2022

Analysing association rates of reef manta rays (Mobula alfredi) situated in Chagos Archipelago

Pollett, L.

Pollett, L. (2022) 'Analysing association rates of reef manta rays (Mobula alfredi) situated in Chagos Archipelago', The Plymouth Student Scientist, 15(2), pp. 42-61.
http://hdl.handle.net/10026.1/20123

University of Plymouth

*The Plymouth Student Scientist, 2022, **15**, (2), 42-61*

Analysing association rates of reef manta rays (*Mobula alfredi)* situated in Chagos Archipelago

Lena Pollett

Project Supervisor: Dr Clare Embling, School of Biological and Marine Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA

Co-supervisor: Joanna L. Harris, University of Plymouth and Manta Trust www.mantatrust.org

Abstract

Reef manta rays (*Mobula alfredi*) are in rapid decline and threatened by multiple anthropogenic pressures. Conservation of this vulnerable marine species requires an understanding of the drivers of their movement patterns and group structuring. Aggregations have been presumed to be a function of resource availability. However, recent studies have suggested that association rates within these areas of aggregation may underpin social behaviour, furthering our understanding of these species' movement and social networking. Here we used acoustic telemetry technology to assess the extent that a group of 26 *M. alfredi* associates within Egmont Atoll, situated within the Chagos Archipelagos, over a one-year period. Social analysis was conducted on this population by assessing dyadic association rates to isolate if these associations were preferred or randomly non-social. A complete but sparse network was found with a high number of detection and dyadic associations observed. However, association rates were not significant, demonstrating a lack of social behaviour and preference between individuals. Furthermore, there was strong site fidelity for Manta Alley, identified primarily as a feeding area, at which the majority of detections and associations (32.1%) were recorded. This suggests that these associations are driven predominantly by site function, such as feeding or individual behaviour in relation to a resource rather than social aspects. Therefore, further research into association rates should focus predominately on cleaning stations and consider how anthropogenic pressures may influence *M. alfredi* social behaviour.

Keywords: Acoustic telemetry, *Mobula alfredi*, aggregation behaviour, association rates, site function

Introduction

Over the last several decades, elasmobranch species have experienced significant and widespread population declines (Braun *et al.*, 2015). It has been estimated that oceanic sharks and rays have incurred a 71% loss in abundance since 1970 (Pacoureau *et al.*, 2021). Within the family Mobulidae, reef manta rays (*Mobula alfredi*) are listed as Vulnerable on the IUCN Red List of Threatened Species (Marshall *et al.*, 2019), where declining populations may be due to persistent and intensifying anthropogenic pressures. These pressures include practices such as target-fisheries, driven by the demand for gill plates in Asian markets (O'Malley *et al.*, 2017), by-catch (Beale *et al.*, 2019; Venables *et al.*, 2021), ocean pollution, habitat degradation (Venables *et al.*, 2020), and unmanaged tourism (Murray *et al.*, 2020). Furthermore, continually rising sea surface temperatures in response to climate change are reducing potential food availability for *M. alfredi* (Richardson, 2008; Harris *et al.*, 2020). These pressures, combined with the conservative life-history traits of *M. alfredi,* including late maturity, slow growth, and low fecundity (Couturier *et al.*, 2014; Harris *et al.*, 2021), make populations extremely vulnerable to rapid declines. Studies on *M. alfredi* have assessed movement patterns, ecology and site usage within populations globally (Couturier *et al.*, 2011; Jaine *et al.*, 2014; Braun *et al.*,2015; Setyawan *et al.*, 2018; Peel *et al.*, 2019), allowing several international, national, and local management strategies for mobulid rays to be implemented in the last decade to facilitate their protection (Beale *et al.*, 2019). Social structuring in organisms can provide greater insight and understanding of their movement patterns, habitat use, disease transmission and genetic exchange (Perryman *et al.*, 2019). However, with the current gap in behaviour research and minimal literature on elasmobranch social structuring, it remains difficult to establish effective conservation methods.

Reef manta rays (*Mobula alfredi*) are large planktivorous elasmobranchs found semi-circumglobally residing within tropical and subtropical waters, commonly as members of highly fragmented regional populations (Harris and Stevens, 2020). Within these regional populations, the home range of individuals varies, where some may exhibit high levels of fidelity to specific sites (Setyawan *et al.*, 2018), yet travel long distances to productive feeding areas where large aggregations (groups) can form (Harris *et al.*, 2020). The merging and splitting of individuals and groups is known as 'fission-fusion' systems (Couzin, 2006). *Mobula alfredi* aggregation behaviour can be best observed at specific sites, known as 'hotspots' (Harris *et al.*, 2021). Aggregations are thought to occur in relation to the exploitation of resources or courtship rituals (Stevens *et al.*, 2018; Harris and Stevens, 2021), as also documented in other elasmobranch species (Klimley,1983; McKibben and Nelson, 1986; Guttridge *et al.*,2012). However, they may also be areas for socialisation between individuals or groups (Perryman *et al.*,2019; MacGlennon, 2008). *Mobula alfredi* have been increasingly identified as social animals in correspondence with their classification of possessing high brain mass to body size, enabling them to form stable, long-lasting social bonds (Jacoby *et al.*, 2012; Perryman *et al.*, 2021).

The formation of social groups may be initiated by both active and passive processes. Individuals may exhibit active preferences by associating more strongly with familiar individuals, as observed in lemon sharks (*Negaprion brevirostris*) (Couzin, 2006; Guttridge *et al.*, 2010; Jacoby *et al.*, 2012). The social preferences between various partners may develop in relation to the context of the association or the behaviour of individuals (Couzin, 2006; Kurves *et al.*, 2014). Benefits of these preferences include competition, predator avoidance and enhanced social learning, which have profound effects on population dynamics (Ward *et al.*, 2005). Therefore, predictable aggregation sites allow unique opportunities to assess association rates, increasing our understanding of movement patterns and social structuring within *M. alfredi* populations (Couturier *et al.*, 2014).

Comprehensive knowledge of the underlying mechanisms and linkages that drive these social networks is required to plan effective conservation strategies for these species. For example, previous studies identified that female adults were the core links within *M. alfredi* social networks in the Republic of the Maldives, suggesting they are the drivers of social structuring within populations (MacGlennon, 2008). Similar observations on *M. alfredi* populations have also been made along the Eastern coast of Australia (Couturier *et al.*, 2014), where a higher female-to-male ratio was found, suggesting females have a greater number of interactions. Further research highlighted that *M. alfredi* form social preferences, where social interactions determine communities and their possible connection with one another (Perryman *et al.*, 2019). Within this study, females were also encountered most frequently at cleaning stations, as opposed to males, which were more likely to be encountered at feeding areas.

These results highlight the importance of incorporating site function when examining associations in elasmobranchs as it helps identify the type of association occurring. However, whilst Perryman *et al.* (2019) demonstrate a clear importance of how social interactions shape a population, the study methodology lacked fine-scale/constrained time intervals for manta interactions (≤ 10 minutes), potentially confounding the results. Interactions can occur over short periods (seconds) and so require small timeframes; however, Perryman *et al*. (2019) timeframe allows for multiple individuals to enter the same area but not cross paths, resulting in no interaction occurring. While combined, these studies provide invaluable insight into manta behaviour, they remain limited temporally and spatially according to when divers and snorkellers were in the water (Dewar *et al.*, 2008). Furthermore, they are invasive techniques as human presence may influence *M. alfredi* movement patterns and, thus, social behaviour. Subsequently, results may be inadequate or limited, shielding the true scale of community structure within these populations. Acoustic telemetry technology, as an alternative or additional method, can be used extensively to track a wide range of individuals and their habitat uses in various selected areas (Setyawan *et al.*, 2018). The technique consists of acoustic receivers containing an integrated hydrophone submerged to detect transmissions of fixed acoustic tags deployed on the tracked individuals (Donaldson *et al.*, 2014). This method could provide invaluable rigorous data, enabling a deeper understanding of manta associations (Venables *et al.,* 2020). However, due to this difference in methodology, multiple elements of fine-scale time intervals should be assessed (1-10 minutes) to establish a precise timescale for which associations are occurring.

Established as a marine protected area (MPA) and no-take zone since 2010 (Sheppard *et al.*, 2012), the Chagos Archipelago is a unique site to observe this population of *M. alfredi*. Understanding the association rates of individuals in this population can help formulate an idea of its network structuring and interpret the impact of excluding direct anthropogenic pressures. Furthermore, globally 94% of

MPAs allow fishing as they are not designated no-take zones (Costa *et al.*, 2016). A valuable opportunity is therefore provided to assess the scale that the fishing industry has on *M. alfredi* behaviour, where this study serves as a reference, comparable to other studies within areas without the extra protection. This will be key to identifying the way in which conservation efforts can be managed and the most effective strategies for their protection.

