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NOTES ON GEOGRAPHIC DISTRIBUTION

First records of Spinetail Devil Ray, *Mobula mobular* (Bonnaterre, 1788), and Bentfin Devil Ray, *M. thurstoni* (Lloyd, 1908) (Myliobatiformes, Mobulidae), in French Polynesia

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Abstract. The first confirmed sightings of Spinetail Devil Ray, *Mobula mobular* (Bonnaterre, 1788), and Bentfin Devil Ray, *M. thurstoni* (Lloyd, 1908) (Myliobatiformes, Mobulidae), are reported in French Polynesia. An individual of *M. mobular* was observed in the Society Archipelago, and a group of seven *M. thurstoni* were observed in a courtship display in the Marquesas Archipelago. Currently listed as Endangered on the IUCN Red List, they face ongoing threats from environmental change and bycatch in industrial fisheries. There is a need for further research in the region to support conservation efforts of these two species.

Key words. Courtship, distribution, endangered species, South Pacific

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INTRODUCTION

The family Mobulidae (mobulid rays) is composed of 10 valid extant species: the three manta ray species and seven devil ray species (Marshall et al. 2009; White et al. 2018; Notarbartolo di Sciara et al. 2019; Bucair et al. 2025). All mobulids are zooplanktivores which are circumglobally distributed throughout the world's tropical and subtropical oceans (Couturier et al. 2012; Stevens et al. 2018b). They have the lowest fecundity of all elasmobranchs, giving birth to only one pup at a time after long gestation periods and with interbirth intervals ranging from once per year to once every seven years (Dulvy et al. 2014; Stevens et al. 2018a). Studies on the reproductive behavior of mobulid rays have identified seven distinct stages for courtship and mating (Stevens 2016; Stevens et al. 2018a). Courtship comprises the initial four stages (initiation, endurance, evasion, and precopulatory positioning), while mating encompasses the subsequent three stages (copulation, post-copulatory holding, and separation; Stevens et al. 2018a).

Spinetail Devil Ray, *Mobula mobular* (Bonnaterre, 1788), is a large-bodied, epipelagic mobulid (Notarbartolo di Sciara 1987; Croll et al. 2016). It is known for forming large surface aggregations likely linked to prey availability and reproductive behavior (Couturier et al. 2012; Notarbartolo di Sciara et al. 2015). Well known as the "Mediterranean Devil Ray" due to its common presence in the Mediterranean Sea (Notarbartolo di Sciara et al. 2020; Bucair et al. 2022), it has also been reported in the Eastern and Western Atlantic Ocean (Notarbartolo di Sciara et al. 2015, 2019; Lozama-Ochoa et al. 2020; Ozaki 2023; Ozaki et al. 2024), in the Indian Ocean (Lawson et al. 2017; Harris et al. 2024), and in the eastern and western Pacific Ocean (Lezama-Ochoa et al. 2019; Griffiths and Lezama-Ochoa 2021; Palacios et al. 2023).

Bentfin Devil Ray, *M. thurstoni* (Lloyd, 1908), is considered a primarily oceanic species and is sighted primarily individually or in small groups (Couturier et al. 2012; Stevens et al. 2018b). Intermediate in size among mobulids, its occurrence has been confirmed off the coasts of Mexico, Ecuador, West Africa, and Southeast Asia (Marshall et al. 2022b), in the Indian Ocean (Lawson et al. 2017), Brazilian Equatorial Atlantic (Bucair et al. 2022), Southern Gulf of California (Palacios et al. 2023), Chagos Archipelago (Harris et al. 2024), Cabo Verde (Ratão et al. 2017), Adaman Sea (Shirke et al. 2017), Caribbean Sea, and Venezuela (Ehemann et al. 2022). Despite being the most frequently landed mobulid in several regions, little is known about its ecology,

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and evidence suggests it suffers high post-release mortality following accidental capture (Croll et al. 2016; Francis and Jones 2017; Lawson et al. 2017). Information on the reproductive biology is very limited for this species, with only four courtship events documented in the world to date (Carpenter et al. in press): one in Brazil (McCallister et al. 2020) and three in the Gulf of California, Mexico (Pelacios et al. 2023).

In French Polynesia, three mobulid species have been reported: the two manta ray species *M. alfredi* (Krefft, 1868) and *M. birostris* (Walbaum, 1792) have been sighted in all five archipelagoes of French Polynesia (Carpentier et al. 2019) and *M. tarapacana* (Phillipi, 1892) has been reported in the Society and Tuamotu Archipelagos (Séguigne et al. 2023). All mobulid species are protected in French Polynesia since 2021 (Code of the Environment of French Polynesia, by-law no. 1013 CM). Threats in the region have been confirmed on *M. alfredi*, mostly in the Society archipelago, where more than a third of all the identified population has been observed with anthropogenic injuries (Carpentier et al. 2019). The ban on purse-seine fisheries across the entire Exclusive Economic Zone (EEZ) of French Polynesia, which spans 4.8 million square kilometers and is the largest EEZ in the Pacific, provides significant benefits for mobulid rays, as purse-seine fisheries are considered as one of the primary threats to mobulid ray populations (Croll et al. 2016; Lezama-Ochoa et al. 2019). Despite the extensive coverage of the French Polynesian EEZ, all mobulids occurring in these waters are unlikely to be fully protected due to their highly migratory behavior and preference for oceanic habitats, which likely take them beyond national jurisdictions. Long-line fisheries, which represents most of the industrial fishing industry in French Polynesia, have also been reported as a threat for mobulid rays (Ward-Paige et al. 2013; Lezama-Ochoa et al. 2015). Due to their conservative life history traits and anthropogenic threats, *M. mobular* and *M. thurstoni* are both listed as Endangered on the IUCN Red List of Threatened Species (Marshall et al. 2022a, 2022b).

