



# Persistent declines in sightings of manta and devil rays (Mobulidae) at a global hotspot in southern Mozambique

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**Abstract** Mobulid rays are among the most vulnerable of chondrichthyans to overexploitation by fisheries due to their low population growth rates. In locations where catch data are lacking, long-term sightings data can provide valuable insight to infer population trends and status. We recorded underwater sighting data of reef manta rays (*Mobula alfredi*), oceanic manta rays (*M. birostris*), and shorthorned pygmy devil rays (*M. kuhlii*) between 2003 and 2023 in the waters off Praia do Tofo in the Inhambane Province, southern Mozambique, one of the major global hotspots for these rays. We modelled sightings data using a hierarchical generalised linear mixed model framework to account for a suite of environmental variables when examining temporal trends. Raw trend models including only ‘year’ as a predictor showed a 99% decline in sightings of reef manta rays, a 92.5% decline in oceanic manta ray sightings,

and an 81.3% decline in devil ray sightings over the 20-year study period. The declining trends persisted for reef and oceanic manta rays once a suite of temporal and environmental variables were accounted for, indicating that the declines were driven by external factors not tested in the models. For shorthorned pygmy devil rays, models that incorporated environmental variables did not retain year as a significant predictor and showed a reduced overall decline in sightings of 36.5%. This indicates that the tested predictors were responsible for approximately half of the observed decline. Anthropogenic factors, particularly fisheries mortality, are likely to have played a significant role in the declining sightings of these three Threatened species. Improved conservation and management measures at a national and international level are critical to prevent further declines, which may otherwise lead to localised extinction.

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## Introduction

Shark and ray populations are under increasing pressure from human impacts, particularly overfishing, and have suffered pronounced declines on both regional and global scales (Pacoureau et al. 2021; Worm et al. 2024). Global assessments show that the proportion of chondrichthyan species threatened with extinction

has increased from one-quarter in 2014 to one-third in 2021 (Dulvy et al. 2014a, 2021). This is largely due to over-exploitation by directed fisheries and high rates of incidental catches in other fisheries (Dulvy et al. 2021; Pacoureau et al. 2021). Many chondrichthyan species are relatively large and long-lived, with a density-dependent rate of population increase, and their conservative life history characteristics leave them particularly vulnerable to anthropogenic pressures (Pardo et al. 2016; Pacoureau et al. 2021).

Manta and devil rays (genus *Mobula*) consist of nine recognised species, collectively referred to as mobulid rays (White et al. 2018; Notarbartolo di Sciara et al. 2020; Hosegood et al. 2020). These medium to large pelagic rays feed on zooplankton and small nekton and have a global distribution in tropical to warm-temperate oceans (Couturier et al. 2012; Last et al. 2016). As a result of their conservative reproductive strategy (i.e. slow growth, late maturation, low fecundity, and long gestation periods), the mobulid population growth rate is amongst the lowest of all elasmobranchs (Dulvy et al. 2014b; Pardo et al. 2016). The group is extremely susceptible to overexploitation and the nature and extent of human-induced threat has become increasingly obvious (Croll et al. 2016; Lawson et al. 2017; Fernando and Stewart 2021). To combat their declines, all mobulid species have been listed in Appendix II of the Convention on International Trade in Endangered Species (CITES), and Appendices I and II of the Convention on Migratory Species (CMS).

Mobulid rays are caught in directed gillnet, hook and line, and harpoon fisheries (Camhi et al. 2009; Acebes and Tull 2016), with the largest targeted fisheries reported from Sri Lanka, Indonesia, India, and the Philippines (Couturier et al. 2012; Croll et al. 2016; Fernando and Stewart 2021). Target fisheries are primarily driven by the export of gill plates, which are valuable in Asian medicine markets (Zeng et al. 2016; O'Malley et al. 2017). Mobulids are highly susceptible to incidental capture and are caught as bycatch in a range of fisheries and gear types, particularly gillnets, trawl nets, and purse-seine nets targeting tuna (White et al. 2006; Hall and Roman 2013; Francis and Jones 2017). Historically, quantifying these catches and assessing their sustainability has been hampered by a lack of species-specific landing data and poor bycatch monitoring in most locations (White et al. 2006; Lack and Sant 2009; Couturier et al. 2012). However, a few localised studies have revealed declining trends in

locations where mobulids are landed. For example, mobulid catch rates declined by an order of magnitude between 2011 and 2020 in Sri Lanka, revealing unsustainable exploitation levels of mobulid populations accessed by national fisheries (Fernando and Stewart 2021). Substantial declines (~95%) in mobulid landings were also documented in the northern Arabian Sea tuna gillnet fisheries between 2013 and 2018, with a notable decrease in catches after 2014 (Moazzam 2018), and fisher interviews in Bangladesh revealed an anecdotal decline in catches of six mobulid species over the previous decade (Haque et al. 2021). However, mobulid populations are fragmented, and trends have only been assessed in a few locations.

In the absence of fisheries catch data, sighting indices of free-swimming animals are useful for conservation assessments—although biases in survey effort need to be considered when interpreting these results (Witt et al. 2012; Rohner et al. 2013). Southern Mozambique's Inhambane Province has been a focus of mobulid research for the past two decades and is a global hotspot for these species, hosting the largest identified populations of reef and oceanic manta rays in Africa (Marshall et al. 2009, 2023; Venables et al. 2020b; Carpenter et al. 2022). The high frequency of sightings and co-occurrence of species at this site has underpinned the distinction and description of the two manta ray species (Marshall et al. 2009). The region has a growing marine tourism industry, predominantly focused around interactions with megafauna such as whale sharks, humpback whales, and mobulid rays (Tibirica et al. 2011; Venables et al. 2016b). Three mobulid species are regularly encountered—reef manta rays (*Mobula alfredi*), listed as 'Vulnerable' on the IUCN Red List (Marshall et al. 2022a); oceanic manta rays (*M. birostris*), and shorthorned pygmy devil rays (*M. kuhlii*; hereafter referred to as 'devil rays'), which are both listed as 'Endangered' (Marshall et al. 2022b; Rigby et al. 2022). The two larger species, oceanic and reef manta rays, are most commonly observed by divers at rocky reef cleaning stations, whereas devil rays are more often seen swimming mid-water, at times in groups of up to 200 individuals. An ongoing photo-identification database has identified 1368 individual reef manta rays and 298 oceanic manta rays since 2003 (MantaMatcher.org, 2024) in southern Mozambique.

Mobulids in Mozambique are caught in targeted fisheries and as incidental capture (by-catch)

by offshore in tuna purse-seine nets (Romanov 2002; Poisson et al. 2014) and by inshore gillnets set along the coast (Temple et al. 2018). Gillnet use has been increasing in Mozambique since the cessation of conflict in 1992 (Rohner et al. 2018; Temple et al. 2018), and gillnets were actively distributed by fisheries officials in some areas to move fishing effort away from inshore nursery habitats (Leeney 2017). Mobulid catch data for the region is scarce; fisheries-related mortality of reef manta rays, in targeted fisheries and as by-catch, was previously estimated at 20–50 individuals per year in the Inhambane Province (Marshall et al. 2011), and there are extensive but unquantified catches of devil rays (A. Marshall, unpublished data). Previously, we reported an 88% decline in reef manta ray sightings in the waters off Praia do Tofo over a 9-year period (2003–2011), based on dive survey time series data, with no clear trend for oceanic manta rays (Rohner et al. 2013). Four years ago, mobulid species were granted national protection in Mozambique under the Regulamento da Pesca Marítima law (Boletim da República Decreto No. 89 Série Número 192 2020), which prohibits the capture, retention, and sale of listed species. However, the impact of this regulation on catch rates is difficult to assess, as mobulids are typically caught incidentally at remote landing sites, and catch monitoring data are limited.

