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Occurrence of mobulid rays in Northwest Madagascar

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Abstract The waters around Nosy Be in northwest Madagascar are well-known for the occurrence of large planktivores, such as whale sharks (*Rhincodon typus*) and Omura's whales (*Balaenoptera omurai*). Between 2016 and 2022, sighting data on mobulid rays were opportunistically collected during tourism activities. Additional sources, including citizen science submissions, tourism operator reports, and social media records, were used to compile sightings of three mobulid ray species. A total of 255 encounters were documented, with *Mobula mobular* ($n=165$) being the most common, followed by *M. birostris* ($n=60$) and *M. kuhlii* ($n=30$). Notably, the absence of confirmed *M. alfredi* records since 2015 suggests a potential local decline. This study highlights Nosy Be as a habitat for mobulid rays and emphasises the necessity for further species monitoring, ongoing identification of potential threats, and

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management initiatives aiming at reducing mortality from gillnet fishing.

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Introduction

Mobulid rays (genus *Mobula*) are pelagic, planktivorous rays in their own family, Mobulidae, and include the two currently recognised manta ray species: the reef manta ray (*Mobula alfredi*) and the oceanic manta ray (*Mobula birostris*; White et al. 2017), as well as seven other smaller *Mobula* species. The mobulids are one of the most threatened of all vertebrate groups, due largely to overfishing (Dulvy et al. 2021; Pacoureau et al. 2021). Lower levels of mortality occur from numerous lesser threats, such as entanglement in nets, recreational foul-hooking, and vessel strikes (Couturier et al. 2012; Stewart et al. 2018). Photo-identification and sighting-based studies have identified a number of aggregation sites for mobulids within the Indian Ocean, the largest of which may be Mozambique (Marshall et al. 2011) and the Maldives (Stevens 2016). However, movement studies in these species have often shown that a significant portion of the population exhibits high residency, increasing the risk of local depletion and even regional extinction (Marshall et al. 2020, 2022c). Declining global trends have been identified for all nine mobulid species, all of which are now listed as threatened on the IUCN Red List of Threatened Species: seven as Endangered and two as Vulnerable. For the species mentioned in this study: *M. mobular* and *M. birostris* were classified as Endangered in 2018 and 2019, respectively (Marshall et al. 2022a,b). *Mobula alfredi* was Vulnerable (Marshall et al. 2022c), while *M. kuhlii* was assessed as Endangered in 2020 (Rigby et al. 2022).

Northwest Madagascar is a noted hotspot for marine biodiversity (Antonelli et al. 2022). The island of Nosy Be is a popular marine tourism destination (Ziegler et al. 2021), known for its populations of large planktivores such as Omura's whales (*Balaenoptera omurai*; Cerchio et al. 2015) and whale sharks (*Rhincodon typus*; Diamant et al. 2021). Several mobulid species are also present in this area, with manta rays (*M. alfredi* and/or *M. birostris*; this was before the species were split in 2009) reported from dive sites off Nosy Be (Jonahson and Harding 2007) and mobulid rays (*M. birostris*, *M. kuhlii*, and *M. mobular)* are associated with *B. omurai* and *R. typus* near Nosy Be (Cerchio et al. 2018, 2022; Diamant et al. 2021). Mobulids have also been recorded in regional aerial surveys (Laran et al. 2017).

No chondrichthyan species are protected in Madagascar (Humber et al. 2015; Séret 2022), although article 18 of the Code de la Pêche et de l'Aquaculture (Loi n°2015–053) prohibits the capture within Madagascar of all endangered or protected species (it is not specified whether conservation status is national or global, i.e. IUCN Red List). Furthermore, in notice No 156–2022/MPEB/SG, the Ministry of Fisheries and Blue Economy implemented a temporary ban on the capture and export of shark and ray species listed in the appendices of the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES), although this listed all species in the *Manta* genus, not the *Mobula* genus which now includes all mobulid rays (White et al. 2017). Mobulids have been recorded in artisanal fishery landings in northern (Robinson and Sauer 2013; Temple et al. 2019), northwest and southwest Madagascar (WCS unpublished data), and are caught as bycatch in pelagic tuna fisheries (Séret 2022). The IUCN Red List assessments for both *M. alfredi* and *M. birostris* noted that these species are fished in Madagascar, and likely depleted (Marshall et al. 2020, 2022c).

Mobulid rays are frequently caught incidentally as bycatch across their distribution range, occurring in approximately 21 small-scale fisheries spanning 15 countries, as well as in nine large-scale fisheries across 11 countries (Croll et al. 2016; Marshall et al. 2022c). Despite their unintentional capture, these mobulids are often retained due to their considerable commercial value in trade (Marshall et al. 2022c). Mobulid rays are utilised for various purposes including their meat, skin, liver oil, and notably their gill plates (Couturier et al. 2012). The demand for gill plates, particularly in Asian markets where they are prized for their perceived health benefits in traditional tonics, has led to their high commercial value. Global landings of mobulid species have been increasing steadily, mainly due to the growing demand for gill plates since the 1990s (Croll et al. 2016; Marshall et al. 2022c), and many fisheries that were once incidental in nature have transitioned into directed commercial export fisheries (Croll et al. 2016). Even

when discarded alive, their post-release mortality can be high (Francis and Jones 2017; Marshall et al. 2022c).

Here, we report the results from 7 years of field surveys and opportunistic data collection on mobulid sightings and landings in the Nosy Be area. Information regarding landing rates and the value of mobulid meat was recorded through interviews with local artisanal fishermen. This study represents the first dedicated research effort on mobulids in the waters of Madagascar, aiming to document the presence of these threatened planktivores in the region, to understand patterns of occurrence, and identify threats to their survival.

Methods

Site description

Ampasindava Bay in northwest Madagascar is formed by the islands of Nosy Be, Nosy Sakatia, Nosy Komba, and the Ampasindava Peninsula of mainland Madagascar (Fig. 1). The maximum depth of the bay is around 100 m, with a few shallow reefs and sandy plateaus. Water temperature ranges between 24 and 30 °C throughout the year (S. Diamant, pers. obs.). Since 2010, the Wildlife Conservation Society (WCS) has been working with local communities to create and manage, on behalf of the Ministry of Environment, two new Marine Protected Areas (MPAs), covering 70,000 ha of marine habitat. The Ankarea MPA covers a total area of 135,556 ha and is located 50 km northeast of Nosy Be. The Ankivonjy MPA, which is an area of interest in this work, is located 50 km southwest of Nosy Be. It includes the coastal ecosystems of the Ampasindava Peninsula and marine ecosystems between the islands of Nosy Iranja and Ankazoberavina.

