Steep declines in sightings of manta rays and devilrays (Mobulidae) in southern Mozambique

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Abstract

Mobulid rays are one of the most vulnerable chondrichthyan groups due to their low population growth rates and high susceptibility to fisheries. While estimates of human-induced mortality are lacking, sighting trend data can provide an index of their status. We recorded underwater sightings data of *Mobula alfredi*, *M. birostris* and *M. kuhlii* over a 14-year period in southern Mozambique. Generalised linear models were used to standardise sightings and adjust for influences other than time. Standardised sightings of the three species, individually, declined by >90%. Declines in sightings were driven primarily by a rapid decrease between 2003–2007, although the declines continued to 2016. While environmental variables did influence sightings, they did not explain this steep decline over time. Increasing mortality from fisheries is likely to have played a significant role in the declining sightings of these vulnerable species.

Key words: Elasmobranch, Extinction, GLM, Conservation, Time-series, Gillnet

Running head: Mobulid sightings trends
Introduction

Anthropogenic activities have impacted marine species faster than those found on land (Myers & Worm, 2003; McCauley et al., 2015). Shark and ray populations have, in particular, suffered pronounced declines (Dulvy et al., 2014a). Many chondrichthyan species are relatively large and long-lived, with a density-dependent rate of population increase, leaving them particularly vulnerable to human-induced pressures (Musick et al., 2000; Dulvy et al., 2014a). One in four chondrichthyans is now threatened with extinction, largely due to over-exploitation by directed fisheries and high incidental catches in other fisheries (Dulvy et al., 2014a).

Mobulid rays are a group of eight species, all medium to large pelagic rays feeding on zooplankton and small nekton that, as a genus, have a global distribution in tropical and warm-temperate oceans (Couturier et al., 2012; Last et al., 2016). Female mobulids generally reach maturity at a large size, do not immediately reproduce once reaching maturity, have a long gestation period and usually produce a single large offspring, and have a resting period between pregnancies (Rambahiniarison et al. submitted; Notarbartolo-Di-Sciara, 1988; Marshall & Bennett, 2010). This reproductive strategy results in some of the lowest population growth rates found among elasmobranchs (Dulvy et al., 2014b; Pardo et al., 2016). Mobulid rays are among the most vulnerable to over-exploitation of all marine species, and the human threat to these species has become increasingly obvious (Dulvy et al., 2014b; Croll et al., 2015; Lawson et al., 2017). All mobulids have been listed on CITES Appendix II and CMS Appendices I & II between 2013 and 2016.
Mobulids are caught in directed harpoon, hook and gillnet fisheries (Camhi et al., 2009; Acebes & Tull, 2016), with the largest targeted fisheries reported from Sri Lanka, Indonesia, India and the Philippines (Couturier et al., 2012; Croll et al., 2015). Target fisheries are often driven by the export of gill rakers, which are valuable in some markets, fetching USD$130 for *Mobula kuhlii* and ~USD$350 for *M. birostris* in China (Zeng et al., 2016). Mobulids are also taken as bycatch, particularly in driftnets and purse-seine nets targeting tuna (White et al., 2006; Hall & Roman, 2013; Francis & Jones, 2016). Quantifying these catches and assessing their sustainability has been hampered by a lack of species-specific landing data and poor monitoring of bycatch (White et al., 2006; Lack & Sant, 2009; Couturier et al., 2012).

Anecdotal evidence suggests that a decline in mobulid sightings has occurred in some areas in response to increased mobulid fisheries catches (Ward-Paige, Davis & Worm, 2013). Manta ray gill rakers in Chinese markets have decreased from 30% to 11% occupancy among mobulid gill rakers over the past years, suggesting resource exhaustion, although this may also be a result of better protection (Zeng et al., 2016).

In the absence of mortality and effort estimates from fisheries, sighting indices of free-swimming animals are also useful in conservation assessment, although biases in survey effort need to be considered when interpreting these results (Witt et al., 2012; Rohner et al., 2013).

The Inhambane province in southern Mozambique has been an important site for manta ray research over the past decade (Marshall, Compagno & Bennett, 2009; Marshall, Dudgeon & Bennett, 2011), as it contains Africa’s largest populations of both reef manta rays *M. alfredi* (Krefft, 1868) and giant manta rays *M. birostris* (Walbaum, 1792). Anecdotal evidence suggests that manta rays are rarely seen outside this hotspot area in the Inhambane province.
The area has recently become a popular destination for dive tourists (Tibiriçá et al., 2011; Venables et al., 2017).

