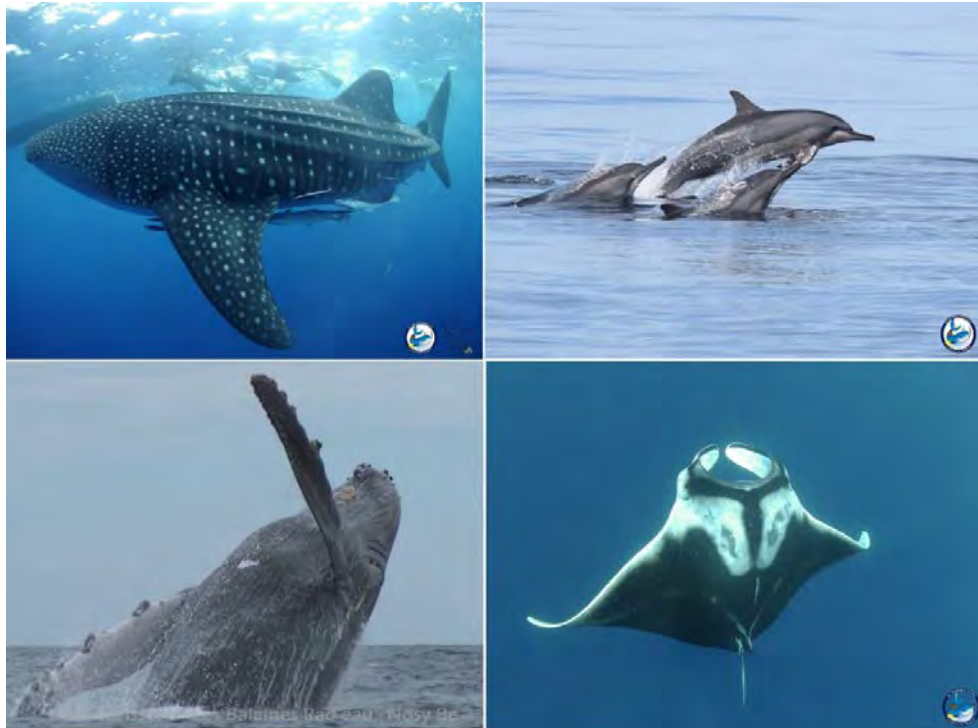


DISTRIBUTION AND HABITAT PREFERENCES  
OF MARINE MEGAFAUNA IN NOSY BE,  
MADAGASCAR



Submitted by

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This thesis is presented for the degree of MASTER OF SCIENCE at

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Photograph credits: *Les Baleines Rand'eau and Madagascar Whale Shark Project*



## Declaration

I declare that the work presented in this thesis was conducted on my own account and has not previously been submitted for examination to any other university.

Alicea Lubbé

February 2023

## Abstract

Marine megafauna have important ecological roles including the top-down regulation of lower trophic levels and the transport of nutrients. They are also charismatic species of socio-economic importance, due to their public appeal and focus for ecotourism. However, these taxa face numerous anthropogenic threats including bycatch, habitat-loss, noise disturbance, prey reductions, pollution, and vessel traffic. Northwest Madagascar has been identified as an important marine mammal area and whale shark aggregation site, yet limited information on megafauna within Madagascar exists. In this thesis, I investigated the community structure, distribution trends, related environmental factors (Chapter 2) and predicted habitat suitability (Chapter 3) using a species distribution modelling approach for marine megafauna around Nosy Be, North-west Madagascar. Data collection consisted of opportunistic boat-based surveys conducted while looking for whale sharks, mobulid rays and cetaceans. These activities were performed by dedicated ‘swim with whale shark’ tourism operators, *Les Baleines Rand'eau* and *Safari Baleine* during tourism activities directed by the *Madagascar Whale Shark Project* over four years (2016-2019). A total of 1792 sightings were reported with 13 identified species, including elasmobranchs: whale shark, *Rhincodon typus*; spinetail mobula ray, *Mobula japonica*; giant oceanic manta ray, *Manta birostris*; shortfin devil ray, *Mobula kuhlii*; balaenids: humpback whale, *Megaptera novaeangliae*; Omura's whale, *Balaenoptera omurai*, delphinids: Indo-Pacific bottlenose dolphin, *Tursiops aduncus*; spinner dolphin, *Stenella longirostris*; pantropical spotted dolphin, *Stenella attenuata*; Indian ocean humpback dolphin, *Sousa plumbea*; false killer whale, *Pseudorca crassidens*; melon-headed whale, *Peponocephala electra* and one cheloniid species: leatherback sea turtle, *Dermochelys coriacea*. Sightings were spatially analysed at a community level according to feeding guilds (i.e., filter feeders vs. predators), and distribution of the megafauna groups

were compared to selected remotely sensed physico-chemical data (sea surface temperature and chlorophyll-a concentration) and bathymetry charts (depth and slope) using generalized linear models (Chapter 2). All four variables had a significant effect on filter feeder distribution. Spatial distribution of filter feeder sightings peaked at an area of steep underwater topography (18-50m; x slope=0.5%) located on the west coast of Nosy Be, where foraging aggregations of large filter feeders (primarily *R. typus* and *B. omurai*) were frequently observed. Only SST had a significant effect on the relative abundance of animals in the predator feeding guild, which demonstrated a more longitudinal distribution along the continental shelf. The maximum entropy model (Maxent) was used for predicting habitat preference for the most frequently sighted species (Chapter 3). The distribution of whale sharks, mobulid rays and Omura's whales were significantly overlapped as they were abundant in two main hotspots, *Grand banc de l'entrée* (~10 km of the west coast) and near Nosy Mitsio island, (~50 km northeast of Nosy Be). Suitable habitat for the dolphins was in relatively shallow waters in temperatures <28°C near areas of steep changes in bathymetry. Bottlenose and spinner dolphins had a more widespread distribution across the continental shelf and humpback dolphin was closely associated with inshore reefs and occur in waters <10m. The coastal and inshore region of Nosy Be is an important habitat for a variety of megafaunal species, and the continental shelf provided essential areas for feeding and breeding. The results were similar to those presented for these species in other regions of the Indian Ocean (i.e., Eastern and Southern Africa; Western Australia; Seychelles) as well as outside of the Indian Ocean (i.e., Indonesia; Caribbean; North Atlantic). Thus the results from this thesis could be considered for management recommendations for marine conservation in the region. The value and limitations of data collected by citizen science were outlined (Chapter 4).

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## Statement of contribution

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## CHAPTER ONE: GENERAL INTRODUCTION

### 1.1. Marine megafauna

The term “marine megafauna” is used to describe large marine animals including marine mammals, such as dolphins and whales, as well as turtles, sharks and rays, certain seabirds, and polar bears. Megafauna are considered keystone species, meaning that they play an important biological role in ecosystems which affects the survival of other species in the community (Caro and O’doherly 1999). The biological role of marine megafauna is often defined by their feeding behaviour or strategy (Estes et al. 2016). These roles include animals ranging from planktivorous filter-feeders to meso and apex predators (Lotze and Worm 2009). In these roles, their top-down and bottom-up influence on ecosystems can be critical for ecosystem functioning (Wells 2009). For example, dolphins can influence ecosystems through top-down control of prey species and by facilitating in the feeding of other animals, including seabirds, as their foraging behaviour aggregates fish and other prey and pushes them to the sea surface (Estes et al. 2016). Sea turtles play an important role in the control of gelatinous zooplankton and contribute to beach health through nutrients from their eggs (Madden et al. 2008). Large filter feeders rely on zooplankton as a main source of food which strongly links them to the environmental conditions and they can thus be employed to indicate environmental change in an ecosystem (Rohner et al. 2013, Putra et al. 2016). By feeding on low trophic level species, filter-feeders control species composition from the bottom up (Heithaus et al. 2008, Putra et al. 2016).

Megafauna also play a vital role in nutrient cycles of marine systems, by consuming and transporting large amounts of nutrients through their short distance and long-distance movements (Kanwisher and Ridgway 1983, Kiszka et al. 2007). Thus, these large animals

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serve as vectors for nutrients, promoting nutrient cycling across ecosystem boundaries (e.g., between offshore/inshore habitats (Aragones et al. 2006, Roman et al. 2014, Temple et al. 2018). Additionally, movement of large species, such as the great whales, may also cause changes in the physical environment by creating drag and turbulence that aids in the mixing of sea water (Roman et al. 2014, Estes et al. 2016). As the spatial distribution of apex and meso-predators often reflect those of their prey and the productivity of the ecosystem (Dewar et al. 2006, Wiley et al. 2011), megafauna can be used as a proxy to assess the health and spatio-temporal variability of a system (Lambert et al. 2017a, 2017b, Augé et al. 2018). Through their feeding and movement strategies, megafauna modify habitats, maintain the community structure, and reflect the health of a system for other species (Kiszka et al. 2007, Heithaus et al. 2008, Temple et al. 2018).

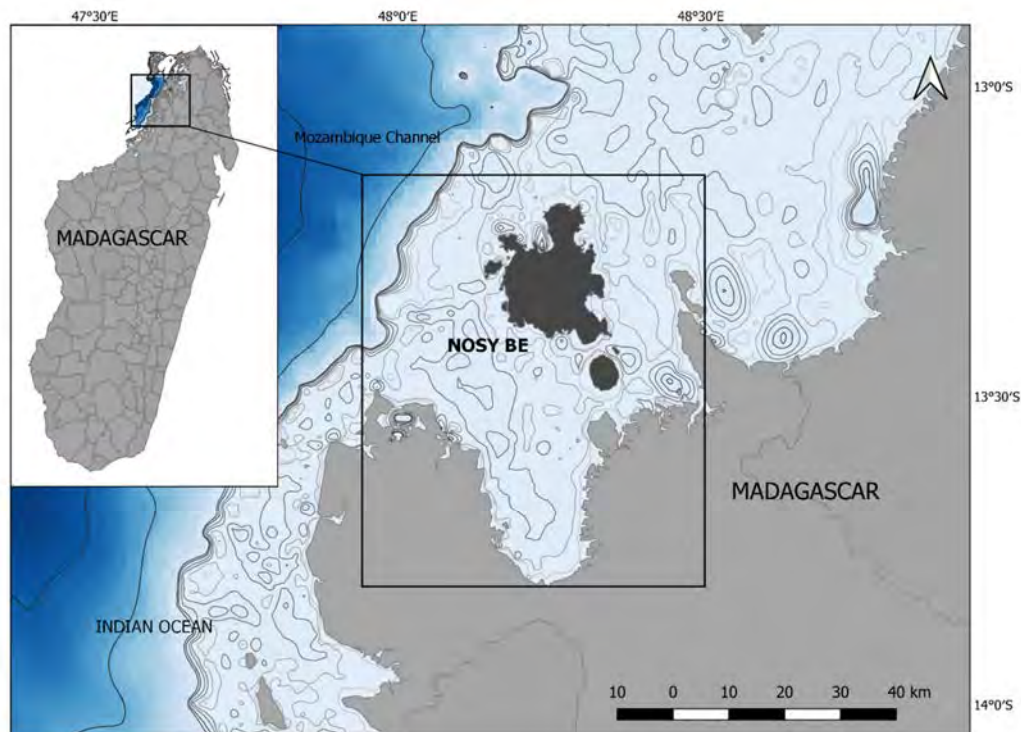
Megafauna are considered iconic charismatic species popular among the general public due to their favourable characteristics and perception of being non-threatening, known as ‘flagship’ species (Caro and O’doherly 1999, Germanov 2020). Many megafauna species are migratory with large home ranges that overlap with many other species, making them ‘umbrella’ species (Germanov and Marshall 2014). Species that are considered both good umbrella and flagship species are those that have: 1) a large body size and long-life spans; 2) large home ranges and long-range movements, but with specialized habitats within their range; 3) smaller population sizes; 4) perceived as non-threatening to the public; and are 5) sensitive to human disturbance. Such species can be employed as ‘surrogate’ species, used to drive conservation initiatives as the public perception of flagship species facilitate awareness, garner financial support, and drive marine conservation action (Caro and O’doherly 1999). Further, the protection of umbrella species requires the protection of large areas and habitats that ultimately protects many other species with overlapping habitats (Caro and O’doherly 1999, Stewart et al. 2018). Marine megafauna meet all the criteria necessary

to be regarded as surrogate species for conservation initiatives (Stewart et al. 2018, Germanov 2020). Thus, our understanding of marine megafaunal ecology is crucial for marine conservation and is needed for any management strategies and monitoring programs. Here, marine megafauna are specifically referring to cetaceans and large filter feeding elasmobranchs commonly occurring in the nearshore waters of north-west Madagascar.

## **1.2. Nosy Be, Madagascar**

Madagascar is the fourth largest island in the world and is located in the Western Indian Ocean (WIO) off the east coast of Africa. The island is separated from the mainland by the Mozambique Channel, surrounded by waters of the Southern Equatorial Current (SEC) and forming part of the Agulhas Large Marine Ecosystem (LME) (Obura et al. 2018). Madagascar's coastline stretches over 5000 km with east & west facing coasts, large latitudinal range and has a marine area of approximately 1300000 km<sup>2</sup> (Metcalf et al. 2007, Kryk et al. 2020). The island has a wide variety of tropical coastal habitats presenting productive habitats. Madagascar is recognised as one of the 25 biodiversity hotspots in the world and is thought to hold the greatest marine ecosystems diversity of any country in the WIO (Cooke et al. 2000, 2022, Bullock et al. 2021). The regions diverse ecosystems and wide western continental shelf have been shaped by the region's geological and oceanographic features (Cooke et al. 2022). Due to the varying physical oceanographic characteristics on the east and west sides of the island, northern Madagascar has a varied diversity of a unique mix of habitats, with many different types of bays, shelves, and islands (Kryk et al. 2020). The west coast has a broad shallow bank with a fossil reef at its edge, sheltering large bay systems. In the east, the narrow continental shelf leads to deep bays with canyons leading to deep waters. Sea temperatures around Madagascar are high and relatively

stable, owing to the surrounding warm waters of the South Equatorial Current. Mean annual sea surface temperatures (SST) range from 22°C in the south to 28°C in the north (Obura et al. 2018, Cooke et al. 2022). The east coast has a marked and constant thermocline at 100 m, whereas the west coast has a poorly defined thermocline at about 150 m (Pripp et al. 2014). Both the west and east coast bays have mixed habitats of seagrass and coral reefs, although there are also complex island systems on the north-west coast, forming an archipelago of several smaller islands originating from volcanic activity (Allen-Waller 2015). This includes the Nosy Be region (12.7°S to 13.7°S), a small island off the northwest coast of Madagascar with smaller surrounding islands of Nosy Komba, Nosy Iranja, and the Nosy Mitsio Archipelago (**Figure 1.1**).



**Figure 1.1.** Location of Nosy Be (12.7°S to 13.7°S), located along the northwest coastline of Madagascar.

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### 1.2.1. *Megafauna of Nosy Be*

Marine megafauna of the Nosy Be archipelago are remarkably diverse with whales, dolphins, dugongs, whale sharks, manta rays and marine turtles reported to be found in the coastal and offshore waters (Cerchio et al. 2015b, 2019, Trudelle et al. 2016, Diamant et al. 2018). Filter feeding elasmobranchs, mainly large sharks and rays includes the family *Rhincodontidae* and *Mobulidae*, from which four known species are found in the coastal water off Nosy Be: the whale shark, *Rhincodon typus*, spinetail devil ray, *Mobula mobular*, giant oceanic manta ray, *Manta birostris* and shortfin devil ray *Mobula kuhlii*. Whale sharks and manta rays are some of the largest fish species in the world with the whale shark reaching a size of at least 12 meters long, the giant manta ray measuring up to 7 meters wide (Colman 1997, McClain et al. 2015). Devil rays are between 1 and 5 meters wide (Stevens 2007, Rohner et al. 2013, Robinson et al. 2016). Whale sharks and mobulid rays are widely distributed, occurring in all tropical, subtropical and warm-temperate seas usually between latitudes 30°N and 35°S (Gunn et al. 1999, Couturier et al. 2012). They are large highly mobile epipelagic migratory species occurring in coastal and oceanic environments that travel long distances feeding on plankton and small fish (Nelson and Eckert 2007). Filter feeding sharks and rays tend to partake in large seasonal feeding aggregations at various sub-tropical and tropical coastal regions where plankton is commonly abundant (Marshall and Bennett 2010, Rohner et al. 2013). Their seasonal aggregations and movement patterns are thought to also be associated with geostrophic current circulation patterns, sea surface temperatures, and in some regions to coincide with increased productivity associated with coral spawning events (Rohner et al. 2020). Manta rays and recently observed devil rays (Murie and Marshall 2016) also regularly aggregate at ‘cleaning stations’ on shallow coastal reefs where ‘cleaner’ fish species remove parasites (O’Shea et al. 2010, Murie and Marshall 2016, White et al. 2018). Whale shark aggregations are known to occur seasonally in many locations with several sites being

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documented in the WIO (i.e., Madagascar, Tanzania, Mozambique and Seychelles), including in the Nosy Be region (Rowat et al. 2009, Diamant et al. 2018). The spatial and abundance patterns of the Malagasy whale shark and mobulid populations are still poorly documented (Diamant et al. 2021). In fact, only three studies exist on whale sharks in Madagascar which provide baseline information on occurrence, movement, and population demographics (Jonahson and Harding 2007, Diamant et al. 2018, 2021). In interview surveys, local fisherman and dive operators identified Nosy Be in the northwest of Madagascar as the region where whale shark sightings most frequently occur (Jonahson and Harding 2007). The coastal region of Nosy Be was only recognized as a possible seasonal feeding site in 2018 through photo-identification documenting 85 individuals in the area over one season (Diamant et al. 2018). To date the Madagascar Whale Shark Project has identified over 400 individuals and have estimated a total population size of approximately 700 sharks using a mark-recapture model (Diamant et al. 2021). To date, the only documentation of manta and mobula rays in Madagascar is through anecdotal reports by fisherman of incidental catch, divers and tourism activities (Kiszka et al. 2009b, Diamant et al. 2021).

Nosy Be also has a diverse marine mammal community with at least 23 of the 90 recognised species of baleen whales (*mysticeti*) and toothed whales (*odontoceti*) (six baleen whales and 16 toothed whales) have been recorded in the coastal and offshore waters surrounding Nosy Be (Cerchio et al., Kiszka et al. 2009a). More recently, an IUCN panel of marine mammal biologists identified northwest Madagascar and northeastern Mozambique Channel as an ‘Important Marine Mammal Area’ (IMMA) (IUCN-MMPATF 2020), largely based on a minimum of 24 marine mammal taxa including 23 cetaceans and the *Dugong dugon*, that have been documented in the region (Laran et al. 2017). Of the baleen whales, humpback, *Megaptera novaeangliae* and Omura’s whales, *Balaenoptera omurai* are sighted most frequently around Nosy Be. Humpback whales have a worldwide distribution (Fossette et al.

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2014, Purdon et al. 2020). Populations off south and east Africa spend summer months in the Southern Ocean. In autumn they move to breeding grounds off east Africa. Humpback whales breed in tropical waters and remain in tropical, sub-tropical, warm-temperate coastal waters for a short period over winter months and then move south-ward (Dulau et al. 2017, Purdon et al. 2020). Madagascar is a well-documented breeding ground for the Southwest Indian Ocean (SWIO) humpback whale population, occurring in all coastal waters during the austral winter (Trudelle et al. 2016). In the nearshore waters of Nosy Be, they are common during the mid and late breeding season, between July and October. The Omura's whale, *Balaenoptera omurai* are reported to occur primarily in tropical and warm-temperate locations (Cerchio et al. 2019). Most reports of sightings are nearshore indicating a predominantly coastal nearshore distribution. To date, the population off the Nosy Be coast is the only confirmed population of living Omura's whales, which occur mainly on the shallow continental shelf. These findings suggest that the population is restricted to the northwest region of Madagascar as a resident breeding population (Cerchio et al. 2015a) which is potentially non-migratory with a fragmented range distribution.

The Indian Ocean humpback dolphin, *Sousa plumbea* and Indo-Pacific bottlenose dolphin, *Tursiops aduncus* occur widely in the northwest region of Madagascar and are the most sighted dolphin species in the coastal waters of Nosy Be (Kiszka et al. 2009a, Cerchio et al. 2015b). *Sousa plumbea* occur in the coastal waters of the western Indian Ocean from approximately E20° to E95° longitude. Encounters are restricted to a narrow strip of shallow, coastal waters from False Bay, South Africa, to approximately the southern tip of India. *Tursiops aduncus* primarily occur in coastal waters in warm temperate and tropical waters of the Indo-Pacific region and often associated with *S. plumbea* off Nosy Be. However, their habitat seems to be more diverse than *S. plumbea* as they are also found in neritic continental shelf habitats. Spinner dolphins, *Stenella longirostris* and pantropical spotted dolphins,

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*Stenella attenuata* are frequently sighted in offshore areas off the Nosy Be coast, often in association with each other (Cerchio et al. 2014). Both species occur widely in all tropical and subtropical waters in coastal and offshore habitats. Small groups of common bottlenose dolphins, *Tursiops truncatus*, are also occasionally sighted in the offshore waters around Nosy Be (Kiszka et al. 2009a). Groups of false killer whale, *Pseudorca crassidens* and melon-headed whales, *Peponocephala electra* of similar size have also been reported in this area (Cerchio et al. In press).

Despite a large variety in size and life-history characteristics, marine megafauna mainly represents k-selected life histories and are considered to be slow growing, late maturing, and long-lived (Norman and Stevens 2007, Stevens 2007). Although there is limited information in the literature on age, growth and reproduction for both *Rhincodontidae* and *Mobulidae*, the whale shark's longevity has been estimated to be at least 80 years (Hsu et al. 2014). Whale sharks are thought to attain sexually maturity at approximately 9 meters in length (Colman 1997). Mobulid rays have a gestation period of one year and one pup every two to three years, making them among the least fecund marine fish in the world (Marshall and Bennett 2010). Detailed information on life-history is limited to relatively few cetacean species. Longevity estimates range from approximately 60 years to well over 100 years among the baleen whales (e.g., Bow head whale) and from 20 years to approximately 100 years for the toothed whales. Cetaceans produce single, large, developed calves with a mean gestation time of 12 months for most species. These slow growth rates and their low fecundity may put megafauna at increased at risk of population declines.

### **1.3. Habitat preference**

Information of the geographical distribution of species and communities in ecosystems is essential to understanding ecosystem functioning and processes, and to address conservation and spatial planning challenges (Ingram and Rogan 2002). In the marine environment there are complex interactions between physical and biological processes resulting in diverse and highly dynamic habitats that vary across multiple spatial and temporal scales (Lambert et al. 2017a, 2018). To exist within the large spatio-temporal variability in marine systems, species have evolved the ability to use target habitats with distinct and predictable oceanographic features for their survival, resulting in species-specific habitats (Lambert et al. 2017a, García-Barón et al. 2020). Many species may use several habitats depending on their availability and quality, while others might be specialised towards a specific habitat type. The high mobility and large home ranges of megafauna makes it costly to obtain distribution data and to identify essential areas to their life and reproduction (McClellan et al. 2014, García-Barón et al. 2020). However, the interaction between habitat variability, resource requirements and social behaviour are factors driving distribution, abundance, and habitat selection of megafauna (Lambert et al. 2017a, García-Barón et al. 2020). Oceanographic and physical features influence resource availability (Bouchet et al. 2015, 2020), which is considered the most crucial factor that determines the spatial distribution and habitat selection of marine species, due to productivity. Therefore, topographical features and temporal changes in physical and biological factors of the environment ultimately affect the spatial and seasonal distribution patterns and habitat use of megafaunal species (Wilson et al. 2007, Copping et al. 2018). Since it is difficult to obtain reliable information about megafauna prey distribution and abundance, physical and biological environmental variables can be used to make predictions about the distribution and habitat preferences of marine species (Augé et al. 2018, García-Barón et al. 2020).

This type of method is widely used to understand the statistical relationships between the occurrence of a species and the environment. Models combine species presence data with underlying environmental data to identify relationships between environmental factors and the occurrence of the species providing insight into prey distribution and identifying areas of high productivity (Guisan et al. 2002, Phillips and Dudík 2008, Zhang and Vincent 2018). By identifying the essential environmental predictors for productivity and prey distribution that best explain a species occurrence in the area, predictive habitat modelling methods can be used to predict suitable habitat for megafauna (Guisan et al. 2002, Phillips et al. 2006). These ecologically meaningful areas can then be defined in the region to inform conservation efforts. Therefore, predictive habitat modelling techniques using environmental predictors have become crucial in addressing conservation issues, especially for megafauna where widespread distributions make traditional boat-based surveys extremely challenging (Gnone et al. 2011). In Nosy Be, baseline ecological information, such as distribution and critical habitats remain unknown. and these questions represent a key knowledge gap that requires further research (Braulik et al. 2015, Cerchio et al. 2015b).

#### **1.4. Ecotourism**

Ecotourism refers to nature-based tourism that has minimal environmental impact, while providing maximum economic benefit to local communities and maximum satisfaction to tourists (Weaver and Lawton 2007). Ecotourism started growing in the 1990s and is since the fastest growing sector of the tourism industry (Moser 2014). Madagascar represents one of the world's most biodiverse areas with high levels of endemism that attracts large numbers of eco-tourists to the islands and surrounding marine environment annually (Cooke et al. 2022). As a result, ecotourism is now one of Madagascar's main industries and is increasing

at around 11% each year (Gardner et al. 2018). The contribution of ecotourism to the Gross Domestic Product is, however, still considered relatively small compared to the other WIO island countries (e.g., Seychelles, Mauritius)(Ziegler et al. 2021). This is due to its growth being severely restricted by political instability, with the most recent and one of the most damaging incidents of political unrest that emerged in 2009. After years of strong growth, international tourist arrivals plummeted by 57% in 2009, from 375,010 to 162,697 (Moser 2014). However, tourism is still considered a large contributor to the island's economy. The Central Bank of Madagascar estimates the tourism industry to contribute approximately US\$ 280 million per year (Moser 2014, Ziegler et al. 2021).