Field surveys

Encounter data were collected from ecotourism vessels between August and December (the peak season for marine megafauna tourism in the area) from 2016 to 2019, and in 2022, as well as opportunistically during research surveys on cetaceans from 2015 to 2019 (see Cerchio et al. 2022). Both survey teams recorded sightings from the surface, and generally entered the water on snorkel for further observations. Researchers and research volunteers were allocated across a maximum of seven marine tourism vessels daily to document opportunistic sightings of marine megafauna, including sharks, rays, marine mammals, and sea turtles. Surveys were not standardised or randomised in terms of coverage, with distance and direction varying according to marine life sightings and ocean conditions (see Diamant et al. 2021). Search effort was highest from 9:00 AM to 1:00 PM due to the regular onset of afternoon winds and associated operator schedules.

The survey area and sightings of the *Mobula* species are shown in Fig. 1. Mobulids were typically encountered within Ampasindava Bay in a known whale shark hotspot (Diamant et al. 2018, 2021). When mobulids were encountered, either when spotted from the vessel or while observers were swimming, encounter data, including geographic position (latitude, longitude), species, and number of individuals were recorded.

For *M. birostris*, when possible, sex was identified by the presence (male) or absence (female) of claspers on the pelvic fins, and classified as 'unknown' if the pelvic fin area could not be observed (Marshall et al. 2009; Stevens et al. 2018). Male maturity was determined by clasper length. Any marks or scars, such as bites or other injuries, were recorded and categorised as bite wounds or anthropogenic scarring, based on the location and shape of the wound or scar. The observed behaviour was also recorded. Foraging was identified when individuals engaged in somersault feeding, visible from the surface, while foraging on zooplankton. Courtship involved mating trains, where multiple individuals followed a female at the surface (Stevens et al. 2018). *Mobula birostris* are individually identifiable based on their unique ventral markings (Marshall et al. 2011). Where possible, a photograph of this ventral region was taken and uploaded to the global manta ray photo-identification library, Manta Matcher (https://mantamatcher.org/; Marshall and Holmberg 2021). Disc width (DW) was visually estimated to 0.5 m based on comparison to snorkelers underwater or to the boat length when rays were near the surface.

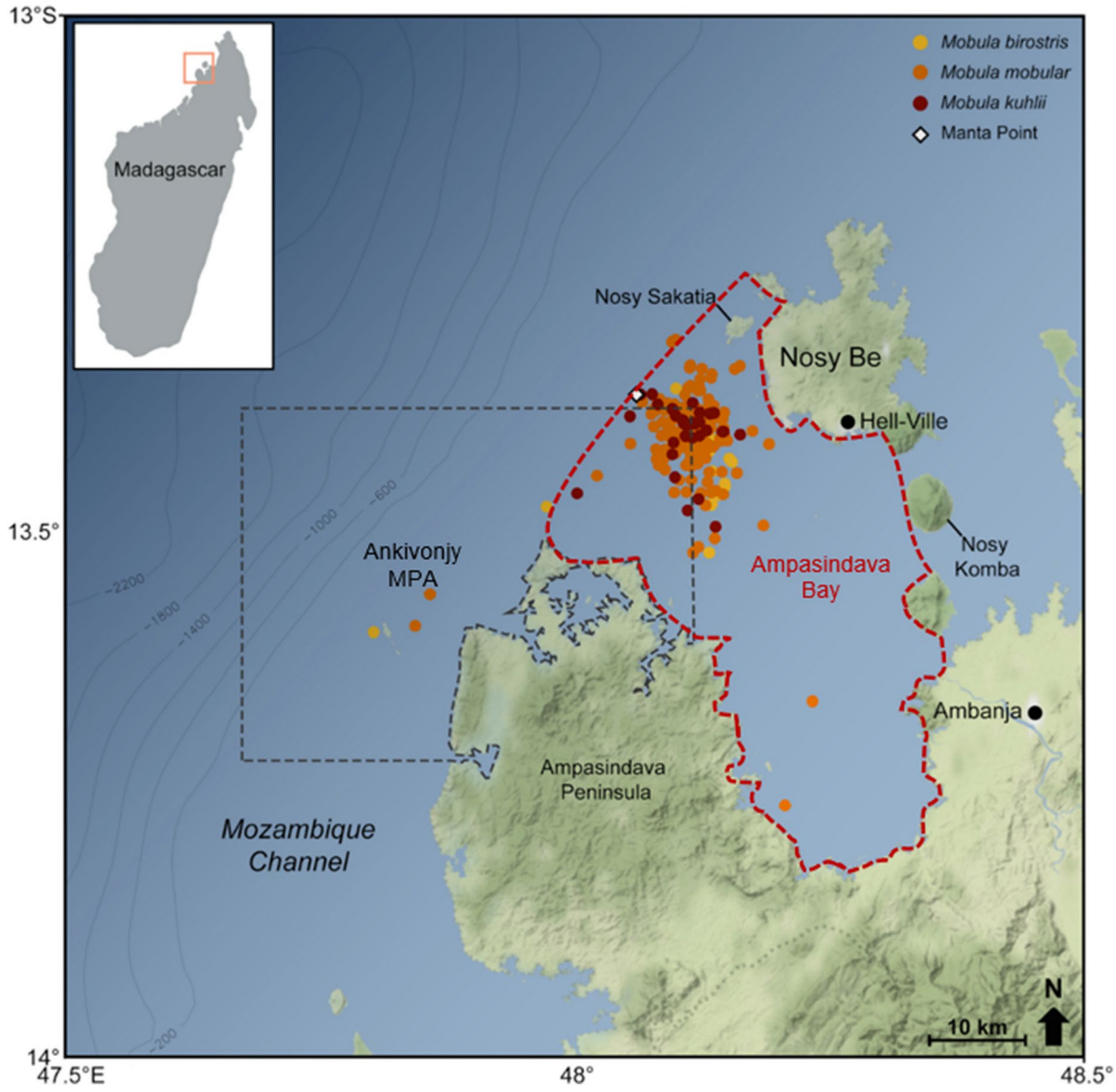

Fig. 1 Map of the study area in northwest Madagascar. The colour dots show the distributions of the encounters of the three identified species across the years ($n = 255$). The red dotted line indicates Ampasindava Bay; the black dashed box shows the Ankivonjy Marine Protected Area. The diamond shows the location of Manta Point, a recreational dive site where manta rays have been regularly seen

Public sighting surveys

To gather additional information on mobulid occurrence in the region, sightings were collated from local tourism operators (i.e. dive centres, wildlife watching operators), community members in the area, citizen science submissions to Manta Matcher, and through searching public records on social media and video platforms. Searches for the keywords 'manta Nosy Be' and 'manta Madagascar' were done on YouTube©, Vimeo©, and Facebook© and were gathered from social media accounts of local diving operators. Records from these sources were obtained between 2012 and 2022. The lead author also conducted informal interviews with long-time dive operators from Nosy Be.