The present study investigates whether, and to what extent, *M. alfredi* at Egmont Atoll in the Chagos Archipelago associate determining their network structuring and if there are preferences between certain groups. The Chagos Archipelagos is a unique site having extensive marine protection and no influence from direct anthropogenic pressures such as, the presence of tourists or fishing industry which may otherwise alter the mantas' behaviour. Furthermore, the use of passive acoustic telemetry to detect associations between *M. alfredi* at known 'hotspots', together with fine-scale time intervals (≤ 5 minutes), will provide an in-depth insight into the accurate scale and magnitude of the population’s structuring. The study aims to expand the current understanding of *M. alfredi* population dynamics by providing detailed insight into their fine-scale association patterns and long-lasting preferences. Based on the existing literature, we predict a high female-biased ratio, with strong links between females and juveniles. Furthermore, site preference will be an important driver of associations and will further demonstrate the importance of protecting these areas of aggregations to conserve *M. alfredi*.

Method

Study site

The Chagos Archipelago is located 450km South of the Maldives in the Central Indian Ocean, lying at the southernmost end of the Lakshadweep–Maldives–Chagos ridge (Sheppard, 2012). Covering 550 00km^2, it is comprised of seven atolls, several large, submerged banks and over 60 low-lying islands (Harris *et al.*, 2021). The zone is a designated no-take marine protected area (MPA) and contains the world's largest contiguous undamaged reef area (Sheppard, 2012). Egmont Atoll is located southwest (Figure 1), containing narrow connecting channel systems surrounding a lagoon system cut off from the ocean by reef crests and flats (Harris *et al.*, 2020).

Data collection

Acoustic tag deployment

Primary data for this study was collected by the Manta Trust in 2019 and 2020. A total of 32 individual reef mantas were tagged at Egmont Atoll, 20 between November 19, 2019, and December 3, 2019, and a further 12 were deployed in March 2020. Due to the staggered establishment of the acoustic receiver array (see section Acoustic receiver array), only acoustic tag detections recorded after the full array was in place are considered in the current study. These data are all tag detections that occurred between April 2020 and April 2021, when 30 tags were at liberty. VEMCO V16-4x acoustic transmitter tags (Vemco Inc.) were deployed on the right dorsal musculature using a modified Hawaiian hand sling while swimming. Before the tagging process, all manta's sex and size class (to allow an estimate of maturity) were recorded along with a photograph of their unique spot pattern on their dorsal side. Size class was split into categories 1-4 for females and 1-3 for males based on size (cm) and external anatomical indicators of individuals shown in table 1, which was adapted from Stevens (2016) categorisation method. All activities were approved by the University of Plymouth Animals in Science Ethics Committee under permit ETHICS-24-2019 and ETHICS-37-2020.

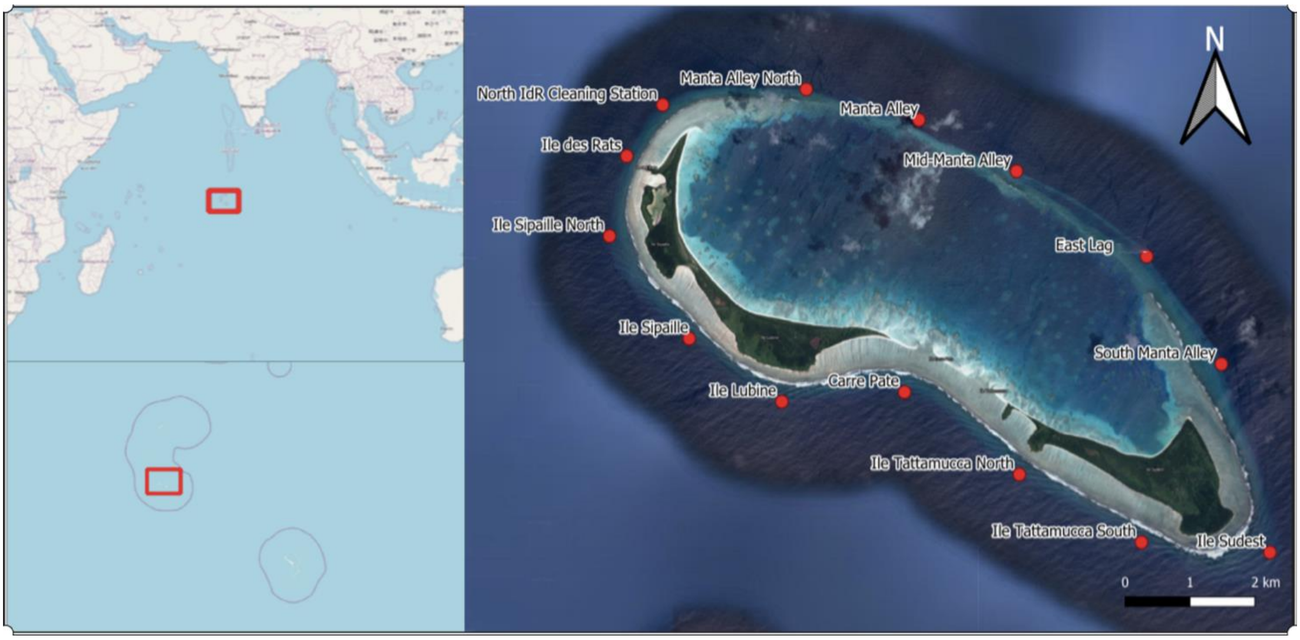


Figure 1: The Chagos Archipelago located in the Central Indian Ocean; British Indian Ocean territory indicated in the red box in top left image. Chagos Archipelagos with Egmont atoll indicated in the red box bottom left image. Egmont atoll with 14 acoustic receivers (AR) located around the surrounding atoll, indicated by red dots in the right image (adapted from Harris *et al.*, 2020). Base map data left: OpenStreetMap ©2022. Base map data right: Google ©2022 Maxar Technologies, Data SIO, NOAA, U.S. Navy, NGA, GEBCO, Imagery ©Landsat / Copernicus, Maxar Technologies, U.S. Geographical Survey, Map data ©2022

Table 1: Categorisation of *M. alfredi* using class sizes as indicators of maturity status (adapted and reproduced with kind permission from Stevens, 2016).

Size		Females			Males		
Size class	Disc width (cm)	Life stage	Maturity status	External anatomical indicators of maturity status	Life stage	Maturity status	External anatomical indicators of maturity status
1	< 210	Juvenile	Immature	None	Juvenile	Immature	Claspers very small and don't extend past posterior edge of pelvic fins
2	210 - 270	Juvenile	Immature	None	Juvenile / Subadult	Immature	Claspers small, not calcified, but may show signs of enlarging and extending past the base of the pelvic fins during the transition to the next size class
3	271-320	Juvenile	Immature	None	Adult	Mature	Claspers fully enlarged and calcified
4	> 320	Adult	Mature	May exhibit mating scars and/or pregnancy bulge	N/A	N/A	N/A

Acoustic receiver array

An acoustic array of 14 VR2W-69 kHz omnidirectional acoustic receivers (Vemco Inc.) was deployed at sites known as manta aggregation areas. Five of the receivers were deployed in November 2019, and the rest were deployed in March 2020. Site function for each site was recorded (Table 2). The depths of the receivers ranged from 12 to 22m below the sea surface. Acoustic tags were detected within approximately 160m radius of the receiver (Harris *et al.,* 2021).

Table 2: Site functions, characteristics and pair associating most frequently at each site.

