Individual variation in residency and regional movements of reef manta rays *Mobula alfredi* in a large Marine Protected Area

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Abstract

Mobulid populations are declining on a global scale as a result of both targeted fisheries and indirect anthropogenic threats. In order to implement effective conservation strategies for species of this taxa, it is crucial that movement patterns at a range of spatiotemporal scales are defined. To gain insight into such patterns, we deployed a combination of acoustic (n = 21) and satellite (n = 12) tags on reef manta rays (*Mobula alfredi*) in the British Indian Ocean Territory Marine Protected Area (BIOT MPA) annually from 2013 through 2016. An extensive array of acoustic receivers (n = 52) were deployed across the archipelago to record the movements of mantas throughout the MPA. Data revealed large individual variation in horizontal movement patterns, ranging from high local site fidelity (<10 km) for up to three years, to large-scale regional movements (>200 km) around the entire MPA. Depth time-series data recorded vertical movement patterns consistent with other epipelagic elasmobranch species, including oscillatory diving and deep dives to greater than 500 m. Though no individuals were directly recorded departing the MPA throughout the study, the gaps in detections and estimated travel speeds documented here indicate that the movements of individuals outside of the BIOT MPA cannot be discounted. Collectively, our data suggests that, with effective enforcement, the current size of the BIOT MPA is providing substantial protection to its reef manta ray population. Characterization of movement patterns across ontogenetic classes, however, is required to fully characterize the spatial ecology of this species and ensure protection across all cohorts of the population.

Keywords: biologging; acoustic telemetry; satellite telemetry; manta; site fidelity; elasmobranch; conservation; Chagos Archipelago

1. INTRODUCTION

A comprehensive understanding of a species' spatiotemporal distribution and movement patterns are key when developing effective management and conservation strategies, or when assessing the efficacy of pre-existing management strategies. Rapidly evolving technologies and analytical methods have facilitated the recent proliferation of electronic tracking studies to better understand the behavior of wild elasmobranchs (Evans et al. 2013, Hussey et al. 2015). The extent to which such studies can accurately describe the movement ecology of a species and augment management and conservation plans, however, depends on factors such as the duration of the tag deployment, the type and resolution of information collected, and the sample size of the study, all common trade-offs in biotelemetry (Hussey et al. 2015, Andrzejaczek et al. 2019, Sequeira et al. 2019).

Two of the most common techniques used for tracking the movements of elasmobranchs are satellite and acoustic tagging (Hammerschlag et al. 2011, Hussey et al. 2015). Advances in tag technology over the last several decades have greatly improved our understanding of the spatial ecology of these animals at a number of different scales (e.g. Heupel et al. 2010, Block et al. 2011), and each method has specific strengths and weaknesses in its capacity to describe movement. Satellite tags can record movements over broad geographical ranges and remotely transmit information to Earth orbiting satellite constellations either when a tagged animal surfaces or the tag detaches from the individual and floats to the surface (i.e. pop-up satellite archival tags: PSATs). These tags also often record additional variables, such as the pressure and ambient temperature encountered by the animal. The accuracy and precision of spatial tracks recorded by satellite tags, however, is often variable at lower latitudes when relying on light-based geolocation estimates, as is often the case with PSATs (Teo et al. 2004, Braun et al. 2015). In addition, these tags rarely record movements for periods exceeding one year (Stewart et al. 2018). Conversely, acoustic tags can provide accurate, fine-scale movement data over many years (currently >10 years) but require the presence of a receiver within a limited detection range (typically < 1 km), and provide no information about movement outside of this range. Thus, a combined approach using both tag types can be used to obtain a more comprehensive understanding of the movement ecology of elasmobranch taxa across a range of spatiotemporal scales (e.g. Jorgensen et al. 2009, Meyer et al. 2010, Braun et al. 2015, Carlisle et al. 2019).

Studies investigating the movement ecology of reef manta rays, *Mobula alfredi* (Marshall et al. 2009, White et al. 2017), have multiplied in recent years following increased awareness, attention and concern over the status of their populations (Stewart et al. 2018). This species, listed as Vulnerable on the IUCN Red List of Threatened Species (Marshall et al. 2019), faces fishing pressure from both targeted (artisanal) and bycatch (artisanal and industrial) fisheries, which is unlikely to be sustainable given its conservative life history (Croll et al. 2016, Marshall et al. 2019). Satellite and acoustic tracking of reef manta rays conducted at aggregations throughout its tropical and subtropical range have reported consistent patterns of residency and site affinity, with limited connectivity to other aggregations (Clark 2010, Braun et al. 2015, Couturier et al. 2018, Setyawan et al. 2018, Peel et al. 2019b). Such results have lent support to the use of Marine Protected Areas (MPAs) as an effective management tool for protecting populations at a regional scale (Peel et al. 2019b). However, a recent study using photographic-identification methods increased the longest known point-to-point movement of this species from 650 km to 1150 km, demonstrating that reef manta rays are indeed capable of performing large scale movements (Armstrong et al. 2019). Collectively, this suggests that reef manta rays may be partial migrants, where some individuals in a population migrate while others remain resident (Chapman et al. 2012). As sample size

and the duration of tag attachment increase, so too will our ability to calculate the proportion of the population that migrates, and, therefore, the efficacy of MPA protection for local populations (Sequeira et al. 2019).

Little is currently known about the distribution and movements of reef manta rays in the British Indian Ocean Territory MPA (BIOT MPA). This MPA is one of the largest no-take MPAs in the world and contains the islands and atolls of the Chagos Archipelago. Illegal, Unreported and Unregulated fishing (IUU), continues to be a significant management concern within the MPA (Ferretti et al. 2018, Tickler et al. 2019), with catches from apprehended vessels found to include manta ray products, some of which were recovered from gear that was deployed within the MPA at the time (IOTC 2015). Telemetry data is therefore critical to determine not only if enforcement of the current MPA design will offer sufficient protection to the local reef manta ray population, but to highlight critical habitats for the species, where the limited MPA enforcement capacity should be prioritized to protect reef manta rays. To date, satellite tags deployed on reef manta rays have revealed coarse, regional-scale movements within the BIOT MPA for up to 254 days, with one of 12 tagged individuals displaying a potential offshore excursion away from the archipelago (Carlisle et al. 2019). To advance these results, finer-scale and longer-term data provided through passive acoustic telemetry studies are required to better characterize reef manta ray movements within the MPA at a range of temporal scales, to highlight areas of critical habitat for the species, and to assess residency in this population. Additionally, depth and temperature data collected by satellite tags will aid in understanding and managing vertical overlap with harmful anthropogenic activities, as well as to increase knowledge of manta ray ecology (Braun et al. 2014, Andrzejaczek et al. 2019).

In this study, we used both acoustic and satellite telemetry to investigate reef manta ray movement patterns in the BIOT MPA at a range of spatiotemporal scales. Specifically, we aimed to (1) assess the extent to which individuals move within the BIOT MPA; (2) determine how the patterns of movement of tagged individuals vary at diel, monthly and seasonal scales; and (3) document the vertical movement patterns of reef manta rays at this location. Results are discussed in the context of the efficacy of the BIOT MPA to protect reef manta rays, and how their movements within the BIOT MPA compare to those of other populations studied around the world.

2. MATERIALS AND METHODS

2.1 Study site

The BIOT MPA comprises a large archipelago of atoll-based reefs and submerged banks in the central Indian Ocean. The MPA is a designated no-take marine reserve of approximately 640,000 km² which includes all of the atolls and waters of the BIOT Exclusive Economic Zone (EEZ), with the exception of a small recreational fishery in the atoll of Diego Garcia (Sheppard et al. 2012). There are currently no human inhabitants within the archipelago, aside from those associated with the military base on Diego Garcia. The northern reefs are approximately 500 km from their nearest neighbour, Addu Atoll, in the southern Maldives.

2.2 Data collection

Between 2013 and 2016, in the months of February to April, reef manta rays were tagged by free-divers in the BIOT MPA with either acoustic tags (V16 coded tags, 69 kHz, transmission interval 30–90 s, battery 1616 days, Vemco, Halifax, Nova Scotia, Canada; n = 21) or pop-up satellite archival tags (MiniPAT models

247A and 348A, Wildlife Computers, Redmond, WA United States; n = 12). All tags were leadered with a three-layer technique, consisting of a ~15-17 cm length of 180 kg monofilament (Moimoi, Kobe, Japan), that was covered with one layer of Spectra and shrink wrap, and attached via a custom-built titanium dart. Tags were externally deployed and embedded off of the midline of the posterior dorsal surface of each manta ray using a tagging pole.

An acoustic receiver array was deployed over several years as described in Carlisle et al. (2019). Briefly, the array primarily consisted of VR2W receivers (Vemco Inc., Nova Scotia, Canada) distributed around the BIOT MPA (Fig. 1). Receivers were deployed between 2014 and 2016 at nine sites, and were typically placed on the fore reefs of atolls at depths of 15-20 m. Of the 52 receivers considered in this study, 13 were deployed among the southern atolls and banks of the archipelago (sites = Egmont Atoll, South Great Chagos Bank, Schwartz seamount) and 39 were deployed among the northern atolls (sites = Peros Banhos and Salomon Atolls, Speakers, North Great Chagos and Victory Banks, Colvocoresses Reef; Fig. 1). Receivers were serviced annually and deployment times were not consistent between sites (Table A1) due to challenges involved in working in this remote region. In addition to the detection data recorded across the receiver array (last downloaded in March 2019), detections recorded between 18th March 2015 and 23rd July 2019 by two VR4 Global units deployed at Salomon Atoll and Egmont Atoll were also included in this study.

All procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care (APLAC) under permit APLAC-10765.

2.3 Acoustic data analysis

Acoustic data were processed and analysed in the R Statistical Environment (R Core Team 2017). A quality control filter was initially applied to the data to remove instances where only one detection occurred at a site in a day (Hoenner et al. 2018). Following quality control, the VTrack package in R was used to calculate detection and dispersal metrics for tagged individuals (Udyawer et al. 2018). Track days (also known as the monitoring or tag deployment period) for individuals were defined by considering the time frame between deployment and the last recorded detection for each tag. This definition of length provides a minimum estimate (i.e. assumes tag loss) relative to estimates that terminate a track at the end date of the study (i.e. assuming tag retention and emigration from the receiver array; Cochran et al. 2019). In this study, the 'minimum' estimate was used to facilitate comparisons with previous studies investigating reef manta ray movements. Additionally, all acoustic tags in this study were externally deployed and were therefore more susceptible to premature detachment. The detection index (DI; Udyawer et al. 2018) was also calculated as a proxy of residency for each individual, and was defined as the detectability of an individual within the acoustic receiver array at BIOT and calculated by:

$$DI = \frac{Number\ of\ days\ detected}{Track\ days}$$

Network maps of movement were constructed by plotting consecutive detections of each tagged individual throughout the receiver array from the first detection to the last using the package 'ggplot2' (Wickham 2016) in R (version 3.6.1; R Core Team 2017).

2.3.1 Generalized additive mixed models

Generalized additive mixed models (GAMMs) were used to investigate the temporal occurrence of acoustically-tagged reef manta rays in the BIOT MPA. To eliminate biases in detection probabilities resulting from the number of receivers present in the array fluctuating over the sampling period, the period for detections under consideration was standardized to those recorded between 15th April 2016 – 14th April 2017 (period outlined in Fig. 2). This period was chosen because it included the highest number of active receivers, while overlapping with most manta tracks. Only receivers that operated for the entirety of this period were included in this analysis (n = 44).

The continuous variables considered here were day of the year (Julian day), time of day (hour of day) and fraction of moon illuminated (0-1), and all were modelled because they have previously been shown to influence manta presence at other locations (Couturier et al. 2018, Peel et al. 2019b). Additional biological (e.g. manta wingspan and sex) and environmental (e.g. tidal range and wind speed and direction) variables investigated in previous studies were not considered due to these data either being unavailable for the period considered or of an inappropriate resolution for the constructed models. Day of year and hour of day were extracted from the detection data. Daily lunar illumination for BIOT were obtained from the United States Naval Observatory http://aa.usno.navy.mil/data/docs/MoonFraction.php). Individual manta ID was included as a random effect. The occurrence of acoustically tagged manta rays (response variable) was quantified for each hour of the standardized period, as either '0' (absent) or '1' (present), based on whether a detection had been recorded for that individual during that time (Peel et al. 2019b).

GAMMs were constructed using a binomial error structure and log link function using maximum likelihood estimations in the package 'mgcv' (Wood 2017). As time of day and day of year are both circular variables, a cyclic smoother was also applied to these variables. All possible combinations of the explanatory variables were modelled during this process and were ranked using weights of Akaike's information criterion (AIC) alongside the null model.

2.4 Satellite tag analysis

Satellite tags were programmed to record ambient light levels, ambient temperature and depth at $3 - 5$ second intervals and to detach from tagged manta rays after 180-360 days (median 190 days). Following release, the tags transmitted summaries of archived data sets to Argos satellites, and data were decoded using the manufacturer's software (Wildlife Computers DAP Processor 3.0). Tracks less than seven days long or with gaps greater than 30 days in length were removed from further analyses. Daily locations were estimated through geolocation of light data following Teo et al. (2004), and the most probable track for each tag generated using a Bayesian state space model (SSM) following Block et al. (2011). As we could not quantify the true distance between the first reported pop-up location of each tag and its real release location, no Argos locations were assigned to the final estimated track end times for each deployment.

Depth and temperature data were summarized into 12- or-24 hour bins, and for five individuals, transmitted time series at 7.5- or 10-minute intervals were available (Table 1). These data were analysed in the R Statistical Environment (R Core Team 2017), and all values are expressed as mean ± standard deviation. Time series data were split into local (Indian Chagos Time) day (7 am-7 pm) and night (7 pm-7 am) periods, and a paired student's t-test was used to compare mean day and nighttime depths for each individual (following tests for normality). Linear least-squares regression was used to assess the relationship between mean nightly depth and moon phase (daily lunar illumination) for both the combined dataset of all five individuals and each individual separately. Daily lunar illumination data were arcsine transformed prior to analysis (Braun et al. 2014).

3.0 RESULTS

3.1 Acoustic data

3.1.1 Detection summary

Acoustic tags were deployed on 21 reef manta rays in the BIOT MPA between February and April in 2015 and 2016, with all tags returning usable tracks following quality control (Table 2). Eighteen individuals were tagged in the south of the MPA near Egmont Atoll, and the remaining three were tagged in the north, near Salomon Atoll (Fig. 1). Track days ranged in length from 10 to 1555 days, with 11 individuals (52%) having minimum tag retention times of at least one year (Table 2). A total of 98,483 detections were recorded across the study period, with one individual being responsible for 37% of these (individual 54832 = 36,929 detections; Table 2). Individuals were detected year-round, on an average of 40 ± 29% of the days they were detected (range 3-100%; Table 2). Individuals tagged in the south had a lower detection index than individuals remaining in the north (0.34 ± 0.28 and 0.75 ± 0.14, respectively). The longest period of time between subsequent detections for any individual was 722 days (individual 59946; tagged in the south), with a total of three individuals reporting gaps in detections of greater than six months.

3.1.2 Regional movements

Tagged reef manta rays were detected at all sites in the BIOT acoustic array (Fig. 2). Areas of highest activity, as determined by the detection frequency of tagged mantas, occurred at Egmont and Salomon Atolls, with these sites collectively responsible for 98% of detections (Fig. 2). All but two individuals remained in the region of the array in which they were tagged (i.e. north or south), and for most individuals, the majority of detections occurred at just one site (Table 2; Fig. 2). All individuals tracked in the northern region of the array were detected at a minimum of two sites. In contrast, 11 of the 18 mantas tagged in the southern region of the MPA were detected only at Egmont Atoll for the entirety of their tracks (10 – 1555 days; Table 2).

In the southern array, three individuals (59931, 59943 and 59932) were detected at both Egmont Atoll and Schwartz seamount. Individual 59931 departed the array from Egmont Atoll and was detected at Schwartz seamount two months later for 16 minutes, before returning to Egmont three days later. Individual 59943 was detected at Egmont Atoll for one month before travelling to Schwartz seamount for one month, after which time no subsequent detections were recorded. Individual 59932 was last detected at Schwartz for three minutes after travelling from Egmont over a period of two days at a minimum speed of approximately 53 km day^{-1}.

Two individuals (59926 and 59937) tagged at Egmont Atoll were detected widely throughout the array, travelling between the southern and northern receivers several times (one-way distance >150 km; Fig. 3). Individual 59926 was recorded at six different sites over 728 tracking days, and was the only individual detected at Colvocoresses Reef; approximately 241 km northeast of Egmont Atoll (Fig. 3A). Individual 59937 made seven one-way crossings between the northern and southern receivers over the 494-day period it was tracked (Fig. 3B). This individual was detected on 59% of its tracking days, at 30 different receivers (Table 2). In the north, individual 59937 also travelled between Salomon and Peros Banhos Atolls several times, and on two occasions detections at receivers from both sites were recorded on the same day (up to 51 km apart; Fig. 3B). The minimum crossing speed between the northern and southern regions of the array, based on the time recorded between subsequent detections, ranged from 13-63 km day^{-1}.

The highest proportion of detections (62.4%) were recorded at Salomon Atoll, more than half of which were attributable to individual 54832. This individual was detected on 906 of its 1074 tracking days (a detection index of 0.84), and spent the majority of its time at Salomon, while performing some regional movements between Peros Banhos Atoll and Victory Bank (Fig. 3C). Individual 54832 also had the longest consecutive number of detections at one receiver, spending over five hours at a receiver inside the lagoon at Salomon, where consecutive is defined as a subsequent detection occurring within 10 minutes at the same receiver. Mantas 59937, 54829 and 54834 were also found to have spent long periods of time (>3 hours) in close proximity to this receiver, which collectively recorded 19.9% of all detections for the study.

