FEATURED STUDENT RESEARCH PAPER

Social preferences and network structure in a population of reef manta rays

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Abstract

Understanding how individual behavior shapes the structure and ecology of populations is key to species conservation and management. Like many elasmobranchs, manta rays are highly mobile and wide-ranging species threatened by anthropogenic impacts. In shallow water environments, these pelagic rays often form groups and perform several apparently socially mediated behaviors. Group structures may result from active choices of individual rays to interact or passive processes. Social behavior is known to affect spatial ecology in other elasmobranchs, but this is the first study providing quantitative evidence for structured social relationships in manta rays. To construct social networks, we collected data from more than 500 groups of reef manta rays (*Mobula alfredi*) over 5 years in the Raja Ampat Regency of West Papua. We used generalized affiliation indices to isolate social preferences from non-social associations, the first study on elasmobranchs to use this method. Longer lasting social preferences were detected mostly between female rays. We detected assortment of social relations by phenotype and variation in social strategies, with the overall social network divided into two main communities. Overall network structure was characteristic of a dynamic fission-fusion society, with differentiated relationships linked to strong fidelity to cleaning station sites. Our results suggest that fine-scale conservation measures will be useful in protecting social groups of *M. alfredi* in their natural habitats and that a more complete understanding of the social nature of manta rays will help predict population responses to anthropogenic pressures, such as increasing disturbance from dive tourism.

Significance statement

In social animals, relationships between individuals have important implications for species conservation. Like many other sharks and rays, manta rays are threatened species, and little is known about their natural behavior or how their populations are structured. This study provides evidence of social structure in a wild, free-ranging population of reef manta rays. We show for the first time that individual manta rays have preferred relationships with others that are maintained over time, and structured societies. This study extends our knowledge of elasmobranch ecology and population structuring. Results suggest that understanding social relationships in manta rays will be important in protecting populations from human impacts and developing sustainable, localized conservation and management initiatives.

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Introduction

Knowledge of how individual behavior drives population structure and dynamics is required to predict the response of populations to human impacts (Sutherland 1998; Sih 2013). In group-living species, social interactions are a fundamental part

of population ecology (Hinde 1976) important in enabling collective behaviors (Couzin et al. 2002; Couzin and Krause 2003; Sumpter 2006), such as cooperative foraging (Sih et al. 2009), predator avoidance (Ward et al. 2011), and social learning (Brown et al. 2011). Social interactions directly affect key ecological and evolutionary processes such as disease transmission, habitat use, and genetic exchange (Kurvers et al. 2014). Social animals are often able to modify their behavior depending on the status of their relationship with various social partners (Krause and Ruxton 2002). Social preferences between individuals may have profound effects on movement decisions that lead to the formation of structured social groups (Bode et al. 2011). Understanding this structure can aid conservation approaches by explaining individual behavior in the context of a population's social environment (Berger-Tal et al. 2011; Krause et al. 2014; Snijders et al. 2017). Social heterogeneity tends to produce organization of animal societies into units that respond differently to environmental conditions, such as in their foraging success (Whitehead and Rendell 2004). This is likely to cause stratification in survival and reproductive success of group members, so it can be misleading to assess population dynamics without considering the impact of this structure (Lusseau et al. 2006). Social network analysis may be used to describe and quantify social structure (Croft et al. 2008) that may be particularly useful for populations in which the existence of social relationships between individuals is not immediately evident, such as in fission-fusion societies (Snijders et al. 2017).

Despite wide literature on social structuring in terrestrial vertebrates and marine mammals (e.g., Baird and Whitehead 2000; Gero et al. 2005; Lusseau et al. 2006; Wolf et al. 2007; Foster et al. 2012), there are few equivalent studies on marine fish. These are particularly lacking for elasmobranchs, despite their high potential for socially structured populations (Jacoby et al. 2010). Sharks and rays are often thought to be solitary creatures, but many species across elasmobranch phylogeny are found in groups or loose aggregations (for review see Jacoby et al. 2012). Where individuals vary in their movements and habitat preferences, some are likely to interact more than others by chance. Group formation via passive processes occurs in elasmobranchs during feeding aggregations (e.g., Heyman et al. 2001) and seasonal migrations (e.g., Heupel and Simpfendorfer 2005; Bass et al. 2017). Many elasmobranchs have developmental shifts in habitat and diet (Wetherbee et al. 2004) that may drive assortment in size- or sex-segregated groups (Wearmouth and Sims 2008). Recently, ex situ studies have shown that some species exhibit complex sociality, including social structure (Jacoby et al. 2010; Mourier et al. 2012), social learning (Guttridge et al. 2013; Thonhauser et al. 2013), and individual personalities (Jacoby et al. 2014; Byrnes et al. 2016). Due to the difficulty in observing multiple interactions between wild elasmobranchs, however, quantitative analysis of the importance of social

relations to the structure of their populations is lacking (but see Guttridge et al. 2011; Mourier et al. 2012). It is usually a considerable challenge to disentangle passive aggregation driven by external forces from active social preferences.

Manta rays (*Mobula* spp.) are excellent candidates for studies on elasmobranch sociality, including social preferences. Individuals can often be easily observed and accurately identified in the wild. Mobulid rays have the largest brains relative to body size of all elasmobranchs (Lisney et al. 2008), with a highly developed central nucleus that has been linked to social intelligence and formation of hierarchical social structures (Ari 2011). Social recognition may be important in mate choice (Marshall and Bennett 2010). Manta rays perform group-based behaviors including collective foraging, following, breaching, copying, play, and curiosity towards humans (Marshall 2008; Deakos 2010; Gadig and Neto 2014; RJYP pers. obs.), which are associated with social functions and reminiscent of highly social marine mammals (Bradbury 1986).

Globally, both species of manta ray (*M. alfredi* and *M. birostris*) are considered vulnerable to extinction (Marshall et al. 2018a, b) due to evidence for recent, large-scale population declines in several regions (e.g., Rohner et al. 2017). Populations are extremely vulnerable to overfishing, among other threats such as ocean pollution, climate change and bycatch (Marshall et al. 2011; Lawson et al. 2017; Stewart et al. 2018), exacerbated by their extremely low reproductive output (Dulvy et al. 2014; Stevens 2016), and high mobility (Germanov and Marshall 2014; Jaine et al. 2014). Populations inhabit subtropical waters, typically those of developing nations where funding for conservation or policing initiatives is scarce, and are unlikely to receive adequate protection from small marine reserves. Indonesia is a globally significant area for both species, having some of the largest identified populations of manta rays in the world (Marshall and Holmberg 2019). Despite receiving protection throughout Indonesian waters in 2014 (Lawson et al. 2017), fishers continue to exploit mobulid rays with impunity, impacting local populations (Couturier et al. 2012; Lewis et al. 2015; Croll et al. 2016). Manta rays are an important attraction in dive tourism (O'Malley et al. 2013; Venables et al. 2016a), and unrestricted growth of this industry may cause disturbance at known aggregation sites (Anderson et al. 2011; Venables et al. 2016b). Understanding the nature of manta ray group and social structuring will aid the implementation of measures to mitigate any negative impacts of dive tourism in these areas.

Research on manta rays to date has focused mainly on broad population demographic and ecological studies (e.g., Marshall and Bennett 2010; Deakos et al. 2011; Kashiwagi et al. 2011; Marshall et al. 2011; Jaine et al. 2012; Couturier et al. 2014), as well as individual-based movement tracking and behavioral studies (e.g., Dewar et al. 2008; Jaine et al. 2014; Stewart et al. 2016a; Ari and D'Agostino 2016).

While these provide comprehensive baseline data for management of manta rays, considering social structure will aid a more nuanced approach, where the behavior of individuals is linked to group- or population-level responses to the environment (Bowler and Benton 2005). Recent studies have shown that individuals within shark populations exhibit large differences in movements, feeding behavior and personality (Jacoby et al. 2014; Matich and Heithaus 2015; Finger et al. 2016, 2017), suggesting that network analyses may be vital to provide reliable data for population ecology and conservation. Though several studies have provided anecdotal evidence of social behavior in manta rays (Deakos 2010; Stevens 2016; Stewart et al. 2016b, 2018), this is the first study to provide a quantitative description of their social organization. Our aims were to describe the temporal and spatial structure of social relations and determine whether manta rays had genuine social preferences (caused by active choice of individuals to interact) by controlling for non-social structural factors, including location, time, phenotype, and individual gregariousness. We expected to find heterogeneity in social relations, as in most social species (Foster et al. 2012). Based on previous knowledge of manta ray ecology and habitat use, we predicted that location fidelity would be an important driver of association and that individuals would have differentiated social strategies. We expected that assortment by phenotype, including sex, maturity, color morph, and reproductive status would be important in structuring the society, potentially enabling the division of the population into distinct social communities.