Our dataset includes individual-based (photo-identified) records of *M. birostris*, as well as sightings of *M. kuhlii* and *M. mobular*, for which photo-identification data were not collected. *Mobula kuhlii* and *M. mobular* could not be reliably distinguished by tourism operators, which particularly affected the results for 2015, 2016, and 2020, as these seasons had a high proportion of public sightings relative to trained researcher observations. Hence, 'encounters' are defined as when individuals or groups of mobulids were recorded, whereas a 'sighting' is defined as a photo-identified individual *M. birostris* recorded on a specific date and site.

Fisher surveys

Five Malagasy fishers from Nosy Be and Nosy Faly were approached by M. Strogoff and C. Scarffe to participate in an independent film project about shark and ray fishing. These fishers volunteered information on the likely product destination, sale prices, and different fishing techniques used to land mobulids in the region. Co-authors had a series of informal discussions and joined the fishers on fishing trips between 2020 and 2023.

Results

Four *Mobula* species were identified within Ampasindava Bay: *M. alfredi*, *M. birostris*, *M. kuhlii*, and *M. mobular*, from a total of 255 encounters of the latter three species recorded during field surveys across the study period (Fig. 2). *Mobula mobular* was the most commonly encountered species ($n = 165$ encounters), followed by *M. birostris* ($n = 60$) and *M. kuhlii* ($n = 30$) (Table 1; Fig. 2). All three species were encountered in the majority of survey years, except for *M. kuhlii*, absent from the data in 2015, 2016, 2018, and 2020, and *M. mobular* was not recorded in

Fig. 2 Mobulid ray species encountered in Ampasindava Bay, Madagascar. **A** School of *Mobula kuhlii*. **B** Courtship behaviour in *M. mobular*, with female in top centre. **C** *Mobula birostris*. **D** Two *M. birostris* feeding at the same time in November 2019, with leucistic individual on left (**A**, **C**, **D** photos: Stella Diamant; B: Simon Pierce)

Table 1 *Mobula birostris* (B), *M. mobular* (M), and *M. kuhlii* (K) encounters reported from Ampasindava Bay per month from 2015 to 2022. 'Tot per month' and 'tot per year' are the sum of species-level encounters per month and year, respectively

	August			September			October			November			December			tot per year		
	B	M	K	B	M	K	B	M	K	B	M	K	B	M	K	B	M	K
2015										3						3		
2016								1		1	1					1	2	
2017				3	3		2	11			16	5	3	4	2	8	34	7
2018	2	2					3	7		9	12		3	3		17	24	
2019					7		9	12	6		16	5		2		9	41	11
2020					2			39		2	25			2		2	68	
2022							5		6	14		5	1		1	20		12
Tot per month	2	2		3	12		19	70	12	29	70	15	7	11	3	**60**	**165**	**30**

2015 and 2022. These potential absences are, however, likely biased by an inability to distinguish the smaller mobulid species from one another from operator reports (see Methods). Mobulid encounters were higher in October and November. The percentage of sightings in the peak months of October and November, relative to the survey season in total, was 80% for *M. birostris*, 84% for *M. mobular*, and 90% for *M. kuhlii*. There was no clear variability in sighting locations between years or months.

Records of *M. alfredi* were obtained solely from historical dive centre records, with cleaning behaviour observed at one particular dive site, 'Manta Point' (Fig. 1), describing the animals slowly hovering over the reef with the presence of cleaning fishes. Dive operators regularly visited Manta Point from 1999 to 2007, due to occasional sightings of manta rays at this cleaning station making this a prime dive location. However, *M. alfredi* and *M. birostris* were not distinguished prior to the split of the then-*Manta* genus in 2009 (Marshall et al. 2009), which made confirmation of species-level identification impossible from operator reports that were not supported with photos. Searches of dive centre social media channels and YouTube videos taken in the bay of Nosy Be, where they routinely dive, confirmed that some of these sightings were *M. alfredi*. Active cleaning was confirmed from public video footage for both *M. alfredi* in November 2012 at an unknown location (i.e. https://www.youtube.com/watch?v=uEKavzcQ8uw) and *M. birostris* in July 2015 at Manta Point (i.e. https://www.youtube.com/watch?v=2VpKmvRNuL0). From 2007 to 2015, sightings of both species became rare according to various dive operators, some specifying they did not visit this site as much due to the inconsistency of manta encounters (pers. comm. representative of Scuba Nosy Be, citing 1 in 15 chances of seeing a manta on a dive at Manta Point after 2007) and the identification of new dive sites that were more popular. As of September 2023, no *M. alfredi* had been observed at this site since 2015 according to representatives from Manta Diving, Aqua Diving, and Scuba Nosy Be. No additional public sightings after 2015 were found in the course of this work. There were no records of feeding behaviour found for *M. alfredi*.

Ecology and behaviour

Mobula kuhlii were seen in groups ranging from an estimated 10–50 individuals. This species was often associated with either *M. birostris* and/or *M. mobular*, though sighting data were not collected in such a way to determine the percentage of time that mixed groups occurred. *Mobula mobular* was seen in numbers ranging from 1 to 50 individuals (estimated), generally in single-species groups. *Mobula birostris* were either solitary or with up to four individuals.

Feeding behaviours were observed in *M. birostris*, *M. mobular*, and *M. kuhlii* during research surveys, with individuals of all three species (separately) somersault feeding at 0–20 m depths while targeting dense patches of zooplankton. On several occasions, once a year on average, unusually large and dense zooplankton patches persisted for 1–3 days, leading to multiple *M. birostris*, *M. mobular*, and *M. kuhlii* feeding concurrently with Omura's whales and whale sharks on the same prey. These events did not

occur at a specific time, being observed in September (in 2023), October (in 2017, 2019, and 2022), and November (in 2018 and 2022). Up to four *M. birostris* were observed feeding within the same patch of krill on three occasions in October (2019 and 2022).

