

Social organisation, social behaviour and collective movements in reef manta rays



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Declarations

This thesis entitled “Social organisation, social behaviour and collective movements in reef manta rays” is an original piece of research which is the result of my own work and includes nothing which is the outcome of work done in collaboration except where this is specifically indicated in the text. This thesis has been substantially accomplished during enrolment in this degree. The research contents have not been submitted for a higher degree to any other university or institution. Any help and assistance that I have received in this research and the preparation of the thesis itself have been appropriately acknowledged. All information sources and literature used are indicated in the text. This thesis does not violate or infringe any copyright, trademark, patent, or other rights whatsoever of any person.

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List of Original Publications

This thesis is based on the following original publications, which are referred to in the text by Roman numbers (Chapters II-V). Original publications are reproduced with permission from their copyright holders.

- II Perryman R. J. Y., Venables S. K., Tapilatu R. F., Marshall A. D., Brown C., Franks D. W. (2019). Social preferences and network structure in a population of reef manta rays. *Behavioral Ecology and Sociobiology*, 73(8), 114.
- III Perryman, R. J. Y., Venables, S. K., Tapilatu, R. F., Setyawan, E., Brown, C. & Mourier, J. Social dynamics in reef manta rays depends on individual differences in movements and site fidelity (submitted to *Frontiers in Marine Science*).
- IV Perryman, R. J. Y., Carpenter, M., Lie, E., Sofronov, G., Marshall, A.D., Brown, C. (2021). Reef manta ray cephalic lobe movements are modulated during social interactions. *Behavioral Ecology and Sociobiology* 75, 51.
- V Perryman, R. J. Y., Kent, M.I.A., Pasian, N., Schaerf, T., Ward, A., Brown, C. (in prep.). Investigating manta ray collective movements via drone surveys.

Other publications

During the course of writing this thesis, I was also involved in the following original publications.

Venables, S. K., Marshall, A. D., Germanov, E. S., Perryman, R. J. Y., Tapilatu, R. F., Hendrawan, I. G., ... & Kennington, W. J. (2019). It's not all black and white: investigating colour polymorphism in manta rays across Indo-Pacific populations. *Proceedings of the Royal Society B*, 286(1912), 20191879. <https://doi.org/10.1098/rspb.2019.1879>

Franks, D. W., Weiss, M. N., Silk, M. J., Perryman, R., & Croft, D. P. (2020). Calculating effect sizes in animal social network analysis. *Methods in Ecology and Evolution*, 12(1), 33-41. <https://doi.org/10.1111/2041-210X.13429>

Kadar, J. P., Vila-Pouca, C., Perryman, R. J. Y., Pini-Fitzsimmons, J., Chambers, S., Gervais, C. & Brown, C. (in press). Behaviour. In: Midway, S., Hasler, C. & Chakrabarty, P. (eds.). *Methods for Fish Biology*, 2nd edition. American Fisheries Society, Bethesda, Maryland, USA.

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Author contributions to data chapters

- II: RJYP and DF conceived the central idea of the manuscript. RJYP, SV, AM and RT collected and input data. RJYP conducted all statistical analyses with input from DF. RJYP was the primary author of the manuscript. DF, CB, AM and SV contributed to editing and manuscript revisions.
- III: RJYP conceived the central idea of the manuscript. RJYP, CB, RT, SV and ES assisted with tagging and receiver maintenance. RJYP performed all data analyses with input from JM. RJYP was the author of the manuscript. CB contributed to editing and manuscript revisions.
- IV: RJYP and MC conceived the central idea of the manuscript. RJYP collected all video recording data from the field study location. MC recorded all behavioural observations from video data, with input from RJYP. RJYP conducted all statistical analyses, except for the Markov based analysis, which was developed by RJYP, GS and EL, and conducted by EL. RJYP wrote the manuscript with input from MC. All authors contributed to editing and manuscript revisions.
- V: RJYP and MK conceived the central idea of the manuscript. RJYP collected all drone video data. RJYP, MK, and NP processed data. RJYP and MK performed data analyses. RJYP wrote the manuscript. All authors contributed to editing and manuscript revisions.

Division of labour in co-authored articles

Data Chapter	II	III	IV	V
Conception and design	RP, DF, CB, AM	RP, CB	RP, CB, MC, AM	RP, CB
Planning and implementation	RP, DF	RP, CB	RP, MC, AM	RP, MK, AW
Data collection	RP, SV, RT	RP, CB, RT, SV, ES	RP, SV	RP
Analysis and interpretation	RP	RP, JM, SV	RP, MC, EL, GS	RP, MK, NP, TS
Writing the article	RP	RP	RP, MC	RP
Overall responsibility	RP	RP	RP	RP

Table 1. Contribution of authors to each of the thesis data chapters.

Key to author initials:

RP= Robert Perryman, AM= Andrea Marshall; CB = Culum Brown; SV = Stephanie Venables; RT = Ricardo Tapilatu; ES = Edy Setyawan; DF = Dan Franks; MK = Mia Kent; TS = Timothy Schaerf; JM = Johann Mourier; AW = Ashley Ward; EL = Eric Lie; GS = Georgy Sofronov; NP = Nicolo Pasian.

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Thesis Abstract

Obtaining data on elasmobranch movements and behaviours in marine environments is a considerable challenge, but is urgently required to implement species management plans. It is important to understand patterns and mechanisms of group formation and cohesion, including social organisation and collective behaviour, that are likely to be adapted to current selective environments. These are key aspects of animal behaviour and behavioural ecology that influence population structuring. Reef manta rays (*Mobula alfredi*) are large and mobile pelagic elasmobranchs that occupy subtropical coastal areas in proximity to developing human populations. They form groups at shallow water aggregation sites, where they are vulnerable to exploitation and disturbance. In this thesis I show that *M. alfredi*: a) have structured societies with active social preferences between individuals, linked to site attachment; b) have strong behavioural heterogeneity that influences social dynamics; c) make gestural movements that may be a form of social communication; and d) alter their collective movements during foraging and courtship events. Our results suggest that conservation strategies should consider the social organisation and social behaviours of manta rays to better understand their spatial ecology and evolutionary dynamics, predict the impact of exploitation by fisheries, and mitigate disturbance from marine ecotourism. Local measures that consider groups as complex structures resulting from interactions between heterogeneous individuals are likely to be most useful for ongoing management.

Quote

“People aren’t continuing like this and not doing anything because they are evil, or because they don’t want to. We aren’t destroying the biosphere because we are selfish. We are doing it simply because we are unaware. I think that is very hopeful, because once we know, once we realise, then we change, then we act”.

Greta Thunberg

Chapter I. General Introduction

The oceans are vast, mysterious and critically important to all life on Earth. Covering more than 90% of the habitable space on our planet, they support a vast complexity of biological systems, whose structures, processes, and dynamics are the result of the evolution of life over billions of years into the extraordinary diversity of marine species, societies, communities, and populations that we are still discovering today. Compared with terrestrial habitats, our understanding of biology in the marine environment is poor (Webb et al. 2012; Tonon and Eveillard 2015), and while our impacts on the ocean have not yet reached the devastating scale of loss caused by the defaunation of the land (McCauley et al. 2015), our actions in the 21st century continue to pose an ever graver threat to their health. If we are to protect marine ecosystems, and continue to benefit from the resources and services that they provide, we must take a holistic and precautionary approach that acknowledges the intricate relationships and inter-dependencies that characterise them (Worm et al. 2006; Webb 2009; Karsenti et al. 2011; Jefferson et al. 2014; Goldenberg et al. 2018; Booth et al. 2019). Though rarely implemented by environmental managers, an ecosystem-based approach to conservation is now recognised as essential (Walters et al. 2005; Levin and Lubchenko 2008; Trochta et al. 2016). With this realisation has come a much-improved understanding of food webs, community assemblages and species interactions in the marine environment (De Ruiter et al. 2005; Essington et al. 2006). Yet there is still a tendency among scientists and wildlife managers to consider populations of marine species as singular, homogenous masses (Trochta et al. 2016; Waugh 2019), rather than as sociobiologically complex structures that emerge from interactions between unique individuals within groups (Snijders et al. 2017; Dulvy et al. 2017; Jolles et al. 2020).

Understanding why some species live in groups, while others live solitary lives, is one of the most important questions in animal behaviour and behavioural evolution (Alexander 1974; Vance et al. 2009). Throughout their lives, animals constantly make decisions to join or leave groups that depend on a complex trade-off of costs and benefits in ecological interactions with both conspecifics and heterospecifics. Direct benefits of grouping include protection from predators (Turner et al. 1986), increased efficiency of movements and foraging (Pitcher and Parrish 1993; Couzin and Krause 2003), and reduced heat loss (Gilbert et al. 2008). Costs include increased competition for resources (Pitcher and Parrish 1993; Pavlov and Kasumyan 2000), conspicuousness to predators and the risk of parasite or disease transmission (Johnson et al. 2002; Ioannou et al. 2011) (for reviews of group-living, see Alexander 1974; Krause et al. 2002). Interacting with others can also have social benefits such as increased access to information (Jones et al. 2017), development of knowledge through social learning (Brown and Laland 2003), formation of alliances (Harcourt and de Waal 1992), and

mutualistic behaviours that increase individual or inclusive fitness such as cooperative breeding (Clutton-Brock 2002), communal territory defence (Port et al. 2011), alloparental care (Riedman 1982) and reciprocal altruism (Silk 2013). How animals balance the costs and benefits of being in a group depends on intrinsic motivations that vary between individuals (e.g. the desire to feed or mate), and extrinsic environmental conditions (e.g. landscape complexity, availability of prey, presence of predators).

Social animals both create, and are influenced by, their interactions and relationships with others. An individual's fitness will depend in part on the size of the group to which it belongs and the structure of relationships within that group, especially its own social relationships (Pulliam and Caraco 1984; Jacoby et al. 2012b). Heterogeneity in social interactions between individuals can cause the structuring of populations into discrete units that respond differently to various density-dependent and density-independent factors (e.g. predation risk, habitat complexity), leading to stratification in the survival and reproductive success of the members of those units (Whitehead and Rendell 2004; Lusseau et al. 2006). Thus, social structures are the result of adaptive evolution (Alexander 1974; Rubenstein 1978) to current selective environments, making social species vulnerable to rapid environmental change or human disturbance, such as the removal of key individuals (Snijders et al. 2017). Conversely, as a key component of a species' biology, social structuring is also a *driver* of species evolution, affecting important ecological and evolutionary processes such as gene flow (Krützen 2003), pathology (Corner et al. 2003), information transfer (McComb et al. 2003; Krause et al. 2010), sexual selection (McDonald et al. 2013) and habitat exploitation (Baird and Dill 1996; Firth et al. 2015; Giraldeau and Caraco 2018). This includes the evolution of social processes such as cooperation or development of social traditions (Perry et al. 2003; Ohtsuki et al. 2006; Ryder et al. 2019). Any disturbance to adaptive social connectivity (e.g. habitat fragmentation, removal of key individuals) may have severe consequences for the resilience and long-term viability of populations (Banks et al. 2007; Snijders et al. 2017; Brakes et al. 2019). Unsurprisingly, group living and social organisation have been the subject of much research by behavioural ecologists. Studies to date have focused primarily on terrestrial vertebrates (e.g. Caro and Collins 1987; Peterson et al. 2002; Bauer et al. 2003; Wittemyer et al. 2005; Strandburg-Peshkin et al. 2015; Ribas et al. 2016), marine mammals (e.g. Baird and Whitehead 2000; Christal and Whitehead 2001; Lusseau et al. 2003; Lusseau et al. 2006; Daura-Jorge et al. 2012) and freshwater teleost fish (e.g. Pitcher & Parrish 1993; Brown & Laland 2003; Croft et al. 2006; Pollen et al. 2007; Maruska 2014; Wilson et al. 2014b; Ward & Webster 2016). It is only in the last decade that research on the social organization of free-ranging marine fish has been undertaken, mainly on sharks.

1.1. Sharks and rays

The elasmobranchs (Chondrichthyes, Elasmobranchii) are ancient, predominantly marine, fishes that are highly functionally diverse and play a hugely important role in marine ecosystems globally. Currently, around 1,160 extant species are recognised, of which ~510 belong to the superorder Selachii (the sharks) and ~650 to the superorder Batoidea (the rays and skates). Over hundreds of millions of years, these species have evolved via adaptive radiation to inhabit the vast majority of aquatic habitats, from inshore coral reefs and sandy areas of the continental shelf to the deep waters and seamounts of the open ocean, from the benthic to the epipelagic, even into estuaries and rivers (Curtis et al. 2011; Medeiros et al. 2015). Elasmobranchs connect habitats and ecosystems by their movements and migrations (Dulvy et al. 2017), control the vertical transfer of energy through trophic levels, and regulate other species' populations and behaviours through predation and risk effects (Creel and Christianson 2008; Heithaus et al. 2008; Ferretti et al. 2010; Williams et al. 2018). Understanding them is critical to our knowledge of the history, biology and ecology of life in the ocean.

Unfortunately, as the human population has exploded in recent decades, so too has its impact on marine life. The global decline in elasmobranch populations has been well documented, and we are now beginning to understand the wider impact of this on the overall functioning of marine ecosystems (Baum et al. 2003; Myers et al. 2007; Heithaus et al. 2010; Ferretti et al. 2010; Dulvy et al. 2014a). Commercial exploitation of sharks and rays is driven by the demand for, and international trade (legal and illegal) in their products. Elasmobranch meat contributes substantially to food security in many developing nations (Pauly et al. 2005; Srinivasan et al. 2010; Simpfendorfer and Dulvy 2017), while their fins are prized in East Asian markets (Clarke et al. 2006; Clarke et al. 2007; Jaiteh et al. 2017; Ferretti et al. 2020). Many populations have been heavily overfished in the recent past (Simpfendorfer and Kyne 2009; Costello et al. 2012; Worm et al. 2013; Dulvy et al. 2017). Elasmobranchs are also killed in large numbers as bycatch due to indiscriminate use of fishing methods such as trawling and longlining (Molina and Cooke 2012; Oliver et al. 2015); ghost fishing by discarded fishing gear (Stelfox et al. 2016); gillnets and drumlines in the guise of protecting surfers and other beach-users (Dudley 1997; Gibbs et al. 2020); and recreational fishing (Gallagher et al. 2017). They suffer from ocean pollution (Fossi et al. 2017; Germanov et al. 2019; Mucientes and Queiroz 2019), and are susceptible to climate related changes to ocean temperature, acidity and currents (Sequeira et al. 2012; Williamson et al. 2019). They are impacted heavily by the over-development of coastal zones, including destruction of the coral reefs, mangrove and kelp forests and seagrass beds (Heithaus et al. 2002; Chin et al. 2012; Ward-Paige et al. 2010; Jewell et al. 2019)

that various species inhabit at different stages of their life-cycle. These combined threats have already had devastating impacts. Many elasmobranch species are now threatened with extinction (Robbins et al. 2006; Bradley and Gaines 2014; Dulvy et al. 2014a; IUCN 2020), and urgent interventions are required, including protection of critical habitats, and in some cases enforcement of near-zero fishing mortality (Baum et al. 2003; Ferretti et al. 2008; Ferretti et al. 2010; Ward-Paige et al. 2010; Nance et al. 2011; Reid et al. 2011; Ward-Paige et al. 2012). Shark and ray fishing mortality is still exceptionally under-managed (Dulvy et al. 2017), however, and the vast majority of populations lack sufficient protection to halt population declines (Lack et al. 2014; Davidson et al. 2016).

Given the multiple anthropogenic threats that elasmobranchs face, it is essential to understand the vulnerability and potential resilience of their populations within wider ecosystems. Despite the temptation for managers and governments to look for 'silver bullet' solutions to complex conservation problems, the functional and ecological diversity of elasmobranchs, and the complex nature of the threats they face, defy simplification (Dulvy et al. 2017). Effective elasmobranch conservation requires specific diagnosis of problems for different species and regions, and interdisciplinary assessment of how to deal with these according to the needs of the whole ecosystem and of the human populations that depend upon it for food or economic security (Dulvy et al. 2014a; Dulvy et al. 2017; Lyons et al. 2019). In particular, it requires detailed knowledge of spatial ecology, such as how elasmobranchs use reproductive and foraging habitats, and their movements (including routes, timing and distribution of individuals) within and between these areas (Bonfil 1997; Simpfendorfer et al. 2010; Speed et al. 2010; Jacoby et al. 2012b; Knip et al. 2012; Hays et al. 2016). Sociality is likely to be a key driver of these processes (Jacoby et al. 2012b). To aid conservation, there is an urgent need to understand the various ways in which elasmobranchs form groups and behave socially, and to link social structuring to wider population demographics and spatial ecology (Jacoby et al. 2012b). Research in these areas will help us understand elasmobranch populations as complex, interdependent systems (Jacoby et al. 2012b; Snijders et al. 2017; Mourier et al. 2018). It is likely to be vital to predict the response of populations to disturbance, prioritise the protection of certain populations or locations that provide connectivity or refuge (Banks et al. 2007; Cartamil et al. 2010; Ledee et al. 2015; Silk et al. 2017; Heupel et al. 2019a; Mourier et al. 2019), and guide the designation of Marine Protected Areas (MPAs) (Espinoza et al. 2014; Lea et al. 2016; Williamson et al. 2019; Peel et al. 2019).

1.2. Elasmobranch group formation

Sharks and rays form groups in many different ways and for a variety of reasons. Passive aggregation is a major driver of spatial distributions among elasmobranch species with a broad range of characteristics and evolutionary histories (for a review see Jacoby et al. 2012b), including both the juvenile and adult phases, in active pelagic as well as sedentary benthic species. Aggregation can occur due to the clumped or patchy distribution of resources (e.g. Heyman et al. 2001; Johnson et al. 2002; Martin et al. 2009; de la Parra Venegas et al. 2011), refuging behaviour (e.g. Sims et al. 2005; Hight and Lowe 2007; Powter and Gladstone 2009), or synchronized patterns of daily or seasonal activity, such as foraging or mating (e.g. Economakis and Lobel 1998; Heupel & Simpfendorfer 2005; Domeier et al. 2008; Speed et al. 2011; Findlay et al. 2016; Bass et al. 2017). When group sizes are below an optimum for the prevailing conditions, for example, individuals may be more inclined to form groups. Dynamic environmental conditions and patchily distributed resources may cause ephemeral group structuring and fission-fusion dynamics (Sumpter 2006; Haulsee et al. 2016). Elasmobranch aggregations may also be assortatively structured by age, size or sex (Springer 1967; Klimley 1987; Hulbert et al. 2005; Jacoby et al. 2012b), often due to developmental or sex-based differences in habitat and dietary preferences (Wetherbee, Cortes & Bizzarro 2004), swimming capabilities, or other factors, such as aggression, that vary by phenotype (Wearmouth and Sims 2008). For example, juveniles of multiple species, including blacktip (*Carcharhinus limbatus*), lemon (*Negaprion brevirostris*) and thresher (*Alopias vulpinus*) sharks are all known to aggregate in nursery areas, probably to protect themselves from predators (Morrissey and Gruber 1993; Heupel and Simpfendorfer 2005; Cartamil et al. 2010). In teleost fishes, phenotypic similarity is known to maximise benefits of shoaling, and is positively selected for by frequency-dependent predation on odd individuals, affecting important ecological flows, such as information transfer and disease transmission through populations (Theodorakis 1989; Hoare and Krause 2003). If assortative structuring is a common feature of elasmobranch populations it is likely to have significant implications for conservation; for example, it may cause differential exploitation of phenotypes where fishing pressure is spatially focused (Mucientes et al. 2009).

1.3. Social behaviour and collective movement

Although many elasmobranch species move and migrate individually, there has long been evidence suggesting that some species behave socially and move in cohesive groups. This is likely to have important implications for their overall biology and ecology (for a review of elasmobranch social behaviour see Jacoby et al. 2012b). Examples of social behaviour in sharks include threat displays,

dominance interactions, and gestural communication during agonistic behaviours (Nelson et al. 1986; Martin 2007), as well as during courtship and feeding. Recent research suggests that elasmobranchs can learn socially (Guttridge et al. 2009; Guttridge et al. 2013; Vila Pouca et al. 2020), and have sophisticated cognitive abilities and varied social personalities (Jacoby et al. 2014; Guttridge and Brown 2014; Byrnes and Brown 2016; Finger et al. 2017). The first investigation of synchronous social movement in groups of sharks was made by Springer (1967) who speculated that groups were structured non-randomly. Since then, polarized schooling behaviours have been recorded in multiple other species, though these studies have usually relied on limited or brief observations (e.g. Blaycock et al. 1989; Rogers et al. 1990). Myrberg Jr. and Gruber (1974) reported following and other apparently social movements in bonnethead sharks (*Sphyrna tiburo*). Reproductive strategies are likely to be a major driver of social and collective behaviours in elasmobranchs (Jacoby et al. 2012b). Basking sharks (*Cetorhinus maximus*) perform following, parallel-swimming and echelon-swimming behaviours over extended time periods, probably linked to courtship (Sims et al. 2000; Wilson 2004). Similarly, spotted eagle rays (*Aetobatus narinari*) perform following and circling behaviours (Tricas 1980) during courtship. Close following behaviour is reported in several other elasmobranch species including the nurse shark (*Ginglymostoma cirratum*), clearnose skate (*Raja eglanteria*), sand tiger shark (*Carcharias taurus*) and whitetip reef shark (*Triaenodon obesus*) (Klimley 1980; Luer and Gilbert 1985; Gordon 1993; Carrier et al. 1994; Whitney et al. 2004). This is often a pre-courtship or pre-copulatory behaviour performed by males, though following may also occur for non-reproductive reasons (Pratt et al. 2005; Guttridge et al. 2011). Myliobatid rays are known to swim and migrate in large mixed-sex schools of thousands of individuals, with group sizes depending on the species and environmental conditions (Notarolo di Sciara 1988; Blaycock et al. 1989; Schwartz et al. 1990; Blaycock et al. 1993). For example, in cownose rays (*Rhinoptera* sp.) and spotted eagle rays, distinct school shapes seem to be dependent on water depth and group behaviour (Silliman 1999; Tagliafico et al. 2019).

Cohesive schooling behaviour is ubiquitous in teleost fishes, and typically occurs due to individuals following simple, localized rules of interaction (such as attraction and alignment at given distances) that enable them to respond rapidly to the motion and state of near-neighbours without requiring familiarity or social information (Couzin and Krause 2003; Couzin et al. 2005; Sumpter 2006). This often has strong anti-predator benefits (e.g. through collective vigilance (Ward et al. 2011), and dilution or confusion effects (Lehtonen and Jaatinen 2016), while improving hydrodynamic efficiency of movements (Hemelrijk et al. 2015) and aiding migration (Berdahl 2018). In many fish species, however, social interactions and collective movements are impacted strongly by familiarity between individuals (Bode et al. 2011; Davis et al. 2017). Species that move in groups, such as hammerhead

sharks (*Sphyrna* spp.) often maintain distances too large to gain hydrodynamic benefits from schooling, and cohesiveness is thought to have social benefits (Klimley 1983; Klimley and Nelson 1984). Likewise, while some elasmobranch group structures are clearly adapted for predator evasion (e.g. Semeniuk and Dill 2006), adults of many large species that occupy apex trophic positions would not benefit from this, yet still form cohesive groups. Selection on homogeneity of individuals within shoals may be weaker or non-existent and is likely to have effects on emergent collective behaviours (Jolles et al. 2017). Social factors that drive cohesive schooling may include improvements in group navigation and foraging success (Ward and Webster 2016; Berdahl et al. 2018) or reproductive benefits (e.g. males may gain reproductive advantages by escorting females- see Deakos 2012, Stevens 2016). As in teleost fish (Pitcher 1983), manta rays and other elasmobranchs may shift from cohesive schooling to less organized shoaling behaviour when behaving socially. We investigate these mechanisms in **Chapter V**.