Methods

Sampling procedure

Data on reef manta ray group compositions were collected from November 2013 to May 2018 in the Dampier Strait region of Raja Ampat, West Papua, by trained researchers diving using SCUBA equipment, or freediving, depending on the position of rays in the water column. Where exact times and locations could be verified, some records (approx. 10% of all data) were obtained by photographic uploads to "MantaMatcher.org," an online citizen-science based catalog (Marshall and Holmberg 2019). It was not possible to record data blind because our study involved observing animals in the field. Sightings of reef manta rays at five sites, including three cleaning stations: Manta Sandy (MS), Manta Ridge (MR) and Rob's Secret Bommie (RSB), and two feeding areas: East Study Area (ESA) and West Study Area (WSA) within a 20-km^2 area were recorded to allow analysis of fine-scale social structure, with data collected from an additional 5km^2 area: Pulau Wai (PW) that was used by manta rays for both feeding and cleaning behaviors. Sampling occasions were dives or snorkels of approx. one hour, at one of these sites, restricted to one sampling occasion at each site per day. The total area covered during a single dive or snorkel was approximately 0.5–1 km^2. We alternated sampling effort by site and time to minimize environmental bias, using variables expected to influence manta ray behavior (location, tidal phase, tidal range, time, and lunar phase) (Jaine et al. 2012). See Appendix Section 1 for details of study area (Appendix Fig. 9) and sampling effort (Appendix Table 4).

Recording individual encounters

Individual reef manta rays were identified by standard photo-ID methods (see Fig. 1), using unique, lifelong spot patterns on the ventral surface (Pierce et al. 2018). Rays were sexed by the presence/absence of claspers, and maturity and reproductive status/sexual activity were estimated as in Marshall and Bennett (2010) using evidence from female pregnancies and mating scars, and male clasper size/calcification. Disc width (DW) was estimated by visual comparison of manta rays to coral structures of known size. Based on 55 individual females of known maturity, size-at-maturity in the population was estimated to be 3–3.5 m DW, similar to populations in Hawaii and Australia (Deakos 2012; Couturier et al. 2014). Where maturity could not be determined using morphological features, females with estimated DW ≥ 3.5 m were considered mature and estimated DW ≤ 3 m immature. Photographic records of each distinct encounter (sighting of an individual) were stored in an online database (www.MantaMatcher.org). For each individual, an "encounter rate" (ER = no. sightings of individual at site, divided by no. sampling occasions at site) was calculated and ranked by site to define individual site preferences. Sex ratios were compared at each study site using exact binomial tests. We constructed logistic mixed effects models using the glmer function of the lme4 package (Bates et al. 2014) in R version 3.4.4 (R Core Team 2018) to compare the probability of encounter of different phenotypes (sex, maturity, color morph) at cleaning stations/feeding sites, and at individual sites, using presence/absence of individuals during a sampling occasion as the dependent variable, site and phenotype as fixed effects, and individual ID as a random effect. We used deviation coding to compare probability of encounter to a grand mean over all sites (see Appendix Section 3, Table 5).

Defining associations

Associations between individuals were defined using the "Gambit of the Group" (GoG) (Whitehead and Dufault 1999), which assumes all individuals observed together are associated, without necessarily interacting socially. This is appropriate where individuals move between groups (Franks et al. 2010), and where direct interactions are difficult to observe regularly, but groups can easily be defined and have
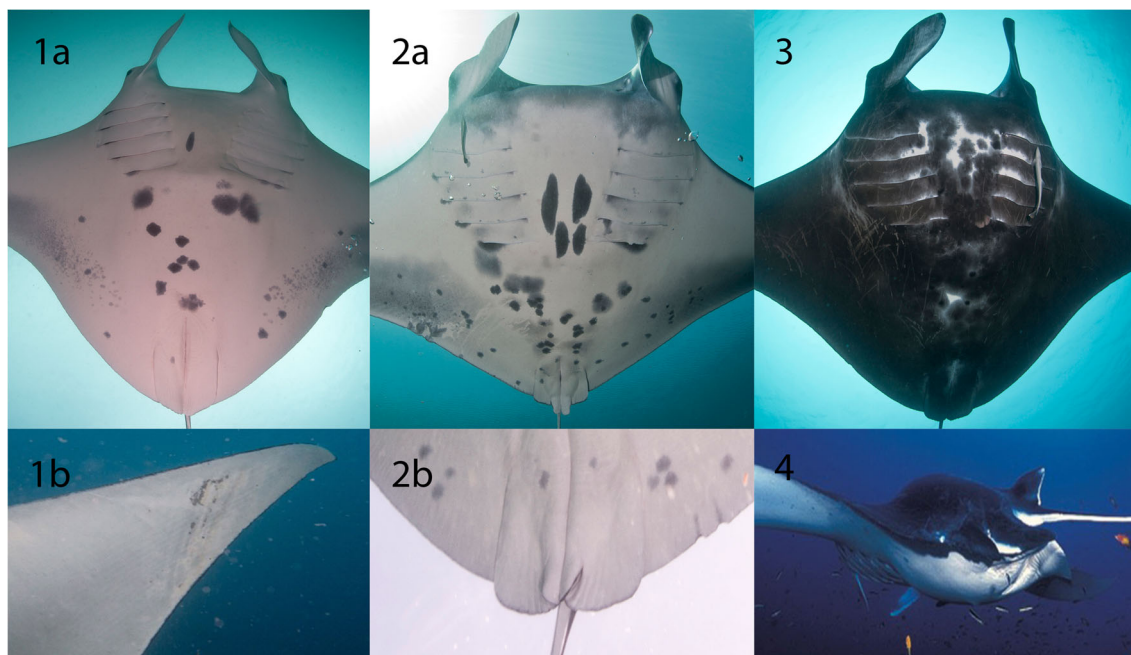
Fig. 1 Identification of reef manta rays: (1a) female typical morph with distinct ventral spot pattern; (1b) mating scars on female indicating maturity; (2a) male typical morph, with claspers; (2b) juvenile male typical morph, with undeveloped claspers; (3) melanistic morph with distinct white patches between gills; (4) pregnant female

meaningful structure (Farine and Whitehead 2015). Each dive was considered an independent sampling occasion (Whitehead 2008a), and all individuals observed during a dive were considered as part of the same group if a gap of < 10 min between encounters occurred (this addressed difficulty in observing a highly mobile species with restricted visibility underwater). In practice, we were confident that observed associations gave an accurate representation of true structure, because groups were spatio-temporally well-defined, and it was usually possible to record the identity of all individuals seen.

Data were recorded in a group by individual binary matrix with rows representing each sampling occasion and columns representing individuals. Network analyses were performed in R, using the asnipe (Farine 2017a), igraph (Csardi and Nepusz 2006), and tnet (Opsahl et al. 2010) packages. Network diagrams were drawn in Gephi 0.9.2 (Bastian et al. 2009). We calculated simple-ratio indices (SRIs) (Cairns and Schwager 1987) to measure strength of association between all pairs. The SRI is the recommended association index (AI) where calibration data are unavailable (Hoppitt and Farine 2018). SRIs were calculated within 45 sampling periods (SPs) of length 15 days. This length was chosen according to results from lagged association rate (LAR) analysis (see "Stability of identifications and associations over time"), and prior knowledge of the species' movements (e.g., Marshall 2008; Deakos 2012), to be short enough that individuals were likely to remain in the area, but long enough to allow sufficient opportunity for swaps between groups required for independence of observations. We identified 112 individuals ≥ 10 times. All individuals

observed < 10 times were removed from subsequent network analyses, because various studies suggest that prioritizing edge accuracy is preferable to including a large proportion of the population (Whitehead 2008b; Franks et al. 2010). We calculated social differentiation (S): the variability of the "true" AIs estimated using maximum likelihood approximation (Whitehead 2008a). Values of S close to 0 indicate homogenous relationships within the population, while values near or greater than 1 indicate highly varied relationships. To determine the accuracy of AIs and their power in testing for social relationships, we calculated the correlation coefficient r, between S and the observed (measured) AIs (Whitehead 2009) as follows: $r = \frac{S}{CV(\text{SRI}_{ab})}$. Sufficient statistical power to test for preferred or avoided associations was accepted when $S^2 \times H > 5$, (where H is the mean no. identifications per individual) (Whitehead 2008b). Standard errors for S and r were estimated using 100 bootstrap replicates of the observed data.

