Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks

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ABSTRACT: Sightings of planktivorous elasmobranchs at their coastal aggregation sites are often linked to biological, environmental and temporal variables. Many large planktivorous elasmobranchs are also globally threatened species, so it is necessary to try and separate population trends from environmentally driven, short-term fluctuations. We investigated the influence of environmental variables on sightings of 3 species of planktivorous elasmobranchs off Praia do Tofo, Mozambique: the reef manta ray *Manta alfredi*, giant manta ray *M. birostris* and whale shark *Rhincodon typus*. We used 8- (2003 to 2011) and 6-yr (2005 to 2011) logbook data for manta rays and whale sharks, respectively, and constructed a generalised linear model with animal sightings as the response. Predictors included temporal (year, month, time of day), biological (plankton categories), oceanographic (water temperature, time from high tide, current direction and strength and wave height) and celestial (moon illumination) indices. These predictors best fitted reef manta ray sightings, a coastal species with high residency, but less so for the wider-ranging giant manta rays and whale sharks. We found a significant decline in the standardised sightings time series for the reef manta ray (88%) and whale shark (79%), but not for the giant manta ray.

KEY WORDS: GLM · Generalised linear model · Decline · Population trend · Seasonality · Environmental variability · *Manta alfredi* · *Manta birostris* · *Rhincodon typus*

INTRODUCTION

Planktivorous elasmobranchs comprise 14 species of mainly large sharks and rays from 5 genera. This group includes the 3 focal species of this study: the whale shark *Rhincodon typus*, reef manta ray *Manta alfredi* and giant manta ray *M. birostris*. While they differ in some aspects of their ecology, they all feed mainly on zooplankton (Stevens 2007, Nakaya et al. 2008, Sims 2008, Couturier et al. 2012). This reliance on zooplankton strongly links sightings of planktivorous elasmobranchs to environmental variables, as

the distribution and abundance of their prey respond rapidly to environmental changes (Boucher et al. 1987, Richardson 2008). By contrast, sightings of higher trophic level species are likely to be less directly influenced by physical factors due to gradual weakening of the immediate environmental signals with each step up the food chain.

Manta rays and whale sharks have a tendency to aggregate on a periodic or seasonal basis at specific sub-tropical and tropical locations around the world (Stevens 2007, Kashiwagi et al. 2011). Foraging is the main driver behind some of these aggregations (Wilson et al. 2001, Anderson et al. 2011), although manta rays also aggregate at 'cleaning stations' on reefs where small fishes remove parasites and dead tissue, or at inshore areas to mate at specific times of the year (Marshall & Bennett 2010a,b). These predictable aggregations have, in some areas, been targeted by fishers or tourism operators (Pravin 2000, Alava et al. 2002). All 3 species in this study are now globally listed as Vulnerable on the IUCN Red List of Threatened Species following significant declines in catches or sightings that have mainly been attributed to targeted fisheries (Norman 2005, Marshall et al. 2011a,c).

The influence of environmental variability on sightings of these highly mobile fishes can complicate the interpretation of trend data. For instance, a decline in whale shark sightings along the eastern coast of South Africa between 1993 and 1998 (Gifford 2001) was included in the successful proposal for listing the species on Appendix II of the Convention on International Trade in Endangered Species (CITES 2002). However, with the benefit of hindsight, the substantial variability in sighting data from this area in summer months (Cliff et al. 2007) and seasonal changes in their oceanic distribution (Sequeira et al. 2012) makes it difficult to attribute these earlier data to a genuine population decline. Even with comparatively robust datasets, such as for whale sharks at Ningaloo Reef in Australia, scientific consensus on population trends has proven difficult to attain due to differences in the underlying assumptions of the models, insufficient data to test which approach is more robust, and the potential influence of environmental variability (Wilson et al. 2001, Meekan et al. 2006, Bradshaw et al. 2007, 2008, Holmberg et al. 2008, 2009, Sleeman et al. 2010a). In another planktivorous elasmobranch, the basking shark *Cetorhinus maximus*, a steep decline in catches in a target fishery off Achill Island in Ireland between 1947 and 1975 was initially attributed to localised stock depletion (Parker & Stott 1965). Re-analysis of these data in

conjunction with concurrent planktonic copepod abundances at this and other sites led Sims & Reid (2002) to suggest that the decrease may have resulted from a shift in prey, and hence basking shark distribution, rather than strictly due to population decline from fishing (Sims & Reid 2002, Sims 2008).

Previous investigations on how environmental variables affect the sightings of planktivorous elasmobranchs have focused primarily on temperature. Whale shark numbers in pelagic surface waters of the western Indian Ocean have been shown to correlate with sea surface temperature (SST) (Sequeira et al. 2012). In coastal waters, SST and wind speed have also been correlated with whale shark numbers in an aerial survey in the Seychelles (Rowat et al. 2009) and SST, chlorophyll *a* (chl *a*) concentration and bathymetry were important predictors of whale shark and manta ray abundance off Ningaloo Reef, Australia (Sleeman et al. 2007). At Komodo Marine Park, Indonesia, the vast majority of reef manta rays have been recorded in water temperatures from 25 to 28°C and when tidal intensity was highest during new and full moons (Dewar et al. 2008). Further, large-scale factors influencing oceanographic processes, such as the Southern Oscillation Index and wind shear at Ningaloo Reef, or monsoon winds in the Maldives, have been linked to shifts in abundance and distribution of planktivorous elasmobranchs (Wilson et al. 2001, Sleeman et al. 2010a, Anderson et al. 2011). These and other environmental factors thus play a role in explaining sighting trends of manta rays and whale sharks. As planktivorous elasmobranchs are often most threatened at their coastal aggregation sites due to their exposure to shore-based fishing and boating activities, it is important to understand drivers of these aggregations and to determine whether observed fluctuations in sightings correspond to short-term environmental variability or whether they represent long-term trends. Standardising sightings data and taking into account environmental covariates are thus potentially important steps in the conservation management of these species.

Here, we aimed to (1) estimate trends in standardised sightings over time, and (2) define the relationships of environmental, spatial and temporal variables on sightings of reef manta rays, giant manta rays and whale sharks at a coastal aggregation site in southern Mozambique. We used a generalised linear model for each species to determine the relative importance of each environmental variable. We hypo-

thesise that sightings of these plantkivorous fishes are influenced by specific environmental variables and that resident reef manta rays are influenced more strongly by local variables than are transient giant manta rays and whale sharks.

