for animals with different residency patterns, and the exploration of environmental changes influencing the population dynamics of manta rays in the region.

In order to estimate the rate of increase in abundance, I added a modification to the POPAN model allowing the estimation of per capita recruitment rate based on the number of females in the two populations. This newly modified POPAN mark recapture method presented in Chapter 3 could be useful in evaluating the effectiveness of conservation and management measures over time.

Furthermore, it could be implemented on other manta ray populations in other regions in Indonesia and other countries, as well as on other species.

The development of drone photogrammetry was a novel approach in understanding the demographics of reef manta rays (see Chapter 4). This method is not only able to estimate the size of manta rays accurately but is also undertaken with minimum or no impact on the animals being measured. This simple method could easily be implemented to obtain accurate measurements of the body size of reef manta rays elsewhere, but also for other marine species that spend considerable time at sea surface, such as oceanic manta rays. Further advancements of this method are currently underway to improve performance through the use of artificial intelligence to automatically estimate the body size.

## 7.4. Science-informed conservation strategies

The increasing abundance of reef manta rays in two MPAs in the Raja Ampat archipelago (Chapter 3), demonstrated the value of the efforts made by the Indonesian government to protect the globally vulnerable species at national and regional levels (Chapter 2). Indonesia has successfully transformed the country from one of the largest shark and ray fishing nations into the world's largest manta ray sanctuary (White et al., 2006; Dharmadi et al., 2015).

With the success of the long-term implementation of management measures in Raja Ampat and the BHS to reduce threats to manta ray populations, my research has highlighted the need for other conservation and management actions that will continue to improve the conservation of reef manta rays. First, further effort should be taken to protect critical aggregation sites that are located outside of MPA boundaries. An example is Eagle Rock, an area previously identified with cleaning stations and feeding areas for reef manta rays (Setyawan et al., 2018; Setyawan et al., 2020), which has been further recognised as an important hub in manta ray movements (Chapter 6). Second, the metapopulation structure of reef manta rays described in Chapter 6 requires managers to consider how best to protect the manta rays over different spatial scales and degrees of connectivity. Future work should also look at the difference between reef manta rays and oceanic manta rays in terms of population demographics, residency patterns, habitat uses, and home ranges in Raja Ampat.

Finally, the protection of critical aggregation sites located within the MPAs needs improvement, especially in relation to manta tourism management. These sites include cleaning sites and feeding areas that are regularly visited by the reef manta rays and are popular sites for diving with manta rays. Currently, there is only one site, Manta Sandy, that has been strictly regulated (Kasmidi, 2017; Kasmidi & Gunadharma, 2017). Further research should investigate the efficacy of these regulations, whether the CoC for diving with manta rays at this site is being adhered to, and measure whether there are any impacts on the behaviours of manta rays visiting this cleaning station. Elsewhere in Raja Ampat, manta diving and snorkelling sites do not have regulations to protect manta rays.

## 7.5. Future research directions

Apart from the specific areas I have covered above, including the value of citizen science, dedicated research in the core study areas such as Dampier Strait and South East Misool, the expansion of surveys and monitoring to other less surveyed areas within Raja Ampat (e.g., Kofiau, Ayau, northwest Waigeo) and neighbouring regions (e.g., Halmahera, Fakfak, and Cenderawasih Bay), and the collection of genetic samples to examine connectivity within and between subpopulations, I also suggest the following areas for future research that would contribute significantly to the conservation and management of manta rays in Indonesia.

### 7.5.1. Telemetry

The rapid development of tracking technology over the last few decades has allowed researchers to follow the horizontal and vertical movements of animals, and record data on their physiology and behaviours (Hays et al., 2016; Watanabe & Papastamatiou, 2023). The tracking devices can now collect not only location data (e.g., Argos, GPS), but also environmental data through various additional sensors integrated with the tags, such as ambient environmental temperature, body temperature, depth, barometric pressure (altitude), heart rate, acceleration, salinity, oxygen levels, light levels (Moses et al., 2022). For example, Werfeli et al. (2022) tracked the migration of birds by using multi-sensor tags to collect light level data to estimate positions, barometric pressures to estimate flight altitude, and acceleration data to flight times. Kneebone et al. (2018) used passive acoustic telemetry with transmitters equipped with tri-axial accelerometers and pressure sensors to examine juvenile tiger sharks *Galeocerdo cuvier*. Brewster et al. (2021) used multi-sensor tags consisting of a video camera, tri-axial accelerometer, gyroscope and magnetometer, temperature, pressure, and light sensors to investigate the behaviours and activity patterns of Goliath groupers *Epinephelus itajara*.

Despite this, planning animal tracking studies, choosing the right tags to collect appropriate data, and deciding on how to deploy the device on animals are not straightforward processes. It requires considerable expertise not only for those initial processes, but also to analyse the data collected to get robust results (Moses et al., 2022). Furthermore, sufficient knowledge on the study species and areas is required to optimise data collection using the tracking device. There are few considerations when choosing electronic tags to track manta rays. Thomas et al. (2011) provided guidelines to choose the best satellite tracking technology for wildlife, which include: (1) data specifications that are required to answer research questions; (2) characteristics of the animal studied and potential constraints of the animals and environment; and (3) costs. For example, satellite tags equipped with GPS for location acquisition cost more than those equipped with Argos or light level geolocations given very high resolution of location data offered by GPS equipped satellite tags. When tracking marine animals, satellite tags with GPS and Argos are best used for animals that spend considerable periods of time at the sea surface. Due to their high-resolution data, satellite tags with GPS are best used to track the fine-scale movements of marine animals over short periods of time up to few months. On the other hand, satellite tags with Argos are more appropriate to be used to track marine animals that migrate long distance. For animals that spend their entire time or almost all their time underwater, acoustic tags and satellite tags with light level geolocation are the best option as GPS and Argos cannot be used to track these animals (Heupel et al., 2006; Moses et al., 2022).

There are many different types of tags available in the market, which can be used to answer various research questions. In this thesis, I used a combination of satellite telemetry and passive acoustic telemetry to track the horizontal movement and residency patterns of reef manta rays at different life stages. However, the vertical movements of the reef manta rays have not been examined to date. Despite the recent global study on the diving behaviours of various elasmobranch species (Andrzejaczek et al., 2022), information on the diving behaviours of manta rays in Indonesia is lacking. Future research should look into the vertical movement ecology of manta ray in Raja Ampat and throughout Indonesian waters, to determine potential threats from fisheries but also to understand the environmental drivers influencing the vertical movements.

Other considerations when tracking wildlife include the periods of tag deployment. The period of tracking depends on the tag's battery life which can span periods of hours to years. On acoustic tags, the battery life can be chosen, but it will impact on the data gathered. Longer battery life requires larger or more batteries, which will impact on the size of the tags. On satellite tags equipped with various sensors, battery life is normally fixed by the manufacturers, therefore, researchers should define the temporal resolution and volume of data to be collected to answer the research questions.

Tracking wildlife should also consider the method of tag deployment to ensure minimal effects on the health, behaviours, and well-being of the tagged animals (Todd Jones et al., 2013; Rosen et al., 2018). Recent developments include the use of novel animal-borne cameras deployed on manta rays using suction cups (Stewart et al., 2019), and a harness to deploy multisensory tags with cameras on manta and mobulid rays (Fontes et al., 2018; 2022). Tags that are equipped with multiple sensors, including cameras, offer a deeper insight into the fine-scale movements and behaviours of animals. Animal borne tags with multiple sensors, however, are only able to track and collect data from animals over few hours or days. In Indonesia, studies on the movement ecology of marine species using satellite and/or acoustic tracking are still limited to few species (e.g., manta rays, whale sharks, thresher sharks) in certain areas (e.g., Papua, Gorontalo, Rote, Sumba, Alor) (Dewar et al., 2008; Setyawan et al., 2018; Meyers et al., 2020). While non-invasive methods for tag deployment are preferred, so far this technology is only able to track animals over short periods of time, which may not be sufficient to answer research questions such as the animals' home range and residency patterns, or whether MPAs provide sufficient protection to protected species. To answer these questions, longer-term tracking methods are still preferrable. To ensure animal welfare standards are met, I suggest that animal tracking studies should be considered and permitted by an animal ethics committee as is done for animals used in laboratory studies in Indonesia.

The field of movement ecology has been growing rapidly over the last few decades and has facilitated enormous data collections around the globe on many species (Hays et al., 2016; Watanabe & Papastamatiou, 2023). Several free, online databases (e.g., Movebank, Ocean Tracking Network, US Animal Telemetry Network, Australia Ocean Data Network) have been commonly used by researchers, government agencies, and conservation organisations from around the world to collect, store, analyse, visualise, and share animal tracking data (Hill et al., 2010; Block et al., 2016; Iverson et al., 2018; Kays et al., 2022). These platforms also support collaborations allowing regional or global studies over large spatial scales. Similar platforms such as Wildbook have also been commonly used to collect images of animals (e.g., whales, manta rays, sea turtles, zebras) that have unique and permanent markers (Town et al., 2013; Berger-Wolf et al., 2017; Blount et al., 2022). These online databases also support data analysis, visualisation, and international collaboration from many users. Moreover, the Australia Integrated Marine Observation System collect various marine and climate data (e.g., currents, sea surface temperature, ocean colours) in Australian waters that are freely available to support research and science Australia and surrounding regions. With the growing number of animal tracking and population demographic studies in Indonesia, it would be very useful to have a single national datasets that can facilitate data collection, storing, analysis, sharing, and collaboration on various different species. This initiative could include several marine species for which population and movement data have been collected, such as manta rays, whale sharks, thresher sharks, and sea turtles.

### 7.5.2. Anthropogenic factors and environmental variables

One of the key questions in marine megafauna movement ecology is how anthropogenic activities affect the movements of marine megafauna (Hays et al., 2016). Despite the successes in reef manta ray populations, there are several potential threats (e.g., marine tourism including manta-based tourism activities, net fishing operating outside of Raja Ampat MPAs) that can have negative impacts on reef manta rays. Understanding anthropogenic impacts should be prioritised to improve the management of the species that generates substantial economic benefits through tourism. Future research should focus on the impact of boating activities and boat traffic around manta ray diving sites. This should include the potential impact of boat noise. Wilson et al. (2022) found that recreational boats generated significant sound pollution (i.e., elevated low frequency soundscape) in shallow habitats and elasmobranch species are sensitive to low frequency sound (Mickle & Higgs, 2021). Investigation into the impact of sound pollution might be worthwhile to improve management measures, not only at manta diving sites, but also in reef manta ray nurseries, such as in Wayag lagoon. The use of acoustic monitoring in Wayag lagoon can also be used to monitor boat traffic, especially in areas that have been designated as no access areas (Indonesian Ministry of Marine Affairs and Fisheries, 2022). Apart from boat traffic and noise pollution, further investigation using satellite telemetry into the home range of manta rays, especially those inhabiting remote areas near the boundaries of Raja Ampat region and MPA network could help understanding the potential risks of manta ray populations from fisheries (e.g., bycatch) or poachers.

Incorporating environmental and climate data into animal tracking data could help understanding habitat preferences, drivers influencing movement patterns, and how the tracked animals respond to changing environmental conditions. Environmental data can be collected both from sensors integrated with tracking device, remote sensing data, or data that are collected by regional and global oceanographic observation systems (Harcourt et al., 2019). Despite using satellite tags that also collected physical environmental data (e.g., ambient temperature), my research did not focus on analyses using these data and other environmental data (e.g., ocean colour, bathymetry, wind speed and direction, moon phases) potentially influencing the movement patterns of tagged reef manta rays. Large- and fine-scale oceanographic processes can affect the movement patterns and presence of reef manta rays over different temporal scales in many regions  (Jaine et al., 2012; Peel et al., 2019b; Harris et al., 2020; Armstrong et al., 2021b; Harris et al., 2021; Harris & Stevens, 2021). Future research should look into the environmental drivers affecting the movement patterns of reef manta rays, not only those juveniles in Wayag lagoon nursery, but also those adult individuals in Raja Ampat and in other regions throughout Indonesia.

With increasing trends in marine animal movement studies in Indonesia, one of critical aspects currently lacking is the availability of oceanographic and climatological data. Data collection effort is not well distributed throughout the country and often the data are not easily accessible and freely available even for research purposes. With such high levels of marine biodiversity and complex oceanographic systems in Indonesian waters, having an integrated oceanographic and climate observation system at national level, such as IMOS  and the Australian Ocean Data Network (AODN) (Harcourt et al., 2019), would be very beneficial and significantly improve marine science and research.

## 7.6. Final thoughts

Apart from threats from fisheries through direct hunting and bycatch, a rapidly emerging potential threat for manta rays and many other ocean-going species is climate change. Warming oceans have shifted the spatial distributions of several marine fishes (Perry et al., 2005; Pinsky et al., 2013). Nearly three decades of monitoring showed that changing climate has impacted prey availability and shifted the foraging grounds of endangered North Atlantic right whales *Eubalena glacialis* northwards to areas with no with protection measures for this species, therefore, putting this species at greater risk of mortality from ship strikes and entanglements from fishing gear (Gavrilchuk et al., 2021; Meyer-Gutbrod et al., 2021; Meyer-Gutbrod et al., 2022). We know little about how the reef manta rays in the Raja Ampat archipelago are coping with the changing climate and how the warming ocean will impact their habitat use, distribution, and movements patterns. Shifts in their distribution and movements patterns could potentially affect the efficacy of Raja Ampat MPA network that has been effective at protecting the reef manta rays and their aggregation sites. Movement to areas outside of the Raja Ampat MPA boundaries could potentially put the reef manta rays at risks from fishing that still operates in many areas in the Bird's Head Seascape (BHS).

The increasing sea surface temperature could affect vertical distribution of marine species (Perry et al., 2005; Dulvy et al., 2008), potentially moving reef manta rays into deeper water. The prolonged La Niña event in 2021, indicated by a higher-than-normal sea surface temperature in southern Raja Ampat waters, especially in the South East Misool MPA, resulted in very low sighting rates of both manta ray species at cleaning stations where they were previously regularly sighted. I hypothesise that they moved to a deeper to exploit prey, a phenomenon observed in other regions (Stewart et al., 2016b; Peel et al., 2019a). The reef manta rays are able to take advantage of the naturally occurring ENSO climate cycle (Chapter 3), however, the impact of warming oceans on the intensity and activity of ENSO is still unclear (Collins et al., 2010). Furthermore, climate change is projected to create considerable impacts on biodiversity in tropical regions (Cheung et al., 2009; Freeman et al., 2018). Future research should look into how manta rays respond to temperature increases and how the changing climate could potentially affect their ability to survive or thrive.

# Appendix

# Appendix A

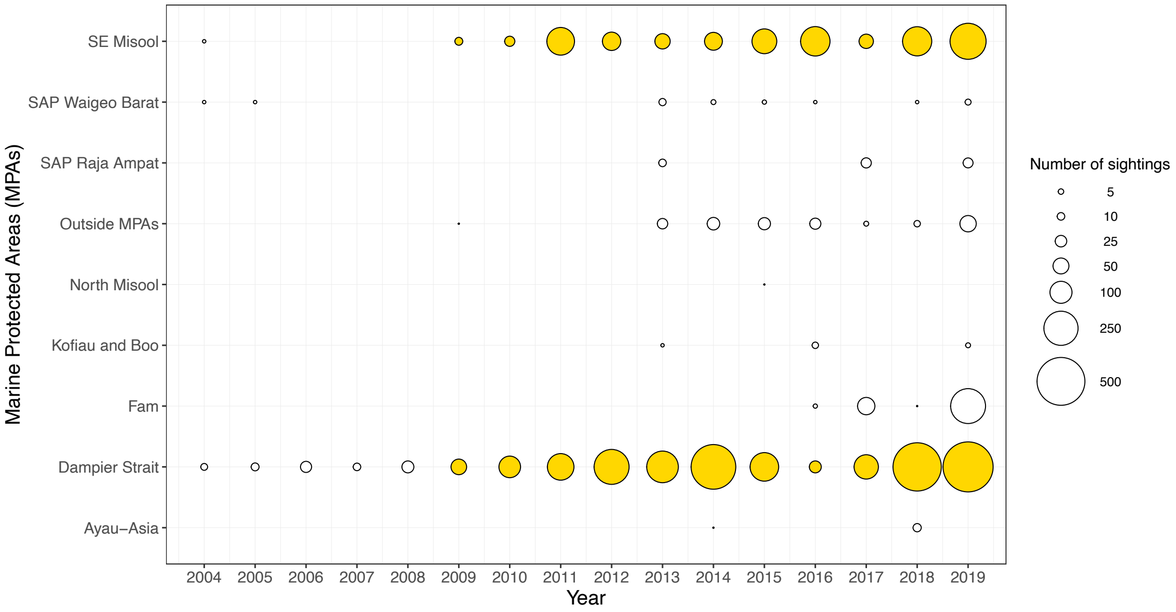

Figure A.1. The annual number of *M. alfredi* sightings within and outside of the nine MPAs in the Raja Ampat archipelago from 2004 to 2019. The circle size represents the number of sightings. Yellow circles represent sighting data used in the analysis.

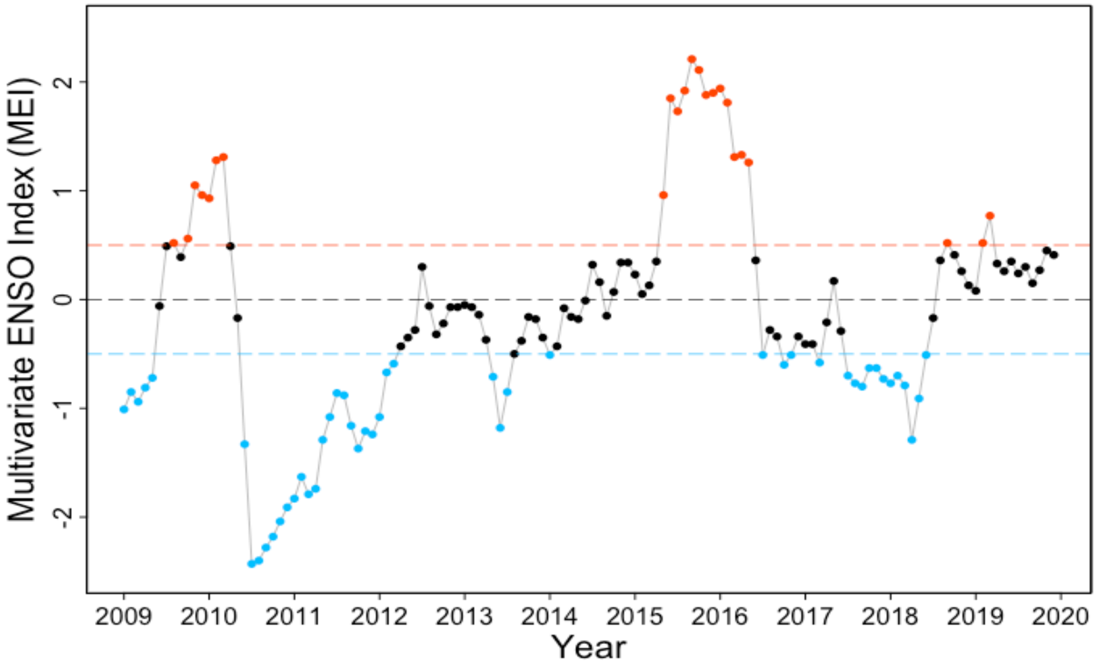

Figure A.2. Bimonthly mean Multivariate El Niño Southern Oscillation (ENSO) Index from 2009 to 2019. The red dots denote indices >0.5 (indicating an El Niño event), blue dots represent indices <-0.5 (indicating a La Niña event), and black dots denote indices ranged from -0.5 to 0.5. The red horizontal dashed line represents index value of 0.5, while the blue horizontal dashed line denotes index value of -0.5.

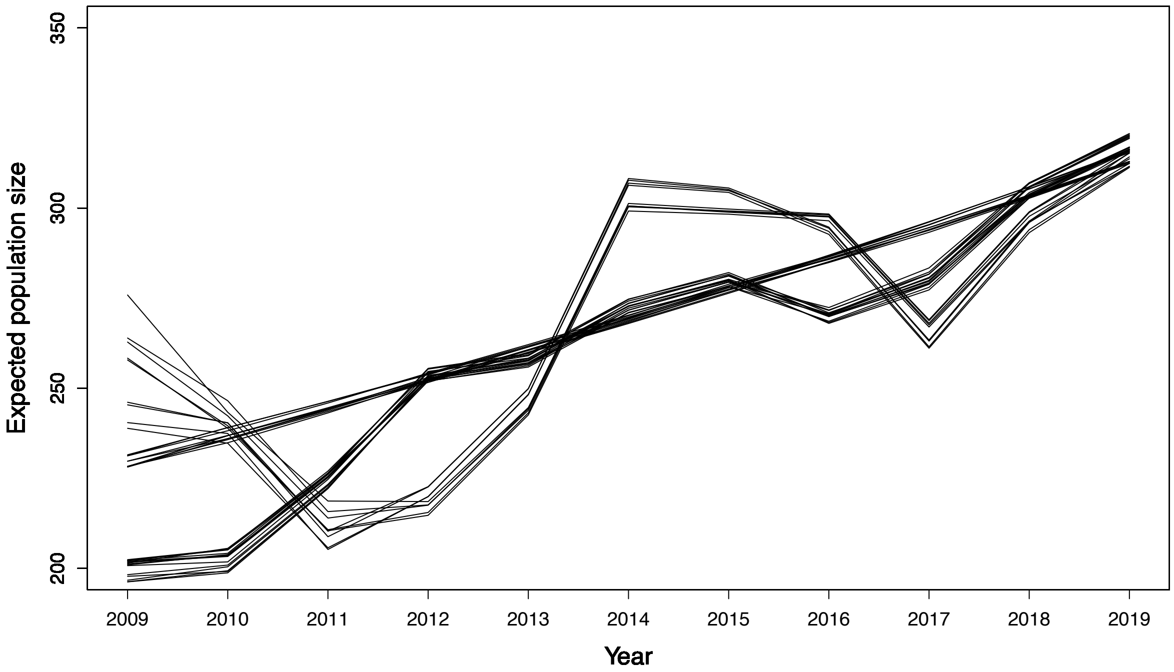

Figure A.3. Annual estimated expected population size of reef manta rays *M. alfredi* for females and males combined in Dampier Strait MPA in 2009–2019. Each line corresponds to the estimated trajectory of each model within 10 QAIC of the best models.

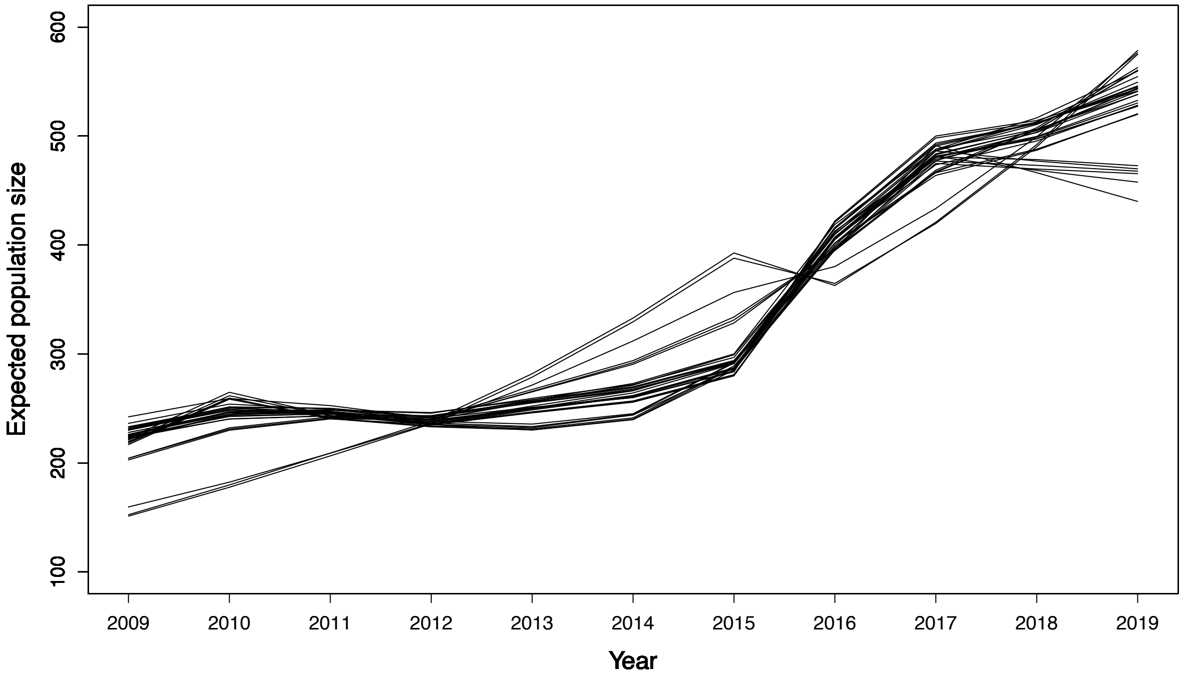

Figure A.4. Annual estimated expected population size of reef manta rays *M. alfredi* for females and males combined in South East Misool MPA in 2009–2019. Each line corresponds to the estimated trajectory of each model within 10 AIC of the best models.

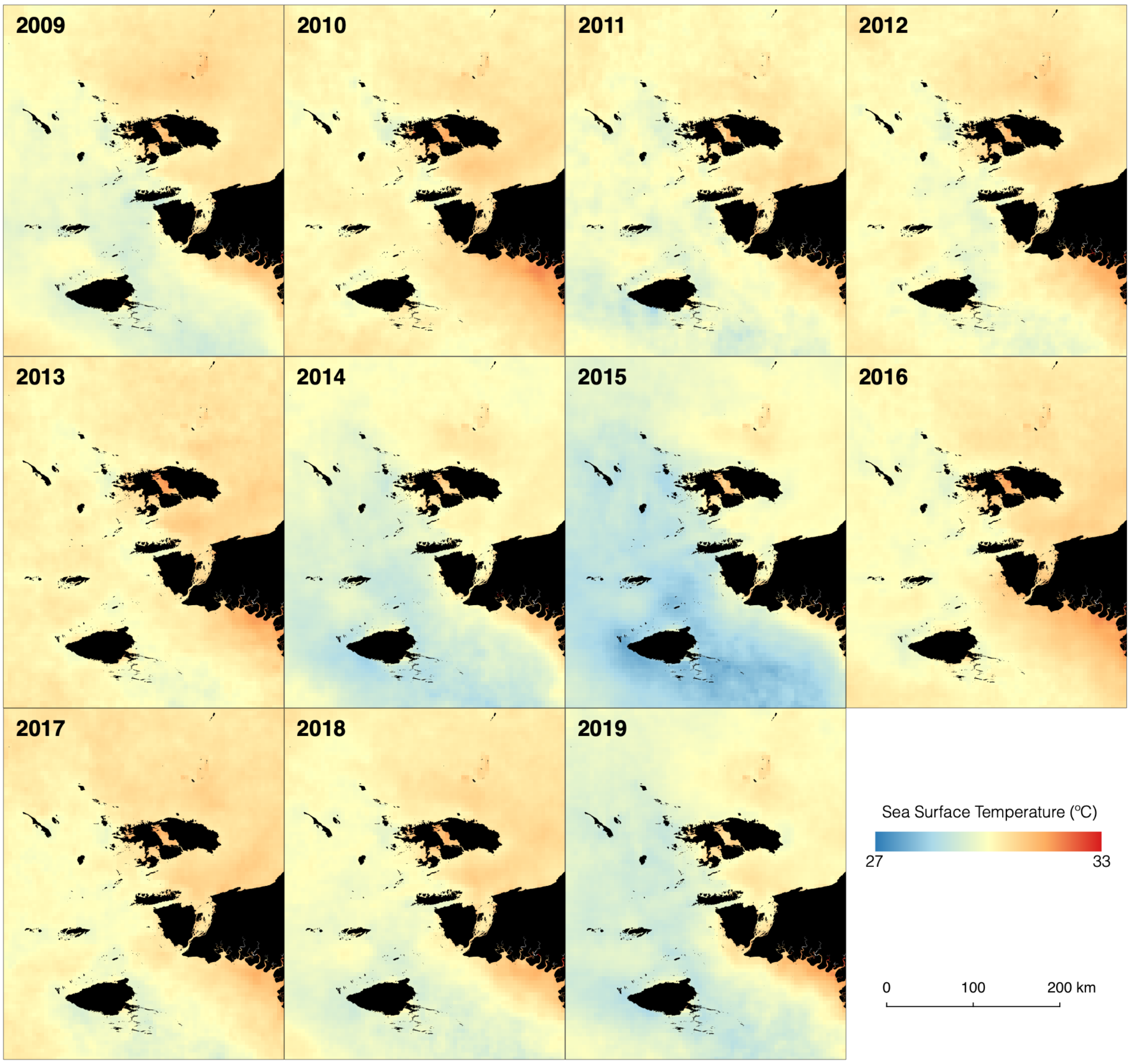

Figure A.5. Annual averaged SST (ºC) distribution across Raja Ampat waters between 2009 and 2019. Islands are coloured black.