Stability of identifications and associations over time

We calculated lagged identification rates (LIRs) (see Appendix Section 3) and LARs (Fig. 5) to describe changes in the presence of individuals in the study area and their relationships over time (Whitehead 1995). For these analyses, we used sampling periods of 1 day. We used LAR rather than standardized LAR because we were confident of identifying most individuals within groups. We calculated three LARs: for all individuals, between females only, and between males

only. Due to large time gaps between study seasons, a maximum time lag of 180 days was used to restrict LARs to within a single study season. We used a moving average (A) over the possible no. of associations (p), multiplied by 0.25 ($A^{p0.25}$), to smooth the line ($A^{p0.25}$ (all individuals) = 3630, $A^{p0.25}$ (females) = 1208, $A^{p0.25}$ (males) = 431). We fit models describing different potential aspects of relationships within animal societies (see Appendix Section 4) and compared LAR to a null association rate (NAR—the expected rate if associations in the population were randomly distributed). Standard errors were obtained using jackknife resampling (Whitehead 1995). All LIR and LAR analyses were run using SOCPROG 2.7 (Whitehead 2009). The most parsimonious LAR model was selected using the quasi-Akaike Information Criterion (QAICc) (Burnham and Anderson 2004; Whitehead 2007).

Quantifying social preferences

Social networks derived using AIs may be the result of many inter-related factors, including joint locational preferences or overlap in time (passive grouping with unknown others), individual gregariousness (active choice to form groups with unknown others), as well as social preferences (active choice to form groups with known others). Manta rays in this study had high location fidelity and phenotypic variation in site preferences (see "Site use and encounter rates" and "Structure of associations"). We needed to disentangle non-social factors from the social preferences that we were interested in. Researchers often use location-constrained permutations for this purpose, but these only change P values and do not control for bias in effect sizes, which can lead to spurious conclusions. We therefore used generalized affiliation indices (GAIs) that control for various non-social factors when constructing network weights (Whitehead and James 2015). GAIs in our study were deviance residuals (divided by the denominator of the corresponding SRI value) from a generalized linear model with a binomial error structure and log link function, with SRIs as the dependent variable, and corresponding matrix elements of predictors of pairwise association as independent variables. High positive values for GAIs indicate affiliation (dyads are more associated than expected given the structural predictor variables), and negative values indicate avoidance. GAIs may therefore be considered an estimate of the strength of social preference between pairs, with variation due to non-social factors statistically removed. Predictor variables used in calculation of GAIs were the following: site use similarity—the Euclidean distance between the encounter rate (see "Recording individual encounters") of each pair at each study site, temporal overlap (custom SRI calculated on whether pairs were observed in the study area within 14 days of each other, within sampling periods of 60 days), gregariousness (based on Godde et al. 2013, joint pairwise gregariousness was calculated as follows: $G_{ab} = \log(\Sigma SRI_a \Sigma SRI_b)$ where

ΣSRI_a and ΣSRI_b are the sums of all the SRIs for individuals a and b, respectively), sex class (male/female, 1 if same sex, 0 if not), maturity class (adult/juvenile, 1 if same maturity class, 0 if not), and color morph class (typical or melanistic, 1 if same color morph, 0 if not). Multiple regression quadratic assignment procedure (MRQAP) tests (Dekker et al. 2007) were used to identify the relative influences of each predictor variable on associations (see Appendix Section 6, Table 8).

Permutation tests

We tested various hypotheses regarding preferred associations, social preferences, assortment by phenotype, and community structure by comparing observed statistics against equivalent statistical distributions produced by data stream permutations of the observed group by individual matrix (Bejder et al. 1998; Croft et al. 2011). All tests used 1000 permutations of the data, with 100 flips per permutation. P values were calculated by the number of times the randomized statistic was higher than the observed statistic. In all cases, permutations were sufficient for P values to stabilize. Permutation tests for SRIs were conducted on all individuals and for GAIs were conducted on subnetworks of individuals divided by the sex and maturity of individuals, as follows: (1) overall network (all ties between all individuals); (2) female:female—female ties with other females; (3) male:male—male ties with other males; (4) female:male—female ties with males; (5) adult:adult—adult ties with other adults; (6) juvenile:juvenile—juvenile ties with other juveniles; (7) adult:juvenile—adult ties with juveniles. This allowed us to retain variation associated with sex or age differences within GAIs while interpreting differences in social relations between sex and age classes. For each network, we tested the hypothesis that there were more preferred and avoided relationships than expected by chance. Short-term preferred relationships were indicated by a significantly lower than expected mean of all tie weights, long-term preferred relationships indicated by a significantly higher than expected SD of all tie weights, and overall preferred relationships indicated by a significantly higher CV of all tie weights (vice versa for avoided relationships), following Whitehead (2009). We used the same permutation method to find dyadic values that were significantly higher than expected within each network. These were used to build a network of estimated social preferences (Fig. 7).

Assortment by phenotype

We tested for assortment in the reef manta ray population by sex, maturity, and color morph, with the null hypothesis that assortment would be no stronger than expected if relationships were random. To test for assortment while controlling for the structure of the dataset, we compared assortativity coefficients (ACs) calculated on observed SRIs (to check if rays assorted

non-socially) and GAI values (to check if social preferences were assorted) to equivalent coefficients calculated from data stream permutations (see "Permutation tests"). ACs were positive if vertices of similar phenotype tended to positively connect, or if vertices of different phenotype tended to negatively connect. ACs were negative if vertices of different phenotype tended to positively connect, or if vertices of similar phenotype tended to negatively connect. GAIs had both negative values (indicating avoidance) and positive values (indicating social preference). Due to the difference in meaning of positive/negative values here, it did not make sense to calculate ACs for all GAI values combined. We therefore tested for assortment among positive and negative GAI values separately.

Community structure

We used the leading.eigenvector.community algorithm in igraph to identify community structure within the overall networks of SRIs/GAIs. This method divided networks successively into clusters, with the most parsimonious network division being that maximized the modularity coefficient, Q (Newman 2006). Data stream permutations (see "Permutation tests") were used to evaluate whether this value was meaningful. We obtained confidence intervals for Q using the method of Lusseau et al. (2008). We assessed robustness of community assignment using a coefficient of assortativity (R_{com}), which directly assessed the degree to which empirical community assignments of nodes agreed with assignments from bootstrap replicates (Shizuka and Farine 2016). We then calculated within-community social differentiation ("Defining associations") to measure social complexity in the population.

Individual network positions

To investigate social strategies and classify overall network structure, we calculated network metrics for individuals within the overall network of GAIs. This allowed us to test hypotheses that individuals of different phenotypic class (sex, maturity status, color morph) or reproductive status (females observed as pregnant at least once/females never observed as pregnant, and females observed as sexually active/never observed as sexually active) had different average network positions. We used the tnet package (Opsahl et al. 2010) in R to calculate the following metrics: weighted degree (summed weight of all connections for each individual), weighted betweenness centrality (measure of how often an individual is located on the shortest path between two others), and local clustering coefficient (measure of how complete the neighborhood of each individual is). For this analysis, all negative GAI values were treated as zeros, because we were primarily interested in the effect of direct social preferences (positive values), rather than avoidance (negative values). Our measure of

weighted betweenness favored shorter paths composed of weaker ties over longer paths with stronger ties (α tuning parameter = 0.5). We compared metrics between phenotypes by calculating the coefficient of the slope of linear models for different levels of each phenotype (Farine 2017b). Empirical slope values were compared to equivalent random values produced via data stream permutations, which provided a null model; P values were obtained as in "Permutation tests."

Results

Individual identification and group structures

A total of 3411 encounters of 594 *M. alfredi* individuals were recorded over 512 sampling occasions. The highest number of sightings of a single individual was 57, with 112 individuals observed $\geq$ 10 times, including 70 females (43 mature, 13 immature, 14 unknown maturity) and 42 males (32 mature, 9 immature, 1 unknown maturity). A declining discovery curve (see Appendix Fig. 10) indicated that most of the total population was recorded at least once. Observed group sizes ranged from 1 to 67 individuals, with most smaller than 20 (mean 6.66 over all sites, 95% CI = 6.03–7.30), median 4 over all sites, 95% CI = 4–5). Feeding sites typically had larger group sizes, but large groups were also observed at cleaning stations (see Appendix Section 2, Fig. 11 for group size and sightings frequency data).