Research on the causes and effects of sociality in elasmobranch populations is required to identify the mechanisms underlying repeated individual interactions (e.g. social recognition, familiarity, social relationships) and the emergent properties of groups (collective behaviours, social organisation). It is important to try to separate and disentangle social and collective structuring that is driven by active social preferences for other individuals from some aggregative and assortative behaviours, which can be largely driven by external forces, locational preferences or linked to phenotypic characteristics. These different types of group-forming mechanisms are likely to result in structures that respond differently to disturbance, with distinct ecological and evolutionary consequences. Disentangling the causes of group formation in wild elasmobranch populations is not a trivial undertaking, as these causes are likely to operate simultaneously and in conjunction with one another (Croft et al. 2011, Mourier et al. 2012). Indeed, social structuring is likely to be highly dependent on movements and habitat use driven by aggregative forces, because pairs or groups of individuals will be more likely to develop social bonds if they repeatedly occupy the same locations. For example, annual site philopatry observed in Port Jackson sharks is clearly structured by sex differences in arrival times, which may cause assortative social structuring or social refuging (Bass et al. 2017). Social systems in hammerhead sharks are also thought to depend on refuging around offshore seamounts, where they aggregate to take advantage of reduced current velocities inside eddies (Klimley 1983; Klimley and Nelson 1984). Such issues require detailed observations of the undisturbed behaviour of elasmobranchs in their natural habitats, and testing of specific, biologically relevant hypotheses on social organization, which is made possible by social network analysis. Over the last decade, considerable progress has been made in the development of methods to describe and quantify the

structure of social relationships in elasmobranchs (see Wilson et al. 2014 and Mourier et al. 2018 for reviews).

1.4. Social network analysis

Network theory (also known as graph theory) has origins in the mathematical and social sciences (including computational science, statistical physics and sociology) but is increasingly utilised in many areas of biology, including genetics, spatial movements, community ecology, epidemiology, information transmission, ethology, sociobiology, evolution and wildlife management (Croft et al. 2008; Wey et al. 2008; Krause et al. 2015; Sosa et al. 2020). Social network analysis (hereafter SNA) is the application of network theory, using a versatile and multi-faceted range of techniques and tools to study the structure of relationships between individuals or groups within societies. SNA enables the quantitative study of social structure across different scales of organisation and is increasingly being applied to address a range of biological problems (Croft 2008). By linking individual behaviour to group-level and population-level phenomena, SNA can provide insights that would not be possible by studying behavioural interactions in isolation; it is therefore essential to robust interpretation of the drivers of population dynamics and species evolution (Lusseau et al. 2006). Hinde's (1976) conceptual framework considers the social organisation of animal groups at three structural levels: the type, quality and duration of behavioural interactions between individuals describe their relationships (including social preferences and the distribution of these between individuals and phenotypes). Patterns of relationships in turn determine the overall social structure or 'surface structure' of populations (including the relative network positions of individuals and the overall distribution of network connectivity). SNA permits the testing of ecologically relevant hypotheses associated with the causes and consequences of social structure within populations (Pinter-Wollman et al. 2012). Social network analyses can be used as an indicator of the changing state of animal societies and the impact of anthropogenic disturbance on them, and are thus valuable for monitoring of population health. For example, they can be used to identify where overharvesting is causing fragmentation of social systems, or interfering with demographically important social processes (Snijders et al 2017). Reduced social stability and increases in aggressive interactions can often be indicators of external stresses to populations.

Social networks consist of nodes representing individuals or social units, and links or 'edges' between these nodes that represent connections between each pair of nodes. Edges may be directional (e.g. one individual passing information to another) or non-directional (e.g. two individuals being in social contact), positive or negative (e.g. affiliation/avoidance), and binary (e.g. observed together/not observed together) or weighted (e.g. frequency/duration of associations). Connections can also be

based on known relationships (such as kinship or mating ties) between individuals or groups, or non-social interactions such as resource sharing or pathogen transmission events. Studies must carefully consider how to define biologically meaningful edges that represent connections of interest, and to record these in a standardized way (Whitehead 2008; Franks et al. 2010; Silk et al. 2015). The choice of an appropriate association index (AI) that accounts for sampling bias and variable reliability of observed edges is critical (Farine and Whitehead 2015; Hoppitt and Farine 2018). Network edges may be based on inferred associations, where individuals are assumed to interact if they are observed in spatiotemporal proximity, known as the 'gambit of the group' (GoG) (Ruxton and James 2002; Franks et al. 2010), or by direct observation of social contact, for example communication between individuals, or touch-based interactions such as grooming in primates (Sueur et al. 2011; Crofoot et al. 2011). The GoG approach is popular in studies on marine species which are difficult or impossible to observe directly and where individuals move between easily defined groups (Franks et al. 2010; Silk et al. 2015). It makes several assumptions (such as that social interactions occur at similar rates between all group members) (Whitehead and Dufault 1999; Farine and Whitehead 2015) that must be dealt with appropriately. Following construction of an appropriate social network, its structural properties may be explored using a range of metrics (summarised in Mourier et al. 2018). Node-level metrics are useful for understanding the position and relative social importance (centrality) of individuals. Other metrics such as average path length, density and network diameter can be used to record whole-network properties such as connectivity and clustering, and compare these among species or populations (Croft et al. 2008). Usually, SNA requires the reliable identification and repeated observation of individual animals and their characteristics, which may include their phenotype, genetic relatedness or behavioural traits. These may then be compared to node-level metrics, for example if an aim is to understand how individual attributes mediate the relationship between social relations and fitness.

Performing social network analyses on wild animals is, however, a complicated process requiring careful consideration of the particular study system, sampling limitations and how to deal with multiple sources of uncertainty and confounding effects (Lusseau et al. 2009; Farine and Strandburg-Peshkin 2015; Davis et al. 2018; Franks et al. 2020). Crucially, due to their relational nature, network data are inherently non-independent and thus cannot be examined using standard statistical methods. Comparison of observed networks to appropriate null models generated by randomisation of the empirical dataset or permutation of node labels is essential (Croft et al. 2011; Farine and Whitehead 2015; Krause et al. 2015; Farine et al. 2017; Farine and Carter 2020). To test specific hypotheses, randomisations can be constrained within particular phenomena of interest (e.g. space, time, phenotype), while maintaining the structure of all other aspects of the network. Failure to adopt

an appropriate null model is likely to produce deceptive or spurious results (James et al. 2009; Franks et al. 2010; Farine et al. 2017; Farine and Aplin 2019). Recently, several studies have found that different types of permutation test (data stream permutations and node label permutations) suffer from high rates of type I and type II errors due to their failure to account for both non-social “nuisance effects” (including sampling biases such as certain individuals being more likely to be observed than others or the non-random spatial structure of sampling procedures), and other confounding effects that are associated with real differences between individuals that affect their connections, besides social preferences (Franks et al. 2020; Puga-Gonzalez et al. 2020; Weiss et al. 2021). The authors involved suggest several methods to solve this, including the inclusion of control variables within regression models, the use of generalized affiliation indices and the division of large datasets to generate replicate networks. Farine and Carter (2020) suggest a double-permutation method, involving both pre- and post-network permutations that deals with the specific weaknesses of each. We apply several of these new methodologies to our analysis of manta ray social structuring in **Chapters II and III**.

Though the application of SNA to studies on elasmobranch populations is still in its infancy, over the last two decades progress in animal SNA has been accelerated by our ability to collect, organize and interpret increasingly large datasets on free-ranging animals. This enables analysis of social behaviours and relationships in a wider population-level context, and it is now possible to conduct studies that uncover the complex interdependent sociobiological processes that may be important in the structuring of elasmobranch populations and the dynamics of elasmobranch behavioural ecology. SNA has recently been used to show that various functionally and phylogenetically diverse elasmobranch species exhibit social structuring (e.g. Jacoby et al. 2010; Guttridge et al. 2011; Mourier et al. 2012; Loiseau et al. 2016). Jacoby et al. (2010; 2012a; 2012c; 2014) conducted studies on captive small-spotted catsharks (*Scyliorhinus canicula*) that investigated flexibility of network structuring, and the effect of environmental changes (e.g. influence of introduced males) on this, as well as variability between groups and individuals. They provided the first empirical evidence that the structure of a shark social network remains consistent over time, and that this was driven by active social preferences rather than preferences for particular group sizes or differences in gregariousness. Studies on semi-captive and free-ranging juvenile lemon sharks (*Negaprion brevirostris*) have shown that active social decisions and assortment by size can influence groupings (Guttridge et al. 2009), and that social preferences occur (Guttridge et al. 2011) that may be based on familiarity between individuals (Keller et al. 2017). In captive studies on this species, Wilson et al. (2015) investigated social dynamics and behavioural phenotypes using Markov chain-based network analysis in combination with data from accelerometer tags, finding that individual sharks did not show

consistency in their social network positions, but did preferentially associate with others of similar locomotor profiles.

Several field-based social network studies on elasmobranchs have utilized large, long-term photographic identification datasets, similar to those used extensively in prior studies on dolphins and other cetacean species (e.g. Lusseau et al. 2003a; 2003b; 2006; Daura-Jorge et al. 2012; Wiszniewski et al. 2012). These typically involve observations of groups recorded at coarse time scales (e.g. once per day), with social network structure inferred by the GoG. The observed group structure is then compared to null models created by randomization of individual observations within 'sampling periods' of a biologically appropriate length of time. Mourier et al. (2012), for example, used data collected during 190 dives over 2 years to show, for the first time, that a shark population was structured into social 'communities' characterized by non-random association preferences, with assortment by sex and size influencing associations in some areas. They also used simulations to show that this network structure was resilient to removal of 25% of individuals (Mourier et al. 2017b). Mourier and Planes (2021) recently undertook the first combined analysis of social structure and population genetics in elasmobranchs, finding that kinship did not predict social relationships in blacktip reef sharks (*Carcharhinus melanopterus*). Findlay et al. (2016) used direct observations of 323 individuals over 6 years to study association preferences in a migratory pelagic species (the white shark *Carcharodon carcharias*), though results suggest that this species does not maintain social preferences. Social networks may also be based on direct observation of social interactions. Such studies may be used to understand complex social behaviours within conserved social groups and formation of cliques or dominance hierarchies (Myrberg and Gruber 1974; Gordon 1993; Pratt and Carrier 2001; Martin 2007; Sperone et al. 2010), as well as collective or cooperative behaviours (Clutton-Brock 2009; Bode et al. 2011; Ryder et al. 2020). Brena et al. (2018), for example, studied dominance interactions and tolerance associations in sicklefin lemon sharks (*Negaprion acutidens*) using remote cameras.

SNA studies on elasmobranchs are now beginning to benefit from the data recording capabilities provided by automated tracking of individuals. Movement networks based on telemetry data from tagged individuals have been used by multiple authors to capture the importance of specific locations and habitats to elasmobranch populations (Jacoby et al. 2012a; Ledee et al. 2015; Stehfest et al. 2015; Papastamatiou et al. 2015; Jacoby and Freeman 2016; Nicol et al. 2016; Heupel et al. 2019b). These can be useful in developing locally-oriented management solutions, for example providing specific guidance for design of Marine Protected Areas (Knip et al. 2012; Lea et al. 2016; Peel et al. 2019). Several recent studies have explored options for reconstructing social relationships between

elasmobranchs from telemetry data. Studying a sedentary benthic species, Armansin et al. (2016) used a passive acoustic receiver array to continuously triangulate the exact location of multiple sharks simultaneously. For active species, an approach using machine learning and Gaussian mixture models (Psorakis et al. 2015; Jacoby et al. 2016) can be used to divide temporal data-streams into biologically meaningful sections for network analysis. This method was used to provide evidence for long-term, spatially extensive social processes in wild grey reef sharks (*Carcharhinus amblyrhynchos*), and showed that some individuals emerge as leaders, with this process being driven by the duration of co-occurrences between individuals (Jacoby et al. 2016). Recently, a study on the same population showed that affiliations between individuals were assorted into spatially explicit social communities (Papastamatiou et al. 2020). We use acoustic telemetry data to construct networks and infer social affiliations between individuals in **Chapter III**.

In summary, the variety of methods now available to study elasmobranch social interactions and group structuring promises to revolutionise the study of their population ecology and movements, and such studies are expected to have important applications to elasmobranch conservation (Mourier et al. 2018). With the exception of one small study on social dynamics in spotted eagle rays (*Aetobatus narinari*) (Krause et al. 2009), however, to the author's knowledge all social network studies of elasmobranchs to date have focused on sharks, with almost no consideration of the importance of sociality in batoids (rays and skates). This thesis is an attempt to provide understanding of the sociobiological processes that appear, to a large extent, to govern the lives of one of the most charismatic and vulnerable elasmobranch species, the reef manta ray.

1.5. Study species- the reef manta ray

Manta rays are large, mobile, and conspicuous filter-feeding rays. Recently reclassified into the genus *Mobula* (White et al. 2018; see also Marshall et al. 2009; Hosegood et al. 2018), they are members of the Myliobatidae family, that evolved from a benthic common ancestor around 28 Mya, and now live a predominantly pelagic existence (Carrier et al. 2012; Aschliman et al. 2012; Poortvliet et al. 2015). The reef manta ray (*Mobula alfredi*) (Krefft 1868) grows to ~5.5m disc-width and inhabits tropical and subtropical coastal regions to approximately 32° latitude, occupying inshore coral reef habitats in coastal regions and around offshore atolls (Kashiwagi et al. 2011; Couturier et al. 2012). It is thought to have diverged less than 1 Mya from the oceanic manta ray (*Mobula birostris*) (Walbaum 1792), largely due to the species' distinct habitat preferences (Kashiwagi et al. 2012). *M. birostris* is the largest extant ray species (up to 7m disc-width) (McClain et al. 2015) and occurs in mosaic sympatry with *M. alfredi* throughout much of its range in the African and Indo-Pacific regions. Its range extends

to higher latitudes, and it tends to occupy cooler waters in habitats further offshore or closer to the edge of continental shelves (Marshall et al. 2011; Kashiwagi et al. 2011; Graham et al. 2012).

Manta rays have highly conservative, K-selected life history strategies. They are naturally long-lived (probably reaching at least 50 years), develop slowly, and have among the lowest reproductive output of all elasmobranchs (Dulvy et al. 2014b; Stevens et al. 2018). Manta and other mobulid rays have the largest brain to body size ratio of any class of fish (Ari 2011), suggesting advanced cognitive abilities, including social intelligence (Dunbar and Shultz 2007). They regularly form groups in shallow waters and are known to perform following, copying and breaching behaviours (Marshall and Bennett 2009; Deakos et al. 2010; Stevens 2016) indicative of sociality. Their populations are typically fragmented, diffuse and small, with subpopulation sizes typically estimated in the hundreds to several thousands (Deakos et al. 2011; Marshall et al. 2011; Kitchen-Wheeler et al. 2012; Couturier et al. 2014; Kashiwagi 2014), and there is thought to be little genetic connectivity between populations (Stevens 2016; Stewart et al. 2018). Such population-level characteristics suggest that evolution in manta rays may have been particularly conducive to the development of sociality, but are also likely to exacerbate anthropogenic impacts on their populations (Banks et al. 2007). Even small negative pressures exerted upon manta ray populations are likely to have severe consequences, and once depleted, population recovery is likely to be extremely slow (Marshall et al. 2011; Dulvy et al. 2014b; Lawson et al. 2016; Stevens 2016).

Unfortunately, manta rays currently face a multitude of anthropogenic threats. The most severe of these is direct, targeted fishing (Alava et al. 1997; White et al. 2006; Lewis et al. 2015; Croll et al. 2016), which has recently been driven by increasing demand for, and international trade in, mobulid gill plates in Asian dried food and 'traditional' Chinese medicine markets (Lawson et al. 2016; O'Malley et al. 2016; O'Malley et al. 2017). In locations such as Hong Kong and Guangzhou, China, their parts are aggressively marketed at high prices as a health tonic purported to treat a variety of ailments (O'Malley et al. 2017). Additionally, manta rays suffer from many of the same general threats to elasmobranchs, including incidental catch (White et al. 2006; Couturier et al. 2012), entanglement in discarded fishing gear (Marshall and Bennett 2010; Deakos et al. 2011; Couturier et al. 2012) and marine pollution (Germanov et al. 2019). Climate change effects, such as disturbance to oceanic currents and ocean acidification, are also likely to have significant effects on their populations due to their impact on oceanographic conditions and the distribution of manta rays' zooplankton prey (Jaime et al. 2012; Rohner et al. 2013). Anthropogenic pressures have already led to documented declines in manta ray sightings (e.g. White et al. 2015; Croll et al. 2016; Rohner et al. 2017b) and data on mobulid ray landings in many areas of manta rays' core range during the 2010s

are of particular concern (Dulvy et al. 2014b; Lewis et al. 2015; Croll et al. 2016). Both species of manta ray are listed as Vulnerable to Extinction on the IUCN Red List of threatened species (Marshall et al. 2018; Marshall et al. 2019). Due to their propensity to cross international boundaries, *M. alfredi* and *M. birostris* are also included in the Convention on Migratory Species of Wild Animals (CMS) and in March 2013 were listed in Appendix II of the Convention on International Trade in Endangered Species (CITES), in an attempt to prevent trade in their parts between signifying countries. Legislation to protect manta rays now exists in multiple nation states (Croll et al. 2016; Lawson et al. 2016).

A major issue for conservation is that manta rays are often distributed along the coastlines of low-income or developing countries with large human populations, where implementing and enforcing strict conservation measures can be problematic. In the large island nation of Indonesia, the intensity of threats to manta rays, and the resources available to combat them vary widely between regions. Despite the declaration of a 'sanctuary' for manta rays throughout Indonesian waters in 2014, large-scale fisheries continue to exploit manta rays with impunity (Germanov and Marshall 2014; Lewis et al. 2015), and to date no comprehensive management strategy exists to protect manta rays in the country. Research and science-based management of populations is urgently required, including rapid assessments of local population status, threats and movements, along with additional resources to employ and train a local workforce to implement conservation measures (Dulvy et al. 2017; Ward-Paige et al. 2017). At the same time, Indonesia is experiencing rapid development of its tourism sector. The long-term sustainability of this industry is highly dependent on the maintenance of healthy marine ecosystems. For example, In Raja Ampat, West Papua, tourism expanded from 998,000 visitors in 2007 to 7.7 million in 2015 (King 2017) and continues to grow year-on-year. Charismatic megafauna species like manta rays are an important attraction for dive-tourists (Couturier et al. 2011; Venables et al. 2016). Approachable, playful and curious towards humans, manta rays are new darlings of environmental popular and social media, with broad outreach to inspire conservation of the ocean. Manta ray watching tourism provides an estimated US\$15m in direct economic benefits to Indonesia annually (O'Malley et al. 2013) and has the potential to be a positive force for elasmobranch conservation (Vianna et al. 2012; Cisneros-Montemayor et al. 2013; Venables et al. 2016; O'Malley et al. 2017). However, currently most wildlife interaction tourism in Indonesia is completely unregulated, and is likely to increase pressure on these animals, particularly at the most popular and accessible dive sites (Gallagher et al. 2015). Unregulated ecotourism brings problems such as the injuries to manta rays from boat strikes, increased pollution and destruction of reef habitats, disturbance to manta rays' natural behaviour and conflict between local people and international tourists. Such pressures can lead to the temporary emigration of manta rays from heavily-used areas (De Rosemont 2008; Deakos 2010; Couturier et al. 2011; RP pers. obs.).

Conservation of mobile species such as manta and other mobulid rays requires explicit knowledge of their spatial ecology and natural behaviour in the wild, in order to detect negative population trends and behaviours that may increase susceptibility to human impacts (Lawson et al. 2016, Stewart et al. 2018). A major priority is to understand the drivers of aggregation and movement into critical habitats (Stewart et al. 2018). The exploitation and disturbance of manta rays in critical habitats is a major conservation concern. Current knowledge of manta rays' movements, habitat use, foraging behaviours and reproductive ecology suggests social behaviour is a particularly important aspect of their ecology, with far-reaching implications for their conservation. In the following sections I discuss what is known about these aspects of manta ray behavioural ecology, and how this knowledge may be enhanced through consideration of their sociality.

1.5.1. Movements, distributions and habitat use

The population demographics, movements and habitat use of manta rays have been studied in multiple locations in the past 20 years. This research has been based largely on mark-recapture analysis of long-term photo-identification datasets, and tracking of individual rays via automated telemetry methods, which either record the presence of tagged individuals in the vicinity of acoustic receiver stations or transmit the location of individuals via satellite GPS when they come to the water surface. Several *M. alfredi* populations have been studied intensively, including in South-East Africa (Marshall et al. 2011; Peel et al. 2019; Venables et al. 2020), the Maldives (Anderson et al. 2011; Kitchen Wheeler et al. 2012; Stevens 2016), Australia (Couturier et al. 2014; Jaine et al. 2014; Armstrong et al. 2020), Hawaii (Clark 2010; Deakos 2010; Deakos et al. 2011), the Red Sea (Braun et al. 2013; Braun et al. 2015), Indonesia (Dewar et al. 2008; Germanov et al. 2019) and Micronesia (Martin et al. 2016). Less is known about *M. birostris* populations, that are often presumed to occupy offshore habitats and to be highly migratory (Graham et al. 2012; Girondot et al. 2015; but see Stewart et al. 2016). *M. alfredi* is known to make long-distance movements of up to 1150km on occasion (e.g. Germanov and Marshall 2014; Armstrong et al. 2019), but is thought to be less migratory and is known to congregate in inshore sandy and coral reef habitats for extended periods. Multiple studies on *M. alfredi* have demonstrated patterns of individual residency to particular locations (Deakos et al. 2011; Jaine et al. 2014; Braun et al. 2015; Marshall et al. 2011). Dewar et al. (2008), for example, found that several acoustically tagged rays spent >90% of their time at the site where they were tagged, and that 81% of subsequent site visits, on different days, were at the same site. These findings indicate that *M. alfredi* individuals occupy preferred home ranges and may repeatedly interact with the same conspecifics. Such site attachment is likely to provide the

opportunity for relationships, including social preferences between individuals, to develop. It is also likely that manta rays will gain benefit from fine-scale, spatially focused, conservation measures such as use of MPAs (Peel et al. 2019; Venables et al. 2020) to protect critical habitats - typically multi-purpose zones in shallow waters, incorporating cleaning stations, and feeding, mating, birthing and nursery grounds (Jaine et al. 2012; Stevens et al. 2016), although specific aggregation sites are often characterised by a single dominant activity (Jaine et al. 2012).