This report presents data on two opportunistic first records of mobulid species in French Polynesia: *M. mobular* in Moorea, in the Society Archipelago, and *M. thurstoni* in Nuku Hiva, in the Marquesas Archipelago.

STUDY AREA

The Society Archipelago is a chain of high volcanic islands located in the central part of French Polynesia (16°S–18°S, 147°W–155°W). Moorea is a high volcanic island located in the Society Archipelago surrounded by a fringing reef and a shallow lagoon, with the outer reef slope dropping steeply into deep oceanic waters exceeding 1,500 m within a few kilometers from shore. These offshore waters are influenced by oceanic currents and episodic upwelling, creating favorable conditions for pelagic species (Leichter et al. 2012). Data was collected in the open ocean Southwest of Moorea Island (17°37′49.75″S, 149°53′15.644″W; Figure 1B).

The Marquesas Archipelago is a remote group of 12 volcanic islands located at the northeast part of French Polynesia (11°S–08°S, 142°W–139°W). All Marquesas Islands are surrounded by rocky shores consisting of steep slopes and deep oceanic trenches, with 500–1500 m depth along the coastlines reaching up to 4000 m in some areas. The Archipelago is renowned for its marine biodiversity and high degree of endemism, influenced by a strong island mass effect creating high phytoplankton biomass (Martinez et al. 2004, 2018). The unique archipelago's natural and cultural importance allowed it to get recognized as a UNESCO World Heritage site in 2024. Data was collected in Hatiheu Bay, located Northeast of the Nuku Hiva Island, in the Marquesas Archipelago (8°49′12.61″S, 140°05′00.73″W; Figure 1A). Hatiheu Bay is approximately 1 km wide, 1.8 km long, and 40 m deep, with a narrow rocky shoreline, surrounded by mountain cliffs and opening on an inhabited valley of less than 400 inhabitants. The bay is known to host a *M. alfredi* aggregation site, with groups of 10–20 individuals frequently seen feeding along the sides of the Bay (Carpentier pers. obs.).

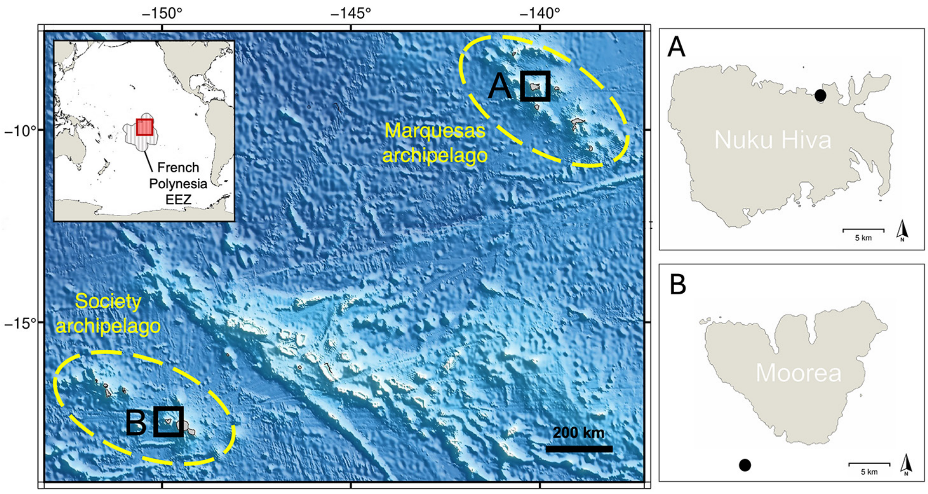

Figure 1. Sighting locations (black points) for the new records of *Mobula mobular* and *M. thurstoni* in French Polynesia. **A.** Observation site of *M. thurstoni* courtship event on 9 February 2023 in Hatiheu Bay, Nuku Hiva Island, Marquesas Archipelago. **B.** Observation site of *M. mobular* on 18 September 2020, offshore of Moorea Island in the Society Archipelago.