Site use and encounter rates

For individuals observed $\geq$ 10 times, especially females, encounters were much more likely at that individual's 1st preference site than any other (Fig. 2). Many individuals were observed multiple times at a single cleaning station, but infrequently or not at all at others (see Appendix Fig. 12), indicating strong site preferences. In general, female rays were more likely to be encountered at cleaning stations than males, while mature males were more likely to be encountered at feeding areas (see Appendix Section 3, Table 5). However, encounter rates at individual cleaning stations MS, MR, and RSB varied considerably between sexes, with different results for each site (Fig. 3). Site MS had a strongly female-biased sex ratio (exact binomial tests N_{enc} = 1198, 77% female, 95% CIs 74.6–80.1% female, P < 0.001), site MR had no difference from parity (N_{enc} = 1052, (53% female, CI = 48.9–56.8% female, P = 0.163), and site RSB (N_{enc} = 321, 40% female, CI 34.2–46.3% female, P = 0.002) had a male-biased sex ratio.

Structure of associations

The population had moderate social differentiation (S = 0.574, SE = 0.067), and estimated AIs were a useful
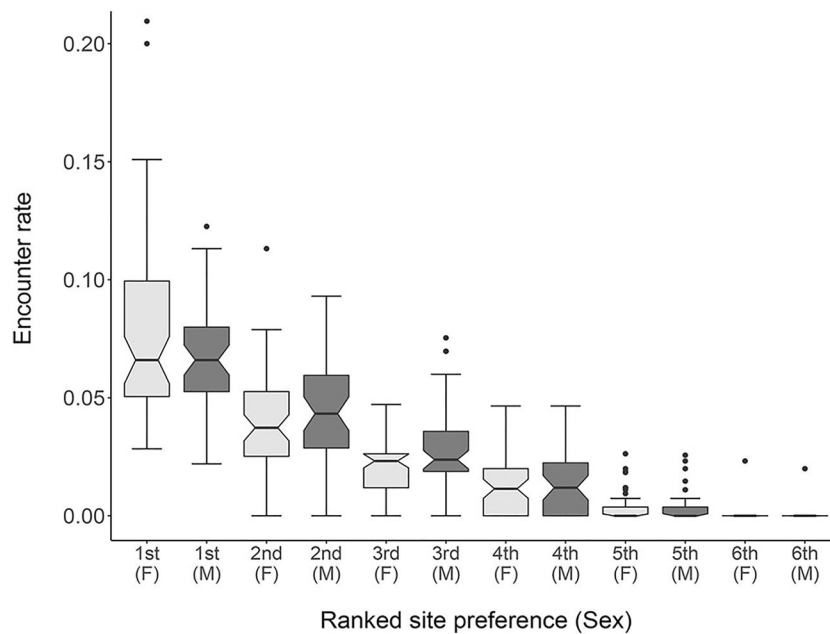
Fig. 2 Encounter rates over all study sites by sex (F females, M males), ranked by site preference. The thick black lines represent the medians, the notches represent the 95% confidence interval of the medians, the boxes encompass the interquartile ranges, the whiskers extend to the most extreme data points within 1.5× the interquartile range outside the box, and the circles show data points beyond the whiskers. Note the much higher average values at first preference sites than other sites, indicating strong site fidelity, particularly for females. There was considerable variability in the level of site fidelity between individuals, but not between sexes

representation of the true AIs ($r = 0.450$, SE $= 0.048$). We had sufficient power to test the hypothesis that reef manta rays had no preferred or avoided relationships ($S^2 \times H = 5.59$). Most pairs that had associated at least once were not strongly associated (70% of recorded associations had an SRI value of ≤ 0.1, and only 3% had a value ≥ 0.2, median non-zero SRI value 0.071). The highest SRI value between any pair of individuals was 0.357. Figure 4
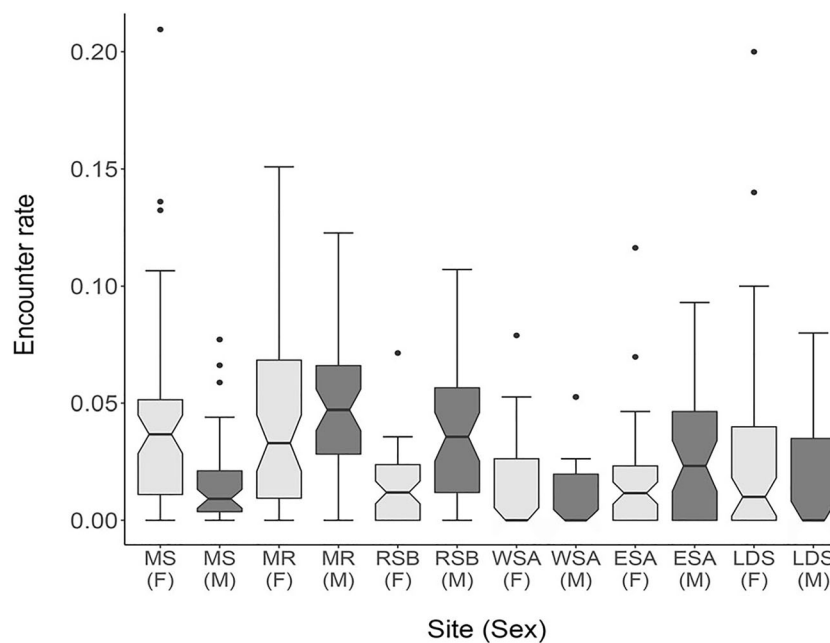

Fig. 3 Encounter rates at each of the six study sites by sex (F females, M males). The thick black lines represent the medians, the notches represent the 95% confidence interval of the medians, the boxes encompass the interquartile ranges, the whiskers extend to the most extreme data points within 1.5× the interquartile range outside the box, and the circles show data points beyond the whiskers. Note the difference between attendance of males and females at the three cleaning stations (MS, MR and RSB), showing marked differences in site preferences. There were a greater number of zero values at the three feeding areas (WSA, ESA and LDS) due to lower sampling effort there
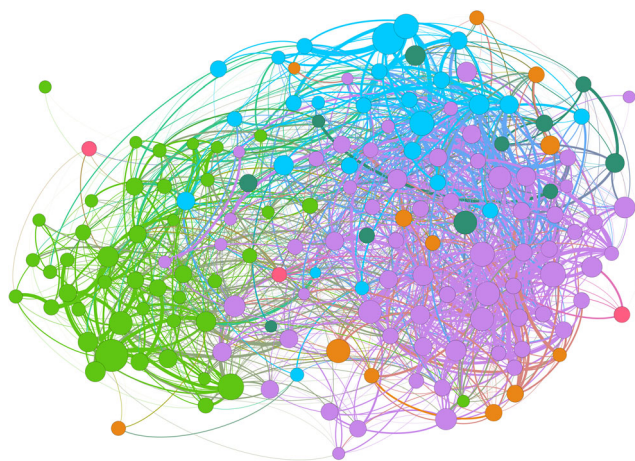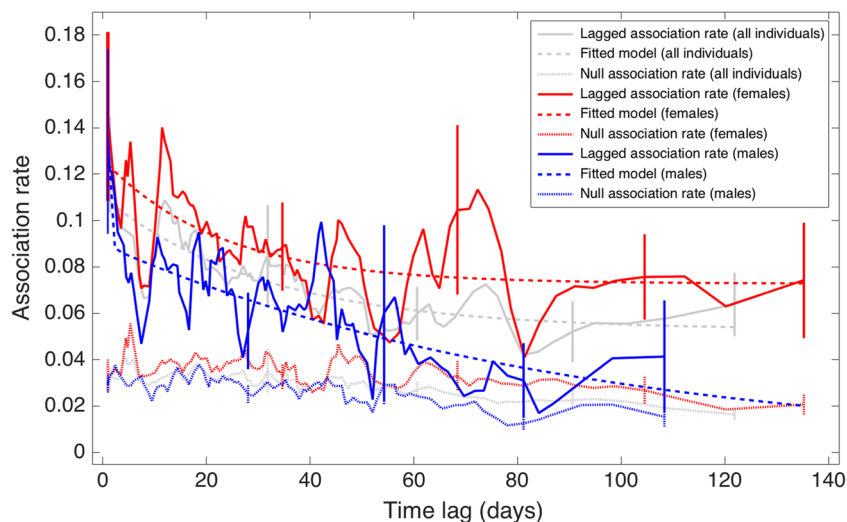
Fig. 4 Network of simple ratio indices. Node colors indicate individual site preferences (green: MS, purple: MR, bottle green: RSB, red = ESA, orange = WSA, blue: LDS). Node size scaled by the SD of encounter rates of an individual at each site, indicating level of overall site fidelity. Edge widths represent weight of SRIs (min = 0.118, max = 0.444). Individuals with 8 or more encounters included as nodes (n=163). Only the 30% highest SRI values were included as edges to show strongest associations. ForceAtlas algorithm was used to construct network

shows the network of associations between individuals in the context of their site preferences, which appear to be an important factor structuring associations. The network was highly connected (56.4% of possible connections realized), but connections among individuals with similar site preferences were more common and typically stronger. Manta rays with preference for site "MS" appeared partly segregated from the rest of the population.