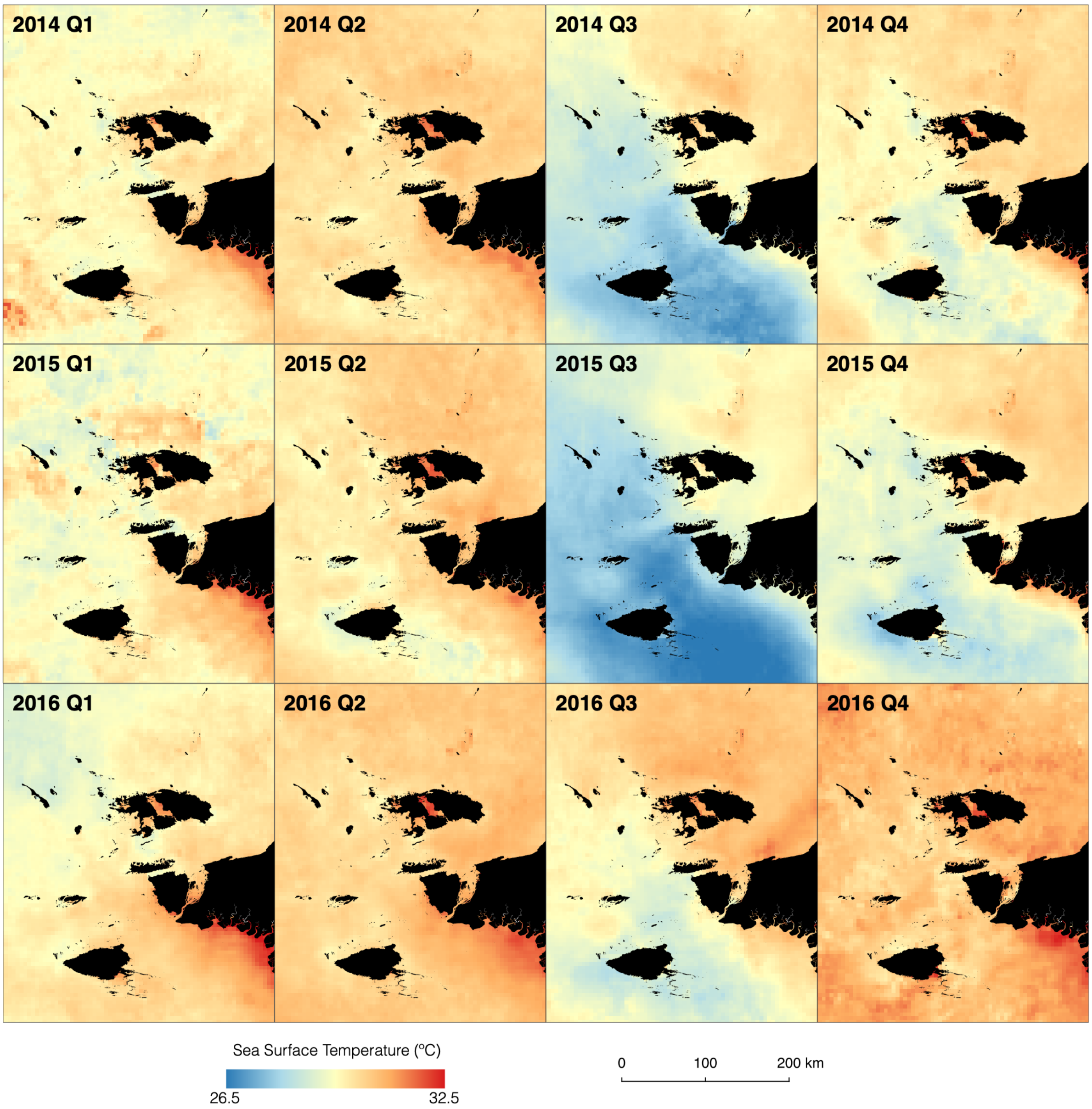

Figure A.6. Seasonal averaged SST (°C) distribution across Raja Ampat waters between 2014 and 2016. Q represents different quarters of the year (e.g., Q1 means the first quarter of the year). Islands are coloured black.

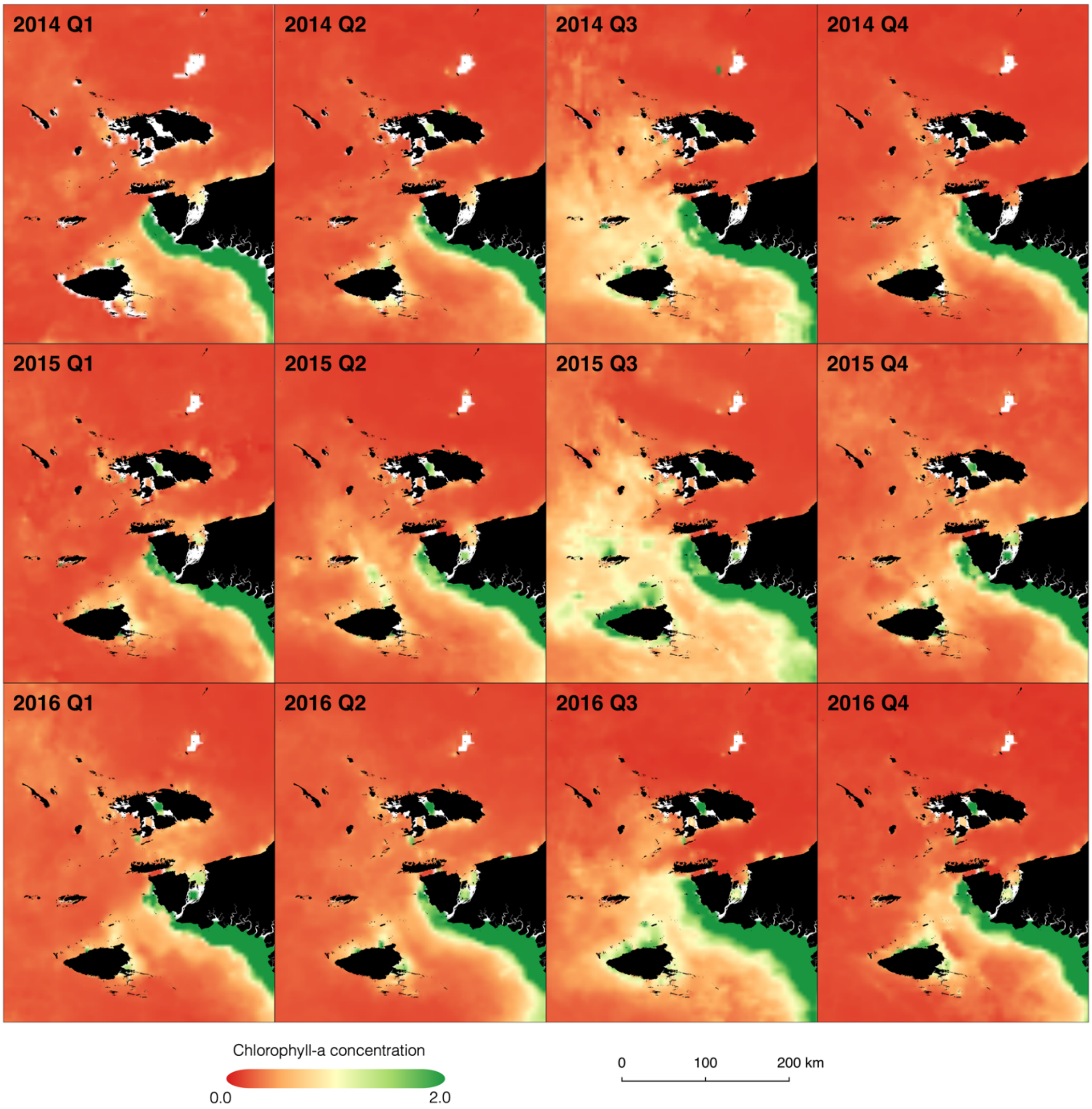

Figure A.7. Seasonal averaged chl-*a* concentration (mg.m$^{-3}$) across Raja Ampat waters between 2014 and 2016. Q represents different quarters of the year (e.g., Q1 means the first quarter of the year). High chl-*a* concentration (green color) along the coast of West Papua (bottom left) is related to run-off and sedimentation, instead of upwelling. Islands are coloured black.

Table A.1. Model selection using Quasi Akaike Information Criterion (QAIC) for the top ten of 33 POPAN mark-recapture models (determined by QAIC < 10) to estimate per capita recruitment rate ($\psi$), survival probability ($\phi$), sighting probability ($p$), and transient probabilities ($\gamma$) of *M. alfredi* in the Dampier Strait MPA.

| **No.** | **Per capita recruitment rate ($\psi$)** | **Apparent survival probability ($\phi$)** | **Sighting probability ($p$)** | **Transient probability ($\gamma$)** | **QΔAIC** |
|---|---|---|---|---|---|
| 1 | $\psi(.)$ | $\phi(.)$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 0.000 |
| 2 | $\psi(\text{MEI})$ | $\phi(.)$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 0.637 |
| 3 | $\psi(.)$ | $\phi(\text{sex})$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 1.778 |
| 4 | $\psi(\text{sex})$ | $\phi(.)$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 1.973 |
| 5 | $\psi(.)$ | $\phi(\text{MEI})$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 1.985 |
| 6 | $\psi(\text{MEI})$ | $\phi(\text{sex})$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 2.414 |
| 7 | $\psi(\text{MEI} + \text{sex})$ | $\phi(.)$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 2.565 |
| 8 | $\psi(\text{MEI})$ | $\phi(\text{MEI})$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 2.587 |
| 9 | $\psi(\text{sex})$ | $\phi(\text{sex})$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 3.658 |
| 10 | $\psi(.)$ | $\phi(\text{MEI} + \text{sex})$ | $p(t + \text{sex})$ | $\gamma(t_1)$ | 3.764 |

Table A.2. Model selection using Akaike Information Criterion (AIC) for the top ten of 32 POPAN mark-recapture models (determined by AIC < 10) to estimate per capita recruitment rate ($\psi$), survival probability ($\phi$), and sighting probability ($p$) of *M. alfredi* in the South East Misool MPA.

| **No.** | **Per capita recruitment rate ($\psi$)** | **Apparent survival probability ($\phi$)** | **Sighting probability ($p$)** | **ΔAIC** |
|---|---|---|---|---|
| 1 | $\psi(\text{MEI})$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t \times \text{sex})$ | 0 |
| 2 | $\psi(\text{MEI} \times \text{sex})$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t + \text{sex})$ | 1.387 |
| 3 | $\psi(\text{MEI} + \text{sex})$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t \times \text{sex})$ | 1.856 |
| 4 | $\psi(\text{MEI} \times \text{sex})$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t)$ | 2.263 |
| 5 | $\psi(\text{MEI})$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t + \text{sex})$ | 2.999 |
| 6 | $\psi(\text{MEI} + \text{sex})$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t)$ | 3.087 |
| 7 | $\psi(\text{MEI} \times \text{sex})$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t \times \text{sex})$ | 3.814 |
| 8 | $\psi(\text{MEI})$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t)$ | 3.920 |
| 9 | $\psi(\text{MEI} + \text{sex})$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t + \text{sex})$ | 3.960 |
| 10 | $\psi(.)$ | $\phi(\text{MEI} \times \text{sex})$ | $p(t \times \text{sex})$ | 4.013 |

# Appendix B. Description of POPAN models

## B.1. Standard POPAN models

To fit a POPAN model by maximum likelihood, we need to specify the probability of obtaining each observed capture history as a function of the model parameters. A capture history is given by $\boldsymbol{\omega} = (\omega_1, \cdots, \omega_k)$, where $\omega_t = 1$ $(t = 1, \cdots, k)$ indicates the individual was detected on occasion *t* of a total of *k* occasions, and $\omega_1 = 0$ indicates the individual was not detected.

Our model has the following parameters:

- $p_t$, detection probability. This parameter is the probability of an individual being detected on occasion $t$.
- $\phi_t$, survival probability. This parameter is the probability of an individual that is alive and in the population on occasion $t$ still being alive and in the population on occasion $t + 1$.
- $\psi_t$, per-capita recruitment rate. This is the expected number of individuals who enter the population on occasion $t + 1$ per individual in the population on occasion $t$.
- $M$, the superpopulation size. Conceptually, this parameter is the number of individuals that are ever at risk of detection during the survey.

We can estimate these parameters separately for each occasion, restrict them to be the same (e.g., $p_t = p$ for all $t$), or model them with available covariates (e.g., $logit(p_t) = \beta_0 + \beta_1 x_t$).

Practitioners often consider the recruitment parameter $p_{e,t}$ (the entry proportions) rather than the per-capita recruitment rate $\psi_t$ we do here, where $p_{e,t}$ is the proportion of the $M$ individuals in the superpopulation that were first available for detection on occasion $t$. We use $\psi_t$ because it involves a proportional relationship between population growth and population size, which is more biologically realistic: all else being equal, larger populations experience larger fluctuations in absolute size over time. Nevertheless, we can calculate the proportion of the $M$ individuals entering the population on each occasion from our $\psi$ and $\phi$ parameters as follows.

Let $N_t$ be the number of individuals alive and in the population on occasion $t$, so the expected number of animals joining the population on occasion $t + 1$ is $\psi_t N_t$. The expected number of individuals that survive between occasions $t$ and $t + 1$ is $\phi_t N_t$, and therefore the expected total number of individuals in the population on occasion $t + 1$, given the number in the population on occasion $t$ is $E(N_{t+1} \mid N_t) = \psi_t N_t + \phi_t N_t = (\psi_t + \phi_t) N_t$ and by taking an average over $N_t$, we obtain

$$E(N_{t+1}) = (\psi_t + \phi_t) E(N_t) \tag{1}$$

We can also express the expected population size at time *t*+1 using proportions of entry as follows:

$$E(N_{t+1}) = \phi_t E(N_t) + p_{e,t+1} M \tag{2}$$

By equating (1) and (2), we have

$$\phi_t E(N_t) + p_{e,t+1} M = (\psi_t + \phi_t) E(N_t)$$

$$p_{e,t+1} M = \frac{\psi_t E(N_t)}{M} \tag{3}$$

By definition, the expected number of individuals in the population on the first occasion is $E(N_1) = p_{e,1}M$. Using the fact that the $p_e$ parameters must sum to one, we can calculate the $p_e$ parameters using (3) and (2) iteratively. Once we have computed the $p_e$ parameters, we can use the standard POPAN model likelihood (Schwarz & Arnason, 1996).

## B.2. POPAN models with transience

Here we consider a variation of the standard POPAN model in which some proportions of recruited individuals are transients. We let $\gamma_t$ be the probability that a randomly selected individual recruited on occasion $t$ is a transient, and so the probability that they are resident is $1 - \gamma_t$. Residents have the standard survival probabilities (i.e., a resident in the population on occasion $t$ remains in the population on occasion $t + 1$ with probability $\phi_t$). However, transients have survival probabilities of zero, and are therefore only available for detection in the occasion on which they were recruited. In other words, a transient recruited on occasion $t$ is guaranteed to have $\omega_{x'} = 0$ for all $t' \neq t$.

We do not observe whether a detected individual is a transient or a resident. If we detect an individual on more than one occasion then we know they are a resident, but we are unable to resolve the status of an individual that was only detected on one occasion: they could be a transient that was detected on the sole occasion they were in the population, but they could still be a resident that evaded detection on the other occasions they were in the population, and indeed some residents are only in the population for a single occasion: for any given resident recruited on time $t$, there is a $(1 - \phi_t)$ probability that they fail to survive beyond this single occasion. We can still use the standard POPAN likelihood as long as we can calculate the entry probability parameters, $p_e$, for our new model.

Let $T_t$ and $R_t$ be the number of transients and residents, respectively, in the population on occasion $t$, so that $N_t = T_t + R_t$. Similar to the standard model described in the previous section, we link recruitment on occasion $t + 1$ to the number of residents in the population on occasion $t$. We assume that the expected number of individuals (transients and residents combined) recruited on occasion $t$ is $\psi_t R_t$, partitioned into transients and residents by the proportions $\gamma_t$ and $(1 - \gamma_t)$, respectively. Therefore, the expected number of residents in the population on occasion $t + 1$, conditional on the number of residents in the population on occasion $t$, is

$$E(R_{t+1} \mid R_t) = \phi_t R_t + (1 - \gamma_{t+1})\, \psi_t R_t$$

where the first term is the expected number of surviving residents from occasion t, and the second term is the number of newly recruited residents. Taking the expectation of both sides over $R_t$, we obtain

$$\begin{aligned} E(R_{t+1}) &= \phi_t E(R_t) + (1 - \gamma_{t+1})\psi_t E(R_t) \\ &= \{\phi_t + (1 - \gamma_{t+1})\psi_t\} E(R_t) \qquad (4) \end{aligned}$$

Similarly, for transients, we have $E(T_{t+1} \mid R_t) = \gamma_{t+1}\psi_t R_t$ and $E(R_{t+1}) = \gamma_{t+1}\psi_t(R_t)$, where we only have a term for recruited individuals, because by definition transients do not survive between occasions.

To find the expected total population size on occasion $t+1$ we can sum the expectations for transients and residents respectively, which gives

$$\begin{aligned} E(N_{t+1}) &= E(T_{t+1}) + E(R_{t+1}) \\ &= (\phi_t + \psi_t)E(R_t) \qquad (5) \end{aligned}$$

and so

$$E(R_t) = \frac{E(N_{t+1})}{\phi_t + \psi_t} \qquad (6)$$

From Equation (4) we have

$$E(R_t) = \{\phi_{t-1} + (1-\gamma_{t+1})\psi_{t-1}\}E(R_{t-1})$$

and via substitution of $E(R_{t-1})$ using (6), we can specify $E(R_t)$ in terms of $E(N_t)$:

$$E(R_t) = \frac{\{\phi_{t-1} + (1-\gamma_t)\psi_{t-1}\}E(N_t)}{\phi_{t-1} + \psi_{t-1}} \qquad (7)$$

This equation applies to the expected number of residents for $t = 2,3,\cdots$. By definition, each individual in the population in the first occasion is a resident with probability $(1-\gamma_t)$ so for $t = 1$, we have

$$E(R_1) = (1-\gamma_1)E(N_1) \qquad (8)$$

For our standard model, we specified the expected population size on occasion *t*+1 in terms of the expected population size on occasion $t$ in Equation (1). We can now achieve something similar here. We have $E(N_{t+1}) = (\phi_t + \psi_t)E(R_t)$ from (5), and similarly to Equation (2) for standard models, we can also express $E(N_{t+1})$ in terms of the superpopulation size and probabilities of entry, where

$$E(N_{t+1}) = \phi_t E(R_t) + p_{e,t+1}M \qquad (9)$$

We can equate (5) and (9) to develop an expression for the probabilities of entries as follows:

$$(\phi_t + \psi_t)E(R_t) = \phi_t E(R_t) + p_{e,t+1}M$$

$$p_{e,t+1} = \frac{\psi_t E(R_t)}{M} \qquad (10)$$

noting that for $p_{e,2}$, corresponding to $t = 1$, we use (8) rather than (7) to calculate the expected number of residents in the population on the previous occasion.

As with the standard models, we can use the fact that the $p_e$ parameters must sum to one, and iteratively calculate the $E(N_t)$ and $p_{e,t}$ terms using (9) and (10).

# Appendix C. Multivariate hierarchical model

In general, we consider a situation in which we have drone measurements of $m$ morphometric dimensions belonging to $G$ different groups, where $n_g$ unique individuals have been measured from the $g$th group. In our specific case here, we have $m$ = 3 morphometric dimensions. For our first model, we analyzed all manta rays as a single group, so $G$ = 1. For our second model, we grouped individuals into into $n_1$ = 30 sexually mature males, $n_2$ = 8 sexually mature females, and $n_3$ = 48 unsexed individuals, so for this analysis $G$ = 3.

Let $p_{gi}$ be the number of drone images captured of the $i$th animal in the $g$th group. For this animal, we observe an $p_{gi} \times m$ matrix $\boldsymbol{Y}_{gi}$. The element in the $j$th row and $k$th column, $y_{gijk}$, is a measurement of the $k$th morphometric dimension in the $j$th image, and is subject to measurement error. Let $\boldsymbol{u}_{gi} = (u_{gi1}, \cdots, u_{gim})$ be a vector containing the unobserved true morphometric dimensions of the $i$th individual in the $g$th group, where $u_{gik}$ is the unobserved true measurement of the $k$th dimension.

## C.1. True Measurements

We assume $\boldsymbol{u}_{gi} \sim \mathrm{MVN}_m(\boldsymbol{\mu}_g, \boldsymbol{\Sigma}_g)$; that is, individuals in the $g$th group have true morphometric dimensions that come from a multivariate normal distribution, where $\boldsymbol{\mu}_g = (\mu_{g1}, \cdots, \mu_{g2})$ is a vector of the underlying mean measurements for the $m$ dimensions in the group's population, and $\boldsymbol{\Sigma}_g$ is an $m \times m$ variance-covariance matrix of the measurements. In this matrix, the $k$th diagonal element, $\Sigma_{gkk} = \sigma_{gk}^2$, is the variance of the $k$th dimension across individuals in the $g$th group's population, while the off-diagonal element in the $k$th row and $k'$th column ($k \neq k'$) is $\Sigma_{gkk'} = \rho_{kk'}\sigma_{gk}\sigma_{gk'}$, the covariance between the $k$th and $k'$th dimension. Here, $\rho_{kk'}$ is the correlation between these morphometric dimensions.

## C.2. Measurement Error

We do not observe true measurements, $\boldsymbol{u}_{gi}$, which precludes direct estimation of the mean vector, $\boldsymbol{\mu}_g$, and variance-covariance matrix $\boldsymbol{\Sigma}_g$ for each group. Instead, we observe the matrix $\boldsymbol{Y}_{gi}$ for each individual, comprising $p_{gi}$ noisy measurements of $\boldsymbol{u}_{gi}$ that are subject to error. We assume the measurement error distribution is itself multivariate normal, and so $\boldsymbol{Y}_{gij} \mid \boldsymbol{u}_{gi} \sim \mathrm{MVN}_m(\boldsymbol{u}_{gi}, \Xi)$. This assumption implies that drone measurements are unbiased: the underlying mean drone measurement of a particular morphometric dimension is equal to the true measurement. The matrix $\Xi$ is a variance-covariance matrix for the measurement error, where the $k$th diagonal element, $\Xi_{kk} = \psi_k^2$, is the measurement error variance of the $k$th dimension, while the off-diagonal element in the $k$th row and $k'$th column ($k \neq k'$) is $\Xi_{kk'} = \phi_{kk'}\psi_k\psi_{k'}$, the covariance between measurement errors for the $k$th and $k'$th dimensions. Here, $\phi_{kk'}$ is the correlation between the measurement errors for these morphometric dimensions. Note that we assume measurement errors are the same across all groups.

## C.3. Model Parameters

The parameters of our model are therefore, the following:

- $\boldsymbol{\mu} = (\boldsymbol{\mu}_1, \cdots, \boldsymbol{\mu}_G)$, where $\boldsymbol{\mu}_g$ contains the underlying population means of the morphometric dimensions for the $g$th group;
- $\boldsymbol{\sigma} = (\boldsymbol{\sigma}_1, \cdots, \boldsymbol{\sigma}_G)$, where $\boldsymbol{\sigma}_g$ contains the underlying population standard deviations of the morphometric dimensions for the $g$th group;
- $\boldsymbol{\rho} = (\boldsymbol{\rho}_1, \cdots, \boldsymbol{\rho}_G)$, where $\boldsymbol{\rho}_g$ contains underlying population correlations between all pairs of morphometric dimensions;
- $\boldsymbol{\psi}$ containing underlying standard deviations of the measurement errors for each of the $m$ dimensions; and
- $\boldsymbol{\phi}$ containing underlying correlations between measurement errors of all morphometric dimensions.

The variance-covariance $\boldsymbol{\Sigma}_g$ can be constructed from parameters $\boldsymbol{\sigma}_g$ and $\boldsymbol{\rho}_g$. Likewise, $\Xi$ can be constructed from $\boldsymbol{\psi}$ and $\boldsymbol{\phi}$. Fitting this model therefore accommodates measurement error, because parameter vectors $\boldsymbol{\psi}$ and $\boldsymbol{\phi}$ characterize the distribution of measurement errors. Our model also allows inference in the distribution of true, unobserved morphometric measurements, which is characterized by parameter vector $\boldsymbol{\mu}$, $\boldsymbol{\sigma}$, and $\boldsymbol{\rho}$.

## C.4. Relationships between Dimensions

Fitting a multivariate normal distribution implies that each of the component variables are linearly related to the others. To determine the linear relationships between true morphometric dimensions in the $g$th group, we can translate $\boldsymbol{\mu}_g$ and $\boldsymbol{\Sigma}_g$ into coefficients of a linear equation that returns the expected value of one morphometric dimension conditional on observed values of any combination of the other dimensions. These coefficients can be interpreted in the same way as those from a standard linear regression model, and allow predictions of unmeasured dimensions based on those that have been measured.

Say we wish to determine the coefficients of the linear equation to calculate the expected value of dimension $p$, conditional on observed values of $s$ other dimensions, $q_1, \cdots, q_s$. So, for example, if we wish to calculate the expected value of the first dimension conditional on observed values of the third and fifth, we have $p = 1$, $s = 2$, $q_1 = 3$, and $q_2 = 5$. Using standard results conditional multivariate distributions, the vector of coefficients for dimensions $q_1, \cdots, q_s$ is given by $\boldsymbol{\beta} = \boldsymbol{\Sigma}_{gA}\boldsymbol{\Sigma}_{gB}^{-1}$, and the intercept is given by $\alpha = \mu_{gp} - \sum_{i=1}^{s} \beta_i \, \mu_{gi}$, where $\boldsymbol{\Sigma}_{gA}$ is the $p$th row of $\boldsymbol{\Sigma}_g$, excluding the $p$th element, and $\boldsymbol{\Sigma}_{gB}$ is an $s \times s$ submatrix of $\boldsymbol{\Sigma}_g$, containing its $q_1$th, $\cdots$, $q_s$th rows and columns. Therefore, the parameters of our model can be used to determine coefficients for linear combinations to describe relationships between any subset of the morphometric dimensions.

## C.5. Parameter Estimation

We fit our hierarchical multivariate normal model by maximum likelihood. The likelihood of our model is:

$$L(\boldsymbol{\theta}) = \prod_{g=1}^{G} \prod_{i=1}^{n_g} \int_{\mathcal{R}^m} f_u\,(\boldsymbol{u}_{gi}; \boldsymbol{\mu}_g, \boldsymbol{\sigma}_g, \boldsymbol{\rho}_g) \prod_{j=1}^{p_{gi}} f_{y|u}\,(\boldsymbol{y}_{gij} \mid \boldsymbol{u}_{gi}; \boldsymbol{\psi}, \boldsymbol{\phi}) d\boldsymbol{u}_{gi} \tag{11}$$

where $f_u(\boldsymbol{u}; \boldsymbol{\mu}, \boldsymbol{\sigma}, \boldsymbol{\rho})$ is the multivariate normal probability density function (PDF) with mean vector $\boldsymbol{\mu}$ and variance-covariance matrix constructed from marginal standard deviations $\boldsymbol{\sigma}$ and correlations $\boldsymbol{\rho}$. Likewise, $f_{y|u}(\boldsymbol{y} \mid \boldsymbol{u}; \boldsymbol{\psi}, \boldsymbol{\phi})$ is the multivariate normal PDF with mean vector $\boldsymbol{u}$ and variance-covariance matrix constructed from marginal standard deviations $\boldsymbol{\phi}$ and correlations $\boldsymbol{\psi}$.

This integrand in Equation (11) is a Gaussian function, so it is available in closed form. Nevertheless, we wrote code to calculate our model's likelihood using the software TMB (Kristensen et al., 2016), which uses the Laplace approximation to evaluate the integral. We used the R function nlminb() to numerically maximize the likelihood.

We wrote additional R functions to predict true measurements of morphometric dimensions, given either drone measurements of new individuals (i.e., not in our original data set that are subject to the same measurement error), true measurements (i.e., not subject to any measurement error), or a combination of both.