1.5.2. Feeding ecology

As filter feeders, mobulid rays use their large mouths, cephalic lobes and modified branchial appendages ('gill plates') to feed, preying primarily on zooplankton, whose distribution is thought to be a primary driver of their movements. Most mobulid species (e.g. *M. birostris*, *M. alfredi*, *M. thurstoni*, *M. tarapacana*, *M. japanica* and *M. mobular*) appear to occupy similar trophic positions, as generalists that prioritise prey biomass rather than taxonomic composition (Rohner et al. 2017a). Manta rays have evolved behavioural adaptations to living in oligotrophic environments where zooplankton are patchily distributed in time and space; these include the ability to survive periods of starvation, to feed efficiently on large pulses of prey, and to vary their dietary intake depending on habitat and season (Rohner et al. 2017a; Burgess et al. 2016; Burgess et al. 2017). They display a high level of flexibility in foraging behaviour, taking advantage of both mesopelagic and demersal sources of prey that are more or less abundant at different times throughout their range, including calanoid copepods (Bennett et al. 2017), krill (Rohner et al. 2017a), mysid shrimps, chaetognathid worms, crustaceans and gelatinous zooplankton (Duffy and Abbott 2003; Essumang 2010; Graham et al. 2012; Armstrong et al. 2016), sometimes even consuming small fishes and fish spawn (Couturier et al. 2012; Hartup et al. 2013; Bessey et al. 2019). Manta rays often feed near to the upper limit of thermoclines (Stewart et al. 2016) and potentially use this as a cue to direct navigation. *M. alfredi* are known to regularly dive to several hundred metres depth during the night (Braun et al. 2014; Stewart et al. 2016; Lassauce et al. 2020), seemingly to take advantage of benthic-associated prey that emerge from the substrate at this time (Osada et al. 2010; Couturier et al. 2013; MacCauley et al. 2014). This provides a potentially important trophic link between coral reefs and adjacent pelagic habitats (Braun et al. 2014). Manta rays' foraging behaviour is closely linked to the lunar phase and tidal cycle (Jaine et al. 2012; Stevens et al. 2016; Hacohe-Domené et al. 2017). In the daytime, they aggregate to feed in shallow surface waters of inshore reef habitats (Stevens et al. 2016), including in Raja Ampat (RP pers. obs.), especially when strong tidal ocean currents bring large blooms of mesopelagic zooplankton to surface waters.

Social behaviour may be an important aspect of feeding ecology in manta rays. As the density of their prey increases, *M. alfredi* are more likely to form groups (Stevens 2016), which can trigger mass feeding events with tens or even hundreds of rays in close proximity (Stevens 2016; Bennett et al. 2017). Unfortunately, such large aggregations are likely to increase the species' susceptibility to fishing, as they enable harpoon fishermen to target large numbers of rays with relatively high catch-per-unit-effort (Dewar 2002; Couturier et al. 2012; Stevens 2016). Reef manta rays' daily movement between deep and shallow water foraging habitats may also have impacts on group formation, by promoting fission-fusion dynamics, with groups forming at shallow water aggregation sites in the morning and breaking apart in the afternoon. Cooperative feeding mechanisms are suspected in several shark species, including blacktip reef, lemon, oceanic whitetip, thresher and sevengill sharks (Strasburg 1958; Budker 1971; Ebert 1991; Morrissey 1993; Castro 1996; Motta and Huber 2004), although these may represent aggregation of individuals to prey (Motta and Wilga 2001; Heithaus 2004). Because mobulid rays feed on zooplankton, which is often patchily and dynamically distributed but highly locally abundant, they may not incur the costs of food-sharing typical during aggregation of other group-forming predators. It is thus likely that efficient patch exploitation by manta rays occurs through social foraging and requires a high level of social intelligence. This might include sharing of information on the location of food patches between familiar individuals that are able to recognise each other's mental states. Abilities in social learning (Pouca et al. 2020; Guttridge et al. 2013), Machiavellian intelligence (Bshary 2011) and reciprocal cooperation (Dugatkin and Mesterton-Gibbons 1996, Brandl and Bellwood 2015) that are reported in teleost fish and elasmobranchs might explain the large brain sizes seen in mobulid rays (Dunbar and Shultz 2007). Indeed, a particularly interesting group-feeding behaviour ('cyclone feeding') has been recorded in the Maldives (Stevens 2016), in which the combined spiral movement of multiple individuals forms a vortex enabling them to cooperate in groups to improve the foraging efficiency of all group members. The organized structure of this behaviour suggests cooperation, as opposed to aggregative or 'feeding-frenzy' behaviour (Motta and Huber 2004; Heithaus 2004). 'Breaching', where manta rays exert a large amount of effort to launch themselves out of the water completely, making a loud noise and vibrational waves through the water, could potentially be a means by which manta rays share information about prey resource availability (Stevens 2016; Domit et al. 2017).

1.5.3. Reproductive ecology

Manta rays are ovoviviparous matrotrophs (Wourms 1993; Dulvy and Reynolds 1997) and become sexually mature at around 8-12 years of age. Females have an annual ovulatory cycle, although in the wild they typically display at least biennial reproductive periodicity (Marshall and Bennett 2010;

Stevens et al. 2016), possibly due to variation in resource availability between years (Stevens et al. 2018). They give birth to a single (occasionally two) large offspring after a gestation period of 12-13 months (Stevens 2016; Nozu et al. 2017; Stevens et al. 2018; Murakumo et al. 2020). Despite this high apparent female investment in offspring, no evidence of parental care has been recorded in either species. The mating system of manta rays appears to be promiscuous, with females advertising their sexual receptivity to attract multiple males, and both sexes are thought to mate with multiple partners (Yano et al. 1999; Stevens et al. 2018). This is likely to have important effects on social behaviour and connectivity within populations. Females are known to synchronise pregnancies, which might involve the exchange of social cues (Stevens 2016). Manta ray reproduction has only rarely been observed in the wild, but pre-copulatory “courtship trains” (Stevens 2016) often occur at shallow-water feeding and cleaning sites (Marshall and Bennett 2010; Deakos 2010; Deakos 2012; Stevens 2018), and appear to be a means of sexual selection for male endurance or athletic ability. These are cohesive mixed groups typically consisting of a single or several fast-swimming females, followed by multiple male escorts. It is likely that females release pheromones to elicit following by males (Hueter et al. 2004; Stevens et al. 2016). Courtship events can last for hours, and consist of following or chasing, including complex series of flips and turns, where males interact with the female by copying her movements, and evasive or avoidance behaviour by the female, or mating (Stevens 2016). Mating behaviour involves males biting the pectoral fin of a female to hold in position, and seems to be highly lateralized, with ‘mating scar’ bites consistently found only on the left pectoral fin of females (Marshall and Bennett 2010). Behavioural lateralization could, therefore, be important to other social behaviours.

In various locations, courtship events appear to occur mainly over several months, during the peak of manta ray numbers, and are clustered throughout this time, with intense courtship activity lasting several days. Breaching (thought to be a form of social communication in other species) is particularly common during courtship periods (Marshall 2008; Medeiros et al. 2015; Stevens et al. 2018). Their reproductive behaviour suggests that manta rays communicate, and choose mating partners, according to social cues. In species with comparable social structure and reproductive systems, such as bottlenose dolphins, individuals are known to adopt a range of complex social strategies to improve their mating prospects (e.g. Owen et al. 2002; Lusseau et al. 2003b; Wiszniewski et al. 2012). Manta ray reproductive ecology may also involve segregation of phenotypes. For example, in Mozambique, a highly biased female sex ratio was reported (Marshall and Bennett 2010) and segregation of individuals by age appears to occur in nursery habitats including estuaries (Medeiros et al. 2015) and lagoons (Setyawan et al. 2018). If human impacts are spatially focused, they may not be evenly distributed throughout a population demographic.

1.6. Summary of knowledge gaps

Animal populations are complex structures that form an intrinsic part of interconnected communities and ecosystems. They comprise individuals that behave differently and interact variably. Current knowledge of the life history characteristics of reef manta rays (including their long life, large brains, tendency to form groups and display site attachment) and other aspects of their movements, foraging and courtship described above, suggest that sociality is a fundamental and adaptive aspect of their behavioural ecology. The study and conservation of manta rays is therefore likely to benefit from a more detailed exploration of their social relationships, collective movements and potential means of communication.

Through a thorough review of the existing literature outlined above, I have identified several gaps in knowledge of manta rays (and of elasmobranchs in general) that I will attempt to address in the following chapters. Firstly, there is still relatively little known about group-living and sociality in wild elasmobranchs. In particular, in many species it is unclear if groups form through aggregative or social mechanisms, or both. We often do not know if social relationships are formed, how long they last, or whether individuals with particular characteristics are more likely to interact socially. Although it is clear that age and sex-based segregation of elasmobranch populations is common, we have little understanding of how this occurs in manta rays, or whether social relationships cause the structuring of manta ray societies into discrete units that could be differentially affected by environmental changes or human disturbance. Second, there is still considerable uncertainty about the extent and frequency of manta ray movements and use of habitats. Studies of reef manta rays using passive acoustic (e.g. Dewar et al. 2008; Setyawan et al. 2018; Venables et al. 2019; Peel et al. 2019) and satellite telemetry (e.g. Graham et al. 2012; Jaine et al. 2014; Andrzejczek et al. 2020) have provided accurate information on individual movements, but, due to logistical constraints, are typically based on data from a few individuals or a small proportion of the overall population. While such studies have undoubtedly been useful in providing comprehensive baseline data for management, it is unclear if results can be applied to whole populations, or used to predict movements of groups, particularly as individual animals of this species are known vary in behaviour. It seems likely that movements of manta rays are partly dependent on social influences, but prior studies have not explored this. Understanding group formation, social relationships within groups, and movements of *M. alfredi* within a network framework will help to guide their conservation. A specific focus on social interactions, and on understanding the social structures that emerge from them (explored in **Chapters II and III**), will enable a more holistic and nuanced approach to conservation that connects the behaviour of individual rays to their population-level demography, ecological dynamics and

evolution (Bowler and Benton 2005). Results may, for example, provide evidence to support the management of subpopulations at a local scale, or as connected metapopulations at wider spatial scales.

Next, despite research going back several decades, we still know little about the social behaviour of elasmobranchs compared to other vertebrate species. Several shark species are known to interact and communicate at a basic level with conspecifics (e.g. to indicate dominance or deference) and with other species such as cleaner fish, but this has rarely been quantitatively analysed. The transfer of social and environmental information between individuals is fundamental to group-living species, affecting many aspects of their behavioural ecology and evolution. In manta rays, despite some investigation of social interactions in both captive and wild settings (Ari and D'Agostino 2016; Stewart et al. 2017) it remains unclear to what extent social communication occurs between individuals, what channels of communication or responses to cues produced by conspecifics or heterospecifics exist, and what type of information might be conveyed. Observations of manta rays at shallow water 'cleaning stations' suggest that these locations are important for social behaviours such as courtship, and as central points for aggregation of groups. This may provide the opportunity for social communication to occur and social relationships to form. However, because of the predictable presence of manta rays in these locations, they are also increasingly impacted by dive tourism. The regular presence of divers at cleaning stations is likely to disturb manta rays' natural behaviour. We investigate the movement of cephalic lobes (a potential mechanism of social communication between rays or other species) in a variety of conditions and contexts at cleaning stations in **Chapter IV**.

Finally, although detailed observations of the foraging and mating behaviours that occur in groups of manta rays have been recorded (Stevens 2016; Stevens et al. 2018), detailed analysis of the structure and dynamics of how individuals interact with each other during these behaviours has not previously been undertaken. Many fish species are known to move collectively, and gain benefits from this such as protection from predators and efficient information transfer. It seems likely that manta rays gain benefits from cohesive movement in groups, but their positioning and movements in relation to one another has not been explored. **Chapter V** aims to uncover the patterns and processes of group-based and collective behaviours in manta rays. Such knowledge will be important to understanding their natural behaviour and the evolution of social behaviours such as group formation, information transfer and possibly cooperation within groups. Both collective behaviour and information transfer may be key aspects of manta ray social behaviour that are vital to the maintenance of healthy populations, but are susceptible to disturbance from humans. The potential negative impacts of dive

tourism on manta rays are still poorly understood, but are likely to occur in areas where large numbers of manta rays congregate seasonally, near to human populations. Boats and divers may disturb the natural behaviour of manta rays, as well as the habitat that they occupy. Though some studies have investigated disturbance to manta rays by human divers (e.g. Venables et al. 2016), no study has explicitly quantified the effect of this on their social behaviour.

Elasmobranch conservation efforts are not helped by indifference and often outright antipathy towards sharks and rays among the general public, which has been, and continues to be stoked by their often negative representation in popular media (Friedrich et al. 2014; Le Busque et al 2019). These species have long been assumed to be asocial and unintelligent, with their reputation as aggressive killing machines encouraged by scientists and authors (e.g. Bigelow and Schroeder 1953, Helm 1961). Though these perceptions may be well entrenched, new research on sociality in elasmobranchs offers a different view that may help improve public attitudes towards them in the 21st Century (Simpfendorfer et al. 2011). In fact, sharks and rays appear to be much more like us than we ever realized. This is the new story about their social lives, that I tell in the following thesis.

1.7. Aims and objectives

The overarching aim of this thesis is to provide a better understanding of group formation, social behaviour, and social structuring in reef manta rays, and thereby contribute to a more comprehensive interpretation of their biology and ecology which can be used to better protect them from human impacts.

My main objectives are:

- a) To describe the structure and dynamics of social relationships within a population of reef manta rays.
- b) To quantitatively determine the extent to which groups are formed due to aggregative or social processes.
- c) To understand how phenotypic and behavioural heterogeneity (e.g. in movements and habitat preferences) impacts social and collective structuring.
- d) To describe and understand socially interactive behaviours, including potential communication between reef manta rays at cleaning stations.
- e) To describe and understand the relative movements and variability in movement behaviour of individual manta rays within groups, including collective behaviours.

- f) To identify the implications of group-based, social and collective behaviours for conservation of reef manta rays, including the potential impacts of disturbance by dive tourism.

1.8. Research context

All research was conducted in the Raja Ampat Regency of West Papua, Indonesia. This archipelago of approximately 1500 islands is part of the Bird's Head Seascape, located in the heart of the Coral Triangle, a region that contains exceptional biodiversity of coral and fish species. The area has high bathymetric structure and is subject to strong tidal influences driving rapid surface currents and complex eddies. It contains a variety of near-pristine habitats including shallow sandy areas and coral reefs, large mangrove forests, lagoons and seagrass beds, in close proximity to deep waters of >2500m depth. A small human population inhabits many of the islands of the archipelago, and artisanal subsistence fishing occurs throughout the area. In the last two decades the area has become popular with dive-tourists, and the provincial government has encouraged the development of tourism. As of 2017, 11 tourist resorts, 40 liveaboard dive boats and more than 40 local homestays operate in Raja Ampat, and the marine tourism industry is expanding rapidly (Atmodjo et al. 2019). Raja Ampat has a long-standing MPA network and was classified as a "marine tourism park" in 2014. This includes six MPAs and numerous "no-take" (no fishing) zones, explicitly managed under the Raja Ampat MPA zonation system (MMAF Ministerial regulation No. 36, 2014) (Maas et al. 2020). It is a priority conservation area for the provincial government and major international non-governmental organizations (McLeod et al. 2009). Raja Ampat is one of the few remaining locations worldwide where both species of manta ray can be regularly encountered. There is no known fishing pressure on manta rays here, and the local *M. alfredi* population appears to be in a healthy state, with large numbers of rays encountered from November to April, including many juveniles as well as mature adult individuals (RP pers. obs.). This population provides an excellent opportunity to enhance understanding of the natural behaviour and social structuring of *M. alfredi* through scientific research in conditions that can be considered near-natural.

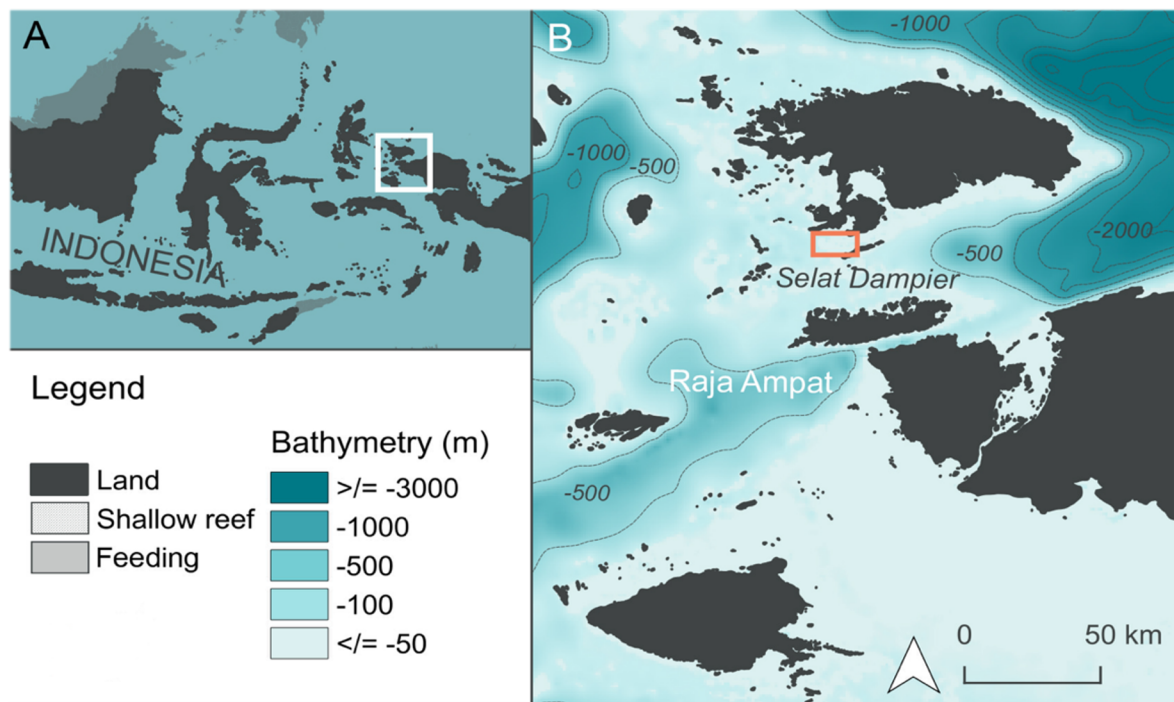


Figure 1. Map of Raja Ampat, West Papua, Indonesia. Panel A shows location of Raja Ampat in West Papua, Indonesia. Panel B shows location of study area in the upper Dampier Strait, Raja Ampat.

1.9. General methods and ethics

The proposed research required the gathering of empirical data on the social behaviour, social organization and collective movement of a large number of wide-ranging elasmobranchs in their natural habitat. This was a challenging task that was achieved by maintaining a regular presence in Raja Ampat over four research seasons during 2015-2019, and by utilising a variety of tools and techniques. All research was in collaboration with Marine Megafauna Foundation www.marinemegafauna.org, and involved direct observation of wild manta rays *in situ*. Chapters II-IV required the use of scuba apparatus and underwater photographic equipment to record observations and identify individual manta rays using standard photo-ID methods (Pierce et al. 2018), while Chapter V relied on video recordings from unmanned aerial vehicles (UAVs or ‘drones’). Over four years of field research, we observed a total of 718 individually-identified reef manta rays. All photographs used for identification can be viewed in the MantaMatcher online database (Town et al. 2013) at www.mantamatcher.org. I recorded more than 60h of underwater video observations of manta rays interacting at cleaning stations, and over 30h of aerial video observations of manta ray groups. I tagged 29 *M. alfredi* with acoustic transmitters. I also obtained data on 10 tagged individuals provided by Edy Setyawan (Conservation International). Further methodological details are included in chapters II-IV of the thesis, as well as in the following section, where I summarise the analytical approach taken in each empirical data chapter.

All applicable international, national, and institutional guidelines for conducting research on animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution at which the corresponding author is based. This research was part of a larger overall project for which ethical approval for all research was granted under an Australian Animal Research Authority permit, number: 2017/037 (Social Behaviour and Social Network Analysis in a Reef Manta Ray Population). No capture, manipulation or significant harm to animals occurred.

1.10. Thesis structure

This thesis comprises six chapters: the present *General Introduction*, four chapters based on original empirical data, and a concluding chapter which summarises the contribution of my research findings to scientific knowledge, and suggests directions for future research. I adopt an interdisciplinary approach throughout, bringing together theory and research methodologies from the complementary disciplines of sociobiology, behavioural ecology, and conservation science. Each of the empirical data chapters investigates different but related aspects of sociality in reef manta rays. These chapters are presented as academic papers and structured according to scholarly conventions. Chapters II and III provide information about the structure of manta ray societies, particularly their connectivity and the importance of key sites, that should be incorporated in local management plans, but use different methods of analysis to focus on different levels of social structuring as defined by Hinde (1976).

Chapter II aims to provide the first comprehensive description of patterns of social structuring (surface structure) within a manta ray population. To this end, I used data collected over several years on a large proportion of individually identified manta rays within the healthy, unfished population of *M. alfredi* in Raja Ampat (including individuals varying in phenotype and behavioural habits). I describe the structure and temporal dynamics of associations between individuals, and perform quantitative analyses to determine various factors that might influence this. To the author's knowledge, this is the first such study in any free-ranging batoid species. Network connections are defined using a GoG approach, where all individuals observed together at aggregation sites are considered to be associated. I use a novel approach to separate the influences of spatiotemporal aggregation and social relationships on observed group structures, involving the calculation of generalised affiliation indices (GAIs) that represent active social preferences between individuals.

I investigate the following questions:

- Do manta rays have preferred social partners?
- What is the influence of habitat preferences on social structuring?
- What is the importance of time and space in structuring associations?
- Are social relationships in reef manta rays assorted by sex, maturity, colour morph or reproductive status?
- Is the population of manta rays segregated into social communities?
- Do particular types of individual occupy influential network positions?

Building on findings from Chapter II, **Chapter III** investigates social network structuring in relation to habitat use, movements and individual heterogeneity in these. However, where Chapter II relies on building a social network through occasional ‘snapshot’ observations of group membership, here automated data collection is used to record the movements and site residency of a selected number of rays in fine detail, focusing on their *relationships* within a broader societal structure. Recently-developed network analysis techniques are applied to reconstruct social networks from continuous passive acoustic telemetry (PAT) data on the presence of reef manta rays at multiple aggregation sites over several months. I utilize Bayesian inference to delineate biologically realistic ‘clustering events’ within the autocorrelated temporal data stream. Pre-network data randomisations are performed within these ‘events’, to construct networks of significantly preferred social associations that controls for ‘nuisance effects’ (Farine and Carter 2020) and differences in the level of spatiotemporal overlap between pairs of individuals. Data are divided by time period to enable analysis of social dynamics.

I investigate the following questions:

- To what extent is an individual’s position within the social network dependent on its movements and site attachment?
- Are social preferences assorted into spatially defined communities?
- Does the structure of social relationships within the population change over time?

In **Chapter IV** I aimed to describe and quantify social behaviour to investigate the potential for social communication by *M. alfredi* at shallow-water cleaning stations, where they are attended by cleaner fish, and often observed by human divers. Many elasmobranch species use body and fin postures in threat displays, or to indicate deference or dominance during conspecific or inter-species encounters. Manta rays have specialized cephalic lobes that are used in tactile manipulation and sensing of

planktonic prey, but seem to be moved frequently and variably in non-feeding contexts. Through focal-follow observations, I describe and quantify the various types of cephalic lobe movements made by free-ranging *M. alfredi*, and test hypotheses on the ecological conditions in which they occur. By investigating the modification of cephalic lobe movements in different behavioural contexts, I provide some indication of their possible functions, including the possibility that these movements are used in gestural communication between rays or during interactions with cleaner fish.