Abbreviation	Site	Site function	Site characteristics	Interlist	Demographic pairs
CP	Carre Pate	Feeding	Sandy bay	131	F3:F2
EL	East Lag	Feeding	Shallow (<15m) close to drop off	46	F4:M3
IdR	Ile des Rats	Feeding	Shallow (<15m) close to drop off	9	F3:F2
IL	Ile Lubine	Feeding	Shallow (<15m) close to drop off	131	F3:F2
ISi	Ile Sipaille	Feeding	Shallow (<15m) close to drop off	123	F3:M2
ISN	Ile Sipaille North	Feeding	Shallow (<15m) close to drop off	68	F3:F3
ISu	Ile Sudest	Cruising	Shallow (<15m) close to drop off	119	F3:F3
ITN	Ile Tattamucca North	Cruising	Steep rocky slope	274	F2:M2
ITS	Ile Tattamucca South	Cruising	Steep rocky slope	115	F3:F3
MA	Manta Alley	Feeding	Outside the lagoon inlet. Location depth approximately 65m	34	F2:M3
MAN	Manta Alley North	Feeding	Shallow (<15m) close to drop off	17	F3:M2
MMA	Mid-Manta Alley	Feeding	Shallow (<15m) close to drop off	116	F3:F4
NICS	North IdR Cleaning Station	Cleaning	Big bommie at 10m close to the drop off	9	F3:F2
SMA	South Manta Alley	Feeding	Shallow (<15m) close to drop off	309	F3:F4

Acoustic tag analysis

Detection data was processed into Tag ID, Date, and Timestamp for when an individual pinged a receiver and site. The data was analysed in R 3.5.2 (R Core Team, 2021) with code written by Joanna Harris to assess the frequency of associations between specific individuals within the detection range of each acoustic receiver. The data were transformed using the R package dplyr (Wickham *et al.*, 2021) to compress data into 5-minute bins and identify when individuals were present within the same 5-min bin. Individuals were acknowledged as associating with one another if more than one acoustic tag was detected within this area for ≤ 5 minutes. This timeframe was chosen after assessing the mean association real rate with mean randomised rates between the time periods 1- 10 minutes analysed using SOCPROG version 2.9 (uncompiled; Whitehead, 2009). Only minor changes in significance were shown, and therefore 5 minutes was chosen to analyse association rates. Furthermore, the timeframe was also chosen based on the ping rate of the acoustic tags. The minimum and maximum ping rates were 30 to 90 seconds, respectively, allowing a gap of up to three minutes between detections of mantas that are at the same location at the same time. This gap between detections may also be influenced by the time of arrival of the two individuals and their position within the detection range of the receiver (Harris and Stevens, 2021); therefore, more conservative five-minute bins were used to ensure overlaps in detections were not missed.

The results were then summarised into the total recorded number of associations between demographic groupings divided by the total number of possible associating pairs and the total number of associations over months divided by the possible number of associating pairs present within each month to mitigate bias in the results. Social analyses were carried out using SOCPROG version 2.9 (uncompiled; Whitehead, 2009) run in Matlab (version 8.2.0.29). Association matrices were produced using the simple ratio index (SRI), where x is the number of sampling periods in which both manta rays a and b were associated, y_{ab} is the number of sampling periods in which both manta rays were detected but not associated, and y_a and y_b are the number of sampling periods in which only a and b, respectively are identified calculated as:

$$x/x + y_{ab} + y_a + y_b$$ (Ginsberg & Young, 1992)

A Monte Carlo randomised method (Bejder *et al.*, 1998) was used to test if associations were preferred or random. The test generates permutations of the original association matrix by randomly rearranging nodes. Individuals are identified as associating if the coefficient of variation (CV) of the observed association indices is greater than the random data (CVr). The proportion of non-zero elements is also compared between the observed and random data to assess for avoidance between individuals.

Results

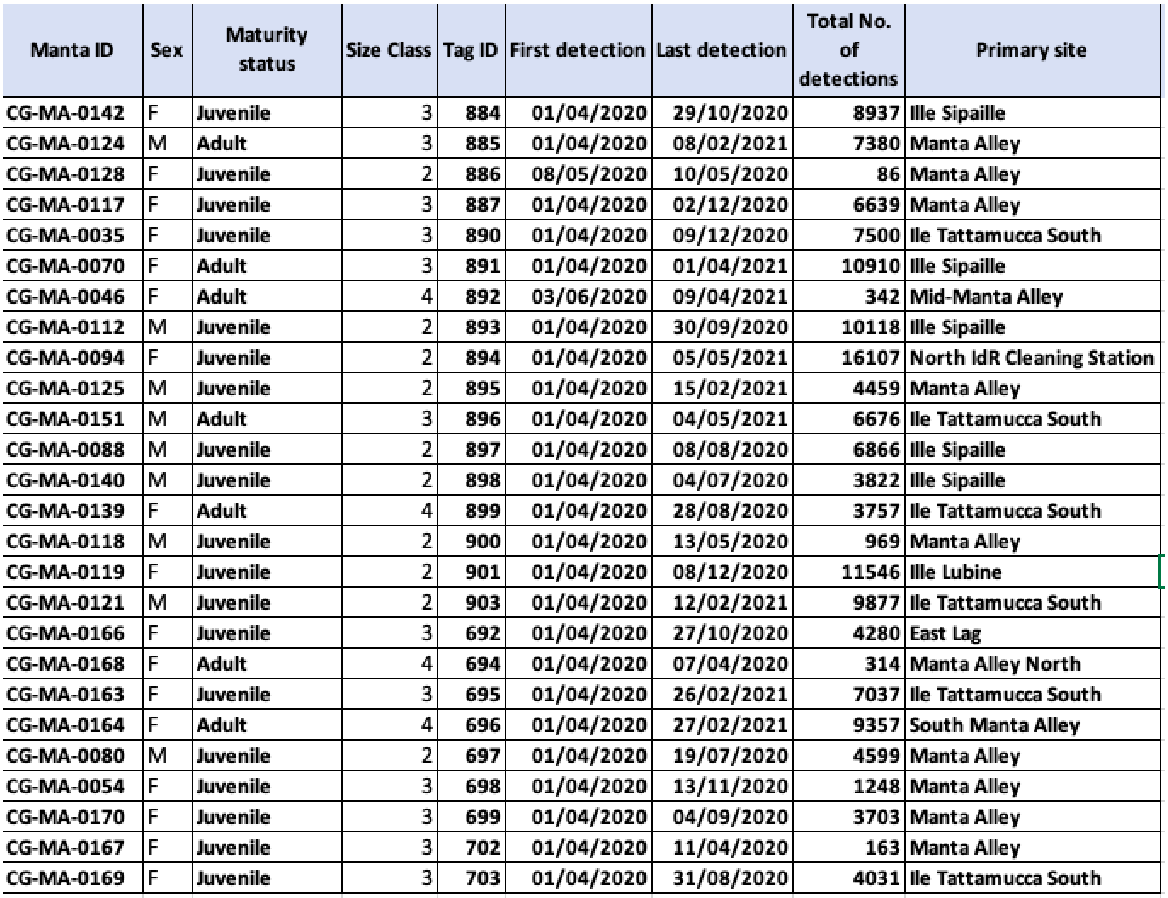
Detection summary

The data used was between the periods 1st April 2020 to 5th May 2021. Overall, 26 acoustic tags of the possible 30 were detected throughout the course of the data collection. The four undetected tags have been labelled as 'unknown' as they were unable to distinguish them as lost or emigration of the individuals from the study area. Detected acoustic tags were deployed on seventeen females (adults=4, juveniles=13) and nine males (adults=2, juveniles=7). A total of 150,723 detections were recorded of the 26 tagged *M. alfredi* individuals across all 14 sites during the study period. The highest number of detections from a single individual was 16,107 by a juvenile female (Manta-ID CG-MA-0094), shown in Table 3. The same individual also had the most frequent visits to 5 of the sites. Males were found to have the highest mean number of detections (6085) compared to female mean detections (5644). Manta Alley was the most visited site, with a total of 20,876 (13.8%) detections from 25 of the individuals (Table 4).

Total associations summary and between demographic groupings

A total of 17,354 associations were recorded between 275 different pairs of *M. alfredi*. From this total, the highest mean number of dyadic associations between males was 67.6 (40%), followed by mixed-sex associations at 55.4 (32%) and female pairs with 47.4 (28%) (Table 5).