3.1.3 Temporal patterns

The final GAMM chosen through the model selection process considered 127,697 observations of presence and absence over a one-year period and retained all explanatory variables. The model described 15.5% of the variation present in these data, with 12.9% of the total variation attributed to the effect of individual mantas (the random effect; Table 3; Table A2). The probability of detecting reef manta rays on the BIOT acoustic array peaked at midday, declining until midnight (Fig. 4A). Individuals were also most likely to be detected in December and January, and during a new moon (Fig. 4B; 4C).

3.2 Satellite tracking

3.2.1 Horizontal movements

Detailed analyses of satellite tag data follow the general findings of Carlisle et al. (2019). Twelve satellite tags were deployed on reef manta rays in the BIOT MPA, with four being deemed unusable for geolocation analyses as a result of short track durations (n = 2) or large gaps in transmissions (≥ 30 days; n = 2) generating unreliable tracks. For the eight remaining tags, track lengths ranged from 16-310 days (mean 157 ± 94 days; Table 1). Four of these tags were deployed in southern region of the MPA at Egmont Atoll, and the remaining four were deployed in the north at either Peros Banhos or Salomon Atolls (Fig. 5). Seven of the eight most-probable tracks indicated that tagged individuals had moved away from their tagging sites and throughout the archipelago, between atolls, islands and banks (Fig. 5). Two of these seven tracks (5213001 and 5214018) crossed between the northern and southern regions of the archipelago (>100 km; Fig. 5A), with the other five generally remaining in the region in which individuals were tagged (Fig. 5). One track (5216008) remained around the southern site of Egmont for the entirety of its 140-day track. The remaining track (5216006) was the only one to perform an extended, return excursion from the archipelago (~2 months and ~100 km offshore), departing Egmont in April 2016 and returning in June of the same year. It is important to note that the individual tracks presented here should be interpreted with caution, given that the extent of latitudinal error surrounding the most-likely position estimates spanned up to two degrees, roughly matching the spatial extent of atolls in this study (Carlisle et al. 2019). Despite this error radius, however, all of the most-probable track paths, including the error estimates encompassing the geolocation and SSM analyses and tag pop-up locations, remained within the BIOT MPA for the duration of every deployment.

3.2.2 Vertical movements and temperature

All satellite tags collected depth and temperature profiles, and five tags collected time-series data at 7.5- or 10-minute intervals that resulted in a total 405 days of depth and temperature time-series data (mean 81 ± 62 days per individual). Mantas here occupied a mean depth of 35.3 ± 27 m (range 0-552 m) and

temperature 27.36 ± 2.4°C (range 9.4-33.2°C). Vertical movement data revealed oscillatory movements, diel vertical movement patterns and deep dives (>200 m; Table 1, Fig. 6). Mean daytime depths (39.7 ± 29.7 m) were significantly deeper than nighttime depths (30.8 ± 24 m) for all individual time-series combined (paired t-test, t = 9.23, df = 493, p-value < 0.001), and for the three individuals with the longest time-series (>86 days; Table 4). Tagged individuals spent the highest proportion of their time at depths between 25 and 50 m (36%), and a further 26.7% at depths of 50 to 100 m, during both the day and night (Fig. 6A). Regression analyses indicated that mean nightly depth was significantly, but weakly, correlated with lunar illumination for the combined time-series dataset (b = 7.7, p < 0.0001, R^2 = 0.04) and for two of the five individuals (Table 4). Three individuals reached maximum depths greater than 500 m (Table 1). The satellite tag deployed on individual 5216006 recorded a maximum depth and minimum temperature of 888 m and 7.3°C respectively, however, popped-up to the surface immediately after these data were logged (Fig. A1). As a result, it cannot be conclusively determined if the tag reached this depth while still deployed on the manta, or if it was reached after a premature release and transported to depth via alternative means.

4.0 DISCUSSION

The BIOT MPA is one of the largest MPAs in the world (~640,000 km^2) and provides a unique opportunity to assess the conservation value of large MPAs for highly mobile marine species, such as the reef manta ray (Carlisle et al. 2019, Tickler et al. 2019). In this study, we combined the use of acoustic and satellite telemetry to obtain a comprehensive view of reef manta ray movements within the BIOT MPA. Though they cannot be discounted, frequent, large-scale movements away from the MPA were not evident throughout the duration of this study, and movements within the MPA varied widely among individuals.

4.1 Horizontal movements

Satellite and acoustic tagged reef manta rays demonstrated variable patterns of residency and regional movements throughout the BIOT MPA. Acoustic telemetry revealed that some individuals travelled widely across the entire acoustic array, whereas others remained resident at specific atoll sites over long periods of time (up to three years). Satellite tracks corroborated this result, with the most-probable tracks for satellite tagged mantas predominately displaying regional movements around the archipelago, and highlighting the residency of individuals to the MPA. Only one individual appeared to conduct an offshore pelagic excursion (~100 km one-way), however, this manta did not exit the boundary of the BIOT MPA during this period. There was no direct evidence to suggest that reef manta rays depart the BIOT MPA, though gaps in acoustic detections (average maximum gap of 115 days, range: 1-722 days), estimated travel speeds, and previous long-distance movement records (e.g. 1,150 km; Armstrong et al. 2019) indicate that long-distance movements to other manta aggregation sites in the western Indian Ocean, such as the Maldives (min. ~450 km) or Seychelles (min. ~1700 km), cannot be discounted. Indeed, based on a conservative speed estimate of 60 km day^{-1} as derived from the movement data presented here, a direct, return trip by a tagged individual to, and from, the Maldives from Egmont Atoll would take 23 days; a journey that would have been possible to complete multiple times within the detection gaps presented in this study. Longer tag attachment durations may show departures from the MPA, but to date, both tag types showed a distinct residency to the study area. The establishment, expansion and connectivity of acoustic arrays in other regions of the Indian Ocean (e.g. Maldives, Seychelles), in addition to photo-ID comparisons and validation among different monitoring sites, will also assist in determining if connections between these populations do exist, but to-date, none have been recorded (pers. comm. J. Lea; Amirante

Island array, Seychelles). Our multi-tagging approach corroborates existing knowledge of reef manta ray spatial ecology (Jaine et al. 2014, Braun et al. 2015, Couturier et al. 2018, Setyawan et al. 2018, Peel et al. 2019b), suggesting that while capable of larger scale migrations, reef manta ray movements predominately occur on a regional scale (<200 km), and therefore, with effective enforcement, BIOT MPA is likely to offer significant refuge to its reef manta ray population. Additionally, this multi-tagging approach is likely to benefit similar studies in other regions and/or species, which also aim to assess the effectiveness of MPAs for marine megafauna by providing a more comprehensive view of their movement patterns.

4.2 Individual variation in residency and site fidelity

Reef manta rays tagged with acoustic and satellite tags displayed high variation in individual movement patterns, with some individuals displaying residency to specific sites within the BIOT MPA, and others moving frequently throughout the entire archipelago (up to 241 km straight-line distance). Collectively, these movement strategies indicate that key habitats for mantas exist at sites where high residency was recorded (i.e. Egmont and Salomon Atolls), and that there is some degree of connectivity between these sites. Residency to the shallow bank and reef habitats of the BIOT MPA, here measured by the detection index (DI), ranged from 3-100% (mean DI = 40 ± 29%). Notable examples include the DI of 84% over 1,074 tracking days for individual 54832 (tagged in the north), and the DI of 3% over 764 tracking days individual 59946 (tagged in the south). Overall, residency was higher for individuals remaining in the northern sites than those tagged in the south (mean DI of 75 ± 14% and 34 ± 26% respectively). Internationally, manta residency levels also vary among other regions where passive acoustic telemetry has been used, ranging from 65% in the Red Sea (Braun et al. 2015) and 62% in the Amirante Islands of Seychelles (Peel et al. 2019b), to 39% in Hawaii (Clark 2010), 28% in West Papua (Indonesia; Setyawan et al. 2018) and 15% in eastern Australia (Couturier et al. 2018). A number of factors may be responsible for these diverging patterns, including the design of the acoustic array (Espinoza et al. 2016, Peel et al. 2019b), the ontogenetic stage of the individuals tracked (Chapman et al. 2015, Peel et al. 2019b), the sample size of the study (Sequeira et al. 2019) and a host of physical and environmental factors that may influence patterns at a given study site (e.g. coastal or island localities, bathymetry, degree of reef isolation) (Espinoza et al. 2015, Peel et al. 2019b). Within the BIOT MPA, the larger spread and density of receivers among northern sites and/or the physical geography of the islands and atolls in this location may have contributed to differences in reported residency rates between the north and south regions of this study. Alternatively, or in addition, there may have been a bias in the maturity and/or sex of the individuals tagged in each region. As juvenile mantas may be less likely to travel longer distances than adults (Peel et al. 2019b), it may be that they were more prevalent in northern regions of the BIOT MPA, however, we did not have the data to assess the life stages or sex of the individuals.