I investigate the following questions:

- What kinds of cephalic lobe movements are made?
- Are these movements performed more frequently or for longer durations during social, cleaning or manta ray-human interactions?
- Do environmental conditions affect social behaviours or cephalic lobe movements?
- Are social behaviours disturbed by the presence of human observers?

In **Chapter V** I focus on describing and quantifying the collective behaviour of reef manta rays. The behaviour of multiple individuals within clearly defined groups is recorded using aerial survey videos taken from a quadcopter drone, and the precise relative movement of all individuals tracked using computer software. Using this data, I test whether manta rays use simple rules of local attraction and alignment in their movement interactions, and the importance of leadership in structuring collective behaviour. I record the movement of rays in several different behavioural contexts, including courtship and feeding, and in different environmental conditions, including disturbance by human divers and tourist boats. I therefore aim to uncover any differences in group-based or collective behaviour in such contexts that may be useful in understanding manta rays' natural behaviour in the wild and developing protocols to mitigate disturbance from dive tourism.

I investigate the following questions:

- Do manta rays change their movement depending on their position and alignment relative to near-neighbours?
- Do manta rays adapt their rules of interaction based in different social or environmental contexts?
- Do individuals respond differently to the movement of near-neighbours, and does this heterogeneity affect the emergent collective behaviour of groups?

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

2.1. Abstract

Understanding how individual behaviour 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 behaviours. Group structures may result from active choices of individual rays to interact, or passive processes. Social behaviour 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 over five 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.

2.2. Introduction

Knowledge of how individual behaviour drives population structure and dynamics is required to predict the response of populations to human impacts (Sutherland 1998; Sih et al. 2013). In group-living species, social interactions are a fundamental part of population ecology (Hinde 1976) important in enabling collective behaviours (Couzin et al. 2002; Couzin & Krause 2003, Sumpter 2006), such as cooperative foraging (Sih et al. 2009), predator avoidance (Ward et al. 2011) and social learning (Brown & Laland 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 behaviour depending on the status of their relationship with

various social partners (Krause et al. 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 how social behaviour between individuals manifests in the social organisation of groups or populations (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 & 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) and 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 & 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 the 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 & Simpfendorfer 2005; Bass et al. 2016). Many elasmobranchs have developmental shifts in habitat and diet (Wetherbee, Cortes & Bizzarro 2004) that may drive assortment in size- or sex-segregated groups (Wearmouth & Sims 2008). Recently, ex-situ studies have shown that some species exhibit complex sociality, including social structure (Jacoby et al. 2010), 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 et al. 2011). Social recognition may be important in mate choice (Marshall & Bennett 2010). Manta rays perform group-based behaviours including collective foraging, following, breaching, copying, play and curiosity towards humans (Marshall 2008; Deakos 2010; Gadig & Neto 2014; RP pers. obs.), that 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; 2018b) 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. 2011a; 2011b; Lawson et al. 2014; Stewart et al. 2018), exacerbated by their extremely low reproductive output (Dulvy et al. 2014; Stevens 2016) and high mobility (Germanov & Marshall 2014; Jaime 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 & 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. 2011b; 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 & Bennett 2010; Deakos et al. 2011; Marshall et al. 2011; Kashiwagi et al. 2011; Jaime et al. 2012; Couturier et al. 2014), as-well as individual-based movement tracking and behavioural studies (e.g. Dewar et al. 2008; Jaime et al. 2014; Stewart et al. 2016a; Ari et al. 2016). While these provide comprehensive baseline data for management of manta rays, considering social structure will aid a more nuanced approach, where the behaviour of individuals is linked to group- or population-level responses to the environment. Recent studies have shown that individuals within shark populations exhibit large differences in movements, feeding behaviour and personality (Jacoby et al. 2014; Matich & 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 behaviour in manta rays (Deakos et al. 2010; Stewart et al. 2016b; Stevens et al. 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 individuals would have differentiated social strategies. We expected that assortment by phenotype, including sex, maturity, colour morph, and reproductive status would be important in structuring the society, potentially enabling the division of the population into distinct social communities.

2.3. Methods

2.3.1. 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 catalogue (Town, Marshall & Sethasathien 2013; Marshall & Holmberg 2019). It was not possible to record data blind because our study involved observing animals in the field. Sightings of reef manta rays recorded at 5 sites (3 cleaning stations and 2 feeding sites) within a 20km² area were used to allow analysis of fine-scale social structure, with data also collected from an additional 5km² site that was used by manta rays for both feeding and cleaning behaviours. Sampling occasions were dives or snorkels of approx. 1h, 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 0.5-1km². We alternated sampling effort by site and time to minimize environmental bias, using variables expected to influence manta ray behaviour (location, tidal phase, tidal range, time, and lunar phase) (Jaine et al. 2012). See Figure 2.1 and Appendix section 2.7.1 for details of study area, and Table 2.1 for summary of sampling effort at each of the main study sites.

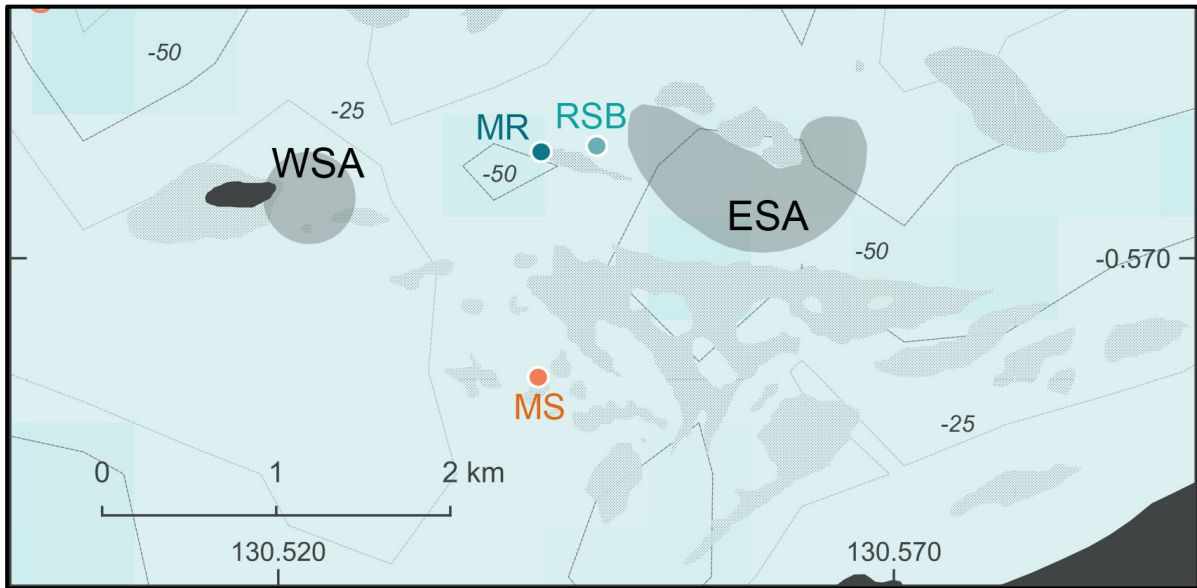


Figure 2.1. Map of study area. Shows location of study sites (cleaning stations MR, MS and RSB) and feeding areas in upper Dampier Strait area of Raja Ampat, West Papua, Indonesia. An additional feeding area (LDS) is not shown. Images from Google Earth, edited in ArcGIS (ESRI 2011).

Season (Nov-May)	Cleaning stations			Feeding areas		
	MS	MR	RSB	LDS	ESA	WSA
2013-14	65	10	0	11	8	20
2014-15	72	67	43	16	20	32
2016-17	48	51	45	19	25	24
2017-18	31	35	25	10	10	36
Total	216	163	113	56	63	112

Table 2.1. Sampling effort by site. Number of sampling dives per season at each of the main study sites.

2.3.2. Individual encounters and encounter rates

Individual reef manta rays were identified by standard Photo-ID methods (see Figure 2.2), using unique, lifelong spot patterns on the ventral surface (Pierce et al. 2018). Rays were sexed by presence/absence of claspers, and maturity and reproductive status/sexual activity were estimated as in Marshall & 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 3-3.5m DW, similar to populations in Hawaii and Australia (Deakos et al. 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, colour 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.

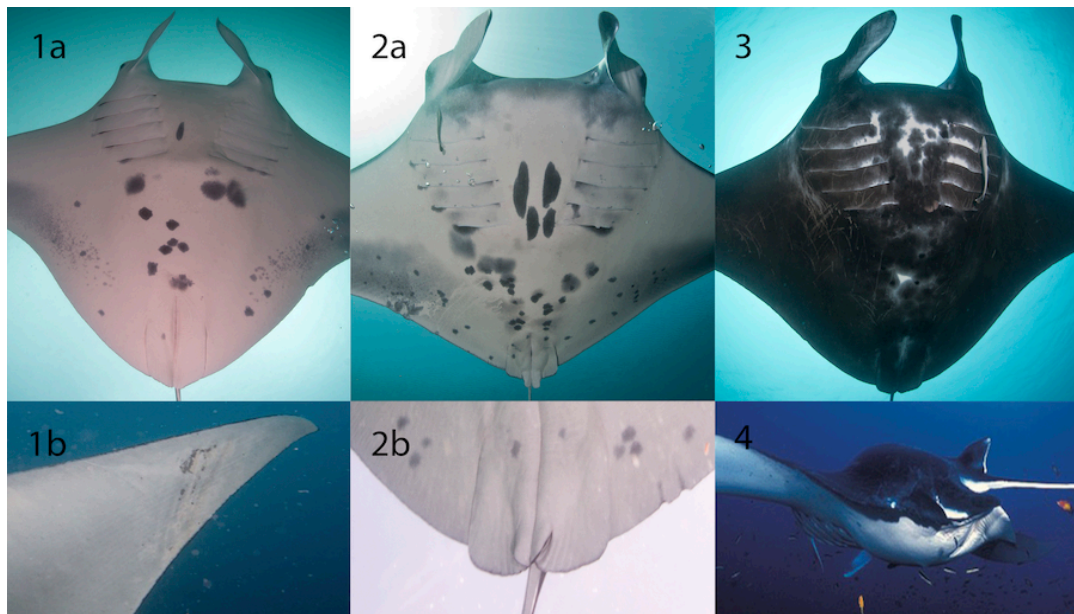


Figure 2.2. Identification of reef manta rays; 1a) female 'normal' morph with distinct ventral spot pattern; 1b) mating scars on female indicating maturity; 2a) male 'normal' morph, with claspers; 2b) juvenile male 'normal' morph, with undeveloped claspers; 3) melanistic morph with distinct white patches between gills; 4) pregnant female.

2.3.3. Defining associations

Associations between individuals were defined using the 'Gambit of the Group' (GoG) (Whitehead & 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 meaningful structure (Farine et al. 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 <10mins 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 & Nepusz 2006), and *tnet* (Opsahl 2010) packages. Network diagrams were drawn in Gephi 0.9.2 (Bastian et al. 2009). We calculated simple-ratio indices (SRIs) (Cairns & Schwager 1987) to measure strength of association between all pairs. The SRI is the recommended association index (AI) where calibration data are unavailable (Hoppitt & Farine 2018). SRIs were calculated within 45 sampling periods (SPs) of length 15 days. This length was chosen according to results from LAR analysis (see section 2.3.4) and prior knowledge of the species' movements (e.g. Marshall et al. 2008; Deakos et al. 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: $r = \frac{S}{CV(SRI_{ab})}$. 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.

2.3.4. Stability of identifications and associations over time

We calculated lagged identification rates (LIRs) and lagged association rates (LARs) 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 one day. LIRs were used to determine over what timescale and rate re-identifications within the study area occurred at the same site as initial observation and at different sites. LIR estimates the probability that an individual identified at time x will be re-identified after a given time lag, in comparison to a randomly chosen individual (Whitehead 2001). LIRs were estimated by: $R(t) = \frac{P(t)}{N}$ where P is the probability that an individual is still present

in the study area after a given time lag (t), and N is the size of the study population (Wimmer & Whitehead 2004). LIR confidence intervals were obtained using 100 bootstrap replicates (Whitehead 2008a). LIR declines as individuals leave the study area, and may increase if these individuals later return (Whitehead 2001). To identify factors affecting LIR decline, we fit exponential decay models to observed LIRs using a combination of demographic parameters: population size (N), mean residence time (a), mean time outside the study area (b), emigration (l), immigration (m) and mortality rates (d), following Whitehead (2001) (see Appendix Table A2.1). Model parameters were estimated by maximizing the summed log likelihoods, with the quasi-Akaike Information criterion QAIC used to select the most parsimonious model (Burnham & Anderson 2002; Whitehead 2007). QAIC was used instead of AIC because of overdispersion of the dataset. Models of exponential decay were fit to lagged association rates using three aspects of societies under fission-fusion dynamics, as follows: constant companionships (i.e. individuals associate permanently); casual acquaintances (i.e. individuals associate longer than time lag d but disassociate and might re-associate); and rapid disassociations (i.e. pairs disassociate during time lag d), following Whitehead (1995). For time-based analyses of associations, we used LARs 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. 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 Table A2.2) 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 & Anderson 2002; Whitehead 2007).

2.3.5. 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 individual social preferences (active choices to group with known individuals). Associations between individuals in our study may be highly influenced by non-social factors (see Table A2.3), including high location fidelity and phenotypic variation in site preferences (see results section 2.4.2). We therefore 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 use generalized affiliation indices (GAIs) that control for various non-social factors when constructing network weights (Whitehead & 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: site use similarity- the Euclidean distance between the encounter rate (see section 2.2.2) 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: $G_{ab} = \log(\sum SRI_a \sum SRI_b)$ where $\sum SRI_a$ and $\sum SRI_b$ 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 colour morph class ('normal' or melanistic, 1 if same colour morph, 0 if not).

2.3.6. Efficiency of non-social predictor variables to explain associations

Multiple regression quadratic assignment procedure (MRQAP) tests (Dekker et al. 2007) were used to identify the relative influences of each predictor variable on associations. MRQAP tests were performed using a stepwise double semi-partialing permutation method (Dekker et al. 2007) to calculate partial correlation coefficients on the overall network, and networks of associations between females only, males only, adults only and juveniles only. For all networks, we found that individual site preference similarity, temporal overlap and similarity in gregariousness were significant predictors of association (see Appendix Table A2.4). These predictors were retained in final calculation of generalized affiliation indices. The maturity and colour morph predictors were non-significant, while the sex predictor was significant in some cases, but not others. These predictors were not included in the final calculation of generalized affiliation indices.

2.3.7. 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 were performed with the *asnipe* package in R, and 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 sub-networks 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 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 standard deviation (SD) of all tie weights, and overall preferred relationships indicated by a significantly higher coefficient of variation (CV) of all tie weights (vice versa for avoided relationships), following Whitehead (2009). Preferred relationships were defined where the pairwise value of the SRI/GAI was higher than 95% of corresponding values produced using data-stream permutations. For GAIs, these values were used to build a network of estimated social preferences.

2.3.8. Assortment by phenotype and community structure

We tested for assortment in the reef manta ray population by sex, maturity and colour morph, with the null hypothesis that assortment would be no stronger than expected if relationships were random. To test for assortment whilst 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. 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.

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 which maximized the modularity coefficient, Q (Newman 2006). Data-stream permutations 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 & Farine 2016). We then calculated within-community social differentiation to measure social complexity in the population.

2.3.9. 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, colour 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 neighbourhood 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 favoured 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, that provided a null model, p-values obtained as in section 2.3.6.

2.4. Results

2.4.1. Individual identification frequencies and group sizes

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 ≥ 10 times, including 70 females (43 mature, 13 immature, 14 unknown maturity) and 42 males (32

mature, 9 immature, 1 unknown maturity). Sightings progress over the research period is shown in Figure 2.3. The overall discovery curve (Panel A) and the individual curves for cleaning station sites (MR, MS and RSB) (Panel B) become gradually shallower as more rays are identified, but do not approach an asymptote. This suggests that a majority (but not all) of the population has been discovered, and that each cleaning station has a core group of individuals that regularly use it. The shallower curve at site MS suggests that the core group here is small (perhaps 50-100 individuals), and other results suggest that this group has strong site fidelity. Steeper curves at sites LDS and ESA suggest that feeding areas are used by a higher proportion of the population, and it is less likely that manta rays have strong fidelity to feeding areas. Insufficient rays were sighted at site WSA to produce a discovery curve for this site. Figure 2.4 shows the distribution of reef manta ray group sizes by site. Observations were mostly of groups of 2-5, or individual rays, though groups of 6-19 individuals were also common. Groups of 20 or more individuals were rare, though these larger groups were more common at sites 'MR' and 'LDS' than other sites. More groups were observed at the cleaning station sites than feeding areas, reflecting the higher sampling effort in these locations.

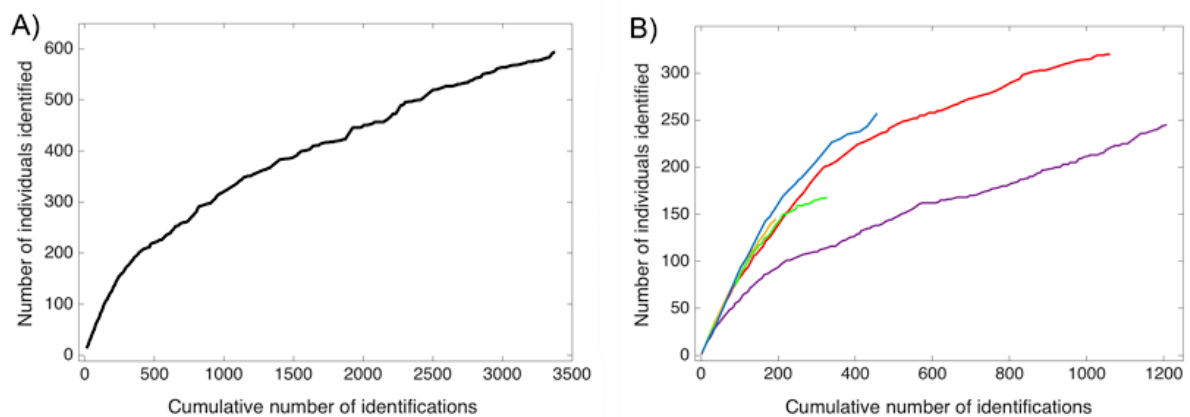


Figure 2.3. Discovery curves of identification progress. For *M. alfredi* in Dampier Strait region, Raja Ampat. Panel A shows identifications at all sites. Panel B shows identifications at each study site separately (red=MR, purple=MS, green=RSB, blue=LDS, orange=ESA).

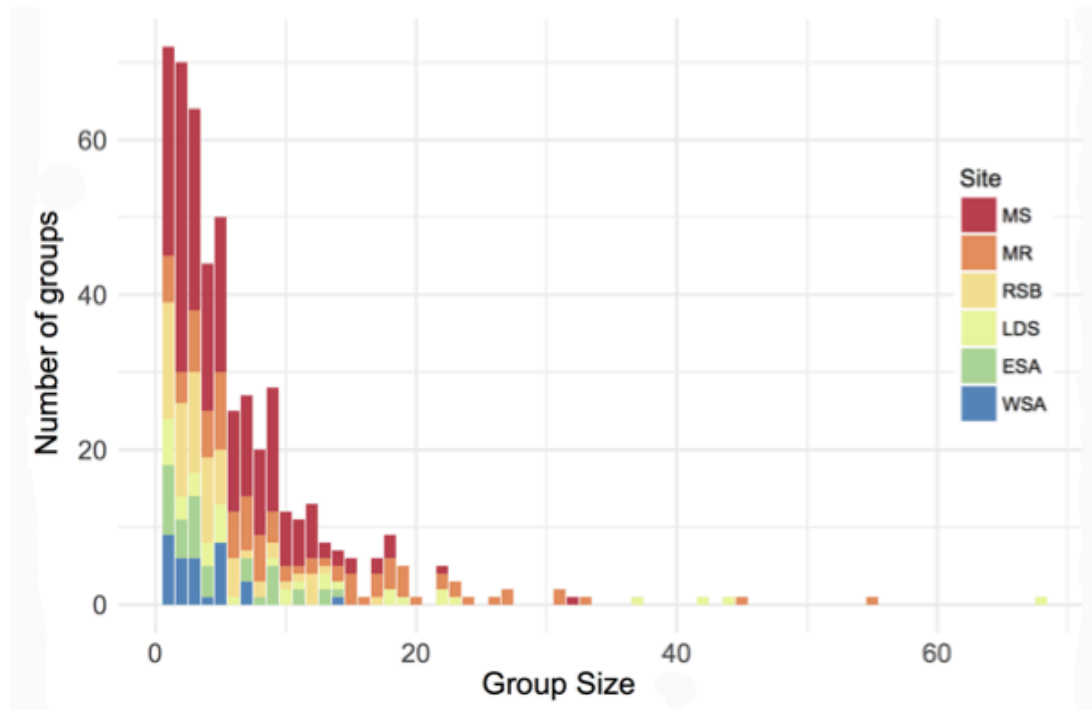


Figure 2.4. Frequency histogram of reef manta ray group sizes at each study site.
Most groups were small, with few larger than 20 individuals.

2.4.2. Site use and encounter rates

For individuals observed ≥ 10 times, especially females, encounters were much more likely at that individual's 1st preference site than any other (Figure 2.5). Many individuals were observed multiple times at a single cleaning station, but infrequently or not at all at others (see Figure 2.6) indicating strong site preferences and strong differences in habitat use between individuals. Many individuals (especially females at site MS) appeared to have strong site fidelity. 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 Table A2.3). The following results are given without Bonferroni correction applied to significance values, but the results with Bonferroni correction can be viewed in Table A2.3). Mature females were also more likely to be encountered at feeding areas than juvenile females. Over all sites, there was no difference in the probability of encounter of male and female rays (adjusted OR- female= 0.953, $p = 0.548$), nor in the probability of encounter of juvenile and adult rays (adjusted OR- juvenile= 1.172, $p = 0.063$), suggesting that there was no sex- or age-based difference in residence to the study area. Melanistic rays were significantly more likely to be encountered than 'normal' colour morph rays (adjusted OR- 'normal'= 0.817, $p = 0.01$) over all sites. This is a surprising result given the lower percentage of melanistic rays detected in the overall population (39%) and suggests that melanistic rays may be particularly resident to our study area. Raja Ampat has the highest known proportion of melanistic manta rays anywhere in the world (Venables et al. 2019). There were large differences, however, in the probability of encounter of

different manta ray phenotypes at individual cleaning stations MS, MR and RSB (Figure 2.7). 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. Compared to a grand mean, females were significantly more likely to be encountered at sites 'LDS' (adjusted OR= 1.451, $p=0.029$) and 'MS' (adjusted OR= 2.127, $p=0$), and significantly less likely to be encountered at sites 'ESA' (adjusted OR= 0.54, $p=0.001$) and 'RSB' (adjusted OR= 0.34, $p=0$), whereas males were significantly more likely to be encountered at sites 'MR' (adjusted OR= 2.208, $p=0$) and 'RSB' (adjusted OR= 1.249, $p=0.013$), and significantly less likely to be encountered at site 'MS' (adjusted OR= 0.562, $p=0$). Adult rays were significantly more likely to be encountered at sites 'LDS' (adjusted OR= 1.291, $p=0.01$) and 'MR' (adjusted OR= 2.326, $p=0$) and significantly less likely to be encountered at site 'RSB' (adjusted OR= 0.771, $p=0.001$). Juveniles were not significantly more likely to be encountered at any site, but were significantly less likely to be encountered at site 'MR' (adjusted OR= 0.658, $p=0.001$). Melanistic colour morph individuals were significantly more likely to be encountered at sites 'LDS' (adjusted OR= 1.434, $p=0.003$) and 'MR' (adjusted OR= 1.852, $p=0$), and significantly less likely to be encountered at sites 'ESA' (adjusted OR= 0.722, $p=0.027$) and 'RSB' (adjusted OR= 0.815, $p=0.04$), while 'normal' colour morph individuals were significantly more likely to be encountered at sites 'ESA' (adjusted OR= 1.455, $p=0.046$) and 'MR' (adjusted OR= 1.257, $p=0.031$), but not significantly less likely to be encountered at any site. These results suggest that various phenotypic factors (sex, maturity and colour morph) have strong influences on site use in manta rays.