Nosy Be is the most well known and most popular tourist destination in the country, contributing the highest revenue to the tourism industry (Cooke et al. 2000). Marine-focused ecotourism including a wide variety of recreational activities such as scuba diving, snorkelling and whale watching primarily focus on marine megafauna. Thus, megafauna in their natural environment provide a large asset to the ecotourism industry. Nosy Be is an ideal scuba diving site with significant marine diversity, many charismatic megafauna, remarkable coral reef diversity and being one of the few seasonal aggregation sites of whale sharks making it a major tourism attraction for Madagascar (Diamant et al. 2018, Ziegler et al. 2021). The whale shark tourism industry in Nosy Be is rapidly growing. Ziegler et al. (2021) reported that the whale shark tourism industry in Nosy Be alone generates approximately US\$ 1.5 million during a three-month season (September – December). The study also found that the majority of tourists in Nosy Be would choose a tourism destination at which whale sharks are protected with tourist and operators supporting the protection of whale sharks and the regulations of tourist and whale shark interactions (Ziegler et al. 2021).

Madagascar is considered one of the poorest nations in the world with 75% of the country's inhabitants living below the poverty line (World Bank). Tourism is currently the second-

largest foreign exchange earner in the country and potentially can provide a way to increase economic growth, and thereby reduce poverty. A shift from previous marine resource extractive industries to tourism focused industries in a number of developing island nations (i.e., Bahamas and Palau) have already generated a higher economic wealth from marine resources (Mazzoldi et al. 2019). Ecotourism in the country is still in the early stages of development and there is large potential for the industry to grow as infrastructure and political stability improves.

#### *1.4.1. Citizen science*

The term "citizen science" here refers to the voluntary collection of data by non-scientific personnel for scientific purposes (Bonney et al. 2009). This data collection method has become increasingly useful in marine science in recent years (Silvertown 2009, Lodi and Tardin 2018b). This increase is largely driven by the need for long-term and large-scale datasets for the implementation of conservation management policies to mitigate marine threats (McKinley et al. 2017). Citizen science has the potential to enhance and facilitate rapid collection of widespread data where there is lack of resources and specialists in the region (Bonney et al. 2009, Matear et al. 2019). The traditional methods used for ecological data collection for megafauna require expensive equipment and most often need to cover large areas over long periods of time (Alessi et al. 2019). This requires a lot of resources and time. Citizen science is, therefore, particularly important for obtaining ecological data and monitoring of biodiversity in developing countries where funding for science is limited and local participation and empowerment is necessary for long-term monitoring. This approach has already contributed vital ecological data for the conservation of megafauna species within critical habitats in developing island countries (Cigliano et al. 2015, McKinley et al. 2017).

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For example, Davies et al. (2012) used citizen science to monitor whale shark populations ultimately leading to protection of habitats to conserve this species.

Despite the potential and benefits citizen science provides, there are concerns of potential problems with data quality and bias regarding the approach of citizen science. Specific concerns include the lack of attention to study design, inconsistent or suboptimal training and absent or problematic standardization and verification methods (Burgess et al. 2017). Some recognized bias relates to tourism operators that target preferred areas and actively search for encounters with closer to ports or launch areas and targeting areas with higher chance of encounters (Burgess et al. 2017, dos Santos and Bessa 2019). Despite these concerns, previous investigations have validated data derived from citizen science with comparisons to rigorous scientific survey data (Kiszka et al. 2007, Oldekop et al. 2011, Davies et al. 2012, Lodi and Tardin 2018). Indeed, it is worth noting that some investigations have even reported volunteer accuracy to be on par with researchers (Oldekop et al. 2011). Citizen science could provide robust long-term ecological data that can fill knowledge gaps in tourism targeted species. As such, the recognition of the importance of citizen science as an important data source for conservation biology by the scientific community is increasing worldwide.

In addition to contributing ecological data on marine species, citizen science creates the opportunity for engagement and educating of the community in the processes involved to policy-making and implementation of management strategies (Germanov and Marshall 2014, dos Santos and Bessa 2019). Furthermore, the participation of the public in citizen science facilitates the awareness of ecological issues in the area and potentially increases stakeholder commitment and involvement in the project. Popular tourism destinations are ideal locations for collecting data through citizen science initiatives on charismatic flagship species that are economically valuable and facilitate greater understanding by the local population (Germanov and Marshall 2014, Stewart et al. 2018, Germanov 2020).

## **1.5. Threats**

Due to their life history and behaviour characteristics, marine megafauna are inherently susceptible to anthropogenic pressures (Halpern et al. 2007, Lotze and Worm 2009). Marine megafauna are facing several threats including being caught as bycatch, hunting, habitat degradation, tourism disturbances, and overfishing of prey species (Razafindrakoto et al. 2008, Braulik et al. 2018). It is estimated that global megafauna populations have declined by 89% from their historical baseline with some exceptions, such as the recent recovery of whale populations post-whaling due to increased protective legislation (Lotze and Worm 2009, Dulvy et al. 2014).

Marine megafauna are directly and indirectly threatened by fishing practices. Some fisheries are still targeting megafaunal species such as sharks and rays, and are frequently caught and killed as bycatch. In particular, the exploitation rates of elasmobranchs by fisheries have increased dramatically since the 1950s in response to a high demand for shark fins, gill rakers, meat and liver from mainly Asian countries (Stevens 2007, Dulvy et al. 2014). This has resulted in the expansion of shark targeted commercial fisheries as well as several small-scale and artisanal fisheries targeting sharks (Couturier et al. 2012, Stewart et al. 2018). Since the year 2000 Madagascar's population has increased by 80% and artisanal fisherman and boats have increased five-fold (McVean et al. 2005). This places more pressure on marine resources, depleting cetacean prey species, increasing by-catch and habitat degradation. Madagascar's elasmobranch populations continue to be exploited with shark finning, overfishing and bycatch known to occur on a daily basis in many areas, including Nosy Be (Razafindrakoto et al. 2008, Cerchio et al. 2015b). Mobulid ray gill rakers are particularly valuable in the international trade and the targeting of large aggregations at critical habitats and migratory channels have been reported and considered a major threat to their populations (Schipper et al., Couturier et al. 2012). Significant declines whale shark sightings have been

noted in well-know hotspots such as Indonesia and Mozambique (Diamant et al. 2018). To curb this decline, the species has been added to Appendix II of the Convention on International Trade in Endangered Species (CITES) and globally endangered on the IUCN Red List of Threatened species in 2016 (Pierce and Norman 2016, Table 1.1). In the WIO, significant declines in sightings of whale sharks have been reported in the well-known hotspots of Mozambique and Seychelles since 2012, and the species remains poorly studied and unprotected in several WIO nations (Sequeira et al. 2012). All *mobulidae* species have recently been added to Appendix II of the Convention on International Trade in Endangered Species (CITES) and to Appendices I and II of the Convention of Migratory Species (CMS) (**Table 1.1**).

The historical exploitation of cetaceans and marine turtles is well documented (Valdivia et al. 2019). However, global conservation efforts have resulted in dramatic declines in the exploitation of these species over the past decades leading to population recoveries for some species. The illegal hunting of dolphins for consumption and international sale, and the exploitation of marine turtles for cultural purposes is still reported by most fishery surveys in Madagascar (Cerchio et al., Razafindrakoto et al. 2008, Kiszka et al. 2009b). Dolphins and whale sharks are also being taken as by-catch (Daimant et al. 2018). Hunting of cetaceans has only been reported to occur opportunistically at a few locations, mainly in southwest Madagascar (Humber et al. 2015). Andrianarivelo (2001) reported that spinner dolphins, bottlenose dolphins and endangered humpback dolphins are the most bycaught species, primarily between August and December (**Table 1.2**). Overexploitation of prey are indirectly affecting megafauna and their habitats. In Madagascar, local coastal communities largely rely on artisanal fishing for their livelihoods, which poses a potential threat to Madagascar's marine megafauna (Razafindrakoto et al. 2008, Kiszka et al. 2009a). Hydrocarbon exploration, coastal industrial development and passive mining also pose a threat to the

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northwest coastal cetacean populations of Madagascar (Cerchio et al. 2015b, 2019). The use of high intensity seismic sound for acoustic mapping of the sea floor and crust, and acoustic imaging of substrata can potentially disturb cetacean behaviour, interfere with vocal communication, and even result physical damage if in close proximity (Southall et al. 2013, Cerchio et al. 2014). Petroleum surveys have occurred in the northwest region of Madagascar since 2005 and impacts on the cetacean populations have been documented. For example, in 2008 a stranding of approximately 200 recorded melon headed whales in the Loza Lagoon system was most likely a response to the acoustic seafloor profiling (Southall et al. 2013). Currently there is extensive offshore petroleum exploration and coastal mining planned in the northwest region of Madagascar, which presents a distinct threat to coastal cetacean populations in the area and potential pollution of the coastal waters surrounding Nosy Be (Cerchio et al. 2014, 2019).

**Table 1.1.** The present marine megafauna in Nosy Be, Madagascar, their IUCN conservation status and known distribution.

<b>Scientific name</b>	<b>Common name</b>	<b>IUCN status</b>	<b>Population trend</b>	<b>Distribution</b>	<b>Habitat</b>
<i>Rhincodon typus</i>	Whale shark	Endangered	Decreasing	Circumglobal tropical and subtropical	Coastal pelagic
<i>Manta birostris</i>	Oceanic manta ray	Endangered	Decreasing	Circumglobal tropical and subtropical	Coastal pelagic
<i>Mobula mobular</i>	Spinetail devil ray	Endangered	Decreasing	Circumglobal tropical, subtropical and temperate	Coastal pelagic oceanic
<i>Mobula kuhlii</i>	Shortfin devil ray	Endangered	Decreasing	Indian Ocean and Western Central Pacific	Coastal pelagic

**Table 1.2.** The present marine megafauna in Nosy Be, Madagascar, their IUCN conservation status and known distribution.

Scientific name	Common name	IUCN status	Population trend	Distribution	Habitat
<i>Megaptera novaeangliae</i>	Humpback whale	Least concern	Increasing	Global	Coastal pelagic and oceanic
<i>Balaenoptera omurai</i>	Omura's whale	Data deficient	Unknown	Tropical, subtropical	Coastal epipelagic
<i>Tursiops aduncus</i>	Indo-pacific bottlenose dolphin	Near threatened	Unknown	Indo-Pacific warm temperate and tropical	Coastal epipelagic and oceanic
<i>Stenella longirostris</i>	Spinner dolphin	Least concern	Unknown	Tropical, subtropical	Coastal pelagic and oceanic
<i>Sousa plumbea</i>	Indian ocean humpback dolphin	Endangered	Decreasing	West, East Indian Ocean and Southeast Atlantic	Coastal pelagic, subtidal intertidal
<i>Stenella attenuata</i>	Pantropical spotted dolphin	Least concern	Unknown	Tropical, subtropical	Coastal pelagic and oceanic
<i>Tursiops truncatus</i>	Common bottlenose dolphin	Least concern	Unknown	Tropical to temperate	Coastal pelagic, oceanic, supratidal, and inland
<i>Pseudorca crassidens</i>	False killer whale	Near threatened	Unknown	Tropical to warm temperate	Pelagic, deep offshore oceanic
<i>Peponocephala electra</i>	Melon headed whale	Least concern	Unknown	Tropical, subtropical	Pelagic, deep offshore oceanic

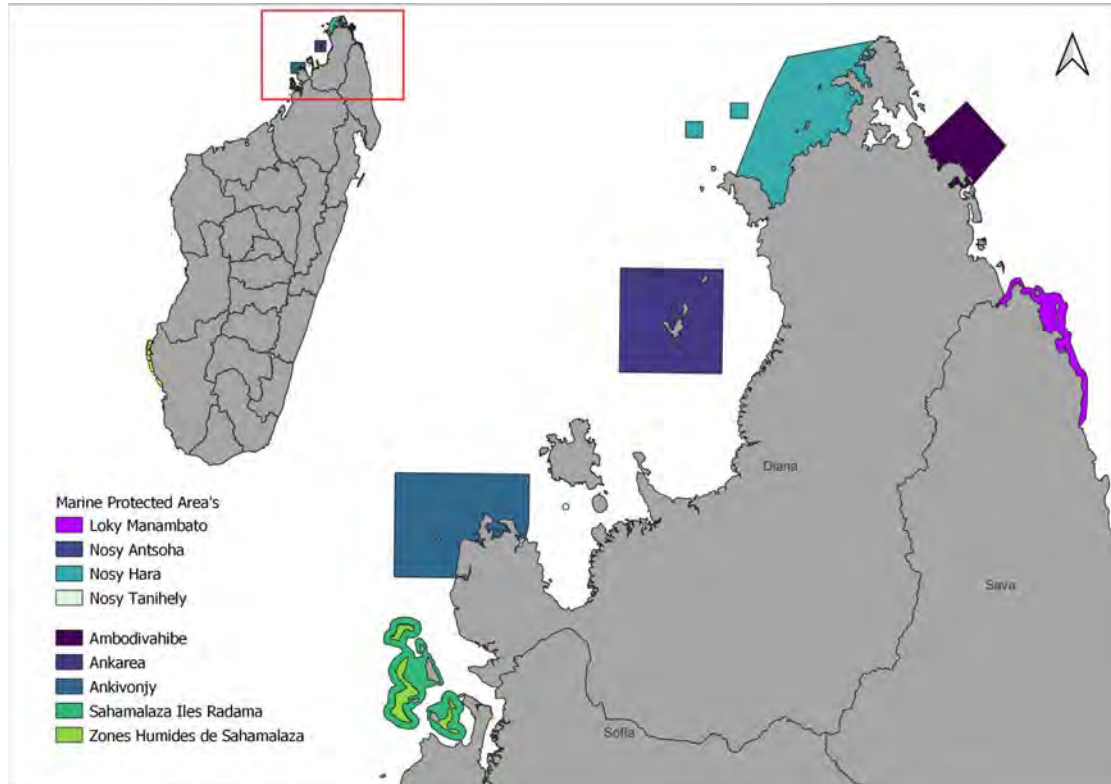
*1.5.1. Conservation*

A conservation status assessment of the WIO found Madagascar's marine region to have the highest species richness index for the entire WIO (Bullock et al. 2021). These authors also reported Madagascar to have the highest number of data deficient species assessed against the IUCN red list. The most prevalent of data deficient species were marine mammals at 30% of all species. Within the northwest region of Madagascar there are currently two established marine protected areas (MPAs), Ankivonji (1394 km<sup>2</sup>) and Ankarea (1356 km<sup>2</sup>), located to the southwest and northeast of Nosy Be respectively, which received permanent protection status in April 2015 by the Wildlife Conservation Society (Gardner et al. 2020) (**Figure 1.2**). These MPAs are community-managed and were designated for economic benefit to local communities by protecting local resources and promoting sustainable fisheries (Gardner et al. 2020).

Information on species distribution and areas of critical habitats are key for management decision making as well as assessing the efficacy of any proposed or existing MPA (Bailey and Thompson 2009, Augé et al. 2018). Madagascar is a data deficient region with limited knowledge and critical habitats of the megafauna community remains unknown. Thus, Nosy Be can greatly benefit from improved knowledge on the species and systems (Humber et al. 2015). Identifying high value biodiversity areas in Nosy Be can provide knowledge to the communities and non-governmental organizations (NGOs) who manage these regions, in order to direct research and improve management measures (Rogers et al. 2010, Ratsimbazafy et al. 2019). Understanding the relationship between species and the environment can contribute to the ecological knowledge and improve our understanding of species. Further it can contribute oceanographical knowledge and give insight to the system and habitat in the region (Davis et al. 2002). Collaborative research among groups and inclusion of the entire marine megafauna community in the Nosy Be region has been

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recommended to further understand the ecological processes that drive the distribution of the groups, and to improve coordinated monitoring of the Nosy Be megafauna community (Cooke et al. 2022). Thus, the area presents a key knowledge gap for further research to aid in the conservation of marine megafauna within the region (Kiszka et al. 2009b, Cerchio et al. 2015b, Temple et al. 2018).



**Figure 1.2.** Current Marine Protected Areas in northern Madagascar.

## 1.6. Aims and Objectives

With this thesis, I aim to provide a basis of key ecological knowledge on the cetacean and filter feeding elasmobranch populations that occur in the coastal waters of the Nosy Be region in northwest Madagascar to aid in the conservation of marine megafauna and critical habitats in the region. Specifically, the main objectives of this thesis are to:

Characterize the marine megafauna community structure for the Nosy Be region, Madagascar (**Chapter 2**),

Determine the distribution trends of the marine megafauna community (i.e., cetaceans, whale sharks and mobulid rays) around Nosy Be (**Chapter 2**),

Identify essential environmental variables influencing the distribution of the megafauna community at fine scale (**Chapter 2**),

Identify high value biodiversity hotspots and suitable marine megafauna habitats on a species level (**Chapter 3**),

Characterize megafauna habitat preference and critical habitats within the area (**Chapter 3**),

Recognize the contributions and limitations of citizen science in the context of marine tourism data (**Chapter 4**) and,

Provide science-based recommendations for marine spatial planning and management strategies in northwest Madagascar (**Chapter 4**)

CHAPTER TWO: TRENDS IN LONG-TERM OCCURRENCE  
AND ESSENTIAL OCEAN VARIABLES OF SIGHTED MARINE  
MEGAFAUNA AROUND NOSY BE, MADAGASCAR



Photo credits: *Stéphanie Floirat*

## 2.1. Abstract

Large marine vertebrates such as cetaceans, elasmobranchs and sea turtles (marine megafauna) have a high socio-economic value in many developing nations, particularly those relying on tourism activities. However, investigating habitat preferences and the distribution of marine megafauna is challenging as collecting data on widespread animals in the field can be costly. Citizen science projects using tourism activities around the globe have proved to be effective in documenting the occurrence of these charismatic species, at little to no cost to the researchers. The aim of this study was to use opportunistic sightings of megafauna from tourism operators collected over four years (2016-2019) to investigate their distribution and the related habitat use off Nosy Be, northwest, Madagascar. Sightings were spatially analysed, and distribution of the megafauna were compared to selected remotely sensed physico-chemical data (water depth; slope; sea surface temperature and chlorophyll-a) and bathymetry charts. A total of 1792 sightings were recorded, including cetaceans and filter feeding elasmobranchs. For community level assessment, data were pooled into two groups according to feeding guilds: filter feeders (i.e. humpback whale; *Megaptera novaeangliae*, Omura's whale; *Balaenoptera omurai*, whale shark; *Rhincodon typus*, spinetail mobula ray; *Mobula japonica*, giant oceanic manta ray; *Mobula birostris*, shortfin devil ray; *Mobula kuhlii* and predators (i.e. Indo-Pacific bottlenose dolphin; *Tursiops aduncus*, spinner dolphin; *Stenella longirostris*, pantropical spotted dolphin; *Stenella attenuata*, Indian ocean humpback dolphin; *Sousa plumbea*, false killer whale; *Pseudorca crassidens*, melon-headed whale; *Peponocephala electra*, leatherback sea turtle; *Dermochelys coriacea*. All four environmental variables had a significant effect on filter feeder distribution (Depth:  $p = 0.0003$ ; Slope:  $p < 0.0001$ ; SST:  $p = 0.021$ ; chl-a:  $p = 0.001$ ). Spatial distribution of sightings peaked off the west coast of Nosy Be in an area of steep underwater topography (Depth: 18-50m,  $p = 0.0003$ ; Slope: slope=0.5%,  $p = <0.0001$ ), where foraging aggregations of large filter feeders

(primarily *R. typus* and *B. omurai*) were frequently observed. Only SST had a significant effect on the relative abundance of predators ( $p < 0.0001$ ) and predators demonstrated a more distribution along the continental shelf. This study shows the potential of citizen science in modelling habitats use to provide important background information, in previously unstudied areas.

### **2.2. Introduction**

In many areas globally, our current understanding of the ecology of many species of marine megafauna is limited, particularly the drivers of their distribution, habitat preference and movement patterns (Cerchio et al. 2014). Given that many megafauna are highly mobile species that have broad home ranges, migrate long distances and spend long periods of time underwater data collection presents logistical constraints, which are resource consuming. Despite these difficulties, this data are critical to management and conservation efforts as marine megafauna populations are increasingly threatened by overfishing, bycatch, habitat degradation, tourism disturbances, and climate change (Cerchio et al. 2015b, 2019, Trudelle et al. 2016, Braulik et al. 2018). The lack of baseline data in many areas, particularly in the developing world, makes it difficult to plan effective conservation actions. Actions, such as implementation of Marine Protected Areas (MPAs), are often needed to protect critical habitats and threatened species; however, an understanding of habitat preference is a key component to achieve this conservation goal (Hueter et al., 2005).

Prey availability is one of the most important factors that determines the spatial distribution and habitat selection of marine species (Bouchet et al. 2015, 2020). Since it is difficult to obtain reliable information of the occurrence of the prey of marine megafauna, physical and biological environmental predictors can be employed as proxies to determine and make predictions about

## Chapter 2: Community Distribution Trends

the distribution and habitat characteristics of marine species (Augé et al. 2018, García-Barón et al. 2020). Essential environmental variables are defined as those variables that best predict the presence of marine megafauna community for a specific area (Lindström and Langenheder 2012, Constable et al. 2016). Using a combination of dynamic ocean variables can help define the environmental drivers of the community occurrence (Wiens and Graham, 2005) and characterize the high value habitats in the area such as feeding sites (i.e., whale sharks and rays) and breeding grounds (i.e., humpback whales). The biological productivity of a region is linked to the oceanography of the area (Guisan and Zimmermann 2000, Reiss et al. 2011, Bradie and Leung 2017), and often predicts distribution of prey species. Thus, the oceanographic features, and temporal changes in the physical and biological factors of the environment can ultimately determine the spatial and seasonal distribution patterns of marine megafauna who follow these prey (i.e., dolphins) (Grémillet et al. 2008, Whitehead et al. 2010, Jones et al. 2019).

Marine megafauna typically has strong site fidelity on a seasonal or yearly basis, targeting habitats with distinct and predictable oceanographic features. This results in species-specific habitats characterized by a unique set of environmental variables (Lambert et al. 2017a, García-Barón et al. 2020). As a result, environmental variables such as bathymetry, water temperature, substrate type and chlorophyll-a concentration can be employed as environmental predictors for mapping essential areas with high megafaunal occurrence.

Nosy Be, Madagascar, is recognised as an important hotspot for large marine species such as the whale shark (*Rhincodon typus*), sea turtles, endangered Indian Ocean humpback dolphin (*Sousa plumbea*) and the rare Omura's whales (*Balaenoptera omurai*) as its nutrient-rich waters concentrate valuable food sources for these larger marine species (Cerchio et al. 2015b, 2019, Trudelle et al. 2016, Diamant et al. 2021). For many of the species that routinely occur off the coast of Nosy Be, there are significant knowledge gaps on population abundance, distribution, and habitat use (Cerchio et al. 2014, Diamant et al. 2018). However, this understanding is

## Chapter 2: Community Distribution Trends

critical both biologically but also socio-economically as Nosy Be is the most visited tourist destination in the country with marine megafauna related activities contributing the highest revenue to the tourism industry (Ziegler et al. 2021). As Nosy Be is a highly diverse but data deficient region, it can benefit from innovative data collection methods, such citizen science during tourism activities, to further marine conservation in the area. Here opportunistic sighting presence-only data collected by tourism operators over a period of 4 years (2016–2019) were used to determine the distribution and habitat preference of the megafaunal community along the coast of Nosy Be, Madagascar. The study aims to characterize habitat preference by assessing the relationship between available environmental variables and their distribution to determine which environmental variables are driving their distribution. Further, the purpose of the study is to provide a basis of baseline ecological knowledge on the cetacean and filter feeding elasmobranch populations and their habitat characteristics in the waters of northwest Madagascar to aid in the conservation of marine megafauna and their critical habitats in this high value region. The rationale for such a multi-taxon ecological study were to collate information on a large range of taxa, to provide baseline distribution maps of the megafauna community in order to identify high value biodiversity hotspots and identify key environmental drivers in the most cost-effective manner.