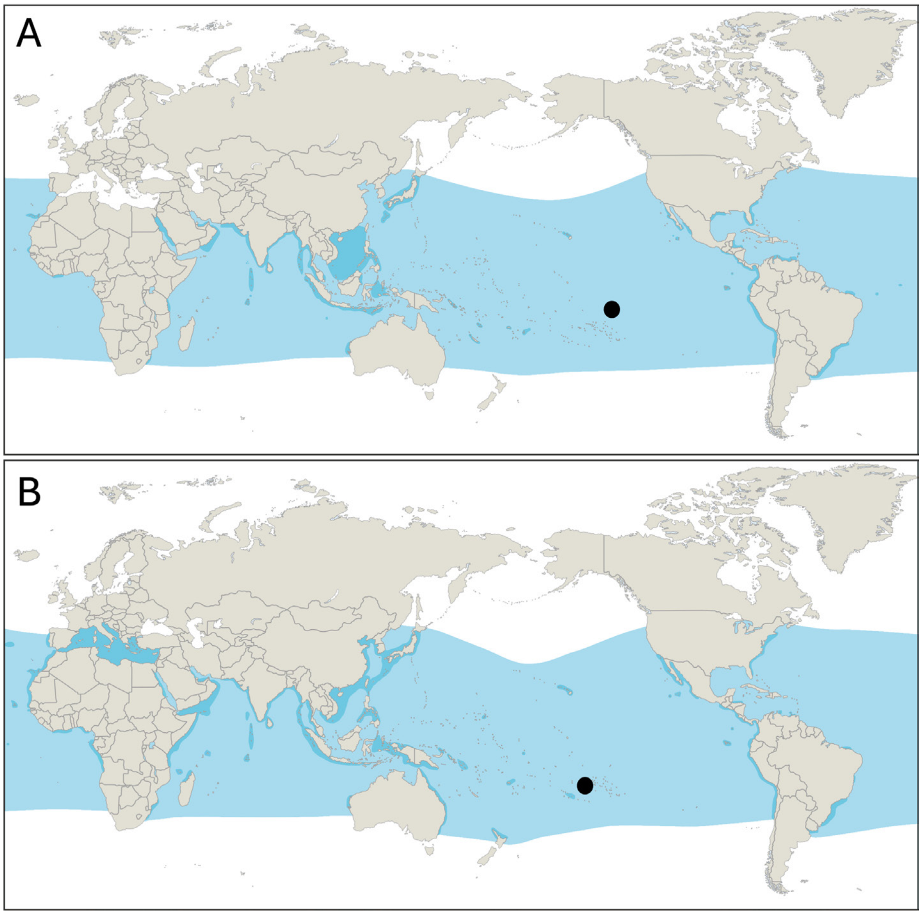

Figure 2. Distribution maps of *M. thrustoni* (**A**) and *M. mobular* (**B**) (credit: Manta Trust). The black points indicate the location for the reported new records for each species in French Polynesia. Lighter blue areas indicate expected range, and darker blue areas indicate confirmed range for each species.

METHODS

The data collected in Moorea Island was obtained through an opportunistic observation by a tour operator. On 18 September 2020, the tour operator's boat was cruising in the open ocean looking for marine pelagic megafauna, when a group of rough-tooth dolphins *Steno bredanensis* (Cuvier in Lesson, 1828) were spotted from the surface. The boat stopped at around 30 m distance from the animals, and two observers went in the water equipped with a GoPro Hero 7 camera. While observing the dolphins, they noticed an oceanic Whitetip Shark, *Carcharhinus longimanus* (Poey, 1861), swimming near the dolphins, and the mobulid ray was spotted at a distance passing by, allowing the observers to gather some photo and video footage that was later reviewed for species identification.

The data from Nuku Hiva Island was collected through a regional research program mandated by the Direction of the Environment of French Polynesia, focusing on manta rays *M. alfredi* and *M. birostris*. As part of this program, a scientific team comprising three members from the Shark Observatory of French Polynesia conducted a three-week expedition to five islands of the Marquesas Archipelago between 28 January and 18 February 2023. During a scientific survey on 9 February 2023, the research boat was slowly cruising parallel to the coast of Hatiheu Bay, Nuku Hiva, while the scientific team scanned the surface for signs of manta ray activity. As tips of pectoral fins were noticed breaking the surface of the water, the scientific team quickly determined that the fins did not correspond to those of manta rays, based on their smaller size and more rounded shape at the tip. The research boat came closer and remained at ~10 m distance from the individuals, allowing two members of the scientific team to go in the water to further investigate. The in-water survey allowed to count the number of individuals, determine their sex by the presence or absence of claspers, and collect video footage using a GoPro Hero 9 and a Canon G7 X Mark II camera. Video footage was later reviewed and analyzed to identify the species using specific morphological features and to further assess the behaviors of the individuals observed. Videos collected from both observations are provided as additional Online Resources.