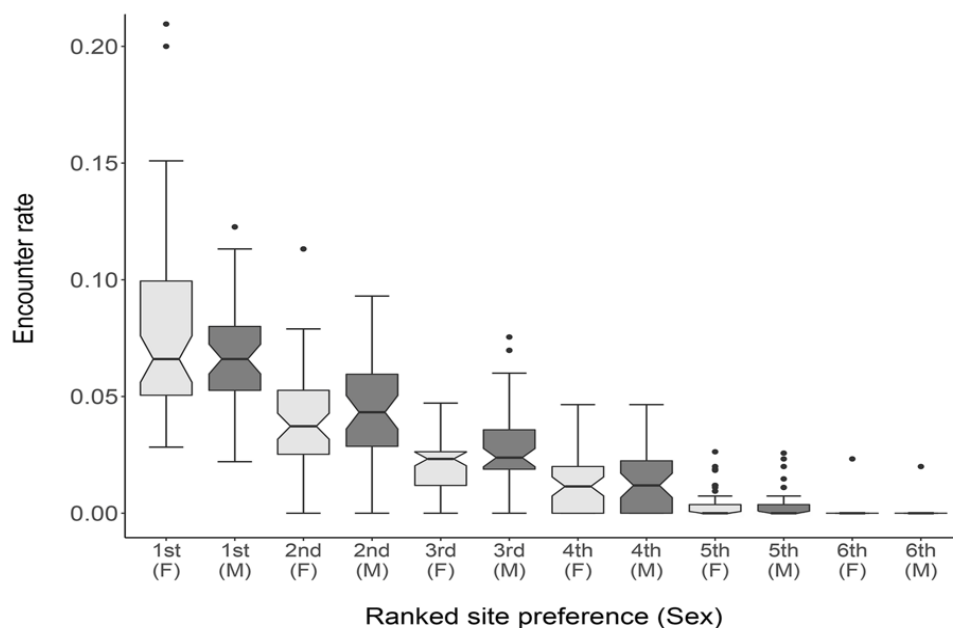


Figure 2.5. Encounter rates over all study sites by sex ranked by site preference. F = females, M= males. The thick black lines represent the medians, the notches represent the 95% confidence interval of the medians, the boxes encompass the interquartile ranges, the whiskers extend to the most extreme data points within 1.5x

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 levels of site fidelity between individuals, but not between sexes.

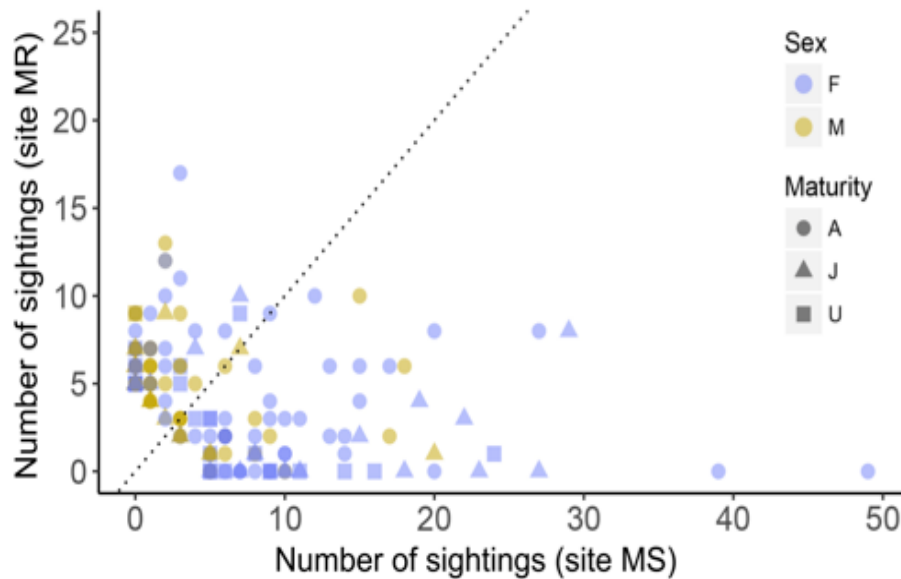


Figure 2.6. Individual sighting frequencies at two main study sites. Dotted line shows equal sightings at both sites. Most individuals were seen predominantly at one site or the other, but not both, despite short distance (approx. 2.5km) between the sites.

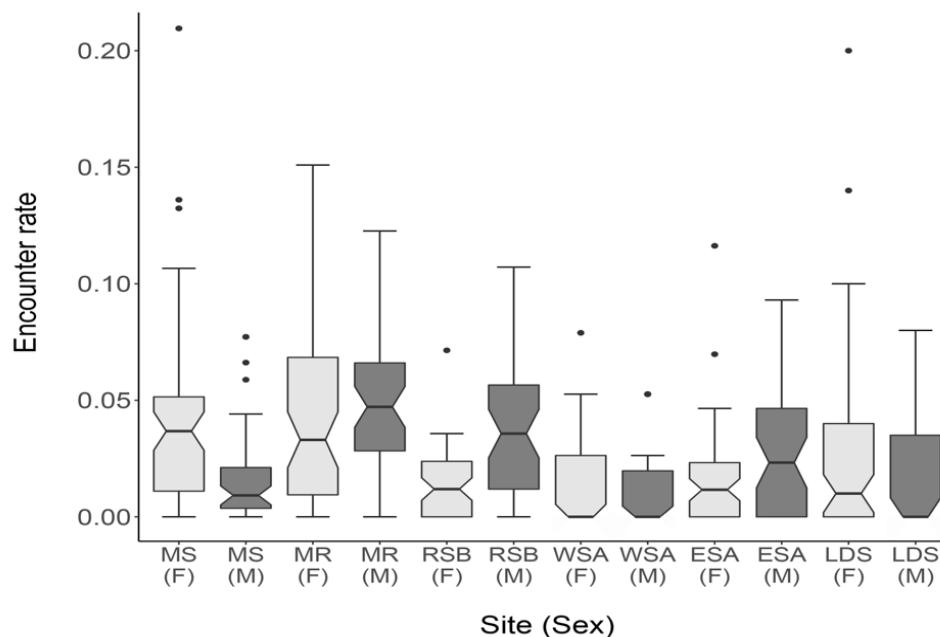


Figure 2.7. Encounter rates at each of the six study sites by sex. F = females, M = males. The thick black lines represent the medians, the notches represent the 95% confidence interval of the medians, the boxes encompass the interquartile ranges, the whiskers extend to the most extreme data points within 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.

2.4.3. Structure of associations

The population had moderate social differentiation ($S = 0.574$, $SE = 0.067$) and estimated AIs were a useful 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 nonzero SRI value: 0.071). The highest SRI value between any pair of individuals was 0.357. Figure 2.8 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.

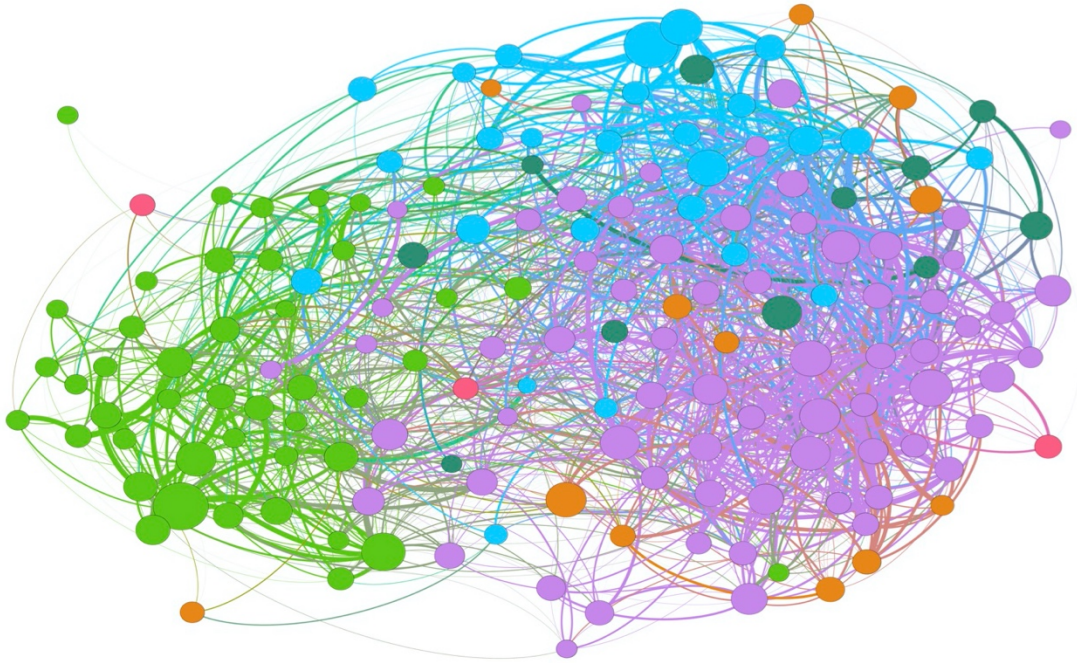


Figure 2.8. Network of associations. Node colours indicate individual site preferences (green: 'MS', purple: 'MR', bottle green: 'RSB', red: 'ESA', orange: 'WSA', blue: 'LDS'). Node size scaled by the SD of encounter rates of an individual at each site, indicating level of overall site fidelity. Edge widths represent weight of simple ratio indices (min= 0.118, max= 0.444). Individuals with 8 or more encounters included as nodes. Only the 30% highest SRI values were included as edges to show strongest associations. ForceAtlas algorithm used to construct network.

2.4.4. Stability of identifications and associations

LIRs fell steeply over the first few days, but remained stable thereafter for at least a year (see Figure 2.9), 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 (see Appendix Table A2.1). LARs (Figure 2.10) 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 Appendix Table A2.2. 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.

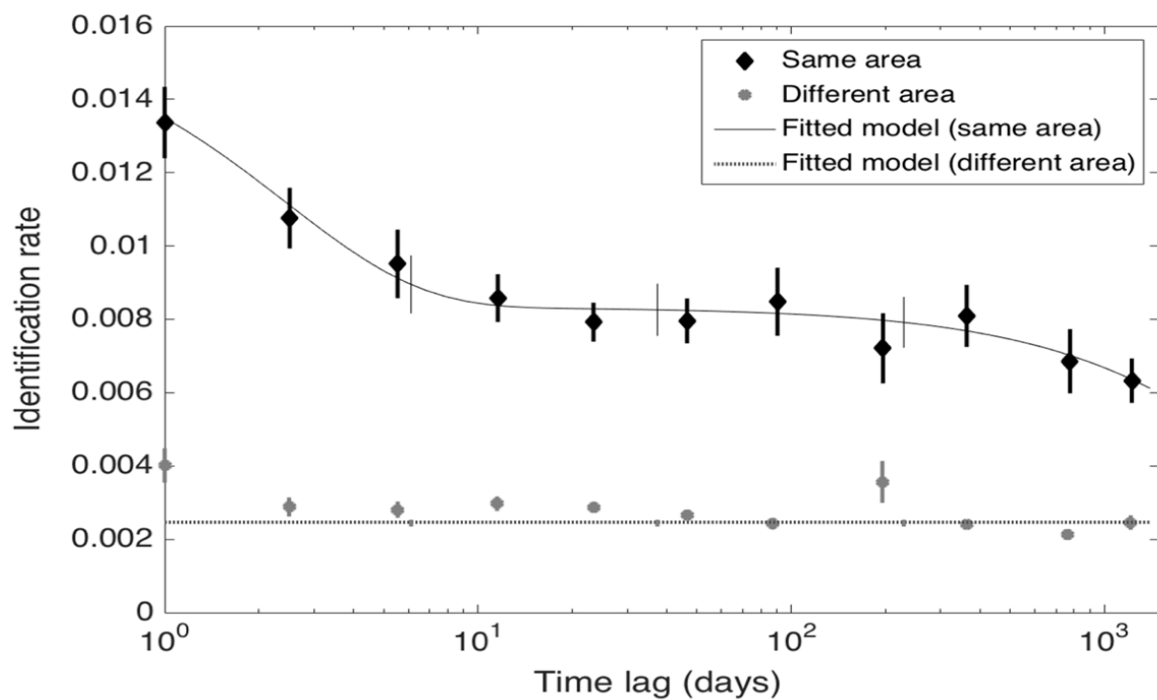


Figure 2.9. Lagged identification rates. For individuals showing rate of re-identification of all 594 individuals at the same location as initial sighting, and at different location. Error bars represent standard errors estimated using 100 bootstrap replicates (Whitehead 2008a).

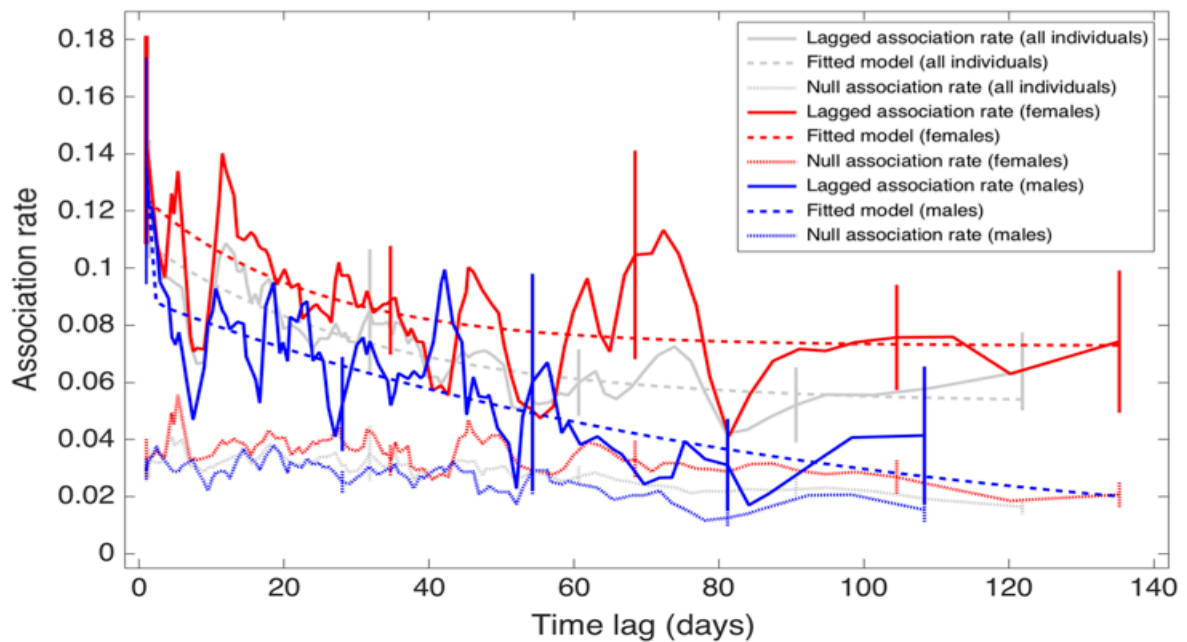


Figure 2.10. Lagged association rates. For all individuals, between females and between males, compared to null association rate. Bars indicate approximate standard errors generated by jackknife resampling. Females dissociated gradually, and LAR did not approach the null rate, whereas males dissociated more rapidly, and LAR approached null rate more frequently.

2.4.5. 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 2.2. Associations (column A) are measured by simple ratio indices (SRIs), whereas social preferences (column B) 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 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. GAIs gave similar results to SRIs in some cases, but not all. Preferred affiliations ($n=636$, indicating social preferences) were more numerous than preferred associations ($n=391$) (Figure 2.11), suggesting that controlling for non-social factors revealed stronger relationships. Most preferred associations were values higher than 0.1, while preferred affiliations spanned a range of high and low values, though the distribution was skewed towards the higher values. 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 lower than expected, indicating that social preferences occurred between all individuals, particularly over short (<15 day) time periods. All statistics for female:female GAIs (Network 2) were 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 was 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 sex (12.6%) (Table 2.2 column C), 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%).

	A) Preferred associations (SRIs)	B) Social preferences (GAIs)			C) Dyadic preferences (GAIs)
Relationship Measures	Overall CV	Overall CV	Short term Mean ($\times 10^{-3}$)	Long term SD ($\times 10^{-2}$)	(% total) Mean ($\times 10^{-3}$)
	Observed value: mean of random values, P-value				
1) Whole net. (n=112:112)	1.14 : 1.10 P= 0.001**	-5.15:-5.44 P=0**	-2.77:-2.58 P= 1**	1.42 : 1.41 P= 0.049	(10.2%) 9.63
Interpretation: Highly significant preferred associations and social preferences (short term)					
2) F:F (n=70:70)	1.07 : 1.04 P= 0.022*	-5.37:-5.58 P=0.045	-2.57:-2.41 P= 0.999**	1.38 : 1.34 P= 0.019*	(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= 0.794	-5.05:-5.25 P= 0.146	-3.15:-2.94 P= 0.978*	1.56 : 1.54 P= 0.151	(4.9%) 23.00
Interpretation: Only short-term social preferences. No preferred associations					
4) F:M (n=70:42)	1.21 : 1.14 P= 0.002**	-5.05:-5.44 P= 0.002**	-2.77:-2.61 P= 0.999**	1.40 : 1.41 P= 0.817	(12.6%) 8.75
Interpretation: Highly significant short-term preferred associations and social preferences, not long-term					
5) A:A (n=75:75)	1.05 : 1.02 P= 0.052	-5.94:-6.06 P= 0.175	-2.40:-2.31 P= 0.932	1.43 : 1.40 P= 0.039	(7.3%) 13.71
Interpretation: No significantly preferred associations or social preferences					
6) J:J (n=22:22)	1.26 : 1.18 P= 0.096	-4.00:-4.85 P= 0.014*	-3.04:-2.58 P= 0.996*	1.21 : 1.21 P= 0.468	(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 P= 0.001**	-5.02:-5.34 P= 0.019*	-2.69:-2.47 P= 0.999**	1.35 : 1.33 P= 0.156	(9.0%) 10.42
Interpretation: Strong short-term preferred associations and social preferences, not long-term					

Table 2.2. Tests for preferred associations and social preferences. Statistics from empirical network compared to random networks. P-values significant at < 0.025 or > 0.975 (two-tailed tests). 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. For P-values, level of significance indicated by: * ≤ 0.05 , ** ≤ 0.005 (two-tailed tests). Column A shows preferred associations. Column B shows social preferences. Column C shows % of all pairwise GAI values that were defined as preferred social relationships, and means of these values. Net. = network, F = female, M = male, A = mature adult, J = juvenile or sub-adult.

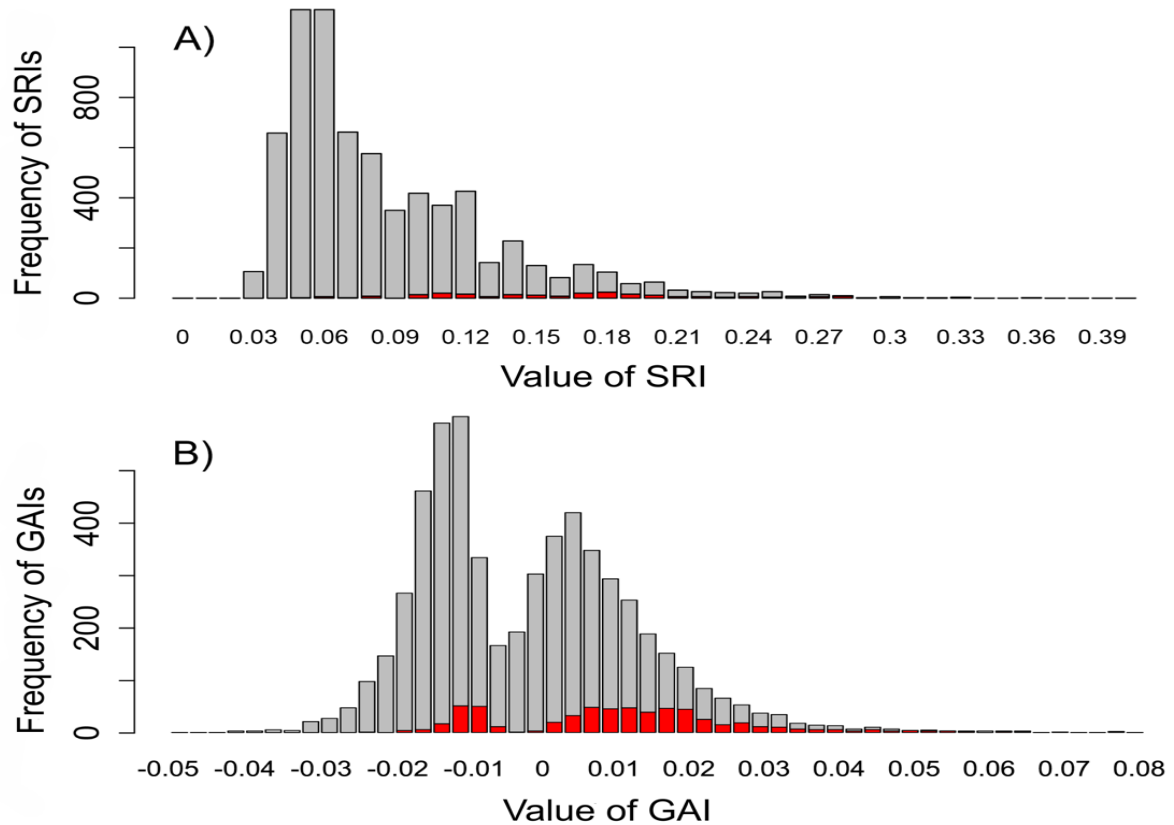


Figure 2.11. Frequency distribution of preferred relationships compared to non-preferred relationships in reef manta rays. Panel A shows associations (SRIs) and panel B shows social affiliations (GAIs). Preferred relationships (red bars) and non-preferred relationships (grey bars) defined according to whether the observed pairwise value was significantly higher than corresponding values produced by data-stream permutations.

2.4.6. Assortment by phenotype

Results for assortment by phenotype are reported in Table 2.2. Assortativity coefficients (ACs) for SRI values were significantly higher than expected when grouping individuals by sex and maturity, indicating that associations were positively assorted by these phenotypic attributes. There was no evidence for assortment of associations by colour 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 indicates that same-sex pairs tend to have social preferences, and do not avoid each other. There was little evidence for assortment of GAIs by maturity or colour morph. Figure 2.12 shows the network of social preferences by sex and maturity. While all individuals are highly connected, there is partial segregation between the sexes.