Here, we reassess mobulid sighting trends in the Inhambane Province over an extended time period of 20 years. Long-term observations are needed to accurately examine sightings and abundance trends in large, slow-growing animals (Rohner et al. 2022), and the two decades here approach the generation length of manta rays (29 years; Marshall et al. 2022a,b). We also expand our scope to include sightings of devil rays which have a shorter generation length and may respond quicker to environmental changes. Given that sightings of these large planktivores are likely affected by environmental factors that can influence both their movements and food sources across short time scales (Richardson 2008), we standardised sightings with generalised linear mixed models (GLMM) to account for environmentally driven variability. We investigate whether declining trends have persisted and whether they are uniform across the three commonly encountered mobulid species. Considering the recent legislation to protect mobulids in Mozambique, our findings will also provide a baseline to monitor the effectiveness of introduced species protection.

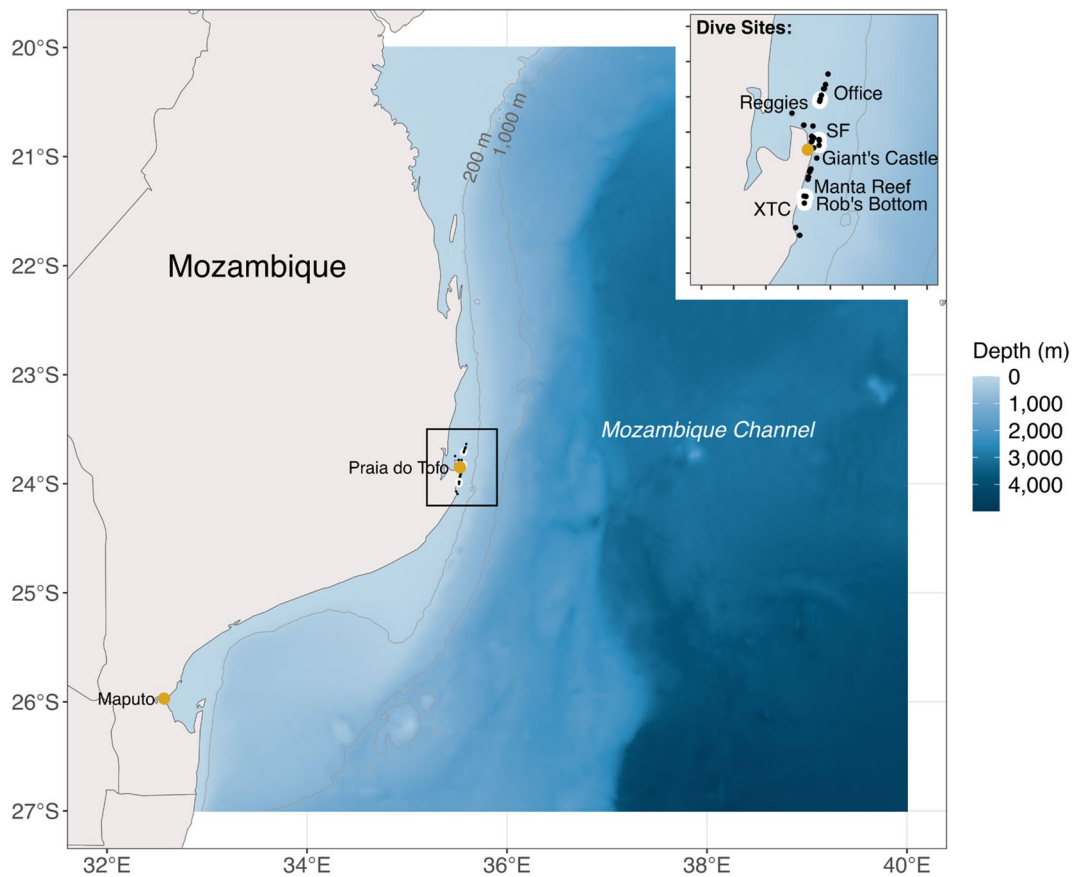
## Methods

### Study site

Praia do Tofo is situated in the Inhambane Province of Mozambique (23.85° S, 35.55° E) (Fig. 1). A series of rocky reefs, ranging from 10 to 30 m deep, lie off a 40 km stretch of coastline near this small town. The reefs have low hard coral diversity, and many serve as ‘cleaning stations’ for larger marine species, particularly larger bony fishes, sharks, and rays. This region has been the subject of a number of studies focusing on mobulid rays (Marshall et al. 2011; Venables et al. 2020b). Oceanographic conditions are dynamic, with underwater horizontal visibility varying from 5 to 30 m, and water temperature varying seasonally from a high of 30 °C during austral summer (Dec–Mar) to 16 °C during the winter (Jul–Sep) (Rohner et al. 2013; Williams et al. 2015). Frequent cold-water intrusions lead to daily temperature amplitudes of up to 7.5 °C in this region (Rohner 2013). Current strength and surface weather conditions are also variable, with occasional strong winds and large swells of > 2.5 m preventing the launching of boats for safety reasons.

### Dive survey protocol

Sightings of reef manta rays, oceanic manta rays, and devil rays were recorded during 4604 dive surveys between 2003 and 2023 (21 years). Surveys were conducted year-round, as opposed to during a specified ‘field season’. The number of surveys varied among years, with the most consistent survey effort from 2010 to 2019 (Supp. Figure 1). Data were collected by trained researchers on SCUBA, using a modified version of the ‘Roving Diver’ Underwater Visual Census (UVC) Technique (Schmitt and Sullivan 1996). Although a typical transect path was followed at each site, observers essentially ‘roved’ freely throughout the site to record marine megafauna species. Our method differed slightly from the standard Roving Diver technique in that we counted the exact number of individuals, where possible, as opposed to recording abundance in categories. Reef and oceanic manta rays were identified based on their natural ventral markings (Fig. 2) using photo-identification (Marshall et al. 2011) and individually counted. By contrast, the number of devil ray individuals was