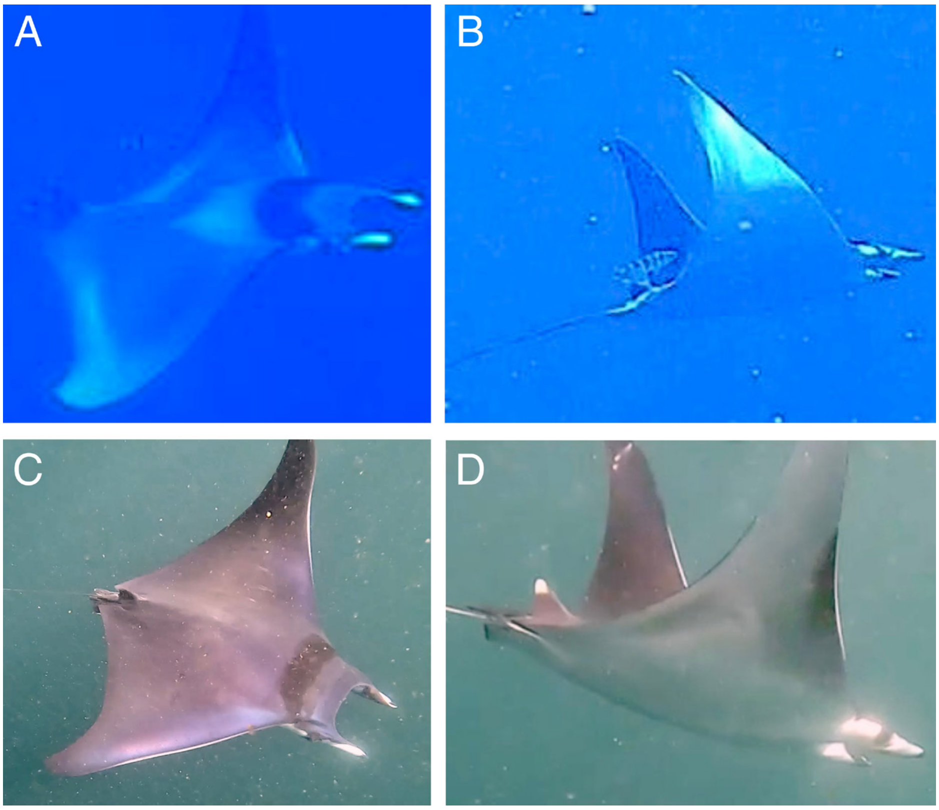

Figure 3. *Mobula mobular* and *M. thurstoni* sighted in French Polynesia showing key characteristics for these species. **A.** Full body view of the dorsal side of individual *M. mobular* photographed on 18 September 2020 offshore of Moorea Island. **B.** Ventral view of the *M. mobular* individual. **C.** Full body view of the dorsal side of an *M. thurstoni* filmed on 9 February 2023, in Nuku Hiva. **D.** Ventral view of the *M. thurstoni* individual. Photos: Nicolas Buray (A, B), Alice Carpentier (C), Toanui Tulasne-Atiu (D).

RESULTS

Order Myliobatiformes
Family Mobulidae
Genus ***Mobula*** Rafinesque, 1810

Mobula mobular **(Bonnaterre, 1788)**
Figure 3A, B

New photographic record. FRENCH POLYNESIA — Society Archipelago • Offshore of Moorea Island; 17°37′49.75″S, 149°53′15.644″W; 0–10 m depth; 18.IX.2020; Buray N, Bui Z obs.; 1 spec.

Estimated disc width 170 cm; data collected during a touristic excursion.; an Oceanic Whitetip Shark, *Carcharhinus longimanus*, and Rough-Toothed Dolphin, *Steno bredanensis*, were observed at the same time of this observation.

Identification. The species observed was confirmed as *M. mobular* after review of the video footage which allowed to distinguish morphological characteristics of this species (Stevens et al. 2018b). The key features include an estimated disc width 170 cm, a thick black band on top of the head that stretches from eye to eye bordered by a lighter grey area continuing along the sides pectoral fin and white-tipped elongated dorsal fin (Figure 3A), as well as a bright white ventral surface (Figure 3B). The tail length was notably longer than the disc length, with an estimated size of ~200 cm.

Mobula thurstoni **(Lloyd, 1908)**
Figures 3C, D, 4A–D

New video record. FRENCH POLYNESIA — Marquesas Archipelago • Nuku Hiva, Hatiheu Bay; 08°49′12.61″S, 140°05′00.73″W; 0–10 m depth; 09.II.2023; Carpentier A, Goyaud A, Tulasne-Atiu T obs.; 1♀, 6♂.

Disc width ~130 cm; data collected during a scientific expedition; Encounter started at 7:37 a.m. and ended at 7:46 a.m. local time, lasting a total of 9 minutes. Individuals were displaying courtship behavior during the observation.

Identification. The species observed was confirmed as *M. thurstoni* after review of the video footage which allowed to distinguish morphological characteristics of this species (Stevens et al. 2018b), including size of ~130 cm, a dark mauve color on the back, a thick black band on top of the head stretching from eye to eye, a white-tipped dorsal fin and a distinctive double curvature of pectoral fins (Figure 3C). Gray shading was present on the curve of the anterior margin of pectoral fins (Figure 3D). The tail length appeared slightly greater than the disc width, with an estimated size of ~150 cm. The spiracle is located above the pectoral fin insertion (Figure 3C).

Reproductive behavior. Courtship behavior was confirmed by the video footage collected during the encounter, following the criteria proposed by Stevens et al. (2018a) for mobulids. A female was being chased by six males swimming at high speed, a stage known as "endurance stage". The males were sometimes aligned, sometimes disordered behind the female (Figure 4A). The female performed erratic movements, and occasionally made abrupt changes of direction, a stage known as "evasion stage", which caused her to sometimes appear in the middle of the chase and continued following the males located at the front (Figure 4B). The female occasionally approached the researchers directly, passing within less than 1 m, closely followed by the males. The group was not observed going deeper than 5–10 m, and the tip of the pectoral fins of the female sometimes breached the surface (Figure 4B). No breaching was observed during the encounter. The female and males appeared similar in both size and coloration, with no evident distinguishing features. The presence of fresh mating wounds was observed on the top (Figure 4C) and underside of the left pectoral fin of the female (Figure 4D). These scars are likely the result of at least one or more recent (within days) mating event, or attempted copulation (Stevens 2016; Stevens et al. 2018a). A rubbing mark is also visible on the female's back (Figure 4C), which were likely caused by friction on the mucus on the ray's dorsal surface, as observed on courtship reef manta rays (Stevens et al. 2018a).