The focal species in this study are Kuhl’s devilray *Mobula kuhlii* (Müller & Henle 1841), a relatively small inshore species measuring up to ~1.35 m disc width (DW; White et al., 2006; Last et al., 2016), *M. alfredi* which grow to ~5.5 m DW, and the largest mobulid species, *M. birostris*, growing to ~7.0 m DW (Marshall, Compagno & Bennett, 2009; Last et al., 2016). Both manta ray species are listed as “Vulnerable” on the IUCN Red List, while *M. kuhlii* is “Data Deficient” (Bizzarro et al., 2009; Marshall et al., 2011a,b). Manta rays in southern Mozambique are usually seen by divers at cleaning stations on rocky reefs, which are also important sites for social behaviours (Marshall & Bennett, 2010; Marshall, Dudgeon & Bennett, 2011). Manta rays spend up to 8 h day⁻¹ at these sites with a mean of 119 min day⁻¹ (Marshall, 2008). Devilrays are, in contrast, most often seen swimming in the water column and encounter times with divers are generally short, although they have also recently been seen cleaning for extended periods at other locations (Murie & Marshall, 2016). Until recently, the two species of manta ray were assigned to the genus *Manta*, but recent DNA analyses indicate that this genus should not be considered separate to *Mobula* (Last et al., 2016). Following this taxonomic revision, but acknowledging the broad use of manta rays as common names, we refer to the family or all three species here as “mobulids”, to *M. kuhlii* as “devilrays”, and to the reef manta and giant manta ray taken together as “manta rays” throughout this work.

Mobulids in Mozambique are caught offshore in tuna purse-seine nets (Romanov, 2002; Amande et al., 2008; Poisson et al., 2014) and in gillnets set along the coast (Fig. 1). Gillnet
use has been increasing in Mozambique since the cessation of conflict in 1992 (Rohner et al. submitted; WWF Eastern African Marine Ecoregion, 2004), and nets have been actively distributed by fisheries officials in some areas to move fishing effort away from inshore nursery habitats (Leeney, 2017). Fisheries-related mortalities of reef manta rays have been previously estimated at 20–50 individuals per year in coastal fisheries in the Inhambane province (Marshall, Dudgeon & Bennett, 2011), and there are extensive but unquantified catches of devilrays (Fig. 1).

Here, we assessed sightings trends of devilrays and manta rays in the Inhambane province, in southern Mozambique, over a 14-year period. We have previously assessed sightings trends of manta rays in southern Mozambique over a shorter time-frame (Rohner et al., 2013), but the perception of continued declines prompted a re-analysis and expansion of scope. We lengthened the time-series of observations from 9 to 14 years, increasing the number of survey dives available for analysis from 855 to 2,524, and have included M. kuhlii sightings for the first time. Mobulids are largely planktivores (Rohner et al. in press; Couturier et al., 2012), and their sightings are likely to be influenced by environmental factors that can influence both their movements and food sources on a short time-scale (Richardson, 2008). We thus standardised sightings with generalised linear models (GLM) to account for environmentally-driven variability in sightings. Sightings of all three mobulid species declined steeply, most likely because of unsustainable catches.