Frequent re-detection events indicated that several acoustically tagged mantas exhibited strong site fidelity to Salomon Atoll, in particular, to one receiver within the lagoon (Figure 2C). This single receiver recorded 19.9% of all of the detections reported in this study (n = 19,593), and four mantas were noted to spend long continuous periods of time (>3 hours) within its detection range. Strong site fidelity in elasmobranchs has been attributed to a range of factors including foraging (Barnett et al. 2011, Couturier et al. 2018), reproduction (DiBattista et al. 2008, Marshall & Bennett 2010), refuge from predators (Michelle et al. 2007, Stevens 2016) and visiting cleaning stations (O'Shea et al. 2010, Perryman et al. 2019). Given that the receiver within the lagoon at Salomon is located next to a channel that feeds in a strong current from outside at high tide, and several mantas have been observed feeding at the channel

mouth (pers. comm. R. Schallert), it is likely that this site represents an important foraging habitat for reef manta rays in the BIOT MPA; likely attracting aggregations of individuals when conditions are suitable. There is also the possibility that the lagoon receiver is located within the vicinity of a cleaning station, as manta foraging and aggregative behaviours are often commonly observed at these sites (O'Shea et al. 2010, Couturier et al. 2018, Peel et al. 2019b), resulting in increased numbers of detections at receivers positioned close by (Peel et al. 2019b). Future work should prioritize the identification of foraging sites and manta cleaning stations within the BIOT MPA, as they are recognized as significant sites for social behaviours including courtship and copulation in reef manta rays (Marshall & Bennett 2010, Stevens et al. 2018, Perryman et al. 2019), and can represent focal points for spatial management strategies aiming to conserve the species.

Variation in regional movements patterns, residency and site fidelity among individuals suggest that reef manta rays are partial migrators, whereby some individuals within a population migrate, and others remain resident (Chapman et al. 2012). Currently, our understanding of the extent to which individual mantas migrate both within and away from the BIOT MPA is limited to a regional (~200 km) scale, however, as discussed, longer distance movements may also occur. Partial migration has been reported in a number of other elasmobranch species, such as grey reef sharks *Carcharhinus amblyrhynchos* (Heupel et al. 2010, Bonnin et al. 2019), tiger sharks *Galeocerdo cuvier* (Papastamatiou et al. 2013) and bull sharks *Carcharhinus leucas* (Espinoza et al. 2016). While long-distance movements benefit partial migrators by connecting distant populations and providing capacity to respond to localized environmental disturbances, they also place individuals at greater risk of encountering threats, such as fishing, that occur outside of MPAs (Jacoby et al. In Review). Alternatively, the observed differences in spatial ecology among tagged individuals may be driven by ontogenetic differences. For instance, larger adult individuals may be travelling larger distances around the study site, while smaller juveniles may remain resident to the shallower sites of the acoustic array, as observed in Peel et al. (2019b). Nevertheless, characterizing the proportion and attributes of the manta population in BIOT that migrates, and documenting the extent of these migrations, is imperative to evaluating population connectivity for this species and to assessing risk of exposure to threats such as targeted fishing, bycatch and habitat degradation (Chapman et al. 2015, Espinoza et al. 2016). Future studies should therefore focus on attaining larger sample sizes, longer attachment durations for satellite tags, and tagging of a representative cross-section of the population (i.e. a range of sexes, sizes and reproductive states; Sequeira et al. 2019).

4.3 Temporal patterns

Both horizontal and vertical movement patterns of reef manta rays were influenced by time of day and, to a weaker extent, lunar phase. Detection frequencies in the BIOT MPA acoustic array peaked at midday and during a new moon, and were substantially higher during daytime hours than nighttime hours. Deeper mean diving depths were exhibited by satellite tagged individuals during the day and a full moon. Increasing use of coastal reef and island arrays in daylight hours has been recorded in several previous studies of reef mantas (Dewar et al. 2008, Clark 2010, Couturier et al. 2018, Setyawan et al. 2018, Peel et al. 2019b), suggesting that tagged individuals travel offshore beyond receiver detection boundaries at night. This behavioural pattern may be a foraging strategy whereby individuals feed in shallow habitats during the day, and migrate to offshore pelagic environments at night to take advantage of the diel vertical migration (DVM) of mesopelagic zooplankton into surface waters (Couturier et al. 2013, Peel et al. 2019a, Peel et al. 2019b). Alternatively, or in addition, daytime use of shallow habitats may be related to social behaviours, where mantas use shallow landmarks to orientate themselves and facilitate intra-specific

social interactions and/or visit cleaning stations (Couturier et al. 2018, Perryman et al. 2019). Notably, reef mantas in the BIOT MPA displayed opposite patterns of DVM to those tagged in the Red Sea, where Braun et al. (2014) documented high surface use by mantas in the day and deeper movements at night (reverse DVM). As the DVM of filter-feeding elasmobranchs is primarily linked with diel movements of plankton (Andrzejaczek et al. 2019), contrasting patterns of normal versus reverse DVM may be a function of the distribution of planktonic prey, which in turn may be influenced by the regional oceanography (Sims et al. 2005). Similarly, the effect of fluctuating lunar illumination levels on manta behaviour may also be connected to changes in the prey distribution. As preferred isolumes of vertically migrating zooplankton move deeper with a full moon, mantas may need to travel into deeper offshore waters to forage, reducing the frequency of detection in coastal acoustic arrays (Braun et al. 2014, Couturier et al. 2018, Peel et al. 2019b). Collectively, regional patterns of horizontal and vertical movement at diel and monthly scales suggests that reef manta rays may act as important links between shallow inshore reefs and offshore pelagic environments in BIOT, potentially transporting important quantities of nutrients between these locations (Williams et al. 2018, Peel et al. 2019a).

Reef manta ray acoustic detections in BIOT peaked in December and January. Seasonality in manta occurrence has previously been associated with both monsoonal cycles and their consequent effects on oceanographic conditions and productivity (Anderson et al. 2011, Setyawan et al. 2018, Peel et al. 2019b), and manta reproductive cycles (Marshall et al. 2011). As climate observations in the BIOT region are extremely sparse (Sheppard et al. 2012), and we lacked the metadata to assess the reproductive status of tagged mantas, it is difficult to disentangle these effects in the present study. It is worth noting, however, that the tuna purse-seine fishery catch historically peaked in BIOT waters in December and January (Mees et al. 2009, Dunn & Curnick 2019), suggesting high primary productivity in the water column at this time. Furthermore, evidence of temporal shifts in resource use towards more pelagic prey during this period has been documented in BIOT previously within other elasmobranch species (Curnick et al. 2019). In addition, peaks in manta detection in the Amirante Islands, Seychelles, from December to February were linked to prevailing trade winds (Peel et al. 2019b). As this latter location and BIOT are both located at a similar latitude in the western Indian Ocean, regional-scale climatic variables resulting in local mesoscale variations in oceanography may be driving these parallel seasonal patterns in reef manta ray movement ecology.

Lastly, it is important to acknowledge that 83% of the deviance explained by the final GAMM in this study was attributed to differences between individual mantas, and that 84.5% of the total variability in detection data remained unexplained. The former may be due to some individuals displaying high site fidelity while others were more transient. The deployment of additional tags, as well as measures of biological variables such as sex and size, will likely help to refine our understanding of movement patterns for this manta ray population (Sequeira et al. 2019). For the latter, the recording of environmental data, such as tides, wind speed and direction, prey fields, temperature, and currents, at ecologically relevant spatial scales, will likely increase the explanatory power of such analyses (Peel 2019). Current work is prioritizing the collection of local environmental data at multiple sites around BIOT and could be used in future studies to examine how these factors influence reef manta ray movement patterns.

4.4 Vertical movements

Dive data revealed vertical movement patterns in reef mantas that were consistent with many other epipelagic elasmobranch species, including oscillatory diving, deep dives to greater than 500 m in depth,

and diel vertical migration (discussed previously) (Andrzejaczek et al. 2019). Throughout a diel cycle, mantas frequently oscillated through depths of 25-50 m (mean depth 35.3 ± 27 m), making occasional forays to both surface and deeper waters. Oscillatory movements have also been recorded by reef mantas in the Red Sea and Hawaii (Clark 2010, Braun et al. 2014), supporting the notion that this behavior is common to these animals throughout their range, and may be a strategy used to optimize prey encounter rates and energy expenditure (Andrzejaczek et al. 2019). Deep dives to ≥200 m were recorded for eight of the twelve satellite-tagged mantas, and the deepest recorded movement of a reef manta ray was extended from 432 m in the Red Sea (Braun et al. 2014) to at least 552 m and possibly 888 m, although it is unconfirmed if the tag was still deployed on the individual at this latter depth. Other mobulids exhibiting deep dives include giant devil rays *Mobula mobular* and Chilean devil rays *M. tarapacana*, which were recorded to reach maximum depths of ~700 m and 1896 m respectively, where it is hypothesized that they were foraging (Canese et al. 2011, Thorrold et al. 2014). For reef mantas, the functionality of deep dives into the mesopelagic remains unconfirmed, but may be associated with prey search, thermoregulation, predator evasion or navigation (Andrzejaczek et al. 2019). The large vertical niche of reef mantas recorded here and elsewhere increases their risk of bycatch by a myriad of fishing gear types (Croll et al. 2016). Consequently, future research into patterns and drivers of vertical movements of these animals should focus on assessing susceptibility to different fishing gears across their range and optimizing management strategies to reduce exposure (Stewart et al. 2018, Andrzejaczek et al. 2019).