MATERIALS AND METHODS

Location

The study was conducted off Praia do Tofo (23.85° S, 35.54° E), Inhambane Province, southern Mozambique (Fig. 1). All trips were conducted in a 40 km stretch of coastal waters. Manta rays aggregate here mainly for cleaning, and they can spend up to 8 h d^{-1} in this activity (Marshall 2009, van Duinkerken 2010). We used SCUBA to observe them at cleaning stations on reefs primarily at Sites 1 and 2. Less frequently surveyed reefs were combined into 3 'northern reefs', 3 'southern reefs' and 7 'central reefs'. Whale sharks were spotted from boats, with search effort concentrated in coastal waters within 8 km south of Praia do Tofo (Fig. 1).

Logbook data

Manta rays

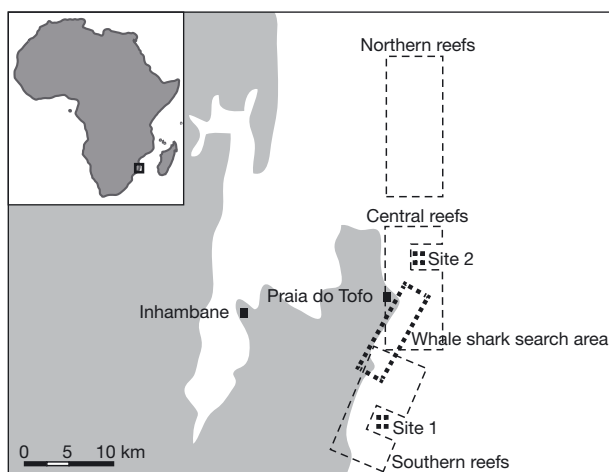Manta ray logbook data were recorded by A. D. Marshall. The dataset comprised 855 dives spanning

Fig. 1. Study location at Praia do Tofo (23.85° S, 35.54° E) in southern Mozambique, indicating the dive sites where manta ray sightings were recorded (thin dashed areas) and the survey area for whale sharks sightings (thick dashed area)

8 yr (May 2003 to April 2011). Sightings of reef and giant manta rays were measured as individuals per dive ('raw sightings' henceforth). In terms of sampling effort, data on dive duration (to standardise each dive over the past 8 yr) was not available. We thus performed a pilot study to assess the influence of dive duration on manta ray sightings. The pilot study included 102 dives over 4 mo in 2012. Dives had a mean duration of 39.3 min and a relatively small SD of 7.67 min. We found no significant relationship between number of manta rays (response variable) and duration of dive (ANOVA; reef manta ray: F = 1.25, p = 0.265; giant manta ray: F = 3.07, p = 0.085). This is likely to be because searches across the reef consistently took the same track over the study period, that manta rays spend most of the day at cleaning stations, and that they are large and conspicuous. Spatial autocorrelation is unlikely to be a major issue for manta rays because the total area of cleaning stations where manta rays congregate and divers searched for them is small (0.5 km^2). Manta rays also show some site fidelity to particular cleaning stations over a period of several hours (Marshall 2009) and it is unlikely that the same manta ray will be seen at different sites on closely spaced dives on the same day. Photographic identification allowed individual animals to be distinguished (Marshall et al. 2011b) and those that were spotted multiple times in the same dive were counted once only. Nine predictors were recorded in the logbook, in addition to sightings of reef and giant manta rays (Table 1).

To account for temporal influences on manta ray sightings, year, month and time of day were recorded for each dive. Dive site was included as a predictor in the manta ray models because manta rays were observed at 5 different sites. This spatial predictor was used to investigate preferences for certain reefs. As a general index of food availability, the major planktonic component during the dive was visually assessed underwater and grouped into 5 categories: (1) zooplankton (i.e. dense visible zooplankton, such as copepods, pteropods or gelatinous zooplankton present in the water), (2) phytoplankton (i.e. visibly green water), (3) no obvious plankton, (4) suspended sediments (i.e. stirred up sediment reducing visibility) and (5) surface slicks (i.e. plankton forming a slick visible only near the surface). As water temperature has previously been correlated with planktivorous elasmobranchs (Dewar et al. 2008, Rowat et al. 2009, Sequeira et al. 2012), we included *in situ* temperature (1°C intervals) recorded at depth on a dive computer. The same computer was

used consistently, which provided the same readings as a temperature recorder (Onset Hobo Pro v2 with ±0.2°C accuracy) in sporadic assessments. To investigate the influence of physical environmental conditions on manta ray behaviour, current direction (N, E, S, W or absent) and strength (absent, light, medium, strong) were assessed underwater visually in relation to the reef. Underwater visibility, visually estimated horizontally at depth in 1 m increments, was included to account for potential sightability effects. Moon phase has been shown to influence biorhythms in other fishes (Colin 1992, Agenbag et al. 2003, Heyman & Kjerfve 2008) and hence moon illumination data were downloaded for the location from NASA's Horizons website (http:// ssd.jpl.nasa.gov/horizons.cgi). Tidal phase and amplitude have also been shown to affect some large planktivores (Dewar et al. 2008) and tide data for Inhambane were obtained from Mobile Geographics (www.mobilegeographics.com).

Whale sharks

Whale shark logbook data were recorded by S. J. Pierce and C. A. Rohner. Observations were made during 720 trips between January 2005 and April 2011. Whale shark numbers were measured as individuals sighted per boat trip ('raw sightings' henceforth). Similar to the methods of Pierce et al. (2010), searches for whale sharks were conducted from 6.5 to 8.2 m long rigid-hull inflatable vessels, often with the addition of a raised spotting chair to enlarge the search area. In terms of sampling effort, most (95%) trips lasted 2 hours (±15 minutes) because of commercial operational constraints. On each trip, we performed a zig-zag search pattern between the beach and 1 km offshore, on the south- and north-ward passes within the 'whale shark area' from Praia do Tofo to 8 km south (Fig. 1). One 'spotter' constantly scanned the surface for whale sharks. 'Site' was not included in the whale shark model because all whale shark observations were made at one site. Spatial autocorrelation is unlikely to be a major issue for whale sharks because the area was small (~8 km^2) and was searched in a consistent way each trip. Individual whale sharks were identified using underwater photographs of the body region immediately posterior to the gills (Arzoumanian et al. 2005). Those that were spotted multiple times in the same trip were counted once only, although there may be some error associated with aggregations of >10 sharks (2.4% of observations)

where not all individuals could be photographed. To account for temporal effects, year, month and time of day were recorded. Moon illumination and tide data were downloaded as described in the manta ray dataset methods. However, as *in situ* observational plankton data were not recorded for this part of the study, we used remotely-sensed chl *a* as a proxy for zooplankton in the model. Despite a possible lag time of zooplankton abundance in response to a phytoplankton bloom (Plourde & Runge 1993, Flagg et al. 1994), phyto- and zooplankton abundance is often correlated (Hutchinson 1967, Richardson & Schoeman 2004, Ware & Thomson 2005) and chl *a* has been used to explain occurrence and movements of marine animals in various studies (Zagaglia et al. 2004, Block et al. 2011), including some on planktivorous elasmobranchs (Sleeman et al. 2007, Graham et al. 2012). Similarly, satellite-derived SST was used in the absence of *in situ* temperature recordings. Chl *a* and SST data at 1 km resolution were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS; http:// modis.gsfc.nasa.gov). These data were composited to 5 d means for the region and extracted for the location off Praia do Tofo (23.893° S, 35.578° E). Due to cloud contamination, minor temporal interpolation was applied (<5%). Surface conditions can affect where and how well whale sharks are visible (Rowat et al. 2009) and we therefore included wave direction and height and wind direction and speed in the initial model. These data were acquired from Buoyweather's hindcast model at 23.85° S, 35.7° E, ~15 km off Praia do Tofo (www.buoyweather.com).