Table C.1. Estimated true measurements of dimensions (DW, DL, and CW), including the lower and upper 95% confidence intervals (CIs), of each individual M. alfredi measured using drones. ♂, ♀, and U denote sexually mature males, sexually mature female, and unsexed individual, respectively. * denotes a large individual that was confirmed to be female based on observations from somersault feeding but recorded here as unsexed because we were not able to observe mating scars in dorsal view by the drone. C and M represent normal "chevron" and melanistic color patterns of the manta rays. WYG = Wayag lagoon, HOL = Hol Gam bay, ARB = Arborek reefs, FAM = Fam islands, YFK = Yefnabi Kecil reef. N repeats = the number of measurement repeats for each individual. Est. = Estimated true measurement, Lower = lower 95% CI, Upper = upper 95% CI.

| ID | Sex | Color morph | Site | N repeats | Disc Width (DW) | | | Disc Length (DL) | | | Cranial Width (CW) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Est. | Lower | Upper | Est. | Lower | Upper | Est. | Lower | Upper |
| 1 | U | C | WYG | 6 | 219.4 | 217.7 | 221.2 | 93.6 | 92.3 | 95.0 | 56.6 | 55.7 | 57.5 |
| 2 | U | C | HOL | 9 | 226.8 | 225.4 | 228.3 | 99.4 | 98.3 | 100.5 | 57.1 | 56.3 | 57.8 |
| 3 | U | M | ARB | 4 | 327.9 | 325.8 | 330.0 | 155.3 | 153.7 | 156.9 | 84.6 | 83.6 | 85.7 |
| 4 | ♀ | C | ARB | 4 | 341.6 | 339.5 | 343.7 | 163.3 | 161.7 | 164.9 | 90.4 | 89.3 | 91.5 |
| 5 | ♂ | M | ARB | 5 | 300.2 | 298.3 | 302.1 | 129.2 | 127.7 | 130.7 | 76.4 | 75.4 | 77.4 |
| 6 | U | M | ARB | 5 | 350.1 | 348.2 | 352.0 | 156.9 | 155.4 | 158.4 | 92.7 | 91.7 | 93.6 |
| 7 | ♀ | C | ARB | 6 | 354.1 | 352.3 | 355.8 | 164.4 | 163.0 | 165.7 | 94.7 | 93.8 | 95.6 |
| 8 | U | M | ARB | 3 | 334.7 | 332.3 | 337.1 | 156.6 | 154.7 | 158.4 | 87.8 | 86.5 | 89.0 |
| 9 | U | M | ARB | 5 | 340.6 | 338.8 | 342.5 | 154.8 | 153.3 | 156.3 | 92.4 | 91.4 | 93.4 |
| 10 | ♂ | C | ARB | 5 | 289.2 | 287.3 | 291.1 | 129.9 | 128.4 | 131.4 | 76.2 | 75.2 | 77.2 |
| 11 | ♂ | C | ARB | 6 | 301.0 | 299.3 | 302.7 | 139.0 | 137.7 | 140.3 | 78.1 | 77.2 | 79.0 |
| 12 | ♂ | C | ARB | 7 | 284.7 | 283.1 | 286.3 | 123.1 | 121.9 | 124.3 | 73.2 | 72.4 | 74.0 |
| 13 | U | C | ARB | 5 | 342.3 | 340.4 | 344.2 | 162.5 | 161.0 | 163.9 | 92.4 | 91.4 | 93.4 |
| 14 | U | M | ARB | 2 | 303.0 | 300.0 | 306.0 | 139.7 | 137.5 | 142.0 | 77.0 | 75.5 | 78.5 |
| 15 | U | M | ARB | 4 | 344.0 | 341.9 | 346.1 | 159.3 | 157.7 | 160.9 | 92.2 | 91.1 | 93.3 |
| 16 | ♀ | C | ARB | 9 | 355.2 | 353.7 | 356.6 | 170.6 | 169.5 | 171.7 | 94.9 | 94.1 | 95.6 |
| 17 | U | M | ARB | 5 | 266.3 | 264.4 | 268.2 | 120.6 | 119.2 | 122.1 | 68.4 | 67.4 | 69.4 |
| 18 | U | C | ARB | 4 | 292.3 | 290.1 | 294.4 | 132.4 | 130.7 | 134.0 | 71.5 | 70.4 | 72.6 |
| 19 | ♂ | C | ARB | 4 | 298.7 | 296.6 | 300.8 | 132.3 | 130.7 | 134.0 | 76.1 | 75.0 | 77.2 |
| 20 | U | M | ARB | 5 | 299.9 | 298.0 | 301.8 | 132.0 | 130.5 | 133.4 | 77.1 | 76.2 | 78.1 |
| 21 | U | C | ARB | 5 | 329.8 | 327.9 | 331.7 | 143.4 | 142.0 | 144.9 | 83.1 | 82.1 | 84.0 |
| 22 | ♂ | C | ARB | 4 | 292.9 | 290.8 | 295.0 | 130.5 | 128.9 | 132.1 | 78.1 | 77.0 | 79.2 |
| 23 | ♂ | C | ARB | 5 | 291.1 | 289.2 | 293.0 | 128.8 | 127.4 | 130.3 | 73.7 | 72.8 | 74.7 |
| 24 | ♂ | C | ARB | 3 | 300.2 | 297.8 | 302.6 | 134.3 | 132.4 | 136.1 | 75.4 | 74.2 | 76.7 |
| 25 | ♂ | C | ARB | 3 | 316.3 | 313.9 | 318.7 | 140.3 | 138.5 | 142.2 | 76.6 | 75.3 | 77.8 |
| 26 | ♀ | C | ARB | 5 | 363.3 | 361.5 | 365.2 | 171.8 | 170.3 | 173.2 | 93.4 | 92.4 | 94.3 |
| 27 | U | M | ARB | 5 | 348.8 | 347.0 | 350.7 | 163.6 | 162.1 | 165.0 | 89.1 | 88.1 | 90.0 |
| 28 | U | C | ARB | 7 | 208.4 | 206.9 | 210.0 | 90.2 | 88.9 | 91.4 | 51.6 | 50.8 | 52.4 |
| 29 | ♂ | C | ARB | 7 | 283.8 | 282.2 | 285.4 | 128.1 | 126.8 | 129.3 | 74.6 | 73.7 | 75.4 |
| 30 | ♀ | C | ARB | 9 | 355.1 | 353.7 | 356.5 | 169.4 | 168.4 | 170.5 | 94.4 | 93.7 | 95.1 |

Table C.1. Estimated true measurements of dimensions (DW, DL, and CW), including the lower and upper 95% confidence intervals (CIs), of each individual M. alfredi measured using drones. ♂, ♀, and U denote sexually mature males, sexually mature female, and unsexed individual, respectively. * denotes a large individual that was confirmed to be female based on observations from somersault feeding but recorded here as unsexed because we were not able to observe mating scars in dorsal view by the drone. C and M represent normal “chevron” and melanistic color patterns of the manta rays. WYG = Wayag lagoon, HOL = Hol Gam bay, ARB = Arborek reefs, FAM = Fam islands, YFK = Yefnabi Kecil reef. N repeats = the number of measurement repeats for each individual. Est. = Estimated true measurement, Lower = lower 95% CI, Upper = upper 95% CI.

| ID | Sex | Color morph | Site | N repeats | Disc Width (DW) | | | Disc Length (DL) | | | Cranial Width (CW) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Est. | Lower | Upper | Est. | Lower | Upper | Est. | Lower | Upper |
| 31 | ♂ | M | ARB | 5 | 276.8 | 274.9 | 278.7 | 125.5 | 124.1 | 127.0 | 72.8 | 71.8 | 73.8 |
| 32 | U | C | ARB | 7 | 352.0 | 350.4 | 353.6 | 165.9 | 164.6 | 167.1 | 92.3 | 91.4 | 93.1 |
| 33 | ♂ | C | ARB | 7 | 290.0 | 288.4 | 291.6 | 126.6 | 125.4 | 127.8 | 76.2 | 75.4 | 77.1 |
| 34 | ♂ | C | ARB | 5 | 285.3 | 283.4 | 287.2 | 128.9 | 127.5 | 130.4 | 73.2 | 72.2 | 74.2 |
| 35 | U | C | ARB | 5 | 313.9 | 312.0 | 315.8 | 141.2 | 139.7 | 142.6 | 83.0 | 82.0 | 83.9 |
| 36 | ♀ | C | ARB | 5 | 362.9 | 361.0 | 364.7 | 172.0 | 170.5 | 173.4 | 96.9 | 95.9 | 97.8 |
| 37 | ♂ | C | ARB | 5 | 281.6 | 279.7 | 283.5 | 135.2 | 133.7 | 136.7 | 79.0 | 78.0 | 79.9 |
| 38 | U | M | ARB | 10 | 307.5 | 306.2 | 308.8 | 140.3 | 139.3 | 141.4 | 80.7 | 80.0 | 81.4 |
| 39 | U | M | HOL | 5 | 254.3 | 252.4 | 256.2 | 108.2 | 106.7 | 109.6 | 61.7 | 60.7 | 62.6 |
| 40 | ♂ | M | ARB | 5 | 278.0 | 276.1 | 279.9 | 126.3 | 124.8 | 127.7 | 72.1 | 71.1 | 73.1 |
| 41 | U | C | ARB | 4 | 268.0 | 265.9 | 270.1 | 125.0 | 123.4 | 126.6 | 71.8 | 70.8 | 72.9 |
| 42 | ♀ | C | ARB | 5 | 323.5 | 321.6 | 325.4 | 147.3 | 145.9 | 148.8 | 82.9 | 81.9 | 83.9 |
| 43 | U | C | ARB | 5 | 318.5 | 316.6 | 320.4 | 140.8 | 139.3 | 142.3 | 81.8 | 80.9 | 82.8 |
| 44 | ♂ | C | ARB | 5 | 288.1 | 286.2 | 289.9 | 131.3 | 129.8 | 132.7 | 72.6 | 71.6 | 73.6 |
| 45 | ♂ | C | ARB | 4 | 284.0 | 281.8 | 286.1 | 123.3 | 121.7 | 124.9 | 72.6 | 71.5 | 73.6 |
| 46 | U | C | FAM | 7 | 266.8 | 265.2 | 268.4 | 115.2 | 114.0 | 116.4 | 66.9 | 66.1 | 67.7 |
| 47 | ♂ | C | ARB | 5 | 283.4 | 281.6 | 285.3 | 129.8 | 128.4 | 131.3 | 75.4 | 74.4 | 76.3 |
| 48 | U | C | ARB | 3 | 212.4 | 209.9 | 214.8 | 88.0 | 86.1 | 89.9 | 49.4 | 48.2 | 50.7 |
| 49 | ♂ | M | ARB | 5 | 282.9 | 281.0 | 284.8 | 123.3 | 121.9 | 124.8 | 70.2 | 69.2 | 71.1 |
| 50 | ♂ | M | ARB | 5 | 297.6 | 295.7 | 299.5 | 137.1 | 135.7 | 138.6 | 75.0 | 74.1 | 76.0 |
| 51 | U | C | FAM | 10 | 360.9 | 359.6 | 362.2 | 167.2 | 166.2 | 168.3 | 96.5 | 95.8 | 97.2 |
| 52 | ♂ | M | ARB | 5 | 283.1 | 281.2 | 285.0 | 132.2 | 130.7 | 133.6 | 73.0 | 72.0 | 74.0 |
| 53 | ♂ | C | FAM | 5 | 290.3 | 288.4 | 292.1 | 127.6 | 126.1 | 129.0 | 76.1 | 75.1 | 77.0 |
| 54 | U | M | ARB | 7 | 339.2 | 337.6 | 340.8 | 163.5 | 162.3 | 164.7 | 86.6 | 85.8 | 87.4 |
| 55 | ♂ | C | ARB | 5 | 274.8 | 272.9 | 276.7 | 129.1 | 127.6 | 130.6 | 71.2 | 70.2 | 72.1 |
| 56 | ♂ | C | ARB | 6 | 281.5 | 279.8 | 283.2 | 128.0 | 126.7 | 129.4 | 74.5 | 73.6 | 75.3 |
| 57 | U | C | WYG | 4 | 218.1 | 216.0 | 220.3 | 103.3 | 101.7 | 105.0 | 59.2 | 58.1 | 60.3 |
| 58 | U | M | YFK | 5 | 243.2 | 241.3 | 245.1 | 107.3 | 105.8 | 108.7 | 61.3 | 60.3 | 62.2 |
| 59 | U | M | YFK | 5 | 206.8 | 204.9 | 208.6 | 94.2 | 92.7 | 95.6 | 54.2 | 53.2 | 55.1 |
| 60 | U | M | YFK | 10 | 225.0 | 223.6 | 226.3 | 99.6 | 98.5 | 100.6 | 54.1 | 53.4 | 54.8 |

Table C.1. Estimated true measurements of dimensions (DW, DL, and CW), including the lower and upper 95% confidence intervals (CIs), of each individual M. alfredi measured using drones. ♂, ♀, and U denote sexually mature males, sexually mature female, and unsexed individual, respectively. * denotes a large individual that was confirmed to be female based on observations from somersault feeding but recorded here as unsexed because we were not able to observe mating scars in dorsal view by the drone. C and M represent normal "chevron" and melanistic color patterns of the manta rays. WYG = Wayag lagoon, HOL = Hol Gam bay, ARB = Arborek reefs, FAM = Fam islands, YFK = Yefnabi Kecil reef. N repeats = the number of measurement repeats for each individual. Est. = Estimated true measurement, Lower = lower 95% CI, Upper = upper 95% CI.

| ID | Sex | Color morph | Site | N repeats | Disc Width (DW) | | | Disc Length (DL) | | | Cranial Width (CW) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Est. | Lower | Upper | Est. | Lower | Upper | Est. | Lower | Upper |
| 61 | U | C | YFK | 10 | 218.9 | 217.6 | 220.3 | 94.8 | 93.8 | 95.8 | 52.4 | 51.7 | 53.1 |
| 62 | U | C | YFK | 10 | 227.7 | 226.4 | 229.0 | 102.0 | 100.9 | 103.0 | 57.9 | 57.2 | 58.6 |
| 63 | U | C | YFK | 9 | 230.2 | 228.8 | 231.6 | 100.7 | 99.6 | 101.8 | 58.9 | 58.2 | 59.6 |
| 64 | U | M | YFK | 10 | 220.5 | 219.2 | 221.9 | 95.8 | 94.7 | 96.8 | 57.5 | 56.8 | 58.2 |
| 65 | U | C | YFK | 6 | 269.5 | 267.8 | 271.2 | 117.7 | 116.4 | 119.1 | 70.1 | 69.2 | 71.0 |
| 66 | U | C | YFK | 8 | 225.1 | 223.6 | 226.6 | 96.4 | 95.2 | 97.6 | 59.0 | 58.2 | 59.8 |
| 67 | U | C | FAM | 7 | 231.2 | 229.6 | 232.8 | 101.8 | 100.6 | 103.1 | 59.8 | 58.9 | 60.6 |
| 68 | U | M | YFK | 4 | 242.5 | 240.4 | 244.6 | 107.3 | 105.7 | 109.0 | 61.1 | 60.0 | 62.2 |
| 69 | U | C | FAM | 10 | 227.5 | 226.2 | 228.9 | 97.9 | 96.9 | 98.9 | 57.9 | 57.2 | 58.6 |
| 70 | U | C | FAM | 6 | 225.0 | 223.3 | 226.7 | 99.6 | 98.2 | 100.9 | 59.7 | 58.9 | 60.6 |
| 71 | U | M | FAM | 3 | 242.9 | 240.5 | 245.4 | 109.4 | 107.5 | 111.2 | 61.0 | 59.8 | 62.3 |
| 72 | U | C | YFK | 5 | 231.2 | 229.3 | 233.1 | 94.9 | 93.4 | 96.3 | 58.4 | 57.4 | 59.4 |
| 73 | ♂ | C | YFK | 8 | 304.9 | 303.4 | 306.4 | 139.4 | 138.2 | 140.6 | 80.7 | 79.9 | 81.5 |
| 74 | ♂ | C | FAM | 8 | 293.7 | 292.3 | 295.2 | 135.9 | 134.7 | 137.1 | 76.0 | 75.3 | 76.8 |
| 75 | ♀ | C | FAM | 9 | 371.8 | 370.4 | 373.2 | 178.6 | 177.5 | 179.7 | 100.4 | 99.7 | 101.2 |
| 76 | ♂ | C | ARB | 8 | 298.1 | 296.6 | 299.5 | 135.8 | 134.7 | 137.0 | 77.9 | 77.1 | 78.7 |
| 77 | ♂ | C | ARB | 7 | 293.2 | 291.7 | 294.8 | 137.8 | 136.5 | 139.0 | 78.6 | 77.7 | 79.4 |
| 78 | ♂ | C | FAM | 8 | 291.3 | 289.8 | 292.8 | 131.6 | 130.4 | 132.8 | 75.9 | 75.2 | 76.7 |
| 79 | ♂ | C | FAM | 8 | 286.1 | 284.6 | 287.6 | 132.3 | 131.2 | 133.5 | 75.9 | 75.1 | 76.6 |
| 80 | U | M | YFK | 8 | 208.7 | 207.2 | 210.2 | 95.2 | 94.1 | 96.4 | 54.2 | 53.5 | 55.0 |
| 81 | U | M | YFK | 7 | 243.4 | 241.8 | 244.9 | 108.9 | 107.7 | 110.1 | 59.4 | 58.5 | 60.2 |
| 82 | U | M | HOL | 5 | 247.6 | 245.7 | 249.5 | 105.1 | 103.6 | 106.5 | 66.5 | 65.5 | 67.4 |
| 83 | U | C | HOL | 6 | 253.2 | 251.4 | 254.9 | 114.0 | 112.6 | 115.3 | 66.6 | 65.7 | 67.5 |
| 84 | U | C | HOL | 5 | 248.9 | 247.0 | 250.8 | 112.3 | 110.9 | 113.8 | 66.7 | 65.7 | 67.7 |
| 85 | U | C | HOL | 4 | 319.1 | 317.0 | 321.2 | 144.6 | 143.0 | 146.2 | 84.6 | 83.6 | 85.7 |
| 86 | U* | M | ARB | 3 | 375.6 | 373.2 | 378.0 | 171.9 | 170.1 | 173.8 | 97.5 | 96.3 | 98.8 |

# Appendix D

Table D.1. Sighting and resighting records of juvenile *M. alfredi* within the Wayag lagoon from 2013 to 2021.

| No. | Manta ID | First sighting date | Second sighting date | Third sighting date | Sighting span (days) |
|---|---|---|---|---|---|
| 1 | RA-MA-0525 | 14 Feb 2018 | 17 Nov 2019 | - | 641 |
| 2 | RA-MA-0750 | 01 Dec 2018 | 16 May 2019 | 19 Oct 2019 | 322 |
| 3 | RA-MA-0838 | 19 Feb 2019 | 18 May 2019 | - | 88 |
| 4 | RA-MA-1322 | 16 May 2013 | 24 Feb 2015 | - | 649 |
| 5 | RA-MA-1454 | 11 Jan 2020 | 12 Jan 2020 | 12 May 2021 | 487 |
| 6 | RA-MA-1456 | 11 Jan 2020 | 11 May 2021 | 12 May 2021 | 487 |
| 7 | RA-MA-1458 | 12 Jan 2020 | 13 Jan 2020 | - | 1 |
| 8 | RA-MA-1459 | 12 Jan 2020 | 12 May 2021 | - | 486 |
| 9 | RA-MA-1503 | 11 May 2021 | 24 May 2021 | 25 May 2021 | 14 |

Table D.2. Young-of-the-year and juvenile *M. alfredi* sighted within the Wayag lagoon from 2013 to 2021, including their sex, color, and estimated disc width (DW) in cm. *measured using drones

| No | Manta ID | Sex | Color | Estimated DW (cm) |
|---|---|---|---|---|
| 1 | RA-MA-0298 | Male | Chevron | 180 |
| 2 | RA-MA-0300 | Female | Chevron | 170 |
| 3 | RA-MA-0304 | Male | Chevron | 150 |
| 4 | RA-MA-0305 | Female | Chevron | 240 |
| 5 | RA-MA-0328 | Male | Chevron | 180 |
| 6 | RA-MA-0333 | Female | Chevron | 230 |
| 7 | RA-MA-0336 | Female | Chevron | 190 |
| 8 | RA-MA-0346 | Male | Chevron | 200 |
| 9 | RA-MA-0347 | Male | Chevron | 220 |
| 10 | RA-MA-0525 | Male | Chevron | 190 |
| 11 | RA-MA-0750 | Female | Chevron | 190 |
| 12 | RA-MA-0838 | Male | Chevron | 190 |
| 13 | RA-MA-1044 | Female | Chevron | 230 |
| 14 | RA-MA-1292 | Unknown | Melanistic | 210 |
| 15 | RA-MA-1293 | Female | Chevron | 210 |
| 16 | RA-MA-1320 | Male | Chevron | 210 |
| 17 | RA-MA-1321 | Female | Chevron | 210 |
| 18 | RA-MA-1322 | Male | Melanistic | 190 |
| 19 | RA-MA-1323 | Female | Chevron | 210 |
| 20 | RA-MA-1324 | Male | Chevron | 210 |
| 21 | RA-MA-1454 | Male | Melanistic | 190 |
| 22 | RA-MA-1455 | Unknown | Melanistic | 210 |
| 23 | RA-MA-1456 | Unknown | Melanistic | 180 |
| 24 | RA-MA-1457 | Unknown | Chevron | 210 |
| 25 | RA-MA-1458 | Unknown | Melanistic | 210 |
| 26 | RA-MA-1459 | Female | Melanistic | 180 |
| 27 | RA-MA-1460 | Unknown | Chevron | 220 |
| 28 | RA-MA-1502 | Unknown | Melanistic | 180 |
| 29 | RA-MA-1503 | Female | Chevron | 200 |
| 30 | RA-MA-1504 | Female | Melanistic | 180 |
| 31 | RA-MA-1505 | Unknown | Chevron | 190 |
| 32 | RA-MA-1506 | Unknown | Chevron | 210 |
| 33 | RA-MA-1507 | Unknown | Melanistic | 190 |
| 34 | RA-MA-1508 | Unknown | Chevron | 210 |
| 35 | Unidentified* | Unknown | Chevron | 218 |
| 36 | Unidentified* | Unknown | Chevron | 219 |

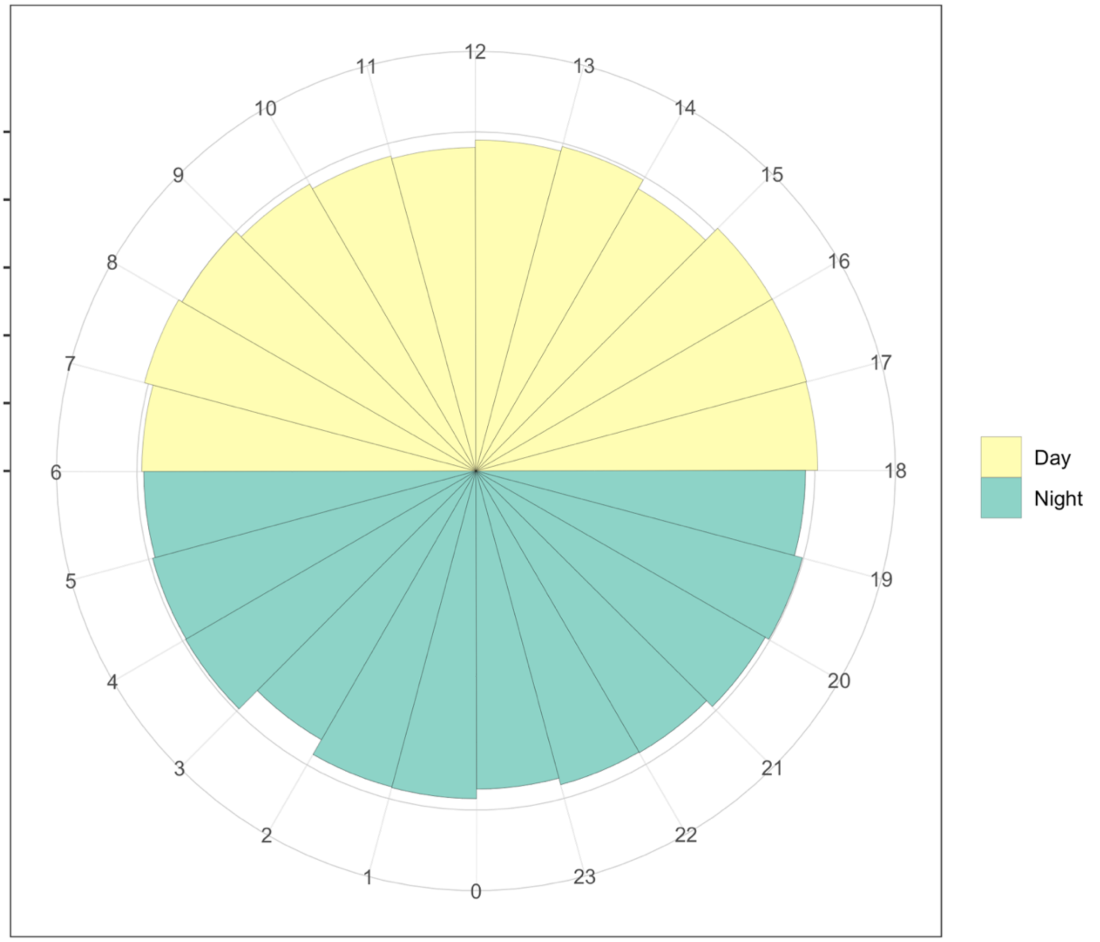

Figure D.1. Hourly total number of acoustic detections from sentinel tag recorded by the receiver at Main Lagoon Entrance from 15–29 May 2021.

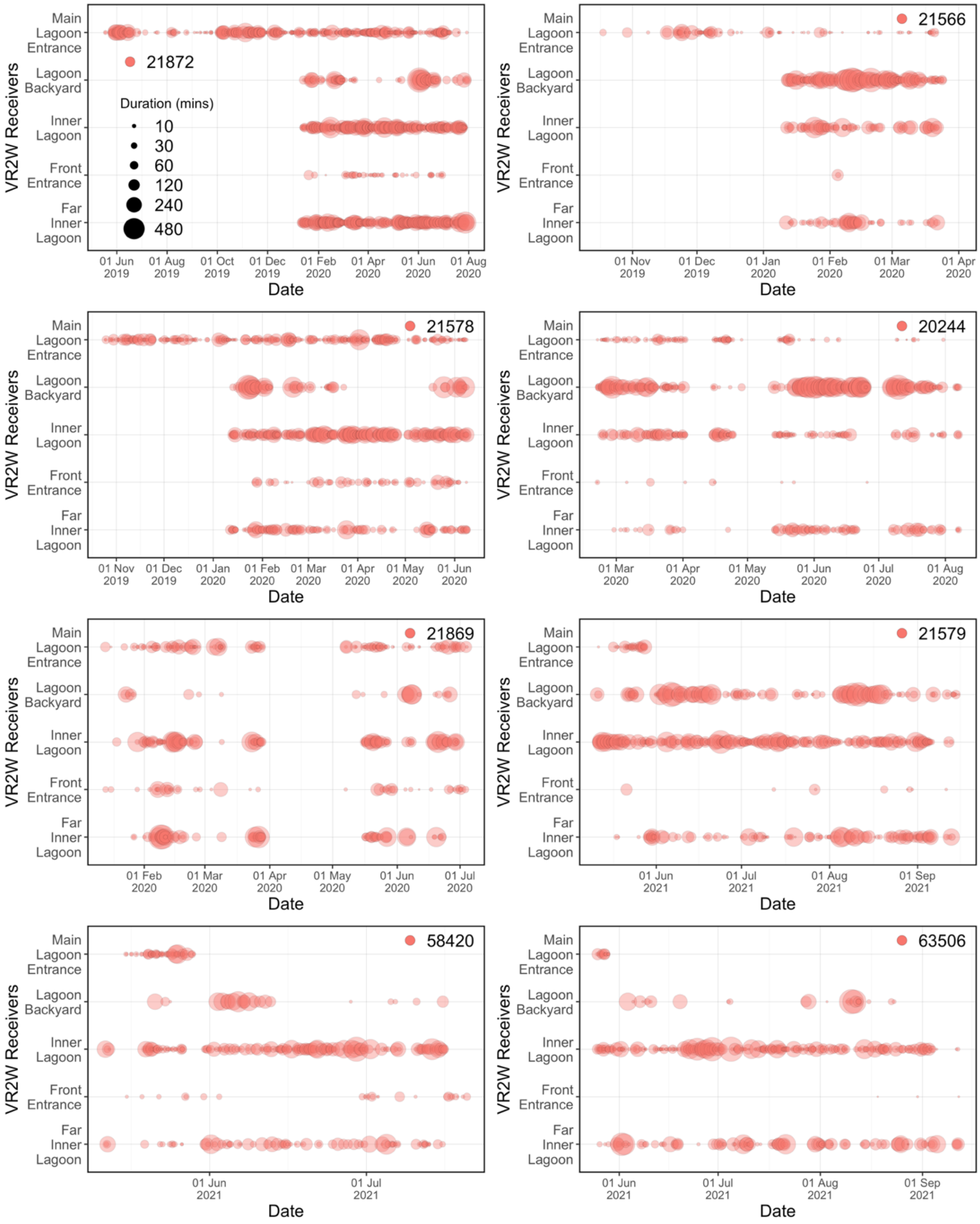

Figure D.2. The duration of visitations (mins) recorded by each receiver for each individual that was detected by five receivers in Wayag lagoon.

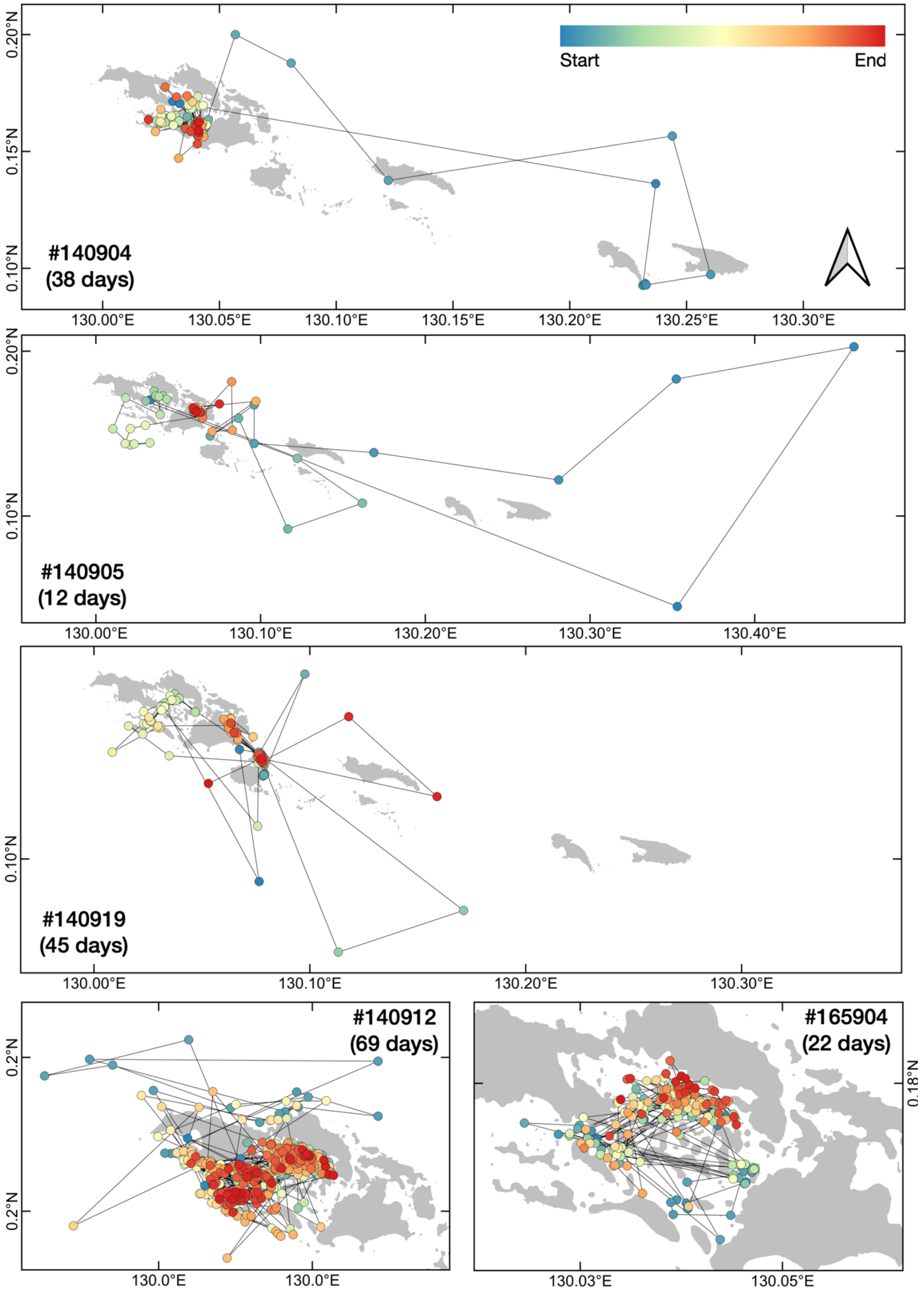

Figure D.3. The raw movement tracks (lines) over time derived from GPS locations (dots) recorded by the satellite transmitters on the five tagged juvenile *M. alfredi*.