	SRI	Positive GAI values	Negative GAI values
Phenotype: Sex AC- real: random mean (SD) P-Value	0.077 : 0.025 (0.012) P= 0.001**	0.101 : 0.037 (0.019) P= 0.002**	-0.046 : -0.017 (0.011) P= 0.995**
Phenotype: Maturity AC- real: random mean (SD) P-value	0.030 : 0.007 (0.009) P= 0.005*	0.028 : 0.006 (0.015) P= 0.068	-0.030 : -0.016 (0.008) P= 0.98**
Phenotype: Colour morph AC- real: random mean (SD) P-value	-0.028 : -0.006 (0.010) P=0.969	-0.034 : -0.006 (0.018) P= 0.944	0.008 : 0.003 (0.011) P= 0.301

Table 2.3. Tests for assortment by sex, maturity and colour morph. For associations (SRIs), and positive and negative affiliations (GAIs). 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. For P-values, level of significance indicated by: * ≤ 0.05 , ** ≤ 0.005 (two-tailed tests)

2.4.7. Community structuring

We found support for sub-division of the observed manta ray society into communities of individuals with stronger in-group relationships. The most parsimonious division of the association (SRI) network (Figure 2.8) was into two communities with a $Q_{\max}$ value of 0.168 (95% CIs- 0.162:0.257) (see Figure 2.13). 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 & Farine, 2016). 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.

2.4.8. Variability in network positions

Results comparing network metrics of GAIs between phenotypes are presented in Table 2.3 and Figure 2.14. 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, colour morph, and for mated and non-mated females.

	Weighted degree			Weighted betweenness			Clustering coefficient		
Phenotype	Mean (95% CIs)	Median (95% CIs)	Observed slope Rand. slope (SD) P value	Mean (95% CIs)	Median (95% CIs)	Observed slope Rand. slope (SD) P value	Mean (95% CIs)	Median (95% CIs)	Observed 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= 0.606	43.3 (28.1-58.5)	22 (14-29)	-0.110 3.400 (4.073) P= 0.802	0.487 (0.480-0.495)	0.483 (0.475-0.491)	0.006 0.006 (0.004) P= 0.480
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= 0.020*	37.3 (26.6- 48.0)	22 (14-32)	19.985 10.388 (5.322) P= 0.029*	0.486 (0.479-0.493)	0.483 (0.475-0.489)	0.008 0.003 (0.004) P= 0.163
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= 0.384	40.3 (28.6-52.0)	27 (16-39)	-5.868 -9.975 (3.623) P= 0.122	0.488 (0.481-0.496)	0.488 (0.478-0.499)	-0.003 -0.002 (0.003) P= 0.643
Normal (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= 0.724	48.0 (20.1- 75.8)	14.5 (9-32)	-9.619 1.176 (4.463) P= 0.992**	0.480 (0.470-0.490)	0.475 (0.465-0.484)	0.016 0.004 (0.004) P= 0.005**
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= 0.243	39.5 (15.4- 63.7)	14 (9-27)	8.552 7.661 (4.582) P= 0.428	0.483 (0.472-0.493)	0.480 (0.470-0.490)	0.011 0.004 (0.004) P= 0.063
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)	

Table 2.4. Phenotypic differences in social network position. Calculated 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 2017). Two-tailed *P* values at *P* ≤ 0.05 indicated in italics, at *P* ≤ 0.01 indicated by *. Rand. = Randomised.

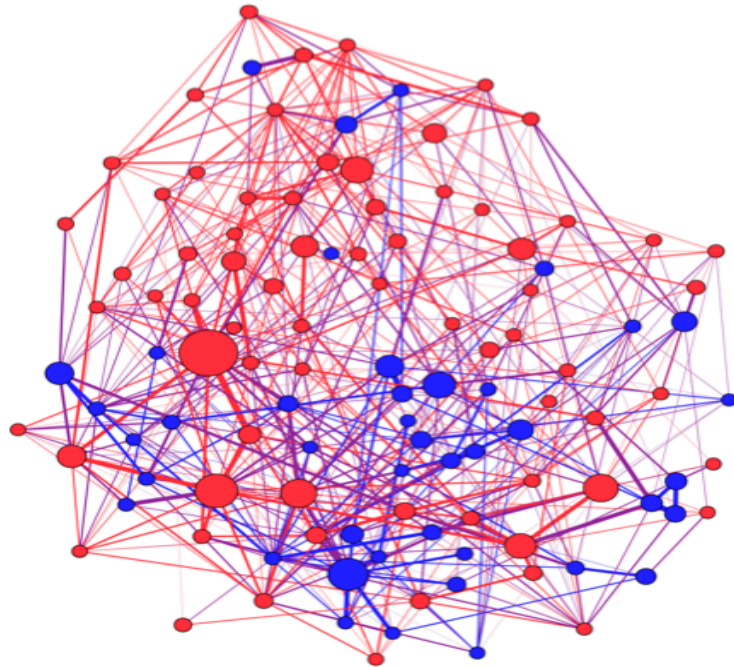


Figure 2.12. Network of social preferences. $N_{edges} = 480$. Node colours indicate sex (red=female, blue=male). Node size indicates that individual's centrality (measured by weighted betweenness). Edge widths represent weights of GAI values. Edge colours represent relations between females (red), between 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.

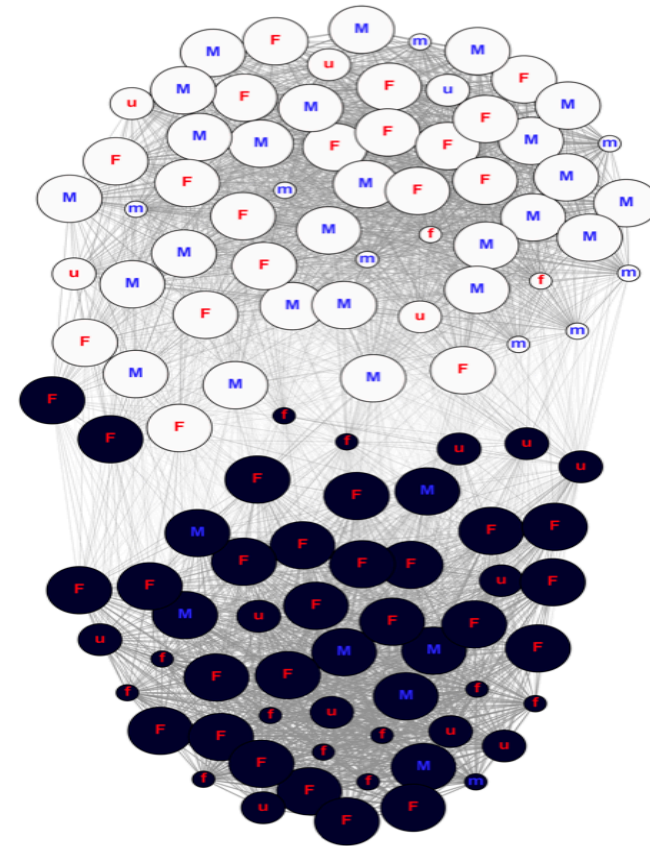


Figure 2.13. Network of community assortativity assignments. Based on SRIs showing how often empirical community assignment of each pair agreed with bootstrap replicate networks (represented by edge widths). Edges < 0.25 removed. Node sizes indicate maturity status: large= adult, small= juvenile, medium= 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.

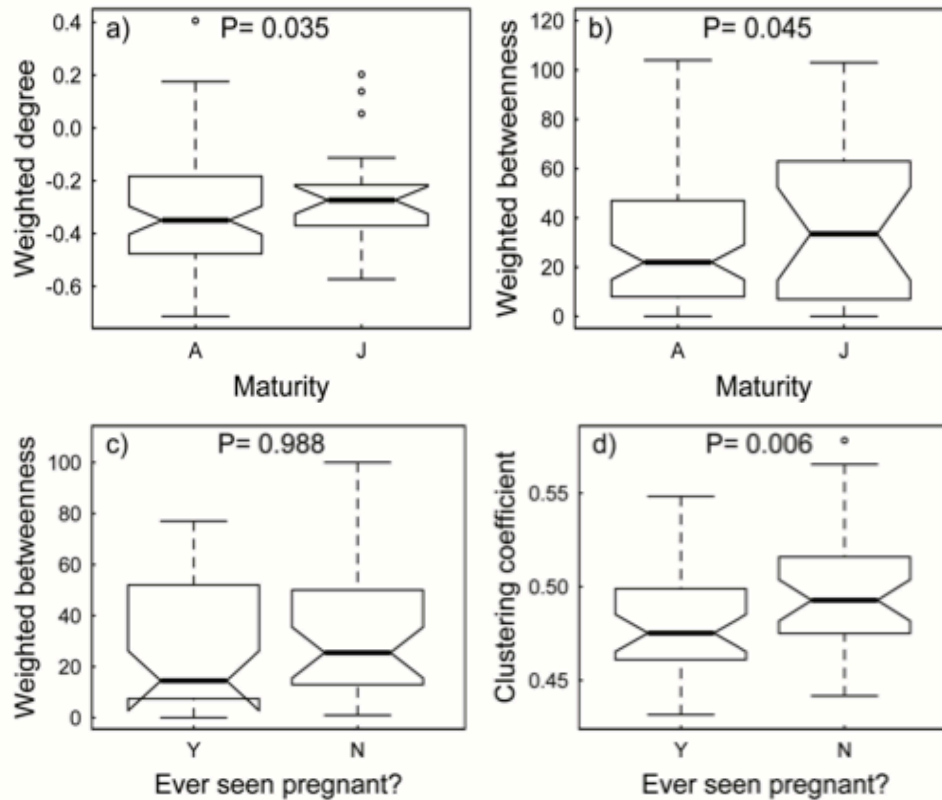


Figure 2.14. Significant differences in network metrics by phenotype. Including; (a) weighted degree for adult (A) and juveniles (J), (b) weighted betweenness for adult (A) and juveniles (J), (c) weighted betweenness for females observed pregnant (Y) and never observed pregnant (N), (d) clustering coefficient 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

2.5. 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; Kalbitzer et al. 2017; Ellis et al. 2017). Familiarity and kin recognition over extended time periods (Griffiths & 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 & 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 & Hamilton 1981; Bruck 2013).

Simultaneous relationships with multiple partners may be required for social behaviours 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 different structure, 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 & Whitehead 2000; Cantor et al. 2015), although in several aspects our findings were comparable to social network studies on bottlenose dolphins (*Tursiops* sp.) including a recent study using GAls (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; Wiszniewski et al. 2012; Bruck et al. 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 & 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 and known wide-ranging movements of the species. Fidelity to areas of coastal reef has been described previously in *M. alfredi* in various locations (Marshall et al. 2011; Deakos 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 smaller 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 95km per day (Jaine et al. 2014; Duinkerken 2010) 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 (RP 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 & Simpfendorfer 2005; Wearmouth & Sims 2008; Guttridge et al. 2011, Krause 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 behaviour 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. 2009; 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 GAs, 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 & Bennett 2010; Deakos et al. 2012; Stevens et al. 2018; RP pers. obs.). 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 et al. 2006) and social factors are known to be drivers of sexual segregation in elasmobranchs (Wearmouth & Sims 2008; Jacoby et al. 2010; Wearmouth et al. 2012).

Fish are 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 & 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 & 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 behaviours with mature males. Our results suggest that mature females do not form long-term social bonds with mature males, though they are likely to form short-term affiliations. When females (including many pregnant individuals) were alone they were often pursued by males (RP pers. obs.). Enabling social behaviour 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. 2016, Perryman et al. 2021). Research into the communicative capabilities of manta rays is warranted.

Our study provides the first evidence for structured social relationships in manta rays. It suggests that detailed information on their social organization (including structure, dynamics, and social preferences) will be important to a fuller understanding of their natural behaviours and response of their populations 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). Our results, therefore, suggest that the structure of social relationships within manta ray populations should be considered as a key aspect of conservation planning. 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, that may cause displacement from certain locations, and changes to social and reproductive behaviours. 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 is 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, 2018b). In the light of these more nefarious threats, network-based studies that link movements and behaviour 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 & 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.

2.6. References

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2.7. Appendix

2.7.1. Study sites and sampling effort

Research dives were conducted at 3 cleaning station sites (where manta rays were cleaned by small reef fish) and 3 larger areas where reef manta rays were regularly observed performing feeding behaviours (see Figure 2.1). Of the cleaning stations, site 'MS' was a sandy area at 14-16m depth, with two small rocks covered in coral structures. Manta rays were observed here in varied current conditions; Site 'MR' was part of a large rocky ridge at 6-9m depth, where manta rays were typically observed during strong currents performing both surface-feeding and cleaning behaviours; Site 'RSB' was a sandy area at 18-20m depth, similar in habitat structure to Site 1, with two rocks covered in coral structures, where manta rays were typically observed during mild currents. Fish species observed to clean manta rays at these sites included *Labroides dimidiatus*, *Chaetodon kleinii* and *Thalassoma lunare*. Of the feeding areas, location 'ESA' was an area of shallow reef in pristine condition and subject to strong tidal currents; location 'WSA' was an area of sloping reef and sandy bottom near to a small island; and location 'LDS' was a shallow sandy area approx. 20km away from the other sites. Sampling effort was higher at cleaning stations than feeding areas, and was spread reasonably evenly between sites, except for the first year of data collection (see Table 2.4).

2.7.2. Stability of identifications and associations

Biological interpretation	LIR model	QAIC	Δ QAIC	
Emigration + mortality (permanent emigration) + reimmigration	$R(d) = \frac{\left(e^{-\left(\delta \times \frac{d}{N}\right)}\right) \times ((b^{-1}) + (a^{-1}) \times e^{-(b^{-1} + a^{-1}) \times d})}{(b^{-1} + a^{-1})}$	104975.73	0	Best model
Emigration + mortality (permanent emigration) + reimmigration	$R(d) = b \times e^{(-N \times d)} + \delta \times e^{(-a \times d)}$	104984.79	9.06	Partial support
Emigration + mortality (permanent emigration)	$R(d) = N^{-1} e^{-\lambda d}$	105007.11	31.38	No support
Emigration + mortality (permanent emigration)	$R(d) = N^{-1} e^{-d/a}$	105007.11	31.38	No support

Emigration + reimmigration	$R(d) = a_2 + a_3 \times e^{(-\lambda \times d)}$	105052.53	76.80	No support
Emigration + reimmigration	$R(d) = \frac{N^{-1} \times ((b^{-1}) + (a^{-1}) \times e^{(-(b^{-1}+a^{-1}) \times d)})}{(b^{-1} + a^{-1})}$	105052.53	76.80	No support
Closed population	$R(d) = 1/N$	105129.50	153.77	No support

Table A2.1. Candidate exponential decay model fits for lagged identification rates. LIRs for reef manta rays between Nov 2013 and May 2018 (total 1651 days), ranked by lowest quasi-Akaike Information Criterion (QAICc). Identification rates of individuals (R), given as a function of time lag (d), related to combinations of the following demographic parameters: population size (N), mean residence time in the study area (a), mean time outside the study area (b), emigration rate (λ) and mortality/permanent emigration rate (δ); other parameters (a_2 , a_3) can be reparametrized as the proportion of the population in the study area at any time ($a_2/(a_2 + a_3)$) and to estimate immigration rate (μ), where $a_2 = \lambda/(N \times (\lambda + \mu))$ and $a_3 = \lambda/(N \times (\lambda + \mu))$; (see Whitehead 2001).

Biological interpretation	LAR model	All individuals		Females		Males	
		QAICc	Δ QAIC	QAICc	Δ QAIC	QAICc	Δ QAIC
Casual acquaintances	$g(d) = e^{-d/\tau_{cas}}$	24190.7	10914.5	13974.0	6235.37	6709.13	2965.84
Two levels casual acquaintances	$g(d) = P_{cas} \times e^{-d/\tau_{cas}} + (1 - P_{cas}) \times e^{-d/\tau_{perm}}$	13279.1	2.92	7742.59	3.89	3743.29	0 (Best)
Rapid dissociation and casual acquaintances	$g(d) = P_{cas} \times e^{-d/\tau_{cas}}$	13287.8	11.61	7746.14	7.44	3746.34	3.05
Rapid dissociation and two levels of casual acquaintances	$g(d) = P_{cas} \times e^{-d/\tau_{cas}} + P_{perm} \times e^{-d/\tau_{perm}}$	13279.6	3.38	7744.09	5.39	3744.95	1.66
Preferred companions and casual acquaintances	$g(d) = P_{cc} + (1 - P_{cas}) \times e^{-d/\tau_{cas}}$	13329.5	53.24	7758.61	19.91	3775.80	32.51
Rapid dissociation and preferred companions	$g(d) = P_{cc} + P_{cas}$	13356.3	80.88	7768.89	30.19	3791.39	48.1
Rapid dissociation, preferred companions, casual acquaintances	$g(d) = P_{cc} + P_{cas} \times e^{-d/\tau_{cas}}$	13276.2	0 (Best)	7738.7	0 (Best)	3748.34	5.05

Table A2.2. Candidate exponential decay model fits for lagged association rates. For reef manta rays in Raja Ampat; all individuals, females only, and males only. Association rate (g), given as a function of time lag (d), related to the proportion of preferred companions (P_{cc}) and the proportion of casual acquaintances (P_{cas}) that lasted for a particular length of time (τ_{cas}), and to the proportion of casual acquaintances (P_{perm}) that lasted for a longer time period (τ_{perm}) (see Whitehead 1995). The lowest quasi-likelihood Akaike Information criterion (QAICc) indicates the best fitting model, and Δ QAIC (difference between QAICc and that of the best model) indicates the degree of support for the other models.

2.7.3. Models of encounter probability

A) Site type by phenotype	Adjusted OR estimate	2.5% CI	97.5% CI	Std. Error	z value	Pr(> z)	Meaning	Sig. level	Significant after Bonferroni correction?
(Intercept)	0.034	0.031	0.036	0.038	-88.2	0.000			
Feeding area: all phenotypes	1.203	1.070	1.350	0.059	3.111	0.002	More likely	**	Yes
Feeding area: Female melanistic adult	0.885	0.707	1.106	0.114	-1.072	0.284	No diff.		
Feeding area: Female 'normal' adult	1.010	0.827	1.232	0.102	0.096	0.924	No diff.		
Feeding area: Female melanistic juvenile	0.442	0.314	0.613	0.170	-4.797	0.000	Less likely	***	Yes
Feeding area: Female 'normal' juvenile	0.673	0.477	0.939	0.172	-2.299	0.021	Less likely	*	Yes
Feeding area: Male melanistic adult	1.793	1.406	2.292	0.125	4.690	0.000	More likely	***	Yes
Feeding area: Male 'normal' adult	1.530	1.192	1.965	0.127	3.338	0.001	More likely	**	Yes
Feeding area: Male melanistic juvenile	1.198	0.814	1.758	0.196	0.923	0.356	No diff.		
Feeding area: Male 'normal' juvenile	1.145	0.754	1.731	0.211	0.641	0.522	No diff.		
Cleaning station: Female melanistic adult	1.320	1.143	1.519	0.073	3.818	0.000	More likely	***	Yes
Cleaning station: Female 'normal' adult	1.025	0.899	1.166	0.066	0.369	0.712	No diff.		
Cleaning station: Female melanistic juvenile	1.651	1.379	1.963	0.090	5.581	0.000	More likely	***	Yes
Cleaning station: Female 'normal' juvenile	1.371	1.117	1.667	0.102	3.098	0.002	More likely	**	Yes
Cleaning station: Male melanistic adult	0.716	0.597	0.852	0.091	-3.685	0.000	Less likely	***	Yes
Cleaning station: Male 'normal' adult	0.723	0.603	0.859	0.090	-3.599	0.000	Less likely	***	Yes
Cleaning station: Male melanistic juvenile	0.717	0.546	0.922	0.133	-2.492	0.013	Less likely	*	No
Cleaning station: Male 'normal' juvenile	0.880	0.657	1.150	0.143	-0.894	0.371	No diff.		
B1) Sex by individual site	Adjusted OR estimate	2.5% CI	97.5% CI	Std. Error	z value	Pr(> z)	Meaning	Sig. level	Significant after Bonferroni correction?
(Intercept)	0.028	0.025	0.031	0.059	-60.35	0.000			
Female: all sites	0.953	0.813	1.118	0.081	-0.601	0.548	No diff.		
Male: ESA	1.248	0.978	1.574	0.121	1.828	0.068	No diff.	.	
Male: LDS	1.165	0.893	1.497	0.132	1.159	0.247	No diff.		
Male: MR	2.208	1.898	2.581	0.078	10.125	0.000	More likely	***	Yes
Male: MS	0.562	0.471	0.670	0.090	-6.421	0.000	Less likely	***	Yes
Male: RSB	1.249	1.048	1.491	0.090	2.479	0.013	More likely	*	No
Female: ESA	0.540	0.371	0.779	0.189	-3.267	0.001	Less likely	**	Yes

Female: LDS	1.451	1.041	2.033	0.170	2.183	0.029	More likely	*	No
Female: MR	1.002	0.811	1.235	0.107	0.014	0.989	No diff.		
Female: MS	2.652	2.127	3.310	0.113	8.650	0.000	More likely	***	Yes
Female: RSB	0.340	0.252	0.454	0.150	-7.190	0.000	Less likely	***	Yes
B2) Maturity by individual site	Adjusted OR estimate	2.5% CI	97.5% CI	Std. Error	z value	Pr(> z)	Meaning	Sig. level	Significant after Bonferroni correction?
(Intercept)	0.027	0.025	0.030	0.047	-76.95	0.000			
Juvenile: all sites	1.172	0.988	1.382	0.085	1.861	0.063	No diff.	.	
Adult: ESA	0.916	0.739	1.124	0.107	-0.818	0.413	No diff.		
Adult: LDS	1.291	1.057	1.564	0.100	2.561	0.010	More likely	*	No
Adult: MR	2.326	2.065	2.625	0.061	13.821	0.000	More likely	***	Yes
Adult: MS	0.997	0.884	1.126	0.062	-0.054	0.957	No diff.		
Adult: RSB	0.771	0.656	0.903	0.082	-3.194	0.001	Less likely	**	Yes
Juvenile: ESA	0.928	0.611	1.379	0.207	-0.363	0.717	No diff.		
Juvenile: LDS	1.232	0.862	1.744	0.179	1.164	0.244	No diff.		
Juvenile: MR	0.658	0.518	0.835	0.122	-3.439	0.001	Less likely	**	Yes
Juvenile: MS	1.000	0.798	1.254	0.115	-0.004	0.997	No diff.		
Juvenile: RSB	1.002	0.740	1.350	0.153	0.016	0.988	No diff.		
B3) Colour morph by individual site	Adjusted OR estimate	2.5% CI	97.5% CI	Std. Error	z value	Pr(> z)	Meaning	Sig. level	Significant after Bonferroni correction?
(Intercept)	0.032	0.028	0.035	0.057	-60.71	0.000			
Normal: all sites	0.817	0.700	0.953	0.079	-2.571	0.010	Less likely	**	No
Melanistic: ESA	0.722	0.534	0.952	0.147	-2.215	0.027	Less likely	*	No
Melanistic: LDS	1.434	1.126	1.805	0.120	2.996	0.003	More likely	**	Yes
Melanistic: MR	1.852	1.587	2.164	0.079	7.794	0.000	More likely	***	Yes
Melanistic: MS	1.076	0.930	1.249	0.075	0.977	0.328	No diff.		
Melanistic: RSB	0.815	0.669	0.989	0.100	-2.051	0.040	Less likely	*	No
Normal: ESA	1.455	1.010	2.118	0.188	1.992	0.046	More likely	*	No
Normal: LDS	0.924	0.667	1.280	0.166	-0.479	0.632	No diff.		
Normal: MR	1.257	1.021	1.548	0.106	2.153	0.031	More likely	*	No
Normal: MS	0.867	0.706	1.064	0.105	-1.370	0.171	No diff.		
Normal: RSB	0.904	0.689	1.186	0.138	-0.733	0.463	No diff.		