Methods

Surveys
Sighting data of *Mobula kuhlii*, *M. birostris* and *M. alfredi* were collected during research dives in the Inhambane province in the south of Mozambique. A complete dataset was available for analysis from 2,524 survey dives conducted over 14 years between 2003 and 2016. The majority of dives (90%, n = 2,262) were conducted from Praia do Tofo (23.85° S, 35.54°E), with an additional 9% of dives (n = 221) from the Bazaruto Archipelago, and 41 dives from elsewhere in the Inhambane region. Effort was uneven among years, with fewer surveys conducted early in the study (Sup. Fig. 1). We partially accounted for this temporal bias by applying a Generalised Linear Model (GLM), and tested the annual number of surveys as a predictor in the models, though it was not retained in the final models (see below). Dive sites in the Praia do Tofo area, with the majority of surveys, were spread over a ~40 km length of coast, with additional dives at locations ~200 km north (Bazaruto) and ~90 km south (Zâvora). Dives lasted between 2–78 minutes (mean ± sd = 40.5 ± 8.6 min), with 97% of surveys lasting between 20–60 min. Each manta ray was identified from the natural markings on their ventral side (Marshall, Dudgeon & Bennett, 2011; Marshall & Pierce, 2012), and individually counted, while the number of devilrays was counted or sometimes estimated for the largest schools. Raw sightings data were plotted as the number of individuals per survey over time, and also as a binomial presence or absence plot, with a loess smoother (Cleveland, Grosse & Shyu, 1992), to examine the temporal trend. Using the individual identification data from *M. alfredi* and *M. birostris*, respectively, we also used two additional indices: (1) the number of individual rays sighted per year, by species; and (2) a simple residency index, measured as the number of manta ray encounters (where an individual was identified) divided by the number of unique individuals, per year. For the latter, a value of one would mean that each manta ray was seen only once in that year. We plotted those indices with a gam smoother trendline and confidence intervals (CI) in grey, which mean that if a horizontal line can be drawn through
the CI the relationship is not significant, and also added a linear regression to calculate
significance. Field work involved visual observations and photographic identification and was
carried out under Mozambique’s Administração Nacional das Áreas de Conservação permit
number 13 for work within the Bazaruto Archipelago National Park. No permit was required
for work outside the park. No animals were restrained, captured or killed.

Sightings were standardised by including a suite of predictor variables (Table 1) in a GLM
constructed in R (R Development Core Team, 2008). Three temporal predictors were used:
year of observation, to test for a long-term trend in sightings; day of year, to adjust for
seasonality; and time of day, to investigate diel variation. The number of surveys per year was
included to account for variation in the annual sample size over the 14-year study. While
multiple dive sites were surveyed over this period, disparity in effort led us to categorise dive
sites as either ‘deep’ (22-32 m mean depth, most of which featured manta cleaning stations)
or ‘shallow’ reefs (10 - 18 m mean depth). Moon illumination data were downloaded from
NASA’s Horizon website (http://ssd.jpl.nasa.gov/horizons.cgi) for the survey area, as moon
phase can influence the presence or behaviour of marine fishes (Agenbag et al., 2003; Jaine
et al., 2012; Rohner et al., 2013). Observers recorded weather conditions in four categories
(sunny, partial overcast (0–50% cloud cover), overcast (51–100% cloud cover), or raining) to
test for atmospheric influences on sightings, and surface swell to adjust for surface water
conditions. Current direction and strength can influence the cleaning behaviour of mantas
(Rohner et al., 2013) and were included in the models. The sightability of animals at these
sites can be influenced by underwater visibility (Williams et al., 2017), so observers estimated
horizontal visibility on each dive. Water temperature can influence mobulid sightings (Jaine
et al., 2012) so we measured the temperature at depth using dive computers and downloaded
8-day mean sea surface temperature data at 4 km resolution from off Praia do Tofo from NASA’s MODIS Aqua satellite (http://modis.gsfc.nasa.gov) using the R package ‘xtractomatic’. We also measured water temperatures every 30 min with a logger (HoboWare) at depth over a 19-month period from three reefs off Praia do Tofo. We use this time-series to illustrate the high variability in temperature at this site, and calculated daily amplitude to show frequent cold water intrusions throughout the year (Sup. Fig. 2). As a general index for food availability, observers recorded plankton densities in four categories: none, when no plankton was visible; green, when phytoplankton was visible; some zooplankton, when the zooplankton density was low; and dense zooplankton, when zooplankton density was high. Surface chlorophyll \(a\) concentration (Chl-\(a\)) data were extracted for off Praia do Tofo at an 8-day mean and 4 km resolution from NASA’s MODIS Aqua satellite. Minor interpolation was applied for missing dates (0.2 % for SST and 5.8% for Chl-\(a\)). Tidal range and time from high tide can affect sightings of manta rays (Jaine et al., 2012; Rohner et al., 2013), so these were also included as potential predictors. Raw data are available in supplementary table 1.