Model

A negative binomial generalised linear model (GLM) with natural splines was constructed using the statistical software R (v.2.13.0; www.r-project. org), with raw sightings set as the response and the aforementioned suite of local variables as predictors (Table 1). Model residuals were visually assessed for normality and homogeneity of variance and an untransformed response with a normal error structure was found to be appropriate. A generalised additive model (GAM; in the mgcv R-package) was used to explore the relationships and define the degrees of freedom (df) to be used for smooth terms in the GLM. This was conservatively set at df = 3 for all smooth terms, unless the GAM plots indicated that df = 4 or 5 more appropriately defined a relationship. The best model was conservatively

Table 1. Predictors used in the generalised linear model for manta rays and whale sharks. RM: reef manta ray *Manta alfredi*; GM: giant manta ray *M. birostris*; WS: whale shark *Rhincodon typus*

Variable	Parameter	Explanation	Type	Units	Mean (±SD)
Manta rays					
Response	RM sightings	Number of individual reef manta rays per dive			2.7 (4)
	GM sightings	Number of individual giant manta rays per dive			0.41 (1.07)
Predictors	Plankton category	Visual assessment of plankton at depth	Categorical	PP = phytoplankton, SS = suspended sediments, ZP = zooplankton, SU = surface slicks, none	
	Moon illumination[a]	Proportion of moon disk illuminated	Continuous	Proportion	0.5 (0.36)
	Water temperature	Water temperature on the reef (20–30 m depth)	Continuous	°C	24.68 (2.17)
	Current direction	Current direction	Categorical	Levels: N, E, S, W or no current	
	Current strength	Current strength	Categorical	Levels: no current, light, medium, strong	
	Tidal range[b]	Difference between high and low tides on the day	Continuous	m	1.87 (0.73)
	Time from high tide[b]	Time difference between observation & closest high tide	Continuous	h	0.66 (3.8)
	Visibility	Estimated underwater visibility	Continuous	m	10.69 (5.36)
	Dive site	Reef or group of reefs	Categorical	Levels: Site 1, Site 2, southern, northern and central reefs	
	Month	Month of observation	Categorical	mo	
	Year	Year of observation	Categorical	yr	
	Time	Time of observation	Continuous	hh	10.22 (1.67)
Whale sharks					
Response	WS sightings	Number of individual whale sharks per trip			2.28 (3.37)
Predictors	Chl *a*[c]	Chl *a* concentration (5 d mean)	Continuous	$mg\,m^{-3}$	0.22 (0.12)
	Moon illumination[a]	Proportion of moon disk illuminated	Continuous	Proportion	0.48 (0.35)
	Wind direction[d]	Wind direction	Continuous	Degrees	115.03 (69.58)
	SST[c]	Sea surface temperature (5 d mean)	Continuous	°C	26.45 (1.83)
	Tidal range[b]	Difference between high and low tides on the day	Continuous	m	1.89 (0.73)
	Time from high tide[b]	Time difference between observation & closest high tide	Continuous	h	−0.38 (4.09)
	Wave direction[d]	Wave direction	Categorical	Levels: N, NE, E, SE, S, SW, W, NW	
	Wave height[d]	Minimal wave height of the day	Continuous	ft	5.18 (1.73)
	Month	Month of observation	Categorical	mo	
	Year	Year of observation	Categorical	yr	
	Time	Time of observation	Continuous	hh	12.52 (0.78)

[a]NASA Horizons, [b]Mobile Geographics, [c]NASA's MODIS satellite, and [d]Buoyweather

assessed using a stepwise Akaike's Information Criterion (AIC) function with the default penalty per parameter set at k = 2 and a dropterm χ^2 function was performed on the AIC-supported model. The significance of each predictor on modelled standardised sightings ('sightings' henceforth) in the final model after the AIC selection process was assessed using a χ^2 test (Venables & Ripley 2002). 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 as a consequence of fewer observations.

Correlations between continuous predictors were assessed with the Pearson method (cut-off = 0.25), and there were no significant correlations between any predictors. Post-hoc Tukey tests were used to perform multiple comparisons among levels of categorical predictors. To estimate % change in megafauna sightings through time, rather than using estimates from the GLM for the last and first yr which are dependent on 2 yr only, we fitted a line through the annual model estimates. Levels of categorical predictors and values of continuous predictors that resulted in highest animal sightings were used for each predictor. A negative exponential fitted best for all species. We then estimated % change from the first to last years from these lines of best fit and used an ANOVA to calculate significance.

RESULTS

Raw sightings

Raw sightings per unit effort were highest for reef manta rays (mean ± SE = 2.7 ± 0.14 ind. dive^{-1}), followed by whale sharks (2.3 ± 0.13 ind. trip^{-1}) and giant manta rays (0.4 ± 0.04 ind. dive^{-1}). Inter-annual variability in raw sightings was high over the study period for all species (Fig. 2). Effort also varied over time, with manta ray searches ranging from 0 to 43 dives mo^{-1} and whale shark searches ranging from 0 to 28 trips mo^{-1} (Fig. 2 insets). We partially accounted for this bias by standardising sightings with a GLM.