Table 3: Summary of M. alfred acoustic tag details, detection and primary site



Manta ID	Sex	Maturity status	Size Class	Tag ID	First detection	Last detection	Total No. of detections	Primary site
CG-MA-0142	F	Juvenile	3	884	01/04/2020	29/10/2020	8937	Ille Sipaille
CG-MA-0124	M	Adult	3	885	01/04/2020	08/02/2021	7380	Manta Alley
CG-MA-0128	F	Juvenile	2	886	08/05/2020	10/05/2020	86	Manta Alley
CG-MA-0117	F	Juvenile	3	887	01/04/2020	02/12/2020	6639	Manta Alley
CG-MA-0035	F	Juvenile	3	890	01/04/2020	09/12/2020	7500	Ile Tattamucca South
CG-MA-0070	F	Adult	3	891	01/04/2020	01/04/2021	10910	Ille Sipaille
CG-MA-0046	F	Adult	4	892	03/06/2020	09/04/2021	342	Mid-Manta Alley
CG-MA-0112	M	Juvenile	2	893	01/04/2020	30/09/2020	10118	Ille Sipaille
CG-MA-0094	F	Juvenile	2	894	01/04/2020	05/05/2021	16107	North IdR Cleaning Station
CG-MA-0125	M	Juvenile	2	895	01/04/2020	15/02/2021	4459	Manta Alley
CG-MA-0151	M	Adult	3	896	01/04/2020	04/05/2021	6676	Ile Tattamucca South
CG-MA-0088	M	Juvenile	2	897	01/04/2020	08/08/2020	6866	Ille Sipaille
CG-MA-0140	M	Juvenile	2	898	01/04/2020	04/07/2020	3822	Ille Sipaille
CG-MA-0139	F	Adult	4	899	01/04/2020	28/08/2020	3757	Ile Tattamucca South
CG-MA-0118	M	Juvenile	2	900	01/04/2020	13/05/2020	969	Manta Alley
CG-MA-0119	F	Juvenile	2	901	01/04/2020	08/12/2020	11546	Ille Lubine
CG-MA-0121	M	Juvenile	2	903	01/04/2020	12/02/2021	9877	Ile Tattamucca South
CG-MA-0166	F	Juvenile	3	692	01/04/2020	27/10/2020	4280	East Lag
CG-MA-0168	F	Adult	4	694	01/04/2020	07/04/2020	314	Manta Alley North
CG-MA-0163	F	Juvenile	3	695	01/04/2020	26/02/2021	7037	Ile Tattamucca South
CG-MA-0164	F	Adult	4	696	01/04/2020	27/02/2021	9357	South Manta Alley
CG-MA-0080	M	Juvenile	2	697	01/04/2020	19/07/2020	4599	Manta Alley
CG-MA-0054	F	Juvenile	3	698	01/04/2020	13/11/2020	1248	Manta Alley
CG-MA-0170	F	Juvenile	3	699	01/04/2020	04/09/2020	3703	Manta Alley
CG-MA-0167	F	Juvenile	3	702	01/04/2020	11/04/2020	163	Manta Alley
CG-MA-0169	F	Juvenile	3	703	01/04/2020	31/08/2020	4031	Ile Tattamucca South

Table 4: Total number of detections at each site.

Site	Number of detections	Number of individuals detected
Carre Pate	11789	23
East Lag	8567	25
Ile des Rats	9724	23
Ile Lubine	13978	22
Ile Sipaille	18316	22
Ile Sipaille North	10708	23
Ile Sudest	3170	21
Ile Tattamucca North	6257	23
Ile Tattamucca South	10454	23
Manta Alley	20876	25
Manta Alley North	10108	23
Mid-Manta Alley	6030	24
North IdR Cleaning Station	11270	22
South Manta Alley	9476	24
Grand Total	150723	N/A

Table 5: Total and mean number of associations separated by sex classes

Sex classes	Total associations	Possible number of associating pairs	Mean number of associations
Female: Female	6451	136	47.4
Male: Male	2433	36	67.6
Female: Male	8470	153	55.4
Grand total	17354	325	170.4

Separating associations by size and sex class indicated that juvenile female pairs (size class=2) had the greatest mean number of associations with a total of 118.7 associations, followed by juvenile females (size class=2) with juvenile males (size class=2) (figure 2). The least associating pairs were found between female adults (size class=4).

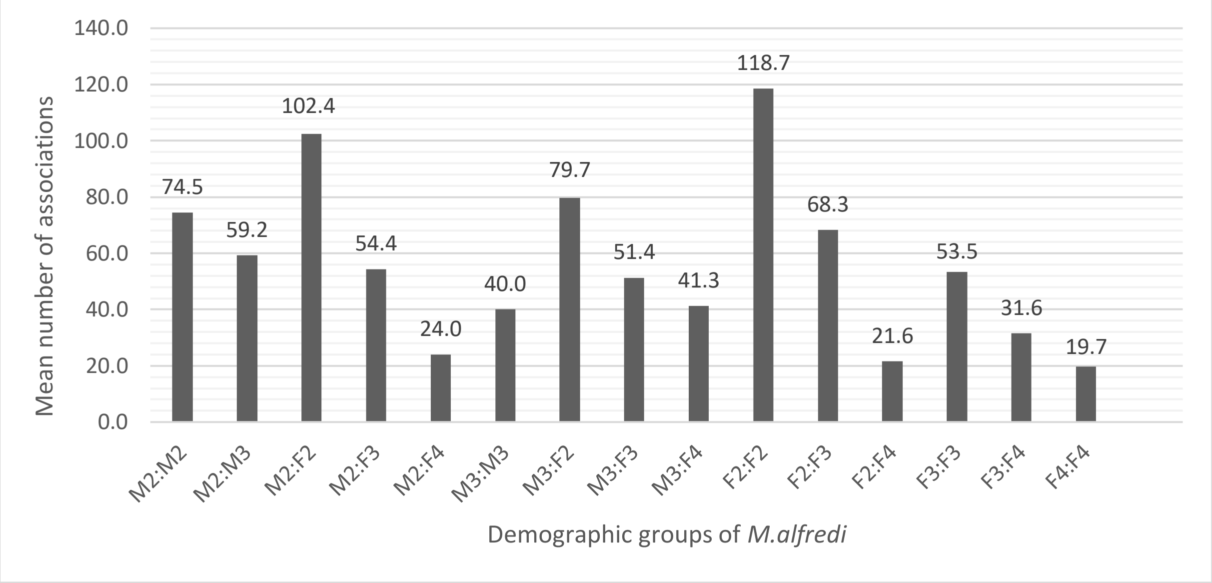


Figure 2: Mean number of associations between demographic groupings separated by sex and size class. F2= Female size class 2, F3= Female size class 3, F4= Female size class 4, M2= Male size class 2, M3= Male size class 3.

Associations between months

May 2020 had the highest mean number of associations from the total possible associating pairs with 22.9. This had a rapid decline in June 2020, followed by a plateau until fluctuating again between November 2020 to April 2021. The months showing the fewest associations were February 2021 (=1.1) and April (=1), with the last association recorded on the 27th April 2021. Overall, there was a decline in associations from the start to the beginning of the study period, as also observed in the detection rates, with a large range between certain months.

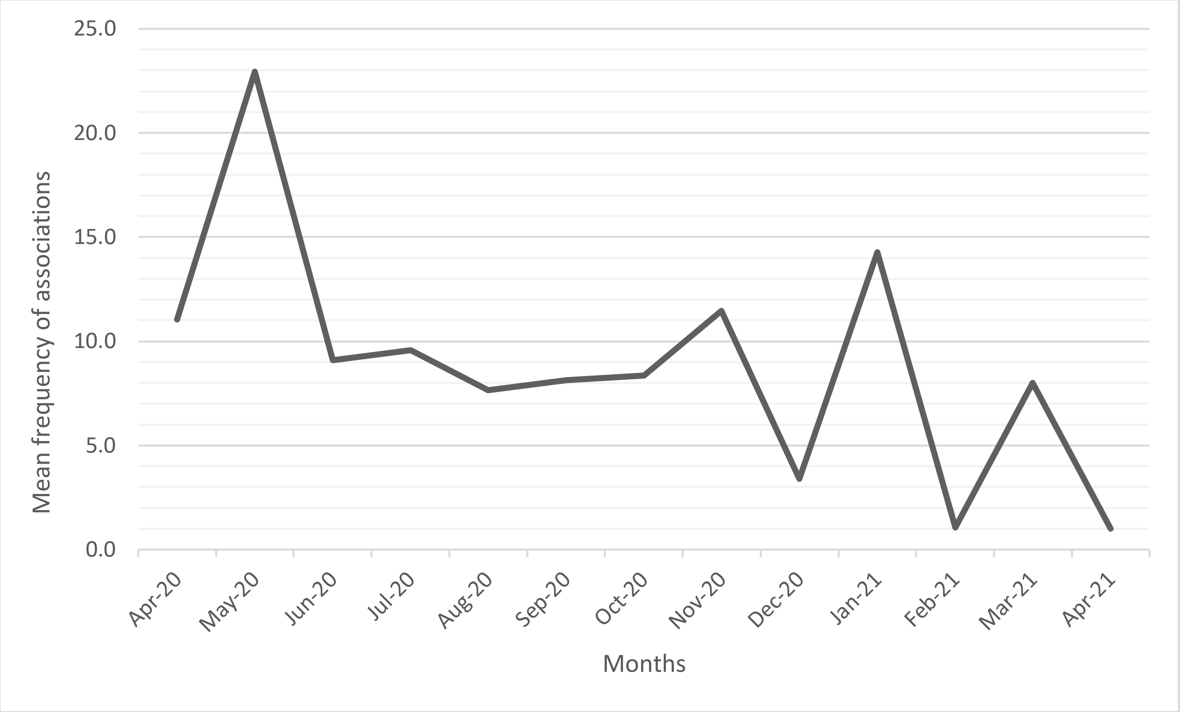


Figure 3: Total mean number of associations over each month divided by the possible number of interacting pairs based on detection of individuals between April 2020 to April 2021.