**Modelling**

Negative binomial generalised linear models (GLM) with natural splines were constructed in R, with sightings as the response and the suite of variables listed above as predictors. A stepwise AIC function was used to evaluate the best predictors in each model using a penalty factor (\(k\)) of 2. A dropterm function with a \(\chi^2\)-test was also used to select significant predictors for the final model (Venables & Ripley, 2002). The deviance explained for each predictor was calculated from an ANOVA of the final model. In the model output figures, the \(y\)-axis is a relative scale, so that a \(y\)-value of zero is the mean effect of the adjusted predictor on the response, a positive \(y\)-value indicates a positive effect on the response, and a negative \(y\)-
value indicates a negative effect on the response. If a horizontal line can be placed between
the 95% confidence limits (dotted lines), this implies that the relationship between the
response and the predictor is not significant. These lines tend to diverge near the extremes
of the range for continuous predictors because of fewer observations. To assess the trends in
sightings over time, we fitted a line through annual model estimates based on modal
(categorical predictors) and median (continuous predictors) input values. A negative
exponential fitted best for all species. We then estimated the percentage change from the
first to last years from these lines of best fit and used an ANOVA to calculate significance.

Results

Raw sightings trends

Mobula kuhlii had the highest mean sightings (1.31 ± 8.4 SD individuals per survey) and largest
groups, with up to 200 individuals seen on a dive. A mean of 1.1 (± 2.75 SD) M. alfredi were
seen per survey, with a maximum of 29. A mean of 0.2 (± 0.75 SD) M. birostris were observed,
with a maximum of 13 individuals on a single dive. Sightings were variable but declined over
time in all three species, with the most pronounced decline in M. alfredi (Fig. 2). In addition
to raw sightings numbers, binary presence also declined for all three species (Fig. 2). For
example, M. alfredi were seen on at least half of all dives until late 2007, but from late 2011
to 2016 they were seen on less than a quarter of all dives. Mobula kuhlii presence was
recorded on less than half the dives over the study, but their group size was often large which
increased their total sighting numbers.

Overall model
The GLMs explained 39.6% of the total variance for *M. alfredi* sightings, 25.8% for *M. kuhlii* and 20.1% for *M. birostris*. The final GLM for *M. kuhlii* retained 10 predictors including year, day of year, underwater visibility, current strength and direction, reef depth, underwater temperature, plankton observations, weather, and surface swell (Fig. 3). Year was the most significant predictor (p<0.0001) for *M. kuhlii* sightings, accounting for 12.7% of the variance. Underwater temperature was also important, with a high significance (p<0.0001), explaining 2.1% of the variance (Table 2).

The final GLM for *M. birostris* retained nine predictors including year, day of year, time of day, underwater visibility, current strength and direction, reef depth, moon illumination, and SST (Fig. 4). Year was the most significant predictor (p<0.0001), accounting for 9.1% of the total variance, while day of year was also significant (p<0.0001) and accounted for 4.9% of the variance (Table 2).

The final GLM for *M. alfredi* retained nine predictors including year, day of year, time of day, underwater visibility, current direction, underwater temperature, Chl-$\alpha$ concentration, plankton observations, and the tidal range (Fig. 5). Year was the most significant predictor (p<0.0001), accounting for 33.9% of the total variance. Current direction, underwater visibility, and day of year were also highly significant (p<0.0001) (Table 2).

**Temporal trends in sightings**

Predictive models based on the final GLMs showed that adjusted sightings declined significantly over time for all species. Modelled sightings of *M. kuhlii* declined by 98.8%, *M. birostris* by 94.2%, and *M. alfredi* by 98% between 2003 and 2016. *Mobula birostris* were seen...
more frequently in the middle of the year (Fig. 4), the cooler months in Mozambique, while
*M. alfredi* were seen more at the start and end of the year (Fig. 5). *Mobula kuhlii* had a low
peak in sightings around ~September (Fig. 3). The time of surveys was significant for manta
rays, with fewer sightings recorded in afternoons, but had no effect on *M. kuhlii* sightings.