### **2.3. Methods and materials**

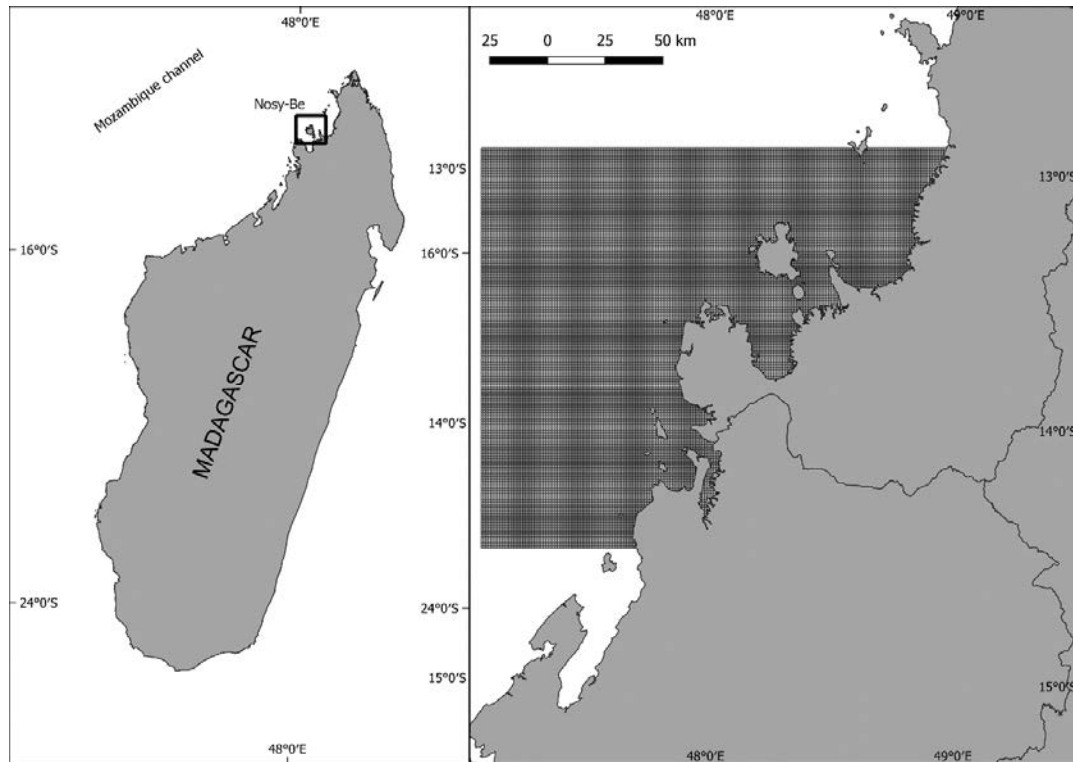
#### *2.3.1. Study site and data collection*

Data were collected using boat-based activities within the waters the islands of Nosy Be, Nosy Sakatia, and the Ampasindava Peninsula of mainland Madagascar (Figure 2.1). Boat surveys were conducted opportunistically during tourism activities looking predominately for whale

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sharks, mobulid rays and cetaceans by dedicated ‘swim with whale shark’ tourism operators, *Les Baleines Rand'eau* and *Safari Baleine* as well as by the *Madagascar Whale Shark Project* in the nearshore region of the island Nosy Be (13.39° S, 48.20° E) in Antsiranana Province in north-western Madagascar (**Figure. 2.1**). Search efforts were focused at approximately 10 to 40 km offshore southwest of Nosy Be depending on the experience of tourism professionals. Surveys were conducted in the morning (between approx. 8:00AM and 12:00PM) on an opportunity basis between 2016 and 2019. Sightings were recorded through recreational marine activities such as diving, snorkelling and whale watching. The information recorded for each sighting included identifying the species of large marine vertebrate, the geographical coordinates or location of the sighting using a Geographic Position System device, time and date of sighting, and group size. Surveys were not standardized or randomized in terms of spatial coverage, with distances covered and search locations varying according to shark sightings and conditions.

The surveyed region was divided into 1 × 1 km grid squares with a grid extent of 13.82° N; 47.07° W, 48.47° E; 12.90° S in QGIS-OSGeo4W-3.22.0 software (**Figure. 2.1**). Sightings of megafauna groups were plotted in QGIS. Species with a sample size <3 were removed. The total number of sightings per 1 km x 1km grid cells was calculated and, taking into account group size, total number of individuals were calculated for each grid cell, giving number of sightings per km<sup>2</sup> (sighting rate) and number of individuals per km<sup>2</sup> (relative abundance) for the study region.



**Figure 2.1.** Location of Nosy Be region ( $13.39^{\circ}$  S,  $48.20^{\circ}$  E), located along the northwest coastline of Madagascar indicating the extent of the study site ( $13.82^{\circ}$  N;  $47.07^{\circ}$  W,  $48.47^{\circ}$  E;  $12.90^{\circ}$  S, shaded grey)

### 2.3.2. *Environmental variables*

Bathymetric features, depth, and slope, and two oceanographic features SST and chlorophyll-*a* concentration (chl-*a*) were included as covariates representing essential environmental variables. Bathymetric data were obtained from the GEBCO dataset in 1 arc second raster format (**Table 2.1**). Slope was calculated in QGIS from the bathymetric data using the slope tool. Monthly level 2 Sea surface temperature (SST) and chlorophyll-*a* (chl-*a*) concentration (Aqua MODIS) measurements were obtained from the Ocean colour database by The NASA Ocean Biology Processing Group (OBPG) (Feldman G.C. and McClain C.R. 2022) from the Aqua MODIS satellite as  $4\text{km}^2$  pixels raster format (**Table 2.1**). The data was processed in the

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software SeaDAS (NASA OBPB) by binning monthly measurements into years and mean long-term values were calculated for all four years during the time the sightings were recorded (2016-2019)(Baith 2001). The environmental data were summarized for each 1kmx1km grid cell in QGIS, where the means for each environmental variable were calculated per km<sup>2</sup> and linked with the sightings data using a spatial join function.

**Table 2.1.** Environmental predictor variables and data sources available for the study area

Predictor	Unit	Source
Topographic:		
Bathymetry	m	GEBCO ( <a href="https://www.gebco.net">https://www.gebco.net</a> )
Slope	%	GEBCO and QGIS derived
Oceanographic:		
Sea surface temperature (SST)	°C	Aqua MODIS - OBPB ( <a href="https://oceancolor.gsfc.nasa.gov">https://oceancolor.gsfc.nasa.gov</a> )
Chlorophyll-a concentration (Chl)	mg.m <sup>-3</sup>	Aqua MODIS - OBPB ( <a href="https://oceancolor.gsfc.nasa.gov">https://oceancolor.gsfc.nasa.gov</a> )

### 2.3.3. *Statistical analysis*

To investigate the occurrence trends and environmental drivers of coastal megafauna sightings around Nosy Be, presence-only positive count data were analysed according to the framework outlined by Zuur et al. (2009) employing R v 4.1.1 software (R Core Team 2021). For general analysis purposes, species were grouped into feeding guilds, i.e., filter feeders and predatory species (Compagno 1984, Balance 2018). Normality was tested using Q-Q plots of residuals and fits, as well as a Shapiro–Wilks test, and response variables were log-transformed where

## Chapter 2: Community Distribution Trends

needed. Due to the unbalanced data collection over the four years and seasons, the data was pooled together for all four years and seasonality was not included in the statistical analysis.

Prior to the analysis, all environmental variables were assessed for collinearity by calculating the pairwise Spearman correlation coefficients ( $r$ ) and the variance inflation factor (VIF; Zuur et al. 2010). None of the pairs of variables showed high correlation ( $r \geq |0.7|$  and  $VIF > 3$ ; Zuur et al. 2010, Dormann et al. 2013) and therefore, all variables were included in the analysis (**Table 2.1**). To identify the most important environmental covariates explaining the distribution of sightings and relative abundance, zero-truncated negative binomial (ZTNB) generalized linear models (GLM), were fitted using the `zerotrunc` function in the `countreg` package (Achim et al. 2008). Separate models were constructed following the Information-Theoretic framework to evaluate the competing models by assessing their relative support based on the AIC value corrected for small sample sizes (AICc) and Akaike weight ( $\omega_i$ ) (Anderson and Burnham 2002) to preserve sample size as logistical constraints of opportunistic data did not warrant a balanced data set. For multivariate models, global models were fitted and then followed a backward stepwise deletion process using the `step` function, to determine the optimal model by selecting that which minimized the Akaike information criterion (AIC), and with a  $\Delta AIC < 2$  (see **Table 2.2**). The influence of the environmental variables (depth, slope, SST, and chlorophyll-a) on the sighting rate and relative abundance of filter feeder and predator species, separately, was assessed using the long-term data set (2016-2019). For the relative abundance of filter feeding and predator species the best fit model included depth + Slope + SST. For filter feeders, the best model of sighting rate included Slope + SST + Chlor-a and SST + chlor-a for the predators (**Table 2.2**).

**Table 2.2.** Model selection using backwards stepwise selection of GLMs, indicating the four best fit models. Models having the lowest AIC and a  $\Delta AIC < 2$  were the best models (in bold).

Subset	Candidate models	AIC	$\Delta AIC$	$w$
<b>Predators</b>				
Relative abundance				
(n=144)	<b>depth + slope + SST</b>	<b>1692.789</b>	<b>0.0000</b>	<b>0.6948</b>
	depth + slope + SST + chlor-a	1694.866	2.0770	0.2459
	slope + SST+ chlor-a	1697.712	4.9227	0.0593
	depth + SST + chlor-a	1712.908	20.1193	0.0000
Sighting rate				
	<b>SST + chlor-a</b>	<b>281.0216</b>	<b>0.0000</b>	<b>0.4779</b>
(n=143)	slope + SST+ chlor-a	282.3826	0.0000	0.4634
	depth + SST + chlor-a	283.1636	0.7811	0.3136
	depth + slope + SST + chlor-a	284.5366	2.1540	0.1579
	depth + slope + SST	286.3081	3.9255	0.0651
<b>Filter feeders</b>				
Relative abundance				
(n=525)	<b>depth + slope + SST</b>	<b>3855.644</b>	<b>0.0000</b>	<b>0.4393</b>
	slope + SST+ chlor-a	3855.880	0.2359	0.3904
	depth + slope + SST + chlor-a	3857.652	2.0084	0.1609
	depth + SST + chlor-a	3863.342	7.6977	0.0094
Sighting rate				
(n=525)	<b>slope + SST + chlor-a</b>	<b>3035.332</b>	<b>0.0000</b>	<b>0.4966</b>
	depth + slope + SST	3036.397	1.0652	0.2916
	depth + slope + SST + chlor-a	3037.082	1.7500	0.2070
	depth + SST + chlor-a	3044.613	9.2806	0.48

## 2.4. Results

### 2.4.1. Occurrence trends

The highest number of sightings were recorded between August and December (84%) due to the increase in whale sharks and rays during this season and thus a higher demand for excursions (**Appendix II**). In total, there were 1754 sightings (1284 elasmobranchs and 460 cetaceans) and an estimated 8576 individuals (2239 elasmobranchs and 6322 cetaceans) from 13 species (**Figure 2.2**). Of the species sighted, two major functional feeding guilds were recognised: filter feeders including balaenopterids (humpback whale; *Megaptera novaeangliae*, Omura's whale; *Balaenoptera omurai*, Ballance 2018) and elasmobranchs (whale shark; *Rhincodon typus*, spinetail mobula ray; *Mobula japonica*, giant oceanic manta ray; *Manta birostris*, shortfin devil ray; *Mobula kuhlii*, Compagno 1984); and predators, including delphinids (Indo-Pacific bottlenose dolphin; *Tursiops aduncus*, spinner dolphin; *Stenella longirostris*, pantropical spotted dolphin; *Stenella attenuate*, Indian ocean humpback dolphin; *Sousa plumbea*, false killer whale; *Pseudorca crassidens*, melon-headed whale; *Peponocephala electra*, Ballance 2018), and one cheloniid species (leatherback sea turtle; *Dermochelys coriacea*). The five most frequently observed species were the whale shark, humpback whale, spinetail devil ray, Omura's whale, and Indo-Pacific bottlenose dolphin which accounted for 90% of all sightings (**Table 2.3**). The whale shark was the most frequently sighted species (accounting for 65% of all observations) whilst spinner dolphins were by far the most abundant species (accounting for 43% of the total counts) (**Figure 2.3**). The less frequently sighted species were the melon-headed whale, false killer whale and pantropical spotted dolphin, but these were some of the largest groups when they were sighted (**Table 2.3**). The maximum group size for melon-headed whales was approximately 800 individuals recorded for 3 different groups ( $n=3$  groups,  $\bar{x}=350$  ind  $\pm$  SD = 396). The second largest groups

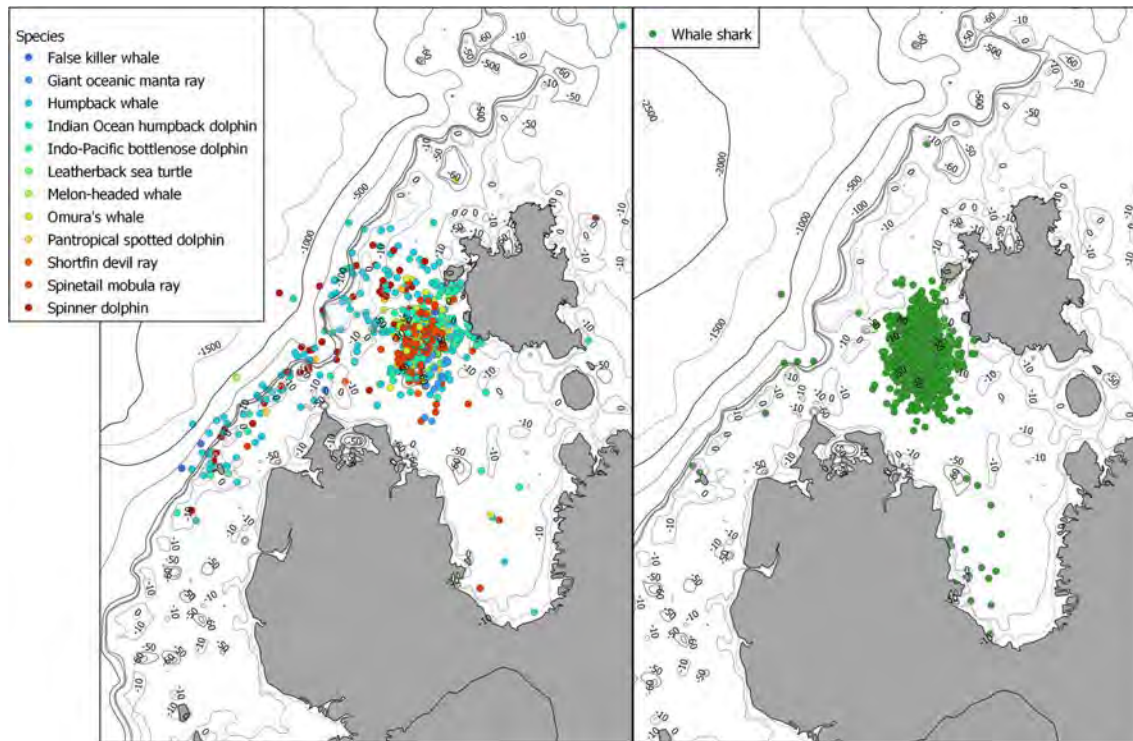
## Chapter 2: Community Distribution Trends

of 500 individuals ( $n=51$  groups,  $x = 80$  ind  $\pm$  SD = 90) were of spinner dolphins. The combined mean group size of the dolphins (Indo-Pacific bottlenose; spinner; spotted dolphin; humpback; false killer whale and melon-headed whale) observed in Nosy Be was 13 individuals ( $n = 72$ ,  $x = 13.0 \pm$  SD = 47.42), ranging from 1 to 800 animals. Mobulid rays (i.e., spinetail devil ray; manta ray and shortfin devil ray) had a mean of 8 individuals ( $n = 144$ ,  $x = 7.63 \pm$  SD = 12.73, median = 3, range 2 – 75). During the four-year period, there was a significant increase in sightings annually with the most sightings in total recorded in 2018 ( $n=603$ ); however, whale sharks encounters were highest during 2019 ( $n=354$ ) and cetacean encounters in 2018 ( $n=46$ ).

**Table 2.3.** Number of sightings and individuals (and proportions) of each encounter, 2016-2019

<b>Species</b>	<b>Common name</b>	<b>Number of sightings</b>	<b>% sightings</b>	<b>Number of individuals</b>	<b>% individuals</b>
<b><i>Filter feeders</i></b>					
<i>Rhincodon typus</i>	<i>Whale sharks</i>	1140	65,0	1140	13,3
<i>Manta birostris</i>	<i>Oceanic manta ray</i>	27	1,5	60	0,7
<i>Mobula kuhlii</i>	<i>Shortfin devil ray</i>	16	0,9	195	2,3
<i>Megaptera novaeangliae</i>	<i>Humpback whale</i>	196	11,2	423	4,9
<i>Mobula japanica</i>	<i>Spinetail devil ray</i>	101	5,8	844	9,8
<i>Balaenoptera omurai</i>	<i>Omura's whale</i>	94	5,4	167	1,9
<b><i>Predators</i></b>					
<i>Tursiops aduncus</i>	<i>Indo-Pacific bottlenose dolphin</i>	78	4,4	580	6,8
<i>Stenella longirostris</i>	<i>Spinner dolphin</i>	51	2,9	3715	43,3
<i>Sousa plumbea</i>	<i>Indian Ocean humpback dolphin</i>	26	1,5	125	1,5
<i>Dermochelys coriacea</i>	<i>Leatherback sea turtle</i>	10	0,6	15	0,2
<i>Stenella attenuata</i>	<i>Pantropical spotted dolphin</i>	6	0,3	119	1,4
<i>Pseudorca crassidens</i>	<i>False killer whale</i>	6	0,3	143	1,7
<i>Peponocephala electra</i>	<i>Melon-headed whale</i>	3	0,2	1050	12,2
	<i>All Species</i>	1754	100	8576	100

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**Figure 2.2.** Presence points recorded for each species in Nosy Be, Madagascar, over the four-year observation period used in the models, bathymetry from GEBCO.



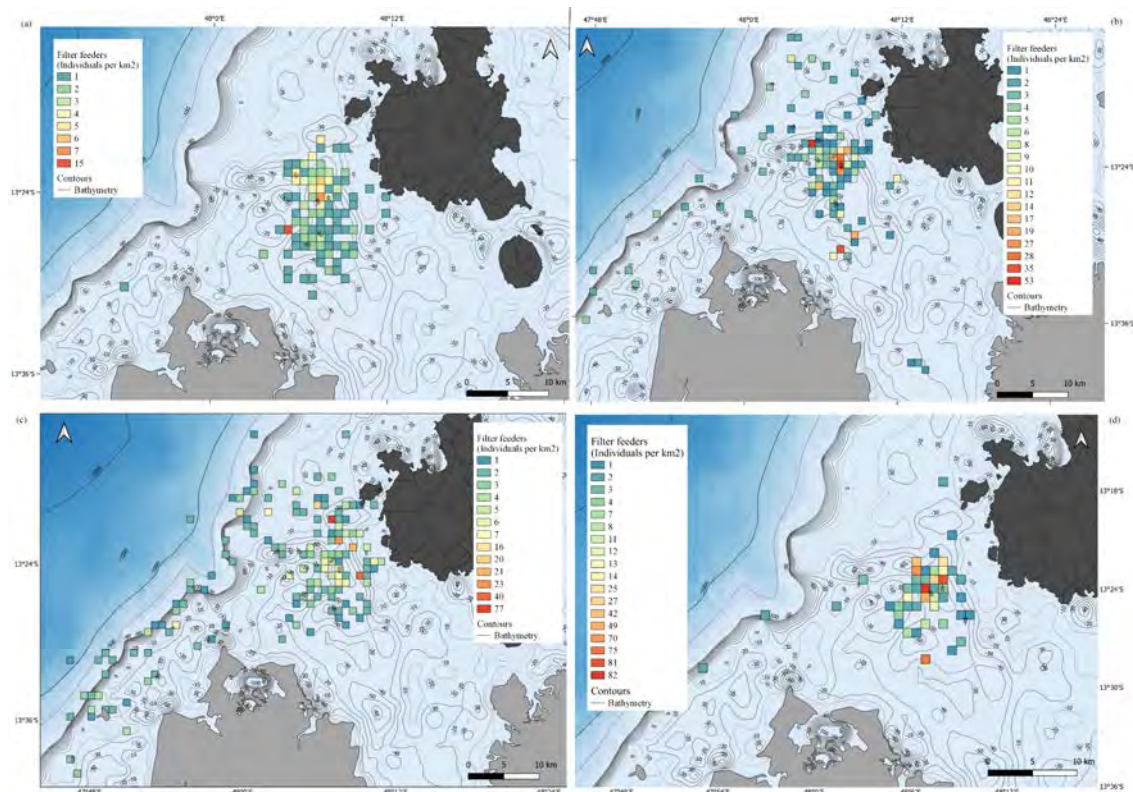
**Figure 2.3.** Five most frequently sighted species in Nosy Be, Madagascar, over the four-year observation period: a) whale shark; *Rhincodon typus*, b) humpback whale; *Megaptera novaeangliae*, c) spinetail mobula ray; *Mobula japonica*, d) Omura's whale; *Balaenoptera omurai*, and e) Indo-pacific bottlenose dolphin; *Tursiops aduncus*, (Credit: *Les Baleines Rand'eau and Madagascar Whale Shark Project*).

#### 2.4.2. Essential environmental variables

Sightings of filter feeding species were recorded in waters of ~60m deep on average ( $x = 63.0$  m  $\pm$  SD = 233.6, median = 35, range 5–3060 m); with an average slope of 1% ( $x = 1.1 \pm$  SD = 1.98; median 0.5, range 0–13.5); sea surface temperatures (SST) in a narrow range from 27.7 to 29.4 °C; ( $x = 28.2 \pm$  SD = 0.2) and a mean total chlorophyll-a concentration (chl-a) of 0.40 mg.m<sup>-3</sup> ( $x = 0.38 \pm$  SD = 0.31, median =0.34, range 0.21 – 1.47). Sighting rate of filter feeders varied significantly with slope (df=1 likelihood ratio test (LRT) = 63.73 p <0.0001), SST (df=1

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LRT = 8.86  $p = 0.003$ ) and total chl-a concentration (df=1 LRT = 53.94  $p < 0.0001$ ). Further, all four environmental variables had a significant effect on the relative abundance of filter feeder species (Depth: df=1 LRT = 13.075  $p = 0.0003$ ; Slope: df=1 LRT = 38.96  $p < 0.0001$ ; SST: df=1 LRT=5.346  $p = 0.021$ ; chl-a: df=1 LRT = 10.48  $p = 0.001$ ; **Table 2.4**). The highest abundance of filter feeders recorded within one of the 1kmx1km grid squares (48,11271° S; 13,40158° E) for all four years was 103 individuals. The second highest abundance was 95 individuals (48,10325° S; 13,38364° E) which was both at a mean depth of 50 meters, a slope of 0.5%, in SST of 28°C and mean chlorophyll-a concentrations of 0.35 mg.m<sup>-3</sup> (**Figure 2.4**; **Figure 2.6**).

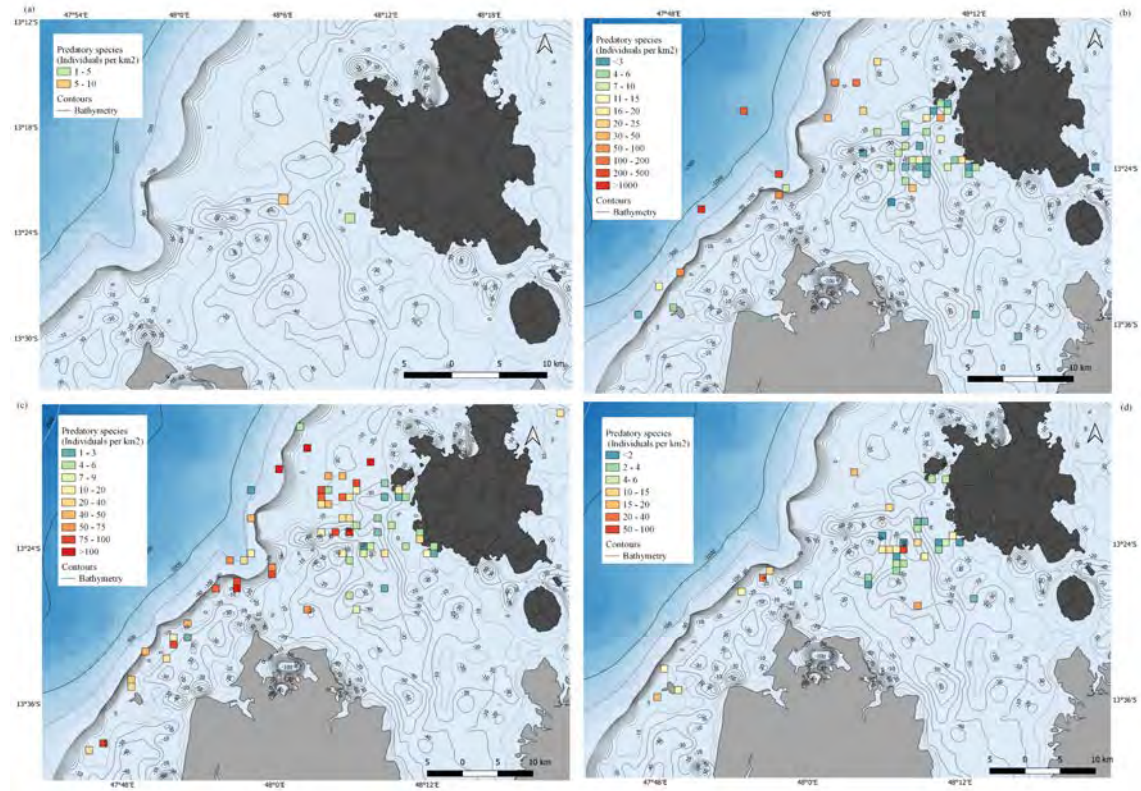


**Figure 2.4.** Sightings of coastal filter feeding megafauna (whale shark; oceanic manta ray; spinetail mobula ray; shortfin ray; humpback whale; Omura’s whale) in terms of the number of individuals sighted per km<sup>2</sup> in the Nosy Be, Madagascar archipelago over the four-year period: (a) 2016, (b) 2017, (c) 2018, and (d) 2019.