Overall model

The final GLM for reef manta rays explained 39.9% of the total variance (Table 2) and had an AIC score of 3226 (model with all predictors: AIC = 3230.0). Ten predictors were retained including year, month, dive site, water temperature, moon illumination, time from high tide, plankton categories, current direction, current strength and time of day (Fig. 3). The final GLM for giant manta rays explained 30.3% of the total variance and had an AIC score of 1260 (model with all predictors: AIC = 1283.5). Five predictors were retained for giant manta rays (Fig. 4), including year, month, dive site, water temperature and moon illumination. The final GLM for whale sharks explained 23.9% of the variance and had an AIC score of 2749.7 (model with all predictors: AIC = 2778.4). Four predictors were retained for whale sharks (Fig. 5), including year, month, time from high tide and wave height. The year factor was the most significant predictor for reef manta rays (χ^2 = 116.0, p < 0.001) and whale sharks (χ^2 = 112.1, p < 0.001), accounting for 24.6 and 13.7% of the variance, respectively. The year factor also explained most (12.2%) of the variance for giant manta rays, while dive site (9.1%) was the most significant predictor (χ^2 = 55.0, p < 0.001). Other strongly significant predictors included water temperature (χ^2 = 29.8, p < 0.001) and dive site (χ^2 = 22.5 p < 0.001) for reef manta rays, month (χ^2 = 42.3, p < 0.001) for giant manta rays, and month (χ^2 = 68.6, p < 0.001) and wave height (χ^2 = 13.9, p = 0.003) for whale sharks (Table 2).

Inter-annual trends

Annual standardised sightings from the predictive model showed a steep decline over time for reef manta rays (88%, ANOVA, *F* = 23.52, p = 0.002; 2003 to 2011) and whale sharks (79%, ANOVA, *F* = 7.39, p = 0.042; 2005 to 2011), while sightings of giant manta rays remained relatively stable (ANOVA, *F* = 1.90, p = 0.21).

Monthly variation

Month was a significant predictor in the GLM for all 3 species. Reef manta ray sightings fluctuated over the year (Fig. 3) but a post-hoc Tukey test showed that sightings were only significantly higher in January/February compared to April. Giant
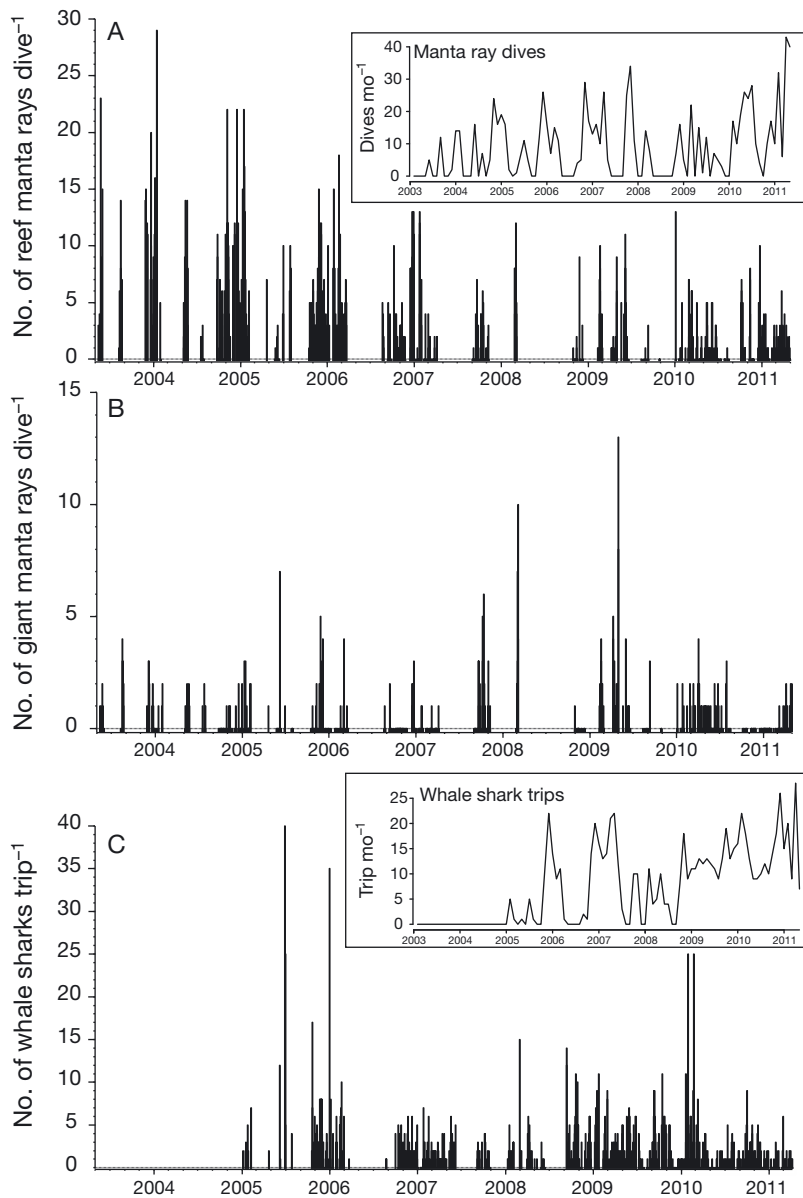
Fig. 2. *Manta alfredi*, *M. birostris* and *Rhincodon typus*. Raw sightings of individual (A) reef manta rays, (B) giant manta rays per dive, and (C) whale sharks per trip, including dives/trips with no sightings (equal to zero). Monthly effort is shown for manta rays (combined) and whale sharks in the insets

manta rays showed a suggestive peak in sightings during April (Fig. 4), which had significantly more sightings than January, February, May, August, October, November and December. Sightings of whale sharks also fluctuated over the course of a year, but showed no clear seasonality. The lower numbers in November and December were significant compared to 5 other months, and the peak in February was significant compared to 4 other months (Fig. 5).

Environmental variables

Water temperature and dive site were strongly significant predictors (χ^2 = 29.2 and 23.2, respectively, both p < 0.001) for reef manta ray sightings. Warmer waters had a positive effect on sightings. More animals were seen at Site 1 than at Site 2, the northern reefs, or southern reefs (Tukey test, p < 0.03). Reef manta rays were sighted less frequently in northward currents compared to the predominant southward currents, and also when currents were absent (p = 0.01 and 0.02, respectively; Fig. 3). Sighting numbers were lower during strong currents, compared to medium currents (p = 0.03), but this was marginally and not significant compared to light and no currents, respectively. More reef manta rays were seen when zooplankton was recorded compared to clear or turbid water conditions (p = 0.003 and 0.03, respectively). The model indicated a suggestive trend towards decreasing sightings at ~09:30 h. Reef manta rays were seen most often during the second quarter of the lunar cycle (~20 to 40% of the moon illuminated). Time from high tide was a significant predictor, but it is difficult to interpret this relationship.

More giant manta rays were observed at Site 1 than at Site 2 and the northern reefs (Tukey test, p = 0.001 and 0.03, respectively; Fig. 4). Water temperature was significant, but had an inconclusive effect on giant manta ray numbers. Sightings were also higher during the first quarter of the lunar cycle (~0 to 25% of the moon illuminated), although this predictor was only marginally significant (χ^2 = 7.8, p = 0.051).