Stability of identifications and associations over time

LIRs fell steeply over the first few days but remained stable thereafter for at least a year (see Appendix Section 4, Fig. 13, Table 6), and individuals were much more likely to be re-sighted at the same site than a different site over the full study

period (1603 days). The re-identification rate at a different site to initial sighting was low, remaining constant throughout the study period. Identifications at the same location were best described using a model that indicated the occurrence of emigration (including permanent emigration from the study area) while re-identifications at a different location were best described by a model indicating a closed population (Appendix Table 6). LARs (Fig. 5) showed that time was an important influence on group structures. Among all individuals, the LAR declined slowly but gradually over several months. Re-associations between females occurred more frequently than those between males, with overall and female LAR remaining higher than equivalent null rates over several months, whereas male LAR approached the null rate after ~ 55 days. Models of exponential decay fit to the LAR data are shown in Table 7 (Appendix). The best-fit model based on QAICc suggested that preferred relationships were important in structuring relationships between females (and among all individuals), while casual acquaintances were important in structuring relationships between males.

Tests for preferred associations and social preferences

Results of tests for association preferences (co-occurrence in time and space) and social preferences (active decisions to interact) are given in Table 1. Associations are measured by simple ratio indices (SRIs), whereas social preferences are measured by generalized affiliation indices (GAIs). The CV of SRIs was significantly higher (observed mean 1.14, mean of random CVs 1.10, $P = 0.001$) than expected, indicating that reef manta rays had preferred associations. These preferences were not evenly distributed throughout the full network. Results were similar for associations between females (F:F network), mixed sex (F:M), and mixed maturity (A:J) associations, indicating preferred associations

Fig. 5 Lagged association rates (LAR) compared to null association rate (NAR) between all individuals, between females and between males. Bars indicate approximate standard errors generated by jackknife resampling. Females dissociated gradually, and LAR did not approach the null rate, whereas males dissociated more rapidly, and LAR approached null rate more frequently. Figure created in SOCPROG

Table 1 Tests for preferred associations and social preferences. Statistics from empirical network compared to random networks. Overall preferred relationships indicated by significantly high CV, short-term (within sampling period) preferred relationships indicated by significantly low mean, long-term (between sampling period) preferred relations indicated by significantly high SD. P values significant at $P = 0.05$ if fewer than 2.5% of the random values were greater than the observed value or if more than 97.5% of the random values were greater than the observed value (two-tailed tests). The two-tailed P values reported are twice the proportion (e.g., the $P = 0.05$ threshold lies at 0.025) and values close to 1 are subtracted from 1 (e.g., a value of 0.975 or above is significant at $P = 0.05$ because $1 - 0.975 = 0.025$) (Farine 2017b). Two-tailed P values at $P \leq 0.05$ are indicated in bold, at $P \leq 0.01$ indicated by *. The right-most column shows percentage of all pairwise GAI values defined as preferred relationships and means of these values

Sub-network	A) Preferred associations (SRIs) Overall (CV)	B) Social preferences (GAIs) Overall (CV)	Short-term (Mean ($\times 10^{-3}$))	Long-term SD ($\times 10^{-2}$)	C) Dyadic preferences (GAIs) (% of all pairs), Mean ($\times 10^{-3}$)
		Observed value: mean of random values, P value			
1) Whole ($n = 112{:}112$)	$1.14 : 1.10$, $\textbf{P = 0.002}$*	$-5.15 : -5.44$, $\textbf{P = 0}$*	$-2.77 : -2.58$, $\textbf{P = 0}$*	$1.42 : 1.41$, $P = 0.098$	(10.2%), 9.63
Interpretation: highly significant preferred associations and social preferences (short term)					
2) F:F ($n = 70{:}70$)	$1.07 : 1.04$, $\textbf{P = 0.044}$	$-5.37 : -5.58$, $P = 0.090$	$-2.57 : -2.41$, $\textbf{P = 0.002}$*	$1.38 : 1.34$, $\textbf{P = 0.038}$	(8.1%), 11.32
Interpretation: preferred associations and social preferences (only network with long-term social preferences)					
3) M:M ($n = 42{:}42$)	$1.13 : 1.15$, $P = 0.412$	$-5.05 : -5.25$, $P = 0.292$	$-3.15 : -2.94$, $\textbf{P = 0.044}$	$1.56 : 1.54$, $P = 0.302$	(4.9%), 23.00
Interpretation: no preferred associations. Only short-term social preferences					
4) F:M ($n = 70{:}42$)	$1.21 : 1.14$, $\textbf{P = 0.004}$*	$-5.05 : -5.44$, $\textbf{P = 0.004}$*	$-2.77 : -2.61$, $\textbf{P = 0.002}$*	$1.40 : 1.41$, $P = 0.366$	(12.6%), 8.75
Interpretation: highly significant preferred associations and short-term social preferences					
5) A:A ($n = 75{:}75$)	$1.05 : 1.02$, $P = 0.104$	$-5.94 : -6.06$, $P = 0.350$	$-2.40 : -2.31$, $P = 0.136$	$1.43 : 1.40$, $P = 0.078$	(7.3%), 13.71
Interpretation: no significantly preferred associations or social preferences					
6) J:J ($n = 22{:}22$)	$1.26 : 1.18$, $P = 0.192$	$-4.00 : -4.85$, $\textbf{P = 0.028}$	$-3.04 : -2.58$, $\textbf{P = 0.008}$*	$1.21 : 1.21$, $P = 0.936$	(8.2%), 6.27
Interpretation: no preferred associations, short-term social preferences, not long term					
7) A:J ($n = 75{:}22$)	$1.17 : 1.08$, $\textbf{P = 0.002}$*	$-5.02 : -5.34$, $\textbf{P = 0.038}$	$-2.69 : -2.47$ $\textbf{P = 0.002}$*	$1.35 : 1.33$, $P = 0.312$	(9.0%), 10.42
Interpretation: strong short-term preferred associations and social preferences, not long term					

within these networks. Associations between adult rays (A:A) and between juvenile rays (J:J) had CV values that were not significantly higher than expected. Associations between males (M:M), however, had a lower than expected CV, indicating that males did not have preferred associations with other males, and may tend to avoid each other.

Associations between individuals in our study may be highly influenced by non-social factors (see Fig. 4 main text, Appendix Table 8). Our use of generalized affiliation indices (GAIs) controlled for this. GAIs gave similar results to SRIs in some cases, but not all. Generally, we found that social preferences were more common than preferred associations (see Appendix Fig. 14). For all networks, the mean of GAI values was negative, indicating that avoidance between pairs was common, particularly between males and between juveniles (the M:M and J:J GAI networks had the lowest means). The CV of all observed GAIs was significantly higher, and the mean of observed GAI values significantly were lower than expected, indicating that social preferences occurred between all individuals, particularly over short (< 15 days) time periods. All statistics for female:female GAIs

(network 2) were significantly (or nearly significantly) different to random expectation, indicating the presence of short and long-term social preferences between female rays. In contrast, for male:male GAIs, only short-term social preferences were significantly stronger than random expectations. There were also a lower percentage of preferred dyadic values between males (4.9%) than between females (8.1%). The highest percentage of preferred dyadic values was between individuals of different sexes (12.6%) (Table 1C), though these appeared to be mainly short-term preferences. Social preferences were not common between adult rays (A:A network). The CV and mean for the J:J and A:J networks indicated that short-term social preferences were stronger than expected between juveniles and between juveniles and mature adults. The percentage of social preferences was similar for all three networks separated by maturity (7.3–9.0%).