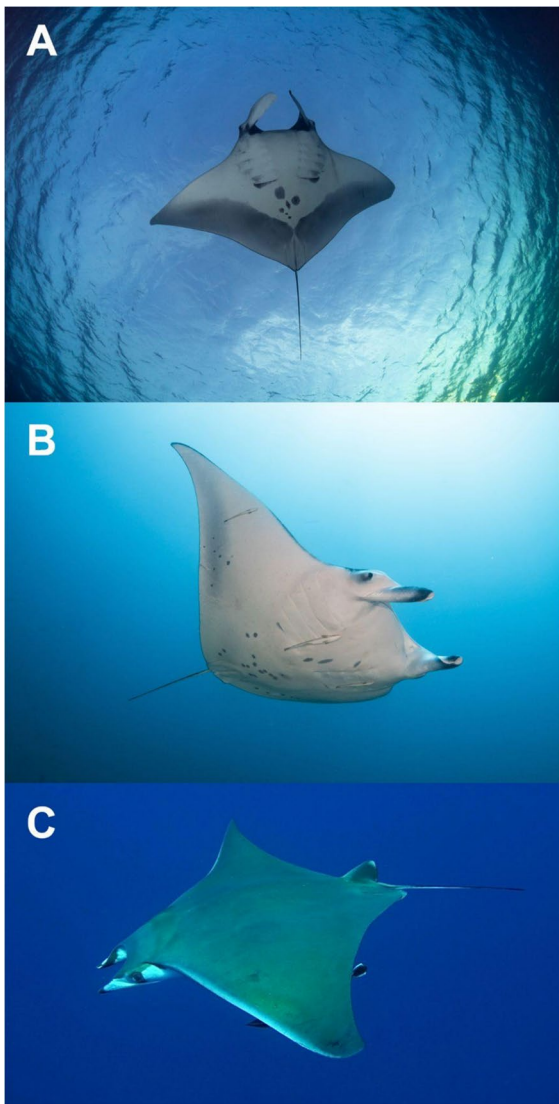
**Fig. 1** Map of the study area around Praia do Tofo in southern Mozambique, with all dive sites in the area indicated (black dots) and the main dive sites highlighted (white points). The inset shows the names and locations of the main dive sites (SF, Sherwood Forest)

counted (for smaller groups of <20 individuals) or estimated when required for larger schools.

Mean dive duration was  $40.3 \pm 6.86$  min based on a subset of dives with duration records ( $n = 3499$ , 76% of all recorded dives). Survey effort was uneven among years, ranging from 32 dives in 2003 to 533 dives in 2019 (Fig. 3). We partially accounted for this temporal bias by using the annual number of surveys as a potential predictor in the models. We only used data from sites that were surveyed > 5 times to exclude exploratory dive sites ( $n = 7$ ) and sites that had at least one mobulid ray recorded once to exclude dive sites on shallow reefs with no chance of observing mobulids ( $n = 4$ ). This eliminated a small proportion (2.5%) of dives. We then grouped 12 sites with < 100 dives as ‘other’ to retain 8 sites as predictors in the models: Giant’s Castle (GC,  $n = 1177$ ), Manta Reef (MR,  $n = 1275$ ), Office Reef (OF,  $n = 423$ ), other (OT,

$n = 448$ ), Rob’s Bottom (RB,  $n = 456$ ), Reggies (RE,  $n = 283$ ), Sherwood Forest (SF,  $n = 176$ ), and Outback (XT,  $n = 341$ ).

Prior to data collection, all observers were trained in a standardised data collection protocol in order to reduce subjectivity. During each survey, observers recorded the diver identity, dive site, start time, and a suite of environmental conditions including (a) surface weather conditions in four categories—sunny, partial overcast (0–50% cloud cover), overcast (51–100% cloud cover), or raining; (b) swell—none, very small, small, medium, or large, based on the Beaufort Sea State Scale; (c) current direction and strength at depth, with strength estimated by the observer in four categories—no current, light, medium, or strong; (d) estimated horizontal underwater visibility at depth (m); (e) water temperature (°C) at depth using dive computers; and (f) overall



**Fig. 2** Photos of the three study species: **A** oceanic manta ray *Mobula birostris*, **B** reef manta ray *M. alfredi*, **C** shorthorned pygmy devil ray *M. kuhlii*, showing the unique ventral markings used for individual identification of reef and oceanic manta rays

plankton density, as a general index for food availability, visually recorded in four categories—no plankton, visible phytoplankton, low zooplankton, or dense zooplankton. We extracted environmental variables (sea surface temperature, chlorophyll-a concentration, salinity, Indian Ocean Dipole index, moon illumination, lunar distance) post hoc, which have been previously related to mobulid sightings (Dewar et al. 2008; Rohner et al. 2013, 2017; Saltzman and White 2023)

to complement the logbook data (Table 1). Further explanation for each potential predictor is given in the Supplementary Materials.

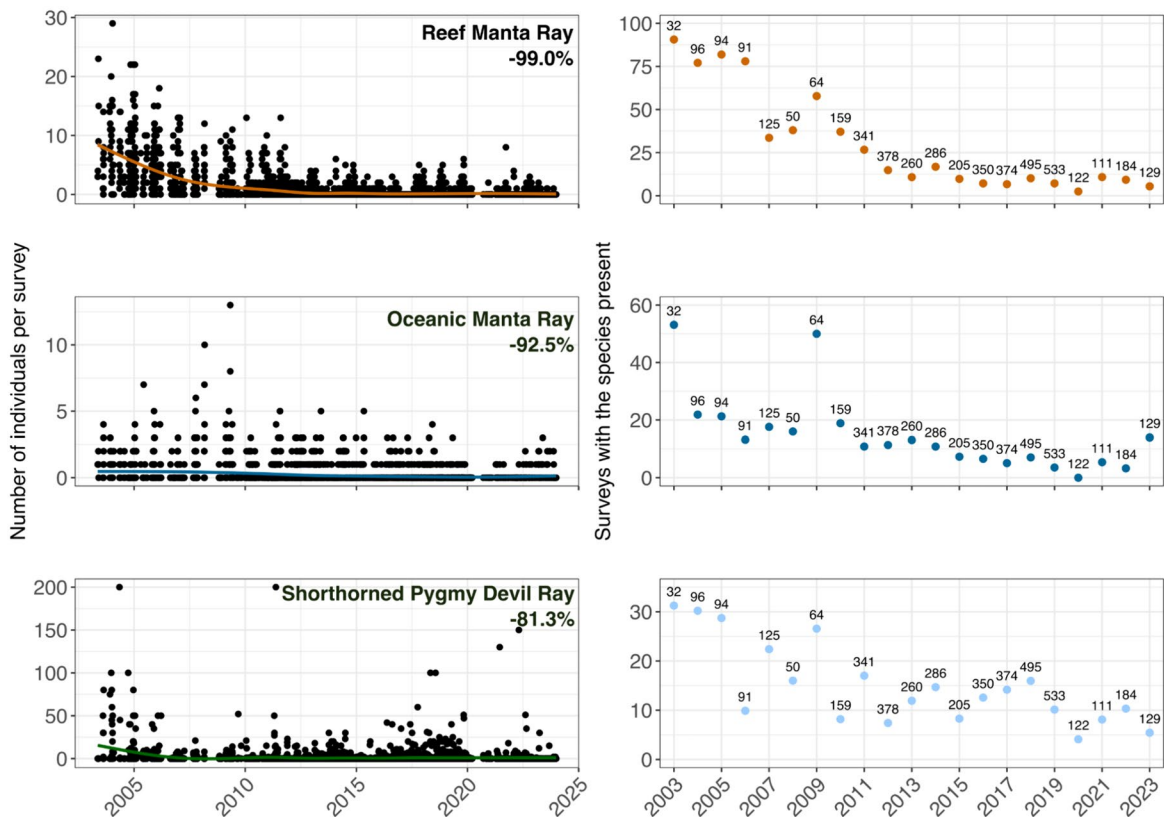
Prior to fitting the models, we examined the correlation among all continuous predictors with a Pearson correlation matrix. Day of year correlated with sea surface temperature (SST;  $r = -0.56$ ) and with temperature at depth ( $r = -0.47$ ), so we only included one of these predictors per model. Temperature and SST also correlated ( $r = 0.65$ ), and we preferentially used temperature at depth, as it is likely to be more influential in this region that is characterised by strong sub-surface upwelling (Roberts et al. 2014). Finally, there was a correlation between effort (number of surveys per year) and year ( $r = 0.43$ ), with more surveys in later years. We excluded effort in all models because estimating the temporal trend was a main objective of this study and therefore required retaining year as a predictor.