Environmental influence on sightings

Temporal factors were the most influential in all three GLMs, but sightings were also affected
by environmental parameters. Underwater visibility had varied influence on sightings among
the species, with more devilrays seen in better visibility (Fig. 3) and more manta rays seen in
lower visibility (Figs. 4,5). Similarly, fewer manta rays were seen in southerly or “other”
current directions (Figs. 4,5), while “other” currents yielded the highest sightings of devilrays
(Fig. 3). Warmer water at depth correlated with lower devilray sightings, while this predictor
was significant but ambiguous in its effect for *M. alfredi*. Water temperature at depth had a
seasonal signal, but was also characterised by numerous cold water intrusions throughout the
year (Sup. Fig. 2). *Mobula kuhlii* and *M. birostris* were both sighted more frequently on deep
reefs. More *M. alfredi* were seen in either green water (i.e. high concentrations of
phytoplankton) or when a high density of zooplankton was recorded, but these parameters
had the opposite influence on devilray sightings. Surface predictors such as weather and swell
were only significant for *M. kuhlii* sightings, with no clear trend (Fig. 3). Sea surface
temperature was retained for *M. birostris*, with an increasing trend for warmer SST. However,
underwater temperature was not significant and was not retained (Fig. 4). Moon illumination
was significant for *M. birostris* but its relationship with sightings was ambiguous. Similarly,
Chl-α concentration was retained in the *M. alfredi* model, but was not significant and without
a clear trend (Fig. 5). Fewer *M. alfredi* were sighted when the tidal range was higher.
Residency influences on sightings

The residency index (sightings/individuals) decreased for M. alfredi over the course of the study, from a maximum of 1.47 in 2004 to a minimum of 1.0 in 2016 (lm F = 16.5, p = 0.0016; Fig. 6a). The number of individual M. alfredi identified per year also broadly decreased over time, with a maximum of 208 in 2004 and a minimum of 19 in 2016 (Fig. 6b), although this relationship was only marginally significant (lm F = 4.7, p = 0.05). Mobula birostris had no clear trend in either the residency index (lm F = 0.18, p = 0.68) or the number of individuals identified each year (lm F = 0.16, p = 0.69; Fig. 6c,d).

Discussion

Sightings of all three mobulid species declined precipitously over the 14-year study period, with modelled sightings of devilrays declining by 98.8%, reef manta rays by 98%, and giant manta rays by 94.2%. The downward trends present in the raw sightings data persisted once a suite of temporal and environmental variables was accounted for by the GLMs. Short-term environmental fluctuations did not explain this longer-term decline. Models explained between 20–40% of the variation in sightings, indicating that while environmental predictors were important, other parameters – not considered here – also played a significant role. The most influential predictor in all three species was the year of observation, underlining the clear declining temporal trend in sightings. This decline is alarming for mobulids in south-eastern Africa because the Inhambane province hosts Africa’s largest identified populations of manta rays (Marshall, Dudgeon & Bennett, 2011) and is the only known hotspot for these species in the region.
We think that the most likely explanation for this decline in sightings is an increase in mortalities in fisheries. The use of large-mesh gillnets, often extending from near the beach to ~500 m offshore, has significantly increased off the Inhambane coast in recent years (Rohner et al. in review). 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. Considering the small population size for *Mobula alfredi* (~800 individuals; Marshall, Dudgeon & Bennett, 2011) and *M. birostris* (~600 individuals; Marshall, 2008), and the low population growth rates of manta rays and devilrays (Dulvy et al., 2014b), even a small number of individuals taken per year could conceivably result in a steep population decline. While increasing gillnet use may be the primary threat, the lack of regional data on mobulid catches in offshore fisheries is also a concern.

Manta rays are long-distance swimmers and deep-divers (Jaine et al., 2014; Braun et al., 2015; Stewart et al., 2016), although their consistent cleaning behaviour does makes them easier to survey underwater than most other large marine species. However, our field survey data have biases that must be acknowledged. Research dives only covered a small proportion of the day and a small fraction of the total habitat available to these rays. Sightings-independent methods, such as acoustic or satellite telemetry, have frequently shown that visual surveys miss a proportion of the individuals that are present (MacNeil et al., 2008; Cagua et al., 2015). It is also possible that over the 14-year survey period, mobulids have shifted to using different reefs along the coast, or deeper reefs outside the depth limits of our surveys. The high significance in the decline over time in our basic residency index for *M. alfredi* supports this hypothesis. Potential drivers of a change in habitat use, such as marine tourism (Venables et
al., 2016) were not investigated here, but should be considered for future studies. Along with a decline in residency, the number of individual _M. alfredi_ identified per year also decreased, suggesting that mortality or permanent emigration is an important driver. We did not find a clear trend in the residency of _M. birostris_.