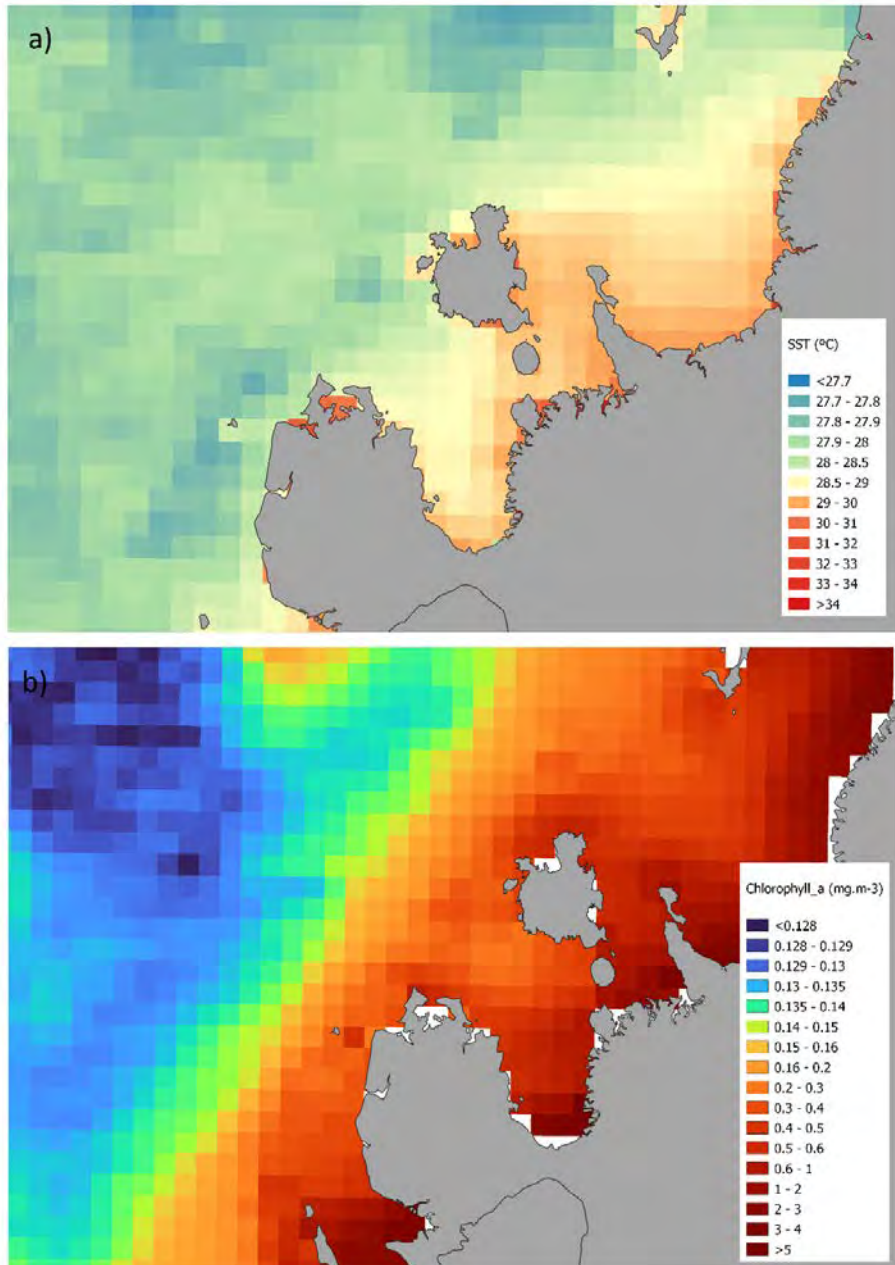
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Predator sightings rate varied significantly with SST ( $df=1$  LRT = 8.86  $p = 0.003$ ) and total chl-a concentration ( $df=1$  LRT = 53.94  $p < 0.0001$ ). However, only SST had a significant effect on relative abundance of sighted predators (SST:  $df=1$  LRT = 25.15  $p < 0.0001$ ; Depth:  $df=1$  LRT = 3.34  $p = 0.07$ ; Slope:  $df=1$  LRT = 2.99  $p = 0.08$ ; **Table 2.2**). Predators were recorded in waters of approximately 80m depth on average ( $x = 79.8 \text{ m} \pm \text{SD} = 269.8$ ; median 20, range 0–2770 m); with the average slope of 1.6% ( $x = 1.58 \pm \text{SD} = 2.61$ ; median 0.5, range 0–13); in SSTs from 27.8 to 29.2 °C; ( $x = 28.2 \pm \text{SD} = 0.2$ ) and mean total chl-a of 0.35  $\text{mg}\cdot\text{m}^{-3}$  ( $x = 0.35 \pm \text{SD} = 0.08$ , median = 0.34, range 0.13 – 0.88; **Figure 2.6**). Dolphin groups were not frequently re-sighted within the same regions (e.g.,  $\text{km}^2$ ) except for six records of similar size humpback dolphin groups which were sighted in the same region on consecutive days. In total, 63% of spinner dolphin, 100% of humpback dolphin and 100% of bottlenose dolphin sightings were in waters less than 60 meters deep, with SSTs of  $28 \text{ }^\circ\text{C} \pm 1.2$ . The two largest groups of dolphins were recorded in the deepest waters (**Figure 2.5**).

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**Figure 2.5.** Relative abundance (number of individuals sighted per km<sup>2</sup>) of coastal cetacean species (spinner dolphin; Indo-Pacific bottlenose dolphin; Indian ocean humpback dolphin; pantropical spotted dolphin; false killer whale; melon headed whale; leatherback Sea turtle) in the Nosy Be archipelago over a period of four years: (a) 2016, (b) 2017, (c) 2018, and (d) 2019.



**Figure 2.6.** Illustration of the mean a) sea surface temperature (°C) and b) Chlorophyll-*a* concentration (mg.m<sup>-3</sup>) in the Nosy Be archipelago for the four years (2016-2019) in 4km<sup>2</sup> resolution binned in SeaDAS and created in QGIS (Aqua MODIS – OBPG).

**Table 2.4.** Results of megafauna occurrence modelling grouped by functional feeding guilds, including whether bottom depth(m), bottom slope (%), SST (sea surface temperature), and chlorophyll-a concentration (Chlor-a) influenced sighting rate and relative abundance off the Nosy Be coast of Madagascar. Presented as p-values, with \* indicating significance ( $p < 0.05$ ), - indicating variable removed from best fit model.

	Filter feeders		Predators	
	Sighting rate	Relative abundance	Sighting rate	Relative abundance
Depth	-	0.00*	-	0.06
Slope	<0.0001*	<0.0001*	-	0.08
SST	0.00 *	0.00*	0.00 *	<0.0001*
Chlor-a	<0.0001*	-	0.14	-

## 2.5. Discussion

Here, I investigated the community structure and spatial trends of megafauna and identified essential ocean variables shaping their fine-scale habitat preferences in Nosy Be, Madagascar. Overall, the marine megafauna community investigated consisted of 13 megafaunal species documented in the study. These included five toothed whale species (Indo-Pacific bottlenose dolphin; Indian Ocean humpback dolphin; Pantropical spotted dolphin; false killer whale; melon-headed whale), two baleen whale species (humpback whale; Omura’s whale), four elasmobranch species (whale shark; spinetail devil ray; shortfin devil ray; manta ray), and one sea turtle species (leatherback sea turtle) (Kiszka et al. 2009a, 2009b, 2010, Diamant et al. 2021). Megafauna sightings increased noticeably annually, this is most probably due to the increase in interest and dedication to the citizen science program by the tourism operators. The

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megafauna community in Nosy Be is diverse in elasmobranchs and cetaceans with six species listed as endangered and two near threatened as their IUCN status documented in this study (Parsons 2016, Pierce and Norman 2016). There was virtually no spatial inter-annual variability for both filter feeders and cetaceans. Megafauna were most frequently sighted in the same regions in all four years, as tourism operators had preferred areas to visit. Nosy Be is a heterogeneous region including shallow bay, shelf, slope, and oceanic waters possibly contributing to a diverse community in a small study area (Kiszka et al. 2010). The majority of megafauna sightings occurred approximately 10 km off the west coast of Nosy Be across a reef edge referred to as *Grand banc de l'entrée* (Jonahson and Harding 2007). Whale shark, mobulid rays, Omura's whales and Indian Ocean humpback dolphin occurrence was particularly high in this area. *Grand banc de l'entrée* is characterized by a steep increase in depth from 18 to 50 meters (i.e., a steep slope) bordering both reef and seagrass habitat together with a large shallow bank (*Banc des, 5m*) on the east and a steep continental shelf (1000m) on the west (Jonahson and Harding 2007, GEBCO 2021). *Grand banc de l'entrée* is a known hotspot to local fisherman and dive operators, who previously identified the site as the region where whale shark sightings occur most frequently (Jonahson and Harding 2007). The offshore dolphins (Indo-Pacific bottlenose dolphin; Pantropical spotted dolphin; spinner dolphin) and humpback whales were most frequently sighted across the continental shelf close to edge near oceanic waters.

### 2.5.1. *Filter feeders*

The sighting rates of filter feeding species were high across the shelf waters of the island during the spring to summer season (i.e., whale shark, spinetail devil ray, humpback whale and Omura's whale) with clear trends in frequency of occurrence. These frequently used regions

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were characterised by waters 40 to 50 meters deep, a mean slope of 1.5%, with SSTs ranging between 28 and 29°C and a total chlorophyll-a concentration of ~0.35 mg milligram per cubic meter. Despite significant influence of all the environmental descriptors used here (depth, slope, SST and chl-a) on the occurrence of filter feeders, these relationships differed slightly between species (García-Barón et al. 2020). Chlorophyll-a concentration and slope had the most influence on the occurrence of the elasmobranchs and Omura's whale. The relationships between filter feeder's distribution and the covariates were not strictly linear but rather results indicated a preferred set of conditions within a narrow range. Extensive previous research shows that marine organisms commonly form predictable aggregations at sites of abrupt bathymetry changes due to the relationship between steep slopes and productivity (Nur et al. 2011, Bouchet et al. 2015). Complex bathymetric features such as continental and reef slopes and shallow banks tend to be areas of high zooplankton abundance and the aggregation of smaller organisms often driving feeding aggregations of megafauna (Afonso et al. 2014). Previous studies conducted in tropical and subtropical regions, such as Australia and Indonesia, have specifically linked bathymetry to whale shark and manta ray aggregations, as well as other filter feeding species (Sims 2008, Rohner et al. 2013, Copping et al. 2018). Mobulid rays in the Gulf of California have been reported to prefer waters <50m in depth and SST >20°C with their distribution associated with to coastal upwelling (Croll et al. 2012, Stewart et al. 2018). Filter feeder species were regularly re-sighted on consecutive days around the same region, suggesting degree of residency in the area (Lezama-Ochoa et al. 2020, Putra et al. 2020). Furthermore, filter feeders were also sighted together with other species on multiple occasions (e.g., spinetail and shortfin devil rays swimming with whale sharks and Omura's whales). Thus, individuals displayed strong inter-annual site fidelity and co-occurrence of the filter feeders in the area. This supports previous and current research that have indicated that this area is an important seasonal habitat for multiple migratory species, particularly the whale sharks

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(Diamant et al. 2018, 2021), humpback whales (Trudelle et al. 2016) and Omura's whales (Cerchio et al. 2015a, 2019).

It is important to note that the coastal waters of Madagascar are a well-documented breeding ground for the Southwest Indian Ocean population of humpback whales. Thus, Nosy Be represents a breeding ground and migration corridor for humpback whales during the wintering months and they do not feed in this region (Trudelle et al. 2016, Dulau et al. 2017). As a result, factors contributing to the productivity in these regions are not a driving factor for their presence, as the main driver behind their presence is reproduction. Only depth showed to be an influencing factor for humpback whale distribution. Here, humpback whales occur in relatively shallow nearshore waters which is consistent with breeding ground habitat, which will be discussed in more detail in chapter 3 (Ersts and Rosenbaum 2003, Bruce et al. 2014, Fossette et al. 2014).

### 2.5.2. *Predators*

The predators demonstrated a clear distribution along the continental shelf edge predominately southwest of Nosy Be along mainland Madagascar as well as around *Grand banc de l'entrée* with some variation between offshore and coastal dolphin species. The occurrence of offshore predators (bottlenose dolphin; spinner dolphin; pantropical spotted dolphin) was in relatively shallow waters, <80m predominantly, along the continental shelf edge and around shallow banks (5m). The coastal dolphin species (i.e., humpback dolphins) were frequently sighted in waters on the west coast of Nosy Be (<30m) over reef habitat and around *Grand banc de l'entrée*. No significant correlation between either sighting rate or relative abundance with depth were found for the predators except for the humpback dolphin, who were exclusively found in shallow coastal waters. These results are supported by similar surveys in other island

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regions of the Indian Ocean investigating cetacean communities (Kiszka et al. 2010, Cerchio et al. 2015b, Vermeulen et al. 2018). However, the two largest groups recorded were sighted in the deepest waters (melon headed whale and spinner dolphins). SST significantly affected sighting rate and SST being the most important descriptor for the relative abundance of predators. The environmental variables had no correlation to spinner dolphin occurrence as they were much more widely distributed across the study area, occurring inshore over the shelf with some large groups sighted in deeper waters. This suggests that these animals are much mobile moving in and out of inshore and offshore habitats. The humpback dolphins showed a preference for warmer surface waters in comparison to the other predators. Spinner, pantropical spotted and bottlenose dolphins preferred cooler offshore waters near the edge of the shelf. Previous research highlights that SST, chl-a concentrations and upwelling are specifically important variables in driving large-scale dolphin distribution patterns due to higher pelagic fish abundance (Grémillet et al. 2008, Correia et al. 2019, García-Barón et al. 2020). Although there were no clear trends in how delphinids respond to chl-a concentrations (i.e., ind. km<sup>2</sup> did not increase with increasing chl-a), higher densities were related to cooler SSTs, often associated with upwelling. Pripp et al. (2014) reported upwelling events to occur off northwest Madagascar close to Nosy Be (13°S) with a strong seasonal change in productivity and distribution of phytoplankton and micronekton (Tew-Kai and Marsac 2009, Obura et al. 2018). SST and chl-a are considered important indicators for delphinids due to variation in the SST and the chl-a possibly being associated with prey availability driving predator distribution and movements suggesting that mechanisms such as prey availability and predator avoidance may be more direct drivers of these species distribution (Cockcroft and Peddemorst 1990, Yen et al. 2004, Whitehead et al. 2008, Correia et al. 2019). Previous research on humpback dolphins in the Nosy Be region have shown similar hotspots as found here, and observations and distribution model results are in line with studies from other parts of the world using

## Chapter 2: Community Distribution Trends

standardized methods (Cerchio et al. 2015b, 2015a, Diamant et al. 2018). Dolphins of the genus *Stenella* (spinner and pantropical spotted dolphin) are commonly shown to have preference for continental shelves in regions with complex bathymetry near islands and isobaths (Benoit-Bird et al. 2003, Herrera et al. 2019). Data were limited for some species, (false killer whale; melon-headed whale; leatherback sea turtle) thus no relationships between species distribution and environmental variables could be made. However, melon-headed whales occur in large groups with one group estimated to have been 800+ individuals. This is a large biomass of predators important to nutrient cycling in the system and important to note these sightings of large groups near Nosy Be (Schmitz et al. 2010).

### 2.5.3. *Filter feeders vs predators*

Overall, there was a spatial overlap in the occurrence of both filter feeders and predators with little variation in preferred environmental conditions between the two feeding guilds. The highest abundance of both groups sighted in waters of approximately 50 deep, at a slope of 1.5%, in waters with SSTs ranging between 28 and 29°C and a total chlorophyll-a concentration of ~0.4 mg milligram per cubic meter. However, the elasmobranchs were more concentrated in certain areas, potentially showing site fidelity within these regions whereas the predators were more widely distributed offshore and across the continental shelf, with a clear preference towards the edge. Filter feeding megafauna occur in feeding aggregations responding to a particular set of environmental conditions including depth, slope, SST and chl-a in these regions with specific oceanographic and bathymetry features, which concentrates or attracts their prey. The predators are more widely distributed, and SST appears to be an important driver for their preferred habitats, possibly related to upwelling. The distribution of lower trophic level animals, like zooplankton, is directly related to the environment (Yen et al. 2004,

## Chapter 2: Community Distribution Trends

García-Barón et al. 2020).. This drives the distribution of their predators, i.e., filter feeders, linking it more closely to the environmental conditions. Animals from mid- and upper-trophic levels (fish, squid, and meso-predators), may respond to changes in prey distribution caused by changes in the environment (Grémillet et al. 2008, Whitehead et al. 2010). Thus, filter feeders have a strong relationship to complex bathymetry such as slope and regions with high chl-a and mechanisms such as prey availability and predator avoidance are more direct drivers of dolphin distribution (Yen et al. 2004). Different prey preferences and foraging methods would possibility lead to differences in distribution between the foraging guilds, although the highly productive habitat off *Grand banc de l'entree* was evidently rich enough to support populations of both filter feeders and predators.

To the authors knowledge, this is the first attempt to assess the habitat characteristics used by megafauna at a community level in Nosy Be, with other long-term studies describing species-specific habitats (Cerchio et al. 2015b, Trudelle et al. 2016, Diamant et al. 2018) or documenting their interactions with anthropogenic activities (Kiszka et al. 2009a, 2009b, Kiszka 2012). This study indicates the shelf waters around Nosy Be are important for marine megafauna with nutrient-rich waters that provide a valuable food source for migrating and resident populations as well as breeding habitats for many large charismatic marine species. Moreover, the region is characterised by high habitat diversity and productivity, which create favourable conditions for many cetacean and elasmobranch species (Kryk *et al.* 2020). These patterns show that this is an important seasonal feeding habitat for whale sharks and other megafauna (i.e., mobulid rays) with the productivity to sustain a large megafaunal community.

### 2.5.4. *Limitations*

Platforms of opportunity, such as tourism operations, are a valuable method of obtaining data on tourism targeted species such as megafauna. However, the use of opportunistic data often encounters limitations in spatial and temporal coverage. Firstly, opportunistic sighting data does not have an even coverage of the survey area, and so we can only interpret the results where the animals were present without knowledge of search effort. However, the use of presence-only data and platforms of opportunity for obtaining ecological information on species is now broadly employed in marine ecology and has been shown to provide valuable and baseline information (Higby et al. 2012, Tonachella et al. 2012, Alessi et al. 2019, Smith et al. 2021, Araujo et al. 2022, Magson et al. 2022). In addition, the data were collected unevenly throughout the year with surveys with an increase in surveys during the spring-summer period. Nonetheless, the start of the monsoon season in January, which persists for up to four months, limits evenly temporal data even for dedicated surveys (Diamant et al. 2018, 2021). Several species investigated occur in Nosy Be waters on a highly seasonal basis and is important to acknowledge the potential limitations by not accounting for temporal changes in distribution to seasonal changes and how this may influence interpretation of the results. As in this case species spatial occurrence were demonstrated on an annual basis, however species presence in the region may vary seasonally. Chl-a and SST vary slightly between wet and dry season in Nosy Be and mean annual conditions does not necessarily reflect the exact conditions at the time the animal was present in the area.

CHAPTER THREE: MAXENT MODEL-BASED PREDICTIONS  
OF SUITABLE MARINE MEGAFAUNA HABITATS AROUND  
NOSY BE, MADAGASCAR

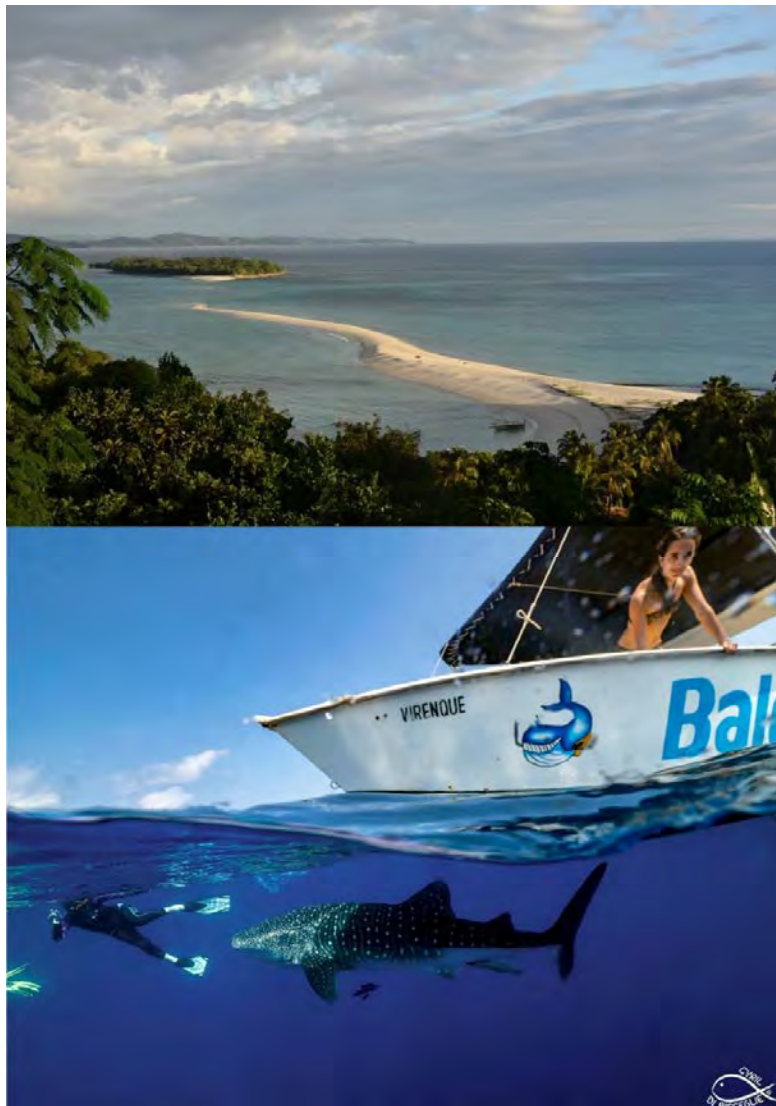


Photo credits: *Les Baleines Rand'eau*

### 3.1. Abstract

Identifying areas where biologically important species, such as megafauna, are likely to be found is critical to direct research and improve management. Despite this importance, there is a paucity of data on megafauna, especially in developing countries, as research in these often-remote areas is expensive and logistically constrained. This chapter describes the suitable habitat of the most frequently sighted marine megafauna in the waters surrounding Nosy Be, in northwest Madagascar. Observations were obtained from tourism vessels during 2016–2019 and environmental data (depth, slope, sea surface temperature and chlorophyll-a) from satellite imagery. The maximum entropy (Maxent) model was employed to predict critical habitats and the environmental conditions characterising these areas for each species. Data obtained included 1729 records of nine frequently sighted species including the whale shark, *Rhincodon typus* (n = 1140), three mobulidae species, *Mobula japonica*; *Mobula kuhlii*; *Manta birostris*; (n = 144), and five cetaceans, humpback whale *Megaptera novaeangliae*, (n = 196); Omura's whale, *Balaenoptera omurai* (n = 94); Spinner dolphin, *Stenella longirostris* (n = 51); Indo-pacific bottlenose dolphin, *Tursiops aduncus* (n = 78); and Indian Ocean humpback dolphin, *Sousa plumbea* (n = 26), recorded during the four years. The Maxent model performed better than random (0.5) and produced an area under the curve scores between 0.860 and 0.991. Chlorophyll-a concentration and sea surface temperature were the variables most strongly related to megafauna suitable habitat for all species. Results predicted high habitat suitability (>70%) for all species in the coastal inshore waters. The findings identified two feeding hotspots for whale sharks, mobulid rays and Omura's whales and demonstrated highest suitable habitat for the dolphins to be in relatively shallow waters. This suggests that the continental shelf is a key habitat for the megafauna community in Nosy Be with a clear range from the shoreline to the edge of the shelf.

### **3.2. Introduction**

The relationship between species and the environment is a central theme in ecological research. Marine species are often associated with specific physical or biological habitats, and there is a growing interest in understanding the role of environmental conditions as drivers of distribution patterns in biologically important species (Elith et al. 2011). The most common approach for estimating the realized or potential geographic distribution of a species is to characterize the environmental conditions that are suitable for the species, and then to identify where suitable environments are distributed within regions (Elith et al. 2006, 2011). To obtain such information, species distribution modelling approach is now a widely used as it elucidates the statistical relationships between the distribution of a species and the environment. This approach combines species presence data with underlying environmental data to identify relationships between environmental factors and the occurrence of the species providing greater insight into the preferred habitats of animals (Phillips and Dudík 2008, Hays et al. 2016). By identifying the essential environmental predictors that best explain a species occurrence in an area, predictive habitat modelling methods can predict potential habitat preferences. As such, predictive habitat modelling has become increasingly common in understanding distribution trends and identifying critical habitats for species (Hays et al. 2016).

Nosy Be exhibits high marine ecosystem diversity, including a large number of marine megafauna. Every year, during August to December, whale sharks, manta and devil rays are observed feeding in the area and it is now recognised as globally important whale shark aggregation site (Diamant et al. 2021). Humpback whales are mainly reported in the region during the austral winter as this area is breeding ground and migratory corridor (Trudelle et al. 2016, 2018). Nosy Be also hosts a large community of other cetaceans year-round, including data deficient Omura's whales and endangered humpback dolphins (Kiszka et al. 2009a,

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Kiszka 2012). The presence of a diverse megafaunal community has contributed to the importance of this region as a tourism destination in Madagascar. Whale watching, swimming with whale shark and scuba diving activities support a highly lucrative tourism industry (Ziegler et al. 2021).

Despite the importance for tourism, information on the ecology of marine megafauna in northwest Madagascar remains scarce. This is likely a result of the cost in studying these animals. Obtaining ecological data on highly mobile, large ranging species such as megafauna often requires the undertaking of costly dedicated surveys covering large geographic areas over protracted periods of time (Alessi et al. 2019). In many developing countries, like Madagascar, the prohibitive cost of ecological research and absence of necessary expertise has contributed to many understudied species within these regions. The use of opportunistic data from pre-existing operations, such as tourism operators used here, represents an excellent opportunity to obtain baseline ecological information on megafauna and indeed has already contributed significantly to data poor regions (Bonney et al. 2009, McKinley et al. 2017).