# Appendix E

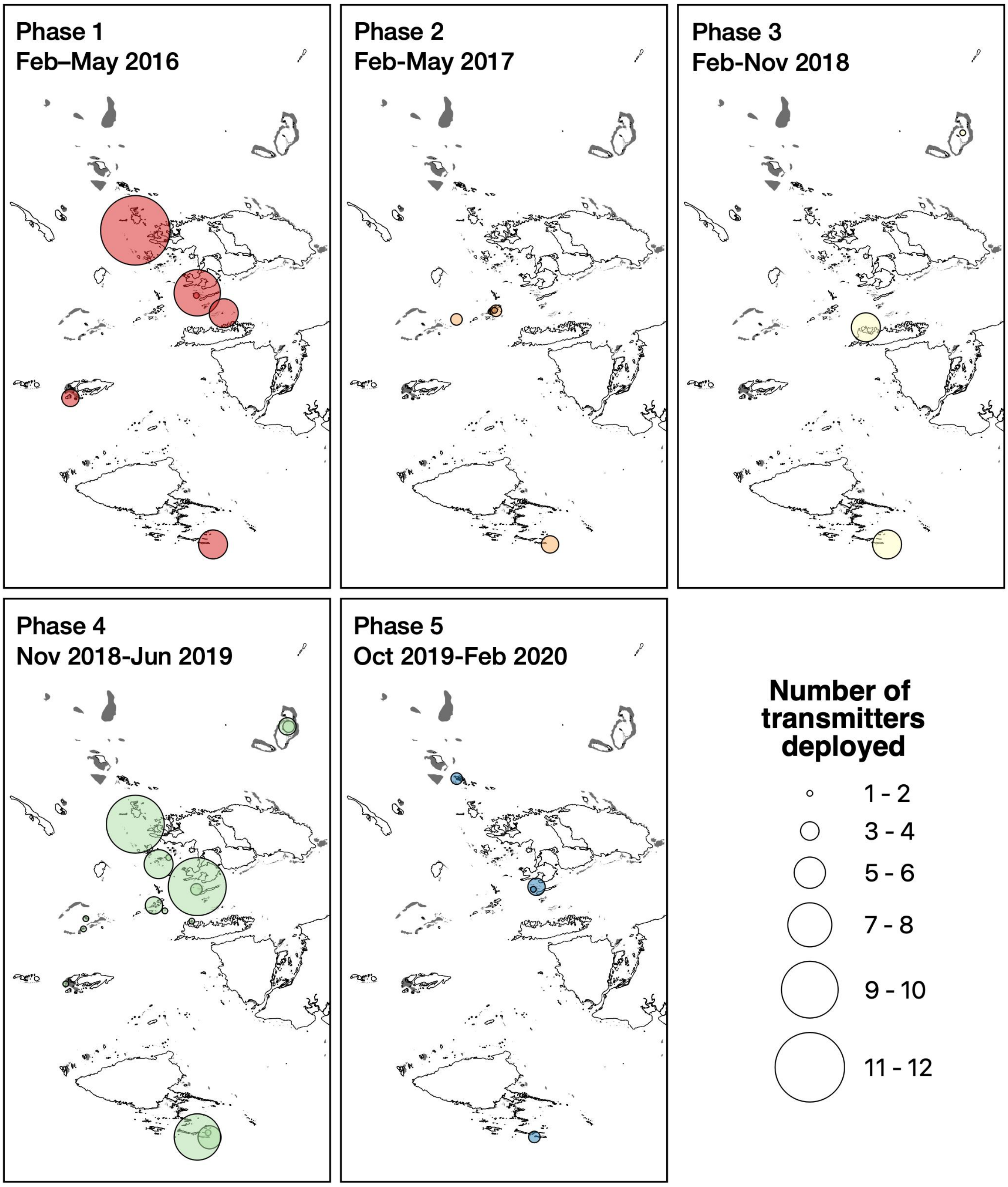

Figure E.1. The number of acoustic transmitters deployed on *M. alfredi* across five tagging phases in Raja Ampat between February 2016 and February 2020. The size of the bubbles represents the number of transmitters deployed.

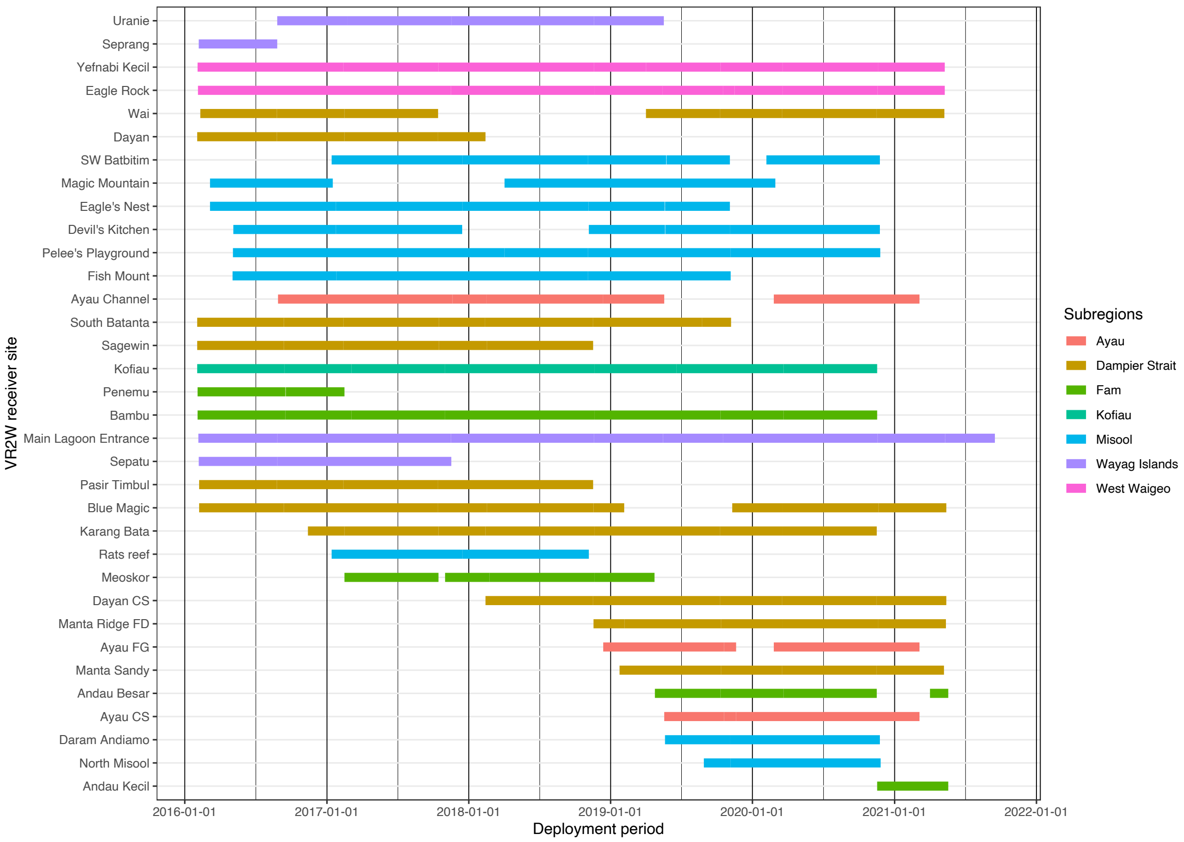

Figure E.2. VR2W acoustic receiver deployment period between February 2016 and September 2021 in Raja Ampat.

Figure E.3. The detection patterns of 94 tagged *M. alfredi* recorded by receivers deployed across the Raja Ampat archipelago between February 2016 and September 2021. The size of the bubbles represents the duration of each detection event at a given site by a tagged *M. alfredi*.

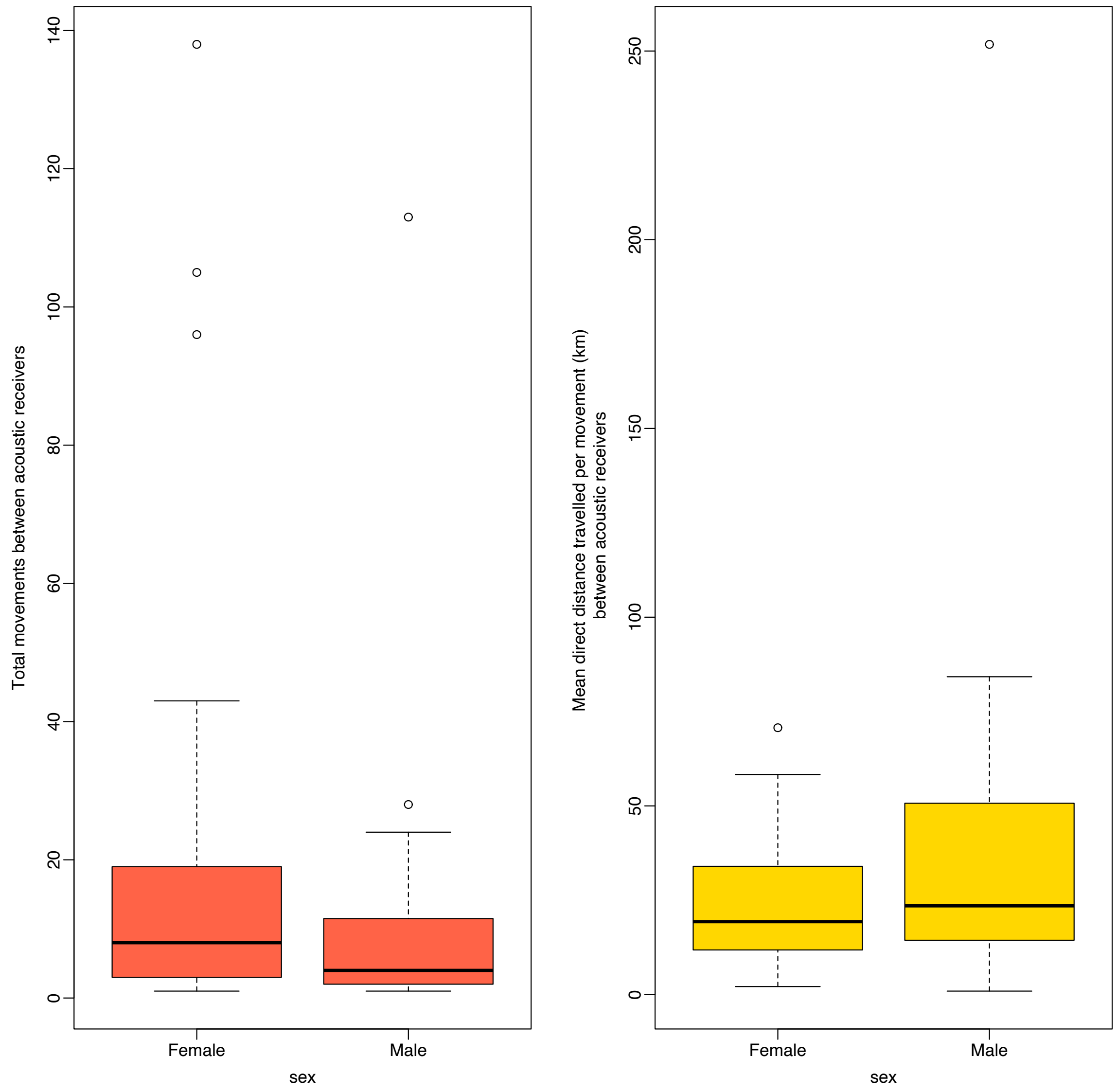

Figure E.4. Boxplots for the total *M. alfredi* movements recorded between two sites based on sex (left panel) and for the mean direct distance travelled by tagged *M. alfredi* per movement (right panel).

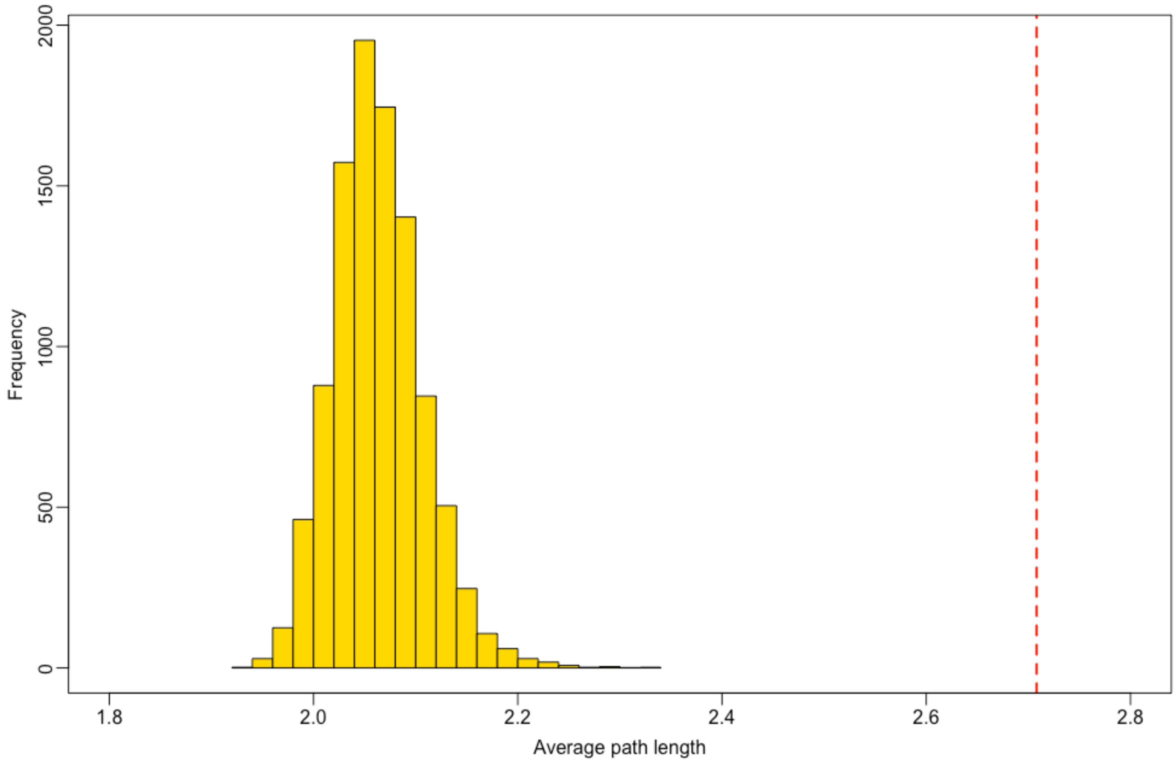

Figure E.5. Distribution of average path length values obtained from permuted random networks (10,000 iterations) compared to the observed value of average path length (red vertical dashed line) of the receiver-based network in Raja Ampat.

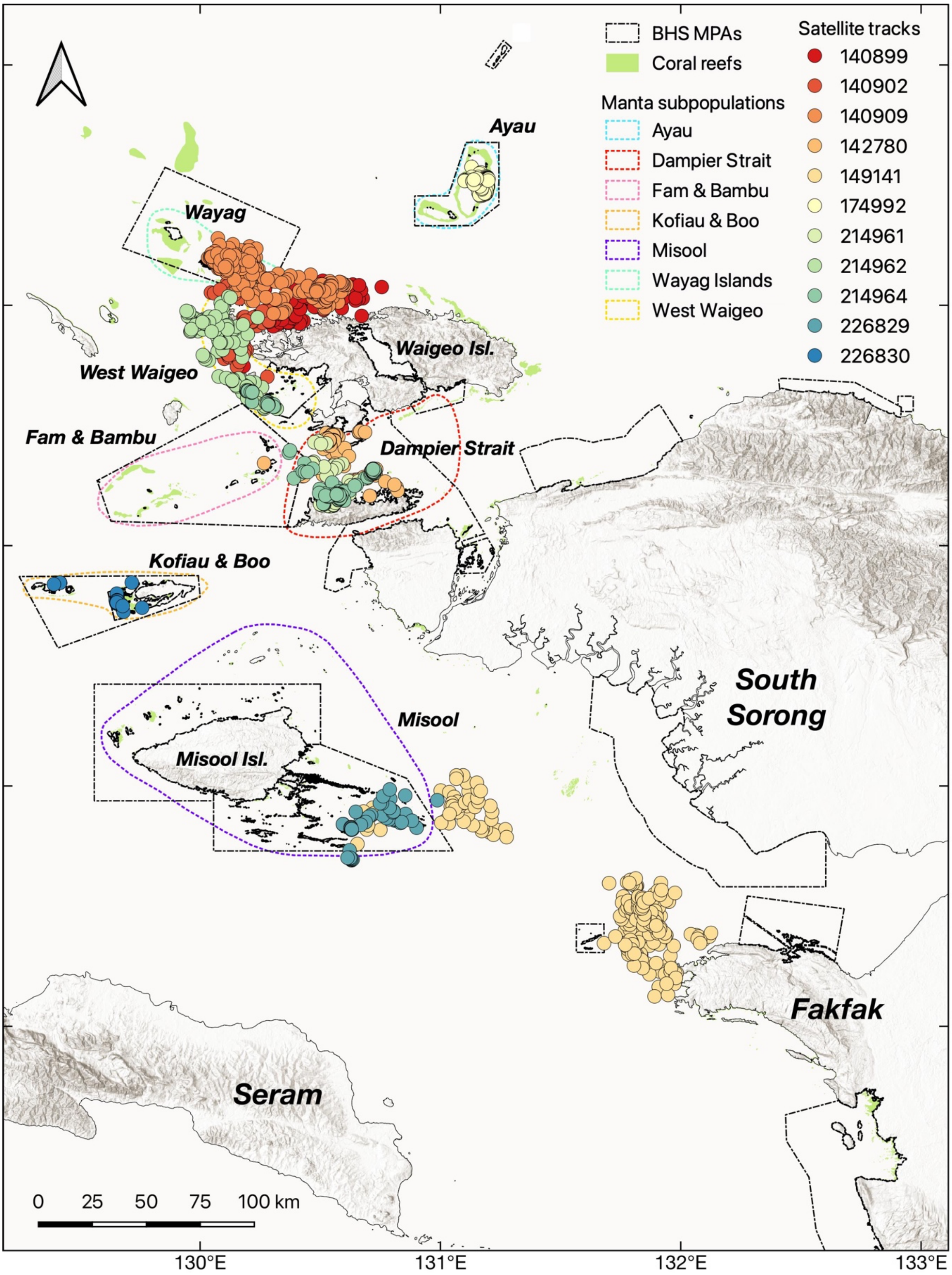

Figure E.6. GPS positions of 11 *M. alfredi* satellite-tracked in Raja Ampat in 2014–2021 overlaid on the boundaries of the Raja Ampat MPA network (dashed lined polygons) and regions occupied by the hypothesised subpopulations (regions denoted by coloured dotted lines). The colours of each GPS positions correspond to each of the *M. alfredi* tagged.

Table E.1. The number of acoustic transmitters deployed on *M. alfredi* in February 2016–February 2020, detected by any acoustic receiver, and detected by two or more acoustic receivers in each tagging region in Raja Ampat.

| Tagging region | Number of acoustic transmitter deployed | Number of acoustic transmitter detected by receiver stations | Number of acoustic transmitters detected by two or more receiver stations |
|---|---|---|---|
| Ayau | 6 | 5 | 4 |
| Dampier Strait | 36 | 31 | 29 |
| Fam & Bambu | 13 | 6 | 3 |
| Kofiau & Boo | 4 | 3 | 1 |
| Misool | 28 | 25 | 24 |
| Wayag | 2 | 1 | 1 |
| West Waigeo | 28 | 23 | 10 |
| **TOTAL** | 117 | 94 | 72 |

Table E.2. The total number of acoustically tagged *M. alfredi* movements (N movements) between receiver stations from February 2016 to September 2021 in Raja Ampat archipelago. The movements occurred from Receiver Station 1 (in Region 1) to Receiver Station 2 (in Region 2).

| No. | Receiver Station 1 | Receiver Station 2 | Region 1 | Region 2 | N movements |
|---|---|---|---|---|---|
| 1 | Magic Mountain | Eagle's Nest | Misool | Misool | 93 |
| 2 | Eagle's Nest | Magic Mountain | Misool | Misool | 73 |
| 3 | Eagle's Nest | Southwest Batbitim | Misool | Misool | 65 |
| 4 | Ayau Besar Feeding Ground | Ayau Besar Cleaning Station | Ayau | Ayau | 60 |
| 5 | Ayau Besar Cleaning Station | Ayau Besar Feeding Ground | Ayau | Ayau | 59 |
| 6 | Southwest Batbitim | Eagle's Nest | Misool | Misool | 57 |
| 7 | Manta Ridge | Manta Sandy | Dampier Strait | Dampier Strait | 38 |
| 8 | Manta Sandy | Manta Ridge | Dampier Strait | Dampier Strait | 37 |
| 9 | Southwest Batbitim | Magic Mountain | Misool | Misool | 32 |
| 10 | Devil's Kitchen | Magic Mountain | Misool | Misool | 28 |
| 11 | Magic Mountain | Devil's Kitchen | Misool | Misool | 25 |
| 12 | Magic Mountain | Southwest Batbitim | Misool | Misool | 23 |
| 13 | Southwest Batbitim | Fish Mount | Misool | Misool | 18 |
| 14 | Devil's Kitchen | Daram Andiamo | Misool | Misool | 17 |
| 15 | Eagle's Nest | Devil's Kitchen | Misool | Misool | 16 |
| 16 | Daram Andiamo | Devil's Kitchen | Misool | Misool | 15 |
| 17 | Eagle's Nest | Fish Mount | Misool | Misool | 15 |
| 18 | Dayan Cleaning Station | Manta Ridge | Dampier Strait | Dampier Strait | 14 |
| 19 | Devil's Kitchen | Eagle's Nest | Misool | Misool | 14 |
| 20 | Manta Sandy | Dayan Cleaning Station | Dampier Strait | Dampier Strait | 12 |
| 21 | Manta Ridge | Wai | Dampier Strait | Dampier Strait | 12 |
| 22 | Fish Mount | Devil's Kitchen | Misool | Misool | 11 |
| 23 | Fish Mount | Magic Mountain | Misool | Misool | 11 |
| 24 | Fish Mount | Southwest Batbitim | Misool | Misool | 11 |
| 25 | Rats Reef | Southwest Batbitim | Misool | Misool | 11 |
| 26 | Yefnabi Kecil | Eagle Rock | West Waigeo | West Waigeo | 11 |
| 27 | Manta Ridge | Dayan Cleaning Station | Dampier Strait | Dampier Strait | 10 |
| 28 | Dayan Cleaning Station | Wai | Dampier Strait | Dampier Strait | 10 |
| 29 | Magic Mountain | Daram Andiamo | Misool | Misool | 10 |
| 30 | Southwest Batbitim | Devil's Kitchen | Misool | Misool | 10 |
| 31 | Fish Mount | Eagle's Nest | Misool | Misool | 10 |
| 32 | Ayau Besar Feeding Ground | Ayau Besar Lagoon Entrance | Ayau | Ayau | 8 |
| 33 | Wai | Dayan Cleaning Station | Dampier Strait | Dampier Strait | 8 |
| 34 | Wai | Manta Ridge | Dampier Strait | Dampier Strait | 8 |
| 35 | Daram Andiamo | Magic Mountain | Misool | Misool | 8 |
| 36 | Eagle's Nest | Rats Reef | Misool | Misool | 8 |

| No. | Receiver Station 1 | Receiver Station 2 | Region 1 | Region 2 | N movements |
|---|---|---|---|---|---|
| 37 | Devil's Kitchen | Southwest Batbitim | Misool | Misool | 8 |
| 38 | Eagle Rock | Yefnabi Kecil | West Waigeo | West Waigeo | 8 |
| 39 | Eagle Rock | Wai | West Waigeo | Dampier Strait | 8 |
| 40 | Ayau Besar Lagoon Entrance | Ayau Besar Feeding Ground | Ayau | Ayau | 7 |
| 41 | Wai | Manta Sandy | Dampier Strait | Dampier Strait | 7 |
| 42 | Dayan Cleaning Station | Manta Sandy | Dampier Strait | Dampier Strait | 6 |
| 43 | Devil's Kitchen | Fish Mount | Misool | Misool | 6 |
| 44 | Magic Mountain | Fish Mount | Misool | Misool | 6 |
| 45 | Wai | Dayan | Dampier Strait | Dampier Strait | 5 |
| 46 | Wai | Pasir Timbul | Dampier Strait | Dampier Strait | 5 |
| 47 | Dayan | Wai | Dampier Strait | Dampier Strait | 5 |
| 48 | Pasir Timbul | Wai | Dampier Strait | Dampier Strait | 5 |
| 49 | Southwest Batbitim | Rats Reef | Misool | Misool | 5 |
| 50 | Ayau Besar Lagoon Entrance | Ayau Besar Cleaning Station | Ayau | Ayau | 4 |
| 51 | Ayau Besar Cleaning Station | Ayau Besar Lagoon Entrance | Ayau | Ayau | 4 |
| 52 | Manta Ridge | Yefnabi Kecil | Dampier Strait | West Waigeo | 4 |
| 53 | Pasir Timbul | Yefnabi Kecil | Dampier Strait | West Waigeo | 4 |
| 54 | Wai | Yefnabi Kecil | Dampier Strait | West Waigeo | 4 |
| 55 | Wai | Blue Magic | Dampier Strait | Dampier Strait | 4 |
| 56 | Blue Magic | Wai | Dampier Strait | Dampier Strait | 4 |
| 57 | Manta Sandy | Wai | Dampier Strait | Dampier Strait | 4 |
| 58 | Rats Reef | Eagle's Nest | Misool | Misool | 4 |
| 59 | Yefnabi Kecil | Pasir Timbul | West Waigeo | Dampier Strait | 4 |
| 60 | Wai | Eagle Rock | Dampier Strait | West Waigeo | 3 |
| 61 | Pasir Timbul | Dayan | Dampier Strait | Dampier Strait | 3 |
| 62 | Dayan Cleaning Station | Karang Bata | Dampier Strait | Dampier Strait | 3 |
| 63 | Blue Magic | Pasir Timbul | Dampier Strait | Dampier Strait | 3 |
| 64 | Manta Ridge | Pasir Timbul | Dampier Strait | Dampier Strait | 3 |
| 65 | Penemu | Yefnabi Kecil | Fam & Bambu | West Waigeo | 3 |
| 66 | Eagle's Nest | Daram Andiamo | Misool | Misool | 3 |
| 67 | Eagle Rock | Manta Sandy | West Waigeo | Dampier Strait | 3 |
| 68 | Eagle Rock | Pasir Timbul | West Waigeo | Dampier Strait | 3 |
| 69 | Manta Ridge | Eagle Rock | Dampier Strait | West Waigeo | 2 |
| 70 | Manta Sandy | Eagle Rock | Dampier Strait | West Waigeo | 2 |
| 71 | Pasir Timbul | Eagle Rock | Dampier Strait | West Waigeo | 2 |
| 72 | Dayan | Yefnabi Kecil | Dampier Strait | West Waigeo | 2 |
| 73 | Manta Ridge | Blue Magic | Dampier Strait | Dampier Strait | 2 |
| 74 | Pasir Timbul | Blue Magic | Dampier Strait | Dampier Strait | 2 |
| 75 | Karang Bata | Dayan Cleaning Station | Dampier Strait | Dampier Strait | 2 |
| 76 | Manta Ridge | Karang Bata | Dampier Strait | Dampier Strait | 2 |

| No. | Receiver Station 1 | Receiver Station 2 | Region 1 | Region 2 | N movements |
|---|---|---|---|---|---|
| 77 | Karang Bata | Manta Sandy | Dampier Strait | Dampier Strait | 2 |
| 78 | Bambu | Andau Besar | Fam & Bambu | Fam & Bambu | 2 |
| 79 | Southwest Batbitim | Pelee's Playground | Misool | Misool | 2 |
| 80 | Fish Mount | Rats Reef | Misool | Misool | 2 |
| 81 | Magic Mountain | Eagle Rock | Misool | West Waigeo | 2 |
| 82 | Eagle Rock | Dayan Cleaning Station | West Waigeo | Dampier Strait | 2 |
| 83 | Yefnabi Kecil | Wai | West Waigeo | Dampier Strait | 2 |
| 84 | Dayan | Eagle Rock | Dampier Strait | West Waigeo | 1 |
| 85 | Dayan Cleaning Station | Eagle Rock | Dampier Strait | West Waigeo | 1 |
| 86 | Dayan Cleaning Station | Yefnabi Kecil | Dampier Strait | West Waigeo | 1 |
| 87 | Dayan | Devil's Kitchen | Dampier Strait | Misool | 1 |
| 88 | Wai | Kofiau | Dampier Strait | Kofiau & Boo | 1 |
| 89 | Dayan Cleaning Station | Bambu | Dampier Strait | Fam & Bambu | 1 |
| 90 | Karang Bata | Bambu | Dampier Strait | Fam & Bambu | 1 |
| 91 | Dayan Cleaning Station | Meoskor | Dampier Strait | Fam & Bambu | 1 |
| 92 | Manta Sandy | Meoskor | Dampier Strait | Fam & Bambu | 1 |
| 93 | Dayan | Penemu | Dampier Strait | Fam & Bambu | 1 |
| 94 | Wai | Ayau Besar Lagoon Entrance | Dampier Strait | Ayau | 1 |
| 95 | South Batanta | Dayan | Dampier Strait | Dampier Strait | 1 |
| 96 | Blue Magic | Manta Ridge | Dampier Strait | Dampier Strait | 1 |
| 97 | Wai | Sagawin | Dampier Strait | Dampier Strait | 1 |
| 98 | Sagawin | South Batanta | Dampier Strait | Dampier Strait | 1 |
| 99 | Bambu | Dayan Cleaning Station | Fam & Bambu | Dampier Strait | 1 |
| 100 | Meoskor | Dayan Cleaning Station | Fam & Bambu | Dampier Strait | 1 |
| 101 | Meoskor | Manta Ridge | Fam & Bambu | Dampier Strait | 1 |
| 102 | Meoskor | Southwest Batbitim | Fam & Bambu | Misool | 1 |
| 103 | Bambu | Eagle Rock | Fam & Bambu | West Waigeo | 1 |
| 104 | Andau Besar | Yefnabi Kecil | Fam & Bambu | West Waigeo | 1 |
| 105 | Andau Kecil | Andau Besar | Fam & Bambu | Fam & Bambu | 1 |
| 106 | Andau Besar | Bambu | Fam & Bambu | Fam & Bambu | 1 |
| 107 | Andau Besar | Meoskor | Fam & Bambu | Fam & Bambu | 1 |
| 108 | Kofiau | Wai | Kofiau & Boo | Dampier Strait | 1 |
| 109 | Magic Mountain | Sepatu | Misool | Wayag | 1 |
| 110 | Southwest Batbitim | Daram Andiamo | Misool | Misool | 1 |
| 111 | Daram Andiamo | Eagle's Nest | Misool | Misool | 1 |
| 112 | Pelee's Playground | Eagle's Nest | Misool | Misool | 1 |
| 113 | Rats Reef | Fish Mount | Misool | Misool | 1 |
| 114 | Pelee's Playground | Magic Mountain | Misool | Misool | 1 |
| 115 | Eagle's Nest | Pelee's Playground | Misool | Misool | 1 |

| No. | Receiver Station 1 | Receiver Station 2 | Region 1 | Region 2 | N movements |
|---|---|---|---|---|---|
| 116 | Magic Mountain | Rats Reef | Misool | Misool | 1 |
| 117 | Daram Andiamo | Southwest Batbitim | Misool | Misool | 1 |
| 118 | Pelee's Playground | Southwest Batbitim | Misool | Misool | 1 |
| 119 | Sepatu | Eagle Rock | Wayag | West Waigeo | 1 |
| 120 | Seprang | Eagle Rock | Wayag | West Waigeo | 1 |
| 121 | Main Lagoon Entrance | Yefnabi Kecil | Wayag | West Waigeo | 1 |
| 122 | Yefnabi Kecil | Ayau Besar Cleaning Station | West Waigeo | Ayau | 1 |
| 123 | Yefnabi Kecil | Dayan | West Waigeo | Dampier Strait | 1 |
| 124 | Yefnabi Kecil | Manta Ridge | West Waigeo | Dampier Strait | 1 |
| 125 | Yefnabi Kecil | Manta Sandy | West Waigeo | Dampier Strait | 1 |
| 126 | Yefnabi Kecil | Andau Kecil | West Waigeo | Fam & Bambu | 1 |
| 127 | Eagle Rock | Penemu | West Waigeo | Fam & Bambu | 1 |
| 128 | Yefnabi Kecil | Penemu | West Waigeo | Fam & Bambu | 1 |
| 129 | Eagle Rock | Magic Mountain | West Waigeo | Misool | 1 |
| 130 | Eagle Rock | Sepatu | West Waigeo | Wayag | 1 |
| 131 | Eagle Rock | Seprang | West Waigeo | Wayag | 1 |