There were multiple observations throughout the survey period (approximately 10% of the encounters towards the end of the season, i.e. December) of *M. mobular* exhibiting (single-species) courtship behaviours and/or mating trains (Fig. 2b).

Photo-identification of *M. birostris*

No individual photo-identifications of *M. alfredi* were obtained. Sixty sightings of *M. birostris* individuals were recorded, of which 18 were photo-identified, including six females, three males (all mature), and nine of unknown sex. Only ventral photos were available for the identified individuals, but, of these, five (28%; three females, two unknown) were leucistic based on their relatively light ventral colouration. All photo-identified individuals had an estimated DW between 300 and 450 cm. One inter-annual resighting was recorded (MA0004B), of a female sighted over a 6-year period in October 2016, December 2017, November 2020, and November 2022. Photo-identification data were uploaded to Manta Matcher; no prior or subsequent sightings of these individuals had been recorded from outside the Ampasindava Bay area or elsewhere as of March 2024.

Scars were present on the dorsal surface of 19 individual *M. birostris*, including fishing gear entanglement injuries, propeller scars, and shark bites (Fig. 3a, b). The majority of scars were attributed to anthropogenic origins (13 individuals), including fishing gear entanglement injuries (12), or propellers or boat engines (1). Two of the bites were categorised as shark bites (unidentified species). For the four remaining injured individuals, the origins of their scars remain uncategorised due to an absence of high-resolution images or healing of the original injury.

Mobulid ray fishing and trade

Mobulids are targeted by local artisanal fishers in the area, particularly off the eastern shores of the islands of Nosy Be and nearby Nosy Faly. Mobulids are routinely ensnared in net fisheries, and often retained for local consumption as both meat and broth within communities, or preserved through drying methods to create a product known as ‘masikita’. Masikita is a common commodity found in local markets, typically sold by weight, ranging from 4000 to 7000 Ariary (Ar) per kilogram (approx. 0.9 to 1.57 US$).

Landings of *M. birostris* were infrequent, happening only every few years due to their large size and weight, making them impractical to lift from the water (see Fig. 4a). Typically, the entire animal commanded a price range of 300,000 to 350,000 Ar (approx. 67.71 to 79.01 US$). Catches of *M. mobular*

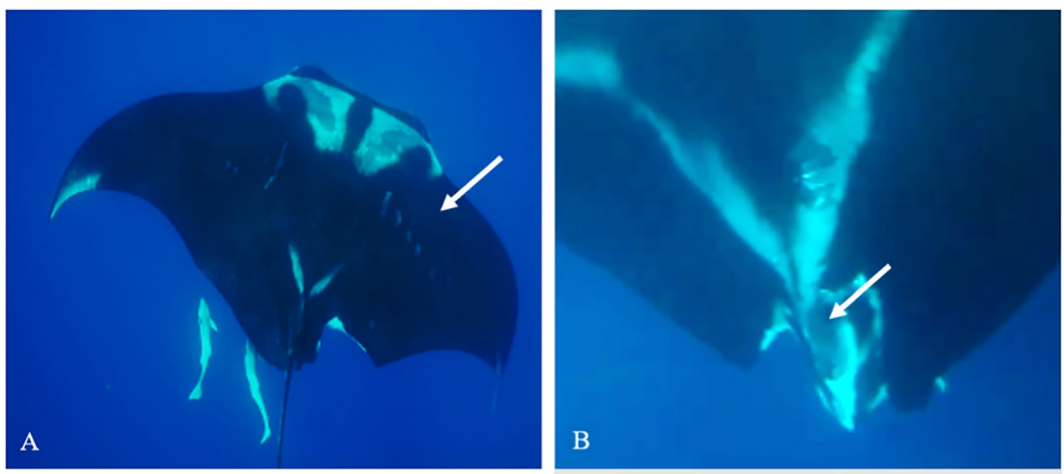

Fig. 3 Scars observed on *Mobula birostris* observed off Nosy Be, Madagascar. **A** Propeller and shark bite scars; **B** Entanglement scars (Photos: Madagascar Whale Shark Project)

Fig. 4 **a** *Mobula birostris* landed in Mananara Nord, East Madagascar on July 2, 2021 (Photo: Vaovao Farany) **b** *M. mobular* being processed by local fishers on Madirokely Beach, Nosy Be, on September 27, 2022 (Photo: Stella Diamant)

and *M. kuhlii* were more common. Slices of fresh meat from these species fetched prices ranging from 15,000 (3.39 US$) to 40,000 Ar (9.04 US$), varying depending on the landing site. For instance, a whole *M. mobular* landed on Nosy Faly may cost approximately 80,000 to 100,000 Ar (approx 18.06 to 22.57 US$).

The majority of mobulid meat originating from the northwest region is transported to markets in the northeast region, including Vohemar, Sambava, and Antalaha (Fig. 5), likely for eventual export. The nearby Comoros islands are frequently identified as importers of mobulids, likely serving as trading hubs with Asian markets. Notably, gill rakers are neither retained for export nor featured in local markets.

Fixed bottom-set gillnets, locally known as 'barazy,' are used off the eastern coasts of Nosy Be and Nosy Faly. These nets, with a mesh size of approximately 20 cm, span 1 to 2 km in length, reach heights of 6 to 8 m, and are deployed at depths of 20 to 35 m, primarily from October to March. Barazy nets target elasmobranchs and other large coastal species, with observations of up to 30 mobulid rays caught per net in a single night. Additionally, bowmouth guitarfish (*Rhina ancylostomus*), Indo-Pacific leopard shark (*Stegostoma tigrinum*), ocellated eagle ray (*Aetobatus ocellatus*), and bull shark (*Carcharhinus leucas*) are common catches, as are hawksbill turtles (*Eretmochelys imbricata*). With similar intentions, nets known as 'Kirara' are deployed overnight to the sea bottom during moonless nights, spanning 1.5 to 2 km in length and reaching heights of 8 to 12 m. These nets drift until the moon rises, targeting large pelagic fishes such as tunas (*Euthynnus affinis* and *Thunnus albacares*), sailfish (*Istiophorus platypterus*), and marlin (*Istiompax indica* and *Tetrapturus audax*) with mobulids caught as bycatch. Notably, larger animals like sea turtles and whale sharks are released because they are forbidden from capture or break the collectively owned nets. Occasionally, line fishers fishing at night on the west side of Nosy Be capture species such as *A. ocellatus*, as well as mobulids, which are visible upon their return in the morning when the catches are cut up on the beach (see Fig. 5b).