Table A2.3. Logistic mixed effects models of probability of encounter by phenotype. Feeding areas and cleaning sites (A), and at 5 individual sites (B1, B2, B3) by phenotype (sex, maturity and colour morph). The model coefficient for 'Feeding area: all phenotypes' represents the overall probability of encounter of manta rays at feeding areas compared to cleaning stations. Similarly, the model coefficients for 'Female: all sites', 'Juvenile: all sites', 'Normal: all sites' represent the overall probability of encounter at all sites, compared respectively to males, mature adults, and melanistic morph rays. All other model coefficients represent the difference in probability of encounter of the given phenotype at the given location (feeding area/cleaning station or individual site) compared to a grand mean over all phenotypes/locations. Fixed effect intercepts represent A) cleaning stations, B1) males, B2) adults, B3) melanistic rays. Adjusted odds ratio (OR) estimates, 95% upper and lower confidence intervals, standard errors, Wald z statistics and p values are reported. No diff. = No difference.

2.7.4. Efficiency of non-social predictor variables to explain associations

	All individuals		Females		Males		Adults		Juveniles	
Predictor	Partial correlation	P-value	Partial correlation	P-value	Partial correlation	P-value	Partial correlation	P-value	Partial correlation	P-value
Intercept	-0.075	0	-0.077	0	-0.037	0.014	-0.101	0	-0.078	0
Site preference similarity	-0.293	0	-0.283	0	-0.338	0	-0.296	0	-0.37	0
Gregariousness similarity	0.035	0	0.035	0	0.028	0	0.043	0	0.038	0
Temporal overlap	0.109	0	0.135	0	0.089	0	0.108	0	0.150	0
Sex class similarity*	0.006	0	-	-	-	-	0.004	0.029	0.012	0.06
Maturity class similarity*	0.002	0.30	-0.002	0.300	-0.002	0.592	-	-	-	-
Colour morph class*	-0.002	0.20	-0.0004	0.810	-0.000	0.985	-0.0003	0.896	-0.006	0.31

Table A2.4. MRQAP tests of predictor variables on association indices. For networks of: all individuals (n= 112); females only (n=70); males only (n=42); adults only (n=75); juveniles only (n=22), shown using partial correlation coefficients- method of Dekker et al. (2007) with 1000 replications. *Predictor variable not included in calculation of generalized affiliation indices

Chapter III. Reef manta ray social dynamics depend on individual differences in movements and site fidelity

3.1. Abstract

Knowledge about the fine-scale spatial ecology of wide-ranging marine species is vital for their conservation. For social species, movements and habitat use are likely to be strongly influenced by relationships between individuals. This may cause social units to be subject to different selective pressures and drive population structuring. Here we used passive acoustic telemetry and network-based analyses to investigate the movements, site fidelity and social affiliations of reef manta rays (*Mobula alfredi*) in Raja Ampat, West Papua. Acoustic transmitters were externally deployed on 27 rays and tracked for up to 110 days. Movement data were retrieved from nine acoustic receivers positioned in clusters at aggregation sites, enabling analysis of social processes at various spatial scales. We utilised Bayesian inference and a double permutation method to address issues in sampling and hypothesis testing on social networks constructed from automated telemetry data. We found that *M. alfredi* varied strongly in their movement behaviour, with some individuals regularly moving distances of >20km, while others stayed around a single aggregation area throughout the study period. Social affiliations were assorted into spatially defined communities, with this social structuring stable over time periods of at least weeks, though many affiliations were likely short-lived. Individuals with high levels of site attachment were more likely to be clustered together, while individuals that regularly made longer distance movements were important in connecting different social communities. We suggest, therefore, that the regional management of *M. alfredi* will benefit from identifying how and where social gatherings occur in different regions. This should include how social groups are formed, how long they remain stable, and differences between individuals/groups that influence this. Certain individuals, groups and locations are likely to be important to the integrity of social networks and metapopulation structures, and prioritising their protection may be justified. We recommend several improvements to management of *M. alfredi* in Raja Ampat based on our findings.

3.2. Introduction

Many populations of elasmobranchs are heavily impacted by human activities (Baum et al. 2003; Worm et al. 2013; Dulvy et al. 2014a; Dulvy et al. 2017; MacNeil et al. 2020) and are increasingly threatened with extinction. To effectively protect elasmobranchs, we must understand how they behave in the wild, including their movements and habitat preferences, and the drivers of these

behaviours. Over the last decade, studies have shown that sharks can form social bonds that may have adaptive functions (e.g. in learning or information transfer), and that these bonds can remain stable over time (Jacoby et al. 2010; Guttridge et al. 2011; Mourier et al. 2012; Wilson et al. 2015; Jacoby et al. 2016; Keller et al. 2017; Papastamatiou et al. 2020; Mourier & Planes 2021). Sharks are also known to have highly variable behavioural phenotypes and individual personalities (Jacoby et al. 2014; Wilson et al. 2015; Byrnes et al. 2016; Finger et al. 2017; Finger et al. 2018). This new knowledge suggests that, like highly social birds and mammals, elasmobranch species can form structured societies, and that social dynamics may be a major driver of spatial ecology (Mourier et al. 2012; Papastamatiou et al. 2020). This is important, because animal social network structures are often adapted to contemporary selective environments, leaving populations vulnerable to disturbance and rapid environmental change (Snijders et al. 2017). Changes in social network structure may be used as biological indicators of disturbance or other ecological changes that may negatively impact populations (Snijders et al. 2017; Mourier et al. 2017a).

The reef manta ray (*Mobula alfredi*) is listed as Vulnerable to Extinction (IUCN Red List; Marshall et al. 2018), due to increasing concern over anthropogenic threats to populations, which include targeted and incidental fisheries, and disturbance to natural habitats and behaviours. These threats are exacerbated by the species' conservative life history, and its occurrence in tropical and subtropical coastal waters of developing countries where it is often poorly protected (Dulvy et al. 2014b; Croll et al. 2016; Stewart et al. 2018; Marshall et al. 2018). In Raja Ampat, West Papua, Indonesia, *M. alfredi* are known to maintain social preferences in their associations with conspecifics (Perryman et al. 2019). These preferences may be a key aspect of their behavioural ecology underpinning their distributions, movement patterns and population structuring/demographics (Wilson et al. 2014). If so, understanding social structuring and social connectivity is likely to be important for developing conservation and management plans. In recent years, several studies have investigated manta ray movements and spatial ecology in various locations. Some have revealed high levels of mobility, with individuals making long-distance movements of hundreds of kilometres (e.g. Germanov et al. 2014; Jaine et al. 2014) and over 1000 km (Armstrong et al. 2019). Others have demonstrated high levels of residency and site attachment, especially to shallow, inshore areas around cleaning stations and feeding sites (Braun et al. 2015; Couturier et al. 2018; Setyawan et al. 2018; Germanov et al. 2019; Peel et al. 2019; Perryman et al. 2019; Venables et al. 2020). These somewhat conflicting results suggest a high level of behavioural variability between and/or within individuals which may have important effects on social structuring. Detailed knowledge of species' biology and ecology is required to aid conservation and management of threatened species (Levin and Lubchenko 2008; Snijders et

al. 2017). Protecting elasmobranchs throughout their entire range is likely to be expensive and logistically complex. Thus, prioritising the protection of critical habitats and mitigating locally specific threats (Guidetti et al. 2013; Lascelles et al. 2014) can maximise conservation returns on investment. Moreover, social dynamics and connectivity are key aspects of behavioural ecology, that affect metapopulation structuring (Lusseau et al. 2006). Understanding them will improve our ability to identify population-level disturbance and predict its effects (Snijders et al. 2017).

Research on the behavioural and spatial ecology of mobile elasmobranchs is often performed using passive acoustic telemetry (PAT), a method which utilises fixed acoustic receiver stations, and is especially useful for species such as *M. alfredi* that regularly attend known aggregation sites. PAT enables the continuous and simultaneous monitoring of multiple individuals, including where they move, how long they remain in an area, and how their movements and habitat use vary over time and space (Donaldson et al. 2014; Braun et al. 2015; Hussey et al. 2015; Heupel et al. 2018a). It has broad applications, for example in the estimation of home ranges (Speed et al. 2016; Venables et al. 2020), assessment of environmental drivers of site visitation patterns (Couturier et al. 2018; Peel et al. 2019) and construction of movement networks (Jacoby and Freeman 2016; Heupel et al. 2018b).

Movement networks provide a powerful way to visualise, interpret and interrogate animal tracking data. They can be used to describe and quantify the frequency and duration of animal movements, investigate connectivity between habitats and show the effect of physical habitat and environmental fluctuations on movement behaviour. Acoustic telemetry data can also be used to infer proximity-based social networks (PBSNs) derived from the frequency or longevity of pairwise spatial associations between multiple individuals, with high temporal resolution (Spiegel et al. 2016; Jacoby et al. 2016; Mourier et al. 2018). As yet, however, the fine-scale spatiotemporal structure of social relationships in manta rays has not been studied. Movement and social networks can help to elucidate connectivity at multiple spatial scales, dynamics of social relationships, and the importance of key individuals, groups and locations. As manta rays are ecologically reliant upon core areas of habitat (McCauley et al. 2014), knowledge on where these are and how they are used is crucial (Stewart et al. 2018). Social cohesion among animals that meet regularly (e.g. highly site attached individuals) can lead to the emergence of clusters of individuals with relatively stronger social connections than exist in the population as a whole, and in time can lead to stable social units or communities (Clauset et al. 2004; Lusseau et al. 2006; Salathé et al. 2010). These units may be subject to distinct selective pressures, such as local environmental changes or varying levels of anthropogenic disturbance. They may also be connected by mobile individuals that affiliate with multiple groups in different locations (Shizuka et

al. 2016). Such individuals can play a disproportionate role in maintaining gene flow and overall population genetic viability.

Social analyses require separation of various influences on group structuring because, in addition to reflecting social preferences, the same observed rates of interaction may result from non-social processes, including sampling biases, assortment due to individual preferences for particular habitats, and phenological or resource-based aggregation (Croft et al. 2008; Armansin et al. 2016). Disentanglement of social and non-social processes may be achieved through the construction of null models based on randomisations of observed data, which can account for the dependency structure between interacting individuals and autocorrelation inherent to time-series data. Appropriate null models are vital to bridge the gap between structural patterns and causative process in understanding biological systems (Farine and Whitehead 2015; Jacoby et al. 2016; Farine 2017). PBSNs typically make several assumptions regarding social organisation that must be considered in hypothesis tests. These include that social relationships are transitive, that all individuals observed in the same place are associated (the 'Gambit of the group') (James, Croft and Krause 2008; Franks et al. 2010), as well as that associations within a given time window are biologically meaningful. To deal with these and other issues in sampling and constructing network graphs from automated telemetry data, Psorakis et al. (2012; 2015) and Jacoby et al. (2016) developed a Gaussian mixture modelling approach (GMMevents) with variable Bayesian inference. This takes into account temporal as well as spatial structure by exploiting key statistical properties of the time-series data stream. Results are typically more robust at capturing biological interactions than traditional methods (Psorakis et al. 2015; Farine et al. 2015). Network sampling requires careful consideration of the spatial position of acoustic receiver locations, as well as the number of individuals tagged, duration of tag deployment and detection range of receivers, which can vary strongly depending on several physical and environmental factors (Braun et al. 2015; Hussey et al. 2015; Sequeira et al. 2019).

In Raja Ampat, West Papua, Indonesia, a well-established Marine Protected Area (MPA) system appears to provide good protection for local wildlife while maintaining traditional practices and empowering local communities (McLeod et al. 2009; Boli et al. 2014). However, wildlife-interaction tourism has grown rapidly in Raja Ampat in the past decade, and there is currently little regulation of tourism activities. If not managed appropriately, disturbance from boats, divers and other marine resource users has the potential to negatively impact local wildlife (Trave et al. 2017), including manta rays which are often the focus of dive/snorkel tourism (Venables et al. 2016). We previously recorded a large population of reef manta rays (>700 individuals) that exhibit residency to the Dampier Strait

region of Raja Ampat during December-May each year (Perryman et al. 2019). In that study, we used photographic identification with a ‘snapshot’ approach to construct social networks and identify broad-scale social patterns. We found evidence for social community structuring, but were not able to record detailed data on movements or social dynamics. Our research suggested that female *M. alfredi* displayed high levels of site fidelity, while males were likely to be more mobile. Social patterns in *M. alfredi* are influenced by their predominantly diel visitations to shallow-water cleaning stations and feeding areas, and differences between individuals in their affinity to particular locations. The use of cleaning stations is vital for maintaining health (Grutter 1999; Marshall 2008), but these stations may also provide important opportunities for reproductive and social interactions (Stevens et al. 2018; Perryman et al. 2019).

In this study we aimed to build on previous research examining the social structure of manta rays in Raja Ampat by investigating social dynamics. Using PAT combined with proximity-based social network analyses, we aimed to record round-the-clock data on manta ray presence at known aggregation sites and use this to infer social relationships between rays. In doing this we hoped to provide a more holistic framework for manta ray spatial ecology to aid local conservation measures. We expected to uncover specific social structures and processes relevant to the local population of *M. alfredi*. We decided to record *M. alfredi* movements and site fidelity at clusters of several sites within wider aggregation areas, to investigate the influence of individual behaviour on social connectivity at multiple spatial scales. We hypothesized that sex- and maturity-based differences between individuals would influence their social behaviour and emergent social network structures, and that membership to distinct social communities would occur and remain stable over time.

3.3. Methods

3.3.1. Study area

We collected data on *M. alfredi* in the Dampier Strait area of Raja Ampat, West Papua, Indonesia (0°39′11.8″S, 130°35′04.5″E; see Figure 3.1). Raja Ampat is an archipelago of approximately 1500 islands, containing a variety of near-pristine marine habitats including shallow sandy areas and coral reefs, large mangrove forests, lagoons and seagrass beds, all in close proximity to deep waters of >2500m depth. The region has high bathymetric structure and is subject to strong tidal influences driving rapid surface currents and complex eddies. It is protected by a large network of nine marine protected areas (MPAs) (Setyawan et al. 2020) and numerous ‘no-take’ (no fishing) zones (Atmodjo et al. 2019), managed under the Raja Ampat MPA zonation system (Ministry of Marine Affairs and

Fisheries, regulation No. 36, 2014). The region supports a large population of 1,375 individual *M. alfredi* (Setyawan et al. 2020), which appears to be in a healthy state, comprising many juveniles as well as mature adults. About 150-200 of these individuals are regularly encountered at the study sites (Perryman et al. 2019). Manta rays are observed at numerous cleaning and feeding aggregation sites across the archipelago (Perryman et al. 2019; Setyawan et al. 2020). There is no known fishing pressure on manta rays within Raja Ampat.

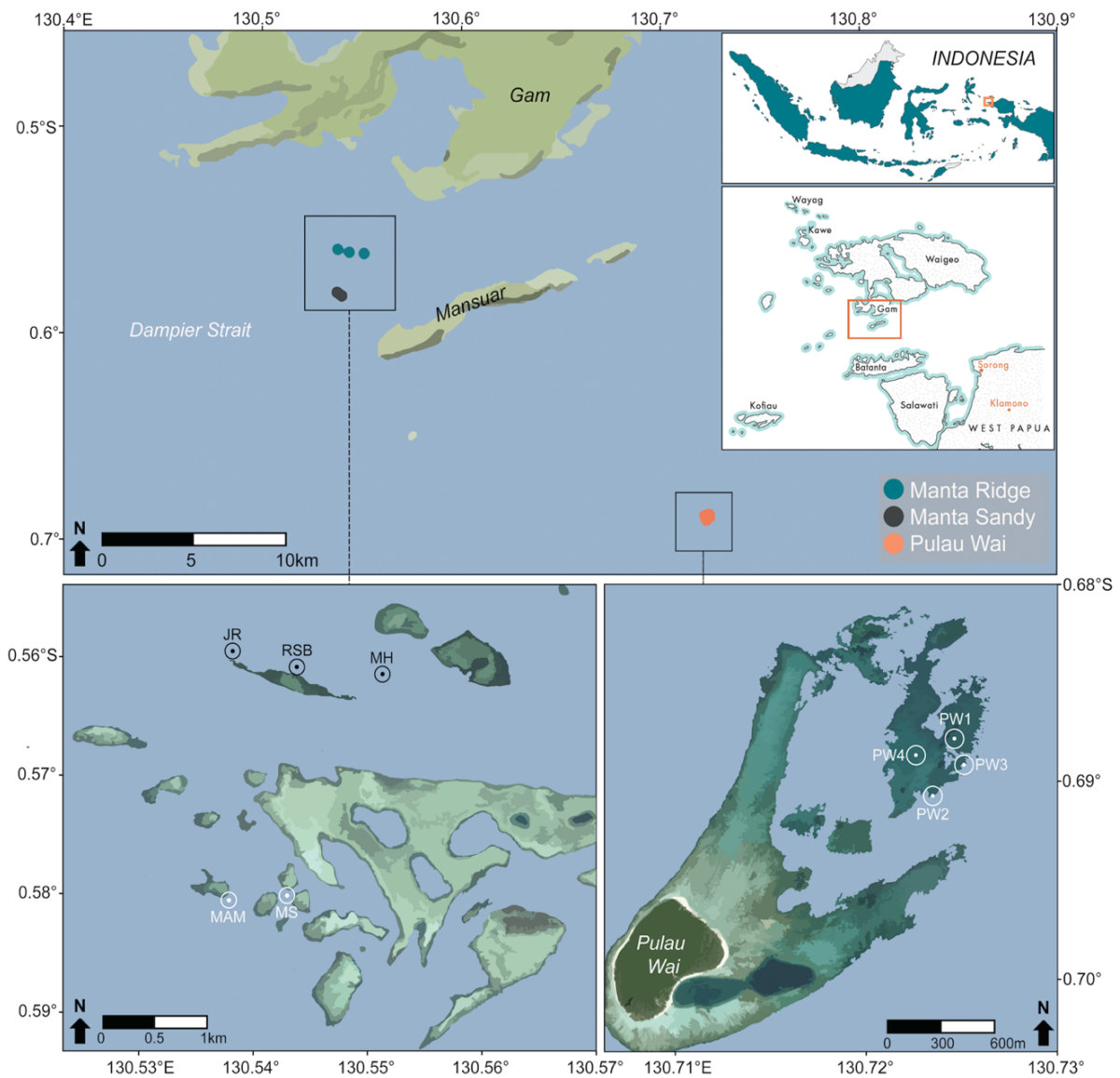


Figure 3.1. Maps of the study area in Dampier Strait, Raja Ampat. Upper main panel: location of all acoustic receiver stations in three *M. alfredi* aggregation areas, including; Manta Ridge; Manta Sandy; Pulau Wai, within Indonesia (upper inset panel); and Raja Ampat (lower inset panel). Lower left main panel: location of two stations (MAM, MS) in Manta Sandy area, and three stations (JR, RSB, MH) in Manta Ridge area. Lower right main panel: location of four stations (PW1, PW2, PW3, PW4) in Pulau Wai area.

3.3.2. Data collection

Acoustic transmitters (Vemco Ltd.) were deployed on *M. alfredi* (n= 27) in the Dampier Strait during 2018-19. Fifteen V13 tags, one V9 tag (all 69 kHz, transmission interval 30-90s), and six V16-6H tags (69kHz, transmission interval 60-120s) were deployed during January and February 2019 by divers on SCUBA in one of three locations (Manta Sandy, Manta Ridge, Pulau Wai) that were previously identified as primary aggregation areas for *M. alfredi* (Perryman et al. 2019). Data were also collected from a further five V16-6H tags deployed on different *M. alfredi* in the same area in February 2018. Tags were externally attached in the musculature of the dorsal side of the pectoral fin of each manta ray, via a custom-built metal dart attached to a tagging pole with Hawaiian sling. Tags were coated in Propspeed™ anti-foul to reduce biofouling build-up and resultant drag. Prior to tagging, all manta rays were photographed to ensure that they could be identified based on unique patterns of pigmentation on their ventral surface, which remain consistent throughout their lifetime (Marshall et al. 2009; Pierce et al. 2018). Rays were sexed according to the presence/absence of claspers. Maturity and reproductive status were estimated using evidence from female pregnancies and mating scars, and male clasper size/calcification (Marshall and Bennett 2010), as in Perryman et al. (2019). Disc width (DW) was estimated by visually comparing manta rays to coral structures of known size.

Manta rays were detected and tracked using nine VR2W acoustic receiver stations (Vemco Ltd.). These were installed between 01/02/2019 and 08/02/2019 at nine individual sites in the three known aggregation areas (Manta Sandy: MS, MAM; Manta Ridge: JR, RSB, MH; Pulau Wai: PW1; PW2; PW3; PW4, see Figure 3.1). Receiver stations were attached securely with cable ties to metal stakes, which were driven into sand or coral rubble at water depths of 10–20m, with the receivers approximately 50cm above the substrate facing up. We conducted detection range tests on V9 and V13 tags *in situ* at each of the aggregation areas by temporary placement of receiver stations in proposed locations. Divers swam gradually away from the chosen location, holding an acoustic transmitter whilst reeling out a large, modified dive reel. We recorded the distance from the receiver station every 30 seconds with a watch that was calibrated to the same clock time as the receiver station, and then matched this to the date-time stamps of tag detections. Detection ranges (i.e. the distance to the nearest 10m beyond which detections were not recorded over three tests at each site) varied from ~40-90m for V-9 tags and ~60-140m for V-13 tags. The Pulau Wai aggregation area had slightly larger detection range on average (mean 83.3m for V-9 tags; mean 116.7m for V-13 tags) than the Manta Sandy (mean 63.3m for V-9 tags; mean 90m for V-13 tags) and the Manta Ridge (mean 73.3m for V-9 tags; 93.3m for V13 tags). The detection range of V-16-6H tags was estimated at ~120-150m, according to a prior study in Raja Ampat (Setyawan et al. 2018). Following range tests, we strategically placed receiver stations

near known cleaning stations or feeding areas - locations frequented by large numbers of *M. alfredi* within each of the chosen aggregation areas. The design of our receiver array and tagging strategy reflect our aim to investigate the influence of individual behaviour on social connectivity at multiple spatial scales. We tagged all individuals in a short time period, aiming to tag several individuals within groups to capture possible social affiliations. This also ensured reduced bias from lack of temporal overlap between tags (Jacoby et al. 2016). All stations were placed in clusters at distances >250m apart (this avoided tag detection overlaps between stations, a requirement for the mixture model analysis), with distances between the clusters varying from 2.5 – 25 km. Detections of tagged *M. alfredi* were recorded at all sites between 08/02/2019 and 20/05/19; these were divided into three 30-day periods for dynamic social analyses (11/02/19 – 12/03/19; 13/03/19 – 12/04/19; 13/04/19 – 12/05/19).