Assortment by phenotype

Results for assortment by phenotype are reported in Table 2. Assortativity coefficients (ACs) for SRI values were significantly higher than expected when grouping individuals by sex

Table 2 Tests for assortment by sex, maturity, and color morph for associations (SRIs), and positive and negative affiliations (GAIs). Assortativity coefficients (ACs) from empirical network compared to random networks. ACs that are significantly larger than expected for SRIs and positive GAIs indicate assortment by phenotype. ACs that are significantly smaller than expected for negative GAIs indicate that similar individuals do not avoid each other. P values significant at $P = 0.05$ if fewer than 2.5% of the random values were greater than the observed value, or if more than 97.5% of the random values were greater than the observed value (two-tailed tests). The two-tailed P values reported are twice the proportion (e.g., the $P = 0.05$ threshold lies at 0.025), and values close to 1 are subtracted from 1 (e.g., a value of 0.975 or above is significant at $P = 0.05$ because $1 - 0.975 = 0.025$) (Farine 2017b). Two-tailed P values at $P \leq 0.05$ indicated in bold, at $P \leq 0.01$ indicated by *

	SRIs	Positive GAI values	Negative GAI values
AC (Phenotype: sex)			
Real:random mean (sd)	0.077:0.025 (0.012)	0.101:0.037 (0.019)	− 0.046:− 0.017 (0.011)
P value	**P = 0.002***	**P = 0.004***	**P = 0.010***
AC (Phenotype: maturity)			
Real:random mean (sd)	0.030:0.007 (0.009)	0.028:0.006 (0.015)	− 0.030:− 0.016 (0.008)
P value	**P = 0.010***	P = 0.136	**P = 0.026**
AC (Phenotype: color morph)			
Real:random mean (sd)	− 0.028:− 0.006 (0.010)	− 0.034:− 0.006 (0.018)	0.008:0.003 (0.011)
P value	P = 0.062	P = 0.112	P = 0.602

and maturity, indicating that associations were positively assorted by these phenotypic attributes. There was no evidence for assortment of associations by color morph. For GAI values, the AC was significantly higher than expected (considering only positive GAI values) and significantly lower than expected (considering only negative GAI values) when grouping by sex. This indicated that same-sex pairs tended to have social preferences and did not avoid each other. There was limited or no evidence for assortment of GAIs by maturity or color morph. Figure 7 shows the network of social preferences by sex and maturity. While all individuals are highly connected, there was partial segregation between the sexes.

Community structuring

We found support for subdivision of the observed manta ray society into communities of individuals with stronger in-group relationships. The most parsimonious division of the association (SRI) network (Fig. 4) was into two communities with a Q_{max} value of 0.168 (95% CIs 0.162-0.257). This indicates that the population had only a weak modular structure, but there was significantly more structure than expected if associations were random (mean of random Q_{max} values = 0.106, $P = 0$). Robustness of community assignment (R_{com}) for SRIs was 0.580, which is considered reliable evidence for the empirical structure (Shizuka and Farine 2016) (see Fig. 6). Within-community social differentiation was quite different for the two communities. Community 1 ($S = 0.393$, observed CV = 0.926, correlation = 0.427) had a moderately differentiated social structure, while community 2 ($S = 0.093$, observed CV = 0.919, correlation = 0.100) had a strongly homogeneous social structure.

Variability in network positions

Results comparing network metrics of GAIs between phenotypes are presented in Table 3 and Fig. 8. They suggest some variation in social strategies between phenotypic groups and according to reproductive status. Juveniles had significantly higher weighted degree and weighted betweenness than mature adults and were therefore more central in the overall network of GAIs. Females observed to be pregnant at least once during the study had significantly lower weighted betweenness and significantly lower clustering coefficients than females with no observed pregnancies. Mature females may therefore be more segregated from the overall network than other individuals. No other metrics were significant, with similar values for degree, betweenness, and clustering between individuals of different sex, color morph, and for mated and non-mated females.

Discussion

Reef manta rays in the Dampier Strait region of Raja Ampat, West Papua formed a complex and heterogeneously structured society, with non-random associations between individuals that divided the population into two distinct communities. Associations were the result of more than just similarities in habitat use, gregariousness, or overlaps in time, indicating that individuals actively chose to group with preferred social partners. As such, this is the first study to provide quantitative evidence for structured social relationships in manta rays. Such relationships may provide survival benefits across a range of contexts (Frère et al. 2010; Ellis et al. 2017;
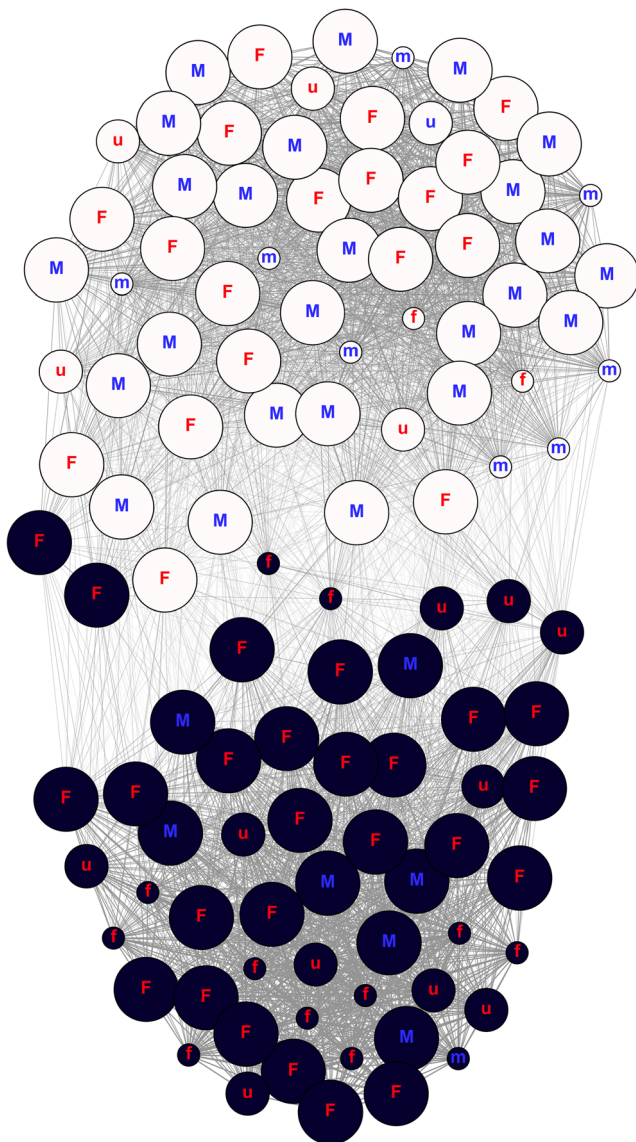
Fig. 6 Network of community assortativity assignments (based on SRIs) showing how often (represented by edge widths) empirical community assignment of each pair agreed with bootstrap replicate networks. Edges < 0.25 removed. Node sizes indicate maturity status: large = adult, small = juvenile, medium = unknown. Community 1 (white nodes) contained an approximately equal no. females (24) and males (34), but community 2 (black nodes) had a strong female bias (46 females, 8 males). ForceAtlas2 algorithm used to construct network

Fig. 7 Network of social preferences ($N_{edges} = 480$). Node colors indicate sex (red = female, blue = male). Node size indicates the centrality of the individual (measured by weighted betweenness). Edge widths represent weights of GAI values. Edge colors represent relations between females (red), between males (blue), and mixed sex relations (purple). While all individuals are highly connected, there is clear partitioning of the network by sex. ForceAtlas algorithm used to construct network

Kalbitzer et al. 2017). Familiarity and kin recognition over extended time periods (Griffiths and Ward 2011) have been shown to enhance the benefits of group living in fishes through antipredator effects (Chivers et al. 1995), increased foraging efficiency (Swaney et al. 2001), reduction in competition (Frostman and Sherman 2004), release of time budget constraints (Griffiths et al. 2004), and improved social learning (Lachlan et al. 1998). However, it is not yet clear to what extent sharks and rays recognize familiar individuals, including their capability for long-term social recognition (LTSR) of
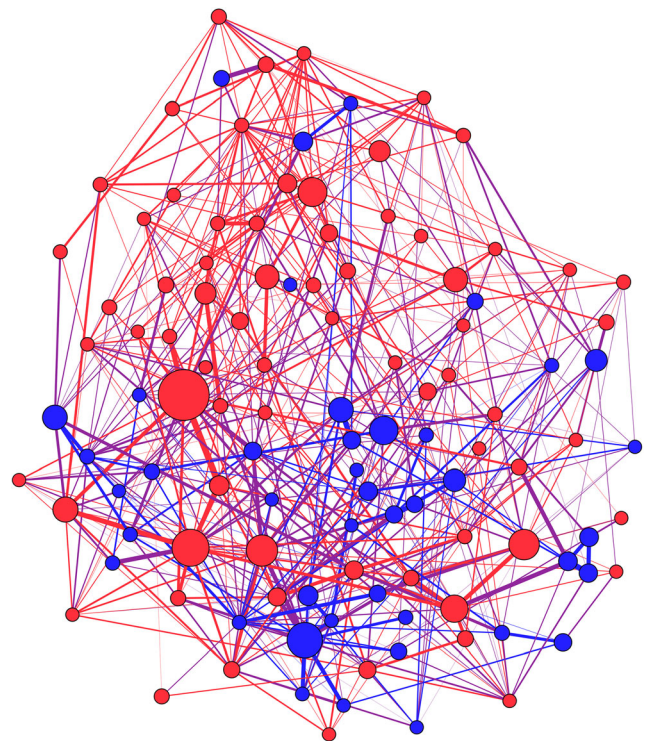
multiple partners and long-term memory of relationship histories.