There was no evidence of *M. alfredi* being caught and landed by local fishers. No small juvenile *M. birostris*, *M. kuhlii*, or *M. mobular* were observed in landings, but some pregnant female *M. mobular* were among the > 30 individuals caught in November 2018 when a drifting fishing net was found at sea and brought back to Madirokely Beach on Nosy Be.

Discussion

Mobulid rays are commonly sighted in the waters around Nosy Be (Table 1). While *M. mobular* was the most frequently recorded species, *M. birostris* and *M. kuhlii* were also encountered in almost every survey year. The absence of encounters of *M. alfredi* since 2015 suggests a population decline in the area. This trend, combined with regular mobulid catches in

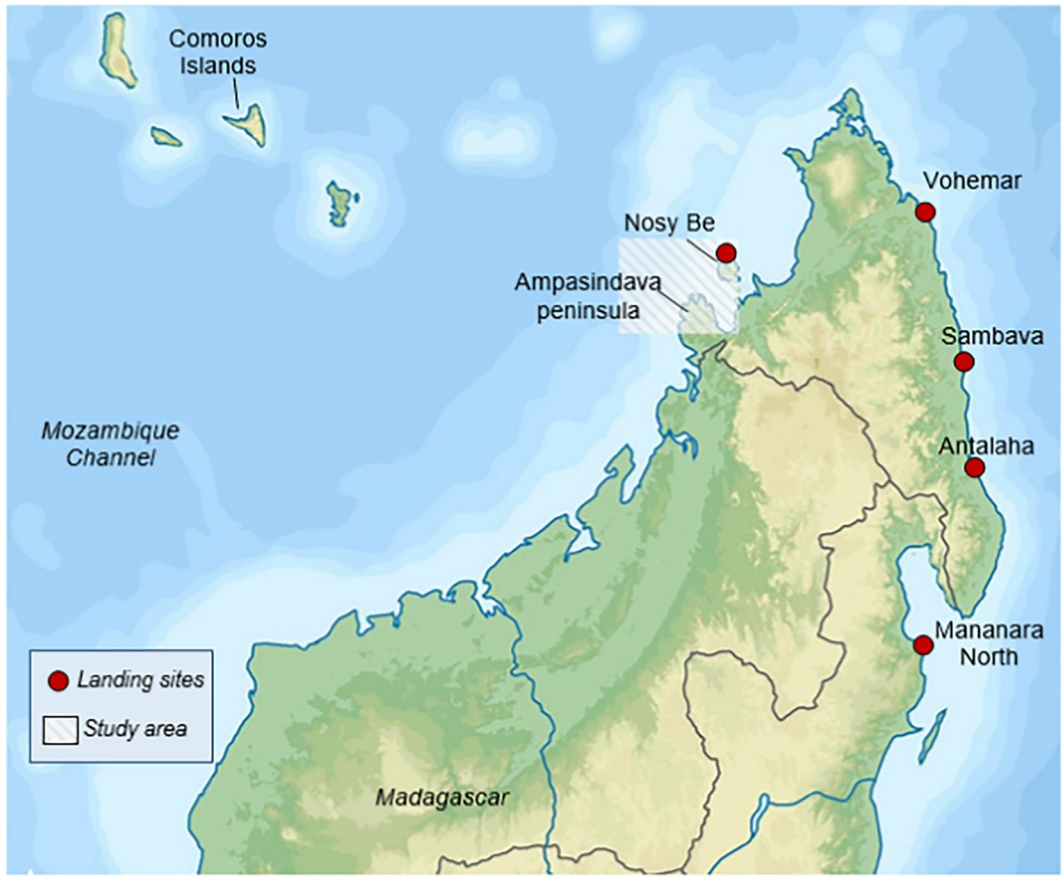

Fig. 5 Map showing the landing sites mentioned in the text as red dots: Nosy Be, Mananara North, Vohemar, Sambava, and Antalaha

nearby fisheries, raises concerns about the conservation of other sympatric *Mobula* species.

Ecology and behaviour

The frequency of mobulid encounters suggests that the Ampasindava Bay area serves as a significant habitat for these species, with regular observations of feeding and foraging behaviours across *M. birostris*, *M. kuhlii*, and *M. mobular*. Courtship behaviours, similar to those described in these species from elsewhere in their distribution (Carpenter and Griffiths 2023; Duffy and Tindale 2018), were also observed in *M. kuhlii* and *M. mobular*.

Sighting trends within the Aug–Dec marine tourism season showed a peak during October and November for the three observed species. This peak coincided with the whale shark season (Diamant et al. 2021) and high levels of feeding activity and vocalisation in Omura's whales (Cerchio et al. 2022). Although mobulids and whale sharks could sometimes be seen feeding together off Nosy Be, whale sharks typically feed on small fishes (Diamant et al. 2021), whereas mobulids primarily forage on zooplankton. Cerchio et al. (2018, 2022) documented Omura's whales feeding on episodically abundant blooms of euphausiids (morphologically identified as *Pseudeuphausia latifrons*), and commonly observed mixed-species aggregations of Omura's whales with large schools of *M. mobular*, and occasionally with *M. birostris*, but less frequently close to feeding whale sharks. Despite the considerable overlap in spatial habitat use in the area surveyed, mobulids may be using areas outside of the primary 'whale shark area', and appear

to be more closely associated with Omura's whales than whale sharks.

Only one *M. birostris* was re-sighted across multiple years, suggesting a lack of site fidelity, though there was a small number of identified individuals. Further work will create a photo library of dorsal images for *M. birostris*, which may help determine the number of unique individuals using the area. However, as the surveys were primarily linked to the whale shark season and search area, it is possible that mobulids are present in higher numbers outside of the survey months or at other locations. Omura's whales have been the subject of broader surveys and tracking work along the NW Madagascan coast (summarised by Cerchio et al. 2022), and the area north of Nosy Be is regularly used by that species—similarly, satellite-tagged whale sharks used that northern Nosy Be area as core habitat (Diament et al. 2018). That area is not frequently visited by whale shark tourism vessels, and thus was not effectively surveyed by this study. Tourism-independent mobulid surveys across a broader area, ideally spanning the months outside of the whale shark season, could provide improved species-specific data on their spatiotemporal patterns of site use and multi-species associations in the region.