Table E.3. Centrality measures (node level metrics) of *M. alfredi* movement network in Raja Ampat between February 2016 and September 2021. The order of the receiver stations is based on the degree centrality (from largest to smallest).

| No | Receiver stations | Subpopulations | In-degree | Out-degree | Degree centrality | Betweenness | Closeness | Eigenvector |
|---|---|---|---|---|---|---|---|---|
| 1 | Wai | Dampier Strait | 9 | 11 | 20 | 0.179 | 0.018 | 1.000 |
| 2 | Eagle Rock | West Waigeo | 11 | 9 | 20 | 0.324 | 0.020 | 0.967 |
| 3 | Yefnabi Kecil | West Waigeo | 9 | 9 | 18 | 0.167 | 0.018 | 0.861 |
| 4 | Dayan Cleaning Station | Dampier Strait | 7 | 8 | 15 | 0.086 | 0.016 | 0.799 |
| 5 | Magic Mountain | Misool | 7 | 8 | 15 | 0.215 | 0.015 | 0.476 |
| 6 | Southwest Batbitim | Misool | 8 | 7 | 15 | 0.049 | 0.013 | 0.372 |
| 7 | Manta Ridge | Dampier Strait | 6 | 8 | 14 | 0.031 | 0.016 | 0.817 |
| 8 | Eagle's Nest | Misool | 7 | 7 | 14 | 0.019 | 0.012 | 0.350 |
| 9 | Manta Sandy | Dampier Strait | 6 | 5 | 11 | 0.028 | 0.016 | 0.719 |
| 10 | Devil's Kitchen | Misool | 6 | 5 | 11 | 0.033 | 0.014 | 0.333 |
| 11 | Pasir Timbul | Dampier Strait | 5 | 5 | 10 | 0.017 | 0.016 | 0.651 |
| 12 | Fish Mount | Misool | 5 | 5 | 10 | 0.009 | 0.011 | 0.290 |
| 13 | Dayan | Dampier Strait | 4 | 5 | 9 | 0.079 | 0.017 | 0.500 |
| 14 | Daram Andiamo | Misool | 4 | 4 | 8 | 0.000 | 0.011 | 0.255 |
| 15 | Rats Reef | Misool | 4 | 3 | 7 | 0.000 | 0.011 | 0.209 |
| 16 | Blue Magic | Dampier Strait | 3 | 3 | 6 | 0.001 | 0.012 | 0.412 |
| 17 | Bambu | Fam & Bambu | 3 | 3 | 6 | 0.018 | 0.014 | 0.263 |
| 18 | Meoskor | Fam & Bambu | 3 | 3 | 6 | 0.034 | 0.014 | 0.305 |
| 19 | Ayau Besar Cleaning Station | Ayau | 3 | 2 | 5 | 0.017 | 0.012 | 0.095 |
| 20 | Ayau Besar Lagoon Entrance | Ayau | 3 | 2 | 5 | 0.015 | 0.012 | 0.105 |

| No | Receiver stations | Subpopulations | In-degree | Out-degree | Degree centrality | Betweenness | Closeness | Eigenvector |
|---|---|---|---|---|---|---|---|---|
| 21 | Karang Bata | Dampier Strait | 2 | 3 | 5 | 0.002 | 0.012 | 0.284 |
| 22 | Andau Besar | Fam & Bambu | 2 | 3 | 5 | 0.030 | 0.014 | 0.148 |
| 23 | Pelee's Playground | Misool | 2 | 3 | 5 | 0.000 | 0.011 | 0.160 |
| 24 | Ayau Besar Feeding Ground | Ayau | 2 | 2 | 4 | 0.000 | 0.009 | 0.033 |
| 25 | Penemu | Fam & Bambu | 3 | 1 | 4 | 0.000 | 0.014 | 0.266 |
| 26 | Sepatu | Wayag | 2 | 1 | 3 | 0.000 | 0.014 | 0.201 |
| 27 | Sagawin | Dampier Strait | 1 | 1 | 2 | 0.026 | 0.012 | 0.088 |
| 28 | South Batanta | Dampier Strait | 1 | 1 | 2 | 0.027 | 0.011 | 0.049 |
| 29 | Andau Kecil | Fam & Bambu | 1 | 1 | 2 | 0.014 | 0.012 | 0.084 |
| 30 | Kofiau | Kofiau & Boo | 1 | 1 | 2 | 0.000 | 0.011 | 0.167 |
| 31 | Seprang | Wayag | 1 | 1 | 2 | 0.000 | 0.012 | 0.161 |
| 32 | Main Lagoon Entrance | Wayag | 0 | 1 | 1 | 0.000 | 0.012 | 0.072 |
| 33 | North Misool | Misool | 0 | 0 | 0 | 0.000 | NA | 0.000 |
| 34 | Uranie | Wayag | 0 | 0 | 0 | 0.000 | NA | 0.000 |

# References

Abrahms, B., Aikens, E. O., Armstrong, J. B., Deacy, W. W., Kauffman, M. J., & Merkle, J. A. (2021). Emerging Perspectives on Resource Tracking and Animal Movement Ecology. *Trends in Ecology & Evolution*, *36*(4), 308-320. https://doi.org/10.1016/j.tree.2020.10.018

Acebes, J. M. V., & Tull, M. (2016). The history and characteristics of the mobulid ray fishery in the Bohol Sea, Philippines. *PLOS ONE*, *11*(8), e0161444. https://doi.org/10.1371/journal.pone.0161444

Agostini, V. N., Grantham, H. S., Wilson, J., Mangubhai, S., Rotinsulu, C., Hidayat, N., . . . Possingham, H. P. (2012). *Achieving Fisheries and Conservation Objectives within Marine Protected Areas: Zoning the Raja Ampat Network*.

Akçakaya, H. R., Mills, G., & Doncaster, C. P. (2007). The role of metapopulations in conservation. In D. Macdonald & K. Service (Eds.), *Key Topics in Conservation Biology* (pp. 64-84). Blackwell Publishing. http://eprints.soton.ac.uk/id/eprint/38499

Alerstam, T., Hedenström, A., & Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos*, *103*(2), 247-260. https://doi.org/10.1034/j.1600-0706.2003.12559.x

Alldredge, A. L., & King, J. M. (1977). Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. *Marine Biology*, *41*(4), 317-333. https://doi.org/10.1007/BF00389098

Allen, A. M., & Singh, N. J. (2016). Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, *3*, 155. https://doi.org/10.3389/fevo.2015.00155

Allen, G. R., & Erdmann, M. V. *Reef Fishes of the East Indies*. Apple App Store. https://geo.itunes.apple.com/us/app/reef-fishes-east-indies-vol./id705188551?mt=8

Allen, G. R., & Erdmann, M. V. (2009). Reef Fishes of the Bird’s Head Peninsula, West Papua, Indonesia. *Check List*, *5*(3), 587-628. https://doi.org/10.15560/5.3.587

Anderson, R. C., Adam, M. S., & Goes, J. I. (2011a). From monsoons to mantas: seasonal distribution of *Manta alfredi* in the Maldives. *Fisheries Oceanography*, *20*(2), 104-113. https://doi.org/10.1111/j.1365-2419.2011.00571.x

Anderson, R. C., Adam, M. S., Kitchen-Wheeler, A.-M., & Stevens, G. (2011b). Extent and economic value of manta ray watching in Maldives. *Tourism in Marine Environments*, *7*(1), 15-27. https://doi.org/10.3727/154427310x12826772784793

Andrzejaczek, S., Chapple, T. K., Curnick, D. J., Carlisle, A. B., Castleton, M., Jacoby, D. M., . . . Block, B. A. (2020). Individual variation in residency and regional movements of reef manta rays *Mobula alfredi* in a large marine protected area. *Marine Ecology Progress Series*, *639*, 137-153. https://doi.org/10.3389/fmars.2020.00558

Andrzejaczek, S., Lucas, T. C. D., Goodman, M. C., Hussey, N. E., Armstrong, A. J., Carlisle, A., . . . Curnick, D. J. (2022). Diving into the vertical dimension of elasmobranch movement ecology. *Science Advances*, *8*(33), eabo1754. https://doi.org/10.1126/sciadv.abo1754

Arauz, R., Chávez, E. J., Hoyos-Padilla, E. M., & Marshall, A. D. (2019). First record of the reef manta ray, *Mobula alfredi*, from the eastern Pacific. *Marine Biodiversity Records*, *12*(1), 1-6. https://doi.org/10.1186/s41200-019-0162-9

Armstrong, A. J., Armstrong, A. O., Bennett, M. B., McGregor, F., Abrantes, K. G., Barnett, A., . . . Dudgeon, C. L. (2020a). The geographic distribution of reef and oceanic manta rays (*Mobula alfredi* and *Mobula birostris*) in Australian coastal waters. *Journal of Fish Biology*, *96*(3), 835-840. https://doi.org/10.1111/jfb.14256

Armstrong, A. J., Armstrong, A. O., McGregor, F., Richardson, A. J., Bennett, M. B., Townsend, K. A., . . . Dudgeon, C. L. (2020b). Satellite tagging and photographic identification reveal connectivity between two UNESCO World Heritage Areas for reef manta rays. *Frontiers in Marine Science*, *7*, 725. https://doi.org/10.3389/fmars.2020.00725

Armstrong, A. O., Armstrong, A. J., Bennett, M. B., Richardson, A. J., Townsend, K. A., & Dudgeon, C. L. (2019). Photographic identification and citizen science combine to reveal long distance movements of individual reef manta rays *Mobula alfredi* along Australia’s east coast. *Marine Biodiversity Records*, *12*(1), 14. https://doi.org/10.1186/s41200-019-0173-6

Armstrong, A. O., Armstrong, A. J., Bennett, M. B., Richardson, A. J., Townsend, K. A., Everett, J. D., . . . Dudgeon, C. L. (2021a). Mutualism promotes site selection in a large marine planktivore. *Ecology and Evolution*, *11*, 5606–5623. https://doi.org/10.1002/ece3.7464

Armstrong, A. O., Armstrong, A. J., Jaine, F. R., Couturier, L. I., Fiora, K., Uribe-Palomino, J., . . . Richardson, A. J. (2016). Prey density threshold and tidal influence on reef manta ray foraging at an aggregation site on the Great Barrier Reef. *PLOS ONE*, *11*(5), e0153393. https://doi.org/10.1371/journal.pone.0153393

Armstrong, A. O., Stevens, G. M., Townsend, K. A., Murray, A., Bennett, M. B., Armstrong, A. J., . . . Richardson, A. J. (2021b). Reef manta rays forage on tidally driven, high density zooplankton patches in Hanifaru Bay, Maldives. *PeerJ*, *9*, e11992. https://doi.org/10.7717/peerj.11992

Asaad, I., Lundquist, C. J., Erdmann, M. V., Van Hooidonk, R., & Costello, M. J. (2018). Designating spatial priorities for marine biodiversity conservation in the Coral Triangle. *Frontiers in Marine Science*, *5*(400). https://doi.org/10.3389/fmars.2018.00400

Atkinson, S. N., Laidre, K. L., Arnold, T. W., Stapleton, S., Regehr, E. V., Born, E. W., . . . Paetkau, D. (2021). A novel mark-recapture-recovery survey using genetic sampling for polar bears Ursus maritimus in Baffin Bay. *Endangered Species Research*, *46*, 105-120. https://www.int-res.com/abstracts/esr/v46/p105-120/

Avgar, T., Street, G., & Fryxell, J. M. (2014). On the adaptive benefits of mammal migration. *Canadian journal of zoology*, *92*(6), 481-490. https://doi.org/10.1139/cjz-2013-0076

Axworthy, J. B., Smith, J. M., Wing, M. S., & Quinn, T. P. (2019). Sex biased individual variation in movement patterns of a highly mobile, near-shore marine planktivore, the reef manta ray *Mobula alfredi*. *Journal of Fish Biology*, *95*(6), 1399-1406. https://doi.org/10.1111/jfb.14148

Babin, A., Fitzpatrick, L., Linnansaari, T., & Curry, R. A. (2019). Detection range of acoustic receivers in a large hydropower reservoir. *Fishes*, *4*(4), 60. https://doi.org/10.3390/fishes4040060

Barnes, R. H. (2005). Indigenous use and management of whales and other marine resources in East Flores and Lembata, Indonesia. *Senri Ethnological Studies*, *67*, 77-85. https://doi.org/10.15021/00002662

Bass, A. (1978). Problems in studies of sharks in the Southwest Indian Ocean. In E. Hodgson & R. Mathewson (Eds.), *Sensory biology of sharks, skates and rays* (pp. 545-594). Office of Naval Research, Department of the Navy.

Beale, C. S., Stewart, J. D., Setyawan, E., Sianipar, A. B., & Erdmann, M. V. (2019). Population dynamics of oceanic manta rays (*Mobula birostris*) in the Raja Ampat Archipelago, West Papua, Indonesia, and the impacts of the El Niño–Southern Oscillation on their movement ecology. *Diversity and Distributions*, *25*, 1472-1487. https://doi.org/10.1111/ddi.12962

Beissinger, S. R., & Westphal, M. I. (1998). On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, *62*, 821-841. https://doi.org/10.2307/3802534

Berger-Wolf, T. Y., Rubenstein, D. I., Stewart, C. V., Holmberg, J. A., Parham, J., Menon, S., . . . Joppa, L. (2017). Wildbook: Crowdsourcing, computer vision, and data science for conservation. *arXiv preprint arXiv:1710.08880*.

Bierlich, K., Schick, R., Hewitt, J., Dale, J., Goldbogen, J., Friedlaender, A., & Johnston, D. (2021). Bayesian approach for predicting photogrammetric uncertainty in morphometric measurements derived from drones. *Marine Ecology Progress Series*, *673*, 193-210. https://doi.org/10.3354/meps13814

Block, B. A., Holbrook, C. M., Simmons, S. E., Holland, K. N., Ault, J. S., Costa, D. P., . . . Kochevar, R. E. (2016). Toward a national animal telemetry network for aquatic observations in the United States. *Animal Biotelemetry*, *4*(1), 6. https://doi.org/10.1186/s40317-015-0092-1

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., . . . Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, *475*(7354), 86-90. https://doi.org/10.1038/nature10082

Blount, D., Gero, S., Van Oast, J., Parham, J., Kingen, C., Scheiner, B., . . . Levenson, J. J. (2022). Flukebook: an open-source AI platform for cetacean photo identification. *Mammalian Biology*, *102*(3), 1005-1023. https://doi.org/10.1007/s42991-021-00221-3

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127-135. https://doi.org/10.1016/j.tree.2008.10.008

Boys, R. M., Oliveira, C., Pérez-Jorge, S., Prieto, R., Steiner, L., & Silva, M. A. (2019). Multi-state open robust design applied to opportunistic data reveals dynamics of wide-ranging taxa: the sperm whale case. *Ecosphere*, *10*(3), e02610. https://doi.org/10.1002/ecs2.2610

Bräger, S., Chong, A., Dawson, S., Slooten, E., & Würsig, B. (1999). A combined stereo-photogrammetry and underwater-video system to study group composition of dolphins. *Helgoland marine research*, *53*(2), 122-128. https://doi.org/10.1007/s101520050015

Branstetter, S. (1990). Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In H. L. Pratt Jr., S. H. Gruber, & T. Taninchi (Eds.), *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries* (pp. 17–28). VIMS Books and Book Chapters.

Braun, C. D., Skomal, G. B., Thorrold, S. R., & Berumen, M. L. (2014). Diving behavior of the reef manta ray links coral reefs with adjacent deep pelagic habitats. *PLOS ONE*, *9*(2), e88170. https://doi.org/10.1371/journal.pone.0088170

Braun, C. D., Skomal, G. B., Thorrold, S. R., & Berumen, M. L. (2015). Movements of the reef manta ray (*Manta alfredi*) in the Red Sea using satellite and acoustic telemetry. *Marine Biology*, *162*(12), 2351-2362. https://doi.org/10.1007/s00227-015-2760-3

Brewster, L. R., Ibrahim, A. K., DeGroot, B. C., Ostendorf, T. J., Zhuang, H., Chérubin, L. M., & Ajemian, M. J. (2021). Classifying Goliath Grouper (*Epinephelus itajara*) Behaviors from a Novel, Multi-Sensor Tag. *Sensors*, *21*(19), 6392. https://doi.org/10.3390/s21196392

Brodie, S., Lédée, E. J. I., Heupel, M. R., Babcock, R. C., Campbell, H. A., Gledhill, D. C., . . . Harcourt, R. G. (2018). Continental-scale animal tracking reveals functional movement classes across marine taxa. *Scientific Reports*, *8*(1), 3717. https://doi.org/10.1038/s41598-018-21988-5

Brown, D., Christian, W., & Hanson, R. M. (2021). *Tracker: video analysis and modeling tool (Version 6.0.1)*. In https://physlets.org/tracker/

Brown, D. D., Kays, R., Wikelski, M., Wilson, R., & Klimley, A. P. (2013). Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry*, *1*(1), 20. https://doi.org/10.1186/2050-3385-1-20

Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J. L. (2005). Distance Sampling. In *Encyclopedia of Biostatistics*. https://doi.org/10.1002/0470011815.b2a16019

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press. http://www.ruwpa.st-and.ac.uk/distance.book/intro.html

Budd, A. M., Schils, T., Cooper, M. K., Lyons, M. B., Mills, M. S., Deinhart, M. E., . . . Strugnell, J. M. (2023). Monitoring threatened species with environmental DNA and open ecological data: Local distribution and habitat preferences of scalloped hammerhead sharks (Sphyrna lewini). *Biological Conservation*, *278*, 109881. https://doi.org/10.1016/j.biocon.2022.109881

Burnett, J. D., Lemos, L., Barlow, D., Wing, M. G., Chandler, T., & Torres, L. G. (2019). Estimating morphometric attributes of baleen whales with photogrammetry from small UASs: a case study with blue and gray whales. *Marine Mammal Science*, *35*(1), 108-139. https://doi.org/10.1111/mms.12527

Butcher, P. A., Colefax, A. P., Gorkin, R. A., Kajiura, S. M., López, N. A., Mourier, J., . . . Raoult, V. (2021). The drone revolution of shark science: A review. *Drones*, *5*(1), 8. https://doi.org/10.3390/drones5010008

Calabrese, J. M., Fleming, C. H., & Gurarie, E. (2016). ctmm: An R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution*, *7*(9), 1124-1132. https://doi.org/10.1111/2041-210X.12559

Campana, S. E. (2005). Chapter 12 - Otolith Elemental Composition as a Natural Marker of Fish Stocks. In S. X. Cadrin, K. D. Friedland, & J. R. Waldman (Eds.), *Stock Identification Methods* (pp. 227-245). Academic Press. https://doi.org/10.1016/B978-012154351-8/50013-7

Campbell, H. A., Watts, M. E., Dwyer, R. G., & Franklin, C. E. (2012). V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. *Marine and Freshwater Research*, *63*(9), 815-820. https://doi.org/10.1071/MF12194

Carpenter, M., Cullain, N., Venables, S. K., Tibiriçá, Y., Griffiths, C., & Marshall, A. D. (2022). Evidence of Závora Bay as a critical site for reef manta rays, *Mobula alfredi*, in southern Mozambique. *Journal of Fish Biology*(n/a). https://doi.org/10.1111/jfb.15132

Carpentier, A. S., Berthe, C., Ender, I., Jaine, F. R., Mourier, J., Stevens, G., . . . Clua, E. (2019). Preliminary insights into the population characteristics and distribution of reef (*Mobula alfredi*) and oceanic (*M. birostris*) manta rays in French Polynesia. *Coral Reefs*, *38*(6), 1197-1210. https://doi.org/10.1007/s00338-019-01854-0

Carreño, A., & Lloret, J. (2021). Environmental impacts of increasing leisure boating activity in Mediterranean coastal waters. *Ocean & Coastal Management*, *209*, 105693. https://doi.org/10.1016/j.ocecoaman.2021.105693

Carroll, E., Childerhouse, S., Fewster, R., Patenaude, N., Steel, D., Dunshea, G., . . . Baker, C. S. (2013). Accounting for female reproductive cycles in a superpopulation capture–recapture framework. *Ecological Applications*, *23*(7), 1677-1690. https://doi.org/10.1890/12-1657.1

Casey, J. G., & Natanson, L. J. (1992). Revised Estimates of Age and Growth of the Sandbar Shark (Carcharhinus plumbeus) from the Western North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*(7), 1474-1477. https://doi.org/10.1139/f92-162

Casselberry, G. A., Danylchuk, A. J., Finn, J. T., DeAngelis, B. M., Jordaan, A., Pollock, C. G., . . . Skomal, G. B. (2020). Network analysis reveals multispecies spatial associations in the shark community of a Caribbean marine protected area. *Marine Ecology Progress Series*, *633*, 105-126. https://doi.org/10.3354/meps13158

Cerchio, S., Yamada, T. K., & Brownell, R. L. (2019). Global distribution of Omura's Whales (*Balaenoptera omurai*) and assessment of range-wide threats. *Frontiers in Marine Science*, *6*(67). https://doi.org/10.3389/fmars.2019.00067

Chapman, B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L. A., & Brönmark, C. (2012). Partial migration in fishes: definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, *81*(2), 479-499. https://doi.org/10.1111/j.1095-8649.2012.03349.x

Chapman, D. D., Feldheim, K. A., Papastamatiou, Y. P., & Hueter, R. E. (2015). There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. *Annual Review of Marine Science*, *7*(1), 547-570. https://doi.org/10.1146/annurev-marine-010814-015730

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., & Pauly, D. (2009). Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, *10*(3), 235-251. https://doi.org/10.1111/j.1467-2979.2008.00315.x

Childs, J. N. (2001). *The occurence, habitat use, and behaviour of sharks and rays associating with topographic highs in the Northwestern Gulf of Mexico* [Master's Thesis, Texas A&M University]. Texas, USA.

Christiansen, F., Dujon, A. M., Sprogis, K. R., Arnould, J. P., & Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere*, *7*(10), e01468. https://doi.org/10.1002/ecs2.1468

Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., & Bejder, L. (2018). Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series*, *592*, 267-281. https://doi.org/10.3354/meps12522

CITES. (2013). Consideration of proposals for amendment of Appendices I and II. Sixteenth meeting of the Conference of the Parties, Bangkok (Thailand), 3–14 March 2013. In (Conference document CoP16 Prop. 46 (Rev.2) ed.). Geneva, Switzerland.

Clark, T. B. (2010). *Abundance, home range, and movement patterns of manta rays (Manta alfredi, M. birostris) in Hawai'i* [Dissertation, University of Hawai'i at Manoa]. Honolulu, USA.

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, *25*(10), 562-573. https://doi.org/10.1016/j.tree.2010.08.002

Collins, M., An, S.-I., Cai, W., Ganachaud, A., Guilyardi, E., Jin, F.-F., . . . Wittenberg, A. (2010). The impact of global warming on the tropical Pacific Ocean and El Niño. *Nature Geoscience*, *3*(6), 391-397. https://doi.org/10.1038/ngeo868

Cooch, E., & White, G. (2001). Goodness of fit testing…. In *Program MARK: A gentle introduction.* (pp. 1-36). http://www.phidot.org/software/mark/docs/book

Cortés, E. (2000). Life History Patterns and Correlations in Sharks. *Reviews in Fisheries Science*, *8*(4), 299-344. https://doi.org/10.1080/10408340308951115

Couturier, L. I., Rohner, C. A., Richardson, A. J., Marshall, A. D., Jaine, F. R., Bennett, M. B., . . . Nichols, P. D. (2013). Stable isotope and signature fatty acid analyses suggest reef manta rays feed on demersal zooplankton. *PLOS ONE*, *8*(10), e77152. https://doi.org/10.1371/journal.pone.0077152

Couturier, L. I. E., Dudgeon, C. L., Pollock, K. H., Jaine, F. R. A., Bennett, M. B., Townsend, K. A., . . . Richardson, A. J. (2014). Population dynamics of the reef manta ray *Manta alfredi* in eastern Australia. *Coral Reefs*, *33*(2), 329-342. https://doi.org/10.1007/s00338-014-1126-5

Couturier, L. I. E., Jaine, F. R. A., Townsend, K. A., Weeks, S. J., Richardson, A. J., & Bennett, M. B. (2011). Distribution, site affinity and regional movements of the manta ray, *Manta alfredi* (Krefft, 1868), along the east coast of Australia. *Marine and Freshwater Research*, *62*(6), 628-637. https://doi.org/10.1071/MF10148

Couturier, L. I. E., Marshall, A. D., Jaine, F. R. A., Kashiwagi, T., Pierce, S. J., Townsend, K. A., . . . Richardson, A. J. (2012). Biology, ecology and conservation of the Mobulidae. *Journal of Fish Biology*, *80*(5), 1075-1119. https://doi.org/10.1111/j.1095-8649.2012.03264.x

Couturier, L. I. E., Newman, P., Jaine, F. R. A., Bennett, M. B., Venables, W. N., Cagua, E. F., . . . Richardson, A. J. (2018). Variation in occupancy and habitat use of *Mobula alfredi* at a major aggregation site. *Marine Ecology Progress Series*, *599*, 125-145. https://doi.org/10.3354/meps12610

Croll, D. A., Dewar, H., Dulvy, N. K., Fernando, D., Francis, M. P., Galván-Magaña, F., . . . Mccauley, D. (2015). Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(3), 562-575. https://doi.org/10.1002/aqc.2591

Crowder, L., & Norse, E. (2008). Essential ecological insights for marine ecosystem-based management and marine spatial planning. *Marine Policy*, *32*(5), 772-778. https://doi.org/10.1016/j.marpol.2008.03.012

Crowder, L. B., & Figueira, W. F. (2006). CHAPTER 15 - Metapopulation Ecology and Marine Conservation. In J. P. Kritzer & P. F. Sale (Eds.), *Marine Metapopulations* (pp. 491-515). Academic Press. https://doi.org/10.1016/B978-012088781-1/50018-2

Croxall, J. P., Butchart, S. H. M., Lascelles, B. E. N., Stattersfield, A. J., Sullivan, B. E. N., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, *22*(1), 1-34. https://doi.org/10.1017/S0959270912000020

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal*, *Complex Systems*(5), 1695. https://igraph.org

Cusick, A. M., Gilmore, R., Bombosch, A., Mascioni, M., Almandoz, G. O., & Vernet, M. (2020). POLAR TOURISM AS AN EFFECTIVE RESEARCH TOOL: Citizen Science in the Western Antarctic Peninsula. *Oceanography*, *33*(1), 50-61. https://doi.org/10.5670/oceanog.2020.101

Davies, T. K., Stevens, G., Meekan, M. G., Struve, J., & Rowcliffe, J. M. (2012). Can citizen science monitor whale-shark aggregations? Investigating bias in mark–recapture modelling using identification photographs sourced from the public. *Wildlife Research*, *39*(8), 696-704. https://doi.org/10.1071/WR12092

Dawson, S. M., Bowman, M. H., Leunissen, E., & Sirguey, P. (2017). Inexpensive aerial photogrammetry for studies of whales and large marine animals. *Frontiers in Marine Science*, *4*, 366. https://doi.org/10.3389/fmars.2017.00366

Deakos, M. H. (2010). Paired-laser photogrammetry as a simple and accurate system for measuring the body size of free-ranging manta rays *Manta alfredi*. *Aquatic Biology*, *10*(1), 1-10. https://doi.org/10.3354/ab00258

Deakos, M. H. (2012). The reproductive ecology of resident manta rays (*Manta alfredi*) off Maui, Hawaii, with an emphasis on body size. *Environmental Biology of Fishes*, *94*(2), 443-456. https://doi.org/10.1007/s10641-011-9953-5

Deakos, M. H., Baker, J. D., & Bejder, L. (2011). Characteristics of a manta ray *Manta alfredi* population off Maui, Hawaii, and implications for management. *Marine Ecology Progress Series*, *429*, 245-260. https://doi.org/10.3354/MEPS09085

Delacy, C. R., Olsen, A., Howey, L. A., Chapman, D. D., Brooks, E. J., & Bond, M. E. (2017). Affordable and accurate stereo-video system for measuring dimensions underwater: a case study using oceanic whitetip sharks *Carcharhinus longimanus*. *Marine Ecology Progress Series*, *574*, 75-84. https://doi.org/10.3354/MEPS12190

Dewar, H. (2002). *Preliminary report: Manta harvest in Lamakera*.