Wave height was the most significant non-temporal predictor for whale shark sightings (χ^2 = 13.9, p = 0.003). More sharks were seen when waves were small (Fig. 5). Sightings were at a consistently lower level when waves were >2 m. Time from high tide was also significant but it was a weak relationship (χ^2 = 7.9, p = 0.048).

Table 2. Percentage of variance explained by the GLM and significance values of a χ^2 test performed on the AIC-supported models, including marginally significant values (p = 0.05–0.1) in *italics*

Predictors	Reef manta ray			Giant manta ray			Whale shark		
	Variance (%)	χ^2	p	Variance (%)	χ^2	p	Variance (%)	χ^2	p
Year	24.62	116.0	<0.001	12.16	62.6	<0.001	13.65	112.1	<0.001
Month	5.60	31.5	0.001	6.30	42.3	<0.001	7.89	68.6	<0.001
Dive site	1.73	23.2	<0.001	9.10	55.0	<0.001	–	–	–
Water temperature	1.68	29.2	<0.001	1.60	11.1	0.026	–	–	–
Moon illumination	1.24	17.8	<0.001	1.13	7.8	*0.051*	–	–	–
Time from high tide	0.21	9.6	0.022	–	–	–	0.80	7.9	0.048
Plankton categories	1.69	16.5	0.003	–	–	–	–	–	–
Current direction	1.76	15.2	0.004	–	–	–	–	–	–
Current strength	0.72	7.3	*0.063*	–	–	–	–	–	–
Time	0.71	10.5	*0.061*	–	–	–	–	–	–
Wave height	–	–	–	–	–	–	1.54	13.9	0.003
Sum	39.9			30.3			23.9		

DISCUSSION

Overall model

The GLM for reef manta rays retained more variables and explained more of the variance than the models for giant manta rays and whale sharks. While in this study, temporal predictors were significant for all 3 species and the spatial (dive site) predictor only used in the manta ray models was significant for both *Manta* species, local environmental variables explained sightings of reef manta rays better than for giant manta rays and whale sharks. This may relate to ecological differences within these planktivorous elasmobranchs in terms of the influence local environmental variables have on their sightings, but also with regards to their respective time spent in our study area and their respective sightability.

Reef manta rays were observed predominantly at known cleaning stations (Marshall et al. 2011b), which are also important sites for social behaviours (Marshall & Bennett 2010b). Although reef manta rays are regularly seen feeding around these reefs, they are not feeding areas per se, but rather multipurpose areas where cleaning is the main behaviour seen by observers. Various cleaning stations are available in the study region and reef manta rays are likely to select favourable environmental conditions to clean in, such as warm water. Reef manta rays are also more strongly resident to the study area than either the giant manta ray or the whale shark (Marshall 2009). Although coastal movements of ~500 km have been recorded in eastern Australia (Couturier et al. 2011), observations from the Hawaiian islands suggest that relatively small geographic distances over deep waters are not traversed by this species

(Deakos et al. 2011). High site residency of reef manta rays has been observed at the current study site (Marshall et al. 2011b) and elsewhere, including Komodo Island, Indonesia (Dewar et al. 2008) and Maui, Hawaii (Deakos et al. 2011). The relatively high site residency of reef manta rays is likely to be a major reason for why local variables were more important drivers of their sightings compared to sightings of giant manta rays and whale sharks.

In contrast to reef manta rays, giant manta rays and whale sharks are wider-ranging species. While the ecology of the giant manta ray remains poorly known, their seasonal appearance in subtropical and temperate areas such as northern New Zealand (Duffy & Abbott 2003) and southern Brazil (Luiz et al. 2009), and their cleaning aggregations at isolated seamounts surrounded by deep oceanic waters (Marshall et al. 2009) suggest that they travel longer distances, tolerate cooler waters, and spend more time in or over deeper water compared to reef manta rays. Considering their offshore movements and less frequent observation by divers off Praia do Tofo, giant manta rays are thus likely to be less influenced by local variables than reef manta rays.