4.5 Conclusion

Our study used a multi-tagging approach to illustrate the highly dynamic nature of reef manta ray movement ecology within a large, remote Indian Ocean MPA, and serves as an important guide to telemetry-based studies of the movement ecology of marine megafauna in remote locations. Movements were recorded at four spatial scales: presence at a single site; movement among atolls, islands, banks and seamounts of BIOT MPA; movement away from the acoustic array and; on a vertical gradient. High individual variation in movement patterns were documented, ranging from high site fidelity to regional movements around the study site, and shallow oscillatory dives to deep mesopelagic dives. If effectively enforced, the BIOT MPA is likely to offer substantial protection to its reef manta ray population, however, better characterization of movement patterns across the life history of these animals is crucial to fully describe the spatial ecology of this species and ensure protection across all cohorts of the population.

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TABLES

Table 1. Summary of satellite tag deployments on reef manta rays *Mobula alfredi* at the British Indian Ocean Territory Marine Protected Area between 2013 and 2016. PDT: profiles of depth and temperature. Series: time-series of depth and temperature at either 7.5- or 10-minute intervals. [a]Tag did not return a usable track. [b]Undetermined if still deployed on manta for this depth record.

Tag ID	Sex	Deploy latitude (°S)	Deploy longitude (°E)	Deployment location	Deployment date	Pop-up date	Days at liberty	Pop-up latitude (°S)	Pop-up longitude (°E)	Available environmental data	Maximum depth (m)
5213001	U	5.28	71.88	Peros Banhos	13-Feb-2013	12-Aug-2013	180	5.36	71.98	PDT	368
5214001[a]	U	6.66	71.36	Egmont	30-Mar-2014	3-Apr-2014	4	6.43	71.26	PDT	112
5214002[a]	U	6.66	71.36	Egmont	30-Mar-2014	2-Apr-2014	3	6.21	72.02	PDT	200
5214018	U	6.66	71.37	Egmont	12-April-2014	1-June-2014	51	6.64	71.31	PDT & Series	168
5215003[a]	U	6.66	71.36	Egmont	25-Mar-2015	20-Sep-2015	179	7.41	72.46	PDT	272
5216006	F	6.64	71.34	Egmont	29-Mar-2016	25-June-2016	88	6.78	71.56	PDT & Series	888[b]
5216007	U	6.64	71.34	Egmont	29-Mar-2016	14-April-2016	16	6.22	71.17	PDT & Series	192
5216008	U	6.64	71.34	Egmont	29-Mar-2016	16-Aug-2016	140	8.05	70.88	PDT & Series	280
5216017	F	5.33	72.26	Salomon	14-April-2016	18-Dec-2016	248	5.30	72.25	PDT	200
5216018	U	5.33	72.26	Salomon	15-April-2016	12-Oct-2016	180	5.34	72.22	PDT & Series	552
5216021	M	5.33	72.26	Salomon	15-April-2016	19-Feb-2017	310	5.92	72.6	PDT	536
5216025†	F	6.66	71.35	Egmont	16-Feb-2016	16-Aug-2016	182	7.4	72.48	PDT	152

Table 2. Summary of acoustic tag deployments on reef manta rays *Mobula alfredi* at the British Indian Ocean Territory Marine Protected Area in 2015 and 2016.

Manta Tag ID	Sex	Deploy lat (°S)	Deploy long (°E)	Deployment Location	Deployment Date	Last Detection	Total No. Detections	Total detection days	Total track days	Detection Index	North/South	No. sites & receivers	
59936	U	6.66	71.36	Egmont	25-Mar-2015	8-May-2015	566	37	44	0.84	South	1	3
59926	U	-6.66	71.36	Egmont	25-Mar-2015	22-Mar-2017	3269	208	728	0.29	Both	6	21
59931	U	-6.66	71.36	Egmont	25-Mar-2015	20-Jun-2019	3086	294	1548	0.19	South	2	7
59934	U	-6.66	71.36	Egmont	25-Mar-2015	23-Oct-2018	2251	147	1308	0.11	South	1	6
59929	U	-6.66	71.36	Egmont	25-Mar-2015	27-Jun-2019	3090	311	1555	0.20	South	1	7
59933	U	-6.66	71.36	Egmont	25-Mar-2015	31-May-2015	106	12	67	0.18	South	1	2
59943	M	-6.65	71.36	Egmont	28-Mar-2016	7-Jun-2016	365	15	70	0.21	South	2	6
59946	F	-6.65	71.36	Egmont	28-Mar-2016	1-May-2018	192	21	764	0.03	South	1	5
59939	F	-6.65	71.36	Egmont	28-Mar-2016	11-May-2016	108	12	44	0.27	South	1	5
59937	F	-6.65	71.36	Egmont	28-Mar-2016	5-Aug-2017	6765	292	494	0.59	Both	4	30
59941	F	-6.65	71.36	Egmont	28-Mar-2016	19-Jul-2017	7522	325	486	0.67	South	1	7
54836	U	-6.64	71.34	Egmont	29-Mar-2016	13-Mar-2017	1088	70	348	0.20	South	1	5
54827	U	-6.66	71.37	Egmont	10-Apr-2016	21-Apr-2016	178	10	10	1	South	1	4
54833	F	-6.66	71.36	Egmont	11-Apr-2016	25-Jun-2016	388	24	75	0.32	South	1	4
54828	F	-6.66	71.36	Egmont	11-Apr-2016	21-Nov-2018	3464	227	954	0.24	South	2	7

54831	U	-6.66	71.36	Egmont	11-Apr-2016	13-Nov-2017	3575	187	580	0.32	South	1	5
54829	U	-5.33	72.26	Salomon	15-Apr-2016	26-Feb-2017	5010	186	316	0.59	North	2	27
54834	F	-5.33	72.26	Salomon	15-Apr-2016	3-April-2017	13843	290	353	0.82	North	2	20
54832	U	-5.33	72.24	Salomon	15-Apr-2016	25-Mar-2019	36929	906	1074	0.84	North	3	12
59930	F	-6.66	71.35	Egmont	16-Feb-2016	7-Jul-2019	6404	400	1237	0.32	South	2	8
59932	U	-6.66	71.35	Egmont	19-Feb-2016	5-Oct-2016	284	33	229	0.14	South	2	6

Table 3. Results of the GAMM constructed to assess the influence of temporal variables on the occurrence of acoustically tagged reef manta rays *Mobula alfredi* at the British Indian Ocean Territory Marine Protected Area. % DE: percent of deviance explained.

Predictor added to model	df	p (χ2)	% DE
Time of day (h)	3	<0.001	2.2
Day of year	5	<0.001	0.34
Fraction of moon illuminated	1.5	<0.001	0.09
Manta ID	17.8	<0.001	12.9
Full model		NA	15.9

Table 4. Statistical results for vertical movements from five MiniPAT-tagged reef manta rays *Mobula alfredi*. T-tests compare mean depths between day (7 am – 7 pm) and night (7 pm – 7 am). Linear regression assessed the relationships between mean nightly depth and the fraction of the moon illuminated for each individual. *Indicates significant result at p<0.05.

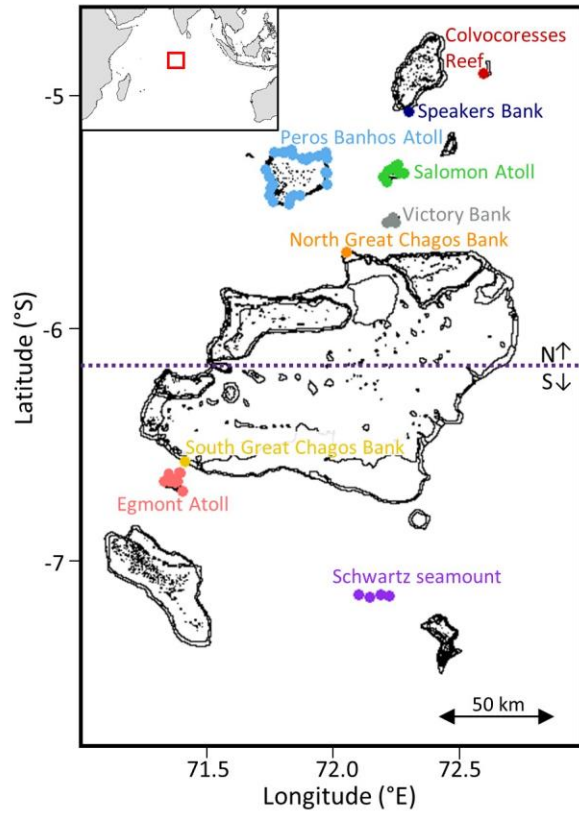| Tag ID	Day depth(m)	Night depth (m)	T-test for equality of means			Linear regression		
	Mean±SD	Mean±SD	df	t	p	b	p	r^2
5214018	12.1 ± 13.9	16.1 ± 16.6	36	-1.48	0.15	1.49	0.63	0.006
5216006	34.2 ± 43.7	28.0 ± 20.4	87	5.12	<0.001*	-0.23	0.93	<0.001
5216007	49.3 ± 20.3	46.9 ± 18.7	16	0.76	0.46	22.4	0.006*	0.410
5216008	31.1 ± 24.1	18.9 ± 22.2	116	5.25	<0.001*	2.21	0.39	0.006
5216018	51.3 ± 17.3	42.8 ± 20.0	172	14.26	<0.001*	9.0	<0.001*	0.180