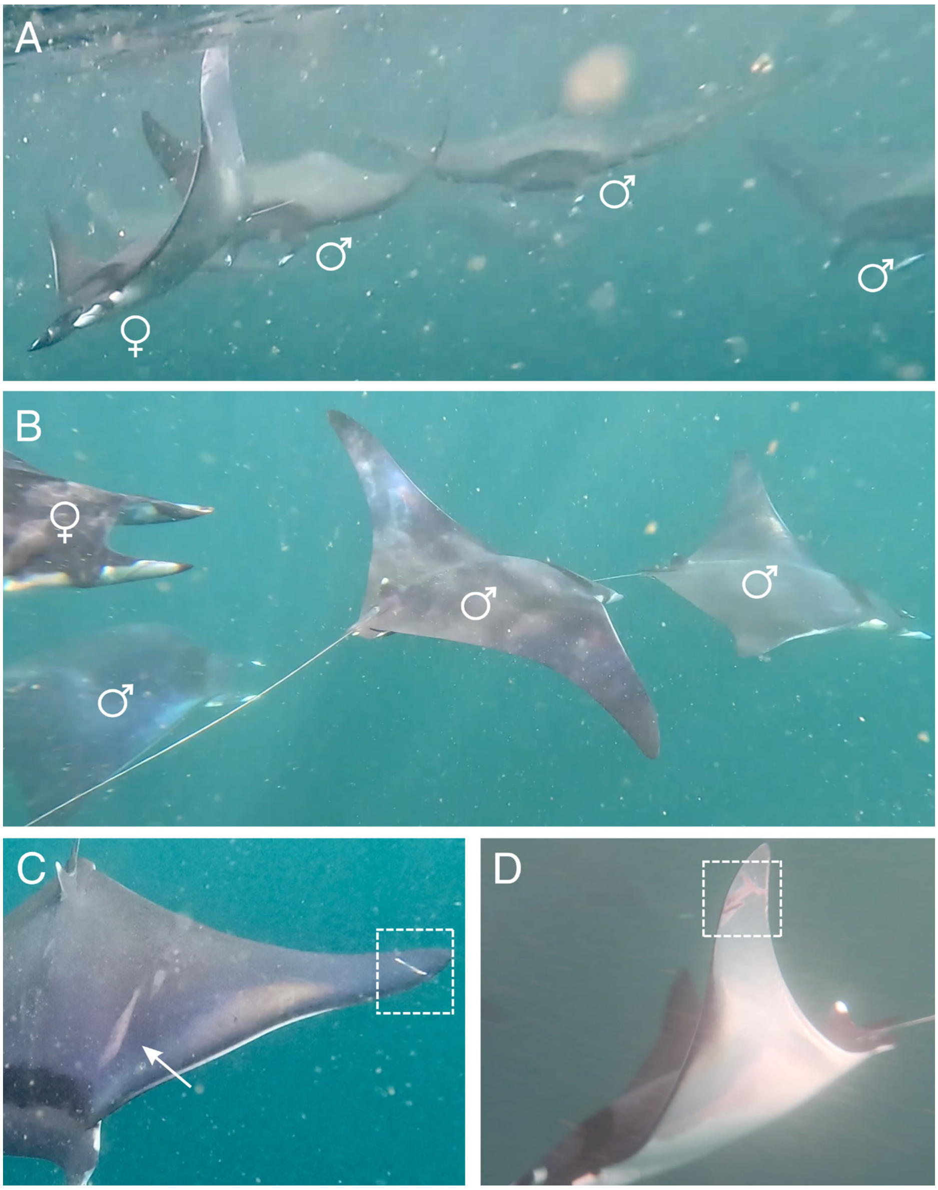

Figure 4. *Mobula thurstoni* courtship behavior filmed on 9 February 2023 at Nuku Hiva, Marquesas Archipelago of French Polynesia. **A.** High-speed pursuit of a female *M. thurstoni* by six males, a behavior indicative of courtship. **B.** Female appearing in the middle of the chase after abrupt turns. **C.** Fresh linear mating wounds indicated by a white dotted rectangle on the dorsal surface of the female *M. thurstoni*, with the white arrow indicating a mark likely resulting from contact with a male during a mating attempt. **D.** Fresh linear mating wounds indicated by a white dotted rectangle on the ventral side of the female *M. thurstoni*. Photos: Toanui Tulasne-Atiu.

DISCUSSION

This report presents the first documented evidence of *Mobula mobular* and *M. thurstoni* occurrence in French Polynesia, based on analysis of photo and video footage collected through an opportunistic observation by a tour operator and during a scientific survey. While both sightings occurred within the expected range of distribution for these species (Figure 2), they represent the first confirmed records from this isolated region of the Pacific Ocean, providing novel and critical evidence that fills a significant geographic gap in their known distribution. Due to their primarily oceanic nature, these species are difficult to observe in the wild and most existing distribution records originate from bycatch or fisheries landings (Rambahiniarison et al. 2018; Lezama-Ochoa et al. 2019; Griffiths and Lezama-Ochoa 2021). Both species have been commonly reported in the Eastern and Western Pacific Ocean (Lezama-Ochoa et al. 2019; Griffiths and Lezama-Ochoa 2021), and sightings across the Central and South Pacific Region are scarce. The two sightings reported in this study represent some of the few direct observations of *M. thurstoni* and *M. mobula* in the South Pacific region and contribute significantly to our understanding their distribution in this region.