#### Modelling

Sightings data were modelled using a hierarchical generalised linear mixed model (GLMM) framework. We included ‘diver’ as a random variable to account for observations made by the same researcher. The response variable for all three species was count data, i.e. the number of individuals sighted per dive. We used zero-inflated mixed models for all three species because of the low frequency of sightings over the study period: reef manta rays were seen on 18.5% of dives, oceanic manta rays on 10% of dives, and devil rays on 13.1% of dives. Models were constructed using the ‘glmmTMB’ package (Brooks et al. 2017) in R version 4.3.1 (R Core Team 2023).

For model selection, we followed Saltzman and White (2023) by generating a selection of models that made biological sense (see below) and comparing the AICc using the ‘AICcmodavg’ package (Mazerolle 2023). Candidate models ranged from simple models with few predictors (e.g. a temporal model with only year, day of year, and time as predictors) to more complex models with a suite of variables (e.g. the best models for the species from (Rohner et al. 2013, 2017; Saltzman and White 2023)). The full list of models (Supp. Table 1) and the model selection process (Supp. Table 2) can be found in Supplementary Materials. To assess the trend in raw sightings over time for each species, we constructed a ‘raw trend’ model that





**Fig. 3** Number of individuals observed per survey with a trendline (left panels) and the percentage of surveys with the species present and the number of surveys (text) (right panels) for reef manta rays (upper panels), oceanic manta rays (middle

panels), and devil rays (lower panels). The percentage decline from the temporal model with only year as a predictor is given in the top right corner of the left panels

included only ‘year’ as a predictor, and ‘diver’ as a random effect, without additional explanatory variables. To assess differences among levels of categorical variables, we used pairwise comparisons with the Tukey method in the ‘emmeans’ package (Lenth 2024) (Supp. Table 4).

## Results

### Temporal trends

Observers counted a mean of  $0.64 \pm 2.01$  and up to 30 individual reef manta rays per survey (Fig. 3). Reef manta rays were seen on 18.5% of surveys. There was a clear temporal trend, with yearly percentages dropping from 90.6% in 2003 to 2.5% in 2020 (Fig. 3). The raw trend model, with only year

( $p < 0.001$ ) as a predictor, showed a 99% decline in sightings over the study period. When excluding the first 4 years with higher sightings rates, there was still an 80.0% decline in sightings from 2007 to 2023. Since the previous assessment, which included data up to 2011 (Rohner et al. 2013), we observed a further 21.5% decline from 2012 to 2023. The overall decline was only slightly lower in the best model (Table 2) that included year ( $p < 0.001$ ) and a suite of environmental predictors (96.9% vs. 99% in the raw trend model).

Oceanic manta rays were seen less frequently and in smaller numbers than reef manta rays, with a mean of  $0.16 \pm 0.61$  individuals and up to 13 seen per survey (Fig. 3). Oceanic manta rays were seen on 10% of surveys, ranging from a maximum of 53.1% in 2003 to a minimum of 0% in 2020 (Fig. 3). The raw trend model with only year ( $p < 0.001$ ) as a predictor

**Table 1** Description and source of predictors included in generalised linear mixed models for all three mobulid species

Predictor	Description	Source	Fixed or random	Type	Units	Range (5th–95th percentile)
Year	Year of study	Logbook	Fixed	Categorical		2003–2023*
DOY	Day of the year	Logbook	Fixed	Continuous		2–366*
Time	Time of day	Logbook	Fixed	Continuous	Hour	7–17*
Temperature	Water temperature at depth	Logbook	Fixed	Continuous	°C	20–27
SST	Sea surface temperature	AVHRR dataset (daily, 0.25 resolution); <a href="https://upwell.pfeg.noaa.gov/erddap">https://upwell.pfeg.noaa.gov/erddap</a>	Fixed	Continuous	°C	23.7–28.8
Plankton	Plankton categories (no plankton, visible phytoplankton, low zooplankton, or dense zooplankton)	Logbook	Fixed	Categorical		
Chl-a	Chlorophyll-a concentration	MODIS Aqua satellite (8-day mean, 0.25 resolution)	Fixed	Continuous	mg m <sup>3</sup>	0.13–0.72
Salinity	Water salinity	Ocean and Climate. Surface salinity (monthly, 0.5 resolution to 2021, then 1 resolution) <a href="http://www.ocean.iap.ac.cn/ftp/cheng/CZ16_v0_IAP_Salinity_0p5_gridded_1month_netcdf/">http://www.ocean.iap.ac.cn/ftp/cheng/CZ16_v0_IAP_Salinity_0p5_gridded_1month_netcdf/</a>	Fixed	Continuous	g kg <sup>-1</sup>	33.94–34.06
Indian Ocean Dipole	Indian Ocean Dipole index	<a href="https://sealevel.jpl.nasa.gov/overlay-iod">https://sealevel.jpl.nasa.gov/overlay-iod</a>	Fixed	Continuous	Week	–1.76–2.04
Moon Illumination	Percentage of the moon illuminated	Lunar <sup>r</sup> package (Lazaraidis 2022)	Fixed	Continuous	%	0.006–0.996
Lunar distance	Distance to the moon	Lunar <sup>r</sup> package (Lazaraidis 2022)	Fixed	Continuous	Earth radii	56.6–63.7
Visibility	Underwater visibility, visually estimated	Logbook	Fixed	Continuous	m	5–25
Weather	Weather category (sunny, partial overcast (0–50%), overcast (51–100%), rain)	Logbook	Fixed	Categorical		
Swell	Ocean surface swell (none, very small, small, medium, large)	Logbook	Fixed	Categorical		
Current direction	Grouped (north, east, south, west, no current)	Logbook	Fixed	Categorical		
Current strength	Grouped (no current, light, medium, strong)	Logbook	Fixed	Categorical		
Dive sites	Dive sites ( <i>n</i> = 8)	Logbook	Fixed	Categorical		
Diver	Identity of the observer ( <i>n</i> = 92)	Logbook	Random	Continuous		

\*indicates full range

showed a 92.5% decline in sightings from 2003 to 2023. Much of the decline occurred since the last assessment (Rohner et al. 2013), with a 73.5% decline over the period from 2012 to 2023. The overall decline was slightly lower in the best model (Table 2), which included year ( $p < 0.001$ ) and a suite of other predictors (89.4% vs. 92.5% in the raw trend model).