Species distribution modelling methods for handling citizen science, such as the Maximum Entropy model (Maxent) is a reliable model for analysing species distributions with presence-only data (Phillips et al. 2006, Norberg et al. 2019, Melo-Merino et al. 2020, Smith et al. 2021). It is a modelling technique for simulating a species's geographic spread by producing probabilistic habitat suitability evaluations detailing the geographical and temporal range of a specific species using a 'general-purpose machine-learning approach' (Halvorsen 2013). Maxent models have strong predictive capacity even with small sample sizes and offer the benefit of merging presence-only data with environmental characteristics (Phillips et al. 2006, Phillips and Dudík 2008). Maxent will calculate the environmental needs for a species based on a collection of data points identifying the locations where it has been observed and the environmental factors associated with each at the time the observations were taken. The range

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and distribution of this species are then estimated using the data in areas that were not sampled but where the environmental factors are known. The model generates a probability distribution over the pixels in a grid of the study area indicating suitable habitat ranging from 0 – 100% probability of a species presence in the area (Merow et al. 2016). Its logistic output can be interpreted as the relative environmental suitability of each pixel in relation to the background of the study area (Phillips et al. 2006, Phillips and Dudík 2008). Maxent has been widely applied in species distribution modelling studies (Merow et al. 2013), including on species with limited data (Elith et al. 2011). It is one of the most widely used SDM techniques in recent scientific research largely due to the extensive predictive ability with small sample sizes and at imprecise locations (Meyers et al. 2017, Norberg et al. 2019). Furthermore, this method has been successfully used with whale sharks (Hacohen-Domené et al. 2015), manta rays (Hacohen-Domené et al. 2017) and marine mammals (Ca et al. 2002, Spyarakos et al. 2011, Jones et al. 2019).

The marine megafauna community structure and distribution around Nosy Be were described in chapter 2 by calculating sighting rate and relative abundance and comparing them to selected remotely sensed physico-chemical data and bathymetry charts using generalized linear models. The purpose of this chapter is to identify and describe predicted high value biodiversity areas and critical habitats for marine megafauna at the species levels in the coastal waters of the Nosy Be, using Maxent, a predictive modelling approach to demonstrate suitable habitat for the most frequently occurring species. From the species identified and investigated in chapter 2: the whale shark; three mobulidae species, *Mobula japonica*; *Mobula kuhlii*; *Manta birostris*; humpback whale, *Megaptera novaeangliae*; Omura's whale, *Balaenoptera omurai*; Spinner dolphin, *Stenella longirostris*; Indo-pacific bottlenose dolphin, *Tursiops aduncus* and Indian Ocean humpback dolphin, *Sousa plumbea* are investigated. Specifically using presence-only records obtained from tourism activities of these species to determine fine-scale suitable

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habitats and key environmental factors associated with whale shark and mobulid ray feeding aggregations, humpback whale breeding/migratory areas, and dolphin occurrence in the region. The results of this study will contribute ecological knowledge to aid in identifying potential habitats of key indicator species for monitoring within the Nosy Be region. This will assist in conservation initiatives such as spatial planning and monitoring to conserve and protect marine megafauna as well as this unique highly productive poorly studied system.

### 3.3. Methods

Sighting data of marine megafauna were recorded in Nosy Be, Madagascar, as per Chapter 2 methods. This included presence-only sightings data collected opportunistically during the spring-summer season over four years (2016-2019) around the island Nosy Be (13.39° S, 48.20° E) in Antsiranana Province, north-western Madagascar (outlined in 2.3.1). Maxent software version 3.4.4 (Phillips et al. 2006, [www.cs.princeton.edu/~schapire/maxent](http://www.cs.princeton.edu/~schapire/maxent)) was selected as a suitable method to model the potential distribution of the megafauna within the region of investigation (see Chapter 2). In the Maxent model, the study area was restricted to a small geographical extent across the Nosy Be archipelago to ensure that the background data were subjected to approximately the same spatial bias as the occurrence data, to improve model performance (Phillips et al. 2009). Four remotely sensed uncorrelated environmental variables related to topographic features (i.e., slope (%), depth (m)) and oceanographic conditions (i.e., SST (°C) and chlorophyll-a (chl-a) concentration ( $\text{mg}\cdot\text{m}^{-3}$ )) were included in the models (refer to 2.3.2, **Table 2.1**). Environmental variables were selected based on known ecological relationships which have been shown to influence habitat selection in filter-feeding sharks and cetaceans (Ca et al. 2002, Hacothen-Domené et al. 2015, 2017, Correia et al. 2019, Purdon et al. 2020). According to the model requirements, all the environmental layers were clipped to

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the same geographical extent with a pixel resolution of 4 km and converted to ASCII files using the 'raster' package in R v 4.1.1 software (R Core Team 2021). To compare the models on consistent data, the data was divided into training and testing sets with 25% of the data used as test data allowing the performance of the model to be tested using a random selection of 25% of the species location points and 75% used for the model training. Cross validation was maintained in the replicate run, and iterations were fixed as 500. To avoid over fitting of the test data, 0.1 was used as the regularization number (Phillips and Dudík 2008). The number of model replications was set to 15, which creates 15 versions of the model and averages the results. The resulting model is theoretically more robust than any single replication. This process was repeated for seven separate models of each species: whale shark; mobulidae family; humpback whale; Omura's whale; spinner dolphin; bottlenose dolphin and humpback dolphin. Area under the receiver operating curve (AUC) was used for the model evaluation, ranging from 0.5 (random) to 1.0 (perfect discrimination). Maxent predicts the probability (0 – 1) of species an area being preferred habitat by identifying areas with habitat conditions most similar to the species current known range. This is presented in continuous raster files with values from 0 – 1 representing habitat suitability. To determine which variables contribute most to the model, the Jackknife method was used to assess the importance of variables (%) in the final model (Kunsch 1989). The Jackknife analysis calculates percentages based on the increase in regularized gain and added or subtracted to the contribution of the corresponding variables of the training process (Kunsch 1989). Final outputs of the model predictions were exported to QGIS-OSGeo4W-3.22.0 software for further analysis and interpretation. The response of the presence of megafauna to the environmental conditions in the area were tested using partial dependence plots. These plots suggest that the probability of the presence of an individual in the study area is higher at a set of specific conditions (Phillips et al. 2006, Phillips and Dudík 2008, Elith et al. 2011)(see **Appendix III**).

**3.4. Results**

In total, the megafauna presence data included 1729 presence points of the nine most frequently sighted species in the region over four years (2016–2019), whale shark, (n = 1140), Mobulidae consisting of the three ray species (*Mobula japonica*, *Mobula kuhlii*, *Manta birostris*) (n =144), humpback whale, (n =196), Omura’s whale, (n = 94), spinner dolphin, (n = 51), Indo-pacific bottlenose dolphin, (n = 78) and Indian Ocean humpback dolphin, (n = 26). All models performed better than random, and the AUC scores ranged between 0.860 and 0.991 (**Table 3.1**). Both the internal Jackknife test of variable importance and variable contribution (%) showed that chl-a and SST were the two most useful variables for estimating the habitat suitability of the megafauna community during the study (**Table 3.1; Appendix III**). Similar results were obtained between species models with the most influential environmental variable being chl-a concentration in the distribution for species: whale shark (62%), Mobulid rays (51%), humpback whale (70%), Omura’s whale (77%), spinner dolphin (84%), Indo-pacific bottlenose dolphin (68%). This was followed by SST for whale shark (37%), Mobulid rays (47%), humpback whale (25%), Omura’s whale (23%) and bottlenose dolphin (23%). The most important variables for humpback dolphins were SST (69%), followed by chl-a (30%). High environmental suitability (higher than 70%) for most species was observed in areas with sea surface temperatures 27°C - 28°C, Chl- a concentration 0.3 – 0.5 mg.m<sup>-3</sup>, in relatively shallow waters (<50 m), and a bottom slope >0.5% with some variation between species (**see Appendix III**).

**Table 3.1.** The AUC values and the permutation importance percentage of each of the environmental variables used in the seven Maxent models.

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Whale shark	Mobulid rays	Humpback whale	Omura’s whale	Spinner dolphin	Humpback dolphin	Bottlenose dolphin
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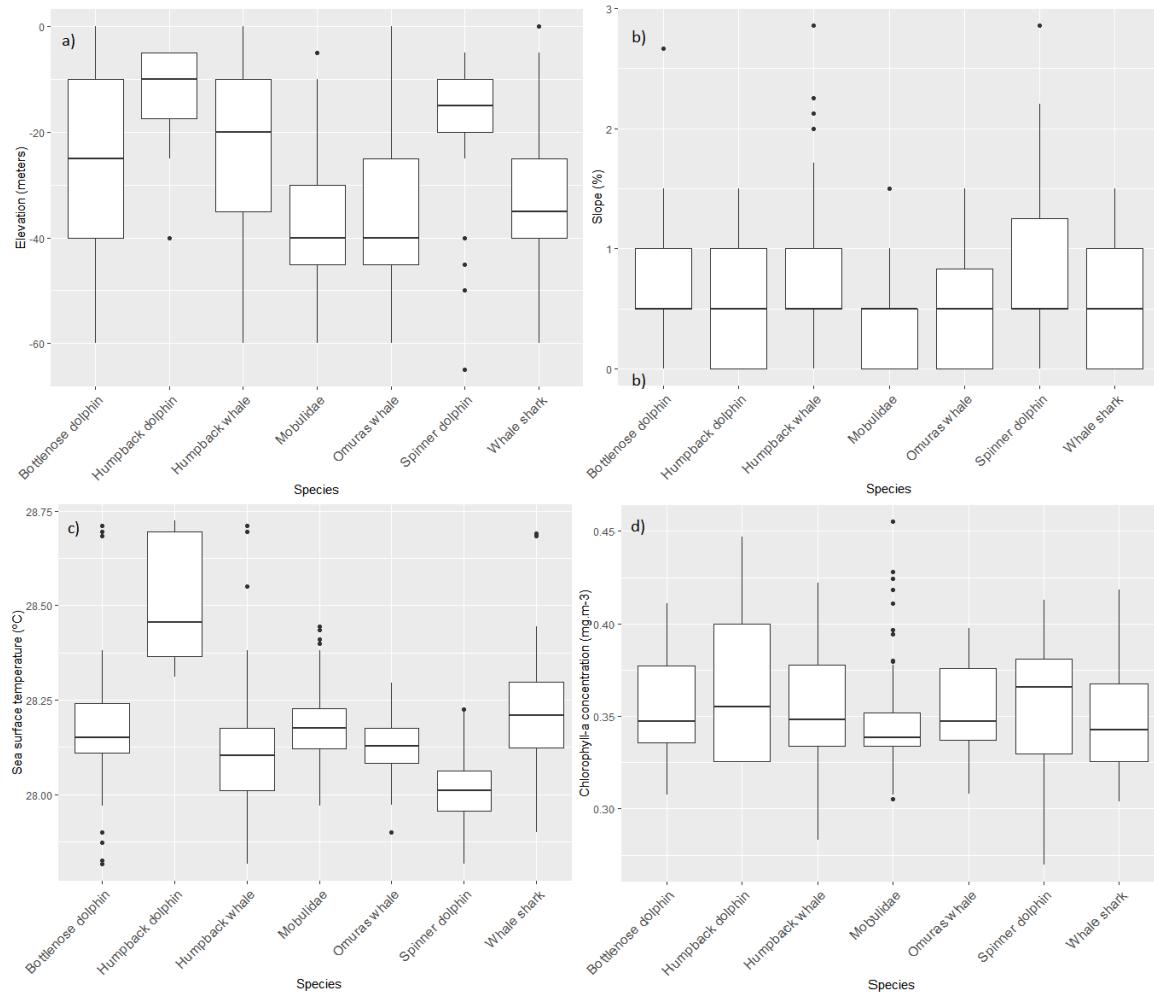
AUC	0.948	0.984	0.951	0.985	0.860	0.991	0.961
Chl-a	62.0	50.6	69.5	77.0	83.7	29.9	68.1
SST	37.0	47.3	25.4	22.7	7.0	68.5	22.6
Slope	0.5	1.7	2.3	0.0	2.1	1.1	1.6
Depth	0.5	0.3	2.7	0.3	7.2	0.5	7.6

Whale sharks were recorded in waters with a mean depth of  $37.8 \text{ m} \pm \text{SD} = 80$ , with an average slope of  $0.7 \pm \text{SD} = 1.08$ ; mean SST  $28.2 \pm \text{SD} = 0.2$  and a mean chl-a  $0.40 \pm \text{SD} = 0.33$  (**Figure 3.1**). The predicted potential distribution map for the whale shark indicated that two areas, one on the southwest and one offshore of the north coast, had the highest environmental suitability ( $>80\%$ ). Records with suitable habitat were in waters of  $\sim 50\text{m}$  depth, close to shallow banks reef edges (**Figure 3.2**). The mobulid rays had a similar trend, with an environmental suitability  $>80\%$  predicted at the same sites and depths (**Figure 3.2**). The *mobulidae* species were recorded in waters with a mean depth of  $36.3 \text{ m} \pm \text{SD} = 12$ , with an average slope of  $0.4 \pm \text{SD} = 0.4$ ; mean SST  $28.2 \pm \text{SD} = 0.13$  and a mean chl-a  $0.40 \pm \text{SD} = 0.32$ . Humpback whales were recorded in waters with a mean depth of  $120.8 \text{ m} \pm \text{SD} = 403$ , with an average slope of  $2 \pm \text{SD} = 3.05$ ; mean SST  $28.1 \pm \text{SD} = 0.2$  and a mean chl-a  $0.37 \pm \text{SD} = 0.33$  (**Figure 3.1**). The highest habitat suitability for humpback whale ( $>70\%$ ) within the region of investigations was along the edge of the continental shelf in relatively shallow waters ranging from  $10 - 100\text{m}$  (**Figure 3.3**). Omura's whales were recorded in waters with a mean depth of  $33.8 \text{ m} \pm \text{SD} = 17$ , with an average slope of  $0.57 \pm \text{SD} = 0.53$ ; mean SST  $28.1 \pm \text{SD} = 0.1$  and a mean chl-a  $0.36 \pm \text{SD} = 0.05$  (**Figure 3.1**) and were predicted to occur in similar areas as the whale shark and mobulid rays, with habitat suitability of  $>70\%$  in those areas. These were at a depth of  $50 - 60\text{m}$  and on the edge of the continental shelf around shallow banks ( $0-5\text{m}$ ) and steep slope ( $0.5 - 1\%$ ) (**Figure 3.3**). The spinner dolphin was recorded in waters with a mean depth of  $167.4 \text{ m} \pm \text{SD} = 458.3$ , with an average slope of  $2.6 \pm \text{SD} = 3.4$ ; mean SST  $28.0 \pm \text{SD} = 0.14$  and a mean chl-

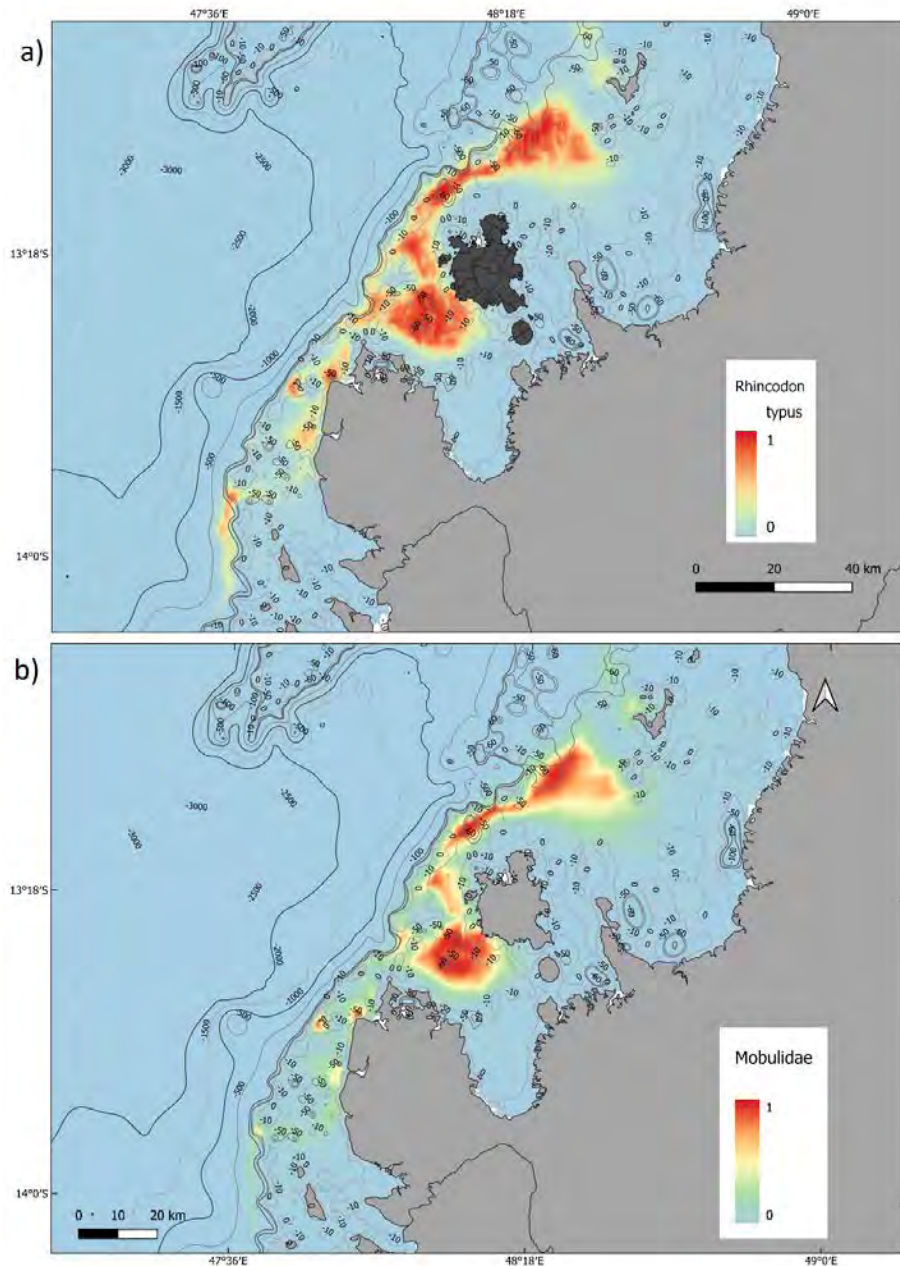
### Chapter 3: Habitat Preferences

a  $0.32 \pm \text{SD} = 0.07$  (**Figure 3.1**). Areas of higher than 60% predicted probability for spinner dolphins were patchy throughout the coastal region with widespread suitable habitat (**Figure 3.4**). Bottlenose dolphins were sighted in relatively shallow waters with a mean depth of  $25.2 \text{ m} \pm \text{SD} = 17.95$ , with an average slope of  $0.77 \pm \text{SD} = 0.79$ ; mean SST  $28.2 \pm \text{SD} = 0.2$  and a mean chl-a  $0.36 \pm \text{SD} = 0.07$  (**Figure 3.1**). Predicted suitability for bottlenose dolphin (>60%) was close to the southwest coast of Nosy Be in shallow waters <20m and in a narrow strip on the edge of the shelf and around shallow banks. The humpback dolphins occurred exclusively in shallow waters with a mean depth of  $4.2 \text{ m} \pm \text{SD} = 16.5$ , with an average slope of  $0.77 \pm \text{SD} = 0.79$ ; mean SST  $28.2 \pm \text{SD} = 0.2$  and a mean chl-a  $0.4 \pm \text{SD} = 0.14$  (**Figure 3.1**). Predicted environmental suitability higher than 50% for the humpback dolphin was only in a small region close to the southwest shore almost exclusively at a depth of approximately 10m (**Figure 3.4**).

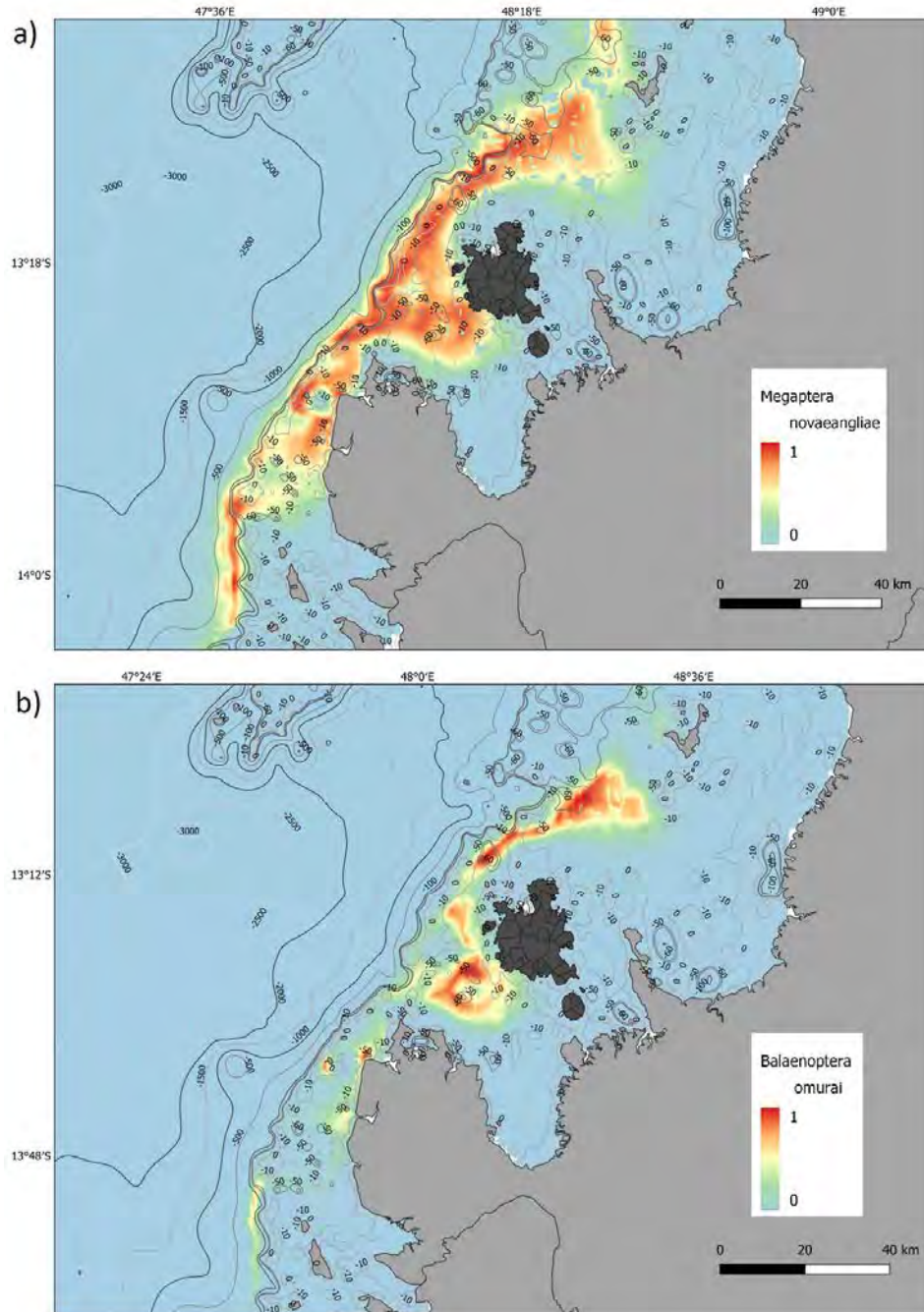
### Chapter 3: Habitat Preferences



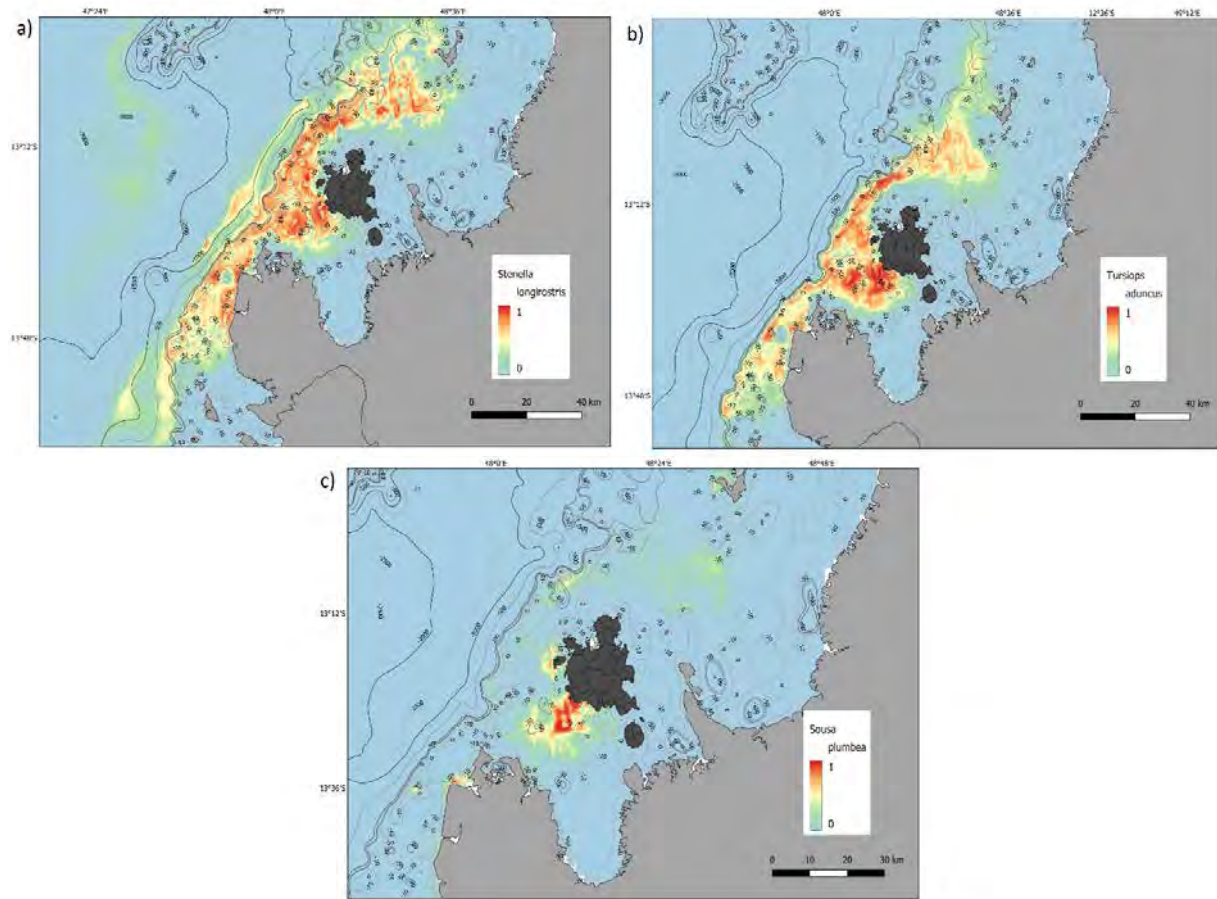
**Figure 3.1.** Boxplot indicating environmental factors: a) elevation; b) Slope; c) sea surface temperature; and d) chlorophyll-a concentration associated with megafauna distribution sighted off Nosy Be, Madagascar, for each species (mobulidae including 3 species). Outliers were removed.