Fig. 1. Distribution of acoustic receivers throughout the British Indian Ocean Territory Marine Protected Area (BIOT MPA; n=52). Inset displays location of the BIOT MPA in the Indian Ocean. Receivers are coloured by site, with the number of acoustic receiver stations per site being as follows: Egmont Atoll = 8, South Great Chagos Bank = 1, Peros Banhos Atoll = 24, North Great Chagos Bank = 1, Salomon Atoll = 9, Victory Bank = 3, Speakers Bank = 1, Colvocoresses Reef = 1 and Schwartz seamount = 4. Middle dashed line indicates the division between northern and southern BIOT MPA. MPA borders occur outside of the boundaries of the main map.
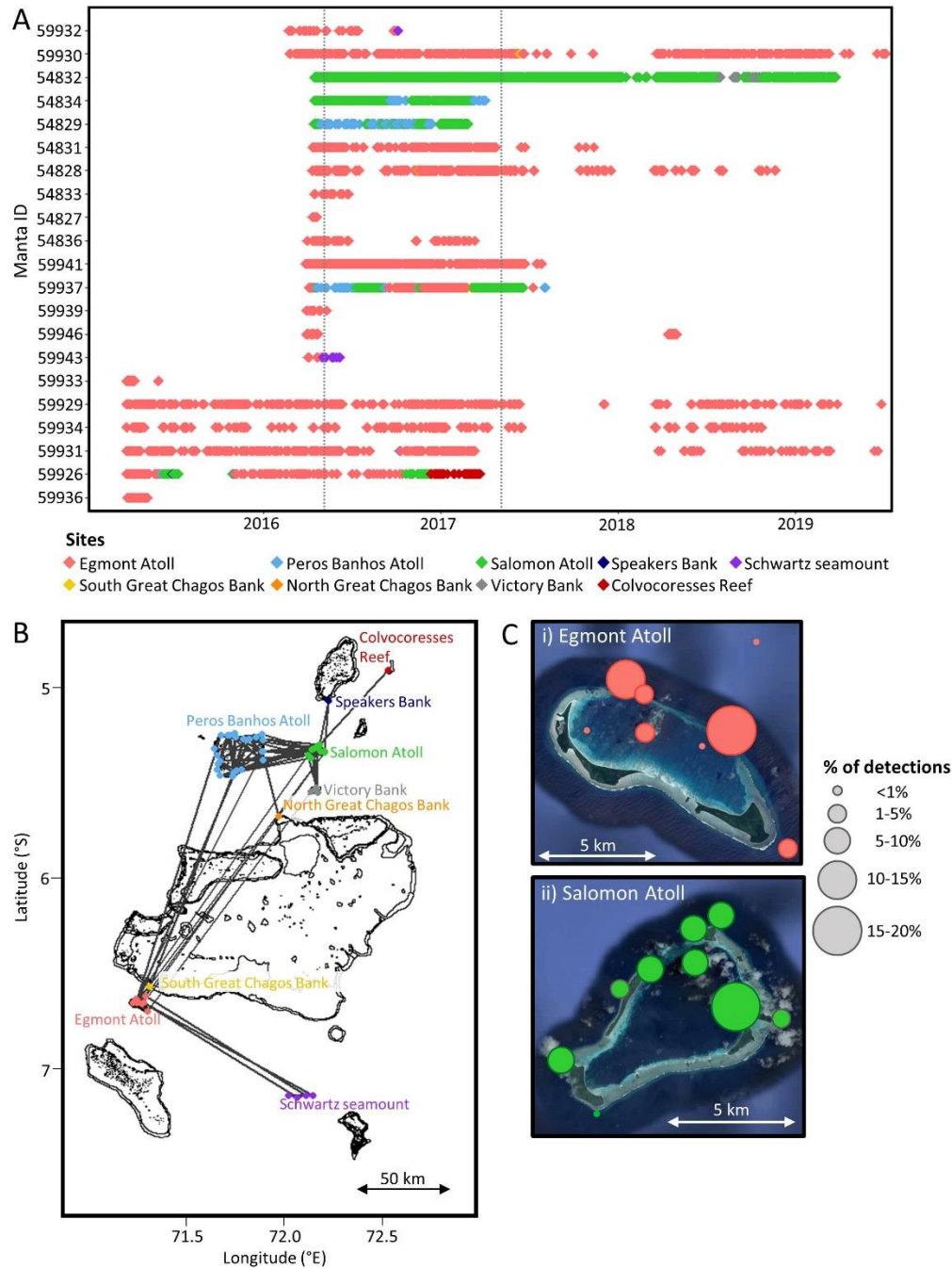
Fig. 2. Summary of acoustic data. A) Acoustic detections over time for each tagged reef manta ray from March 2015 to June 2019 throughout the entire British Indian Ocean Territory Marine Protected Area acoustic array (n=52 receivers). Dashed line indicates period considered in temporal models of occurrence. B) Network map of the BIOT MPA receiver array, indicating movements of all individuals among receivers in the array. Each track starts and ends at a tagged individual's first and last detection respectively. C) Proportion of total reef manta ray detections ecorded for each receiver at the detection hotspots of i) Egmont and ii) Salomon Atolls. Note that at each other site within the BIOT MPA array, no receiver recorded >1% of the total detections.
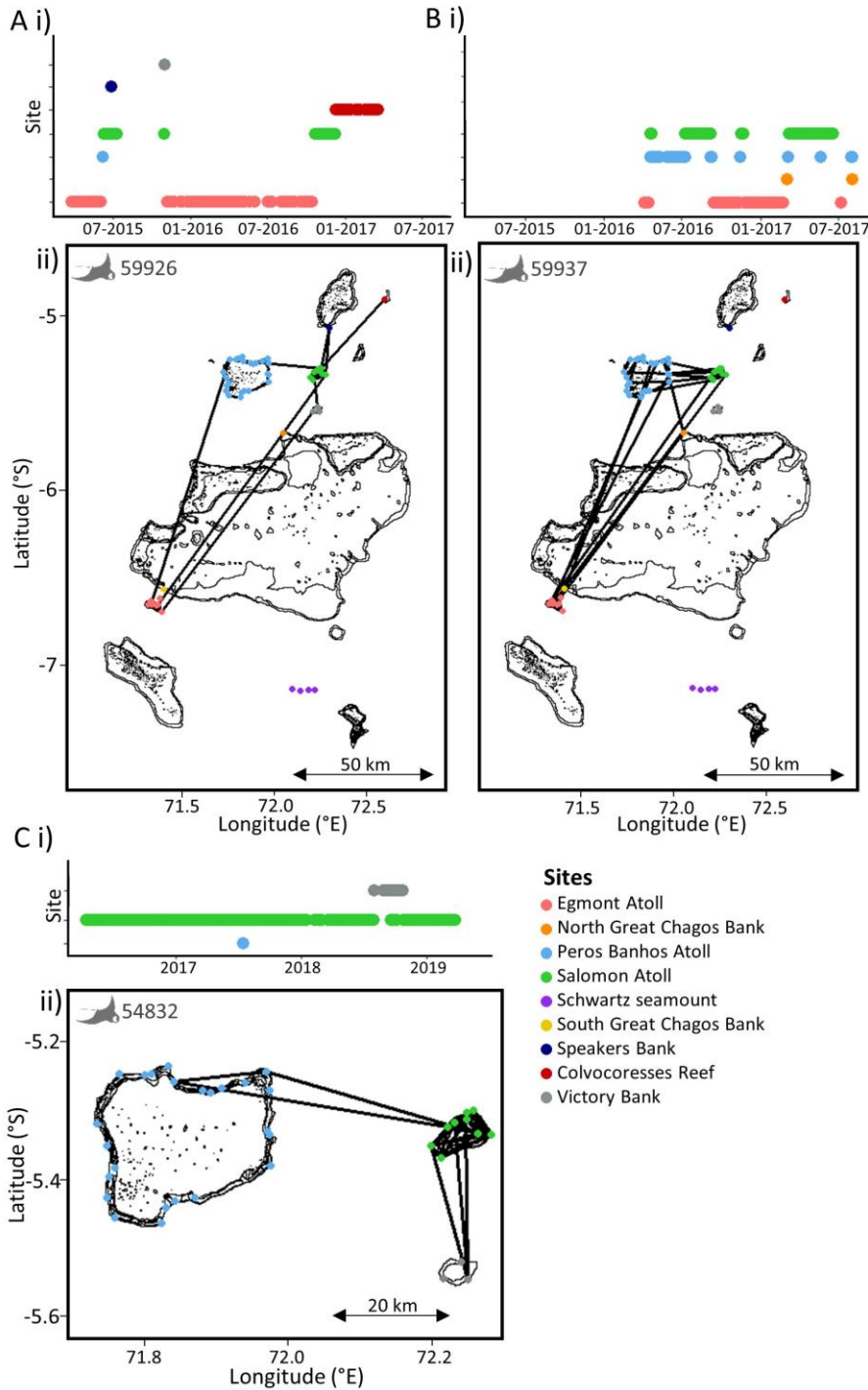
Fig. 3. Detection data for three individual reef manta rays in the British Indian Ocean Territory Marine Protected Area acoustic array: A) 59926 (track time = 728 days); B) 59937 (track time = 494 days); and C) 54832 (track time = 1074 days). (A) and (B) were tagged near Egmont Atoll, and (C) at Salomon Atoll. i) in each instance displays acoustic detections over time, and ii) the network map, for each individual. Note that the time scale and areas represented differ slightly between individuals.