A mean of  $1.2 \pm 7.77$  devil rays, and up to 200 individuals, were seen per survey from 2003 to 2023 (Fig. 3). The species was recorded on 13.1% of all surveys, ranging from a high of 31.2% in 2003 to a low of 4.1% in 2020 (Fig. 3). The raw trend model with only year ( $p = 0.003$ ) as a predictor showed an 81.3% decline in sightings over the full study period. Much of that decline occurred in the first half of the study, with an increase of 143.6% from 2012 to 2023. By contrast, the best model with year and a suite of other predictors (Table 2) showed a smaller overall decline from 2003 to 2023 (36.5% vs 81.3% in the raw trend model), and year ( $p = 0.45$ ) was not significant.

Environmental models

We used a variety of models with different combinations of predictors to examine their influence on mobulid sightings off Praia do Tofo (Table 1; Supp. Table 1). The best model for reef manta rays included nine fixed predictors (year, sea temperature, weather, current strength, swell, salinity, dive site, plankton, chlorophyll-a) and ‘diver’ as a random variable (Table 2; Supp. Table 3). This model explained 14.3% of the variance for the fixed predictors. Year was significant ( $p < 0.001$ ), with a declining trend over the study period (96.9%; Fig. 4). Salinity was also significant ( $p < 0.001$ ) with an increasing trend

in sightings with higher salinity. Fewer reef manta rays were predicted with increasing chl-a ( $p = 0.01$ ). Most reef manta ray sightings were predicted when current strength was ‘medium’, during which sightings were predicted to be 53% higher than in no current ( $p = 0.004$ ) and 76% higher than in strong currents ( $p = 0.03$ ). There were no differences with the other pairwise comparisons. Sunny weather conditions resulted in 42% more predicted reef manta ray sightings than partial overcast ( $p = 0.01$ ). Medium swell was predicted to have 70% more sightings than no swell ( $p = 0.007$ ) while small swell was marginally significant ( $p = 0.07$ ) compared to medium swell. Among the dive sites, Office Reef and ‘other’ had lower predicted sightings than all other dive sites, except for Reggies (Fig. 4).

The best model for oceanic manta rays included the same predictors as the best reef manta ray models, although not all the same predictors were significant (Table 2; Supp. Table 3). This model explained 25.3% of the variance for fixed predictors. Year was a significant predictor ( $p < 0.001$ ) with a declining trend over time (Fig. 5). Salinity was also significant ( $p = 0.03$ ), with fewer sightings predicted for increasing salinity values. Weather conditions also had an influence, with sunny weather resulting in 42% more sightings than in partial overcast and 57% more than in overcast conditions. Among the dive sites, Office Reef, other, and Reggies had fewer sightings than most other sites, while Manta Reef had the most predicted sightings. No plankton resulted in 53% higher predicted sightings for oceanic manta rays than when dense zooplankton was observed (Fig. 5).

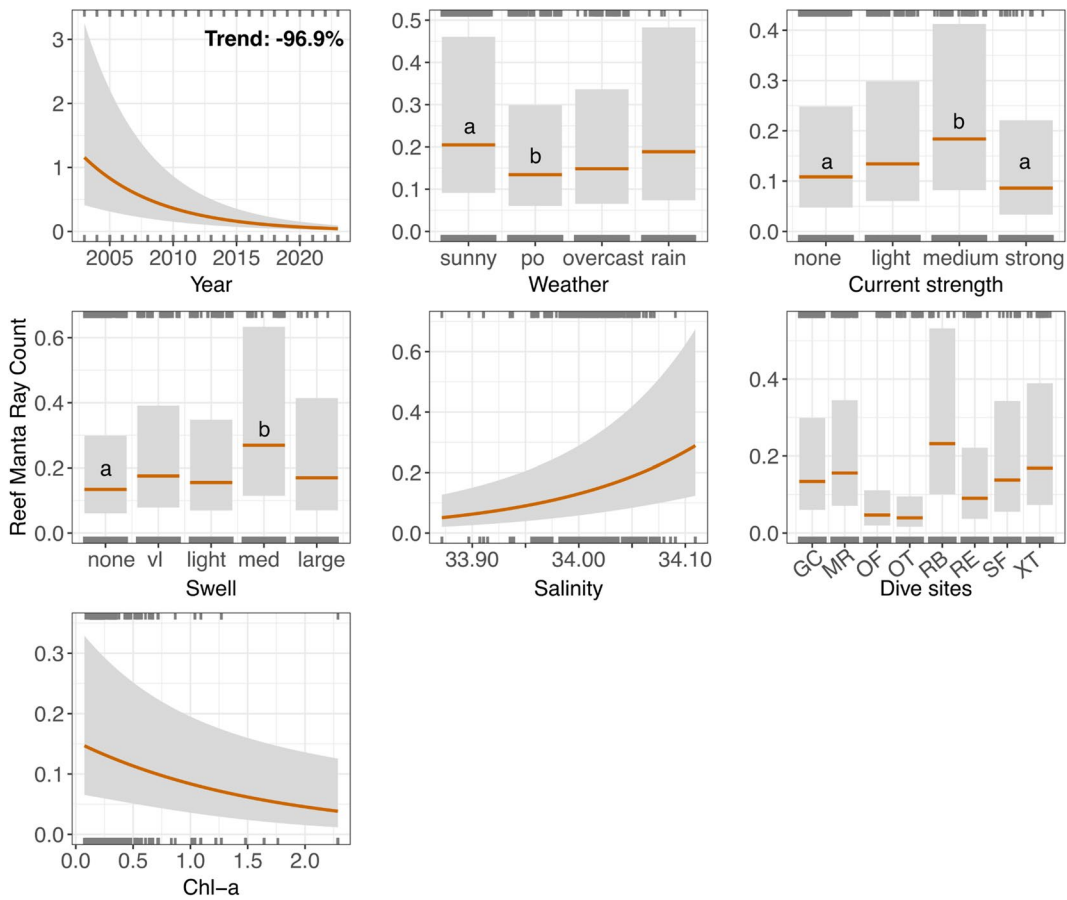
The best model for devil rays included 15 fixed predictors (year, sea temperature, underwater visibility, current direction, current strength, moon

**Table 2** Summary table of percentage occurrence and best model for the three mobulid species

Species	% surveys with species present	Best model
Reef manta ray	18.50%	Year* + temperature + weather* + current strength* + swell* + salinity* + sites* + plankton + Chl-a*
Oceanic manta ray	10%	Year* + temperature + weather* + current strength + swell + salinity* + sites* + plankton* + Chl-a
Shorthorned pygmy devil ray	13.10%	Year + temperature* + visibility* + current direction* + current strength + moon illumination + salinity + Indian Ocean Dipole + weather* + swell* + sites* + plankton + time + lunar distance + Chl-a

\*indicates significant predictor. Chl-a chlorophyll-a





**Fig. 4** Predicted counts of reef manta rays for significant predictors in the best model. Letters indicate differences between levels of categorical variables from pairwise comparisons (i.e. ‘a’ is different from ‘b’). No letters were added to ‘Dive