Whale sharks also undertake large-scale oceanic movements (Eckert & Stewart 2001, Hsu et al. 2007, Rowat & Gore 2007, Sleeman et al. 2010b), e.g. one whale shark that was satellite-tagged immediately adjacent to the current study area travelled ~1200 km in 87 days (Brunnschweiler et al. 2009). Individual whale sharks at Praia do Tofo are generally seen for up to a few days before they move elsewhere (S. J. Pierce unpubl.). Similar to giant manta rays, their sightings at coastal sites are therefore likely to be driven more by broader-scale processes than local conditions. Other studies support this hypothesis,
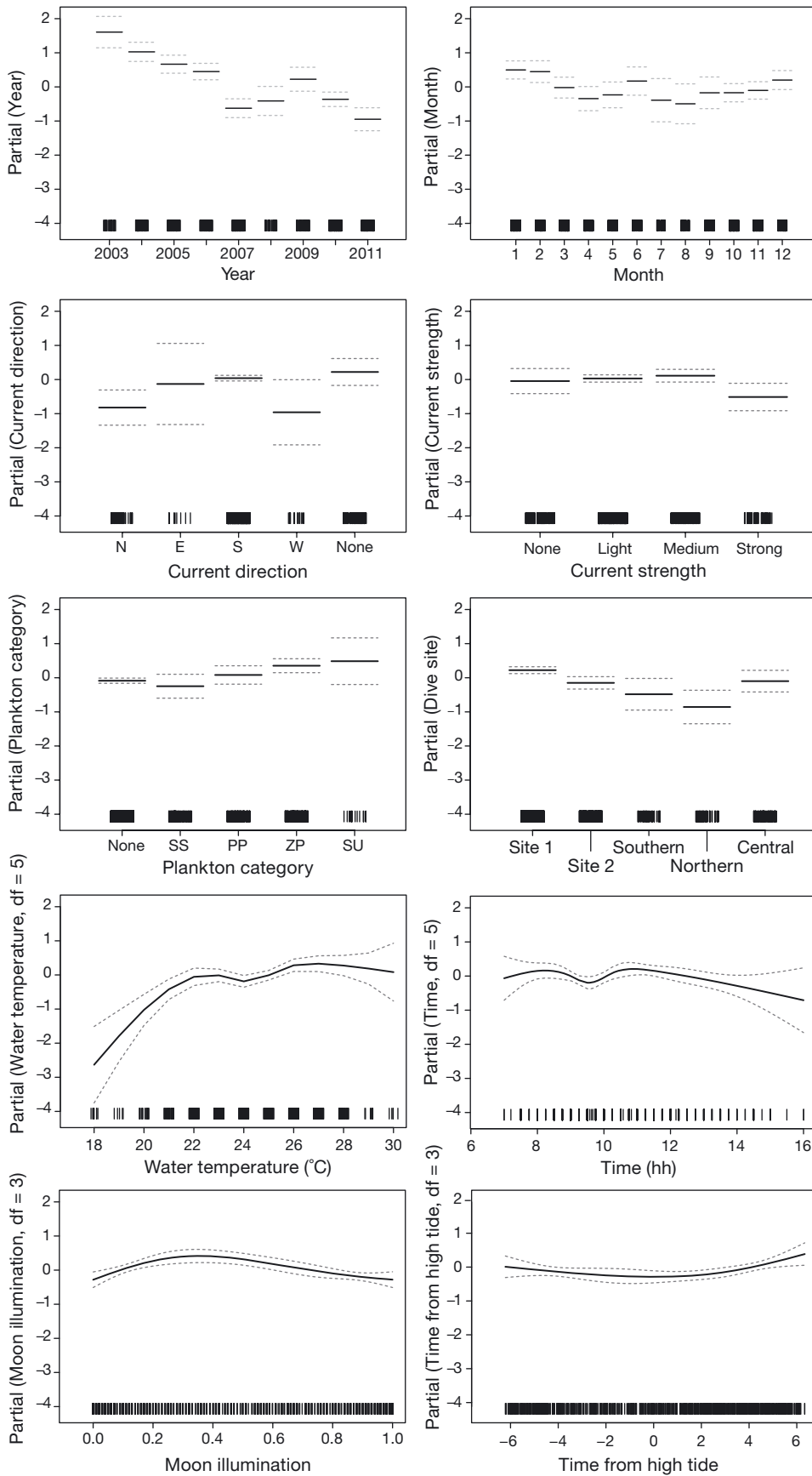
Fig. 3. *Manta alfredi*. Reef manta ray GLM model outputs showing the relationship between their sightings and all significant predictors. The rug plot along the *x*-axis indicates sampling effort and dotted lines mark the 95% confidence interval. See Table 1 for details
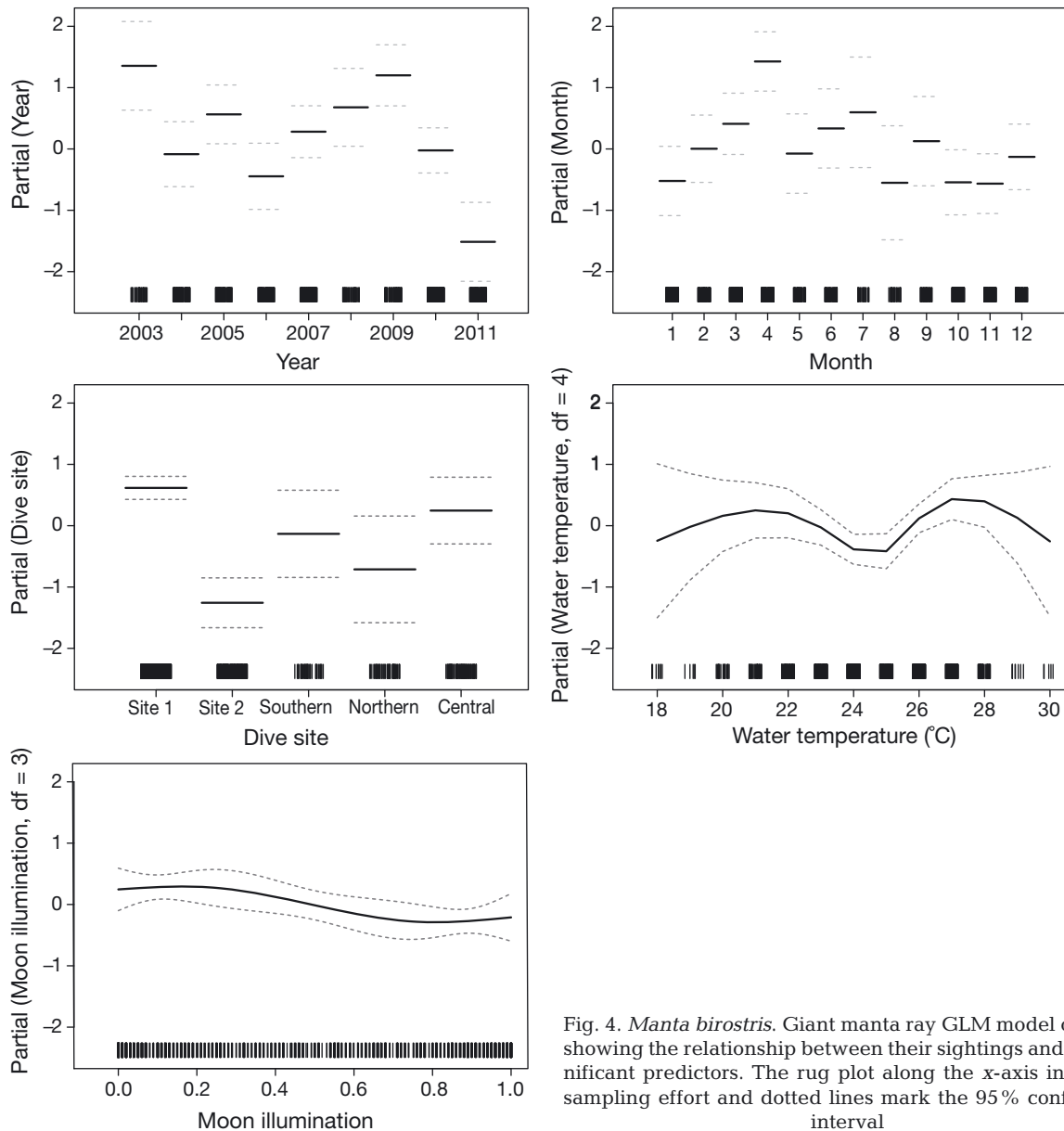
Fig. 4. *Manta birostris*. Giant manta ray GLM model outputs showing the relationship between their sightings and all significant predictors. The rug plot along the *x*-axis indicates sampling effort and dotted lines mark the 95% confidence interval

with sightings at Ningaloo Reef, Australia, partly linked to the Southern Oscillation Index that influences the strength of the Leeuwin Current (Wilson et al. 2001, Sleeman et al. 2010a).