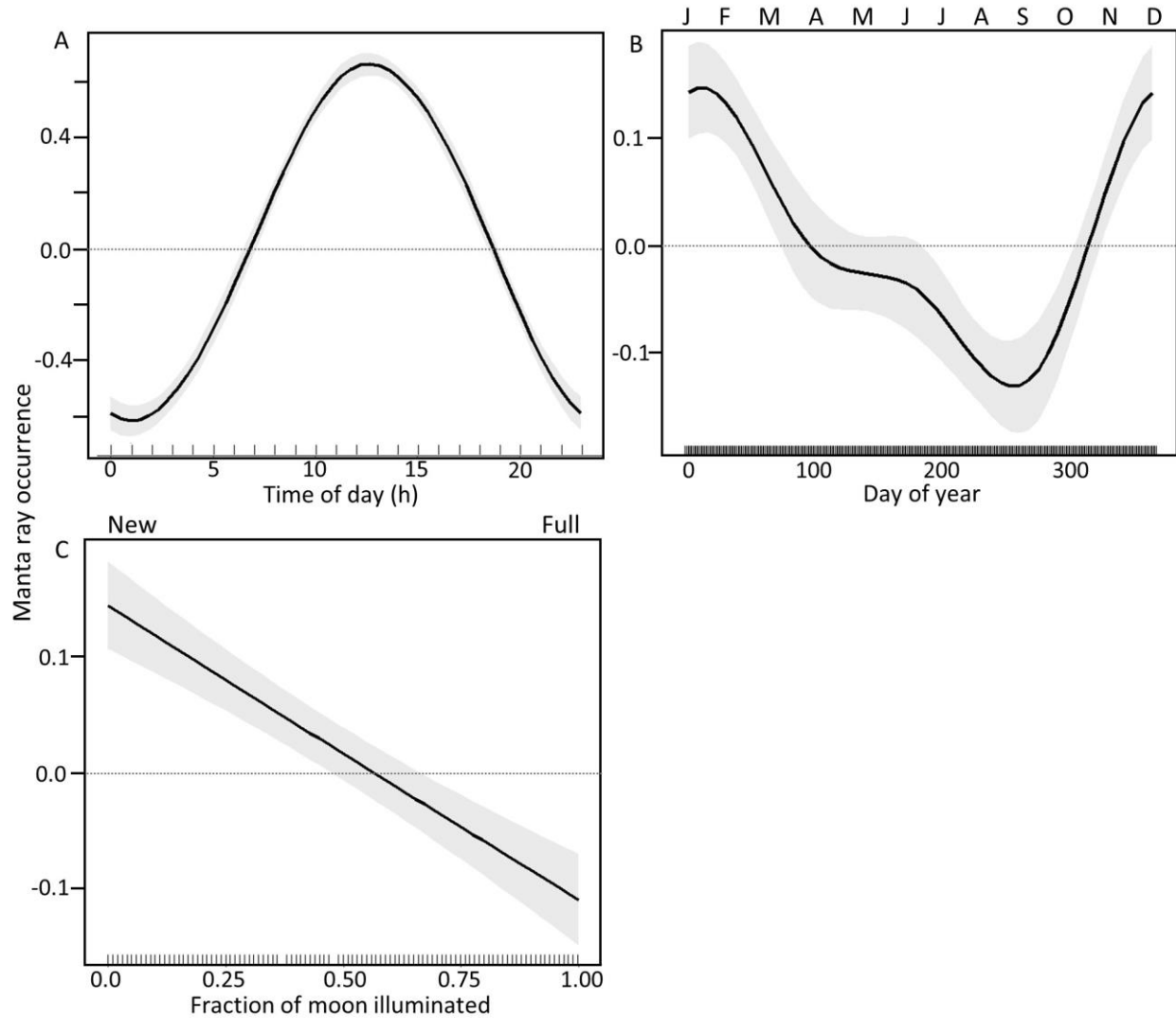
Fig. 4. Marginal effect plots derived from the top ranked binomial GAMM indicating the significant effects of (A) time of day, (B) day of year and (C) fraction of moon illuminated on the relative likelihood of detecting acoustically-tagged reef manta rays within the British Indian Ocean Territory Marine Protected Area receiver array between April 2016 and 2017. For each plot, the y-axis is a relative scale, and its magnitude reflects the importance of each variable. The shaded bar around each line represents the 95% confidence interval.
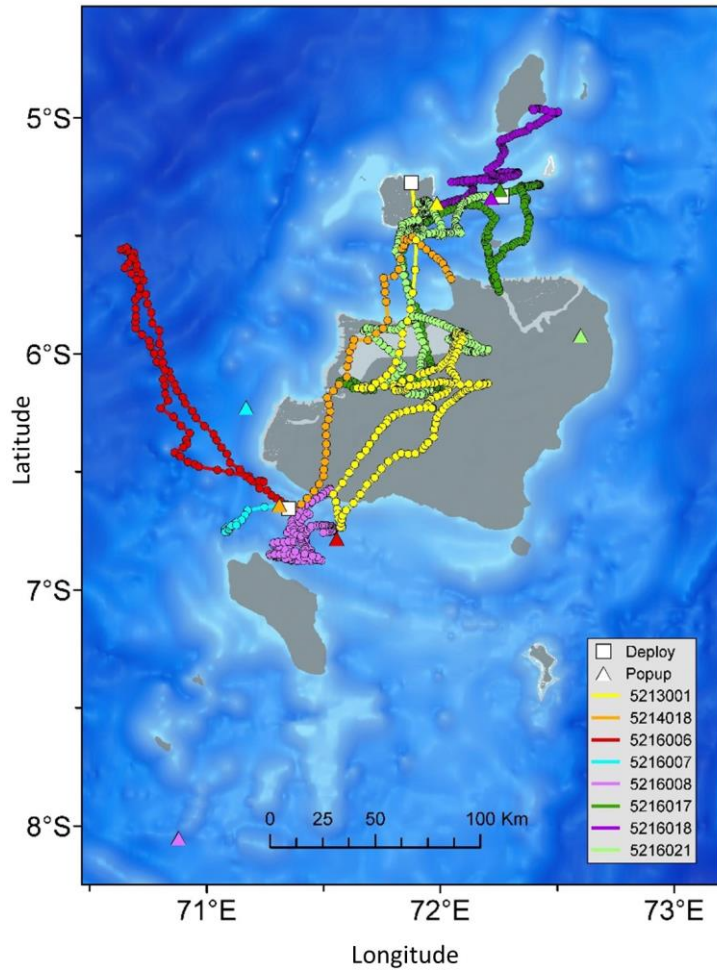
Fig. 5. Daily most-probable positions for eight reef manta rays *Mobula alfredi* fitted with satellite tags within the British Indian Ocean Territory Marine Protected Area. Tracks and pop-up positions are coloured by individual and deployment positions are coloured white. Note that pop-up locations are those first recorded by the tag, and may not accurately reflect the real popup location from the tagged individual as a result of delayed data transmissions. MPA boundaries lay outside of the borders of the map.
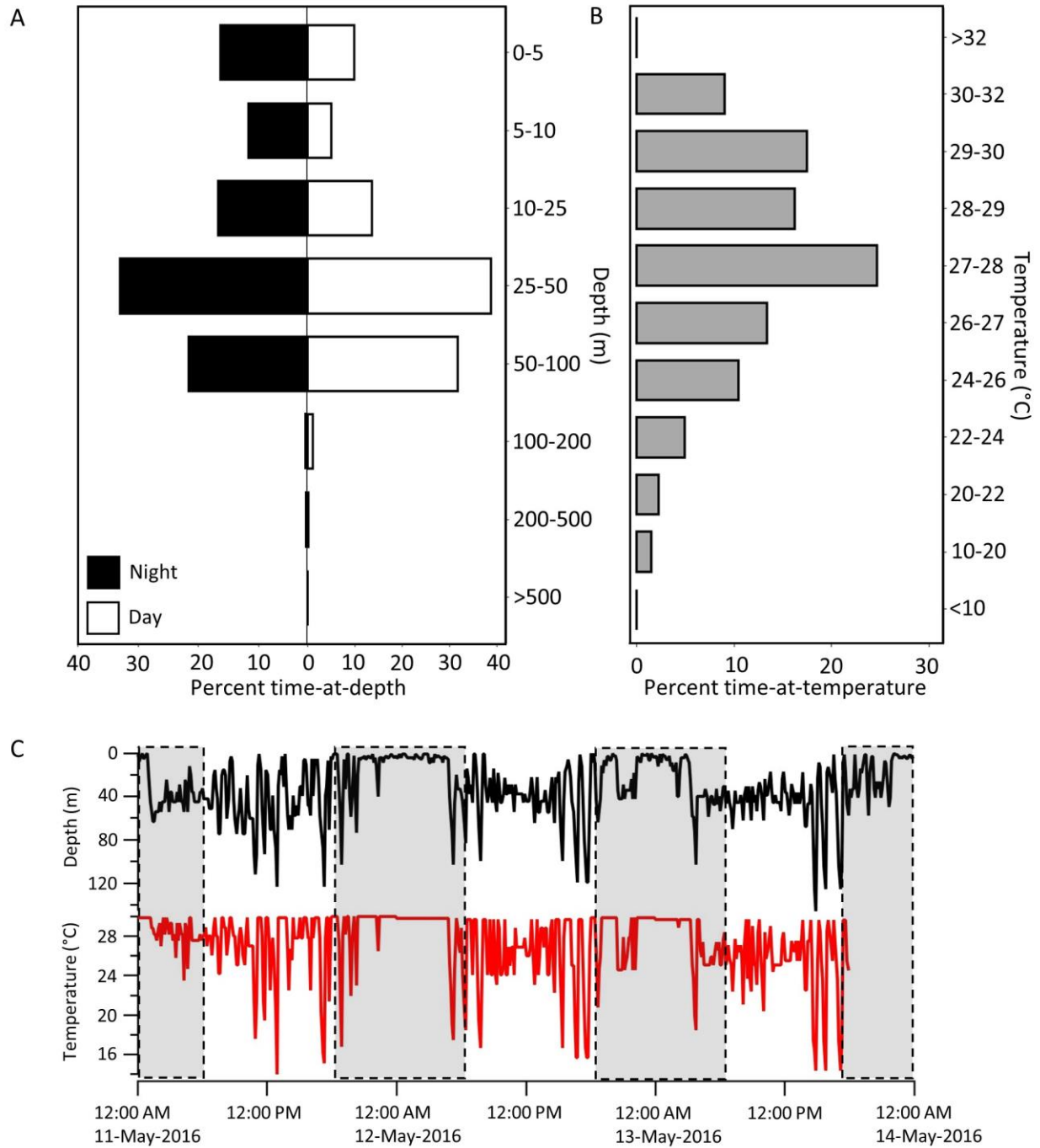
Fig. 6. MiniPAT time series data from reef manta rays *Mobula alfredi* in the British Indian Ocean Territory Marine Protected Area. A) Percent time spent at depth at night (7pm – 7am; grey shading) and day (7am – 7pm). B) Percent time spent at temperature. Both A and B represent summarized data from a total of approximately 405 days of time series data from six individuals. C) An example of raw depth and temperature time series data from individual 5216008, demonstrating both oscillatory and diel vertical movement patterns.