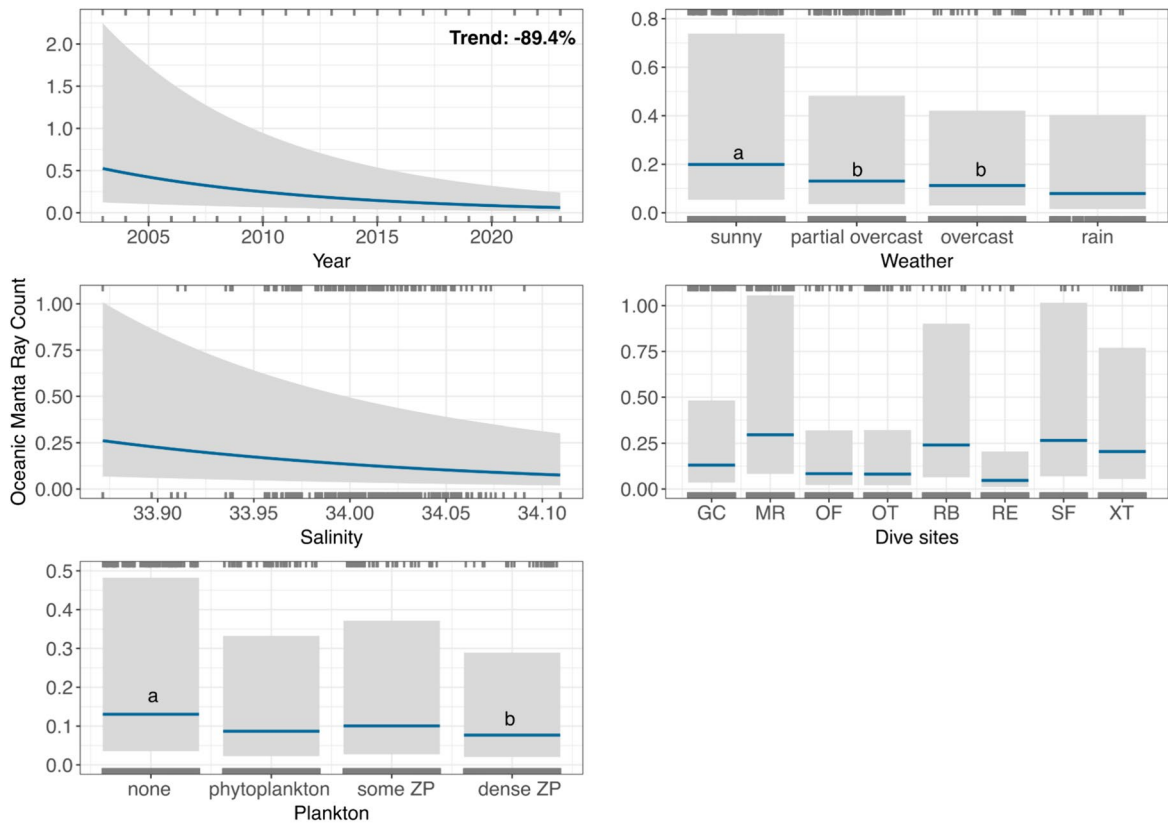
sites’ because of the many and varied significant combinations (See Supp. Table 4 ). The trend over time is shown in the top-right corner of the Year panel. Note the variable Y-axis scales. Po, partial overcast; vl, very light; med, medium

illumination, salinity, Indian Ocean Dipole, weather, swell, dive site, plankton, time, lunar distance, chlorophyll-a) and ‘diver’ as a random variable (Table 2; Supp. Table 3). This model explained 16.4% of the variance for fixed predictors. This was the only species that did not have year as a significant predictor. Water temperature was significant ( $p < 0.001$ ), with fewer predicted sightings with increasing temperature (Fig. 6). Underwater visibility was also significant ( $p = 0.004$ ), with more individuals predicted when visibility increased. More devil rays were predicted with an eastward current compared to a southward current ( $p = 0.02$ ), while the other pairwise comparisons were not significant. There were also more individuals predicted under partial overcast compared to sunny weather conditions ( $p = 0.02$ ). Although the

swell was a significant predictor, none of the pairwise comparisons showed a trend. Among the dive sites, Office Reef and Manta Reef had the highest predicted counts of devil rays (Fig. 6).

**Discussion**

Sightings of all three mobulid species declined dramatically over the 20-year study period in the waters off Praia do Tofo. Raw trend models showed a 99%, 92.5%, and 81.3% decrease in sightings of reef manta rays, oceanic manta rays, and devil rays, respectively. For reef and oceanic manta rays, these declining trends persisted after a range of environmental variables were accounted for by the models, indicating that



**Fig. 5** Predicted counts of oceanic manta rays for significant predictors in the best model. Letters indicate differences between levels of categorical variables (i.e. ‘a’ is different from ‘b’). No letters were added to ‘Dive sites’ because of the many

and varied significant combinations (See Supp. Table 4). The trend over time is shown in the top-right corner of the Year panel. Note the variable Y-axis scales.

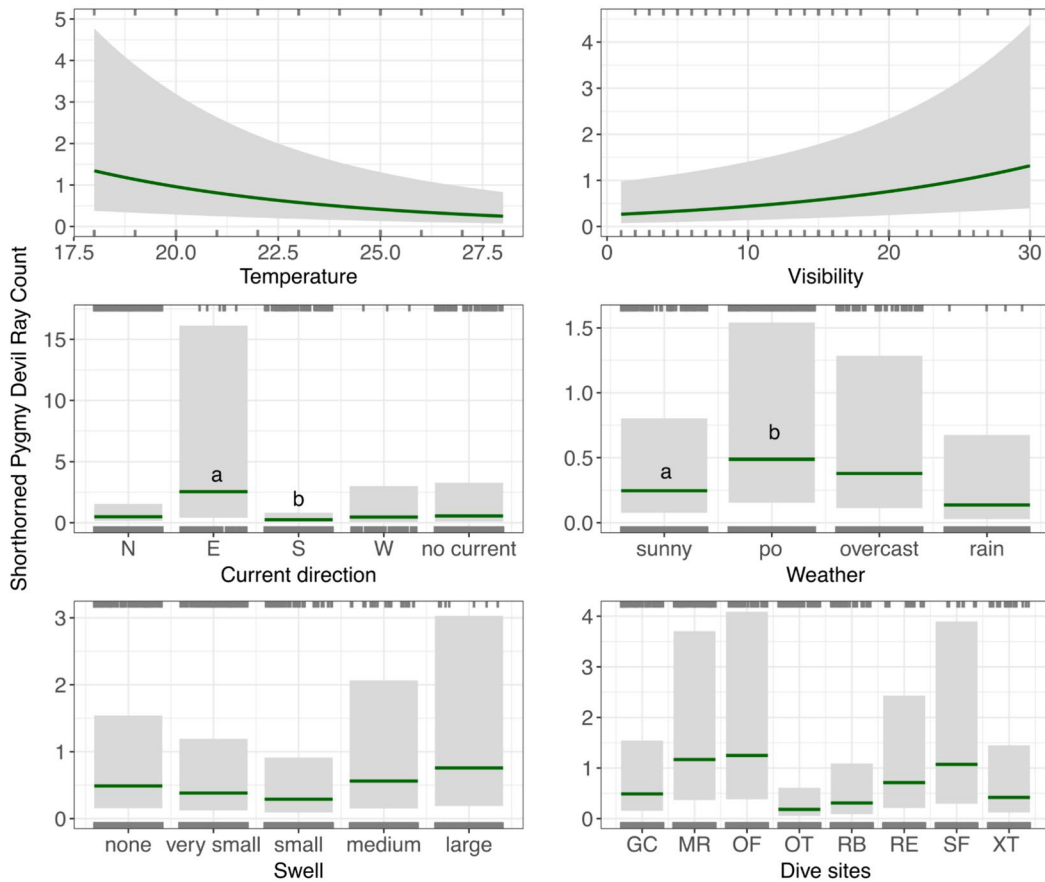
the declines were largely driven by other parameters not considered here—likely overfishing, as discussed below. By contrast, year was not a significant predictor in the best model for devil rays, which showed a reduced overall decline of 36.5%, indicating that environmental factors were responsible for approximately half of the decline in sightings. This decline in reef and oceanic manta ray sightings is alarming for mobulids in the Western Indian Ocean because the Inhambane Province hosts the largest identified populations of these species in Africa.