Elsewhere, seasonal *M. birostris* presence has been correlated with surface water temperature, El Niño–Southern Oscillation, salinity, windspeed, and productivity (Beale et al. 2019; Domínguez-Sánchez et al. 2023; Harty et al. 2022), which likely influence the broad-scale movements of this highly mobile species. Tracking work on *M. birostris*, and the less-studied *M. kuhlii* and *M. mobular*, would therefore be a useful next step to build on these results and provide a sighting-independent means of better understanding their regional movement ecology.

Mobula alfredi was not seen during surface surveys or dive tourism activities for this study. The last confirmed photographic record of the species in this region was from 2015. While the species is known to be highly vulnerable to decline from small-scale fisheries (Marshall et al. 2022c; Rohner et al. 2013), in the absence of long-term species-specific local catch records, the cause of this apparent depletion cannot be confirmed.

Human threats and management implications

Mobulid rays are a valuable resource in ecotourism, with whale sharks, manta rays (now solely *M. birostris* based on these results), and cetaceans being the main draw cards for participants in marine tourism experiences in Nosy Be (Ziegler et al. 2021). This industry was estimated to be worth US$1.5 million to the local economy over the September–December season in 2019 alone. The apparent disappearance of *M. alfredi* from dive sites in recent years shows that the continued presence of this group cannot be taken for granted.

Mobulids are prone to boat strikes when near the surface (Pate and Marshall 2020; Strike et al. 2022), as shown here by propeller scarring on *M. birostris*. Whale sharks in the same area are also affected by boat strikes, with 19% of individuals bearing scars (Diamant et al. 2021). Whale shark tourism operators have expressed concern regarding vessel overcrowding around sharks (Ziegler et al. 2021), which was also observed for mobulids, particularly in *M. birostris* encounters, which remain high up on the tourist "bucket list". In February 2024, the Malagasy decree N°33,626 regulating interactions with marine megafauna was updated officially to include codes of conduct protecting sea turtles, whale sharks, and cetaceans. The careful application of a similar marine tourism code of conduct, or expansion of the existing code to include mobulid rays, and subsequent measures to mitigate the impacts of tourism and boat operations, would also benefit mobulids (i.e. Venables et al. 2016).

The increasing use of bottom-set gillnets in the vicinity of Nosy Be poses a direct threat to mobulids and several other globally threatened species, which are opportunistically captured for local consumption and likely export. The lack of data on landings, or catch per unit effort, underscores the need to monitor fisheries in the region to allow for the assessment of potential impacts on mobulids and other threatened species. An interpretation of The Code de la Pêche et de l'Aquaculture (Article 18) defines 'endangered aquatic organisms' as protected species in Madagascar, therefore including mobulids, indicating they should not be targeted and should be released if incidentally captured. Furthermore, the official announcement 156–2022/MPEB/SG defines the exploitation and exportation of sharks, rays and sea cucumbers

listed on CITES as 'temporarily suspended'. Madagascar's fisheries law (Law No. 2015–053) does not specifically protect mobulid rays but does prohibit fishing of 'endangered or protected' species under national and international conventions. Madagascar is a signatory to the Convention on the Conservation of Migratory Species of Wild Animals (CMS), mandating strict protection for all species listed in Appendix I, which includes all *Mobula* species. A revision of this law to reflect CMS listings, as well as measures and provisions of other multilateral agreements, such as retention bans under the Indian Ocean Tuna Commission (IOTC), and clearly defining species that are prohibited, should be a priority for improved conservation of elasmobranchs in the country.

The CMS Appendix I listing of mobulids also mandates spatial protection of their important habitats. The Nosy Be area has recently been identified as an Important Shark and Ray Area (ISRA) based partially on the presence of mobulid rays (ISRA Western Indian Ocean e-atlas). Mobulid rays do use the Ankivonjy Marine Protected Area (MPA) in the western Ampasindava Bay but, similar to whale sharks (Diamant et al. 2018, 2021) and Omura's whales (Cerchio et al. 2015), the existing MPAs in NW Madagascar do not cover important habitat for these large planktivores. The majority of feeding, cleaning, and courtship behaviours observed were outside the current MPA boundary. Extension of Ankivonjy MPA to the northeast, which is taking place through the creation of the Tandavandriva corridor MPA (Arrete No, 03/2020) to join the existing Ankivonjy and Ankarea MPAs, would cover a significant portion of the mobulid ray (and whale shark) feeding area. The management regulations within the new MPA should consider threats to mobulid rays and other marine megafauna using the area. Long-term conservation measures in other mobulid hotspots, such as Raja Ampat in Indonesia, have successfully reduced threats and achieved population growth (Setyawan et al. 2022a,b).

Industrial fishing vessels operating further offshore may also pose a threat to mobulids, often caught as bycatch in longline and gillnet tuna fisheries (FAO ORG). These fisheries fall under the jurisdiction of Indian Ocean Tuna Commission (IOTC) Resolution 19/03, applicable to Madagascar, which bans retention of all mobulid species in member states' fisheries, including (from January 1, 2021) artisanal fisheries, and mandates the prompt release of incidentally caught mobulids alive and unharmed. Most industrial tuna vessels operating in the region are foreign-flagged, with medium-sized longliners from France operating out of La Réunion and large vessels from Korean and Japanese companies often using Mauritius as their base (Marshall et al. 2022c).

The capture of species such as mobulid rays by foreign-flagged vessels often results in retained catches being landed in flag states, not the country in which they were landed—in this case Madagascar. The associated threats include poor or no reporting of such catches, non-permitted exports, and opportunities to move high-value products illegally to international markets. While there is no information on mobulid gill plates being traded from Madagascar, this represents a significant global trade and threat to mobulid rays in other parts of the world. Effective regulation and enforcement of such regulation must be put in place to avoid this threat developing in Madagascar. Other Western Indian Ocean countries should be equally astute in mitigating this threat, to avoid illegal trade through nearby countries.

Enhanced research endeavours focused on mobulids would contribute to redefining their home ranges and pinpointing critical habitats (Setyawan et al. 2024; Venables et al. 2020), thereby facilitating the implementation of effective spatial management strategies. Given Madagascar's prevalent poverty, with over 75% of the population living below the national poverty line in 2022 (World Bank 2023), initiatives aimed at ensuring food security must be integral components of comprehensive conservation initiatives. This necessitates a multifaceted approach that not only balances the financial needs of fishing communities but also promotes sustainable ecotourism and other economic opportunities stemming from the presence of these species. In order to protect mobulid rays in Madagascar, the implementation and enforcement of protective measures outlined in national and international legislation are critical, including the need to regulate the use of gillnets in the region.