This paper describes observed reproductive behaviors for *M. thurstoni*, which indicate that the Marquesas may serve as a reproductive area for this rare and endangered species. The reproductive behavior observed was consistent with the courtship behavior previously described for other species of mobulid rays (Carpenter et al. in press) and other events described for *M. thurstoni* (McCallister et al. 2020; Palacio et al. 2023). This courtship event is the fifth documented for this species in the world and had the highest reported number of males involved in a mating train for this species to date, with six males participating (Carpenter et al. in press). One courtship event was documented in Saint Peter and Saint Paul Archipelago, Brazil, in May 2015 and included one female and three males (McCallister et al. 2020). Three courtship events were documented in the Southern Gulf of California, Mexico, involving one female and four males in June 2021, one female and three males in July 2022, and one female and two males in August 2022 (Palacios et al. 2023). During the courtship event we report here, the female was not darker nor bigger than the males, as opposed to the courtship event reported by McCallister et al. (2020). Based on the seven stages described for mobulid courtship and mating (Stevens 2016; Stevens et al. 2018a), our observation was consistent with the courtship behavior, especially the "endurance" and "evasion" stages. The presence of mating wounds on the female indicates that mating behavior or attempted copulation occurred, although it was not observed directly by the scientific team. These wounds result from the male biting the female's pectoral fins, which allows an abdomen-to-abdomen positioning during copulation (Yano et al. 1999; Marshall and Bennet 2010; Stevens et al. 2018a). In contrast to manta rays, devil ray species have teeth on both jaws (Notarbartolo-di-Sciara 1987; Stevens et al. 2018b), which can leave linear wounds on both sides of the females' pectoral fins during mating, as observed during this event. Prior to biting, the male positions himself on top of the female (Stevens et al 2018a), leaving dorsal marks on the female, which was also observed in this encounter. The presence of several fresh mating wounds on the female while she was still actively engaged in courtship, suggest that *M. thurstoni*, like other mobulid rays, likely mate multiple times with different males during a single mating period (Stevens et al 2018a). This behavioral trait may be linked to sperm competition and/or storage strategies (Stevens 2016; Jordan et al. 2021).

As part of the scientific expedition that permitted the observation in Nuku Hiva, Marquesas Archipelago, surveys were conducted among the local communities, and reports of mobulid rays' bycatch were made by local fishermen on the islands of Ua Pou, Nuku Hiva, and Ua Huka, as well as sightings by professional divers in Hiva Oa and Nuku Hiva. However, no photographic evidence was obtained to confirm the species observed or behaviors (Carpentier unpublished data), nor evaluate the frequency of sightings. It suggests that increased scientific surveys and more systematic identification of mobulid rays during bycatch events are needed to allow for a better understanding of the distribution and habitat use of mobulid rays in this remote Pacific region (Stewart et al. 2018). Given the endangered status of mobulid rays and the government of French Polynesia's commitment to preserve their critical habitats, a better understanding of their ecology and critical sites is essential to improve conservation strategies for these species within French Polynesia waters.

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ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

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Author contributions

Conceptualization: ASC. Data curation: ASC. Formal analysis: ASC. Funding acquisition: ASC, FM. Investigation: ASC, AG, TT, NB, CB. Methodology: ASC, CB. Resources: ASC. Supervision: ASC. Visualization: ASC. Project administration: ASC, VP, MS. Validation: ASC, CB. Writing – original draft: ASC. Writing – review and editing: ASC, GMWS, FM, CB.

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Data availability

All data that support the findings of this study are available in the main text and Supplementary materials.

REFERENCES

Bucair N, Mendonça S, Araújo C, Rangel BS, Gadig OB (2022) Records of Bentfin Devil Ray, *Mobula thurstoni*, in a marine protected area in Brazilian Equatorial Atlantic: implications for the species' distribution and local conservation strategies. Environmental Biology of Fishes 105 (5): 653–661. https://doi.org/10.1007/s10641-022-01266-0

Bucair N, Hinojosa-Alvarez S, Marshall AD, Pate J, Francini CLB, Garrido AG, Capel KCC, Loboda TS, Monteiro JS, Bruno CEM, Vaga CF, Dove ADM, Hoopes LA, Perry C, Kitahara MV (2025) An integrative taxonomy investigation unravels a cryptic species of *Mobula* Rafinesque, 1810 (Mobulidae, Myliobatiformes), from the Atlantic Ocean. Environmental Biology of Fishes (2025): 1–35.

Carpenter M, Klimley AP, Boggio-Pasqua A, Armstrong AO, Hilbourne S, Guerrero M, Lapinski M, Fuentes K, Stevens GMW, Palacios M (in press) A review of manta and devil ray courtship and mating. Environmental Biology of Fishes.

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

Code of the Environment of French Polynesia. Loi du pays n° 2017-25 du 05/10/2017 and Arrêté n° 466 CM du 22/03/2018. https://lexpol.cloud.pf. Accessed on: 2025-07-15.