While temporal variables were the primary influence on sightings of all species, the GLMs also revealed some interesting relationships with other predictors. Lower visibility was associated with higher manta ray sightings, but fewer devilray sightings. This is likely because devilrays have a higher probability of being sighted in clearer water, as they often swim high in the water column. This is similar to results on turtle sightings on the same reef systems, as turtles need to swim to the surface to breathe (Williams et al., 2017). Manta rays, in contrast, are generally associated with cleaning stations that are specifically surveyed by the research team, partially negating the influence of visibility. More devilrays were seen in cooler water temperatures at depth, but during the warmer months at the start and end of the year. This apparent disparity could in fact indicate that devilray presence is associated with upwelling events, which occur throughout the year and create daily amplitudes of up to 11°C (Sup. Fig. 2). Sightings of _M. alfredi_ were lower in cold water (<21°C), but plateaued in warmer water. This is a similar result to that demonstrated for _M. alfredi_ in Australia, which had a pronounced peak at ~22°C when foraging and a general increase in sightings with warmer water (Jaine et al., 2012). The lack of a relationship between water temperature and _M. birostris_ sightings may reflect their broad temperature tolerance, with _M. birostris_ extending further into temperate areas than _M. alfredi_ (Marshall, Compagno & Bennett, 2009). _Mobula kuhlii_ and _M. birostris_ were seen more on deep reefs, as expected for all three species.
Previously, we reported an 88% decline in *M. alfredi* sightings and no clear trend for *M. birostris* sightings within the same study area over a shorter time-frame (Rohner et al., 2013). Here, we increased our previous time-series data for manta rays by 5 years (2003–2011 previously vs. 2003–2016 here) and by nearly tripling the number of survey dives (855 vs. 2,524). Some relationships between manta ray sightings and predictors remained stable, indicating that these are likely to be reliable associations. For example, *M. alfredi* were consistently seen more when water was >21°C, and during the warmer months at the start and end of the year. The decreasing trend of *M. alfredi* sightings continued over time, resulting in a total decline going from 88% to 98% over the longer time-series. *Mobula birostris* sightings had no significant trend between 2003–2011, but this enlarged data-series shows a steep decline over this longer study period. The lack of observable trend 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 mobulid sightings.

Mozambique is a signatory to both CMS, on which all mobulids are recommended for protection, and CITES which promotes sustainable international trade. While international trade in mobulid products is not known to be a driver of contemporary catches in Mozambique, it is a major driver globally (Lawson et al., 2017). Although improved data on catches are required to confirm our hypothesis that mobulid stocks are being rapidly depleted by fisheries, we argue that precautionary management is required for these species. There is a strong economic argument (Tibiriçá et al., 2011; Venables et al., 2017) and conservation imperative to implement legislative protection for mobulids in Mozambique.

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Table 1. Predictors used in the GLMs for *Mobula kuhlii*, *M. alfredi* and *M. birostris*, with an explanation, the type of predictor, the units and mean ± standard deviation.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Explanation</th>
<th>Type</th>
<th>Units</th>
<th>Mean ± SD</th>
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<tr>
<td>Year</td>
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<td>Continuous</td>
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<td></td>
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<tr>
<td>Day of year</td>
<td>Day of observation</td>
<td>Continuous</td>
<td>d</td>
<td></td>
</tr>
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<td>Time of day</td>
<td>Time of day</td>
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<tr>
<td>Surveys per year</td>
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<td>Type of reef</td>
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<td>m</td>
<td>Shallow or deep</td>
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<tr>
<td>Weather conditions</td>
<td>Weather conditions at the surface</td>
<td>Categorical</td>
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<tr>
<td>Moon illumination</td>
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<td>Proportion</td>
<td>0.5 ± 0.36</td>
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<tr>
<td>Underwater temperature</td>
<td>Temperature at depth</td>
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<td>°C</td>
<td>24.3 ± 2.15</td>
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<td>SST</td>
<td>Satellite-derived 8-d mean surface temperature</td>
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<td>°C</td>
<td>26.3 ± 1.77</td>
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<td>Chl-a concentration</td>
<td>Satellite-derived 8-d mean chlorophyll a concentration</td>
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<td>mg m⁻³</td>
<td>0.3 ± 0.39</td>
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<td>Plankton observations</td>
<td>Visual assessment of plankton at depth</td>
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</tr>
<tr>
<td>Current direction</td>
<td>Dominant direction of current at depth</td>
<td>Categorical</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Current strength</td>
<td>Current strength at depth</td>
<td>Categorical</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface swell</td>
<td>Ocean swell at the surface</td>
<td>Categorical</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tidal range</td>
<td>Difference between high and low tide</td>
<td>Continuous</td>
<td>m</td>
<td>2.4 ± 0.39</td>
</tr>
<tr>
<td>Time from high tide</td>
<td>Time from the nearest high tide</td>
<td>Continuous</td>
<td>min</td>
<td>52.9 ± 222.3</td>
</tr>
</tbody>
</table>
Table 2. Model outputs showing the variance explained and the p-values for each predictor retained in the final GLMs for *Mobula kuhlii*, *M. birostris* and *M. alfredi*.