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Data availability *Mobula birostris* photo-ID data are available online at mantamatcher.org. Other data can be provided on request.

Declarations

Ethical approval This study was made possible thanks to research permits obtained every year during the study period by the Ministry of Environment and Sustainable Development of Madagascar, and facilitated by our partners at Institut Halieutique et des Sciences Marines. All research carried out was purely observational.

Competing interests The authors declare no competing interests.

References

Antonelli A, Smith RJ, Perrigo AL et al (2022) Madagascar's extraordinary biodiversity: evolution, distribution, and use. Science 378:eabf0869 https://doi.org/10.1126/science.abf0869

Beale CS, Stewart JD, Setyawan E, Sianipar AB, Erdmann MV (2019) Population dynamics of oceanic manta rays (*Mobula birostris*) in the Raja Ampat Archipelago, West Papua, Indonesia, and the impacts of the El Niño-Southern Oscillation on their movement ecology. Divers Distrib 25:1472–1487. https://doi.org/10.1111/ddi.12962

Carpenter M, Griffiths C (2023) 'Flash Mobula': first observations of courtship behaviour of the shortfin devil ray *Mobula kuhlii*. Afr J Mar Sci 45:51–56. https://doi.org/10.2989/1814232X.2022.2158131

Cerchio S, Andrianantenaina B, Lindsay A, Rekdahl M, Andrianarivelo N, Rasoloarijao T (2015) Omura's whales (*Balaenoptera omurai*) off northwest Madagascar: ecology, behaviour and conservation needs. R Soc Open Sci 2:150301. https://doi.org/10.1098/rsos.150301

Cerchio S, Andrianantenaina B, Zerbini A, Pendleton D, Rasoloarijao T, Cholewiak D (2018) Residency, feeding ecology, local movements and potential isolation of the Madagascar Omura's whale (*Balaenoptera omurai*) population. Paper SC/67B/NH09 presented to the Scientific Committee of the International Whaling Commission, Bled, Slovenia

Cerchio S, Andrianantenaina B, Rasoloarijao T, Andrianarivelo N (2022) *Balaenopteridae omurai*, Omura's whale. In: Goodman SM (ed) The new natural history of Madagascar. Princeton University Press, Princeton, pp 424–429. https://doi.org/10.1515/9780691229409

Couturier LIE, Marshall AD, Jaine FRA, Kashiwagi T, Pierce SJ, Townsend KA, Weeks SJ, Bennett MB, Richardson AJ (2012) Biology, ecology and conservation of the Mobulidae. J Fish Biol 80:1075–1119. https://doi.org/10.1111/j.1095-8649.2012.03264.x

Croll DA, Dewar H, Dulvy NK, Fernando D, Francis MP, Galván-Magaña F, Hall M, Heinrichs S, Marshall A, McCauley D, Newton KM, Notarbartolo-Di-Sciara G, O'Malley M, O'Sullivan J, Poortlivet M, Roman M, Stevens G, Tershy BR, White WT (2016) Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. Aquat Conserv: Mar Freshw 26:562–575. https://doi.org/10.1002/aqc.2591

Diamant S, Pierce SJ, Rohner CA, Graham RT, Guillemain d'Echon A, Guillemain d'Echon T, Sourisseau E, Fidiarisandratra LC, Bakary G, Trélanche S, Andriananrisoa F, Kiszka JJ (2021) Population structure, residency, and abundance of whale sharks in the coastal waters off Nosy Be, north-western Madagascar. Aquat Conserv: Mar Freshw 31:3492–3506. https://doi.org/10.1002/aqc.3743

Diamant S, Rohner CA, Kiszka JJ, d Echon AG, d Echon TG, Sourisseau E, Pierce SJ (2018) Movements and habitat use of satellite-tagged whale sharks off western Madagascar. Endanger Species Res 36:49–58. https://doi.org/10.3354/esr00889

Domínguez-Sánchez PS, Širović A, Fonseca-Ponce IA, Zavala-Jiménez AA, Rubin RD, Kumli KR, Ketchum JT, Galván-Magaña F, Wells RD, Stewart JD (2023) Occupancy of acoustically tagged oceanic manta rays, *Mobula birostris*, in Bahia de Banderas. Mexico Mar Biol 170:128. https://doi.org/10.1007/s00227-023-04278-1

Duffy CA, Tindale SC (2018) First observation of the courtship behaviour of the giant devil ray *Mobula mobular* (Myliobatiformes: Mobulidae). N Z J Zool 45:387–394. https://doi.org/10.1080/03014223.2017.1410850

Dulvy NK, Pacoureau N, Rigby CL, Pollom RA, Jabado RW, Ebert DA, Finucci B, Pollock CM, Cheok J, Derrick DH,

Herman KB (2021) Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. Curr Biol 31:4773–4787. https://doi.org/10.1016/j.cub.2021.08.062

Francis MP, Jones EG (2017) Movement, depth distribution and survival of spinetail devil rays (*Mobula japanica*) tagged and released from purse-seine catches in New Zealand. Aquat Conserv: Mar Freshw 27:219–236. https://doi.org/10.1002/aqc.2641

Harty K, Guerrero M, Knochel AM, Stevens GMW, Marshall A, Burgess K, Stewart JD (2022) Demographics and dynamics of the world's largest known population of oceanic manta rays *Mobula birostris* in coastal Ecuador. Mar Ecol Prog Ser 700:145–159. https://doi.org/10.3354/meps14189

Humber F, Andriamahefazafy M, Godley BJ, Broderick AC (2015) Endangered, essential and exploited: how extant laws are not enough to protect marine megafauna in Madagascar. Mar Policy 60:70–83. https://doi.org/10.1016/j.marpol.2015.05.006

Jonahson M, Harding S (2007) Occurrence of whale sharks (*Rhincodon typus*) in Madagascar. Fish Res 84:132–135. https://doi.org/10.1016/j.fishres.2006.11.023

Laran S, Authier M, Van Canneyt O, Dorémus G, Watremez P, Ridoux V (2017) A comprehensive survey of pelagic megafauna: their distribution, densities, and taxonomic richness in the tropical Southwest Indian Ocean. Front Mar Sci 4:139. https://doi.org/10.3389/fmars.2017.00139