Couturier LIE, Marshall AD, Jaine FRA (2012) Biology, ecology and conservation of the Mobulidae. Journal of Fisheries Biology 80 (5): 1075–1119. http://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, Poortvliet M, Roman M, Stevens G, Tershy BR, White WT (2016) Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. Aquatic Conservation: Marine and Freshwater Ecosystems 26 (3): 562–575. https://doi.org/10.1002/aqc.2591

Dulvy NK, Pardo SA, Simpfendorfer CA, Carlson JK (2014) Diagnosing the dangerous demography of manta rays using life history theory. PeerJ 2: e400. https://doi:10.7717/peerj.400

Ehemann N, Acosta-Rodríguez E, Tagliafico A, Pelletier N, Stevens G (2022) Manta and devil ray species occurrence and distribution in Venezuela, assessed through fishery landings and citizen science data. Journal of Fish Biology 101 (1): 213–225. https://doi.org/10.1111/jfb.15088

Francis MP, Jones EG (2017) Movement, depth distribution and survival of Spinetail Devilrays (*Mobula japanica*) tagged and released from purse-seine catches in New Zealand. Aquatic Conservation 27 (1): 219–236. https://doi.org/10.1002/aqc.2641

Glaus K, Gordon L, Vierus T, Marosi ND, Sykes H (2024) Rays in the shadows: batoid diversity, occurrence, and conservation status in Fiji. Biology 13 (2): 73. https://doi.org/10.3390/biology13020073

Griffiths SP, Lezama-Ochoa N (2021) A 40-year chronology of the vulnerability of Spinetail Devil Ray (*Mobula mobular*) to eastern Pacific tuna fisheries and options for future conservation and management. Aquatic Conservation: Marine and Freshwater Ecosystems 31 (10): 2910–2925. https://doi.org/10.1002/aqc.3667

Harris JL, Collins C, Spalding M, Stevens GM (2024) First records of the Sicklefin (*Mobula tarapacana*), Bentfin (*Mobula thurstoni*), and Spinetail (*Mobula mobular*) Devil Rays in the Chagos Archipelago. Journal of Fish Biology 104 (5): 1628–1632. https://doi.org/10.1111/jfb.15678

Jordan RP, Graham CT, Minto C, Henderson AC (2021) Assessment of sperm storage across different reproductive modes in the elasmobranch fishes. Environmental Biology of Fishes 104: 27–39. https://doi.org/10.1007/s10641-020-01051-x

Lawson JM, Fordham SV, O'Malley MP, Davidson LNK, Walls RHL, Heupel MR, Stevens G, Fernando D, Budziak A, Simpfendorfer CA, Dulvy NK (2017) Sympathy for the devil: a conservation strategy for devil and manta rays. PeerJ 5: e3027. https://doi.org/10.7717/peerj.3027

Leichter JJ, Stewart HL, Miller SL (2012) The island-scale internal wave climate of Moorea, French Polynesia. Journal of Geophysical Research: Oceans 117: C6. https://doi.org/10.1029/2012jc007949

Lezama-Ochoa N, Hall M, Román M, Vogel N (2019) Spatial and temporal distribution of mobulid ray species in the eastern Pacific Ocean ascertained from observer data from the tropical tuna purseseine fishery. Environmental Biology of Fishes 102 (1): 1–17. https://doi.org/10.1007/s10641-018-0832-1

Lezama-Ochoa N, Lopez J, Hall M, Bach P, Abascal F, Murua H (2020) Spatio-temporal distribution of the Spinetail Devil Ray *Mobula mobular* in the eastern tropical Atlantic Ocean. Endangered Species Research 43: 447–460. https://doi.org/10.3354/esr01082

Lezama-Ochoa N, Murua H, Chust G, Ruiz J, Chavance P, de Molina AD, Caballero A, Sancristobal I (2015) Biodiversity in the by-catch communities of the pelagic ecosystem in the Western Indian Ocean. Biodiversity and Conservation 24: 2647–2671. https://doi.org/10.1007/s10531-015-0951-3

Marshall AD, Bennett MB (2010) Reproductive ecology of the reef manta ray *Manta alfredi* in southern Mozambique. Journal of Fish biology 77 (1): 169–190. https://doi.org/10.1111/j.1095-8649.2010.02669.x

Marshall AD, Compagno LJ, 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/10.11646/zootaxa.2301.1.1

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 2022: e.T110847130A214381504. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T110847130A214381504.en

Marshall A, Barreto R, Bigman JS, Carlson J, Fernando D, Fordham S, Francis MP, Herman K, Jabado RW, Liu KM, Pardo SA, Rigby CL, Romanov E, Smith WD, Walls RHL (2022b). *Mobula thurstoni* (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2022: e.T60200A214368409. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T60200A214368409.en

Martinez E, Maamaatuaiahutapu K (2004) Island mass effect in the Marquesas Islands: time variation. Geophysical Research Letters 31 (18): 1–4. https://doi.org/10.1029/2004GL020682

Martinez E, Raapoto H, Maes C, Maamaatuaihutapu K (2018) Influence of tropical instability waves on phytoplankton biomass near the Marquesas Islands. Remote Sensing 10 (4): 640. https://doi.org/10.3390/rs10040640

McCallister M, Mandelman J, Bonfil R, Danylchuk A, Sales M, Ajemian M (2020) First observation of mating behavior in three species of pelagic myliobatiform rays in the wild. Environmental Biology of Fishes 103: 163–173. https://doi.org/10.1007/s10641-019-00943-x

Notarbartolo-di-Sciara G (1987) A revisionary study of the genus *Mobula* Rafinesque, 1810 (Chondrichthyes: Mobulidae) with the description of a new species. Zoological Journal of the Linnean Society 91 (1): 1–91. https://doi.org/10.1111/j.1096-3642.1987.tb01723.x