Our results show that stable, differentiated social relationships lasting over several weeks or months are an important driver of group structures in reef manta rays, which suggests that both familiarity and LTSR are important in structuring their societies. In complex social systems, such capabilities can be essential to identify partners in reciprocal altruism, maintain social hierarchies, and avoid inbreeding (Trivers 1971; Axelrod and Hamilton 1981; Bruck 2013). Simultaneous relationships with multiple partners may be required for social behaviors in manta rays, such as in initiation of mating trains and during collective feeding events. Social preferences were detected mostly between female rays, in mixed sex relations, and between juveniles, with only weak evidence for short-term preferences between males. Time-based analyses suggested that associations between manta rays dissociated gradually over time, but often remained stable over weeks or months (particularly among females). Associations and social preferences were assorted by sex and maturity, and network metrics showed that social relationships were highly differentiated and indicative of varied social strategies. The overall network of observed associations was weakly modular, with two main communities that had quite
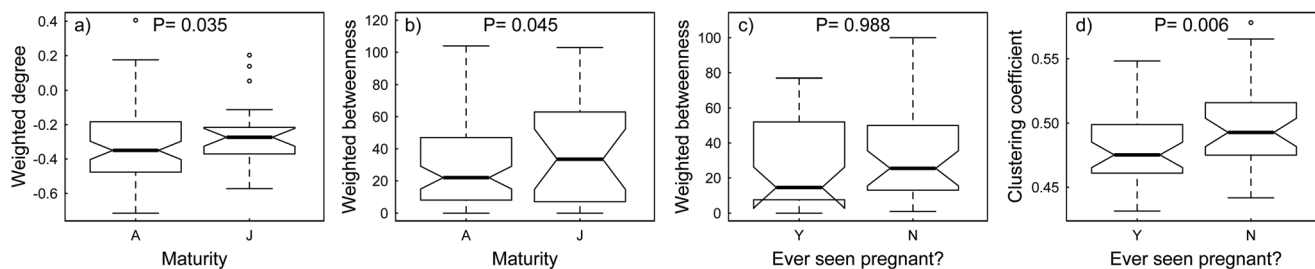
Fig. 8 Significant differences in network metrics by phenotype, including **a** weighted degree for adult (A) and juveniles (J), **b** weighted betweenness for adult (A) and juveniles (J), **c** weighted betweenness for females observed pregnant (Y) and never observed pregnant (N), **d** clustering coefficient for females seen (Y) pregnant and never seen (N) pregnant.

The thick black lines represent the medians, the notches represent the 95% confidence interval of the medians, the boxes encompass the interquartile ranges, the whiskers extend to the most extreme data points within 1.5× the interquartile range outside the box, and the circles show data points beyond the whiskers

different structures, one having a mixed sex ratio with differentiated social relations and the other having a highly biased female sex ratio, with homogeneous social structure. Female reef manta rays therefore appear to choose to associate mostly with other females (in more stable groups) or with males (in more dynamic groups). This decision may depend on factors such as age/maturity and reproductive status, as discussed further below. Reef manta rays did not form tight-knit social groups, such as those observed in many dolphin and larger toothed whale populations (Baird and Whitehead 2000; Cantor et al. 2012), although in several aspects our findings were comparable to social network studies on bottlenose dolphins (*Tursiops* sp.) including a recent study using GAIs (Zanardo et al. 2018). Bottlenose dolphins typically live in open and fluid hierarchical societies with fission-fusion dynamics, LTSR, and a high number of potential affiliates (Lusseau et al. 2003; Gero et al. 2005; Bruck 2013). Social structure in these dolphins is flexible depending on environmental conditions (Lusseau et al. 2003; Karczmarski et al. 2005), enabling efficient flow of information required in foraging and predator avoidance (King and Janik 2015). It is possible that social relationships in reef manta rays have similar structure and functions.

In addition to preferred social relationships, we found that passive aggregation and assortment of individuals with similar phenotypic attributes were important non-social factors influencing network structure. Many rays had strong philopatry to individual cleaning stations, resulting in marked differences in site sex ratios. This was surprising given the close proximity of all sites (Appendix Fig. 9c) and known wide-ranging movements of the species. Fidelity to areas of coastal reef has been described previously in *M. alfredi* in various locations (Deakos et al. 2011; Marshall et al. 2011; Jaine et al. 2014), including in Raja Ampat (Setyawan et al. 2018), but our study is novel in that it demonstrates that this can occur variably at multiple sites in close proximity (at a finer scale than the daily movements of the species). This result suggests that broad processes such as food availability or habitat quality may not be as important as individually

distinct environmental or social preferences in driving manta ray movements and habitat use at fine scales. Associations were closely correlated with individuals' site preferences. Site fidelity is often a prerequisite for sociality in gregarious animals, creating an environment for social relationships to develop (Wolf et al. 2007) and controlling the emergence of social preferences (Mourier et al. 2012). Time was also an important influence on social organization. Being present in the study at the same time was a strong predictor of association between pairs. Re-sightings were increasingly unlikely only a few days after initial sighting but were much more likely to occur at a previously visited site over long time periods. Rather than having broad area residency (where isolation by distance might explain location fidelity), this suggests that individuals typically stayed in a certain location for hours or days and made frequent movements in and out of the study area, returning to visit preferred sites (i.e., philopatry) over several years. It is likely that many individuals ranged widely throughout a larger area than we could cover in the scope of this study. LAR results suggested that casual acquaintances between rays were as important (or more) than preferred companionships to network structure. *M. alfredi* are known to travel up to 95 km per day (van Duinkerken 2010; Jaine et al. 2014) and move to deeper waters during the night (Braun et al. 2014). In Raja Ampat (Setyawan et al. 2018) and other locations (Marshall 2008; Dewar et al. 2008), visits to cleaning station sites occur mainly during daylight hours. Social structure in reef manta rays may therefore depend on daily fission-fusion dynamics. A limitation of our study is that associations between rays were only recorded at a few specific locations for short time periods during daylight hours. Preliminary observations via remotely piloted aircraft show that manta rays often follow each other when leaving cleaning stations or feeding areas (RJYP unpublished) and suggest that group structures formed in these areas are maintained outside them. Therefore, the network of associations that we recorded may underestimate true social relationships.