Declining sightings trends for reef manta rays and whale sharks

Although sightings of giant manta rays were relatively stable over the study period, there was a significant decline in reef manta ray (88%) and whale shark (79%) sightings. By including various temporal and environmental variables in the GLM, the standardised sightings trend was adjusted for these variables. Although other local biophysical predictors — not included in the GLM — may also influence sightings, external anthropogenic pressures or larger-scale oceanographic influences are likely to be involved. Reef manta rays are actively fished in southern Mozambique (Marshall et al. 2011b), with an estimated 20 to 50 individuals killed by fishers annually along the 50 km of coastline encompassing the present study area (A. D. Marshall unpubl.). This reef manta ray population is naturally small, as demonstrated in the superpopulation estimate of 802
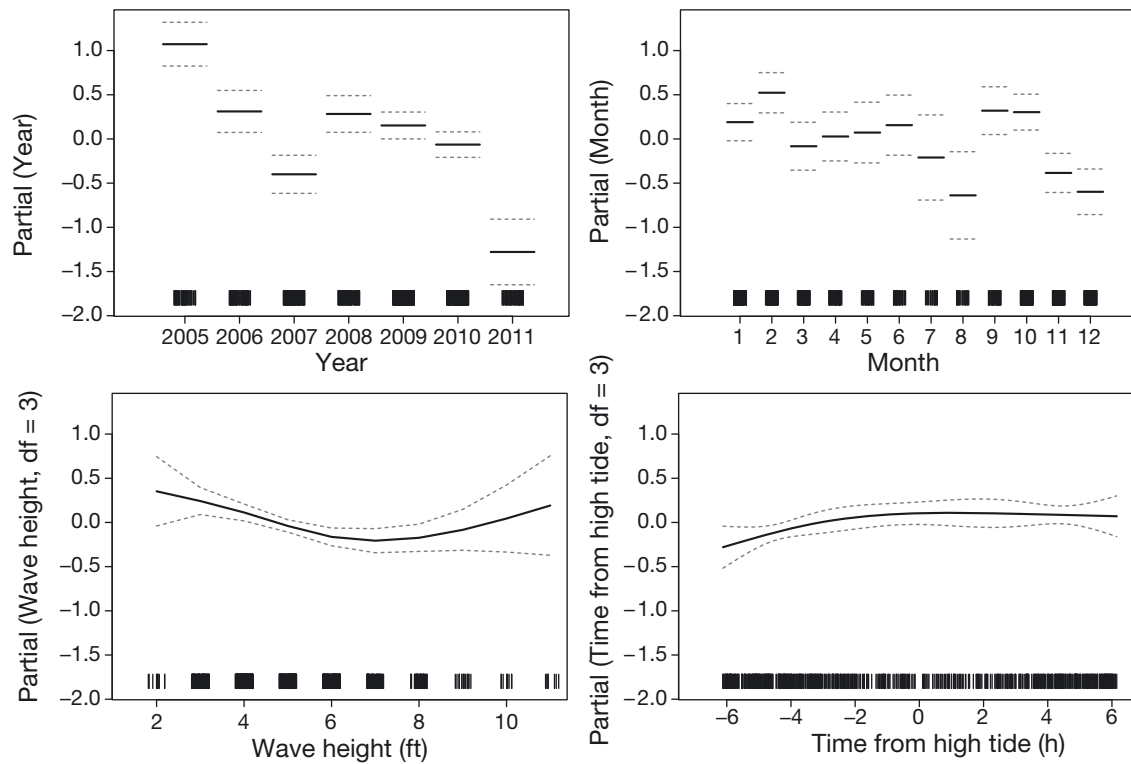
Fig. 5. *Rhincodon typus*. Whale shark GLM model outputs showing the relationship between their sightings and all significant predictors. The rug plot along the *x*-axis indicates sampling effort and dotted lines mark the 95% confidence interval

individuals in our study area, with annual population estimates ranging from 149 to 454 rays between 2003 and 2007 (Marshall et al. 2011b). As this species has a conservative life history strategy with a low level of recruitment, fishing pressure is likely to substantially impact this population (Marshall & Bennett 2010b, Marshall et al. 2011b). Some of the reefs in the study area have also been increasingly subjected to SCUBA diving ecotourism pressure, with up to 11 regular commercial scuba diving operators, most with multiple boats, active in 2011. Only 4 operators were active at the start of our study period, and the steady increase in diver traffic could interrupt cleaning activities and otherwise disturb the manta rays. Cleaning is an important daily activity and reef manta rays spend particularly long periods at cleaning stations in the present study area (Marshall 2009). Approximately 76% of individuals bear bite wounds of predatory sharks, and removal of dead tissue around injuries is thought to facilitate wound healing and prevent secondary infection (Marshall & Bennett 2010a). Giant manta rays are less affected by bite injuries (~35%; Marshall 2009) and visit cleaning stations less regularly. As they spend less time at these reefs, they are likely to be less affected by the

recreational diving activities that focus on these sites. Further, only one giant manta ray has been observed to be caught in the local fishery over the past 8 years (A. D. Marshall pers. obs.), suggesting that fishing pressure on this species is low in comparison to the reef manta ray.

A significant decline in whale shark sightings was also observed. There is no present-day fishery for whale sharks in Mozambique, although occasional catches have taken place in the local area during the study period (S. J. Pierce unpubl.). Tuna purse-seine fishers spot whale sharks in the Mozambique Channel (Sequeira et al. 2012) and their accidental catches could have negative impacts on the sharks (Floch et al. 2012). Also, some live sharks at Praia do Tofo bear scars attributable to net entanglement and propeller strikes (Speed et al. 2008). Given that whale sharks are capable of long-distance movements, it is plausible that negative human impacts elsewhere could affect sightings at Praia do Tofo, as has been suggested for this species at Ningaloo Reef, Australia (Bradshaw et al. 2007, 2008) and in the Andaman Sea, Thailand (Theberge & Dearden 2006). Initial findings from the global whale shark database have shown little connectivity among distant aggregation

sites in the Indian Ocean (Brooks et al. 2010, ECO-CEAN 2012), and no link between sharks from Praia do Tofo and areas with active whale shark fisheries (such as Taiwan). However, the limited knowledge of whale shark movements in the Western Indian Ocean preclude a full assessment of this possibility (Gifford et al. 2007, Brunnschweiler et al. 2009, Brooks et al. 2010). Alternatively, regional- to large-scale oceanographic parameters, not accounted for in our models, may also influence local whale shark sightings, as has been shown for Ningaloo Reef, Australia (Wilson et al. 2001, Sleeman et al. 2010a). Of particular importance may be the mesoscale eddies that dominate the flow of the Mozambique Channel (de Ruijter et al. 2002). These eddies exhibit high inter-annual variability (Schouten et al. 2003) and create strong fronts often associated with high biomass (Lima et al. 2002, Tew Kai & Marsac 2010), suggesting that further investigation of mesoscale eddies will be important for understanding the strong inter-annual signal in whale shark sightings at Praia do Tofo.

Is megafauna visitation seasonal?

The model results suggested that the highest giant manta ray sightings were in April, although the 95% confidence limits do overlap with March and July. Such a pattern may imply an annual migration past Praia do Tofo during the austral autumn/winter, although additional sightings of giant manta rays were made throughout the year. Sightings of giant manta rays at other aggregation sites, such as south-eastern Brazil (Luiz et al. 2009) and New Zealand (Duffy & Abbott 2003), similarly are seasonal and indicate that this species undertakes seasonal movements.