APPENDIX

Table A1. Summary of acoustic receiver deployments within the British Indian Ocean Territory Marine Protected Area between March 2014 and July 2019.

Site name	Receiver deployment	Receiver recovery	Total days deployed	Deployed for full study period (Y/N)	% Total Detections
Colvocoresses Reef	7-Apr-2016	1-May-2017	389	N	0.26
Speakers Bank	29-Mar-2015	7-Apr-2016	375	N	<0.01
Peros Banhos Atoll	20-Mar-2015	24-Apr-2018	1131	N	1.3
Salomon Atoll	26-Mar-2014	23-Jul-2019	1945	Y	62.4
Victory Bank	22-Mar-2015	14-Apr-2016	763	N	0.09
	14-Apr-2016	21-Mar-2019			
North Great Chagos Bank	5-Jun-2016	12-Mar-2018	645	N	<0.01
South Great Chagos Bank	27-Mar-2015	16-Mar-2018	1085	N	<0.01
Egmont Atoll	26-Mar-2015	23-Jul-2019	1580	Y	35.6
Schwartz seamount	12-Apr-2016	28-Apr-2017	381	N	0.4

Table A2. All models involved in the model selection process. Model comparisons were made using Akaike's Information Criterion (AIC). ΔAIC displays deviance in AIC scores from top ranked models. All models are generalized additive mixed models and were ran using the mgcv package in R with manta identity as a random variable. All null models include the random effect.

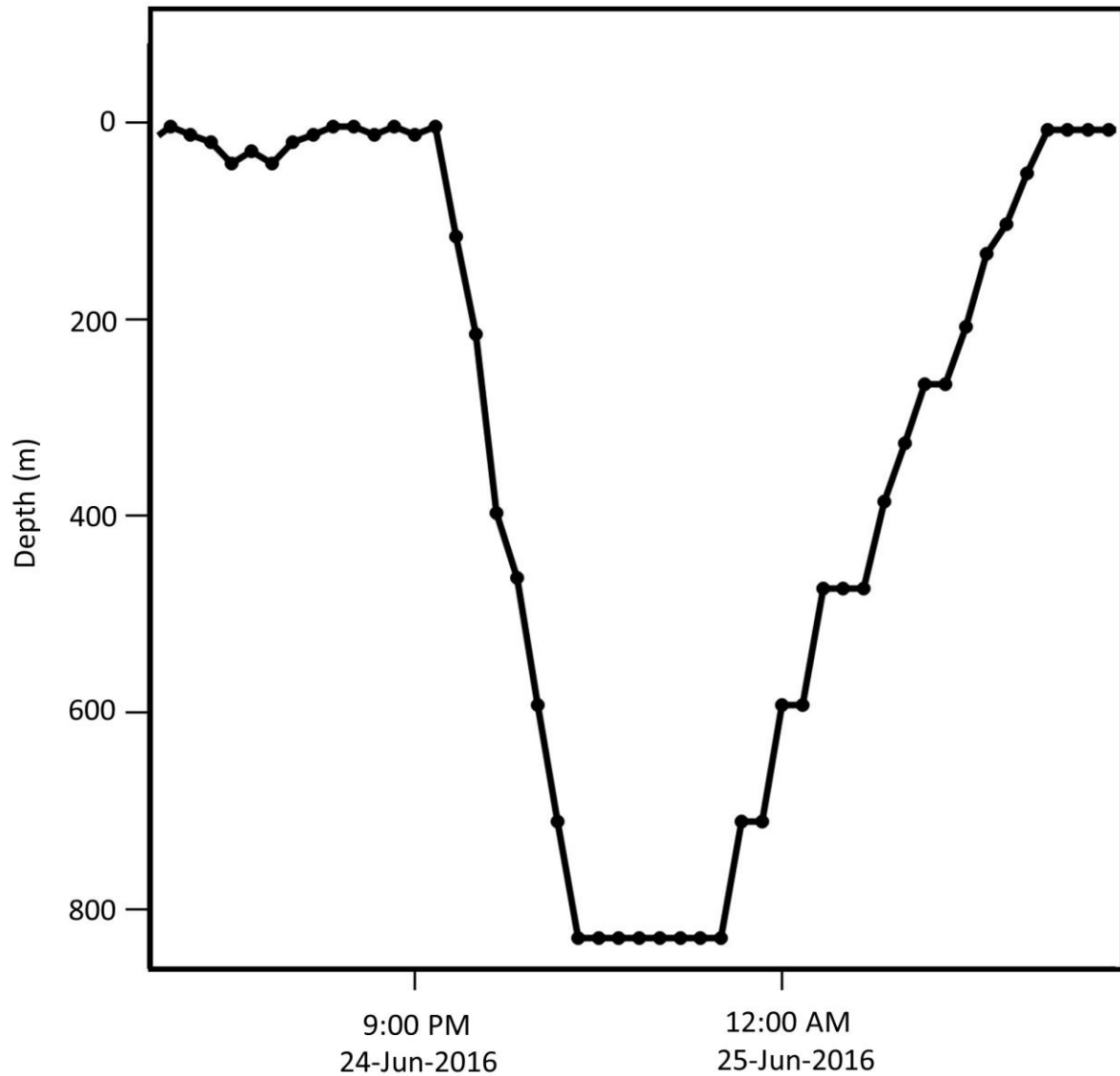| Model	AIC	ΔAIC
Presence ~ ToD + DoY + MoonFraction	57922	0
Presence ~ ToD + DoY	57984	62
Presence ~ ToD + MoonFraction	57973	51
Presence ~ DoY + MoonFraction	59295	1373
Presence ~ DoY	59616	1694
Presence ~ ToD	58031	109
Presence ~ MoonFraction	59605	1683
Presence ~ 1	59662	1740

Fig. A1. A dive to 888 m recorded by a satellite tag (recording depth at 10 minute intervals; Mini-PAT; Wildlife Computers) externally deployed on a reef manta ray (*Mobula alfredi*; individual 5216006) in the British Indian Ocean Territory Marine Protected Area. Tag popped to surface following this record, and it cannot be conclusively determined if the tag reached this depth while still deployed on the manta, or if it was reached after a premature release and transported to depth via alternative means.