**Figure 3.2.** Habitat suitability in the nearshore and coastal regions of northwest Madagascar of a) whale shark, *Rhincodon typus* b) the family mobulidae (*Mobula japonica*, *Mobula kuhlii*, *Manta birostris*). The scale illustrates the predicted probability of suitable habitat. The maps were developed using a QGIS-OSGeo4W-3.22.0 software (WG84).



**Figure 3.3.** Habitat suitability in the nearshore and coastal regions of northwest Madagascar of a) humpback whales, *Megaptera novaeangliae* b) Omura's whales, *Balaenoptera omurai*. The scale illustrates the predicted probability of suitable habitat.



**Figure 3.4.** Habitat suitability in the nearshore and coastal regions of northwest Madagascar of a) Spinner dolphin, *Stenella longirostris* b) Indo-pacific bottlenose dolphin, *Tursiops aduncus*, c) Indian Ocean humpback dolphin, *Sousa plumbea*.

### 3.5. Discussion

The present chapter established a series of baseline habitat models for whale sharks, mobulid rays, humpback whales, Omura's whales, spinner dolphins, bottlenose dolphins and humpback dolphins in a data-limited setting. The habitat models show fine-scale habitat preference of marine megafauna based on environmental variables, which influence their spatial distribution within the Nosy Be archipelago region, in north-western Madagascar. This study highlights

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important areas for the selected megafauna providing areas for implementation of management plans for conservation. This is the first study to model the habitat suitability for the megafauna community in this region. To investigate the essential environmental variables associated with their occurrence trends, Maximum Entropy modelling was employed coupled with opportunistic sightings from 2016 to 2019. The results demonstrate that Maximum Entropy modelling is a useful technique for predicting species habitat preferences in situations where there are only presence data available and with small sample sizes. Main findings suggest that chl-a and SST are most important predictors of megafauna distribution and can be used as proxies for their occurrence where no sighting data are available.

### 3.5.1. *Whale sharks and mobulid rays*

Whale sharks and mobulid rays, such as the manta ray and devil rays, are highly mobile epipelagic migratory species that occur in coastal and oceanic environments in tropical sub-tropical regions around the world, typically travelling long distances for feeding (Nelson and Eckert 2007, Couturier et al. 2012). These animals often form large seasonal feeding aggregations at various sub-tropical and tropical coastal regions where plankton are abundant (Rohner et al. 2013, Murie and Marshall 2016). The results demonstrated a clear distribution of whale sharks and three ray species spinetail devil ray, giant oceanic manta ray, and shortfin devil ray across the coastal waters of the island during the late spring to summer season. The most important environmental factor identified in the model is total chl-a concentration. Previous studies investigating the drivers for both whale shark and manta rays at more well-known seasonal feeding sites (i.e., Mexico and Australia) have also reported chl-a concentration and related primary productivity to be amongst the most important variables in driving habitat preferences of these species (Nelson and Eckert 2007, Rohner et al. 2013, 2020,

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Copping et al. 2018, Garzon et al. 2021). In areas with high marine productivity, it is common to observe abundant megafauna due to increased food availability and foraging opportunities (Rohner et al. 2013). In the context of using environmental proxies to model distribution, chl-a concentration does not itself determine the distribution of these species but is a proxy for other biological factors for example, high zooplankton biomass, which provides food for many plankton feeders such as the whale shark, devil and manta rays (Nelson and Eckert 2007, Mourier 2012). The tropical and sub-tropical regions of the worlds' oceans are generally characterised by low primary productivity. However, areas with steep continental shelves results in the advection of nutrient rich deep waters into surface waters contributing to higher chl-a levels in these regions (Wilson et al. 2007). Although the model did not identify slope and depth to be as important to elasmobranch distribution as SST and chl-a, there is a preference for shallower waters in the region and for areas of complex bathymetry. Rohner et al. (2013) suggested that presence of whale sharks is mostly associated with the distance from the continental shelf edge, where animals are in proximity to but not on the steepest sloping areas in Western Australia. This has been reported in multiple studies and is a reoccurring trend across different aggregation sites which suggest that whale shark habitat preference globally is mostly associated with areas of complex bathymetry (Sleeman et al. 2010, Hacohe-Domené et al. 2015, 2017, Austin et al. 2019, Ehemann et al. 2022). It is also thought that their occurrence in some regions coincides with increased productivity associated with fish spawning events (Hacohe-Domené et al. 2015, Rohner et al. 2020). For instance, de la Parra Venegas et al. (2011) demonstrated large whale shark aggregations in the Mexican Caribbean due to the presence of dense patches of fish eggs of little tunny (*Euthynnus alletteratus*). Similarly, in Western Australia, the presence of large filter feeders coincides to with coral spawning events (Rohner et al. 2013). These potential drivers could not be monitored but could be contributing to elasmobranch distribution.

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The second most important environmental contributing factor of the elasmobranch's distribution was SST. The model predict the probabilities of both whale shark and mobulidae sightings to be associated with water temperatures between 28 °C and 29°C. Whale shark distribution in the pelagic waters of the broader western Indian Ocean has previously been correlated with very similar SST (Sequeira et al. 2012). Sequeira et al. (2012) reported 65% of the whale shark sightings to occurred between 27.5 and 29°C with clear isolines of minimum 26°C and maximum 30°C. In Seychelles, similar relationships were identified during aerial surveys with SST as well as high chl-a levels and fish schools being important indicators for whale shark numbers relating to zooplankton abundance (Rowat et al. 2009, 2011). These consistent results demonstrate the importance of oceanographic and environmental features in influencing the distribution of feeding aggregation sites with higher probability of presence in areas of high productivity and within a set temperature range.

The environmental conditions that were considered potential habitat of whale sharks and mobulid rays mainly occur the west coast of Nosy Be approximately 10 km's offshore in the shallow bay. The model demonstrated *Grand banc de l'entrée* as suitable habitat with high probability of occurrence (predicted value of 0.9) and is likely to be a seasonal ray seasonal hotspot during spring-summer. Indeed, this is supported by anecdotal information from local fisherman and diver centre data (Jonahson and Harding 2007). However, the model also showed a suitable habitat for both whale shark and rays further off the north coast of Nosy Be further offshore (~ 40km's inshore from mainland and 20 km's North from Nosy Be). No sightings were recorded in that area although the model identified it as possible important habitat. This region is not a highly visited tourist destination and the lack of sightings is due to the fact that it is not readily visited or accessible to tourist operators as it is on the far side of the island from their launch and is possibly too far from shore for safety requirements. This highlights the value of SDM's in identifying habitat preference in non-accessible areas. The

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model predictions are supported by previous research in the area (Diamant et al. 2018, 2021) in which eight whale sharks were tagged off Nosy Be (Diamant et al. 2018, 2021). These sharks did frequent the area on the north coast of Nosy Be, as well as the hotspot off the southwest coast.

### 3.5.2. *Baleen whales*

The Maxent model showed a wide distribution of humpback whales across the entire coastal region of the study area over the continental shelf, with a clear range limit of the edge of the continental shelf. Humpback whales have a worldwide distribution and migrate large distances between feeding and breeding grounds (Andrews-Goff et al. 2018). The annual humpback whale migration cycle alternates seasonally driven by feeding in productive high latitudes in the summer to breeding in the winter in low latitudes (Clapham and Mead 1999). Thus, in the Southwest Indian Ocean (SWIO) humpback whales occur mainly in winter and spring during their breeding season (Cerchio et al. 2013, Dulau et al. 2017). Humpback whales breed in tropical waters and remain in tropical warm-temperate regions for a short period and then move south-ward. The coastal waters of Madagascar is a well-documented breeding ground for the Southwest Indian Ocean population of humpback whales (Fossette et al. 2014, Dulau et al. 2017, Trudelle et al. 2018). With the use of satellite transmitters, Trudelle et al. (2016) found that humpback whales occur in all coastal waters off Madagascar during the austral winter. They also indicated that humpback whales prefer the continental shelf waters, which is consistent with the Maxent model results and with what has been observed in other breeding areas in the Indian Ocean (Ersts and Rosenbaum 2003, Bruce et al. 2014, Fossette et al. 2014). Trudelle et al. (2016) investigated the influence of environmental factors on the habitat use and movement of the humpback whale across the Madagascar breeding ground and reported it to

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be significantly related to bathymetric features, preferring regions of higher chl-a levels. Rasmussen et al. (2007) showed that SST drives migrations at a basin scale between feeding and breeding habitats but suggested that it is not an important driver of occurrence at a fine scale. Here, chl-a was the most important predictor of humpback whale occurrence with a preference for higher chl-a levels over the continental shelf. The association with shallow banks at breeding habitats have been described for the species and highlighted in previous studies at breeding grounds in other regions (Craig and Herman 2000, Garrigue et al. 2015). Dulau et al. (2017) showed extensive use of seamounts and shallow banks by humpback whales between Madagascar and Reunion breeding grounds. However, the Jackknife analysis did not demonstrate a large importance of bathymetric features in the model of the humpback whale, the highest habitat suitability (>70%) in the region was along the edge of the shelf with steep slopes due to the presence of shallow banks and small islands. Humpback whale occurrence was high and widespread throughout the region, indicating that Nosy Be archipelago's complex bathymetry and steep continental shelf could be a preferred habitat on a broader scale. Most humpback whale sightings were during September and October (68%) but sightings were reported from July to November in Nosy Be. Although there is a seasonal imbalance in the data skewed towards the spring-summer season, it has been mentioned in previous studies that humpback whales are more common around Nosy Be during the late breeding season as it is a late season migratory corridor and a possible stopover during their migration southward (Cerchio et al. 2013, Fossette et al. 2014, Dulau et al. 2017). Previous literature has found depth and distance from shore to be important factors in winter grounds with mother and calves preferring shallow coastal regions (<30m) due social organization during the breeding season (Ersts and Rosenbaum 2003). It is suggested that the reason for these preferences at and between breeding grounds could be related to social structure and behaviour, but some

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speculation suggests that perhaps this is an indicator of an early onset of feeding in their southern migration towards feeding grounds (Rasmussen et al. 2007).

By contrast, Omura's whales are hypothesized to be a non-migratory species with previous studies showing that the resident breeding population is largely restricted to the northwest region of Madagascar (Cerchio et al. 2015b, 2019). The Maxent model results for the Omura's whale were similar to those of the whale shark and mobulids, with a clear habitat preference for shelf waters. The most important environmental factors identified in the model of Omura's whale's occurrence were chl-a and SST respectively. The predictive suitability map also illustrates the high probability of Omura's whale presence northeast of Nosy Be near Nosy Mitsio, though no sightings were reported in the area through boat-based activities. Cerchio et al. (2015) indicate that scuba diving operators in the region have reported unconfirmed sightings of Omura's whales near Nosy Mitsio island, approximately 50 km northeast of Nosy Be, supporting this region as preferred habitat for the species however this needs further investigation.

### 3.5.3. *Delphinids*

The results showed that spinner and bottlenose dolphins may be widely distributed across the continental shelf. Spinner dolphins are widespread globally, occurring in the Atlantic, Indian, and Pacific Oceans, and are thought to be associated with oceanic habitats and feed on epipelagic to mesopelagic prey (Dolar et al. 2003). Results from the current investigation suggest that the highest suitable habitat in the Nosy Be region for spinners dolphins was at relatively shallow depths (10 – 100m). Studies of spinner dolphins in other regions support this and have found them to occur in shallow waters with a range to ~100m (Benoit-Bird et al. 2003, Lammers 2005, Thorne et al. 2012). The most important environmental factor identified

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for the spinner dolphin distribution was chl-a concentration with the other factors having a relatively small contribution to the model. Spinner dolphins are known to have rest habitats in shallow bays for long periods of the day and move into deeper waters at night for foraging (Thorne et al. 2012). Herrera et al. (2019) found spinner dolphins to have a strong preference for steep slopes and to mainly occur in productive coastal regions and near islands. Thus, the bathymetry around Nosy Be with shallow bays and steep changes in depths provide ideal habitat for this. Benoit-Bird et al. (2003) suggested that their shelf distribution is due to the vertical migration of mesopelagic fish that is an important part of their diet. Lammers (2005) reported similar trends and identified a relationship with isobaths and strong site fidelity at these areas. Although their distribution in the region did not show a strong relationship with slope, most suitable habitat was across the edge of the continental shelf and areas of shallow banks (0 – 5m) with possible further offshore occurrence. A correlation to higher chl-a concentration indicates a preference for productive regions with possibly higher prey availability in these regions. Suitable habitat for spinner dolphins seems to be much more widespread, providing evidence for their cosmopolitan distribution with a preference for productive regions near islands. Preferred prey availability and specific bathymetry features is perhaps an important driver for these species which has previously been suggested (Benoit-Bird et al. 2003, Thorne et al. 2012).

The Indo-pacific bottlenose dolphin has an Indo-Pacific warm temperate and tropical distribution and predominantly occur in shallow coastal waters and reef habitats, feeding on inshore prey although reported to occur in waters up to 200m deep (Cribb et al. 2013, Sprogis et al. 2016). The model results showed the habitat preference of bottlenose dolphins tended to be concentrated across the continental shelf waters in near shore habitats, similar to the spinner dolphin but with highest suitable habitat at shallow depths (~20m), suggesting that bottlenose dolphin have a more inshore distribution. This has been reported in other areas of the Western

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Indian Ocean such as Mayotte (Kiszka et al. 2011) La Réunion (Dulau-Drouot et al. 2008), Zanzibar (Stensland E et al. 2006) and South Africa (Caputo et al. 2021). For instance, in Mayotte bottlenose dolphins were observed in waters of less than 40 m and to have a coastal and shallow water distribution (Kiszka et al. 2010, 2011). However, both spinner and bottlenose dolphin appear to be highly mobile species who inhabit a variety of areas through a wide distribution (Ingram and Rogan 2002b, Thorne et al. 2012). The most important environmental factors identified were chl-a concentration and SST for the bottlenose dolphin distribution. SST, chl-a and upwelling are important variables in driving large-scale dolphin distribution patterns as it is associated with higher pelagic fish abundance in these regions (Grémillet et al. 2008, Correia et al. 2019, García-Barón et al. 2020). This could possibly explain the strong relationship between delphinid occurrence and chl-a in the region. On the other hand, some studies have stressed the importance of benthic habitat type on the occurrence of bottlenose dolphins with sea grass beds and rocky and coral reefs as the most important habitats (Cribb et al. 2013, Herrera et al. 2019). (Kiszka et al. (2010b) found bottlenose dolphins to make extensive use of outer reef edges in Mayotte, however, Cribb et al. (2013) found bottlenose dolphins to be present mostly over sandy habitats with a shift towards seagrass beds during spring and summer in South Australia. Coral reefs and seagrass beds generally have high productivity by creating habitat for smaller species that provide resources for larger species. Therefore, habitat type (i.e., reef, seagrass, sandy.) may also be a driver of delphinid occurrence and may be an influencing factor for other delphinids as well. The Nosy Be coastal and shelf regions area a mix of sandy, coral reef and extensive seagrass beds, which could be another factor contributing the productivity and food availability in the area relating to suitable cetacean habitat.

The Indian ocean humpback dolphin are typically found in shallow waters of less than 20 m generally around islands, close to the coast and associated with river mouths, mangroves, tidal

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channels, and inshore reefs (Cerchio et al. 2015b) All humpback dolphin species are obligate shallow water species (Kiszka et al. 2010, Keith et al. 2013, Vermeulen et al. 2018), and off Nosy Be all encounters of humpback dolphins occurred in depths of <25 m, with average depths of 8.2m . The Maxent model showed a very narrow distribution of humpback dolphins with a much smaller range of suitable habitat than for bottlenose and spinner dolphin with highest predicted suitable habitat in shallow waters of <10m. Preferred habitat seems limited to the southwest coast of the Nosy Be and some coastal regions of mainland Madagascar with a strong relationship to SST. Mean SST for the region over the four years had higher SST values on average for the east coast of Nosy Be compared to the west coast (+3°C). However, (Cerchio et al. 2015b) recorded humpback dolphin sightings on the east coast of Nosy Be and suggested that their distribution is heterogeneous, with more widespread distribution of these animals in inshore waters around Nosy Be. Tourism boats operate mainly offshore likely overseeing many coastal dolphins occurring closer inshore. The interpretation of the results for humpback dolphin are, therefore, limited as more survey effort would be needed in inshore waters to get accurate predictability of how they use inshore habitat all around Nosy Be.

#### 3.5.4. *Conclusions and limitations*

The findings of this study demonstrate the importance of the shelf and coastal region of northwest Madagascar to marine megafauna. The models performed well with the use of opportunistic location data and small sample sizes for all species. In addition, environmental factors identified as descriptor variables for the habitat of the megafauna species investigated are in agreement with previous studies conducted both locally and elsewhere in the world. With the results from this study and previous supporting literature, the ecological drivers of habitat preference appear to be defined by increased productivity in a region relating to resource

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availability and the distribution and abundance of prey. This thesis provides the first formal record of Nosy Be as habitat for three ray species, manta rays, spinetail and shortfin devil rays and a potential seasonal feeding site. Important areas for megafaunal species in northwest Madagascar are presented and give information on important areas for implementation of management plans for its conservation which will be discussed in chapter 4.

The study highlights the use of citizen science/presence-only data used in creating models of occurrence even in absence of sighting data for all regions. However, due to their opportunistic nature of the data collected here there is an inherent spatial bias. Considering that areas known for high occurrences are much more often visited by tourism boats rather than areas that are not. Maxent relies on an unbiased sample so efforts in collecting a comprehensive set of presence records or dealing with biases are important (Elith et al. 2006). Providing background data with similar biases to those in the presence data used in this study is considered a main alternative dealing with inherent biases (Elith et al. 2011). However, this does not account for the bias in the dataset completely and is not considered as efficient as presence-absence records. For presence-absence models, sample bias affects both presence and absence records, and therefore the effect of the bias cancels out (Elith et al. 2011, Norberg et al. 2019). Furthermore, the dataset limits the understanding of the complexities behind temporal variation in species distribution. In the current study the model predicts suitable spatial habitat year-round for all species by not including seasonal models which is not the case. For example, a species such as the whale shark are only present in spring-summer but would be absent during the winter. Thus, the predicted suitable habitat may vary temporally for different species. When interpreting the results of this study it is important to consider these potential sources of error, especially when applying these data for spatial planning, management, and conservation.

## CHAPTER FOUR: GENERAL DISCUSSION

Marine megafauna are widely recognised as key indicator species of the status and health of the marine environment (Hooker et al. 1999, Hooker and Gerber 2004, Lewison et al. 2014, Santos and Pierce 2015). Given the important role they play in nutrient and energy cycling within marine systems, declines in megafauna populations are likely to have far reaching bottom-up and top-down consequences on ecosystems and result in cascading impacts (Estes et al. 2016). The loss of vulnerable marine megafauna has potential consequences for ecosystem structure and function, with implications across spatial and temporal scales and thus their protection can ultimately result in the protection of whole ecosystems (Caro and O'doherty 1999). Despite the importance of marine megafauna in marine ecosystem functioning, ecological knowledge is limited for many species and in many geographic regions (Copping et al. 2018, García-Barón et al. 2020). Indeed, the effective conservation of marine habitats is often hampered by a lack of general ecological knowledge, such as the distribution, and characteristics of target habitats for megafauna (Hays et al. 2016). Understanding the habitat preference of megafauna is important in identifying critical habitats for conservation and management decision making as well as assessing the efficacy of any proposed or existing marine protected area (MPAs) (Bailey and Thompson 2009, Augé et al. 2018).

In the marine environment, megafauna niche or distribution models have been developed based on environmental factors, such as chlorophyll-a and sea surface temperature, since megafauna species may use oceanographic variables as cues for locating prey as well as responding to specific conditions (Austin et al. 2019, Louzao et al. 2019, Melo-Merino et al. 2020). To describe these habitats for the Nosy Be region those ecological descriptors that

best explain species distribution were identified for their realized occurrence and for their predicted occurrence. By obtaining spatial trends and predictions for multiple species, ecologically meaningful areas can be defined which may inform future conservation efforts (García-Barón et al. 2020). Citizen science is emerging as a promising tool to gather large amounts of sightings data particularly in isolated or economically poor regions of the world's oceans (McKinley et al. 2017, dos Santos and Bessa 2019).

The main findings from this thesis are summarized below and further discussed in the following sections on the marine megafauna community in the region (Chapters 2), their distribution trends and related environmental variables (Chapter 2 and 3) and predicted habitat suitability in the region (Chapter 3). Considering the findings from this thesis the contributions and limitations of citizen science in the context of marine tourism data and the implications for the conservation of the Nosy Be marine region is discussed.

#### **4.1. The marine megafauna community**

In recent years, Nosy Be has been identified as a seasonal feeding aggregation site for whale sharks (*Rhincodon typus*) (Diamant et al. 2018), an important humpback whale (*Megaptera novaeangliae*) breeding ground and migratory corridor (Trudelle et al. 2016), a host of a resident population of the rare Omura's whale (*Balaenoptera omurai*) (Cerchio et al. 2015a), and a hotspot for a diversity of dolphin species including the endangered Indian Ocean humpback dolphin (*Sousa plumbea*) (Cerchio et al. 2015b). With the help of tourism operations, presence records were obtained opportunistically in conjunction with the Madagascar Whale shark project during the spring-summer period over four years (2016-2019). A substantial number of megafauna comprising 13 identified species were recorded

in the Nosy Be region ( $x = 13$  individuals/km<sup>2</sup>) over the four-year period. Six cetacean species were sighted: Indo-Pacific bottlenose dolphin (*Tursiops aduncus*); Indian ocean humpback dolphin (*Sousa plumbea*); spinner dolphin (*Stenella longirostris*) pantropical spotted dolphin (*Stenella attenuate*); false killer whale (*Pseudorca crassidens*) and melon-headed whale (*Peponocephala electra*), two baleen whale species: humpback whale (*Megaptera novaeangliae*); Omura's whale (*Balaenoptera omurai*), four elasmobranch species: whale shark (*Rhincodon typus*); spinetail devil ray (*Mobula japonica*); shortfin devil ray (*Mobula kuhlii*); manta ray (*manta birostris*), and one sea turtle species: leatherback sea turtle (*Dermochelys coriacea*) (Chapter 2). Among the 13 species identified, whale shark, humpback whale, spinetail devil ray, Omura's whale, and Indo-Pacific bottlenose dolphin were sighted most frequently (~90%). Sighting rate was highest for the whale shark ( $x = 6$  sightings/km<sup>2</sup>) while the dolphin species were often sighted in larger groups and were consequently thus the most abundant group ( $x = 36$  individuals/km<sup>2</sup>). The information presented in this thesis provides further evidence that Nosy Be region supports a diverse community of large marine megafauna and represents a significant hotspot for many threatened marine megafauna species including whale sharks (Diamant et al. 2018, 2021), mobulid rays (this study), cetaceans (Cerchio et al. 2015b, 2015a) and sea turtles.

#### 4.1.1. *Habitat preference*

Distribution trends from known sighting records were investigated at the community level to better understand the importance of Nosy Be as a high value biodiversity area for marine megafauna (Chapter 2). The megafauna within the region were found primarily coastal inshore and across the continental shelf with a narrow distribution range which was

concentrated on the westerly boundary of Nosy Be and approximately 10 km off the west coast across a reef edge referred to as *Grand banc de l'entrée* (Jonahson and Harding 2007). *Grand banc de l'entrée* is characterized by a steep drop from 18 to 50 meters bordering both reef and seagrass habitat together with a large shallow bank (*Banc des*, 5m) on the east, and a steep continental shelf (1000m) on the west, lower mean sea surface temperatures (SST) (27.5 - 28°C) and relatively high Chlorophyll-a concentrations (chl-a) (0.3 – 0.5 mg.m<sup>-3</sup>) (Jonahson and Harding 2007, GEBCO 2021, Figure 4.1). Annual site fidelity was evident in the filter feeders as little inter-annual variability was observed in the spring-summer season between the four years with the same site identified to be the most visited every year. These patterns might reflect the factors driving megafauna occurrence in the region. The predictive habitat model identified two hotspots in the area for whale sharks, mobulid rays and Omura's whales, *Grand banc de l'entrée* on the west coast of Nosy Be, as found in the environmental modelling, approximately 10 km's offshore in the shallow bay and of the north coast of Nosy Be further offshore between Nosy Be and Nosy Mitsio (~ 40km's from mainland and 20 km's North from Nosy Be, Chapter 3). These two hotspots were associated with depths of 50 – 60m, SST of 27 - 28°C, slope of 0.5 – 1% and total chl-a concentration ranging from 0.3 to 0.5 mg.m<sup>-3</sup>.