Marshall AD, Compagno LJV, Bennett MB (2009) Redescription of the genus *Manta* with resurrection of *Manta alfredi* (Krefft, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae). Zootaxa 2301:1–28. https://doi.org/10.5281/zenodo.191734

Marshall AD, Dudgeon CL, Bennett MB (2011) Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique. Mar Biol 158:1111–1124. https://doi.org/10.1007/s00227-011-1634-6

Marshall A, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Derrick D, Herman K, Jabado RW, Liu KM, Rigby CL, Romanov E (2020) Mobula birostris. IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T195459A68632178.en

Marshall A, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Herman K, Jabado RW, Liu KM, Rigby CL, Romanov E (2022a) *Mobula mobular* (amended version of 2020 assessment). The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T110847130A214381504.en

Marshall A, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Derrick D, Herman K, Jabado RW, Liu KM, Rigby CL, Romanov E (2022b) *Mobula birostris* (amended version of 2020 assessment). The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T198921A214397182.en

Marshall A, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Herman K, Jabado RW, Liu KM, Pacoureau N, Rigby CL, Romanov E, Sherley RB (2022c) *Mobula alfredi* (amended version of 2019 assessment). The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T195459A214395983.en

Marshall AD, Holmberg J (2021) Manta Matcher Photo-identification Library. https://mantamatcher.org/

Pacoureau N, Rigby CL, Kyne PM, Sherley RB, Winker H, Carlson JK, Fordham SV, Barreto R, Fernando D, Francis MP, Jabado RW (2021) Half a century of global decline in oceanic sharks and rays. Nature 589:567–571. https://doi.org/10.1038/s41586-020-03173-9

Pate JH, Marshall AD (2020) Urban manta rays: Potential manta ray nursery habitat along a highly developed Florida coastline. Endang Species Res 43:51–64. https://doi.org/10.3354/esr01054

Rigby CL, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Jabado RW, Liu KM, Marshall A, Romanov E (2022) *Mobula kuhlii* (amended version of 2020 assessment). The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T161439A214405747.en

Robinson L, Sauer WHH (2013) A first description of the artisanal shark fishery in northern Madagascar: implications for management. Afr J Mar Sci 35:9–15. https://doi.org/10.2989/1814232X.2013.769906

Rohner CA, Pierce SJ, Marshall AD, Weeks SJ, Bennett MB, Richardson AJ (2013) Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. Mar Ecol Prog Ser 482:153–168. https://doi.org/10.3354/meps10290

Rohner CA, Burgess KB, Rambahiniarison JM, Stewart JD, Ponzo A, Richardson AJ (2017) Mobulid rays feed on euphausiids in the Bohol Sea. R Soc Open Sci 4:161060. https://doi.org/10.1098/rsos.161060

Séret B (2022) Chondrichthyan fishes (sharks, rays, and chimaeras). In: Goodman SM (ed) The new natural history of Madagascar. Princeton University Press, Princeton, pp 368–380 https://doi.org/10.2307/j.ctv2ks6tbb.48

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

Setyawan E, Erdmann MV, Mambrasar R, Ambafen O, Hasan AW, Izuan M, Mofu I, Putra MIH, Sianipar AB, Constantine R, Stevenson BC, Jaine FRA (2024) Spatial connectivity of reef manta rays across the Raja Ampat archipelago. Indonesia R Soc Open Sci 11:230895. https://doi.org/10.1098/rsos.230895

Setyawan E, Stevenson BC, Erdmann MV, Hasan AW, Sianipar AB, Mofu I, Putra MIH, Izuan M, Ambafen O, Fewster RM, Aldridge-Sutton R, Mambrasar R, Constantine R (2022b) Population estimates of photo-identified individuals using a modified POPAN model reveal that Raja Ampat's reef manta rays are thriving. Front Mar Sci 9:1014791. https://doi.org/10.3389/fmars.2022.1014791

Stevens G, Fernando D, Di Sciara GN (2018) Guide to the manta and devil rays of the world. Princeton University Press, Princeton

Stewart JD, Jaine FR, Armstrong AJ, Armstrong AO, Bennett MB, Burgess KB, Couturier LI, Croll DA, Cronin MR, Deakos MH, Dudgeon CL, Fernando D, Froman N, Germanov ES, Hall MA, Hinojosa-Alvarez S, Hosegood JE, Kashiwagi T, Laglbauer BJL, Lezama-Ochoa N, Marshall AD, McGregor F, Notarbartolo di Sciara G, Palacios MD, Peel LR, Richardson AJ, Rubin RD, Townsend KA, Venables SK, Stevens GMW (2018) Research priorities to support effective manta and devil ray conservation. Front Mar Sci 5:314. https://doi.org/10.3389/fmars.2018.00314

Strike EM, Harris JL, Ballard KL, Hawkins JP, Crockett J, Stevens GMW (2022) Sublethal injuries and physical abnormalities in Maldives manta rays, *Mobula alfredi* and *Mobula birostris*. Front Mar Sci 9:773897. https://doi.org/10.3389/fmars.2022.773897

Temple AJ, Wambiji N, Poonian CN, Jiddawi N, Stead SM, Kiszka JJ, Berggren P (2019) Marine megafauna catch in southwestern Indian Ocean small-scale fisheries from landings data. Biol Conserv 230:113–121. https://doi.org/10.1016/j.biocon.2018.12.024

Venables S, McGregor F, Brain L, van Keulen M (2016) Manta ray tourism management, precautionary strategies for a growing industry: a case study from the Ningaloo Marine Park, Western Australia. Pac Conserv Biol 22:295–300. https://doi.org/10.1071/PC16003

Venables SK, van Duinkerken DI, Rohner CA, Marshall AD (2020) Habitat use and movement patterns of reef manta rays *Mobula alfredi* in southern Mozambique. Mar Ecol Prog Ser 634:99–114. https://doi.org/10.3354/meps13178

White WT, Corrigan S, Yang L, Henderson AC, Bazinet AL, Swofford DL, Naylor GJP (2017) Phylogeny of the manta and devil rays (Chondrichthyes: Mobulidae), with an updated taxonomic arrangement for the family. Zool J Linn Soc 182:50–75. https://doi.org/10.1093/zoolinnean/zlx018

Ziegler JA, Diamant S, Pierce SJ, Bennett R, Kiszka JJ (2021) Economic value and public perceptions of whale shark tourism in Nosy Be, Madagascar. Tour Mar Environ 16:167–182. https://doi.org/10.3727/154427321X16223819324721