<table>
<thead>
<tr>
<th>Predictor</th>
<th><em>M. kuhlii</em> Variance (%)</th>
<th><em>M. birostris</em> Variance (%)</th>
<th><em>M. alfredi</em> Variance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>12.7</td>
<td>9.1</td>
<td>33.9</td>
</tr>
<tr>
<td>Day of year</td>
<td>0.9</td>
<td>4.9</td>
<td>1.0</td>
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<tr>
<td>Underwater visibility</td>
<td>1.4</td>
<td>0.6</td>
<td>1.1</td>
</tr>
<tr>
<td>Current direction</td>
<td>1.0</td>
<td>0.9</td>
<td>2.2</td>
</tr>
<tr>
<td>Current strength</td>
<td>1.6</td>
<td>0.6</td>
<td>1.1</td>
</tr>
<tr>
<td>Reef depth</td>
<td>0.5</td>
<td>0.1</td>
<td>0.423935</td>
</tr>
<tr>
<td>Underwater temperature</td>
<td>2.1</td>
<td>&lt;0.0001</td>
<td>0.0</td>
</tr>
<tr>
<td>Plankton observations</td>
<td>1.5</td>
<td>0.005658</td>
<td>0.6</td>
</tr>
<tr>
<td>Weather</td>
<td>1.8</td>
<td>0.001132</td>
<td>0.001182</td>
</tr>
<tr>
<td>Surface swell</td>
<td>2.3</td>
<td>0.001601</td>
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</tr>
<tr>
<td>Time of day</td>
<td>2.0</td>
<td>&lt;0.0001</td>
<td>0.3</td>
</tr>
<tr>
<td>Moon illumination</td>
<td>1.0</td>
<td>0.006055</td>
<td>0.1</td>
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<td>SST</td>
<td>0.9</td>
<td>0.008499</td>
<td>0.4</td>
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<td>Chl-a concentration</td>
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<td></td>
<td>0.26538</td>
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<tr>
<td>Tidal range</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Sum</strong></td>
<td>25.8</td>
<td>20.1</td>
<td>39.6</td>
</tr>
</tbody>
</table>
Fig. 1. Mobulids caught in gillnets in the Inhambane province of Mozambique, with (a) and (b) *M. alfredi* and (c) and (d) *M. kuhlii*. 
**Fig. 2.** Raw, unadjusted sightings (left panels) and binomial presence (right panels) over time for *Mobula kuhlii*, *Manta birostris* and *M. alfredi* (top to bottom).
Figure 3. Model output for the *Mobula kuhlii* GLM, showing the relationship between sightings and all significant predictors. The rug plot along the x-axis shows sampling effort and the dotted lines mark the 95% confidence intervals.
**Figure 4.** Model output for the *Mobula birostris* GLM, showing the relationship between sightings and all significant predictors. The rug plot along the x-axis shows sampling effort and the dotted lines mark the 95% confidence intervals.
Figure 5. Model output for the *Mobula alfredi* GLM, showing the relationship between sightings and all significant predictors. The rug plot along the x-axis shows sampling effort and the dotted lines mark the 95% confidence intervals.
Figure 6. The residency index and number of individuals sighted per year for *M. alfredi* (a,b) and *M. birostris* (c,d) with a gam-based trendline in colour with confidence intervals in grey, and a linear regression line in black.
Supplementary Figure 1: Survey effort showing dives per month between 2003–2016.
Supplementary Figure 2: Underwater temperature plots from three reefs (Manta Reef 22 m depth; Giant’s Castle 28 m; Office Reef 24 m) off Praia do Tofo over a 19-month period, with (A) time-series of temperature readings every 30 min; and (B) amplitude of temperature variation over 24h periods.