Notarbartolo di Sciara G, Stevens G, Fernando D (2020) The Giant Devil Ray *Mobula mobular* (Bonnaterre, 1788) is not giant, but it is the only Spinetail Devil Ray. Marine Biodiversity Records 13(1): 1–5. https://doi.org/10.1186/s41200-020-00187-0

Notarbartolo di Sciara G, Lauriano G, Pierantonio N, Cañadas A, Donovan G, Panigada S (2015) The devil we don't know: investigating habitat and abundance of endangered Giant Devil Rays in the north-western Mediterranean Sea. PLoS ONE 10 (11): e0141189. https://doi.org/10.1371/journal.pone.0141189

Notarbartolo di Sciara G, Adnet S, Bennett M, Broadhurst MK, Fernando D, Jabado RW, Laglbauer BJ, Stevens G (2019) Taxonomic status, biological notes, and conservation of the longhorned pygmy devil ray *Mobula eregoodoo* (Cantor, 1849). Aquatic Conservation 30 (1): 104–122. https://doi.org/10.1002/aqc.3230

Ozaki R (2023) Chasing rays: distribution and habitat-use of mobulid rays in the northeastern continental shelf of Aotearoa New Zealand. PhD thesis, University of Auckland, Auckland, New Zealand, 194 pp.

Ozaki R, Stephenson F, Pinkerton M, Finucci B, Green L, Penna AD, Sila-Nowicka K (2024) Evidence of environmental niche separation between threatened mobulid rays in Aotearoa New Zealand: insights from species distribution modelling. Journal of Biogeography 51 (11): 2117–2135. https://doi.org/10.1111/jbi.14976

Palacios MD, Trejo-Ramírez A, Velázquez-Hernández S, Huesca-Mayorga SA, Stewart JD, Cronin MR, Lezama-Ochoa N, Zilliacus KM, González-Armas R, Galván-Magaña F, Croll DA (2023) Reproductive behavior, seasonality, and distribution of three devil ray species (*Mobula mobular*, *M. thurstoni*, and *M. munkiana*) in the southern Gulf of California, Mexico. Marine Biology 171 (1): 12. https://doi.org/10.21203/rs.3.rs-3050468/v1

Rambahiniarison JM, Lamoste MJ, Rohner CA, Murray R, Snow S, Labaja J, Araujo G, Ponzo A (2018) Life history, growth, and reproductive biology of four mobulid species in the Bohol Sea, Philippines. Frontiers in Marine Science 5: 269. https://doi.org/10.3389/fmars.2018.00269

Ratão SS, Dias D, Stiebens V (2017). First record of smoothtail mobula *Mobula thurstoni* (Myliobatidae) in Cabo Verde. Zoologia Caboverdiana 6: 11–14.

Séguigne C, Mourier J, Clua É, Buray N, Planes S (2023) Citizen science provides valuable data to evaluate elasmobranch diversity and trends throughout the French Polynesia's shark sanctuary. PLoS ONE 18 (3): e0282837. https://doi.org/10.1371/journal.pone.0282837

Shirke SS, Nashad M, Sukham MD, Pradeep HD (2017). A first record of the Bentfin Devil Ray *Mobula thurstoni* (Lloyd, 1908) (Myliobatiformes: Mobulidae) from the Indian EEZ of the Andaman Sea. Journal of Threatened Taxa 9 (12): 11074–11080. https://doi.org/10.1088/1755-1315/137/1/012048

Stevens GMW (2016) Conservation and population ecology of manta rays in the Maldives. PhD thesis, University of York, York, United Kingdom, 207 pp.

Stevens GMW, Hawkins JP, Roberts CM (2018a) Courtship and mating behavior of manta rays *Mobula alfredi* and *M. birostris* in the Maldives. Journal of Fish Biology 93: 344–359. https://doi.org/10.1111/jfb.13768

Stevens GMW, Fernando D, Dando M, Notarbartolo–di–Sciara G (2018b) Guide to the manta and devil rays of the world. Princeton University Press, Princeton, New Jersey, USA. https://doi.org/10.2307/j.ctvs32s7t

Stewart JD, Jaine FR, Armstrong AJ, Armstrong AO, Bennett MB, Burgess KB, Couturier L, Croll D, Cronin M, Deakos M, Dudgeon C, Fernando D, Froman N, Germanov E, Hall M Hinojosa-Alvarez S, Hosegood J, Kashiwagi T, Laglbauer B, Lezama-Ochoa N, Marshall A, McGregor F, Notarbartolo di Sciara G, Palacios M, Peel L, Richardson A, Rubin R, Townsend K, Venables S, Stevens GM (2018) Research priorities to support effective manta and devil ray conservation. Frontiers in Marine Science 5: 314. https://doi.org/10.3389/fmars.2018.00314

Ward-Paige CA, Davis B, Worm B (2013) Global population trends and human use patterns of Manta and Mobula rays. PLoS ONE 8 (9): e74835. https://doi.org/10.1371/journal.pone.0074835

White WT, Corrigan S, Yang L, Henderson AC, Bazinet AL, Swofford DL, Naylor GJP (2018) Phylogeny of the manta and devil rays (Chondrichthyes: Mobulidae), with an updated taxonomic arrangement for the family. Zoological Journal of the Linnean Society 182: 50–75. https://doi.org/10.1093/zoolinnean/zlx018

Yano K, Sato F, Takahashi T (1999) Observations of mating behavior of the Manta Ray, *Manta birostris*, at the Ogasawara Islands, Japan. Ichthyological Research 46 (3): 289–296.