Dewar, H., Mous, P., Domeier, M., Muljadi, A., Pet, J., & Whitty, J. (2008). Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. *Marine Biology*, *155*(2), 121-133. https://doi.org/10.1007/s00227-008-0988-x

Dharmadi, Fahmi, & Satria, F. (2015). Fisheries management and conservation of sharks in Indonesia. *African Journal of Marine Science*, *37*(2), 249-258. https://doi.org/10.2989/1814232X.2015.1045431

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., . . . Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525-537. https://doi.org/10.1016/j.biocon.2019.06.033

Dingle, H., & Drake, V. A. (2007). What Is Migration? *Bioscience*, *57*(2), 113-121. https://doi.org/10.1641/b570206

Distefano, E. (2005). *Human-Wildlife Conflict worldwide: collection of case studies, analysis of management strategies and good practices*. FAO.

Dudgeon, C. L., Noad, M. J., & Lanyon, J. M. (2008). Abundance and demography of a seasonal aggregation of zebra sharks *Stegostoma fasciatum*. *Marine Ecology Progress Series*, *368*, 269-281. https://doi.org/10.3354/meps07581

Dudley, N. (Ed.). (2008). *Guidelines for applying protected area management categories*. IUCN.

Dujon, A. M., Lindstrom, R. T., & Hays, G. C. (2014). The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods in Ecology and Evolution*, *5*(11), 1162-1169. https://doi.org/10.1111/2041-210X.12286

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., . . . Derrick, D. H. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology*, *31*, 4773–4787. https://doi.org/10.1016/j.cub.2021.08.062

Dulvy, N. K., Pardo, S. A., Simpfendorfer, C. A., & Carlson, J. K. (2014). Diagnosing the dangerous demography of manta rays using life history theory. *PeerJ*, *2*, e400. https://doi.org/10.7717/peerj.400

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., & Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, *45*(4), 1029-1039. https://doi.org/10.1111/j.1365-2664.2008.01488.x

Dulvy, N. K., Simpfendorfer, C. A., Davidson, L. N. K., Fordham, S. V., Bräutigam, A., Sant, G., & Welch, D. J. (2017). Challenges and priorities in shark and ray conservation. *Current Biology*, *27*(11), R565-R572. https://doi.org/10.1016/j.cub.2017.04.038

Durban, J. W., Moore, M. J., Chiang, G., Hickmott, L. S., Bocconcelli, A., Howes, G., . . . LeRoi, D. J. (2016). Photogrammetry of blue whales with an unmanned hexacopter. *Marine Mammal Science*, *32*(4), 1510-1515. https://doi.org/10.1111/mms.12328

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., . . . Berkhout, J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, *506*(7487), 216-220. https://doi.org/10.1038/nature13022

Elith, J., & Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual review of ecology, evolution, and systematics*, *40*(1), 677-697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Emmons, C. K., Hanson, M. B., & Lammers, M. O. (2021). Passive acoustic monitoring reveals spatiotemporal segregation of two fish-eating killer whale Orcinus orca populations in proposed critical habitat. *Endangered Species Research*, *44*, 253-261. https://doi.org/10.3354/esr01099

Encalada, S. E., Bjorndal, K. A., Bolten, A. B., Zurita, J. C., Schroeder, B., Possardt, E., . . . Bowen, B. W. (1998). Population structure of loggerhead turtle (*Caretta caretta*) nesting colonies in the Atlantic and Mediterranean as inferred from mitochondrial DNA control region sequences. *Marine Biology*, *130*(4), 567-575. https://doi.org/10.1007/s002270050278

Ender, A. I., Mangubhai, S., Wilson, J. R., & Muljadi, A. (2014). Cetaceans in the global centre of marine biodiversity. *Marine Biodiversity Records*, *7*, e18. https://doi.org/10.1017/S1755267214000207

Erdmann, M. V. (2011). Regional Profile: Indonesia. Bird's Head Seascape, 2001-2009. In L. Alonso, J. Deichmann, S. McKenna, P. Naskrecki, & S. Richards (Eds.), *Still counting…: Biodiversity Exploration for Conservation – the first 20 years of the Rapid Assessment Program* (pp. 272-276). Conservation International.

Erdmann, M. V. (2013, 20 September 2021). Newest 'walking' shark heralds brighter future for Indonesia's sharks and rays. http://blog.conservation.org/2013/08/newest-walking-shark-heralds-brighter-future-for-indonesias-sharks-and-rays/

Erdmann, M. V. (2014a). *Indonesia Gives Mantas A New 'Ray of Hope'*. Retrieved 20 September 2021 from https://birdsheadseascape.com/diving/indonesia-gives-mantas-a-new-ray-of-hope-by-mark-erdmann-ph-d/

Erdmann, M. V. (2014b). *New MMAF-CI-SEAA manta tagging program launched*. Retrieved 14 October 2021 from https://birdsheadseascape.com/conservation-science/new-mmaf-ci-seaa-manta-tagging-program-launched/

Espinoza, M., Heupel, M. R., Tobin, A. J., & Simpfendorfer, C. A. (2016). Evidence of Partial Migration in a Large Coastal Predator: Opportunistic Foraging and Reproduction as Key Drivers? *PLOS ONE*, *11*(2), e0147608. https://doi.org/10.1371/journal.pone.0147608

Eurostat. (2002). *Glossary of statistical terms: true value*. Retrieved 21 October 2021 from https://stats.oecd.org/glossary/detail.asp?ID=4557

Fernando, D., & Stewart, J. D. (2021). High bycatch rates of manta and devil rays in the "small-scale" artisanal fisheries of Sri Lanka. *PeerJ*, *9*, e11994. https://doi.org/10.7717/peerj.11994

Fleming, C., Sheldon, D., Fagan, W., Leimgruber, P., Mueller, T., Nandintsetseg, D., . . . Sianipar, A. (2018). Correcting for missing and irregular data in home-range estimation. *Ecological Applications*, *28*(4), 1003-1010. https://doi.org/10.1002/eap.1704

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2015). Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology*, *96*(5), 1182-1188. https://doi.org/10.1890/14-2010.1

Fontes, J., Baeyaert, J., Prieto, R., Graça, G., Buyle, F., & Afonso, P. (2018). New non-invasive methods for short-term electronic tagging of pelagic sharks and rays. *Marine Biology*, *165*(2), 34. https://doi.org/10.1007/s00227-018-3289-z

Fontes, J., Macena, B., Solleliet-Ferreira, S., Buyle, F., Magalhães, R., Bartolomeu, T., . . . Afonso, P. (2022). The advantages and challenges of non-invasive towed PILOT tags for free-ranging deep-diving megafauna. *Animal Biotelemetry*, *10*(1), 39. https://doi.org/10.1186/s40317-022-00310-1

Ford, A. T., Cooke, S. J., Goheen, J. R., & Young, T. P. (2017). Conserving megafauna or sacrificing biodiversity? *Bioscience*, *67*(3), 193-196. https://doi.org/10.1093/biosci/biw163

Francis, M. P. (2006). Morphometric minefields—towards a measurement standard for chondrichthyan fishes. *Environmental Biology of Fishes*, *77*(3-4), 407-421. https://doi.org/10.1007/s10641-006-9109-1

Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V., & Fitzpatrick, J. W. (2018). Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences*, *115*(47), 11982-11987. https://doi.org/10.1073/pnas.1804224115

Fretwell, P. T., Staniland, I. J., & Forcada, J. (2014). Whales from space: counting southern right whales by satellite. *PLOS ONE*, *9*(2), e88655. https://doi.org/10.1371/ journal.pone.0088655

Friess, C., Lowerre-Barbieri, S. K., Poulakis, G. R., Hammerschlag, N., Gardiner, J. M., Kroetz, A. M., . . . Griffin, L. P. (2021). Regional-scale variability in the movement ecology of marine fishes revealed by an integrative acoustic tracking network. *Marine Ecology Progress Series*, *663*, 157-177. https://doi.org/10.3354/meps13637

Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., . . . Richardson, A. J. (2009). Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology & Evolution*, *24*(7), 360-369. https://doi.org/10.1016/j.tree.2009.01.011

Gaudioso, V., Sanz-Ablanedo, E., Lomillos, J. M., Alonso, M. E., Javares-Morillo, L., & Rodríguez, P. (2014). “Photozoometer”: A new photogrammetric system for obtaining morphometric measurements of elusive animals. *Livestock Science*, *165*, 147-156. https://doi.org/10.1016/j.livsci.2014.03.028

Gavrilchuk, K., Lesage, V., Fortune, S. M. E., Trites, A. W., & Plourde, S. (2021). Foraging habitat of North Atlantic right whales has declined in the Gulf of St. Lawrence, Canada, and may be insufficient for successful reproduction. *Endangered Species Research*, *44*, 113-136. https://doi.org/10.3354/esr01097

Gell, F. R., & Roberts, C. M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution*, *18*(9), 448-455. https://doi.org/10.1016/S0169-5347(03)00189-7

Genovart, M., & Pradel, R. (2019). Transience effect in capture-recapture studies: The importance of its biological meaning. *PLOS ONE*, *14*(9), e0222241. https://doi.org/10.1371/journal.pone.0222241

Germanov, E. S., Bejder, L., Chabanne, D. B., Dharmadi, D., Hendrawan, I. G., Marshall, A. D., . . . Loneragan, N. R. (2019). Contrasting habitat use and population dynamics of reef manta rays within the Nusa Penida marine protected area, Indonesia. *Frontiers in Marine Science*, *6*, 215. https://doi.org/10.3389/fmars.2019.00215

Germanov, E. S., & Marshall, A. D. (2014). Running the gauntlet: regional movement patterns of *Manta alfredi* through a complex of parks and fisheries. *PLOS ONE*, *9*(10), e110071. https://doi.org/10.1371/journal.pone.0110071

Germanov, E. S., Pierce, S. J., Marshall, A. D., Hendrawan, I. G., Kefi, A., Bejder, L., & Loneragan, N. (2022). Residency, movement patterns, behavior and demographics of reef manta rays in Komodo National Park. *PeerJ*, *10*, e13302. https://doi.org/10.7717/peerj.13302

Gimenez, O., Lebreton, J.-D., Choquet, R., & Pradel, R. (2018). R2ucare: An R package to perform goodness-of-fit tests for capture-recapture models. *Methods in Ecology and Evolution*, *9*, 1749–1754. https://doi.org/10.1111/2041-210X.13014

Glowka, L., Burhenne-Guilmin, F., Synge, H., McNeely, J. A., & Gündling, L. (1994). A guide to the convention on biological diversity.

Gordon, A. L. (2005). Oceanography of the Indonesian seas and their throughflow. *Oceanography*, *18*(4), 14-27. https://doi.org/10.5670/oceanog.2005.01

Gordon, L., & Vierus, T. (2022). First photographic evidence of oceanic manta rays (*Mobula birostris*) at two locations in the Fiji islands. *PeerJ*, *10*, e13883. https://doi.org/10.7717/peerj.13883

Government of Berau. (2019). *Regency Law 16/2019 on Full Protection of Sharks, Manta Rays, Certain Fish Species, and Coral Reefs*. Berau, East Kalimantan, Indonesia: Government of Berau

Government of Indonesia. (2004a). *Law 31/2004 on Fisheries*. Jakarta, Indonesia: Government of Indonesia

Government of Indonesia. (2004b). *Law 32/2004 on Regional Governance*. Jakarta, Indonesia: Government of Indonesia

Government of Indonesia. (2014). *Law 23/2014 on Regional Governance*. Jakarta, Indonesia: Government of Indonesia

Government of Manggarai Barat. (2013). *Regency Edict DKPP/1309/VIII/2013 on Banning Shark and Ray fishing in Manggarai Barat waters*. Manggarai Barat, Indonesia: Government of Manggarai Barat

Government of Papua Barat. (2019). *Special Provincial Law 10/2019 on Sustainable Development in West Papua*. Manokwari, West Papua, Indonesia: Government of Papua Barat

Government of Raja Ampat. (2007). *Regency Regulation 66/2007 on Marine Protected Areas in Raja Ampat*. Waisai, Raja Ampat, Indonesia: Government of Raja Ampat

Government of Raja Ampat. (2008). *Regency Law 27/2008 on Raja Ampat Marine Protected Areas*. Waisai, Raja Ampat, Indonesia: Government of Raja Ampat

Government of Raja Ampat. (2009). *Regency Regulation 5/2009 on Raja Ampat Marine Protected Areas*. Waisai, Raja Ampat, Indonesia: Government of Raja Ampat

Government of Raja Ampat. (2010). *Regency Edict 430/2010 on Banning the Use of Destructive Fishing Methods and Fishing Activities within No Take Zones*. Waisai, Raja Ampat, Indonesia: Government of Raja Ampat

Government of Raja Ampat. (2012). *Regency Law 9/2012 on Fishing Ban on Sharks, Manta Rays, and Certain Fish Species in Raja Ampat waters*. Waisai, Raja Ampat, Indonesia

Graham, N. A., Spalding, M. D., & Sheppard, C. R. (2010). Reef shark declines in remote atolls highlight the need for multi-faceted conservation action. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *20*(5), 543-548. https://doi.org/10.1002/aqc.1116

Graham, R. T., & Roberts, C. M. (2007). Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. *Fisheries Research*, *84*(1), 71-80. https://doi.org/10.1016/j.fishres.2006.11.026

Gravel, R., Lai, S., & Berteaux, D. (2023). Long-term satellite tracking reveals patterns of long-distance dispersal in juvenile and adult Arctic foxes (<i>Vulpes lagopus</i>). *Royal Society Open Science*, *10*(2), 220729. https://doi.org/10.1098/rsos.220729

Gray, P. C., Bierlich, K. C., Mantell, S. A., Friedlaender, A. S., Goldbogen, J. A., & Johnston, D. W. (2019). Drones and convolutional neural networks facilitate automated and accurate cetacean species identification and photogrammetry. *Methods in Ecology and Evolution*, *10*(9), 1490-1500. https://doi.org/10.1111/2041-210X.13246

Grecian, W. J., Lane, J. V., Michelot, T., Wade, H. M., & Hamer, K. C. (2018). Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *Journal of The Royal Society Interface*, *15*(143), 20180084. https://doi.org/10.1098/rsif.2018.0084

Grémillet, D., Chevallier, D., & Guinet, C. (2022). Big data approaches to the spatial ecology and conservation of marine megafauna. *ICES Journal of Marine Science*, *79*(4), 975-986. https://doi.org/10.1093/icesjms/fsac059

Grimm, V., Reise, K., & Strasser, M. (2003). Marine metapopulations: a useful concept? *Helgoland marine research*, *56*(4), 222-228. https://doi.org/10.1007/s10152-002-0121-3

Grorud-Colvert, K., Sullivan-Stack, J., Roberts, C., Constant, V., Horta e Costa, B., Pike, E. P., . . . Lubchenco, J. (2021). The MPA Guide: A framework to achieve global goals for the ocean. *Science*, *373*(6560), eabf0861. https://doi.org/10.1126/science.abf0861

Gu, Z., Gu, L., Eils, R., Schlesner, M., & Brors, B. (2014). circlize Implements and enhances circular visualization in R. *Bioinformatics*, *30*(19), 2811-2812. https://doi.org/10.1093/bioinformatics/btu393

Guttridge, T. L., Gruber, S. H., DiBattista, J. D., Feldheim, K. A., Croft, D. P., Krause, S., & Krause, J. (2011). Assortative interactions and leadership in a free-ranging population of juvenile lemon shark *Negaprion brevirostris*. *Marine Ecology Progress Series*, *423*, 235-245. https://doi.org/10.3354/meps08929

Harcourt, R., Sequeira, A. M. M., Zhang, X., Roquet, F., Komatsu, K., Heupel, M., . . . Fedak, M. A. (2019). Animal-Borne Telemetry: An Integral Component of the Ocean Observing Toolkit [Systematic Review]. *Frontiers in Marine Science*, *6*. https://doi.org/10.3389/fmars.2019.00326

Harris, J. L., Hosegood, P., Robinson, E., Embling, C. B., Hilbourne, S., & Stevens, G. M. (2021). Fine-scale oceanographic drivers of reef manta ray (*Mobula alfredi*) visitation patterns at a feeding aggregation site. *Ecology and Evolution*, *11*(9), 4588-4604. https://doi.org/10.1002/ece3.7357

Harris, J. L., McGregor, P. K., Oates, Y., & Stevens, G. M. (2020). Gone with the wind: Seasonal distribution and habitat use by the reef manta ray (*Mobula alfredi*) in the Maldives, implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*. https://doi.org/10.1002/aqc.3350

Harris, J. L., & Stevens, G. M. (2021). Environmental drivers of reef manta ray (*Mobula alfredi*) visitation patterns to key aggregation habitats in the Maldives. *PLOS ONE*, *16*(6), e0252470. https://doi.org/10.1371/journal.pone.0252470

Hartup, J., Marshell, A., Stevens, G., Kottermair, M., & Carlson, P. (2013). *Manta alfredi* target multispecies surgeonfish spawning aggregations. *Coral Reefs*, *32*(2), 367-367. https://doi.org/10.1007/s00338-013-1022-4

Harvey, E., Fletcher, D., & Shortis, M. (2002). Estimation of reef fish length by divers and by stereo-video: A first comparison of the accuracy and precision in the field on living fish under operational conditions. *Fisheries Research*, *57*(3), 255-265. https://doi.org/10.1016/S0165-7836(01)00356-3

Haussmann, M. F., & Vleck, C. M. (2002). Telomere length provides a new technique for aging animals. *Oecologia*, *130*(3), 325-328. https://doi.org/10.1007/s00442-001-0827-y

Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., . . . Cuevas, E. (2019). Translating marine animal tracking data into conservation policy and management. *Trends in Ecology & Evolution*, *34*(5), 459-473. https://doi.org/10.1016/j.tree.2019.01.009

Hays, G. C., Ferreira, L. C., Sequeira, A. M., Meekan, M. G., Duarte, C. M., Bailey, H., . . . Costa, D. P. (2016). Key questions in marine megafauna movement ecology. *Trends in Ecology & Evolution*, *31*(6), 463-475. https://doi.org/10.1016/j.tree.2016.02.015

He, F., Zarfl, C., Bremerich, V., Henshaw, A., Darwall, W., Tockner, K., & Jähnig, S. C. (2017). Disappearing giants: a review of threats to freshwater megafauna. *WIREs Water*, *4*(3), e1208. https://doi.org/10.1002/wat2.1208

Hearn, A. R., Acuna, D., Ketchum, J. T., Penaherrera, C., Green, J., Marshall, A., . . . Shillinger, G. (2014). Elasmobranchs of the Galapagos marine reserve. In *The Galapagos marine reserve* (pp. 23-59). Springer.

Heinrichs, S., O'Malley, M., Medd, H., & Hilton, P. (2011). *The Global Threat to Manta and Mobula Rays*. Manta Ray of Hope.

Hellström, G., Lennox, R. J., Bertram, M. G., & Brodin, T. (2022). Acoustic telemetry. *Current Biology*, *32*(16), R863-R865. https://doi.org/10.1016/j.cub.2022.05.032

Heupel, M. R., Carlson, J. K., & Simpfendorfer, C. A. (2007). Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series*, *337*, 287-297. https://doi.org/10.3354/meps337287

Heupel, M. R., Kanno, S., Martins, A. P., & Simpfendorfer, C. A. (2019). Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. *Marine and Freshwater Research*, *70*(7), 897-907. https://doi.org/10.1071/MF18081

Heupel, M. R., Kessel, S. T., Matley, J. K., & Simpfendorfer, C. A. (2018). Acoustic telemetry. In J. C. Carrier, M. R. Heithaus, & C. A. Simpfendorfer (Eds.), *Shark Research: Emerging Technologies and Applications for the Field and Laboratory*. CRC Press.

Heupel, M. R., Reiss, K. L., Yeiser, B. G., & Simpfendorfer, C. A. (2008). Effects of biofouling on performance of moored data logging acoustic receivers. *Limnology and Oceanography: Methods*, *6*(7), 327-335. https://doi.org/10.4319/lom.2008.6.327

Heupel, M. R., Semmens, J. M., & Hobday, A. J. (2006). Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research*, *57*(1), 1-13. https://doi.org/10.1071/MF05091

Hight, B. V., & Lowe, C. G. (2007). Elevated body temperatures of adult female leopard sharks, Triakis semifasciata, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoregulation? *Journal of Experimental Marine Biology and Ecology*, *352*(1), 114-128. https://doi.org/10.1016/j.jembe.2007.07.021

Hill, K., Moltmann, T., Proctor, R., & Allen, S. (2010). The Australian Integrated Marine Observing System: delivering data streams to address national and international research priorities. *Marine Technology Society Journal*, *44*(6), 65-72. https://doi.org/10.4031/MTSJ.44.6.13

Hindell, M. A., Reisinger, R. R., Ropert-Coudert, Y., Hückstädt, L. A., Trathan, P. N., Bornemann, H., . . . Raymond, B. (2020). Tracking of marine predators to protect Southern Ocean ecosystems. *Nature*, *580*(7801), 87-92. https://doi.org/10.1038/s41586-020-2126-y

Hodgson, J. C., Mott, R., Baylis, S. M., Pham, T. T., Wotherspoon, S., Kilpatrick, A. D., . . . Koh, L. P. (2018). Drones count wildlife more accurately and precisely than humans. *Methods in Ecology and Evolution*, *9*(5), 1160-1167. https://doi.org/10.1111/2041-210X.12974

Holmberg, J., Norman, B., & Arzoumanian, Z. (2009). Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo-identification. *Endangered Species Research*, *7*(1), 39-53. https://doi.org/10.3354/esr00186

Homma, K. (1997). Biology of the manta ray, *Manta birostris* Walbaum, in the Indo-Pacific. 5th Indo-Pacific Fish Conference, Nouméa, New Caledonia.

Hooker, S. K., Cañadas, A., Hyrenbach, K. D., Corrigan, C., Polovina, J. J., & Reeves, R. R. (2011). Making protected area networks effective for marine top predators. *Endangered Species Research*, *13*(3), 203-218. https://doi.org/10.3354/esr00322

Horton, T. W., Hauser, N., Zerbini, A. N., Francis, M. P., Domeier, M. L., Andriolo, A., . . . Clapham, P. J. (2017). Route Fidelity during Marine Megafauna Migration. *Frontiers in Marine Science*, *4*. https://doi.org/10.3389/fmars.2017.00422

Hua, N., Tan, K. U. N., Chen, Y., & Ma, Z. (2015). Key research issues concerning the conservation of migratory shorebirds in the Yellow Sea region. *Bird Conservation International*, *25*(1), 38-52. https://doi.org/10.1017/S0959270914000380

Huffard, C. L., Erdmann, M. V., & Gunawan, T. (Eds.). (2012a). *Geographic Priorities for Marine Biodiversity Conservation in Indonesia*. Ministry of Marine Affairs and Fisheries and Marine Protected Areas Governance Program.

Huffard, C. L., Wilson, J., Hitipeuw, C., Rotinsulu, C., Mangubhai, S., Erdmann, M. V., . . . Mondong, M. (2012b). *Ecosystem based management in the Bird's Head Seascape Indonesia: turning science into action*. Conservation International, The Nature Conservancy, and World Wildlife Fund Indonesia.

Hupman, K., Stockin, K. A., Pollock, K., Pawley, M. D. M., Dwyer, S. L., Lea, C., & Tezanos-Pinto, G. (2018). Challenges of implementing mark-recapture studies on poorly marked gregarious delphinids. *PLOS ONE*, *13*(7), e0198167. https://doi.org/10.1371/journal.pone.0198167

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., . . . Kocik, J. F. (2015). Aquatic animal telemetry: a panoramic window into the underwater world. *Science*, *348*(6240), 1255642. https://doi.org/10.1126/science.1255642

Hussey, N. E., Wintner, S. P., Dudley, S. F. J., Cliff, G., Cocks, D. T., & Aaron MacNeil, M. (2010). Maternal investment and size-specific reproductive output in carcharhinid sharks. *Journal of Animal Ecology*, *79*(1), 184-193. https://doi.org/10.1111/j.1365-2656.2009.01623.x

Huveneers, C., Simpfendorfer, C. A., Kim, S., Semmens, J. M., Hobday, A. J., Pederson, H., . . . Heupel, M. R. (2016). The influence of environmental parameters on the performance and detection range of acoustic receivers. *Methods in Ecology and Evolution*, *7*(7), 825-835. https://doi.org/10.1111/2041-210X.12520

Ihaka, R., & Gentleman, R. (1996). R: a language for data analysis and graphics. *Journal of computational and graphical statistics*, *5*(3), 299-314. https://doi.org/10.2307/1390807

Indonesian Ministry of Marine Affairs and Fisheries. (2009a). *Ministerial Decree 64/2009 on the Establishment of National Marine Protected Area of Raja Ampat Islands and its Surrounding waters in Papua Barat Province*. Jakarta, Indonesia: Indonesian Ministry of Marine Affairs and Fisheries

Indonesian Ministry of Marine Affairs and Fisheries. (2009b). *Ministerial Decree 65/2009 on the Establishment of National Marine Protected Area in Waigeo Barat and its Surrounding Waters in Raja Ampat*. Jakarta, Indonesia: Indonesian Ministry of Marine Affairs and Fisheries

Indonesian Ministry of Marine Affairs and Fisheries. (2013). *Ministerial Decree 18/2013 on the Full Protection of Whale Sharks in Indonesian waters*. Jakarta, Indonesia: Indonesian Ministry of Marine Affairs and Fisheries

Indonesian Ministry of Marine Affairs and Fisheries. (2014). *Ministerial Decree 4/2014 on the Full Protection of Manta Rays in Indonesian waters*. Jakarta, Indonesia: Indonesian Ministry of Marine Affairs and Fisheries

Indonesian Ministry of Marine Affairs and Fisheries. (2015). *National Plan of Action: Manta Ray Conservation Period 1: 2016–2020*. Jakarta, Indonesia: Indonesian Ministry of Marine Affairs and Fisheries

Indonesian Ministry of Marine Affairs and Fisheries. (2022). *Ministerial Decree 23/2022 on Waigeo Barat and its Surrounding Waters and Raja Ampat Islands and its Surrounding Waters MPAs in West Papua Province.* Jakarta, Indonesia: Indonesian Ministry of Marine Affairs and Fisheries

Indonesian Ministry of National Development Planning. (2021). *Road Map of SDGs Indonesia Towards 2030*. Jakarta, Indonesia: Indonesian Ministry of National Development Planning

Iverson, S. J., Fisk, A. T., Hinch, S. G., Flemming, J. M., Cooke, S. J., & Whoriskey, F. G. (2018). The Ocean Tracking Network: Advancing frontiers in aquatic science and management. *The Ocean Tracking Network: Advancing aquatic research and management*, *01*(01), 1041-1051. https://doi.org/10.1139/cjfas-2018-0481

Jacoby, D. M., Ferretti, F., Freeman, R., Carlisle, A. B., Chapple, T. K., Curnick, D. J., . . . Block, B. A. (2020). Shark movement strategies influence poaching risk and can guide enforcement decisions in a large, remote marine protected area. *Journal of Applied Ecology*, *57*(9), 1782-1792. https://doi.org/10.1111/1365-2664.13654

Jacoby, D. M. P., Brooks, E. J., Croft, D. P., & Sims, D. W. (2012a). Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods in Ecology and Evolution*, *3*(3), 574-583. https://doi.org/10.1111/j.2041-210X.2012.00187.x

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

Jacoby, D. M. P., & Freeman, R. (2016). Emerging Network-Based Tools in Movement Ecology. *Trends in Ecology & Evolution*, *31*(4), 301-314. https://doi.org/10.1016/j.tree.2016.01.011

Jaine, F., Rohner, C., Weeks, S., Couturier, L., Bennett, M., Townsend, K., & Richardson, A. (2014). Movements and habitat use of reef manta rays off eastern Australia: Offshore excursions, deep diving and eddy affinity revealed by satellite telemetry. *Marine Ecology Progress Series*, *510*, 73-86. https://doi.org/10.3354/meps10910

Jaine, F. R., Couturier, L. I., Weeks, S. J., Townsend, K. A., Bennett, M. B., Fiora, K., & Richardson, A. J. (2012). When giants turn up: sighting trends, environmental influences and habitat use of the manta ray *Manta alfredi* at a coral reef. *PLOS ONE*, *7*(10), e46170. https://doi.org/10.1371/journal.pone.0046170

Jaiteh, V. F., Lindfield, S. J., Mangubhai, S., Warren, C., Fitzpatrick, B., & Loneragan, N. R. (2016). Higher abundance of marine predators and changes in fishers' behavior following spatial protection within the world's biggest shark fishery. *Frontiers in Marine Science*, *3*, 43. https://doi.org/10.3389/fmars.2016.00043

Jeffreys, G., Rowat, D., Marshall, H., & Brooks, K. (2013). The development of robust morphometric indices from accurate and precise measurements of free-swimming whale sharks using laser photogrammetry. *Marine Biological Association of the United Kingdom. Journal of the Marine Biological Association of the United Kingdom*, *93*(2), 309. https://doi.org/10.1017/S0025315412001312

Jirik, K. E., & Lowe, C. G. (2012). An elasmobranch maternity ward: female round stingrays Urobatis halleri use warm, restored estuarine habitat during gestation. *Journal of Fish Biology*, *80*(5), 1227-1245. https://doi.org/10.1111/j.1095-8649.2011.03208.x

Johnson, A. R., Wiens, J. A., Milne, B. T., & Crist, T. O. (1992). Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology*, *7*(1), 63-75. https://doi.org/10.1007/BF02573958

Johnston, D. W. (2019). Unoccupied aircraft systems in marine science and conservation. *Annual Review of Marine Science*, *11*, 439-463. https://doi.org/10.1146/annurev-marine-010318-095323

Jones, A. G., & Ardren, W. R. (2003). Methods of parentage analysis in natural populations. *Molecular Ecology*, *12*(10), 2511-2523. https://doi.org/10.1046/j.1365-294X.2003.01928.x

Jones, B. (2021). *MPA's added to the BHS MPA network*. Retrieved 20 September 2021 from https://birdsheadseascape.com/conservation-science/mpas-added-to-the-bhs-mpa-network/

Jones, B., Shimlock, M., Erdmann, M., & Allen, G. R. (2011). *Diving Indonesia's Bird's Head Seascape*. Conservation International.