Temporal trends and potential drivers

Of the three species, reef manta rays exhibited the largest decline in sightings from 2003 to 2023 (99% in the raw trend model). Since the previous assessment that included data up to 2011 (Rohner et al. 2013),

we observed a further 21.5% decline in reef manta ray sightings from 2012 to 2023, showing that much of the decline occurred in the first half of the study, although it persists at a lower rate. This is also evident in photo-ID data for both species; in the 9-year period between 2003 and 2011, we recorded 1299 encounters of 1039 photo-identified individual reef manta rays, whereas only 201 encounters of 193 individuals were recorded in the 11-year period between 2012 and 2023. Similarly, 201 unique individual oceanic manta rays were recorded from 225 encounters during 2003–2011, compared to 178 encounters of 166 individuals in the second half of the study period (2012–2023) (MantaMatcher.org, 2024).

When including a variety of temporal and environmental predictors, the best model showed a decrease in sightings of 96.9%, indicating that the observed decline was driven by something other than the



**Fig. 6** Predicted counts of devil rays for significant predictors in the species’ best model. Letters indicate differences between levels of categorical variables (i.e. ‘a’ is different from ‘b’).

No letters were added to ‘Dive sites’ because of the many and varied significant combinations (See Supp. Table 4). Note the variable Y-axis scales. Po, partial overcast

variables included in the models. A slightly lower decline was observed for oceanic manta rays over the 20-year study period: 92.5% in the raw trend model. The last assessment reported a stable trend in sightings for this species from 2003 to 2011 (Rohner et al. 2013), which means that the majority of this decline occurred in the most recent decade, with a 73.5% decline in sightings from 2012 to 2023. After the incorporation of environmental and temporal predictors, the best model showed a slightly lower overall decline (89.4%), with year retained as a significant predictor.

Our findings strongly suggest that declines in reef and oceanic manta ray sightings are driven by external factors that were not accounted for in the models. These external factors are likely to be human-induced, although other large-scale factors may also

have contributed by shifting the hotspot of sightings outside our area of observations. An increase in fisheries mortality is the most likely explanation for these declines. The use of large-mesh gillnets (set and drift nets), often extending from nearshore to ~500 m offshore, has significantly increased off the Inhambane coast in recent years (Rohner et al. 2018; Temple et al. 2018). Due to their non-selective nature, there are high capture rates of elasmobranchs and other megafauna in gillnets in Mozambique (Temple et al. 2018). While landings from these artisanal fisheries are presently unquantified along this remote coast, the gillnet fishery poses a clear threat to marine megafauna in this region. Although the number of identified individuals (1368 reef manta rays, 298 oceanic manta rays; MantaMatcher.org, 2024) is relatively high compared to other manta ray aggregation sites

globally, the low population growth rates of these species (Dulvy et al. 2014b) suggest that even a small number of individuals captured annually is likely to lead to population declines. While increased use of non-selective fishing gears may be the primary threat, the lack of regional data on mobulid catches in off-shore fisheries is also a concern.

An alternative explanation for the observed declines is a shift in habitat use. The surveyed sites predominantly serve as cleaning stations for reef and oceanic manta rays and therefore represent only a small portion of their overall range. Cleaning stations serve as vital habitat for manta rays and are the main sites globally where the species are regularly observed. Apart from the health benefits of parasite removal and wound healing (Grutter 1999; Marshall 2008), these sites are also important for reproductive and social interactions (Stevens et al. 2018; Perryman et al. 2019). Acoustically tagged reef manta rays spent up to 8 consecutive hours at cleaning stations in Mozambique and returned to the same reefs over periods of multiple months, demonstrating the importance of these sites (Venables et al. 2020b). It is possible that, over the 20-year study period, mobulids have shifted to using different reefs along the coast or deeper reefs (> 40 m deep) that are outside of the depth limit of recreational dive surveys.

While our study only includes data collected on surveys off Praia do Tofo, both reef and oceanic manta rays are seen at other sites along the Inhambane Province coastline, including Zavora, Pomene, Morrungulo, the San Sebastian Peninsula, and the Bazaruto Archipelago (Venables et al. 2020b; Carpenter et al. 2022; Marshall et al. 2023). Investigating trends in sightings at these locations will be useful to determine whether individuals that previously frequented Praia do Tofo may have shifted habitat preferences to other locations along the coast. Photo-ID and telemetry studies have revealed connectivity between Mozambique and South Africa for reef and oceanic manta rays (Marshall et al. 2023; Authors unpublished data), with strong potential for genetic connectivity along this continuous coastline (Venables et al. 2020a). Overall manta ray catches in the KwaZulu-Natal bather protection program in South Africa increased between 1981 and 2000 then showed a significant decline between 2000 and 2021 (Carpenter et al. 2023), suggesting that this trend may be uniform along the south-east African coastline.

Both reef and oceanic manta rays are highly mobile, inhabiting wide home ranges and moving extensively on the vertical plane (Stewart et al. 2016, 2018; Armstrong et al. 2020; Andrzejczek et al. 2022), yet consistent cleaning behaviour and site fidelity lend to these species being easier to survey underwater than most other marine megafauna. However, our field survey data have biases that should be acknowledged. Acoustically tagged reef manta rays showed diurnal visitation patterns to the surveyed reefs, with cleaning station visits peaking between 9:00 and 14:00, which overlapped with survey times (Venables et al. 2020b). However, research dives only covered a small proportion of the day and a small fraction of the total habitat available to these rays, with sightings being limited by the survey path and underwater visibility. Sightings-independent telemetry methods have frequently shown that visual surveys miss a proportion of the individuals that are present (MacNeil et al. 2008; Cagua et al. 2015). While our survey paths covered the known reef cleaning stations at each site, mobulid rays could have been present in the general area, but not visible to the observer. However, given that the survey method remained consistent, we are confident that these trends are reflective of the number of individuals visiting these sites over the course of the study period.

Tourism pressure can impact manta ray behaviour, and sustained pressure has the potential to result in long-term shifts in habitat use (Venables et al. 2016a; Murray et al. 2019). Dive tourism in Mozambique is a growing industry, and Praia do Tofo has become one of the best-known dive destinations in Mozambique (Tibirica et al. 2011; Venables et al. 2016b). Marine wildlife tourism activities have increased throughout the 20-year study period. Dive tourism as a potential driver of a change in manta ray habitat use was not investigated here but should be considered for future studies.