The Maxent results showed that the habitat preference of spinner and bottlenose dolphins was concentrated across the continental shelf waters in nearshore region. The predictive distribution model results indicated similar patterns for the spinner and Indo-pacific bottlenose dolphin with highest suitable habitat in this region corresponding to shallow depths, 10 – 100m and cooler SST range (27 to 27.5 °C). However, spinner dolphins were further offshore across the region. Both spinner and bottlenose dolphins are highly mobile species and inhabit a variety of coastal habitats through a heterogenous distribution (Benoit-Bird et al. 2003, Thorne et al. 2012). Both dolphin species were also recorded at *Grand banc*

*de l'entrée*, where suitable habitat was identified at edge of the continental shelf and around the pinnacle. This is in line with cetacean distribution studies which indicate that continental shelves are highly productive habitats which frequently support high densities of marine predators, particularly cetaceans (Lambert et al. 2018). The high densities of cetaceans within these regions can be linked to increased food availability where the interaction between bathymetry and oceanographic features lead to upwelling which aggregates plankton close to the surface waters (Croll et al. 2012). This, in turn, attracts planktivores such as small fish and their predators to the region. The importance of continental shelves and island coastal regions to (Benoit-Bird et al. 2003, Wilson et al. 2007, Kiszka et al. 2011, Cribb et al. 2013) whale sharks, manta rays and cetaceans has been highlighted in numerous studies worldwide (Benoit-Bird et al. 2003, Sleeman et al. 2010, Herrera et al. 2019, Ehemann et al. 2022).

#### 4.1.2. *Essential environmental variables*

Results from this investigation and numerous previous studies have highlighted the importance of food availability in determining the distribution megafauna (Benoit-Bird et al. 2003, Bouchet et al. 2015, 2020). The modelling approach presented here provide fine-scale environmental processes for Nosy Be highlight the importance of essential environmental variables as predictors for prey availability in driving the distribution of marine megafauna. The potential of foraging areas was characterised according to selected variables including total chl-a, SST and sea topography. Whale shark and ray aggregation sites correlation with SST and chl-a have been reported for multiple sites across the world (e.g., Sleeman et al. 2010, Sequeira et al. 2012, Hacoheh-Domené et al. 2015, Austin et al. 2019, Ehemann et al. 2022). Further the current results demonstrate similar trends for cetaceans than what has been indicated for other regions of the world. Chl-a, upwelling and SST have been identified as

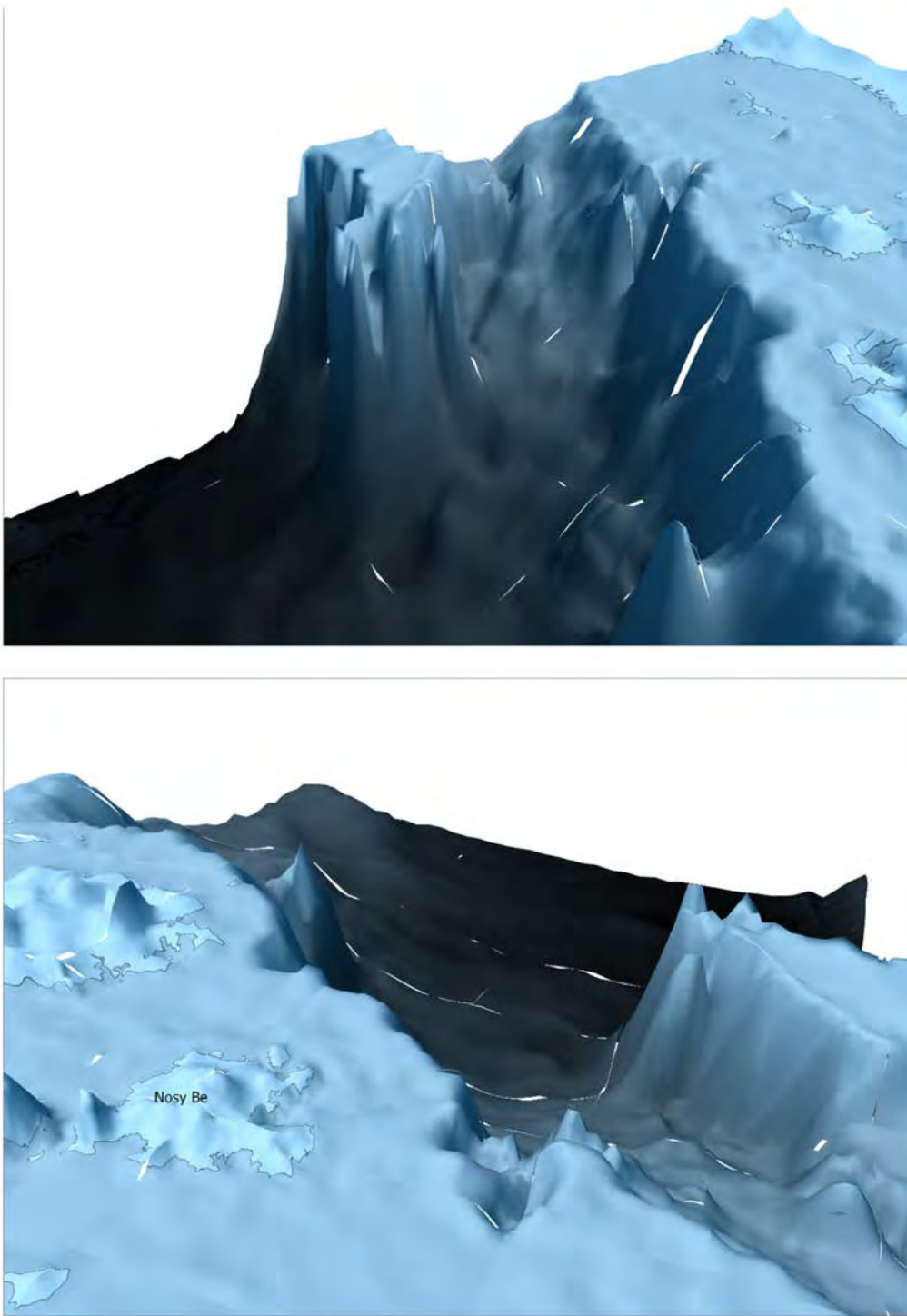
important predictors for cetacean distribution in more well studied regions such as Australia, South Africa (Grémillet et al. 2008), North Atlantic (Correia et al. 2019, 2021), French waters (Kiszka et al. 2007, Lambert et al. 2018) and the Caribbean (Herrera et al. 2019).

The importance of SST and chl-a as important drivers of megafauna distribution can be explained by the relationship between these factors and the provision of nutrient-rich waters and planktonic productivity (Friedland et al. 2012). Nosy Be waters are characterised by stable levels of chl-a year-round with slightly higher levels recorded during austral winter (Kryk et al. 2020). The open waters of oligotrophic tropical regions of the world's oceans are characterised by low total chl-a concentrations reflecting low macronutrient availability within these regions. By contrast, coastal inshore waters within the region typically have higher levels indicated by elevated pigmentation (Benny 2002). The elevated pigment concentrations within these regions reflect increased nutrient availability due to the upwelling of nutrient rich waters into the surface waters driven by topographic steering (water is upwelled along the steep seabed) and, on occasions, freshwater outflow from riverine systems (Pripp et al. 2014, Allen-Waller 2015, Obura et al. 2018). The fine-scale oceanography of northwest Madagascar is poorly studied, although upwelling events have been documented close to Cape Saint André (16°S) and Nosy Be (13°S) (Pripp et al. 2014). Moreover, mesoscale eddies occur on the western edge of the Mozambique channel propagating southwards along the channel edge which play a major role in water enrichment across this region (Pripp et al. 2014, Obura et al. 2018). These eddies transport and export inorganic and organic particles from the Mozambican continental shelf westward supporting strong seasonal changes in productivity and distribution of phytoplankton and micronekton in northwest Madagascar (Tew-Kai and Marsac 2009). Seasonal monsoons may also contribute to the seasonal productivity in the area. For example, alternating monsoons were reported to result in year-round productivity in the Maldives supporting the largest manta ray population in the

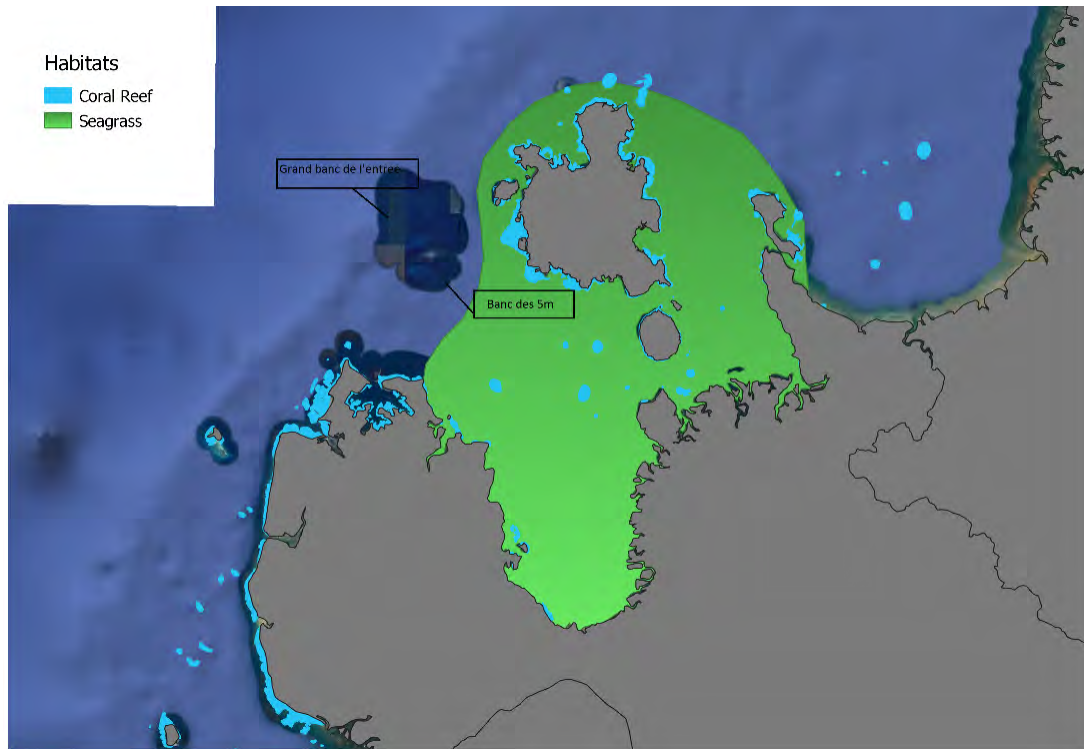
world (Kitchen-Wheeler et al. 2012, Kitchen-Wheeler 2013). January is typically the start of the cyclone season in Nosy Be with prevailing rainfall until April (Diamant et al. 2018, 2021). As a result, freshwater run off may further enhance nutrient availability in shallow coastal waters within the region. Pripp et al. (2014) found high biological productivity adjacent to river mouths along the western shelf of Madagascar. Twelve freshwater sources drain into the marine environment on the south coast of the island from the forested mountains in the Lokobe National Park in Nosy Be (Allen-Waller 2015).

In addition to water chemistry, habitat heterogeneity also plays a strong role in ecosystem productivity and diversity (Bouchet et al. 2015, 2020). Complex bathymetry and habitat patchiness are typically in areas of high productivity creating suitable habitats for smaller species (Nur et al. 2011). Northern Madagascar represents the eastern boundary of the Northern Mozambique Channel with a diversity of habitats (Obura et al. 2018). Nosy Be area is a highly heterogeneous habitat with a shallow bay, steep continental slope, shelves, small islands and a mix of seagrass, reef and oceanic habitats (**Figure 4.1; Figure 4.2**). Cooke et al. (2022) reported about 90% of all coral reefs and 98% of all mangroves of Madagascar to occur within the Nosy Be archipelago. Tidal range combined with the drainage of Madagascar's largest rivers into the Mozambique Channel, transport large volumes of fresh water and sediment which serve to reduce the salinity, increase turbidity, and contribute to nutrient and organic matter pools within the region. The complex bathymetry, hydrodynamics and physio-chemical variables contribute to the formation of unique habitats which sustain high levels of biodiversity. A compilation of previous studies found 62 genera and 323 species of coral in the northwest region of Madagascar alone, and a very rare and diverse diatom flora within the region (Kryk et al. 2020). The physical environment is a large contributing factor to this region being a diversity hotspot for multiple species with different biogeographic ranges (Obura et al. 2018). Areas surrounding regions of complex bathymetry

with sudden changes in depth such as reef edges, the continental shelf edge and shallow banks were all areas highlighted as suitable habitat for megafauna species (**Figure 4.1**). Areas with complex bathymetric features tend to be areas of high marine productivity, owing to higher densities of zooplankton (Yen et al. 2004, Nur et al. 2011). These complex features and habitat heterogeneity provide suitable habitats for smaller species such as invertebrates and fish enhancing foraging opportunities for upper-level predators (Bouchet et al. 2020). This is supported by literature from a large range of species and regions and is considered an important predictor variable for large filter feeding seasonal aggregation sites such as the whale shark, manta ray and basking shark (Sims 2008, Rohner et al. 2013, Copping et al. 2018). This thesis notes that the shelf and coastal region surrounding Nosy Be provide the food and habitat requirements for marine megafauna to forage, improving the understanding as to why this region supports such high diversity and abundance of marine megafauna.



**Figure 4.1.** Detailed 3D visualization topography model of the sea floor of the Nosy Be marine archipelago produced in QGIS, data source GEBCO.



**Figure 4.2.** Marine benthic habitats of Nosy Be, indicating *Grand banc de l'entrée* and *Banc des 5m* from ESRI satellite view, habitat information from GEBCO.

#### 4.2. Citizen science wins and shortcomings

There is a real need for long-term ecological data to adequately monitor marine megafauna populations necessary for successful conservation initiatives (Hays et al. 2016, Temple et al. 2018). In order to classify the parameters and conditions associated with identifying a species critical habitat, long-term datasets over large spatial scales are required (McClellan et al. 2014, Stewart et al. 2018). Obtaining such information is time and resource consuming, resulting in data gaps in marine megafauna literature. However, the citizen science-based data, such as from coordinated programs with the tourism sector used in this thesis, is proving to be valuable in providing data over longer periods of time than what could be possible by

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scientific surveys, though should be interpreted with caution (McKinley et al. 2017, dos Santos and Bessa 2019).

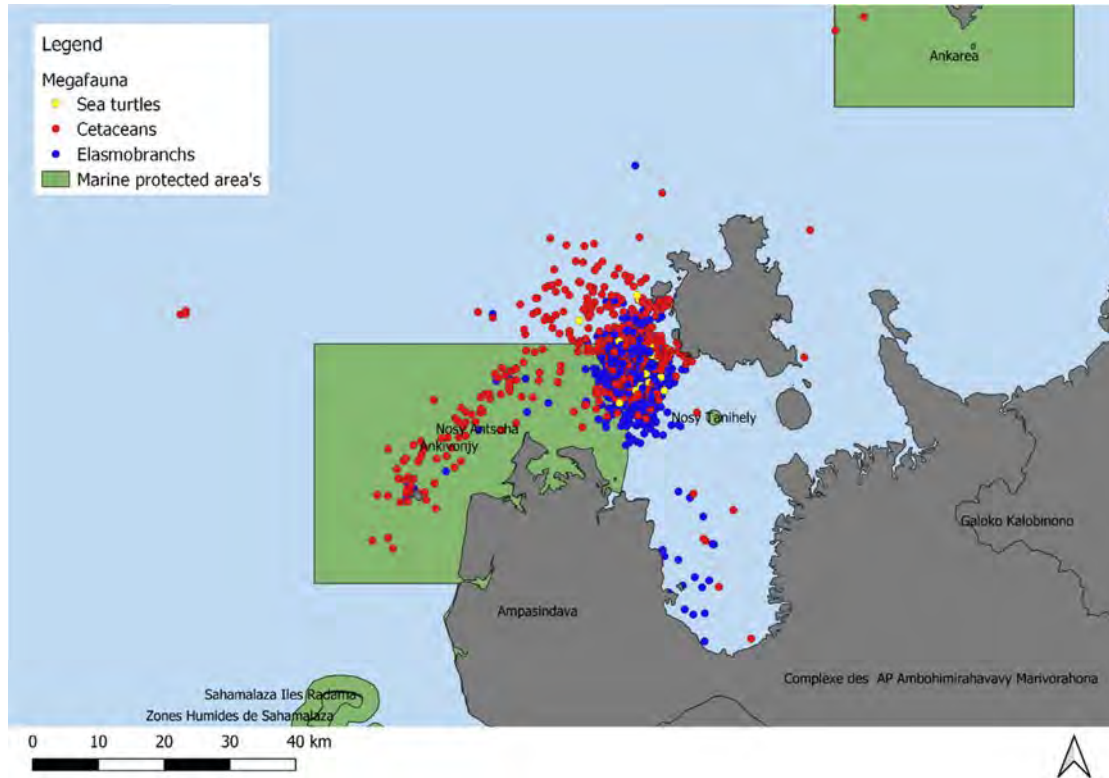
A number of concerns have been raised about the quality data collected in citizen science studies science, see Bird et al. 2014. These include the lack of attention to study design, inconsistent or suboptimal training and absent or problematic standardization and verification methods (Burgess et al. 2017). Some recognized bias related to tourism data were evident in the study, as preferred areas with high encounter probability is targeted and operators often actively search for encounters with closer navigation and higher chance of encounters (Burgess et al. 2017, dos Santos and Bessa 2019). Search effort cannot be accounted for as it was not recorded. The lack of search effort data creates a bias based on areas sampled with no information on areas outside of the limited study range. This limits the model performance and increases overinterpretation of the results. However, the use of these methods in marine ecology has increased and further been assessed and validated (Oldekop et al. 2011, Tonachella et al. 2012, Vianna et al. 2014). In context of the current study, local knowledge (i.e., the knowledge from tourism operators of where to find animals; correctly identifying animals) is an important component in identifying high value sites and biodiversity hotspots (Noble et al. 2020). Areas with high occurrences is known through observations and is a key component to identifying critical habitat and understand the drivers behind these diverse regions (Noble et al. 2020, Pottie et al. 2021). Statistical methods have been developed to account for some of the concerns relating to the quality of citizen science (Merow et al. 2016, Untalan et al. 2019). However, the methods implemented in the maxent model do not fully account for the inherent bias in the data. When interpreting the results of this study, these biases were taken into account and is important to be aware of this when applying the information for identifying high value regions.

Citizen science is particularly important in developing countries and islands where funding for science is limited. These areas are commonly situated in the tropics and most often provide critical habitats for large and diverse megafauna populations (Mwango'mbe et al. 2021, Ehemann et al. 2022, Magson et al. 2022). Citizen science can offer a cost and time efficient tool to obtain such data that would not have been available otherwise. Here citizen science initiatives by Madagascar Whale Shark Project, tourism sector and local participation have provided valuable knowledge on the megafauna community in the region. However, information from such data is limited and used here for identifying general community trends, it is still valuable and can provide information in this previously understudied area (Lodi and Tardin 2018, Natoli et al. 2022). The Maxent model clearly demonstrates the Nosy Be megafauna hot spot regularly visited by operators however, unstudied spots not visited by tourism operators such as northeast of Nosy Be near Nosy Mitsio was also identified as suitable habitat with high predicted occurrence that could potentially be highly biodiverse and need conserving. This demonstrates the importance and value of such data for these understudied and under populated regions and the possibilities of effective citizen science programs. Coordinated programs with the tourism sectors have achieved long-term successful monitoring of megafauna in other regions such as whale sharks in Ningaloo Reef, Australia (Mau, 2008) and manta rays in Raja Ampat, Indonesia (Kasmidi & Gunadharma, 2017). We found that presence-only citizen science provided a valuable contribution to the understanding of the occurrence and distribution of the megafauna community off the Nosy Be coast and that tourism can be effectively utilized for contributing to megafauna research, especially in data-poor regions and, finally, inform management and conservation practices, however, should be interpreted with caution. Going forward, citizen science data collection should be continued in Nosy Be as it has the potential to serve as an important tool for long-term population monitoring, community engagement and empowerment.

### 4.3. Conservation implications

The marine environment around Nosy Be is recognized as a Key Biodiversity Area (Key Biodiversity Areas, 2021). The year-round presence of the large and diverse megafauna community and diverse coral reefs contributes to Nosy Be being of high ecological value both locally and globally. Moreover, the high biodiversity sustains a thriving ecotourism industry which translates into substantial economic benefit to Madagascar. The identification of megafauna biodiversity hotspots and their critical habitats is crucial to conservation and protection efforts of marine systems by assisting in the implementation of new marine protected areas (MPAs), identifying gaps in current MPAs and assisting in the allocation of efforts and resources for the best outcomes (García-Barón et al., 2019; Lambert et al., 2017b). Effective habitat protection is important, benefitting the large and small fauna and the health of the system. Results from this thesis provide invaluable information towards the implementation of management measures for the megafauna of Nosy Be. The results demonstrate suitable habitat with high probability of occurrence for nine frequently occurring species of megafauna (of which five are listed as endangered under the IUCN) in the area. The critical megafauna habitats identified are located within the community managed Ankivonjy MPA (1,394 km<sup>2</sup>, **Figure 4.2**). It is, however, recommended that the Ankivonjy MPA be expanded to incorporate all the critical habitats of the megafauna. The expansion of the MPA is also likely to have far reaching effects on the marine ecosystem of Nosy Be since it would incorporate poorly conserved habitats such as fringing reefs (Allen-Waller 2015, Diamant et al. 2021). Currently the only protection in the coastal waters of Nosy Be is a fringing reef surrounding the southern coast under the Lokobe MPA. The expansion of Lokobe MPA further east and south across *Grand banc de l'entrée* is a possible consideration for the region. A further hotspot identified by the model was located adjacent the Ankarea

MPA, surrounding Nosy Mitsio. The expansion of the Ankarea MPA should also be considered; however, this region needs further investigation (**Figure 4.2**). Diamant et al. (2018) reported low risk of fishing-related mortalities and injuries for whale sharks within the Ankivonjy and Ankarea MPAs. Thus, the expansion of the MPAs over the identified critical habitats could benefit all megafauna as fishing mortality is a common threat for all these species (Andrianarivelo 2001, Razafindrakoto et al. 2008, Cerchio et al. 2014). Elasmobranchs continue to be exploited by shark targeted commercial fisheries as well as several small-scale and artisanal fisheries in Madagascar. Cetaceans and elasmobranchs are caught as bycatch which is the number one threat to endangered humpback dolphin populations. In Madagascar, bottlenose dolphins and humpback dolphins are the most bycaught species (Andrianarivelo 2001). Most of Madagascar's coastal human population relies on artisanal fishing for their livelihoods. Considering the importance of prey availability to the occurrence of megafauna in this region, overfishing of prey species present a large threat to the cetacean community and the management of subsistence fishing within the MPAs could benefit the megafauna in the region. Diamant et al. (2018) also observed a strong association between whale sharks and mackerel tuna schools hence directed management of fisheries in these regions could benefit filter feeding and predatory megafauna.



**Figure 4.3.** Existing Marine Protected Areas in relation to the documented distribution of the marine megafauna community in the Nosy Be region.

#### 4.4. Recommendations and future direction

Presence-only citizen science data have proven to be valuable for contributing baseline knowledge on distribution and habitat preference of megafauna for Nosy Be. However, there are several ways to account for the aforementioned limitations in the study. To account for the bias in opportunistic sightings data Global Positioning System (GPS) tracks can be recorded during each trip to track survey effort as well as logging the hours of active searching and total hours of the trip. This can make for a more standardized approach to the data collected by tourism operators and mitigate the concerns regarding citizen science by providing information on where search effort is focussed, and days boats went out, but no

sightings were recorded. This can also help to more accurately define the observational area covered by the tourism operators. Further modelling could also be completed including other factors, such as primary productivity and zooplankton samples (Putra et al. 2016). Since it is difficult to collect data evenly through seasons in the region, accounting for search effort can provide for including a seasonal component to the models. This is important for investigating the effects of climate shifts on megafauna. The Maxent model has been shown to have high predictive power in demonstrating how changes in the environment will affect species. This could particularly be important for key foraging grounds such as Nosy Be. Models could include predicted future environmental conditions and its effects on megafauna distribution.

Further, species abundance and population density estimates are critical information for the long-term monitoring of megafauna populations to support future research and assess the efficacy of MPAs in a region and management strategies put in place (Tyne et al. 2014, Robinson et al. 2016, Diamant et al. 2021). Estimating population abundance for species requires systematic surveys for capture-recapture data collection and these study designs can be costly. One potential solution that allows for collecting such data is photographic identification of individuals from tourists and operators, which can be implemented for both elasmobranchs and cetaceans (Rowat et al. 2009, Tonachella et al. 2012, Couturier et al. 2014). There are concerns and limitations regarding these methods, however, they can be used and have already contributed greatly to population estimates for the whale shark population in Nosy Be by the Madagascar Whale shark Project (Diamant et al. 2021).. Various capture-recapture models can then be implemented in the program MARK and compared which have different assumptions depending on whether individuals will have equal probabilities of recapture (Kitchen-Wheeler et al. 2012, Tyne et al. 2014, 2016).

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Distance sampling is another potential method for obtaining reliable density and abundance estimations (Dick and Hines 2011). This can be done through ship-based to small-boat based surveys along a set of line transects and recording sighting distances and angles. Density is estimated along the set of transects via a detection function fitted to the perpendicular distances from the line to the detected animal (Mullin and Fulling 2003). These estimates can then be projected for the whole study region. Distance sampling line transect surveys have been used successfully all over the world to estimate cetacean abundance (Mullin and Fulling 2003, Dick and Hines 2011, Hammond et al. 2013). The population status of seven out of the nine cetaceans recorded in this study are unknown, a major hindrance to their protection. Expanding on these surveys in the area for the cetacean populations should be considered for future research.