Sex, age, and size-based assortment are common in shark aggregations (Heupel and Simpfendorfer 2005; Wearmouth

Table 3 Network metrics comparing individual positions in GAI network structure by phenotype, by comparing the coefficient of the observed (obs) slope of empirical linear models to random (rand) slope models. Mean and median values reported with confidence intervals. P values significant at $P = 0.05$ if fewer than 2.5% of the random values were greater than the observed value, or if more than 97.5% of the random values were greater than the observed value (two-tailed tests). The two-tailed P values reported are twice the proportion (e.g., the $P = 0.05$ threshold lies at 0.025), and values close to 1 are subtracted from 1 (e.g., a value of 0.975 or above is significant at $P = 0.05$ because $1 - 0.975 = 0.025$) (Farine 2017b). Two-tailed P values at $P \leq 0.05$ indicated in italics, at $P \leq 0.01$ indicated by *

Phenotype	Weighted degree Mean (95% CIs)	Weighted degree Median (95% CIs)	Weighted degree Obs slope: Rand slope (SD) P value	Weighted betweenness (alpha = 0.5) Mean (95% CIs)	Weighted betweenness Median (95% CIs)	Weighted betweenness Obs slope: Rand slope (SD) P value	Clustering coefficient Mean (95% CIs)	Clustering coefficient Median (95% CIs)	Clustering coefficient Obs slope: Rand slope (SD) P value
Female ($N=70$)	−0.282 (−0.34:−0.23)	−0.313 (−0.37:−0.27)	−0.074:−0.070 (0.016) $P=0.788$	43.3 (28.1–58.5)	22 (14–29)	−0.110: 3.400 (4.073) $P=0.396$	0.487 (0.480–0.495)	0.483 (0.475–0.491)	0.006: 0.006 (0.004) $P=0.960$
Male ($N=42$)	−0.356 (−0.41:−0.30)	−0.354 (−0.47:−0.29)		43.2 (29.7–56.7)	34 (14–29)		0.494 (0.484–0.503)	0.489 (0.483–0.501)	
Adult ($N=75$)	−0.314 (−0.37:−0.26)	−0.350 (−0.40:−0.29)	*0.055: 0.012 (0.020) $P=0.040$*	37.3 (26.6–48.0)	22 (14–32)	19.985: 10.388 (5.322) $P=0.058$	0.486 (0.479–0.493)	0.483 (0.475–0.489)	0.008: 0.003 (0.004) $P=0.326$
Juvenile ($N=22$)	−0.258 (−0.35:−0.17)	−0.273 (−0.37:−0.22)		57.3 (17.9–96.7)	33.5 (7–50)		0.494 (0.477–0.511)	0.490 (0.471–0.511)	
Melanistic ($N=55$)	−0.322 (−0.38:−0.27)	−0.328 (−0.40:−0.28)	−0.024:−0.029 (0.016) $P=0.768$	40.3 (28.6–52.0)	27 (16–39)	−5.868: −9.975 (3.623) $P=0.244$	0.488 (0.481–0.496)	0.488 (0.478–0.499)	−0.003: −0.002 (0.003) $P=0.714$
Typical ($N=57$)	−0.298 (−0.36:−0.24)	−0.334 (−0.39:−0.26)		46.1 (28.2–64.0)	24 (13–35)		0.491 (0.482–0.501)	0.483 (0.477–0.491)	
Pregnant ($N=36$)	−0.248 (−0.33:−0.16)	−0.310 (−0.38:−0.18)	−0.069:−0.056 (0.021) $P=0.552$	48.0 (20.1–75.8)	14.5 (9–32)	*−9.619: 1.176 (4.463) $P=0.016$*	0.480 (0.470–0.490)	0.475 (0.465–0.484)	0.016: 0.004 (0.004) $P=0.010*$
Not pregnant ($N=34$)	−0.317 (−0.38:−0.25)	−0.333 (−0.44:−0.26)		38.4 (26.1–50.6)	25.5 (16–43)		0.495 (0.483–0.508)	0.493 (0.482–0.503)	
Mated (F) ($N=39$)	−0.267 (−0.35:−0.19)	−0.331 (−0.41:−0.23)	−0.034:−0.048 (0.020) $P=0.486$	39.5 (15.4–63.7)	14 (9–27)	8.552: 7.661 (4.582) $P=0.856$	0.483 (0.472–0.493)	0.480 (0.470–0.490)	0.011: 0.004 (0.004) $P=0.126$
Unmated (F) ($N=31$)	−0.301 (−0.37:−0.23)	−0.303 (−0.36:−0.25)		48.1 (30.7–65.4)	29 (18–50)		0.493 (0.481–0.506)	0.488 (0.474–0.499)	

and Sims 2008; Guttridge et al. 2011), so it was not surprising to detect phenotypic structuring here. Sex ratios at manta ray aggregation sites are often female dominated (Marshall et al. 2011), though here we document a male-dominated site. Assortment may occur without any individual recognition capability, for example, if individuals differ in behavior or motivation, they may spontaneously form closer associations to similar individuals, known as "self-sorting" (Couzin 2006). Social preferences are, however, often important in creating assortative structures in dynamic systems (Croft et al. 2015), and assortative interactions suggestive of active partner preference are reported in a wild elasmobranch (Guttridge et al. 2011). Here we detected sex and maturity-based assortment of GAIs, suggesting that social preferences were a driver of assortative structuring. This could be linked to reef manta rays' reproductive strategy, which is not yet well described, but appears to be promiscuous (Stevens 2016). In several *M. alfredi* populations, most non-juvenile male and female manta rays display evidence of reproductive activity, males initiate courtship with multiple females at different times, while females may take part in mating chains with multiple males (Marshall and Bennett 2010; Deakos 2012; Stevens et al. 2018; RJYP unpublished data). A single female manta ray has been observed to mate with two males in close succession (Yano et al. 1999). Sexual conflict in promiscuous systems is common (Parker 2006), and social factors are known to be drivers of sexual segregation in elasmobranchs (Wearmouth et al. 2012). Fish are also known to avoid mating with familiar conspecifics in promiscuous systems (e.g., Simcox et al. 2005), and the use of familiarity is often varied between sexes (e.g., Griffiths and Magurran 1997; Croft et al. 2003). While both sexes may have equal ability to recognize familiar individuals, they may not have equal motivation—for example, males may only behave differently towards familiar individuals in the context of mate choice (Griffiths and Ward 2011). Differences in motivation to be social in manta rays could explain why social preferences were rare between males and why pregnant females were significantly less central and less connected to the overall population than non-pregnant females. Mature females often appeared to dominate cleaning stations and were rarely observed performing cleaning behaviors with mature males. When females (including many pregnant individuals) were alone, they were often pursued by males (RJYP, pers. obs.). Enabling social behavior may be a primary cause of manta ray visitations to cleaning stations, that act as "social gathering points" (Stevens 2016). Hierarchical social organization in these locations could allow mature females to group with preferred social partners and simultaneously avoid unwanted mating attempts by mature males. Familiarity has been shown to reduce aggression among sharks within recently established social hierarchies (Brena et al. 2018). Social gathering points could also facilitate exchange of information (e.g., regarding the distribution

of ephemeral food patches) in species which appear to lack the ability to communicate over medium-long distances, for example, breaching may be used as a social signal of food availability (Stevens 2016). Some elasmobranchs use body positioning and fin movements in gestural communication (Martin 2007; Sperone et al. 2012), and this may occur in reef manta rays (Stewart et al. 2016b; RJYP unpublished). Research into the communicative capabilities of manta rays is warranted.

Our study provides the first evidence for structured social relationships in manta rays and suggests that detailed information on their social organization (including structure, dynamics, and social preferences) will help to understand their natural behaviors and response to human and environmental impacts. Social preferences may lead to formation of distinct social units that are differentially at risk of disturbance (Jacoby et al. 2012). Social structures may be adapted to current selective environments, so rapid environmental changes may have severe consequences in disrupting demographically important social processes, influencing population genetic and demographic structure. Species that occur in small, isolated populations, with a low rate of reproduction, and a high reliance on social interactions are likely to be vulnerable to sudden population crashes due to changes in social structure (Snijders et al. 2017). We recommend long-term monitoring of manta rays in the Raja Ampat marine park to understand the effects of dive tourism, including increases in boating and SCUBA diving activities, which may cause displacement from certain locations and changes to social and reproductive behaviors. Knowledge on social interactions and fine-scale site fidelity in manta rays may be used to prioritize the protection of key sites and develop guidelines for sustainable ecotourism. It is important, however, to stress that fine-scale monitoring and protection within small MPAs are not likely to protect these highly mobile species from target fisheries, bycatch, environmental change, or ocean pollution, which are the major global dangers that manta rays face (Marshall et al. 2018a, b). In the light of these more nefarious threats, network-based studies that link movements and behavior to population ecology are required. These might combine social information with animal tracking technology (Wilson et al. 2015; Jacoby et al. 2016) or information on genetic relatedness (Frère et al. 2010); use temporal networks to investigate social stability and assortativity in the context of a changing environment (Blonder et al. 2012); determine network resilience to removal of individuals (Williams and Lusseau 2006; Mourier et al. 2017); link habitat connectivity to social connectivity (Snijders et al. 2017); or model disease, information, and gene flow using a network approach (Hamede et al. 2009). Such studies will improve our understanding of the ecology and evolution of mobulid rays and other elasmobranchs and help to provide a more holistic approach to their conservation.

Compliance with ethical standards

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