Associations and demographics between sites

The site found to have the highest percentage of associations was Manta Alley (32.1%), followed by Manta Alley North (13%) and Ille Sipaille (8.9%), as shown in figure 4. Overall, juveniles most frequently associated with each other across 10 of the 14 sites. These associating juveiles were either between female or mixed-sex pairs. Manta-ID CG-MA-0119 and Manta-ID CG-MA-0070 (juvenile female size classes 2 and 3) were found to associate most frequently at both Carre Pate and Ile Lubine. A further two juvenile females (size classes=2 and 3) with Manta-ID CG-MA-0094 and Manta-ID CG-MA-0142 were found associating most frequently at North IdR Cleaning Station and Ile des Rats (Table 2). The pair associating at Manta Alley most frequently were Manta-ID CG-MA-0124 (Male size class=3) and Manta-ID CG-MA-0094 (Female size class= 2).

Are these preferred associations or random aggregations?

The coefficient of variation of the observed indices was significantly similar to the mean of the random data. (Monte Carlo test: CV= 0.744, CVr= 0.744, P>0.05, one-tailed). No clear preferred associations were found between sex class, size class or between sites except for Manta Alley, which showed to have a significant difference between the observed and the random data; however, no statistical significance was found (Monte Carlo test: CV= 1.03, CVr= 0.001, P>0.05, one-tailed). Additionally, all tests showed no difference between the proportion of non-zero elements between the real and random datasets, indicating no avoidance.

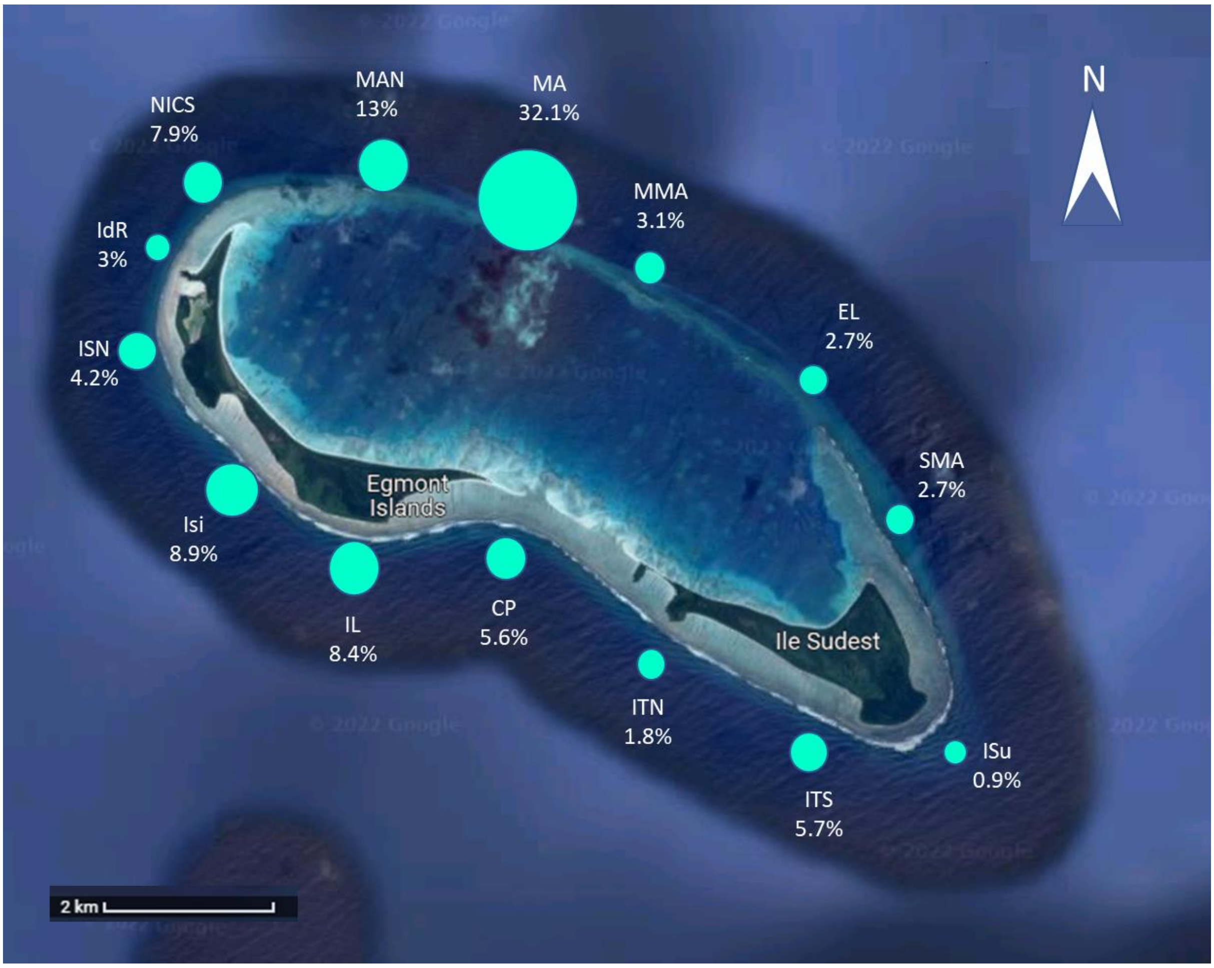


Figure 4: Percentage associations of *Mobula alfredi* across sites surrounding Egmont atoll. Dots identify locations of the acoustic receivers (AR), and size corresponds to the percentage of associations occurring across sites. Base map data: Google ©2022 Data SIO, NOAA, U.S. Navy, NGA, GEBCO, Landsat / Copernicus, Maxar Technologies, Imagery ©2022 TerraMetrics, Map data ©2022.

Discussion

Research outcomes

Overall, *M. alfredi* detection rates at Egmont atoll are frequent, which supports previous reports that Egmont atoll provides key habitat for these species (Andrzejaczek *et al.*, 2020; Harris *et al.*, 2021). However, association patterns were found to be randomly distributed when analysing the population. These results suggest that the associations are not preferred but are random aggregations due to similarities in habitat use or the utilisation of resources. Although not significant, these findings provide data on movement patterns of this population surrounding Egmont atoll and the importance of particular sites. These findings, therefore, will contribute to the limited data on drivers of aggregation behaviour of *M. alfredi* in certain areas, which will influence conservation management strategies for these vulnerable species.

Importance of site function

High detection rates observed across all sites may be a result of passive habitat preference or site fidelity in relation to the function of the site. Aggregation behaviour is commonly a result of animals being drawn to aggregate because of a resource such as food or specific site requirements (Jacob *et al.*, 2012). Feeding grounds are areas of large aggregations of *M. alfredi* having high plankton prey density (Richardson, 2008; Armstrong *et al.*, 2016). Overall, 71% of the study areas were categorised as feeding grounds, which included Manta Alley, Manta Alley North and Ile Sipaille. These three sites all showed the highest association rates across all sites, with Manta alley showing 32% of the total associations, indicating a high level of site fidelity. Aggregations within this area have observed 40+ individuals feeding at one time and were found to have no indications of cleaning activity (Harris *et al.*, 2021). MacGlennon's (2008) study in the Republic of the Maldives found significant associations at locations restricted to behaviours such as cleaning, courtship and travelling but not feeding. Furthermore, few *M. alfredi* engaged in cleaning behaviour together were also found feeding together (MacGlennon, 2008). This suggests feeding behaviour maybe exclusively an individual activity that does not incorporate preferred social assocaitions but random assocaitions as a result of aggregations. However, cleaning stations can be areas of important socialisation among individuals, with observations of *M. alfredi* interacting with other mantas for more extended periods, only engaging in cleaning activity for short periods (Stevens, 2016). Here, the only cleaning area, North IdR cleaning station (NICS), was found to have few associations (7.9%), which suggests they may be used solely for resource purposes within this population. Furthermore, 21% of the sites within this study were categorised as cruising grounds. Two of these sites (Ile Sudest and Ile Tattamucca North) showed the lowest percentages of associations (<2%), which may suggest they are predominately areas where aggregation behaviour does not occur. This may be because they are only passed during travel and not related to a particular resource. These findings highlight that site function is an important aspect to consider when analysing association rates in *M. alfredi.* Furthermore, although the cleaning station within this population showed no significance in association rates, there should still be a focus on cleaning stations when examining social behaviour in *M. alfredi* populations in future studies.