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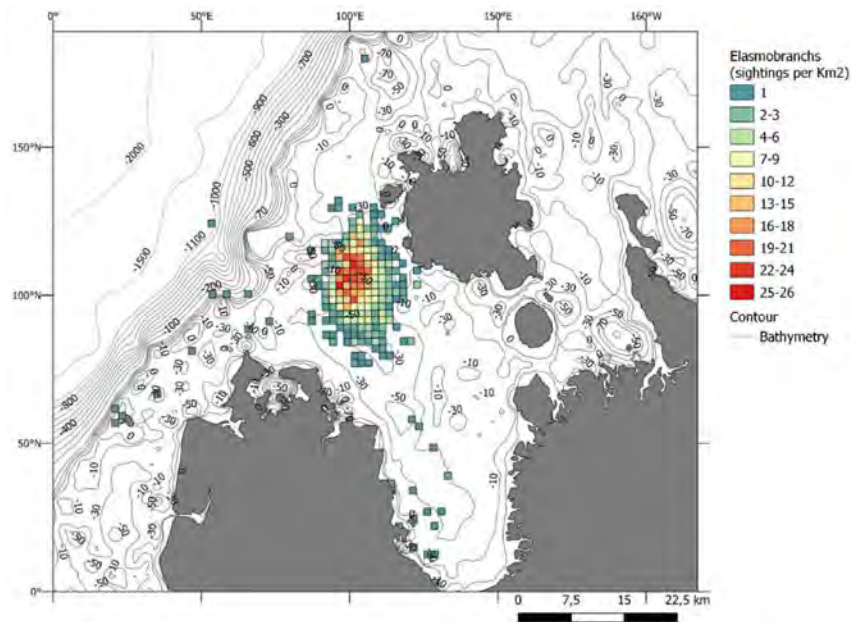
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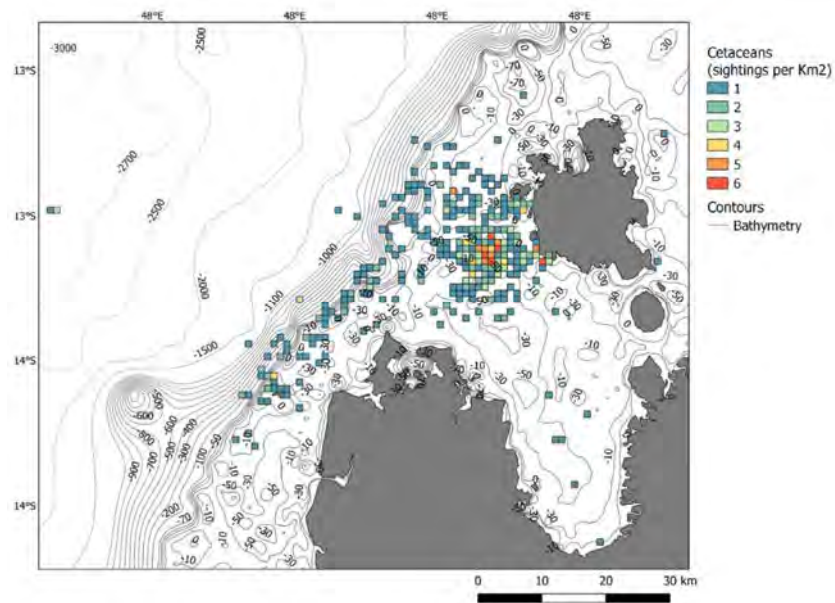
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## APPENDIX I: SPATIAL TRENDS

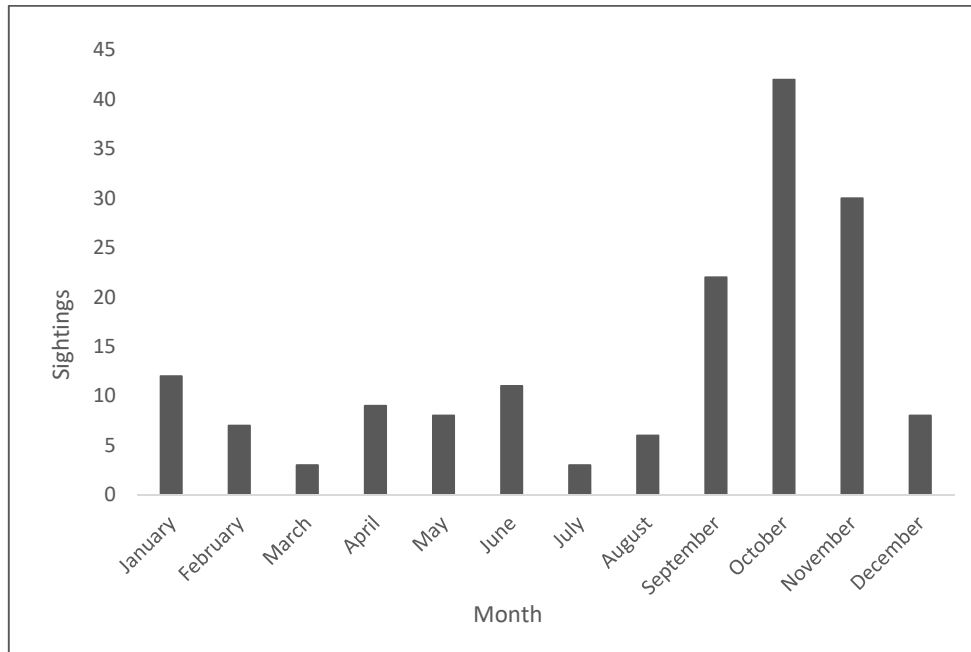


**Supplementary Figure I.1.** The sighting rate (sightings/km<sup>2</sup>) of coastal elasmobranchs in the Nosy Be study area over a period of four years (2016-2019)

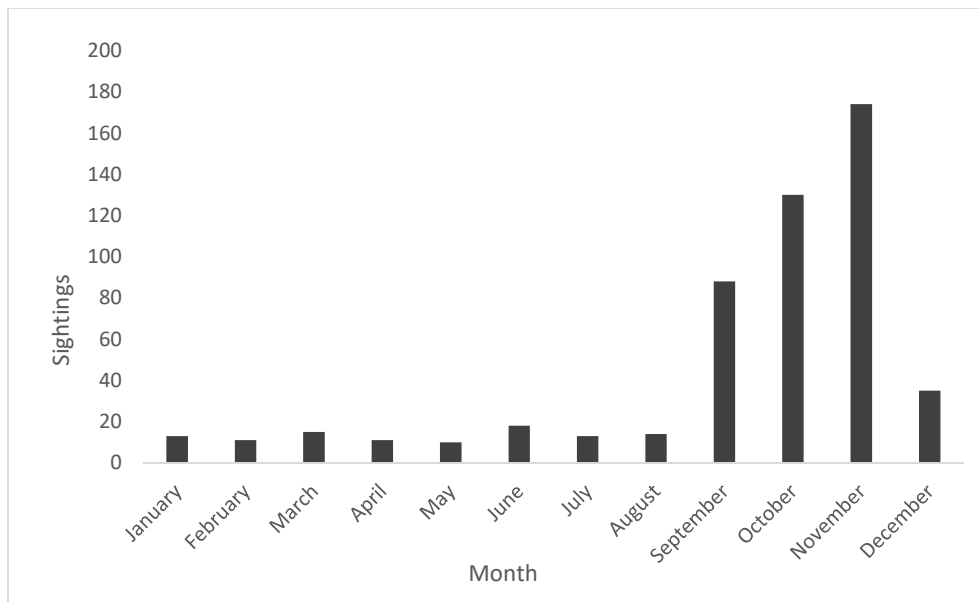


**Supplementary Figure I.2.** The sighting rate (sightings/km<sup>2</sup>) of cetacean species in the Nosy Be study area over a period of four years (2016-2019)

## APPENDIX II: TEMPORAL TRENDS

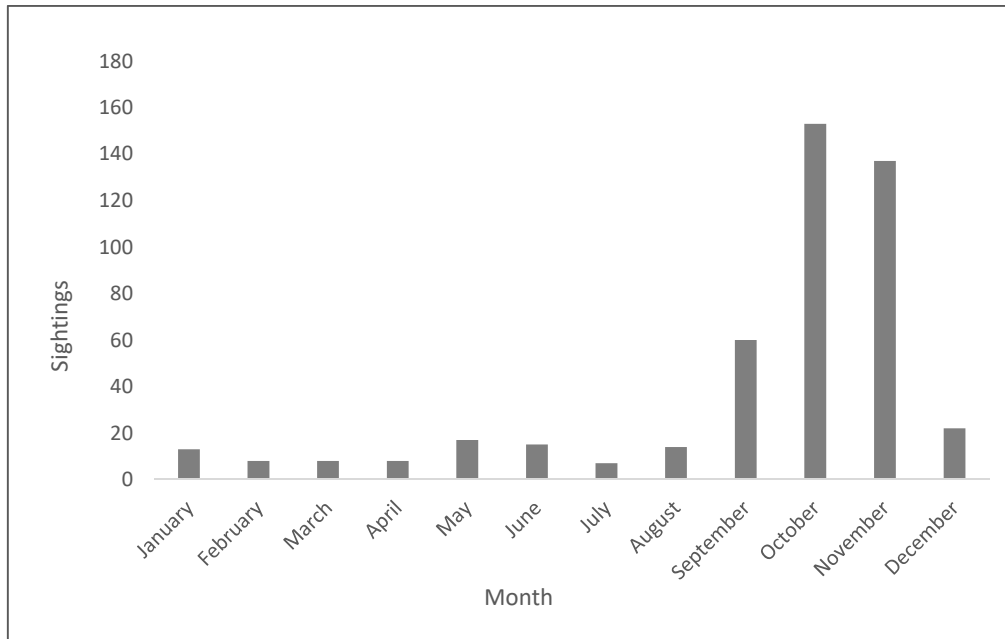


**Supplementary Figure II.1.** Total number of megafauna sightings for each month in 2016

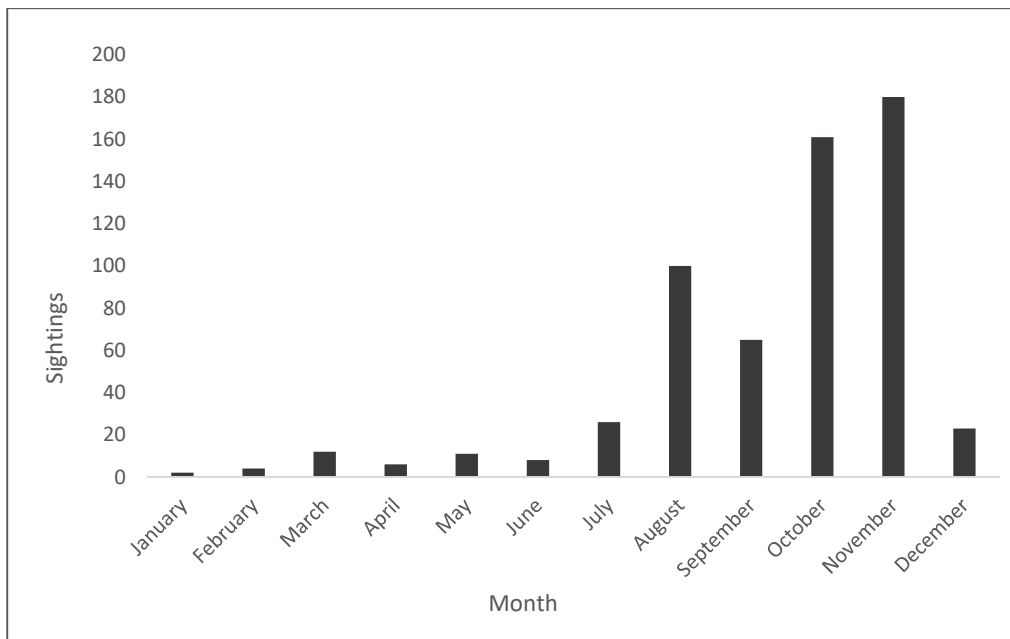


**Supplementary Figure II.2.** Total number of megafauna sightings for each month in 2017

Appendix II

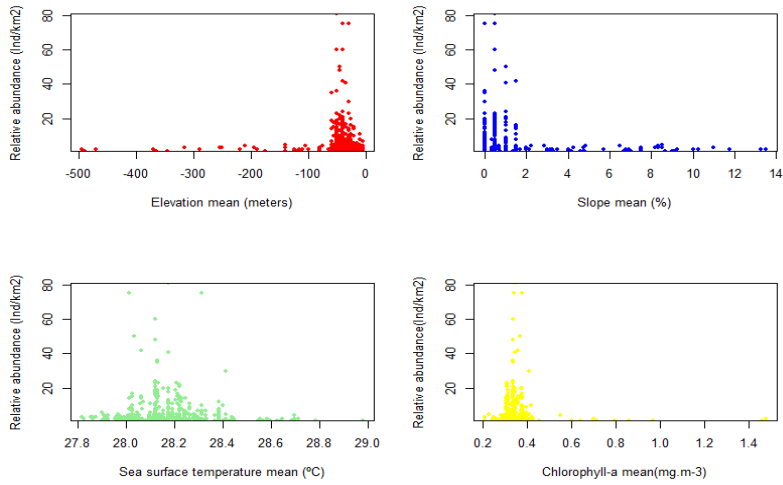


**Supplementary Figure II.3.** Total number of megafauna sightings for each month in 2018

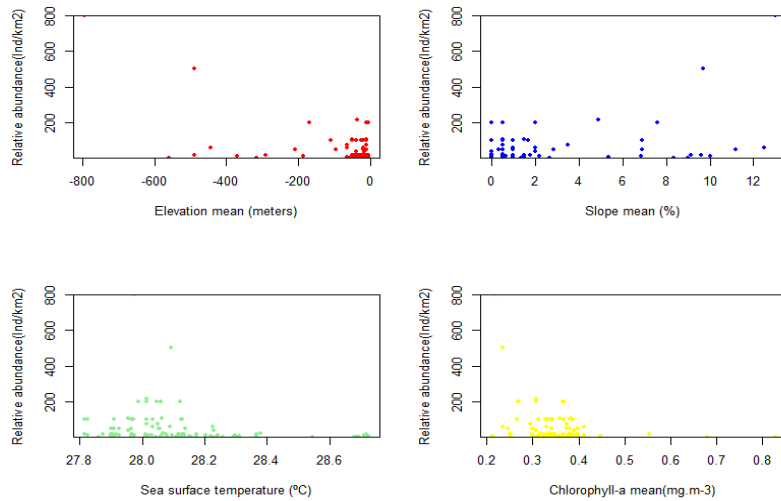


**Supplementary Figure II.4.** Total number of megafauna sightings for each month in 2019

### APPENDIX III: ENVIRONMENTAL TRENDS

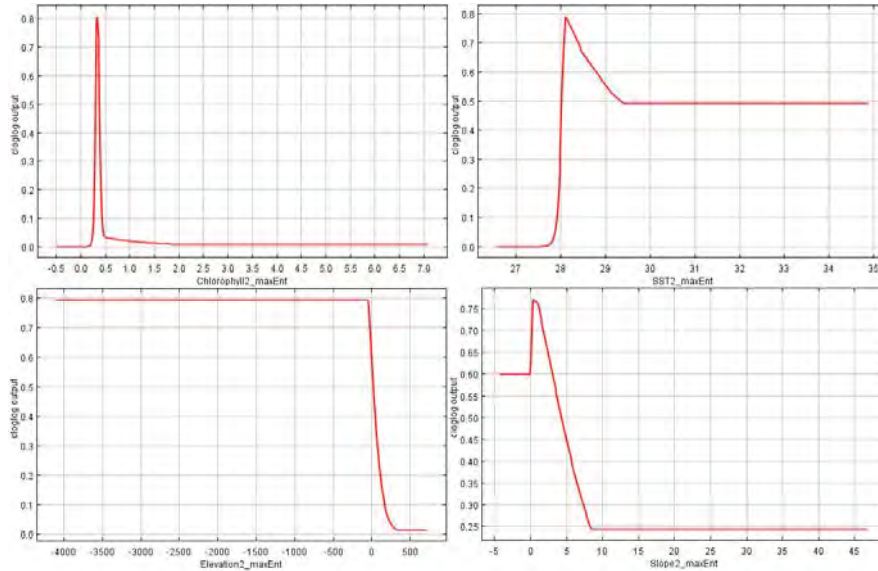


**Supplementary Figure III.1.** Relative abundance (ind./km<sup>2</sup>) of filter feeder megafauna sighted off the coast of Nosy Be, Madagascar and the related mean environmental variables (Elevation, slope, SST, chl-a).

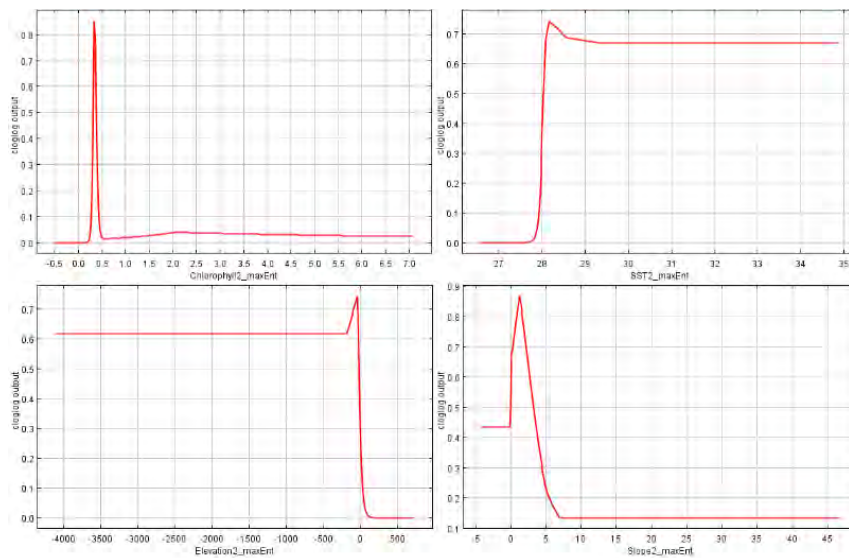


**Supplementary Figure III.2.** Relative abundance (ind./km<sup>2</sup>) of *delphinids* sighted off the coast of Nosy Be, Madagascar and the related mean environmental variables (Elevation, slope, SST, chl-a).

## Appendix III

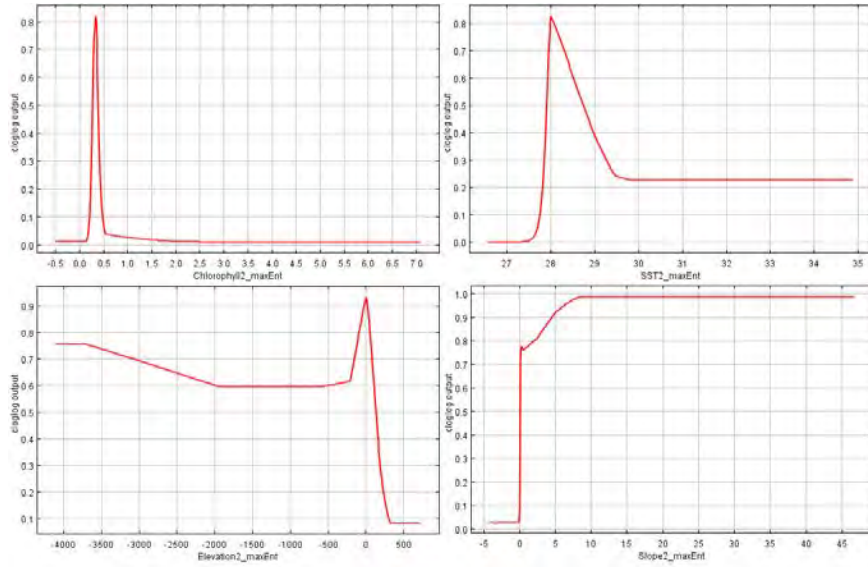


**Supplementary Figure III.3.** The response curves of whale shark; *Rhicondon typus* (probability of presence related to environmental conditions) to each environmental variable as explained by Maxent.

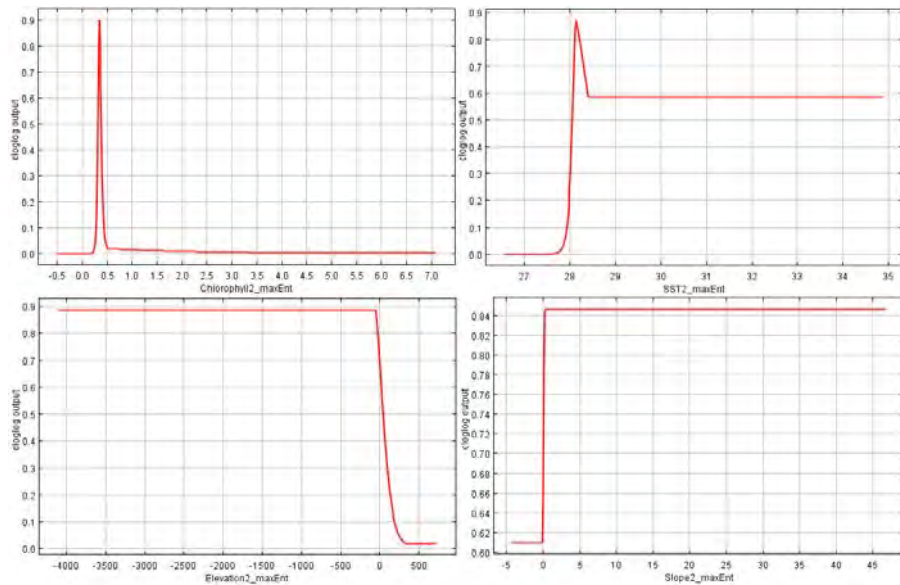


**Supplementary Figure III.4.** The response curves of Mobulidae; *Mobula japonica*, *Mobula kuhlii*, *Manta birostris* (probability of presence related to environmental conditions) to each environmental variable as explained by Maxent.

### Appendix III

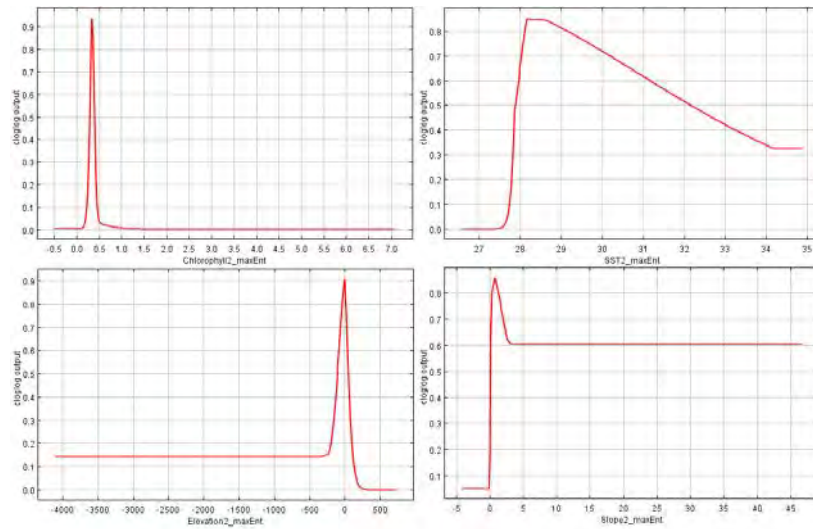


**Supplementary Figure III.5.** The response curves of humpback whale; *Megaptera novaeangliae* (probability of presence related to environmental conditions) to environmental variable as explained by Maxent.

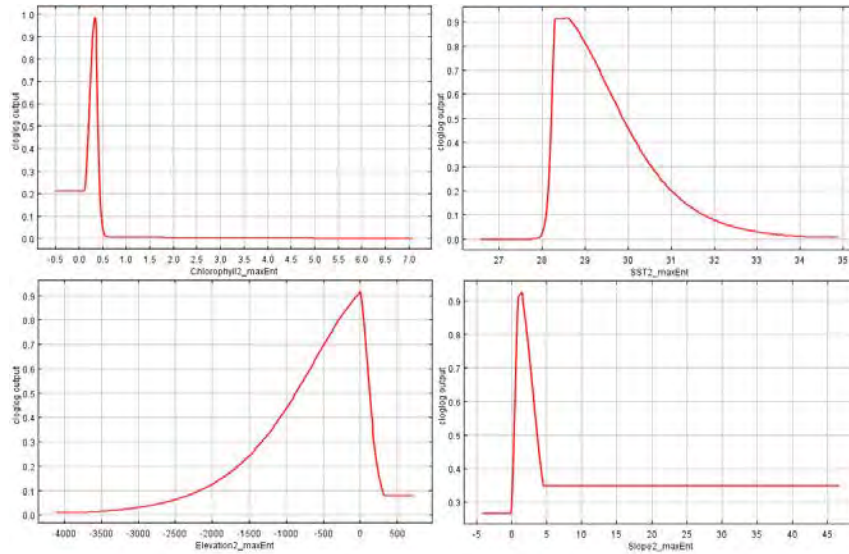


**Supplementary Figure III.6.** The response curves of Omura's whale; *Balaenoptera omurai* (probability of presence related to environmental conditions) to each environmental variable as explained by Maxent.

## Appendix III



**Supplementary Figure III.7.** The response curves of Indo-pacific bottlenose dolphin; *Tursiops aduncus* (probability of presence related to environmental conditions) to each environmental variable as explained by Maxent.



**Supplementary Figure III.8.** The response curves of Indian Ocean humpback dolphin; *Sousa plumbea* (probability of presence related to environmental conditions) to each environmental variable as explained by Maxent.