Jonsen, I., & Patterson, T. (2020). *foieGras: fit latent variable movement models to animal tracking data for location quality control and behavioural inference*. In (Version R package version 0.7–6) The Comprehensive R Archive Network.

Jonsen, I. D., McMahon, C. R., Patterson, T. A., Auger-Méthé, M., Harcourt, R., Hindell, M. A., & Bestley, S. (2019). Movement responses to environment: fast inference of variation among southern elephant seals with a mixed effects model. *Ecology*, *100*(1), e02566. https://doi.org/10.1002/ecy.2566

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

Kashiwagi, T. (2014). *Conservation biology and genetics of the largest living rays: manta rays* [Dissertation, The University of Queensland]. Brisbane, Australia.

Kashiwagi, T., Ito, T., & Sato, F. (2010). Occurrences of reef manta ray, *Manta alfredi*, and giant manta ray, *M. birostris*, in Japan, examined by photographic records. *Report of Japanese Society for Elasmobranch Studies*, *46*, 20-27. https://doi.org/10.1371/journal.pone.0088655

Kashiwagi, T., Marshall, A. D., Bennett, M. B., & Ovenden, J. R. (2011). Habitat segregation and mosaic sympatry of the two species of manta ray in the Indian and Pacific Oceans: *Manta alfredi* and *M. birostris*. *Marine Biodiversity Records*, *4*. https://doi.org/10.1017/s1755267211000479

Kasmidi, M. (2017). *Manta Sandy's Monitoring Post: Managing one of the 'busiest' dive sites*. Retrieved 20 September 2021 from https://birdsheadseascape.com/diving/manta-sandys-monitoring-post-managing-one-busiest-dive-sites-raja-ampat-meidiarti-kasmidi/

Kasmidi, M., & Gunadharma, N. A. (2017). *Diving in Manta Sandy? Here's what you need to know!* Retrieved 20 September 2021 from https://birdsheadseascape.com/diving/diving-manta-sandy-heres-need-know-meidiarti-kasmidi-nikka-amandra-gunadharma/

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Kays, R., Davidson, S. C., Berger, M., Bohrer, G., Fiedler, W., Flack, A., . . . Wikelski, M. (2022). The Movebank system for studying global animal movement and demography. *Methods in Ecology and Evolution*, *13*(2), 419-431. https://doi.org/10.1111/2041-210X.13767

Kelly, R., Fleming, A., Pecl, G. T., von Gönner, J., & Bonn, A. (2020). Citizen science and marine conservation: a global review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1814), 20190461. https://doi.org/10.1098/rstb.2019.0461

Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S., & Fisk, A. T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, *24*(1), 199-218. https://doi.org/10.1007/s11160-013-9328-4

Kessel, S. T., Elamin, N. A., Yurkowski, D. J., Chekchak, T., Walter, R. P., Klaus, R., . . . Hussey, N. E. (2017). Conservation of reef manta rays (*Manta alfredi*) in a UNESCO World Heritage Site: Large-scale island development or sustainable tourism? *PLOS ONE*, *12*(10), e0185419. https://doi.org/10.1371/journal.pone.0185419

Kitchen-Wheeler, A., Ari, C., & Edwards, A. J. (2011). Population estimates of Alfred mantas (*Manta alfredi*) in central Maldives atolls: North Male, Ari and Baa. *Environmental Biology of Fishes*, *93*(4), 557-575. https://doi.org/10.1007/s10641-011-9950-8

Kitchen-Wheeler, A.-M. (2010). Visual identification of individual manta ray (*Manta alfredi*) in the Maldives Islands, Western Indian Ocean. *Marine Biology Research*, *6*(4), 351-363. https://doi.org/10.1080/17451000903233763

Kneebone, J., Winton, M., Danylchuk, A., Chisholm, J., & Skomal, G. B. (2018). An assessment of juvenile sand tiger (Carcharias taurus) activity patterns in a seasonal nursery using accelerometer transmitters. *Environmental Biology of Fishes*, *101*(12), 1739-1756. https://doi.org/10.1007/s10641-018-0821-4

Knip, D. M., Heupel, M. R., & Simpfendorfer, C. A. (2012). Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biological Conservation*, *148*(1), 200-209. https://doi.org/10.1016/j.biocon.2012.01.008

Knochel, A. M., Hussey, N. E., Kessel, S. T., Braun, C. D., Cochran, J. E. M., Hill, G., . . . Berumen, M. L. (2022). Home sweet home: spatiotemporal distribution and site fidelity of the reef manta ray (*Mobula alfredi*) in Dungonab Bay, Sudan. *Movement Ecology*, *10*(1), 22. https://doi.org/10.1186/s40462-022-00314-9

König, H. J., Kiffner, C., Kramer-Schadt, S., Fürst, C., Keuling, O., & Ford, A. T. (2020). Human–wildlife coexistence in a changing world. *Conservation Biology*, *34*(4), 786-794. https://doi.org/10.1111/cobi.13513

Kool, J. T., Moilanen, A., & Treml, E. A. (2013). Population connectivity: recent advances and new perspectives. *Landscape Ecology*, *28*(2), 165-185. https://doi.org/10.1007/s10980-012-9819-z

Kranstauber, B., Smolla, M., & Scharf, A. K. (2021). *move: Visualizing and Analyzing Animal Track Data*. In (Version R package version 4.1.6) https://CRAN.R-project.org/package=move

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., & Bell, B. M. (2016). TMB: Automatic differentiation and Laplace approximation [automatic differentiation; AD; random effects; latent variables; C++ templates; R]. *Journal of Statistical Software*, *70*(5), 21. https://doi.org/10.18637/jss.v070.i05

Kritzer, J. P., & Sale, P. F. (2006). CHAPTER 16 - The Future of Metapopulation Science in Marine Ecology. In J. P. Kritzer & P. F. Sale (Eds.), *Marine Metapopulations* (pp. 517-529). Academic Press. https://doi.org/10.1016/B978-012088781-1/50019-4

Kritzer, J. P., & Sale, P. F. (2010). *Marine metapopulations*. Elsevier.

Kubelka, V., Sandercock, B. K., Székely, T., & Freckleton, R. P. (2022). Animal migration to northern latitudes: environmental changes and increasing threats. *Trends in Ecology & Evolution*, *37*(1), 30-41. https://doi.org/10.1016/j.tree.2021.08.010

Laidre, K. L., Heide-Jørgensen, M. P., Logsdon, M. L., Hobbs, R. C., Dietz, R., & VanBlaricom, G. R. (2004). Fractal analysis of narwhal space use patterns. *Zoology*, *107*(1), 3-11. https://doi.org/10.1016/j.zool.2003.09.001

Landeo-Yauri, S. S., Ramos, E. A., Castelblanco-Martínez, D. N., Niño-Torres, C. A., & Searle, L. (2020). Using small drones to photo-identify Antillean manatees: A novel method for monitoring an endangered marine mammal in the Caribbean Sea. *Endangered Species Research*, *41*, 79-90. https://doi.org/10.3354/esr01007

LaRue, M., Salas, L., Nur, N., Ainley, D., Stammerjohn, S., Pennycook, J., . . . Rotella, J. (2021). Insights from the first global population estimate of Weddell seals in Antarctica. *Science Advances*, *7*(39), eabh3674. https://doi.org/10.1126/sciadv.abh3674

Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., . . . Tetley, M. J. (2014). Migratory marine species: their status, threats and conservation management needs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(S2), 111-127. https://doi.org/10.1002/aqc.2512

Lassauce, H. (2021). *Caractéristiques biologiques, écologie spatiale et structure de la population de raies manta de récif (Mobula alfredi) de Nouvelle-Calédonie* [Dissertation, University of New Caledonia]. Nouméa, New Caledonia.

Lassauce, H., Chateau, O., Erdmann, M. V., & Wantiez, L. (2020). Diving behavior of the reef manta ray (*Mobula alfredi*) in New Caledonia: More frequent and deeper night-time diving to 672 meters. *PLOS ONE*, *15*(3), e0228815. https://doi.org/10.1371/journal.pone.0228815

Lassauce, H., Dudgeon, C. L., Armstrong, A. J., Wantiez, L., & Carroll, E. L. (2022). Evidence of fine-scale genetic structure for reef manta rays *Mobula alfredi* in New Caledonia. *Endangered Species Research*, *47*, 249-264. https://doi.org/10.3354/esr01178

Last, P., Naylor, G., Séret, B., White, W., de Carvalho, M., & Stehmann, M. (2016). *Rays of the World*. CSIRO publishing.

Lawrence, L. (2018). *Manta Sandy ranger station: A aommunity based approach to sustainable tourism in Raja Ampat*. Retrieved 20 September 2021 from https://birdsheadseascape.com/regional/manta-sandy-ranger-station-community-based-approach-sustainable-tourism-raja-ampat-lynn-lawrance-ed-nikka-amandra-gunadharma/

Lédée, E. J. I., Heupel, M. R., Taylor, M. D., Harcourt, R. G., Jaine, F. R. A., Huveneers, C., . . . Simpfendorfer, C. A. (2021). Continental-scale acoustic telemetry and network analysis reveal new insights into stock structure. *Fish and Fisheries*, *22*(5), 987-1005. https://doi.org/10.1111/faf.12565

Lédée, E. J. I., Heupel, M. R., Tobin, A. J., Knip, D. M., & Simpfendorfer, C. A. (2015). A comparison between traditional kernel-based methods and network analysis: an example from two nearshore shark species. *Animal Behaviour*, *103*, 17-28. https://doi.org/10.1016/j.anbehav.2015.01.039

Lee, D. E., Lohay, G. G., Cavener, D. R., & Bond, M. L. (2022). Using spot pattern recognition to examine population biology, evolutionary ecology, sociality, and movements of giraffes: a 70-year retrospective. *Mammalian Biology*. https://doi.org/10.1007/s42991-022-00261-3

Lennox, R. J., Aarestrup, K., Cooke, S. J., Cowley, P. D., Deng, Z. D., Fisk, A. T., . . . Young, N. (2017). Envisioning the Future of Aquatic Animal Tracking: Technology, Science, and Application. *Bioscience*, *67*(10), 884-896. https://doi.org/10.1093/biosci/bix098

Letessier, T. B., Juhel, J.-B., Vigliola, L., & Meeuwig, J. J. (2015). Low-cost small action cameras in stereo generates accurate underwater measurements of fish. *Journal of Experimental Marine Biology and Ecology*, *466*, 120-126. https://doi.org/10.1016/j.jembe.2015.02.013

Lewis, S. A., Setiasih, N., Fahmi, Dharmadi, O'Malley, M. P., Campbell, S. J., . . . Sianipar, A. B. (2015). Assessing Indonesian manta and devil ray populations through historical landings and fishing community interviews. *PeerJ Preprints 6:e1334v1*. https://doi.org/10.7287/peerj.preprints.1334v1

Lindenmayer, D. B., Likens, G. E., Andersen, A., Bowman, D., Bull, C. M., Burns, E., . . . Liddell, M. J. (2012). Value of long-term ecological studies. *Austral Ecology*, *37*(7), 745-757. https://doi.org/10.1111/j.1442-9993.2011.02351.x

Lindsey, P. A., Chapron, G., Petracca, L. S., Burnham, D., Hayward, M. W., Henschel, P., . . . Dickman, A. (2017). Relative efforts of countries to conserve world’s megafauna. *Global Ecology and Conservation*, *10*, 243-252. https://doi.org/10.1016/j.gecco.2017.03.003

Lowe, W. H., & Allendorf, F. W. (2010). What can genetics tell us about population connectivity? *Molecular Ecology*, *19*(15), 3038-3051. https://doi.org/10.1111/j.1365-294X.2010.04688.x

Lyons, M. B., Brandis, K. J., Murray, N. J., Wilshire, J. H., McCann, J. A., Kingsford, R. T., & Callaghan, C. T. (2019). Monitoring large and complex wildlife aggregations with drones. *Methods in Ecology and Evolution*, *10*(7), 1024-1035. https://doi.org/10.1111/2041-210X.13194

Lyrholm, T., & Gyllensten, U. (1998). Global matrilineal population structure in sperm whales as indicated by mitochondrial DNA sequences. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1406), 1679-1684. https://doi.org/10.1098/rspb.1998.0488

Magson, K., Monacella, E., Scott, C., Buffat, N., Arunrugstichai, S., Chuangcharoendee, M., . . . Araujo, G. (2022). Citizen science reveals the population structure and seasonal presence of whale sharks in the Gulf of Thailand. *Journal of Fish Biology*, *3*, 540-549. https://doi.org/10.1111/jfb.15121

Mangubhai, S., Erdmann, M. V., Wilson, J. R., Huffard, C. L., Ballamu, F., Hidayat, N. I., . . . Purba, G. (2012). Papuan Bird’s Head Seascape: Emerging threats and challenges in the global center of marine biodiversity. *Marine Pollution Bulletin*, *64*(11), 2279-2295. https://doi.org/10.1016/j.marpolbul.2012.07.024

Mangubhai, S., Wilson, J. R., Rumetna, L., & Maturbongs, Y. (2015). Explicitly incorporating socioeconomic criteria and data into marine protected area zoning. *Ocean & Coastal Management*, *116*, 523-529. https://doi.org/10.1016/j.ocecoaman.2015.08.018

Marquez, M. C. (2022). *World’s Oldest Known Manta Ray Spotted Again On Great Barrier Reef*. Forbes. Retrieved 2 Feb 2023 from https://www.forbes.com/sites/melissacristinamarquez/2022/10/11/worlds-oldest-known-manta-ray-spotted-again-on-great-barrier-reef/?sh=2378b4ae702c

Marshall, A., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., . . . Romanov, E. (2020). *Mobula birostris. The IUCN Red List of Threatened Species 2020: e.T198921A68632946.* https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T198921A68632946.en

Marshall, A., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., . . . Sherley, R. B. (2022). *Mobula alfredi (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2022: e.T195459A214395983*. IUCN. Retrieved 18 February 2023 from https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T195459A68632178.en

Marshall, A. D., & Bennett, M. B. (2010). Reproductive ecology of the reef manta ray *Manta alfredi* in southern Mozambique. *Journal of Fish Biology*, *77*(1), 169-190. https://doi.org/10.1111/j.1095-8649.2010.02669.x

Marshall, A. D., Compagno, L. J., & Bennett, M. B. (2009). Redescription of the genus *Manta* with resurrection of *Manta alfredi* (Krefft, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae). *Zootaxa*, *2301*, 1-28. https://doi.org/10.11646/ZOOTAXA.2301.1.1

Marshall, A. D., Dudgeon, C., & Bennett, M. (2011). Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique. *Marine Biology*, *158*(5), 1111-1124. https://doi.org/10.1007/s00227-011-1634-6

Marshall, A. D., & Pierce, S. J. (2012). The use and abuse of photographic identification in sharks and rays. *Journal of Fish Biology*, *80*(5), 1361-1379. https://doi.org/10.1111/j.1095-8649.2012.03244.x

Marshall, A. D., Pierce, S. J., & Bennett, M. B. (2008). Morphological measurements of manta rays (*Manta birostris*) with a description of a foetus from the east coast of Southern Africa. *Zootaxa*, *1717*(1717), 24-30. https://doi.org/10.11646/zootaxa.1717.1.2

Martín, G., Espinoza, M., Heupel, M., & Simpfendorfer, C. A. (2020). Estimating marine protected area network benefits for reef sharks. *Journal of Applied Ecology*, *57*(10), 1969-1980. https://doi.org/10.1111/1365-2664.13706

Mason, N., Ward, M., Watson, J. E. M., Venter, O., & Runting, R. K. (2020). Global opportunities and challenges for transboundary conservation. *Nature Ecology & Evolution*, *4*(5), 694-701. https://doi.org/10.1038/s41559-020-1160-3

Matley, J. K., Klinard, N. V., Barbosa Martins, A. P., Aarestrup, K., Aspillaga, E., Cooke, S. J., . . . Fisk, A. T. (2022). Global trends in aquatic animal tracking with acoustic telemetry. *Trends in Ecology & Evolution*, *37*(1), 79-94. https://doi.org/10.1016/j.tree.2021.09.001

McAllister, T. G., Beggs, J. R., Ogilvie, S., Kirikiri, R., Black, A., & Wehi, P. M. (2019). Kua takoto te mānuka: mātauranga Māori in New Zealand ecology. *New Zealand Journal of Ecology*, *43*(3), 1-7. https://doi.org/10.20417/nzjecol.43.41

McCauley, D. J., DeSalles, P. A., Young, H. S., Papastamatiou, Y. P., Caselle, J. E., Deakos, M. H., . . . Micheli, F. (2014). Reliance of mobile species on sensitive habitats: a case study of manta rays (*Manta alfredi*) and lagoons. *Marine Biology*, *161*(9), 1987-1998. https://doi.org/10.1007/s00227-014-2478-7

McIntosh, R. R., Holmberg, R., & Dann, P. (2018). Looking Without Landing—Using Remote Piloted Aircraft to Monitor Fur Seal Populations Without Disturbance. *Frontiers in Marine Science*, *5*. https://doi.org/10.3389/fmars.2018.00202

McKenna, S. A., Allen, G. R., & Suryadi, S. (Eds.). (2002). *A Marine Rapid Assessment of the Raja Ampat Islands, Papua Province, Indonesia*. Conservation International.

McKinney, J. A., Hoffmayer, E. R., Holmberg, J., Graham, R. T., Driggers III, W. B., de la Parra-Venegas, R., . . . Dove, A. D. (2017). Long-term assessment of whale shark population demography and connectivity using photo-identification in the Western Atlantic Ocean. *PLOS ONE*, *12*(8), e0180495. https://doi.org/10.1371/journal.pone.0180495

McLeod, E., Szuster, B., & Salm, R. (2009). Sasi and marine conservation in Raja Ampat, Indonesia. *Coastal Management*, *37*(6), 656-676. https://doi.org/10.1080/08920750903244143

Meekan, M. G., Bradshaw, C. J., Press, M., McLean, C., Richards, A., Quasnichka, S., & Taylor, J. G. (2006). Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. *Marine Ecology Progress Series*, *319*, 275-285. https://doi.org/10.3354/meps319275

Meekan, M. G., Duarte, C. M., Fernández-Gracia, J., Thums, M., Sequeira, A. M. M., Harcourt, R., & Eguíluz, V. M. (2017). The Ecology of Human Mobility. *Trends in Ecology & Evolution*, *32*(3), 198-210. https://doi.org/10.1016/j.tree.2016.12.006

Menesatti, P., Costa, C., Antonucci, F., Steri, R., Pallottino, F., & Catillo, G. (2014). A low-cost stereovision system to estimate size and weight of live sheep. *Computers and Electronics in Agriculture*, *103*, 33-38. https://doi.org/10.1016/j.compag.2014.01.018

Meyer, C. G., Papastamatiou, Y. P., & Holland, K. N. (2010). A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. *Marine Biology*, *157*(8), 1857-1868. https://doi.org/10.1007/s00227-010-1457-x

Meyer-Gutbrod, E. L., Davies, K. T. A., Johnson, C. L., Plourde, S., Sorochan, K. A., Kenney, R. D., . . . Greene, C. H. (2022). Redefining North Atlantic right whale habitat-use patterns under climate change. *Limnology and Oceanography*. https://doi.org/10.1002/lno.12242

Meyer-Gutbrod, E. L., Greene, C. H., Davies, K. T. A., & Johns, D. G. (2021). OCEAN REGIME SHIFT IS DRIVING COLLAPSE OF THE NORTH ATLANTIC RIGHT WHALE POPULATION. *Oceanography*, *34*(3), 22-31. https://www.jstor.org/stable/27051387

Meyers, M. M., Francis, M. P., Erdmann, M., Constantine, R., & Sianipar, A. (2020). Movement patterns of whale sharks in Cenderawasih Bay, Indonesia, revealed through long-term satellite tagging. *Pacific conservation biology*, *26*(4), 353-364. https://doi.org/10.1071/PC19035

Mickle, M. F., & Higgs, D. M. (2021). Towards a new understanding of elasmobranch hearing. *Marine Biology*, *169*(1), 12. https://doi.org/10.1007/s00227-021-03996-8

Minor, E. S., & Urban, D. L. (2007). Graph theory as a proxy for spatially explicit population models in conservation planning. *Ecological Applications*, *17*(6), 1771-1782. https://doi.org/10.1890/06-1073.1

Moll, R. J., Millspaugh, J. J., Beringer, J., Sartwell, J., & He, Z. (2007). A new 'view' of ecology and conservation through animal-borne video systems. *Trends in Ecology & Evolution*, *22*(12), 660-668. https://doi.org/10.1016/j.tree.2007.09.007

Molnár, Z., & Babai, D. (2021). Inviting ecologists to delve deeper into traditional ecological knowledge. *Trends in Ecology & Evolution*, *36*(8), 679-690. https://doi.org/10.1016/j.tree.2021.04.006

Moses, K., Katsis, L., Griffith, P., Kemp, R., & Dancer, A. (2022). *An introduction to satellite technologies for tracking wildlife*. Zoological Society of London.

Mourier, J. (2012). Manta rays in the Marquesas Islands: first records of *Manta birostris* in French Polynesia and most easterly location of *Manta alfredi* in the Pacific Ocean, with notes on their distribution. *Journal of Fish Biology*, *81*(6), 2053-2058. https://doi.org/10.1111/j.1095-8649.2012.03449.x

Mourier, J., Lédée, E., Guttridge, T., & Jacoby, D. (2018). Network Analysis and Theory in Shark Ecology—Methods and Applications. In J. C. Carrier, M. R. Heithaus, & C. A. Simpfendorfer (Eds.), *Shark Research: Emerging Technologies and Applications for the Field and Laboratory* (1st ed., pp. 392). CRC Press.

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

Mueller, T., & Fagan, W. F. (2008). Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos*, *117*(5), 654-664. https://doi.org/10.1111/j.0030-1299.2008.16291.x

Mueller, T., Olson, K. A., Fuller, T. K., Schaller, G. B., Murray, M. G., & Leimgruber, P. (2008). In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology*, *45*(2), 649-658. https://doi.org/10.1111/j.1365-2664.2007.01371.x

Muff, S., Nilsen, E. B., O'Hara, R. B., & Nater, C. R. (2021). Rewriting results sections in the language of evidence. *Trends in Ecology & Evolution*. https://doi.org/10.1016/j.tree.2021.10.009

Muhajir, P., Mangubhai, S., Wilson, J., & Ardiwijaya, R. (2012). *Marine Resource Use in Kofiau and Boo Islands Marine Protected Area, Raja Ampat, West Papua. 2006-2011*. The Nature Conservancy, Indo-Pacific Division.

Murakumo, K., Matsumoto, R., Tomita, T., Matsumoto, Y., & Ueda, K. (2020). The power of ultrasound: observation of nearly the entire gestation and embryonic developmental process of captive reef manta rays (*Mobula alfredi*). *Fishery Bulletin*, *118*(1), 1-8. https://doi.org/10.7755/fb.118.1.1

Murphy, S. E., Farmer, G., Katz, L., Troëng, S., Henderson, S., Erdmann, M. V., . . . Putra, K. S. (2021). Fifteen years of lessons from the Seascape approach: a framework for improving ocean management at scale. *Conservation Science and Practice*, *3*(6), e423. https://doi.org/10.1111/csp2.423

Murray, A., Garrud, E., Ender, I., Lee-Brooks, K., Atkins, R., Lynam, R., . . . Stevens, G. (2020). Protecting the million-dollar mantas; creating an evidence-based code of conduct for manta ray tourism interactions. *Journal of Ecotourism*, *19*(2), 132-147. https://doi.org/10.1080/14724049.2019.1659802

Möller, L. M., Attard, C. R. M., Bilgmann, K., Andrews-Goff, V., Jonsen, I., Paton, D., & Double, M. C. (2020). Movements and behaviour of blue whales satellite tagged in an Australian upwelling system. *Scientific Reports*, *10*(1), 21165. https://doi.org/10.1038/s41598-020-78143-2

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci U S A*, *105*(49), 19052-19059. https://doi.org/10.1073/pnas.0800375105

Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., . . . Jarić, I. (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*, *375*(6582), eabg1780. https://doi.org/10.1126/science.abg1780

Newman, M. (2018). Measures and metrics. In *Networks* (2nd ed., pp. 158–217). Oxford University Press. https://doi.org/10.1093/oso/9780198805090.003.0007

Newman, M. E. J. (2004a). Analysis of weighted networks. *Physical Review E*, *70*(5), 056131. https://doi.org/10.1103/PhysRevE.70.056131

Newman, M. E. J. (2004b). Fast algorithm for detecting community structure in networks. *Physical Review E*, *69*(6), 066133. https://doi.org/10.1103/PhysRevE.69.066133

Newman, M. E. J. (2006). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences*, *103*(23), 8577-8582. https://doi.org/10.1073/pnas.0601602103

Niella, Y., Butcher, P., Holmes, B., Barnett, A., & Harcourt, R. (2022). Forecasting intraspecific changes in distribution of a wide-ranging marine predator under climate change. *Oecologia*, *198*(1), 111-124. https://doi.org/10.1007/s00442-021-05075-7

Noad, M. J., Kniest, E., & Dunlop, R. A. (2019). Boom to bust? Implications for the continued rapid growth of the eastern Australian humpback whale population despite recovery. *Population Ecology*, *61*(2), 198-209. https://doi.org/10.1002/1438-390X.1014

Norris, K. (2004). Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology*, *41*(3), 413-426. https://doi.org/10.1111/j.0021-8901.2004.00910.x

Notarbartolo Di Sciara, G. (1987). A revisionary study of the genus *Mobula* Rafinesque, 1810 (Chondrichthyes: Mobulidae) with the description of a new species. *Zoological Journal of the Linnean Society*, *91*(1), 1-91. https://doi.org/10.1111/j.1096-3642.1987.tb01723.x

O'Malley, M. P., Townsend, K. A., Hilton, P., Heinrichs, S., & Stewart, J. D. (2017). Characterization of the trade in manta and devil ray gill plates in China and South-east Asia through trader surveys. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*(2), 394-413. https://doi.org/10.1002/aqc.2670

O’Malley, M. P., Lee-Brooks, K., & Medd, H. B. (2013). The global economic impact of manta ray watching tourism. *PLOS ONE*, *8*(5), e65051. https://doi.org/10.1371/journal.pone.0065051

Ohlhorst, S. L. (1982). Diel migration patterns of demersal reef zooplankton. *Journal of Experimental Marine Biology and Ecology*, *60*(1), 1-15. https://doi.org/10.1016/0022-0981(81)90176-3

Oleksyn, S., Tosetto, L., Raoult, V., Joyce, K. E., & Williamson, J. E. (2021a). Going batty: The challenges and opportunities of using drones to monitor the behaviour and habitat use of rays. *Drones*, *5*(1), 12. https://doi.org/10.3390/drones5010012

Oleksyn, S., Tosetto, L., Raoult, V., & Williamson, J. E. (2021b). Drone-based tracking of the fine-scale movement of a coastal stingray (*Bathytoshia brevicaudata*). *Remote Sensing*, *13*(1), 40. https://doi.org/10.3390/rs13010040

Pacoureau, N., Carlson, J. K., Kindsvater, H. K., Rigby, C. L., Winker, H., Simpfendorfer, C. A., . . . Dulvy, N. K. (2023). Conservation successes and challenges for wide-ranging sharks and rays. *Proceedings of the National Academy of Sciences*, *120*(5), e2216891120. https://doi.org/10.1073/pnas.2216891120

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., . . . Dulvy, N. K. (2021). Half a century of global decline in oceanic sharks and rays. *Nature*, *589*(7843), 567-571. https://doi.org/10.1038/s41586-020-03173-9

Pakiding, F., Matualage, D., Salosso, K., Purwanto, Anggriyani, I. R., Ahmad, A., . . . Mascia, M. B. (2020). *State of the Bird's Head Seascape marine protected area network 2019*. University of Papua, Yayasan Konservasi Alam Nusantara-TNC, World Wildlife Fund, and Conservation International.

Palacios, M. D., Hoyos-Padilla, E. M., Trejo-Ramírez, A., Croll, D. A., Galván-Magaña, F., Zilliacus, K. M., . . . González-Armas, R. (2021). Description of first nursery area for a pygmy devil ray species (*Mobula munkiana*) in the Gulf of California, Mexico. *Scientific Reports*, *11*(1), 132. https://doi.org/10.1038/s41598-020-80506-8

Papastamatiou, Y. P., DeSalles, P. A., & McCauley, D. J. (2012). Area-restricted searching by manta rays and their response to spatial scale in lagoon habitats. *Marine Ecology Progress Series*, *456*, 233-244. https://doi.org/10.3354/meps09721

Parrott, B. B., & Bertucci, E. M. (2019). Epigenetic Aging Clocks in Ecology and Evolution. *Trends in Ecology & Evolution*, *34*(9), 767-770. https://doi.org/10.1016/j.tree.2019.06.008

Pate, J. H., & Marshall, A. D. (2020). Urban manta rays: potential manta ray nursery habitat along a highly developed Florida coastline. *Endangered Species Research*, *43*, 51-64. https://doi.org/10.3354/esr01054

Pattanayak, H. S., Verma, H. K., & Sangal, A. L. (2022). Lengthening of average path length in social networks due to the effect of community structure. *Journal of King Saud University - Computer and Information Sciences*, *34*(10, Part A), 8401-8421. https://doi.org/10.1016/j.jksuci.2020.10.014

Peel, L. R. (2019). *Movement patterns and feeding ecology of the reef manta ray (Mobula alfredi) in Seychelles* [Dissertation, University of Western Australia]. Perth, Australia.