Population dynamics and demographics

Overall, a highly biased female sex ratio was found during tagging (1.9:1), which was expected as it has been identified in previous studies (Couturier *et al.*, 2014; Marshall *et al.*, 2011; Perryman *et al.*, 2019). Juvenile females (Manta-ID CG-MA-0094) showed the highest number of detections at five of the fourteen sites, indicating high site fidelity. Furthermore, two pairs associating most frequently at four of the sites were all females. These findings agree with previous studies that have shown female elasmobranch, including *M. alfredi*, to show philopatry behaviour and higher site fidelity than males (Marshall *et al*., 2011; Stevens, 2016). This sex-specific site selection may be as a result of factors including proximity to food sources, birthing grounds, and reproduction opportunities (Marshall & Bennett, 2010). McCauley *et al.* (2014) highlighted the reliance *M. alfredi* have on specific sites for such factors and how this may be altered in disturbed settings. Therefore, species showing a high degree of site fidelity must be carefully managed as fishing impacts or other anthropogenic factors can have more directed effects on the depletion of individuals in a specific region (Marshall *et al.*, 2011).

Males showed the highest mean number of detections and associations across all sites. While male elasmobranchs tend to show male-biased dispersal (Pardini *et al.*, 2001; Daly-Engel *et al.*, 2012; Roycroft *et al.*, 2019; Phillips *et al.*, 2021), the majority of tagged male *M. alfredi* were found to stay within or near Egmont atoll as shown by their last detection date. This frequent male detection may also be a result of the majority of study sites being categorised as feeding areas. Comparatively, Berumen *et al.*'s (2014) study also identified a male-bias in whale sharks' (*Rhincodon typus*) feeding aggregations despite a female bias sex ratio within the population. Conversely, Perryman *et al.*'s (2019) study observed that female *M. alfredi* were encountered most frequently at cleaning stations, as opposed to feeding areas. This may imply *M. alfredi* male dominance in feeding areas, possibly identifying a further line of inquiry into the demographics of feeding behaviours in future studies. Furthermore, previous studies identified that females show strong preference with each other and were the core links within social networks, observed best within cleaning stations (MacGlennon, 2008; Perryman *et al.*, 2019). These findings further highlight that site function is an important factor when analysing social structuring in *M. alfredi* populations.

Juveniles were found to associate most with one another overall, either between females or mixed-sex pairs. This was predicted based on Perryman *et al.*'s (2019) findings demonstrating long-term preferences between *M. alfredi* juveniles being attributed to factors including age/maturity and similar phenotypes. Juveniles were also observed associating most frequently across the majority of the study sites. Juvenile *M. alfredi* have also been found to show high site fidelity attributed to factors such as foraging (Couturier *et al.*, 2018), shelter, and refuge from predators (e.g., large sharks) (Marshall & Bennett, 2010). Furthermore, due to their small sizing, juveniles are unable to emigrate the vast distances that full-grown adults do. Therefore they reside within particular areas with easy accessibility to feeding grounds (Stevens, 2016). Similar factors also influence other juvenile elasmobranchs (Gruber *et al.*, 2001; Heupel *et al.*, 2018); however, Guttridge (2010) demonstrated active partner preferences were driving association patterns in juvenile free-ranging lemon sharks. Although social behaviour was not observed in this study, it is possible that juveniles may learn the locations of the desired feeding and cleaning grounds by simply following other juveniles or adults, reflecting simple imitation behaviour. Further research should therefore focus on *M. alfredi* juvenile assocaitions with the underlining need for greater protection of the aggregation sites they frequestly use.

Emigration and movement patterns

The general decline in associations over the study period is consistent with a decline in detection rate and high emigration of the species outside of Egmont Atoll, as estimated using acoustic telemetry technology (Andrzejaczek *et al.*, 2020). Andrzejaczek *et al.* (2020) found *M. alfredi* have large-scale regional movements (>200km) inside the MPA which may relate to prey density (Armstrong *et al.*, 2016), induced by environmental drivers (Harris and Stevens, 2021) or lack of cleaning stations around Egmont atoll (Harris *et al.*, 2021). Furthermore, three individuals disappeared within ten days after tagging; although impossible to determine, this may be a result of tag failure, tag loss, mortality or dispersal of individuals (Braun *et al.*, 2015), which could be another reason for the lack of significance in the data set.

Implications for manta ray conservation

Effective design and implementation of conservation measures for *M. alfredi* requires an understanding of drivers for their movement patterns and community structuring (Couturier *et al.*, 2018; Perryman *et al.*, 2019). Recent uses in telemetry technology have allowed large-scale assessment of movement patterns within various *M. alfredi* populations (Clark, 2010; Braun *et al.*, 2015; Edy and Ronald, 2018; Peel *et al.*, 2019), identifying frequently used habitats that can be targeted with focused management, for example, marine protected areas (Sims, 2010). However, although there has been a lot of research into the functions of aggregations, there is little knowledge on aspects driving these groupings and the associations occurring within them. The current study provides a powerful means of assessing associations between *M. alfredi* and offers invaluable insight into the drivers of aggregations to particular sites. As a designated MPA and no-take zone, the Chagos Archipelago's *M. alfredi* population receives a high level of protection; however, other areas are exposed to multiple anthropogenic pressures. These anthropogenic disturbances, such as tourism, may lead to changes in social behaviour observed in populations, as identified previously in Southern stingrays (Semeniuk and Rothley, 2008). Therefore, the use of this technique within other areas may also identify how these pressures affect these associations and further how these may influence the overall structuring of *M. alfredi* populations. Using Chagos as a reference site can allow a more in-depth understanding of *M. alfredi* behaviour at key aggregation sites and population structuring, leading to more manta-focused MPAs to be implemented globally in line with these highly mobile species.

Conclusion

This study used social network analysis and fine-scale passive acoustic telemetry to quantitatively demonstrate a lack of preferred associations in a population of *M. alfredi*. Although these findings do not indicate social structuring within this population, they confirm that feeding areas lack observed social behaviour within these elasmobranchs and are primarily areas for feeding activity. Future research would benefit from further investigation into other aggregation sites within Chagos Archipelago, such as cleaning stations. Furthermore, using this site as a comparison to other areas influenced by anthropogenic pressures may provide insight into the extent disturbances, such as tourism, may have on the social behaviour of *M. alfredi.* Given the vulnerability of *M. alfredi* aggregations to fishing pressures (Venables *et al.*, 2021), shedding further light on drivers for aggregation behaviour will not only enhance our understanding of their population dynamics and movement but will also contribute to their conservation.

Future work

This study further illustrates the benefits of using multiple shorter windows that record more accurate associations, especially when using remote technology such as acoustic telemetry. Although effective, Perryman *et al*. (2019) method using 10 minute windows to acknowledge interactions lacked temporal restrictions and prevented accurate social behaviour to be recorded. Recommendations for future research would include the use of JSATS 208kHz transmitters that possess a 5-second ping rate (Li *et al*., 2020). This would allow a smaller timeframe to be used when examining associations, ensuring results are more precisely recorded. Furthermore, the use of GPS locators that provide the locations of the individuals when inside the designated area would pinpoint where the associations transpire (Braun *et al*., 2015).

Acknowledgements
This study would not have been possible without the funding from the Garfield Weston Foundation and Bertarelli Foundation, and it’s contributions to the Bertarelli Programme in Marine Science. I also owe a special thanks to Clare Embling, Joanna Harris and the Manta Trust for their supervision and support. A particular thanks to Joanna Harris, Chagos Manta Ray Project Leader, who provided me with the data and also assisted me with my data analysis providing me with the necessary R code. Data collection complies with the current laws of the country in which it was performed in.

Copyright statement (Manta Trust)

This research has been conducted in collaboration with the Manta Trust (represented by Joanna Harris), who has officially authorised me to use the data to support this research. The author and the Manta Trust give permission to use this research for consultation and to copy parts of it for personal use. Every other use is subject to the copyright of this journal; more specifically the source must be specified when using results from this work.