For devil rays, the raw trend model showed an 81.3% decline in sightings over the study period. Much of this decline occurred in the first half of the study (2003–2011), with sightings increasing by 143.6% from 2012 to 2023. Models that incorporated environmental predictors did not retain year as a significant predictor and showed a reduced overall decline in devil ray sightings of 36.5%. This indicates that the tested predictors were responsible for approximately half of the observed decline in sightings.

While this decline is much lower in comparison to those observed for reef and oceanic manta rays, it still represents a substantial declining trend in devil ray sightings over the past two decades.

### Environmental predictors

While temporal variables were the primary influence on sightings of reef and oceanic manta rays, the models also revealed interesting relationships with other predictors. Dive site was significant for both manta ray species, indicating preferential site visitation to particular cleaning station reefs, something which was also revealed by acoustic telemetry studies on reef manta rays in the region (Venables et al. 2020b). Current strength influenced reef manta ray sightings, with increased sightings during medium currents. When cleaning, manta rays typically hover above the reef to allow cleaner fishes to approach them; medium currents may be more energy efficient by reducing the effort required to hover over the reef, whereas light or strong currents may require active swimming to remain in the optimal posture and position for cleaning (Rohner et al. 2013; Murie et al. 2020). Sightings of reef manta rays were reduced when chl-a levels increased. This may be due to a reduction in visibility in the greener water, although visibility was not found to be a significant predictor. Here, we are using chl-a as a proxy for productivity; therefore, this species may spend more time feeding and less time at cleaning stations during times of increased prey availability, hence the lower sightings at our survey reefs. Oceanic manta ray sightings were higher when no visible zooplankton was observed, which may also be related to feeding activities. When zooplankton is available in higher concentrations, it is expected that filter feeders prioritise targeting prey at feeding sites over visiting cleaning stations (Armstrong et al. 2016). Salinity levels had opposing effects on reef and oceanic manta rays with higher reef manta ray sightings with increased salinity, but lower oceanic manta ray sightings. Increased salinity was related to an increased abundance of mobula rays in the Cocos Island National Park off Costa Rica, but had no significant effect on the occurrence of manta rays (Saltzman and White 2023). While the link between salinity and manta ray sightings in our study remains unclear, it is worth considering in future investigations into the environmental drivers of

these species. In our previous assessment, water temperature was found to influence reef manta ray sightings, with this species seeming to avoid colder water, between 18 and 21 °C, while no trend was apparent for oceanic manta rays (Rohner et al. 2013). Water temperature has also been found to influence manta ray sightings in other locations (Jaine et al. 2012; Peel et al. 2019; Saltzman and White 2023); however, it was not a significant predictor of sightings of either species in this study. While it is unclear exactly why the trend seen in our previous study did not persist, it is likely that the additional 12 years of data included in our updated models have introduced variability that masked the previously observed relationship. The waters off Praia do Tofo experience a broad temperature range, with high daily temperature variability on survey reefs (Rohner 2013). Given the high-temperature tolerance of reef and oceanic manta rays (e.g. Lassaue et al. 2020; Stewart et al. 2019), it is feasible that other environmental factors are stronger predictors of sightings in this region. Alternatively, the increased number of surveys with no sightings of reef manta rays since our previous assessment may have influenced the relationship with temperature to mask their absence in cool temperatures.

By contrast, water temperature was a significant predictor for devil ray sightings, with sightings decreasing as water temperature increased. A similar trend was observed in sightings of *Mobula* spp., in the waters surrounding Cocos Island off Costa Rica (Saltzman and White 2023). In Mozambique, this may represent a seasonal trend, with increased sightings in winter with colder water temperatures, or may signify an increase in devil rays during upwelling events, which occur throughout the year and create daily amplitudes of up to 7.5 °C (Rohner 2013). Devil ray sightings increased with increasing underwater visibility, which is likely because devil rays have a higher probability of being sighted in clearer water; they often swim high in the water column, typically above observers that are swimming slightly above the reef. Current direction, surface weather conditions and swell were all identified as significant predictors of devil ray sightings; however, the relationships here were less clear. Among the study sites, two locations had higher predicted devil ray sightings—Office Reef, in the far north of the study area, and Manta Reef, one of the most southerly sites. These reefs have shallower average depths compared to other survey sites



(18–24 m, compared to 24–28 m); thus, observers may have increased visibility up into the water column, which is where devil rays are most commonly observed.

#### Implications for conservation and management recommendations

In a previous assessment, we reported an 88% decline in reef manta ray sightings, with no clear trend for oceanic manta ray sightings within the same study area, over a shorter time frame of 2003–2011 (Rohner et al. 2013). After increasing the time-series data to 20 years and the number of surveys from 855 to 4604, we show a continuing decline in reef manta ray sightings and reveal a concurrent decline in oceanic manta ray sightings, particularly through the most recent decade. The lack of observable trend for oceanic manta rays in the earlier assessment was influenced by a short-lived increase in sightings in 2009, underlining the need for long-term observations to assess trends in long-lived species (Rohner et al. 2022) and the necessity for re-assessments as datasets are extended. While the initial study did not assess trends in devil ray sightings, we find here that the tested predictors were responsible for approximately half of the > 80% observed decline in sightings in raw trend models.

The Inhambane Province has long been recognised as a global hotspot for reef and oceanic manta rays (Marshall 2008; Marshall et al. 2011; Venables et al. 2020b). However, the continued decline in sightings—and an indication that external, and likely anthropogenic, factors are driving these declines—are major causes for concern. Mozambique is a signatory to both CMS, on which all mobulid species are recommended for protection, and CITES, which promotes sustainable international trade. While international trade in mobulid products has not specifically been identified as a driver of contemporary catches in Mozambique, it is a major driver in other locations and globally (Lawson et al. 2017; Fernando and Stewart 2021). We therefore recommend mobulids are listed on CITES Appendix I to fully prohibit commercial trade of these species and increase protection on an international level. While regional catch data are required to confirm that mobulid stocks are being rapidly depleted by fisheries in Mozambique, we argue that precautionary management is urgently required for these

species. Reducing threats such as targeted fishing pressure and incidental capture in non-selective fishing gears should be a priority. The implementation of legislative protection for mobulid species found in Mozambican waters under Regulamento da Pesca Marítima law (Boletim da República Decreto No. 89 Série Número 192 2020) is an excellent first step, prohibiting the capture, retention, and sale of listed species. Adequate enforcement, however, is crucial for such regulations to have tangible conservation impacts. This poses a challenge due to Mozambique's vast and remote coastline, and lack of infrastructure and resources to ensure such enforcement outside of major fishing hubs. As a precautionary measure, it is also important that marine wildlife tourism activities, such as SCUBA diving and 'ocean safaris', are carried out to international best practice standards. Adherence to codes of conduct for megafauna interactions and minimising the numbers of boats and divers at cleaning station sites are recommended to reduce potential disturbance to mobulids.

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**Data availability** Datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

#### Declarations

**Ethics approval and consent to participate** Fieldwork involved visual observations and photographic identification and was carried out with the permission of Instituto Oceanográfico de Moçambique (InOM). No animals were caught, handled, or removed from their natural habitat. All research was conducted in accordance with the requirements of the Marine Megafauna Foundation Animal Ethics policy.

**Conflict of interest** The authors declare no competing interests.

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