Peel, L. R., Daly, R., Keating Daly, C. A., Stevens, G. M., Collin, S. P., & Meekan, M. G. (2019a). Stable isotope analyses reveal unique trophic role of reef manta rays (*Mobula alfredi*) at a remote coral reef. *Royal Society Open Science*, *6*(9), 190599. https://doi.org/10.1098/rsos.190599

Peel, L. R., Stevens, G. M., Daly, R., Keating Daly, C. A., Collin, S. P., Nogués, J., & Meekan, M. G. (2020). Regional movements of reef manta rays (*Mobula alfredi*) in Seychelles waters. *Frontiers in Marine Science*, *7*, 558. https://doi.org/10.3389/fmars.2020.00558

Peel, L. R., Stevens, G. M. W., Daly, R., Daly, C. A. K., Lea, J. S. E., Clarke, C. R., . . . Meekan, M. G. (2019b). Movement and residency patterns of reef manta rays *Mobula alfredi* in the Amirante Islands, Seychelles. *Marine Ecology Progress Series*, *621*, 169-184. https://doi.org/10.3354/meps12995

Péron, C., & Grémillet, D. (2013). Tracking through life stages: Adult, immature and juvenile autumn migration in a long-lived seabird. *PLOS ONE*, *8*(8), e72713. https://doi.org/10.1371/journal.pone.0072713

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate Change and Distribution Shifts in Marine Fishes. *Science*, *308*(5730), 1912-1915. https://doi.org/10.1126/science.1111322

Perryman, R. J., Venables, S. K., Tapilatu, R. F., Marshall, A. D., Brown, C., & Franks, D. W. (2019). Social preferences and network structure in a population of reef manta rays. *Behavioral Ecology and Sociobiology*, *73*(8), 114. https://doi.org/10.1007/s00265-019-2720-x

Perryman, R. J. Y., Mourier, J., Venables, S. K., Tapilatu, R. F., Setyawan, E., & Brown, C. (2022). Reef manta ray social dynamics depend on individual differences in behaviour. *Animal Behaviour*, *191*, 43-55. https://doi.org/10.1016/j.anbehav.2022.06.010

Perryman, W. L., & Lynn, M. S. (1993). Identification of geographic forms common dolphin (*Delphinus delphis*) from aerial photogrammetry. *Marine Mammal Science*, *9*(2), 119-137. https://doi.org/10.1111/j.1748-7692.1993.tb00438.x

Peter, T. S., Judith, A., Phillip, J. C., Nancy, F., Steven, K. K., Finn, L., . . . Philip, S. H. (2003). North Atlantic humpback whale abundance and rate of increase four decades after protection from whaling. *Marine Ecology Progress Series*, *258*, 263-273. https://doi.org/10.3354/meps258263

Phardana, T., Subhan, B., Naulita, Y., Sani, L. M. I., & Madduppa, H. (2022). Low genetic diversity and a mixing population of the reef Manta ray (*Mobula alfredi*, Krefft 1868) between three populations across Indonesian seas revealed by Mitochondrial DNA. *IOP Conference Series: Earth and Environmental Science*, *1033*(1), 012038. https://doi.org/10.1088/1755-1315/1033/1/012038

Phillips, N. M., Devloo-Delva, F., McCall, C., & Daly-Engel, T. S. (2021). Reviewing the genetic evidence for sex-biased dispersal in elasmobranchs. *Reviews in Fish Biology and Fisheries*, *31*(4), 821-841. https://doi.org/10.1007/s11160-021-09673-9

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine Taxa Track Local Climate Velocities. *Science*, *341*(6151), 1239-1242. https://doi.org/10.1126/science.1239352

Pirotta, V., Grech, A., Jonsen, I. D., Laurance, W. F., & Harcourt, R. G. (2019). Consequences of global shipping traffic for marine giants. *Frontiers in Ecology and the Environment*, *17*(1), 39-47. https://doi.org/10.1002/fee.1987

PISCO. (2007). *The Science of Marine Reserves (2nd Edition, International Version)*. www.piscoweb.org

Pistorius, P. A., Sydeman, W. J., Watanuki, Y., Thompson, S. A., & Orgeret, F. (2023). Chapter 8 - Climate change: The ecological backdrop of seabird conservation. In L. Young & E. VanderWerf (Eds.), *Conservation of Marine Birds* (pp. 245-276). Academic Press. https://doi.org/10.1016/B978-0-323-88539-3.00020-0

Pradel, R., Hines, J. E., Lebreton, J.-D., & Nichols, J. D. (1997). Capture-recapture survival models taking account of transients. *Biometrics*, *53*, 60-72. https://doi.org/10.2307/2533097

Prasetyo, A. P., McDevitt, A. D., Murray, J. M., Barry, J., Agung, F., Muttaqin, E., & Mariani, S. (2021). Shark and ray trade in and out of Indonesia: Addressing knowledge gaps on the path to sustainability. *Marine Policy*, *133*, 104714. https://doi.org/10.1016/j.marpol.2021.104714

Purwanto, Andradi-Brown, D. A., Matualage, D., Rumengan, I., Awaludinnoer, Pada, D., . . . Ahmadia, G. N. (2021). The Bird's Head Seascape Marine Protected Area network–Preventing biodiversity and ecosystem service loss amidst rapid change in Papua, Indonesia. *Conservation Science and Practice*, e393. https://doi.org/10.1111/csp2.393

Putra, M. I. H., Setyawan, E., Laglbauer, B. J. L., Lewis, S., Dharmadi, D., Sianipar, A., & Ender, I. (2020). Predicting mobulid ray distribution in coastal areas of Lesser Sunda Seascape: Implication for spatial and fisheries management. *Ocean & Coastal Management*, *198*, 105328. https://doi.org/10.1016/j.ocecoaman.2020.105328

QGIS.org. (2021). *QGIS Geographic Information System*. In QGIS Association. https://www.qgis.org/

Queiroz, N., Humphries, N. E., Couto, A., Vedor, M., da Costa, I., Sequeira, A. M. M., . . . Sims, D. W. (2019). Global spatial risk assessment of sharks under the footprint of fisheries. *Nature*, *572*(7770), 461-466. https://doi.org/10.1038/s41586-019-1444-4

R Core Team. (2021). *R: A language and environment for statistical computing*. In R Foundation for Statistical Computing. http://www.R-project.org/

Rambahiniarison, J., Agustines, A., Alexopoulos, K., Araujo, G., Armstrong, A. O., Arnold, S., . . . Barr, Y. (2022). Distribution of the reef manta ray *Mobula alfredi* and the oceanic manta ray *Mobula birostris* in the Philippines: A collaborative effort for conservation. *Journal of Fish Biology*, *n/a*(n/a). https://doi.org/10.1111/jfb.15283

Rambahiniarison, J. M., Lamoste, M. J., Rohner, C. A., Murray, R., Snow, S., Labaja, J., . . . Ponzo, A. (2018). Life history, growth, and reproductive biology of four mobulid species in the Bohol Sea, Philippines. *Frontiers in Marine Science*, *5*(269). https://doi.org/10.3389/fmars.2018.00269

Rayfield, B., Fortin, M.-J., & Fall, A. (2011). Connectivity for conservation: a framework to classify network measures. *Ecology*, *92*(4), 847-858. https://doi.org/10.1890/09-2190.1

Reinke, B. A., Miller, D. A. W., & Janzen, F. J. (2019). What have long-term field studies taught us about population dynamics? *Annual review of ecology, evolution, and systematics*, *50*(1), 261-278. https://doi.org/10.1146/annurev-ecolsys-110218-024717

Reisser, J., Proietti, M., Kinas, P., & Sazima, I. (2008). Photographic identification of sea turtles: method description and validation, with an estimation of tag loss. *Endangered Species Research*, *5*(1), 73-82. https://doi.org/10.3354/esr00113

Riedel, R., Caskey, L. M., & Hurlbert, S. H. (2007). Length-weight relations and growth rates of dominant fishes of the Salton Sea: implications for predation by fish-eating birds. *Lake and Reservoir Management*, *23*(5), 528-535. https://doi.org/10.1080/07438140709354036

Riekkola, L., Zerbini, A. N., Andrews, O., Andrews-Goff, V., Baker, C. S., Chandler, D., . . . Constantine, R. (2018). Application of a multi-disciplinary approach to reveal population structure and Southern Ocean feeding grounds of humpback whales. *Ecological Indicators*, *89*, 455-465. https://doi.org/10.1016/j.ecolind.2018.02.030

Robinson, O. J., Ruiz-Gutierrez, V., Fink, D., Meese, R. J., Holyoak, M., & Cooch, E. G. (2018). Using citizen science data in integrated population models to inform conservation. *Biological Conservation*, *227*, 361-368. https://doi.org/10.1016/j.biocon.2018.10.002

Rodríguez, J. P., Fernández-Gracia, J., Thums, M., Hindell, M. A., Sequeira, A. M. M., Meekan, M. G., . . . Eguíluz, V. M. (2017). Big data analyses reveal patterns and drivers of the movements of southern elephant seals. *Scientific Reports*, *7*(1), 112. https://doi.org/10.1038/s41598-017-00165-0

Rogers, T. D., Cambiè, G., & Kaiser, M. J. (2017). Determination of size, sex and maturity stage of free swimming catsharks using laser photogrammetry. *Marine Biology*, *164*(11), 213. https://doi.org/10.1007/s00227-017-3241-7

Rohner, C., Pierce, S., Marshall, A., Weeks, S., Bennett, M., & Richardson, A. (2013). Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. *Marine Ecology Progress Series*, *482*, 153-168. https://doi.org/10.3354/meps10290

Rohner, C. A., Flam, A. L., Pierce, S. J., & Marshall, A. D. (2017). Steep declines in sightings of manta rays and devilrays (Mobulidae) in southern Mozambique. *PeerJ PrePrints*. https://doi.org/10.7287/peerj.preprints.3051v1

Rojas López, K. E., Guadalupe, J. J., Gordillo-Romero, M., Montero-Oleas, A., Pazmiño, D. A., Guerrero, M., & Torres, M. L. (2022). Exploring the genetic diversity and population structure of *Mobula birostris* in two key aggregation zones in the Eastern Tropical Pacific. *Marine Ecology Progress Series*, *699*, 75-89. https://doi.org/10.3354/meps14171

Rojas, Y. E. T., Osuna, F. P., Herrera, A. H., Magaña, F. G., García, S. A., Villalobos Ortíz, H., & Sampson, L. (2014). Feeding grounds of juvenile scalloped hammerhead sharks (Sphyrna lewini) in the south-eastern Gulf of California. *Hydrobiologia*, *726*(1), 81-94. https://doi.org/10.1007/s10750-013-1753-9

Rosen, D. A. S., Gerlinsky, C. G., & Trites, A. W. (2018). Telemetry tags increase the costs of swimming in northern fur seals, Callorhinus ursinus. *Marine Mammal Science*, *34*(2), 385-402. https://doi.org/10.1111/mms.12460

Ruzzante, D. E., McCracken, G. R., Førland, B., MacMillan, J., Notte, D., Buhariwalla, C., . . . Skaug, H. (2019). Validation of close-kin mark–recapture (CKMR) methods for estimating population abundance. *Methods in Ecology and Evolution*, *10*(9), 1445-1453. https://doi.org/10.1111/2041-210X.13243

Sabatini, A. M., & Genovese, V. (2014). A sensor fusion method for tracking vertical velocity and height based on Inertial and barometric altimeter measurements. *Sensors*, *14*(8), 13324-13347. https://doi.org/10.3390/s140813324

Sandoval-Castillo, J., & Beheregaray, L. B. (2015). Metapopulation structure informs conservation management in a heavily exploited coastal shark (*Mustelus henlei*). *Marine Ecology Progress Series*, *533*, 191-203. https://doi.org/10.3354/meps11395

Schenk, T. (2005). *Introduction to photogrammetry* (Vol. 106). The Ohio State University.

Schoeman, R. P., Patterson-Abrolat, C., & Plön, S. (2020). A Global Review of Vessel Collisions With Marine Animals [Review]. *Frontiers in Marine Science*, *7*. https://doi.org/10.3389/fmars.2020.00292

Schofield, G., Esteban, N., Katselidis, K. A., & Hays, G. C. (2019). Drones for research on sea turtles and other marine vertebrates–A review. *Biological Conservation*, *238*, 108214. https://doi.org/10.1016/j.biocon.2019.108214

Schwarz, C. J., & Arnason, A. N. (1996). A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics*, *52*, 860-873. https://doi.org/10.2307/2533048

Sequeira, A. M., Thums, M., Brooks, K., & Meekan, M. G. (2016). Error and bias in size estimates of whale sharks: implications for understanding demography. *Royal Society Open Science*, *3*(3), 150668. https://doi.org/10.1098/rsos.150668

Setiawan, R., Wirasatriya, A., Hernawan, U., Leung, S., & Iskandar, I. (2020). Spatio-temporal variability of surface chlorophyll-*a* in the Halmahera Sea and its relation to ENSO and the Indian Ocean Dipole. *International Journal of Remote Sensing*, *41*(1), 284-299. https://doi.org/10.1080/01431161.2019.1641244

Setyawan, E., Duffy, C. A., Erdmann, M. V., Green, L., & Tindale, S. (2021, 5-8 July 2021). *First insights into the spatial ecology of endangered Mobula birostris in Aotearoa* New Zealand Marine Sciences Society Conference, Tauranga, New Zealand.

Setyawan, E., Erdmann, M. V., Gunadharma, N., Gunawan, T., Hasan, A. W., Izuan, M., . . . Constantine, R. (2022a). A holistic approach to manta ray conservation in the Papuan Bird's Head Seascape: Resounding success, ongoing challenges. *Marine Policy*, *137*, 104953. https://doi.org/10.1016/j.marpol.2021.104953

Setyawan, E., Erdmann, M. V., Lewis, S. A., Mambrasar, R., Hasan, A. W., Templeton, S., . . . Cerutti-Pereyra, F. (2020). Natural history of manta rays in the Bird's Head Seascape, Indonesia, with an analysis of the demography and spatial ecology of *Mobula alfredi* (Elasmobranchii: Mobulidae). *Journal of the Ocean Science Foundation*, *36*, 49–83. https://doi.org/10.5281/zenodo.4396260

Setyawan, E., Erdmann, M. V., Mambrasar, R., Hasan, A. W., Sianipar, A. B., Constantine, R., . . . Jaine, F. R. A. (2022b). Residency and use of an important nursery habitat, Raja Ampat's Wayag Lagoon, by juvenile reef manta rays (*Mobula alfredi*). *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.815094

Setyawan, E., Sianipar, A. B., Erdmann, M. V., Fischer, A. M., Haddy, J. A., Beale, C. S., . . . Mambrasar, R. (2018). Site fidelity and movement patterns of reef manta rays (*Mobula alfredi*: Mobulidae) using passive acoustic telemetry in northern Raja Ampat, Indonesia. *Nature Conservation Research*, *3*(4), 17-31. https://doi.org/10.24189/ncr.2018.043

Setyawan, E., Stevenson, B. C., Erdmann, M. V., Hasan, A. W., Sianipar, A. B., Mofu, I., . . . Constantine, R. (2022c). Population estimates of photo-identified individuals using a modified POPAN model reveal that Raja Ampat's reef manta rays are thriving. *Frontiers in Marine Science*, *9*, 1014791. https://doi.org/10.3389/fmars.2022.1014791

Setyawan, E., Stevenson, B. C., Izuan, M., Constantine, R., & Erdmann, M. V. (2022d). How big is that manta ray? A novel and non-invasive method for measuring reef manta rays using small drones. *Drones*, *6*(3), 63. https://doi.org/10.3390/drones6030063

Sherman, C. S., Simpfendorfer, C. A., Pacoureau, N., Matsushiba, J. H., Yan, H. F., Walls, R. H. L., . . . Dulvy, N. K. (2023). Half a century of rising extinction risk of coral reef sharks and rays. *Nature Communications*, *14*(1), 15. https://doi.org/10.1038/s41467-022-35091-x

Simpfendorfer, C. A., Kyne, P. M., Noble, T. H., Goldsbury, J., Basiita, R. K., Lindsay, R., . . . Jerry, D. R. (2016). Environmental DNA detects Critically Endangered largetooth sawfish in the wild. *Endangered Species Research*, *30*, 109-116. https://doi.org/10.3354/esr00731

Simpfendorfer, C. A., & Milward, N. E. (1993). Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. *Environmental Biology of Fishes*, *37*(4), 337-345. https://doi.org/10.1007/BF00005200

Simpson, S. J., Humphries, N. E., & Sims, D. W. (2021). Habitat selection, fine-scale spatial partitioning and sexual segregation in Rajidae, determined using passive acoustic telemetry. *Marine Ecology Progress Series*, *666*, 115-134. https://doi.org/10.3354/meps13701

Sims, D. W., Witt, M. J., Richardson, A. J., Southall, E. J., & Metcalfe, J. D. (2006). Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1591), 1195-1201. https://doi.org/10.1098/rspb.2005.3444

Snider, S., & Brimlow, J. (2013). An introduction to population growth. *Nature Education Knowledge*, *4*(4), 3. https://www.nature.com/scitable/knowledge/library/an-introduction-to-population-growth-84225544/

Sollmann, R., Gardner, B., Williams, K. A., Gilbert, A. T., & Veit, R. R. (2016). A hierarchical distance sampling model to estimate abundance and covariate associations of species and communities. *Methods in Ecology and Evolution*, *7*(5), 529-537. https://doi.org/10.1111/2041-210X.12518

Speed, C. W., Cappo, M., & Meekan, M. G. (2018). Evidence for rapid recovery of shark populations within a coral reef marine protected area. *Biological Conservation*, *220*, 308-319. https://doi.org/10.1016/j.biocon.2018.01.010

Stevens, G. M. W. (2016). *Conservation and population ecology of manta rays in the Maldives* [Dissertation, University of York]. York, United Kingdom.

Stevens, G. M. W., Fernando, D., & Di Sciara, G. N. (2018a). *Guide to the Manta and Devil Rays of the World*. Princeton University Press. https://doi.org/10.2307/j.ctvs32s7t

Stevens, G. M. W., Hawkins, J. P., & Roberts, C. M. (2018b). Courtship and mating behaviour of manta rays *Mobula alfredi* and *M. birostris* in the Maldives. *Journal of Fish Biology*, *93*(2), 344-359. https://doi.org/10.1111/jfb.13768

Stewart, J. D., Beale, C. S., Fernando, D., Sianipar, A. B., Burton, R. S., Semmens, B. X., & Aburto-Oropeza, O. (2016a). Spatial ecology and conservation of *Manta birostris* in the Indo-Pacific. *Biological Conservation*, *200*, 178-183. https://doi.org/10.1016/j.biocon.2016.05.016

Stewart, J. D., Hoyos-Padilla, E. M., Kumli, K. R., & Rubin, R. D. (2016b). Deep-water feeding and behavioral plasticity in *Manta birostris* revealed by archival tags and submersible observations. *Zoology*, *119*(5), 406-413. https://doi.org/10.1016/j.zool.2016.05.010

Stewart, J. D., Jaine, F. R. A., Armstrong, A. J., Armstrong, A. O., Bennett, M. B., Burgess, K. B., . . . Deakos, M. H. (2018a). Research priorities to support effective manta and devil ray conservation. *Frontiers in Marine Science*, *5*, 314. https://doi.org/10.3389/fmars.2018.00314

Stewart, J. D., Nuttall, M., Hickerson, E. L., & Johnston, M. A. (2018b). Important juvenile manta ray habitat at Flower Garden Banks National Marine Sanctuary in the northwestern Gulf of Mexico. *Marine Biology*, *165*(7), 111. https://doi.org/10.1007/s00227-018-3364-5

Stewart, J. D., Smith, T., Marshall, G., Abernathy, K., Fonseca-Ponce, I. A., Froman, N., & Stevens, G. M. W. (2019). Novel applications of animal-borne Crittercams reveal thermocline feeding in two species of manta ray. *Marine Ecology Progress Series*, *632*, 145-158. https://doi.org/10.3354/meps13148

Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, *7*(6), 533-555. https://doi.org/10.1007/BF01237820

Teitelbaum, C. S., & Mueller, T. (2019). Beyond Migration: Causes and Consequences of Nomadic Animal Movements. *Trends in Ecology & Evolution*, *34*(6), 569-581. https://doi.org/10.1016/j.tree.2019.02.005

Tetley, M. J., Braulik, G. T., Lanfredi, C., Minton, G., Panigada, S., Politi, E., . . . Hoyt, E. (2022). The Important Marine Mammal Area Network: A Tool for Systematic Spatial Planning in Response to the Marine Mammal Habitat Conservation Crisis [Original Research]. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.841789

Thomas, B., Holland, J. D., & Minot, E. O. (2011). Wildlife tracking technology options and cost considerations. *Wildlife research (East Melbourne)*, *38*(8), 653-663. https://doi.org/10.1071/WR10211

Thomson, J. A., Börger, L., Christianen, M. J. A., Esteban, N., Laloë, J. O., & Hays, G. C. (2017). Implications of location accuracy and data volume for home range estimation and fine-scale movement analysis: comparing Argos and Fastloc-GPS tracking data. *Marine Biology*, *164*(10), 204. https://doi.org/10.1007/s00227-017-3225-7

Todd Jones, T., Van Houtan, K. S., Bostrom, B. L., Ostafichuk, P., Mikkelsen, J., Tezcan, E., . . . Seminoff, J. A. (2013). Calculating the ecological impacts of animal-borne instruments on aquatic organisms. *Methods in Ecology and Evolution*, *4*(12), 1178-1186. https://doi.org/10.1111/2041-210X.12109

Torres, L. G., Nieukirk, S. L., Lemos, L., & Chandler, T. E. (2018). Drone up! Quantifying whale behavior from a new perspective improves observational capacity. *Frontiers in Marine Science*, *5*, 319. https://doi.org/10.3389/fmars.2018.00319

Town, C., Marshall, A., & Sethasathien, N. (2013). Manta Matcher: automated photographic identification of manta rays using keypoint features. *Ecology and Evolution*, *3*(7), 1902-1914. https://doi.org/10.1002/ece3.587

Towner, A. V., Wcisel, M. A., Reisinger, R. R., Edwards, D., & Jewell, O. J. (2013). Gauging the threat: the first population estimate for white sharks in South Africa using photo identification and automated software. *PLOS ONE*, *8*(6), e66035. https://doi.org/10.1371/journal.pone.0066035

Treves, A., & Santiago-Ávila, F. J. (2020). Myths and assumptions about human-wildlife conflict and coexistence. *Conservation Biology*, *34*(4), 811-818. https://doi.org/10.1111/cobi.13472

Trierweiler, C., Klaassen, R. H. G., Drent, R. H., Exo, K.-M., Komdeur, J., Bairlein, F., & Koks, B. J. (2014). Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20132897. https://doi.org/10.1098/rspb.2013.2897

Udyawer, V., Dwyer, R. G., Hoenner, X., Babcock, R. C., Brodie, S., Campbell, H. A., . . . Heupel, M. R. (2018). A standardised framework for analysing animal detections from automated tracking arrays. *Animal Biotelemetry*, *6*(1), 17. https://doi.org/10.1186/s40317-018-0162-2

Urban, D., & Keitt, T. (2001). Landscape Connectivity: A Graph-Theoretic Perspective. *Ecology (Durham)*, *82*(5), 1205-1218. https://doi.org/10.1890/0012-9658(2001)082[1205:LCAGTP]2.0.CO;2

Urban, D. L., Minor, E. S., Treml, E. A., & Schick, R. S. (2009). Graph models of habitat mosaics. *Ecology Letters*, *12*(3), 260-273. https://doi.org/10.1111/j.1461-0248.2008.01271.x

VanderWright, W. J., Dudgeon, C. L., Erdmann, M. V., Sianipar, A., & Dulvy, N. K. (2021). Extinction risk and the small population paradigm in the Micro-Endemic radiation of epaulette sharks. *Reference Module in Earth Systems and Environmental Sciences*. https://doi.org/10.1016/B978-0-12-821139-7.00130-6

Varkey, D. A., Ainsworth, C. H., Pitcher, T. J., Goram, Y., & Sumaila, R. (2010). Illegal, unreported and unregulated fisheries catch in Raja Ampat Regency, Eastern Indonesia. *Marine Policy*, *34*(2), 228-236. https://doi.org/10.1016/j.marpol.2009.06.009

Venables, S. K. (2020). *Ecology and conservation of a threatened reef manta ray (Mobula alfredi) population in southern Mozambique* [Dissertation, The University of Western Australia]. Perth, Australia.

Venables, S. K., Duinkerken, D. I., Rohner, C., & Marshall, A. D. (2020). Habitat use and movement patterns of reef manta rays *Mobula alfredi* in southern Mozambique. *Marine Ecology Progress Series*, *634*, 99-114. https://doi.org/10.3354/meps13178

Venables, S. K., Marshall, A. D., Armstrong, A. J., Tomkins, J. L., & Kennington, W. J. (2021). Genome-wide SNPs detect no evidence of genetic population structure for reef manta rays (Mobula alfredi) in southern Mozambique. *Heredity*, *126*(2), 308-319. https://doi.org/10.1038/s41437-020-00373-x

Veron, J. E., Devantier, L. M., Turak, E., Green, A. L., Kininmonth, S., Stafford-Smith, M., & Peterson, N. (2009). Delineating the coral triangle. *Galaxea, Journal of Coral Reef Studies*, *11*(2), 91-100. https://doi.org/10.3755/galaxea.11.91

Ward-Paige, C. A., Davis, B., & Worm, B. (2013). Global population trends and human use patterns of *Manta* and *Mobula* Rays. *PLOS ONE*, *8*(9), e74835. https://doi.org/10.1371/journal.pone.0074835

Ward-Paige, C., Keith, D., Worm, B., & Lotze, H. K. (2012). Recovery potential and conservation options for elasmobranchs. *Journal of Fish Biology*, *80*(5), 1844-1869. https://doi.org/10.1111/j.1095-8649.2012.03246.x

Warren, V. E., Constantine, R., Noad, M., Garrigue, C., & Garland, E. C. (2020). Migratory insights from singing humpback whales recorded around central New Zealand. *Royal Society Open Science*, *7*(11), 201084. https://doi.org/10.1098/rsos.201084

Watanabe, Y. Y., & Papastamatiou, Y. P. (2023). Biologging and Biotelemetry: Tools for Understanding the Lives and Environments of Marine Animals. *Annual Review of Animal Biosciences*, *11*(1), 247-267. https://doi.org/10.1146/annurev-animal-050322-073657

Weeks, S. J., Magno-Canto, M. M., Jaine, F. R. A., Brodie, J., & Richardson, A. J. (2015). Unique sequence of events triggers manta ray feeding frenzy in the Southern Great Barrier Reef, Australia [Article]. *Remote Sensing*, *7*(3), 3138-3152. https://doi.org/10.3390/rs70303138

Wei, S., Dan, G., & Chen, H. (2016). Altitude data fusion utilising differential measurement and complementary filter. *IET Science, Measurement & Technology*, *10*(8), 874-879. https://doi.org/10.1049/iet-smt.2016.0118

Weimerskirch, H., Cherel, Y., Delord, K., Jaeger, A., Patrick, S. C., & Riotte-Lambert, L. (2014). Lifetime foraging patterns of the wandering albatross: Life on the move! *Journal of Experimental Marine Biology and Ecology*, *450*, 68-78. https://doi.org/10.1016/j.jembe.2013.10.021

Werfeli, M., Ranacher, P., & Liechti, F. (2022). Gone with the wind: Inferring bird migration with light-level geolocation, wind and activity measurements. *Methods in Ecology and Evolution*, *13*(6), 1265-1274. https://doi.org/10.1111/2041-210X.13837

White, W. T., Corrigan, S., Yang, L., Henderson, A. C., Bazinet, A. L., Swofford, D. L., & Naylor, G. J. P. (2017). Phylogeny of the manta and devilrays (Chondrichthyes: mobulidae), with an updated taxonomic arrangement for the family. *Zoological Journal of the Linnean Society*, *182*(1), 50-75. https://doi.org/10.1093/zoolinnean/zlx018

White, W. T., Giles, J., Dharmadi, & Potter, I. C. (2006). Data on the bycatch fishery and reproductive biology of mobulid rays (Myliobatiformes) in Indonesia. *Fisheries Research*, *82*(1), 65-73. https://doi.org/10.1016/j.fishres.2006.08.008

Whitney, J. L., Coleman, R. R., & Deakos, M. H. (2023). Genomic evidence indicates small island-resident populations and sex-biased behaviors of Hawaiian reef Manta Rays. *BMC Ecology and Evolution*, *23*(1), 31. https://doi.org/10.1186/s12862-023-02130-0

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. In Springer-Verlag New York. https://ggplot2.tidyverse.org

Williams, K. A., Frederick, P. C., & Nichols, J. D. (2011). Use of the superpopulation approach to estimate breeding population size: an example in asynchronously breeding birds. *Ecology*, *92*(4), 821-828. https://doi.org/10.1890/10-0137.1

Wilson, L., Pine, M. K., & Radford, C. A. (2022). Small recreational boats: a ubiquitous source of sound pollution in shallow coastal habitats. *Marine Pollution Bulletin*, *174*, 113295. https://doi.org/10.1016/j.marpolbul.2021.113295

Womersley, F. C., Humphries, N. E., Queiroz, N., Vedor, M., da Costa, I., Furtado, M., . . . Sims, D. W. (2022). Global collision-risk hotspots of marine traffic and the world’s largest fish, the whale shark. *Proceedings of the National Academy of Sciences*, *119*(20), e2117440119. https://doi.org/10.1073/pnas.2117440119

Woodroffe, R., Thirgood, S., & Rabinowitz, A. (2005). *People and wildlife, conflict or co-existence?* (Vol. 9). Cambridge University Press.

Wright, G., Rochette, J., Gjerde, K. M., & Levin, L. A. (2018). Protect the neglected half of our blue planet. *Nature*, *554*(7691), 163-165.

Yokota, L., & Lessa, R. P. (2006). A nursery area for sharks and rays in Northeastern Brazil. *Environmental Biology of Fishes*, *75*(3), 349-360. https://doi.org/10.1007/s10641-006-0038-9

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R* (Vol. 574). Springer.