References

Andrzejaczek, S., Chapple, T.K., Curnick, D.J., Carlisle, A.B., Castleton, M., Jacoby, D.M., Peel, L.R., Schallert, R.J., Tickler, D.M. and Block, B.A. (2020). Individual variation in residency and regional movements of reef manta rays Mobula alfredi in a large marine protected area. *Marine Ecology Progress Series*, *639*, 137-153. https://doi-org.plymouth.idm.oclc.org/10.3354/meps13270

Armstrong, A.O., Armstrong, A.J., Jaine, F.R., Couturier, L.I., Fiora, K., Uribe-Palomino, J., Weeks, S.J., Townsend, K.A., Bennett, M.B. and Richardson, A.J. (2016). Prey density threshold and tidal influence on reef manta ray foraging at an aggregation site on the Great Barrier Reef. *PloS one*, *11*(5), https://doi.org/10.1371/journal.pone.0153393

Beale, C.S., Stewart, J.D., Setyawan, E., Sianipar, A.B. and Erdmann, M.V. (2019). Population dynamics of oceanic manta rays (Mobula birostris) in the Raja Ampat Archipelago, West Papua, Indonesia, and the impacts of the El Niño–Southern Oscillation on their movement ecology. *Diversity and Distributions*, *25*(9), 1472-1487. https://doi.org/10.1111/ddi.12962

Bejder, L., Fletcher, D. & Brager, S. (1998). A method for testing association patterns of social animals. *Animal behaviour*, 56(3),719-725. https://doi.org/10.1006/anbe.1998.0802

Berumen, M.L., Braun, C.D., Cochran, J.E., Skomal, G.B. and Thorrold, S.R. (2014). Movement patterns of juvenile whale sharks tagged at an aggregation site in the Red Sea. *PLoS One*, *9*(7), e103536. https://doi.org/10.1371/journal.pone.0103536

Braun, C.D., Skomal, G.B., Thorrold, S.R. and Berumen, M.L. (2015). Movements of the reef manta ray (Manta alfredi) in the Red Sea using satellite and acoustic telemetry. *Marine biology*, *162*(12), 2351-2362. https://doi.org/10.1007/s00227-015-2760-3

Costa, B.H., Claudet, J., Franco, G., Erzini, K., Caro, A. and Gonçalves, E.J. (2016). A regulation-based classification system for Marine Protected Areas (MPAs). *Marine Policy*, *72*, 192-198. https://doi.org/10.1016/j.marpol.2016.06.021

Couturier, L.I., Jaine, F.R., Townsend, K.A., Weeks, S.J., Richardson, A.J. and Bennett, M.B.(2011). Distribution, site affinity and regional movements of the manta ray, Manta alfredi (Krefft, 1868), along the east coast of Australia. *Marine and Freshwater Research*, *62*(6), 628-637. https://doi.org/10.1071/MF10148

Couturier, L.I., Dudgeon, C.L., Pollock, K.H., Jaine, F.R.A., Bennett, M.B., Townsend, K.A., Richardson, A.J. (2014) Population dynamics of the reef manta ray Manta alfredi in eastern Australia. Coral Reefs 33, 329–342. https://doi.org/10.1007/s00338-014-1126-5

Couturier, L.I.E., Newman, P., Jaine, F.R.A., Bennett, M.B., Venables, W.N., Cagua, E.F., Townsend, K.A., Weeks, S.J. and Richardson, A.J. (2018). Variation in occupancy and habitat use of Mobula alfredi at a major aggregation site. *Marine Ecology Progress Series*, *599*, 125-145. https://doi.org/10.3354/meps12610

Couzin, I.D., 2006. Behavioural ecology: social organisation in fission–fusion societies. *Current Biology*, *16*(5), pp.R169-R171. https://doi.org/10.1016/j.cub.2006.02.042

Daly-Engel, T.S., Seraphin, K.D., Holland, K.N., Coffey, J.P., Nance, H.A., Toonen, R.J. and Bowen, B.W. (2012). Global phylogeography with mixed-marker analysis reveals male-mediated dispersal in the endangered scalloped hammerhead shark (Sphyrna lewini). *PLoS One*, *7*(1), e29986. https://doi.org/10.1371/journal.pone.0029986

Dewar, H., Mous, P., Domeier, M., Muljadi, A., Pet, J. and Whitty, J. (2008). Movements and site fidelity of the giant manta ray, Manta birostris, in the Komodo Marine Park, Indonesia. *Marine Biology*, *155*(2), 121-133. https://doi.org/10.1007/s00227-008-0988-x

Donaldson, M.R., Hinch, S.G., Suski, C.D., Fisk, A.T., Heupel, M.R. and Cooke, S.J. (2014). Making connections in aquatic ecosystems with acoustic telemetry monitoring. *Frontiers in Ecology and the Environment*, *12*(10), 565-573. https://doi.org/10.1890/130283

Edy, S., and Ronald, M. (2018). Site fidelity and movement patterns of reef manta rays (Mobula alfredi: Mobulidae) using passive acoustic telemetry in northern Raja Ampat, Indonesia. *Nature Conservation Research. 3*(4), 17-31. http://dx.doi.org/10.24189/ncr.2018.043

Ginsburg, J. R., and Young, T. P.(1992) Measuring association between individuals or groups in behavioural studies. *Animal behaviour*, 44, 377-379. https://psycnet.apa.org/doi/10.1016/0003-3472(92)90042-8

Gruber, S.H., De Marignac, J.R. and Hoenig, J.M. (2001). Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark–depletion experiments. *Transactions of the American Fisheries Society*, *130*(3), pp.376-384. https://doi.org/10.1577/1548-8659(2001)130%3C0376:SOJLSA%3E2.0.CO;2

Guttridge, T.L., Gruber, S.H., Krause, J. and Sims, D.W. (2010). Novel acoustic technology for studying free-ranging shark social behaviour by recording individuals' interactions. *PLoS One*, *5*(2), e9324. https://doi.org/10.1371/journal.pone.0009324.

Harris, J.L., McGregor, P.K., Oates, Y. and Stevens, G.M. (2020). Gone with the wind: Seasonal distribution and habitat use by the reef manta ray (Mobula alfredi) in the Maldives, implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *30*(8), 1649-1664. https://doi.org/10.1002/aqc.3350

Harris, J.L., Hosegood, P., Robinson, E., Embling, C.B., Hilbourne, S. and Stevens, G.M. (2021). Fine-scale oceanographic drivers of reef manta ray (Mobula alfredi) visitation patterns at a feeding aggregation site. *Ecology and evolution*, *11*(9), 4588-4604. https://doi.org/10.1002/ece3.7357

Harris, J.L. and Stevens, G.M., 2021. Environmental drivers of reef manta ray (Mobula alfredi) visitation patterns to key aggregation habitats in the Maldives. *PLOS ONE*, *16*(6), e0252470. https://doi.org/10.1371/journal.pone.0252470

Heupel, M.R., Kanno, S., Martins, A.P. and Simpfendorfer, C.A. (2018). Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. *Marine and Freshwater Research*, *70*(7), 897-907. https://doi.org/10.1071/MF18081

Jacoby, D.M., Croft, D.P. and Sims, D.W. (2012). Social behaviour in sharks and rays: analysis, patterns and implications for conservation. *Fish and Fisheries*, *13*(4), 399-417. https://doi.org/10.1111/j.1467-2979.2011.00436.x

Jaine, F.R.A., Rohner, C.A., Weeks, S.J., Couturier, L.I.E., Bennett, M.B., Townsend, K.A. and Richardson, A.J. (2014). Movements and habitat use of reef manta rays off eastern Australia: offshore excursions, deep diving and eddy affinity revealed by satellite telemetry. *Marine Ecology Progress Series*, *510*, 73-86. https://doi.org/10.3354/meps10910

Klimley, A.P. (1983). Social organisation of schools of the scalloped hammerhead shark*, Sphyrna lewini (Griffith and Smith),* in the Gulf of California. University of California, San Diego. https://escholarship.org/uc/item/2qg6s9t5

Kurvers R.H., Krause, J., Croft, D.P., Wilson, A.D. and Wolf, M. (2014) The evolutionary and ecological consequences of animal social networks: Emerging issues. *Trends Ecol Evol,* 29, 326–335. https://doi.org/10. 1016/j.tree.2014.04.002

Li H., Deng Z.D., Lu J., Martinez J.J., Wu B. and Zang X. (2020) A miniaturised long-life acoustic transmitter for animal tracking in marine environments. In *Global Oceans 2020: Singapore–US Gulf Coast* 1-4. doi: 10.1109/IEEECONF38699.2020.9389355.