Reef manta rays were sighted throughout the year without exhibiting a clear seasonal signal. The model suggested higher sightings in the austral summer, although numbers from January/February were only significantly higher than April. More sightings in the austral summer are likely as this is when they mate and give birth in the study area (Marshall & Bennett 2010b).

Whale sharks appear seasonally at most of their coastal aggregation sites around the world, with their visitation normally coinciding with increased prey availability (Taylor 1996, Nelson & Eckert 2007, Riley et al. 2010, de la Parra Venegas et al. 2011, Rowat et al. 2011). The lack of a seasonal signal in whale shark sightings in this study indicates a departure from this general rule. Despite their non-seasonal appearance

at Praia do Tofo, whale shark sightings fluctuated during the study. This is likely to be a consequence of their movement patterns and the variable local zooplankton abundance influenced by the dynamic regional oceanography dominated by event-scale, non-seasonal eddies (Schouten et al. 2003).

Environmental influences on megafauna sightings

Water temperature was a strongly significant predictor for reef manta rays, less so for giant manta rays, and SST was removed from the final model for whale sharks. Reef manta rays appeared to avoid cold water (18 to 21°C), while giant manta rays had an unclear relationship with water temperature. The distribution of these 2 species overlap in parts of their range, but giant manta rays extend further into colder temperate areas (Kashiwagi et al. 2011, Couturier et al. 2012), which could explain why temperature is not as strong a predictor of their presence as it is for reef manta rays. Water temperatures on the reefs off Praia do Tofo fluctuated up to 7.5°C d^{-1} (C. A. Rohner pers. obs.), with cool-water intrusions recorded in all seasons. Reef manta rays preferentially selected episodes of warmer water irrespective of season. Water temperature was not supported for the whale shark model. Whale sharks can tolerate cold waters, as they have a wide distribution extending into areas with cold surface waters (Turnbull & Randell 2006) and can undertake deep dives into water as cold as 3.4°C (Brunnschweiler et al. 2009). In the western Indian Ocean, 90% of whale shark sightings have been suggested to occur in a narrow surface temperature band (26.5 to 30°C) (Sequeira et al. 2012). SST is likely to strongly influence whale shark sightings offshore, where fronts are a major driver of the spatial dynamics of predators (Zainuddin et al. 2008, Tew Kai & Marsac 2010). The lack of a relationship with SST in our study was either because such oceanic fronts may have less influence on coastal surface waters, or because remotely sensed SST data was inadequate for our purpose.

Site 1 was the preferred reef for both manta ray species, while Site 2 was also often visited by the reef manta ray, but not the giant manta ray. Sightings of the latter were also marginally more common on southerly reefs than at Site 2. Site 1 and the southern group are wide reefs that offer a large area for cleaning, while Site 2 is narrower and has relatively small cleaning stations. Giant manta rays, because of their large body size, may prefer larger reefs that enable them to remain close to cleaning stations, especially

as they tend to get cleaned in groups, which may require more space to maneuver and alternate passes over the cleaning stations.

Minimum wave height impacted the sightings of whale sharks, with more individuals seen when waves were small. This may simply reflect an increase in sightability during these more favourable conditions rather than an actual change in whale shark presence or behaviour. Sharks may swim at greater depths when surface waters are rough and hence may be present, but not seen by surface-based observers (Rowat et al. 2009). Time from high tide had a weak effect on sightings of reef manta rays and whale sharks, with slightly more reef manta rays at low tide. Moon illumination was a supported predictor for both *Manta* species, with more sightings made when less than half the moon was illuminated. These results are in contrast with reef manta rays in Lombok, Indonesia, where their numbers increased during full and new moon when the tidal flux was highest (Dewar et al. 2008).

Significantly more reef manta rays were seen when zooplankton dominated the water column compared to when there was no plankton or when suspended sediment was present. Sediment-rich water could negatively affect normal gill ventilation for respiration and filter-feeding, and it is possible that large, mobile planktivores will avoid such conditions. Higher numbers of reef manta rays seen at cleaning stations when zooplankton was locally abundant may indicate that they preferentially visit cleaning stations that are in close proximity to good feeding areas.

Reef manta rays were sighted less frequently during northward currents compared to the predominant south- and eastward currents. Fewer reef manta rays were also seen in strong currents compared to medium and light currents, but were not significantly different from absent currents. We therefore interpret this relationship with caution. It appears that, given reef manta ray presence at the reefs was generally related to routine cleaning behaviour, this may indicate stronger currents are sub-optimal for cleaning. This is likely because it would be difficult for the small cleaner fishes to maintain their position above the reef in strong currents, or perhaps because reef manta rays preferentially avoid cleaning when it is energetically costly to hold their position relative to the reef. Time of day was marginally significant for reef manta rays, with a suggestive low in sightings from 08:30 to 10:00 h. This observation may reflect the relatively high amount of ecotourism boat traffic and diver numbers close to the reefs at those times.

Broader applications and implications for conservation

Praia do Tofo in southern Mozambique is one of the few coastal hotspots for all 3 species discussed in this study (Pierce et al. 2010, Marshall et al. 2011b). As whale sharks and manta rays are globally threatened, it is important to separate environmentally driven short-term fluctuations from significant long-term trends. This can be a challenge in these migratory species as sighting data are often from a single geographical locality within their broader range. Standardisation of catch data with multivariate models, which take into account a suite of environmental variables, has become common practice for fisheries managers (e.g. Agenbag et al. 2003, Zagaglia et al. 2004, Hazin & Erzini 2008, Zainuddin et al. 2008) and here we have shown that GLMs are also a useful tool for examining sightings trends of planktivorous elasmobranchs. While, on a broad scale, changing ocean climate has the potential to shift historical aggregation sites through influencing environmental conditions and zooplankton composition and density, in this case sightings of *M. birostris* showed no significant trend in the limited study period. The observed data suggest a decline in sightings of reef manta rays and whale sharks, and this is confirmed by the GLM after taking into account a suite of local predictors in the model. While larger-scale oceanographic variables could drive the fluctuating numbers of whale shark sightings, the decline in sightings of reef manta rays may represent a true decline driven by mortality due to fishing or by avoidance of reefs visited by increasing numbers of dive tourists. However, the data in the present study do not unambiguously identify the reasons for an apparent decline in sightings of reef manta rays, but given that Praia do Tofo is a global hotspot for these species and also hosts a burgeoning marine tourism industry, potential threats such as increased fishing and tourism pressure require immediate attention by scientists and managers.

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