MacGlennon, G. (2008). Social Structure and Behaviour of the Manta Ray (Manta birostris) in the Republic of the Maldives (Doctoral dissertation). Bangor University.

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

Marshall, A.D., Dudgeon, C.L. and Bennett, M.B. (2011). Size and structure of a photographically identified population of manta rays Manta alfredi in southern Mozambique. *Marine Biology*, *158*(5), 1111-1124. https://doi.org/10.1007/s00227-011-1634-6

Marshall, A., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M.P., Herman, K., Jabado, R.W., Liu, K.M., Pacoureau, N., Rigby, C.L., Romanov, E. & Sherley, R.B. (2019). *Mobula alfredi*. *The IUCN Red List of Threatened Species* 2019 e.T195459A68632178. https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T195459A68632178.en (Accessed on 20 March 2022).

McCauley, D.J., DeSalles, P.A., Young, H.S., Papastamatiou, Y.P., Caselle, J.E., Deakos, M.H., Gardner, J., Garton, D.W., Collen, J.D. and Micheli, F. (2014). Reliance of mobile species on sensitive habitats: a case study of manta rays (Manta alfredi) and lagoons. *Marine biology*, *161*(9), pp.1987-1998. https://link.springer.com/article/10.1007/s00227-014-2478-7

McKibben, J.N. and Nelson, D.R. (1986). Patterns of movement and grouping of gray reef sharks, Carcharhinus amblyrhynchos, at Enewetak, Marshall Islands. *Bulletin of Marine Science*, *38*(1), 89-110. https://www.ingentaconnect.com/content/umrsmas/bullmar/1986/00000038/00000001/art00010#.

Murray, A., Garrud, E., Ender, I., Lee-Brooks, K., Atkins, R., Lynam, R., Arnold, K., Roberts, C., Hawkins, J. and Stevens, G. (2020) 'Protecting the million-dollar mantas: Creating an evidence-based code of conduct for manta ray tourism interactions', *Journal of Ecotourism*, *19*(2), pp.132-147. https://doi.org/10.1080/14724049.2019.1659802.

O'Malley, M.P., Townsend, K.A., Hilton, P., Heinrichs, S. and Stewart, J.D. (2017). Characterisation of the trade in manta and devil ray gill plates in China and South-east Asia through trader surveys. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*(2), 394-413. https://doi-org.plymouth.idm.oclc.org/10.1002/aqc.2670.

Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P. and Jabado, R.W. (2021). Half a century of global decline in oceanic sharks and rays. *Nature*, *589*(7843), 567-571. https://doi.org/10.1038/s41586-020-03173-9.

Pardini, A.T., Jones, C.S., Noble, L.R., Kreiser, B., Malcolm, H., Bruce, B.D., Stevens, J.D., Cliff, G., Scholl, M.C., Francis, M. and Duffy, C.A. (2001). Sex-biased dispersal of great white sharks. *Nature*, *412*(6843), 139-140. https://doi.org/10.1038/35084125

Peel, L.R., Stevens, G.M., Daly, R., Daly, C.A.K., Lea, J.S., Clarke, C.R., Collin, S.P. and Meekan, M.G. (2019). Movement and residency patterns of reef manta rays Mobula alfredi in the Amirante Islands, Seychelles. *Marine Ecology Progress Series*, *621*, 169-184. https://doi.org/10.3354/meps12995.

Perryman, R. J. Y., Venables, S. K., Tapilatu, R. F., Marshall, A. D., Brown, C. and Franks, D. W. (2019) 'Social preferences and network structure in a population of reef manta rays', *Behavioural Ecology and Socio-Biology*, *73*(8), 114. https://doi.org/10.1007/s00265-019-2720-x

Phillips, N.M., Devloo-Delva, F., McCall, C. and Daly-Engel, T.S. (2021). Reviewing the genetic evidence for sex-biased dispersal in elasmobranchs. *Reviews in Fish Biology and Fisheries*, *31*(4), 821-841. https://doi.org/10.1007/s11160-021-09673-9

R Core Team (2021) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Available at: https://www.R-project.org (Accessed: 3 November 2021).

Richardson, A.J. (2008). In hot water: zooplankton and climate change. *ICES Journal of Marine Science*, *65*(3), 279-295. https://doi.org/10.1093/icesjms/fsn028

Roycroft, E.J., Le Port, A. and Lavery, S.D. (2019). Population structure and male-biased dispersal in the short-tail stingray Bathytoshia brevicaudata (Myliobatoidei: Dasyatidae). *Conservation Genetics*, *20*(4), 717-728. https://doi.org/10.1007/s10592-019-01167-3

Semeniuk, C.A. and Rothley, K.D. (2008). Costs of group-living for a normally solitary forager: effects of provisioning tourism on southern stingrays (*Dasyatis americana)*. *Marine Ecology Progress Series*, *357*, 271-282. https://doi.org/10.3354/meps07299

Setyawan, E., Sianipar, A.B., Erdmann, M.V., Fischer, A.M., Haddy, J.A., Beale, C.S., Lewis, S.A. and Mambrasar, R. (2018). Site fidelity and movement patterns of reef manta rays (Mobula alfredi): Mobulidae using passive acoustic telemetry in northern Raja Ampat, Indonesia. *Nature Conservation Research*, *3*(4), 1-15. http://dx.doi.org/10.24189/ncr.2018.043

Stevens, G.M.W. (2016) '*Conservation and population ecology of manta rays in the Maldives',* (Doctoral dissertation, University of York).

Stevens, G.M.W., Hawkins, J.P., Roberts, C.M. (2018). Courtship and mating behaviour of manta rays Mobula alfredi and M. birostris in the Maldives. J Fish Biol. 93(2), 344–59. https://doi.org/10.1111/jfb.13768

Sheppard, C. R. C., Ateweberhan, M., Bowen, B. W., Carr, P., Chen, C. A., Clubbe, C., Craig, M. T., Ebinghaus, R., Eble, J., Fitzsimmons, N., Gaither, M. R., Gan, C.-H., Gollock, M., Guzman, N., Graham, N. A. J., Harris, A., Jones, R., Keshavmurthy, S., Koldewey, H. and Yesson, C. (2012) 'Reefs and islands of the Chagos

Archipelago, Indian Ocean: Why it is the world's largest no-take marine protected area', *Aquatic Conservation: Marine and Freshwater Ecosystems*, *22*(2), 232–261. https://doi.org/10.1002/aqc.1248

Sims, D.W. (2010). Tracking and analysis techniques for understanding free-ranging shark movements and behaviour. In J.C. Carrier, J.A. Musick, and M.R. Heithaus, (Eds.), Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation (pp. 351–392). CRC Press.

Venables, S.K., Marshall, A.D., Armstrong, A.J., Tomkins, J.L. and Kennington, W.J. (2021) Genome-wide SNPs detect no evidence of genetic population structure for reef manta rays (Mobula alfredi) in southern Mozambique, *Heredity*, *126*(2), 308-319. https://doi.org/10.1038/s41437-020-00373-x.

Venables, S.K., van Duinkerken, D.I., Rohner, C.A. and Marshall, A.D. (2020) Habitat use and movement patterns of reef manta rays Mobula alfredi in southern Mozambique, *Marine Ecology Progress Series*, *634*, 99-114. https://doi.org/10.3354/meps13178

Ward, A.J., Holbrook, R.I., Krause, J. and Hart, P.J. (2005) Social recognition in sticklebacks: the role of direct experience and habitat cues, *Behavioral Ecology and Sociobiology*, *57*(6), 575-583. https://doi.org/10.1007/s00265-004-0901-7

Whitehead, H. (2009). SOCPROG programmes: analysing animal social structures. Behaviour Ecology and Sociobiology. 63, 765-778. https://doi.org/10.1007/s00265-008-0697-y

Wickham, H., François, R., Henry, L. & Müller, K. (2021). dplyr: A Grammar of Data Manipulation. R package version 1.0.4. https://CRAN.R-project.org/package=dplyr

Wilson, A.D., Brownscombe, J.W., Krause, J., Krause, S., Gutowsky, L.F., Brooks, E.J. and Cooke, S.J. (2015). Integrating network analysis, sensor tags, and observation to understand shark ecology and behavior. *Behavioral Ecology*, *26*(6), 1577-1586. https://doi.org/10.1093/beheco/arv115

Wilson, A.D.M., Croft, D.P. and Krause, J. (2014). Social networks in elasmobranchs and teleost fishes. *Fish and Fisheries*, *15*(4), 676-689. https://doi.org/10.1111/faf.12046