3.3.3. Acoustic detection data processing

Acoustic telemetry data were processed using VUE software (Vemco Ltd.) and MS Excel, and all further analyses were performed in R (R Core Team 2017). We first filtered data for active tag IDs, removed any false positive detections and corrected for any receiver clock-drift (Lea et al. 2016). We then examined detection data visually, removing any detections recorded prior to tagging (due to handling of transmitters by divers), and ensuring that no tags had been shed within range of receiver stations by checking for periods of >24h of consecutive detections. We used the 'VTrack' package (Campbell et al. 2012) to calculate summary statistics for each tagged individual and a detection index (DI) (Udyawer et al. 2018), which described the detectability of each individual, as a proxy of residency to the whole study area. This was defined as:

$$DI (\%) = \frac{\text{No. days detected}}{\text{No. days between first and last detection}} \times 100$$

All summary statistics were tested to check assumptions of normality and homogeneity using Shapiro-Wilk and Levene's tests. None were normally distributed, so we used Kruskal-Wallis tests to compare these statistics by sex and maturity status (due to low sample sizes, juveniles and sub-adults were considered as immature, versus mature adults), to investigate any possible impact of physical characteristics on behavioural phenotypes.

3.3.4. Site attachment and movements

To investigate levels of site attachment and movements at various scales, we extracted 'residence events' at each receiver station and movements between stations using the 'RunResidenceExtraction' function (VTrack). A residence event was recorded when a manta ray was detected consecutively at a

receiver three or more times and terminated if the ray was detected at another station, or was not detected at any station for 3 hours. For each individual, an 'Area Fidelity Score' was calculated as the standard deviation of the mean frequency of residence events at each of the three main aggregation areas. For this we included six receiver stations (MS, MAM, RSB, JR, PW1, PW3). Residency data from three other stations (JR, PW3, PW4) were removed to compare two sites that were visited most frequently in each aggregation area). Movements were extracted from departure and arrival profiles between residence events at each receiver station. Average (mean) movement speeds for each individual were calculated by dividing the distance of each individual movement by its duration, excluding all movements with durations >24h (these were assumed not to represent direct movements between sites). To investigate differences between individual movement patterns, we recorded the frequency and duration of movements within and between aggregation areas for each tagged individual, dividing these into 'short' (<500m), 'medium' (500m-3km) and 'long' (>20km) distance movements. We used ANOSIM tests with 9999 permutations (Vegan package; Oksanen et al. 2019) to compare counts of residence events at all nine receiver stations, and counts of movements at the different spatial scales, by sex and maturity status. These counts were $\log(x+1)$ transformed to allow for better comparisons among individuals with differing observation frequencies (Meyer et al. 2010; Papastamatiou et al. 2010; Peel et al. 2019).

3.3.5. Network analyses

Movement networks and social networks were constructed for 25 individuals that were detected > 200 times over the entire study period using the 'igraph' package (Csardi & Nepusz 2006). Both types of network were also constructed as time-aggregated networks that were used to examine social dynamics. These were constructed over 30-day periods during February-May (when detections were most frequent) for 15 individuals that were detected at least 100 times in each of those periods. For movement networks, each acoustic receiver station was considered as a node, with edges representing movements between stations (for all individuals) extracted using VTrack and weighted by the total number of movements made (Jacoby et al. 2012). In order to place social organisation in the context of habitat use and movements before quantifying social structuring, we derived 'communities' from the collective movement network (Papastamatiou et al. 2020) using the cluster.walktrap algorithm (igraph) to reveal clusters of movements (this algorithm was the most robust in simulations by Finn et al. 2014). The statistical significance of each spatial community was calculated by two-sample Wilcoxon tests using the DcommSignif function in package 'dnet' (Fang and Gough, 2014). We then assigned individual manta rays to spatial communities based on the community in which they recorded the highest number of residence events at a single receiver.

Social networks were constructed through a Gaussian mixture modelling approach with variational Bayesian inference (GMMEvents) using code modified for the R environment (Vbmix package) (Jacoby et al. 2016). This procedure delineates biologically appropriate ‘gathering’ events within the raw detection data enabling the time window in which associations are recorded to be variable and based on the structure of detections, rather than set arbitrarily (Psorakis et al. 2012; Psorakis et al. 2015). Significant associations were calculated via randomizations of the individual-by-location bipartite graph, constrained within ‘gathering’ events. This controlled for various “nuisance” sampling biases (Farine and Carter 2020), including differences in individual detection frequencies and the number of clustering events in which each individual was recorded, as well as controlling for individual spatial preferences, with the result that significant associations may be considered as social *affiliations*. The method assumes that individuals visit aggregation areas in groups and that membership within a group denotes social affiliation (‘gambit of the group’ approach; Franks et al. 2010), which both seem reasonable in *M. alfredi*. The GMMEvents procedure produced an adjacency matrix showing the number of separate events in which dyads were detected together, which was used to construct networks representing the frequency of social affiliations between *M. alfredi*.

3.3.6. Effect of individual variation on social relations

To investigate the impact of behavioural phenotypes (movement profiles, site attachment, spatial community membership) on *M. alfredi* social relations, we needed to control for various ‘social’ factors (Farine and Carter 2020) that were not controlled within GMMEvents (e.g. potential differences in gregariousness by sex, individuals having limited numbers of possible close associates). To do this we performed additional edge rearrangement (reassignment of edge weight) randomisations on the edge lists of each social adjacency matrix using the ‘tnet’ package (Opsahl et al. 2010), constraining the total number of edges in the network, and the number of individuals per community. This ‘double permutation’ method (Farine and Carter 2020) produced 10,000 randomised social network permutations that were used as a null model against which observed network statistics could be compared (i.e. data-stream randomisations performed in GMMEvents produced a network of social affiliations based on ‘gathering events’, and the edge weights in this network were then randomly reassigned 10,000 times to generate a null model). The overall and 30-day time-aggregated social networks were tested for weighted assortative mixing (r_w^d) by spatial community membership using the ‘*assortment.discrete*’ function in the package ‘*assortnet*’ (Farine et al. 2014). The significance of this assortment was calculated by comparing the observed assortativity coefficient to a posterior distribution of r_w^d values derived from the permutations. To test for stability in social connections between the monthly time-aggregated networks, we performed Mantel tests (with 10,000 node label

permutations) using the ‘vegan’ package (Oksanen et al. 2019), which tested the significance of the correlation in dyadic association strengths between the 30-day sampling periods.

To test the influence of differences between individuals in habitat use and movement profiles on their importance to the social network, we used tnet (Opsahl et al. 2010) to calculate the following weighted social network metrics describing the relative position of an individual to others in the network: degree (summed weight of all connections for each individual); betweenness centrality (measure of how often an individual is located on the shortest path between two others); and local clustering (measure of how complete the neighbourhood of each individual is). We calculated betweenness centrality using a tuning parameter ($\alpha = 0.5$) which prioritizes short paths composed of weaker ties over longer paths with stronger ties as in Perryman et al. (2019). We then constructed linear models of sex, body size, the number of movements within and between spatially-defined communities, and area fidelity scores against social network metrics, including an offset term to control for differences in the number of days on which individuals were detected. We tested the significance of the influence of these variables on social network metrics by comparing the empirical model coefficients to randomised coefficients from equivalent models (Farine 2017), using the same ‘double permutation’ method as previously.

3.4. Results

3.4.1. Acoustic detection data summary

Of the 27 acoustic tags deployed on *M. alfredi*, 25 returned usable data (see Figure 3.2 and Table A3.1, including a total of 51,871 detections (mean 1997 ± 783 per individual; all confidence levels given at 95% level). Females ($n = 15$, mean disc width $3.45 \pm 0.19\text{m}$) accounted for 59.5% of detections, and males ($n = 10$, mean disc width $2.98 \pm 0.19\text{m}$) for 40.5% of detections; no difference in detectability by sex was found (Kruskal-Wallis KW χ^2 value = 0.25, $p = 0.62$). Individual rays were detectable (no. days from first to last detection) for a mean of 63.52 ± 11.58 days and detected on a mean of 26.76 ± 6.59 days (MS area: 4.86 ± 2.67 ; MR area: 5.06 ± 4.25 ; PW area: 12.82 ± 5.63). There was no difference in the number of detections or number of days detected by tag type (V9, V13, V16-6H; KW tests; all p values > 0.4). Of the female rays, one was a juvenile and 14 were adults (1.0 and 58.5% of total detections respectively). Of the males, five were juvenile or sub-adult, and five were adults (20.4 and 20.1% of total detections respectively). There was no difference in detectability between mature and immature individuals (Kruskal-Wallis χ^2 value = 0.94, $p = 0.33$). Residency to the study area over all individuals was $47.7 \pm 10.3\%$ (range?) and was slightly higher for males ($57.5 \pm 11.8\%$) than females

($41.1 \pm 8.7\%$), but this difference was not statistically significant (Kruskal-Wallis χ^2 value = 2.16, $p=0.14$). There was little phenotypic variability in behaviour, but individual manta rays varied strongly in the frequency of their recorded movements at different spatial scales and in their tendency to display philopatry to aggregation areas. We found no difference in the total distance recorded between residence events (mean 67.5 ± 27.3 km, range 0.72-251.89 km), number of receiver stations visited (mean 6.24 ± 0.77 , range 3-9) or movement speeds (mean 2.46 ± 0.43 km/h, range 1.26-6.18 km/h), by sex (KW tests; all p values > 0.18) or maturity status (KW tests; all p values > 0.22).

3.4.2. Movements

Tagged rays were detected at all study sites in the Dampier Strait, though detection frequencies were much higher in the 'Pulau Wai' aggregation area than other areas (83.7% detections). We recorded a total of 2,553 movements between receiver stations in the same aggregation area and 101 movements between aggregation areas. 1,036 within area movements were made by eight rays that were only detected in one area, while 13 individuals made four or more between area movements, including 10 individuals that made four or more movements of >20 km. For female and male rays, movements to different sites within the same aggregation area were recorded at similar, highly variable frequencies (means of 103.7 ± 36.4 , and 104.7 ± 49.8 movements; ranges 12-298, and 4-410 movements, respectively) and movement frequencies between aggregation areas were also similarly varied (means of 4.6 ± 1.29 , and 3.7 ± 1.99 movements; ranges 0-9, and 0-16 movements, respectively). There was no difference in movement frequencies at various spatial scales (<500 m, 500m-3km, >20 km) by sex (ANOSIM R statistic: 0.082, $p=0.11$) or maturity status (ANOSIM R statistic: 0.163, $p=0.083$), though the 'Manta Sandy' and 'Manta Ridge' areas appeared to be used mainly by females and males, respectively (see Figure 3.3A).



Figure 3.2. Chronology of residence events recorded by receiver station. February – May 2019. Minimum 3 detections, 3 hr timeout period for residence event to be recorded. Receivers in the same cluster are shown by different shades of the same colour; red: Manta Sandy area; blue: Manta Ridge area; green: Pulau Wai area. Where residence events were recorded at multiple sites on the same day, the site with the most events is shown. Most individuals were detected in only one receiver cluster, but several (e.g. tag IDs ‘28055’, ‘12486’, ‘3304’) moved regularly between clusters.

3.4.3. Site residency

Nineteen individuals were recorded attending the 'Manta Sandy' area (mean 4.9 ± 2.7 detection days per individual), 15 individuals were recorded at the 'Manta Ridge' area (mean 5.1 ± 4.2 detection days per individual) and 21 individuals were recorded at the 'Pulau Wai' area (mean 12.8 ± 5.6 detection days per individual). Ten individual rays were recorded at all three aggregation areas, while four rays were recorded in only the 'Manta Sandy' and 'Manta Ridge' areas, five rays were recorded in only the 'Manta Sandy' and 'Pulau Wai' areas, 1 ray was recorded in only the 'Manta Ridge' and 'Pulau Wai' areas, and five individuals were only recorded in the 'Pulau Wai' area. A total of 973 residence events (mean 38.9 ± 10.8 events) were recorded at the six sites for which data were compared. A total of 192 residence events were recorded in the 'Manta Sandy' area (sites 'MS' and 'MAM', mean 7.7 ± 4.2 events), 218 in the 'Manta Ridge' area (sites 'RSB' and 'MH', mean 8.7 ± 7.8 events), and 563 in the 'Pulau Wai' area (sites 'PW1', 'PW2', mean 38.9 ± 10.8 events). Levels of fidelity to each aggregation area varied strongly between individuals (mean area fidelity score 8.15 ± 2.99) but were similar for females and males (mean 8.01 ± 3.14 and 8.35 ± 3.27 , respectively), with similar residence event patterns by sex (ANOSIM R statistic: 0.039, $p = 0.231$) and maturity status (ANOSIM R statistic: 0.184, $p = 0.082$).

3.4.4. Social affiliations, dynamics and community structure

The overall movement network was divided into two distinct movement communities, with a moderate level of community modularity k ($Q = 0.275$), suggesting that although movements were much more common within aggregation areas, there was a reasonable level of connectivity between communities (see Figure 3.3A). Results were broadly similar for the separate monthly time-aggregated networks ($Q = 0.35, 0.218$ and 0.219), although the northern-most community was further divided into two-sub communities for months 1 and 2 (see Figure 3.4A). Social affiliations were assorted by spatial community in the overall network and in months 1 and 2, indicating that the spatial communities shown represent separate social units (see Table 3.1). Because the vast majority of manta ray detections were recorded during diel periods (see Figure 3.5), the social affiliations described only reflect structuring during the daytime (approximately 06:00 – 18:00) rather than at night. Mantel tests revealed that association strengths for pairs of individuals were correlated in adjacent months, and that there was strong correlation over the entire study period, although there was no significant correlation between months 1 and 3 (see Table 3.2 and Figure 3.4B). This suggests

that social relationships are several weeks, and in some cases last over several months, but also that many social affiliations are short-lived.

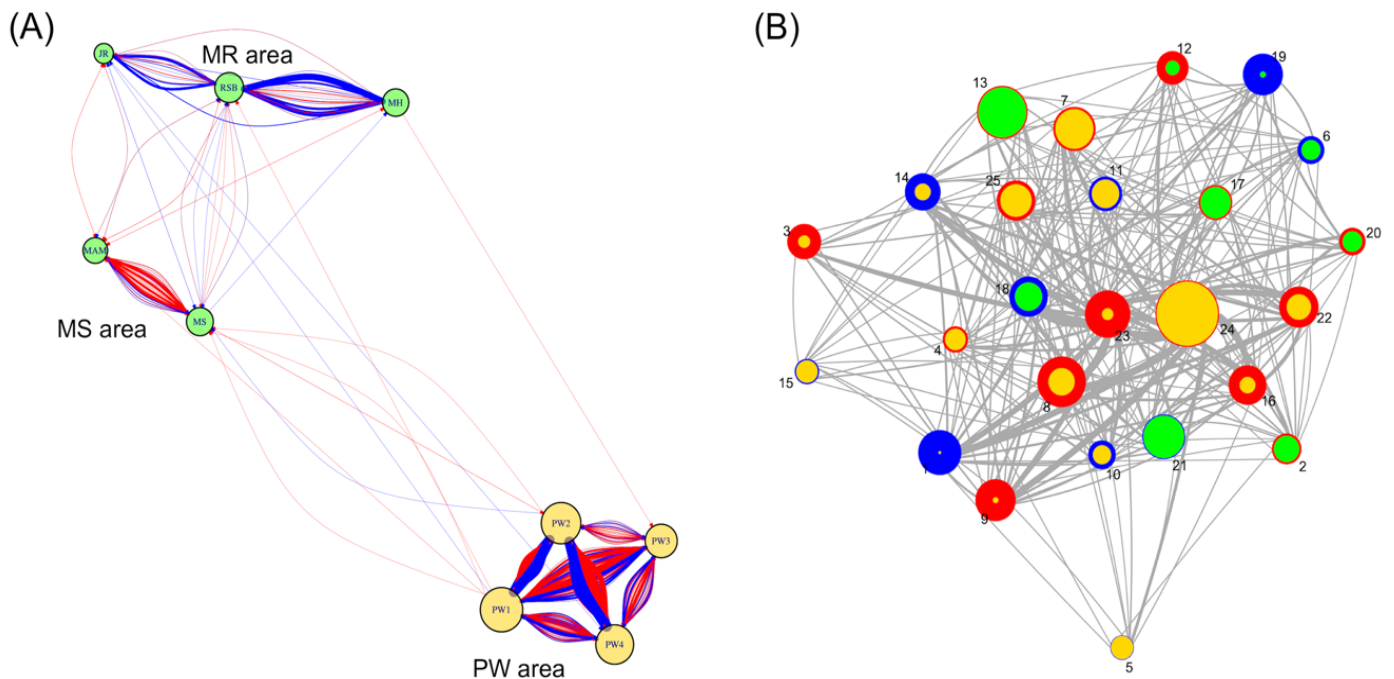


Figure 3.3. Spatial and social assortment of reef manta rays in Raja Ampat, West Papua. (A) Overall movement network. Each node represents an acoustic receiver. The position of each node is representative of its true geographic position, but distances between the three aggregation sites (clusters of top three, middle two, and bottom four stations) have been reduced in scale to allow for easier visual interpretation of movement frequencies. Node size represents the number of detections recorded there. Node colours represent spatial communities defined using cluster.walktrap algorithm. Edges represent movements between each station. Edge colours represent movements by females (red) and males (blue). (B) Overall social network. Each node represents an individual manta ray. Blue outer circles show males, red outer circles show females. Yellow and green inner circles show membership to two spatially defined communities based on residence events. Node size (not including border) represents level of site fidelity based on 'area fidelity score'. Node border thickness represents number of long-distance movements (>20km) made by that individual. Edges represent social affiliations between rays. Edge thickness represents strength of social affiliation (based on number of 'gathering events' in which two individuals were socially affiliated).

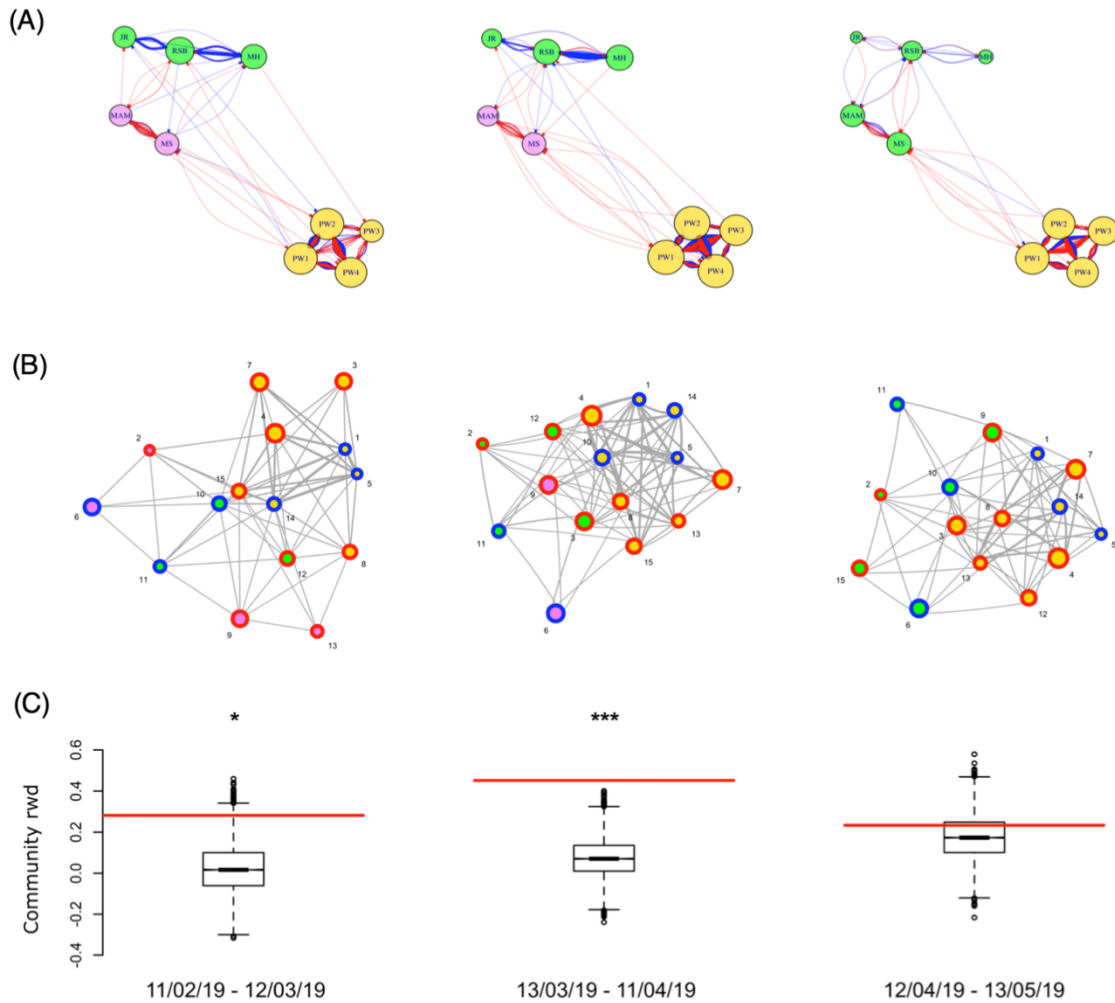


Figure 3.4. Time aggregated networks showing spatial and social assortment of reef manta rays. (A) Movement networks. Each node represents an acoustic receiver. The position of each node is representative of its true geographic position, but distances between the three aggregation sites (clusters of top three, middle two, and bottom four stations) have been reduced in scale to allow for easier visual interpretation of movement frequencies. Node size represents the number of detections recorded there. Node colours represent spatial communities defined using cluster.walktrap algorithm. Edges represent movements between each station. Edge colours represent movements by females (red) and males (blue). (B) Social networks. Each node represents an individual manta ray. Blue outer circles show males, red outer circles show females. Yellow and green inner circles show membership to two spatially defined communities based on residence events. Node size (not including border) represents level of site fidelity based on ‘area fidelity score’. Node border thickness represents number of long-distance movements (>20km) made by that individual. Edges represent social affiliations between rays. Edge thickness represents strength of social affiliation (based on number of ‘gathering events’ in which two individuals were socially affiliated). (C) Boxplots show distribution of weighted assortativity coefficients (r_w^d) for social affiliations into communities defined by spatial movement networks for 10,000 random social networks, compared to empirical values (red lines) over three months.

	Overall network	Month 1	Month 2	Month 3
No. communities (modularity)	2 (0.275)	3 (0.35)	3 (0.218)	2 (0.219)
Community P values	0.012*; 0.029*	0.22; 0.1; 0.029*	1; 0.1; 0.029*	0.012*; 0.029*
Observed r_w^d (SE)	0.159 (0.054)	0.303 (0.083)	0.393 (0.072)	0.263 (0.079)
Random r_w^d (SE)	0.044 (0.092)	0.065 (0.096)	0.075 (0.086)	0.206 (0.113)
Assortativity P value	0.021*	0.015*	< 0.001***	0.298

Table 3.1. Spatial community modularity and social assortativity coefficients. Communities assigned via cluster.walktrap algorithm. Assortativity coefficients r_w^d for those communities compared to 10,000 social network permutations, showing that social affiliations are assorted by spatial community structure for the overall networks and first two monthly networks. Significance values: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

	Mantel test r	95% quantiles (permutations)	P value	Significance level
Month 1 : Month 2	0.659	0.295	0.0003	***
Month 2 : Month 3	0.362	0.318	0.0334	*
Month 1 : Month 3	0.178	0.299	0.1345	
Months 1 : 2 : 3	0.648	0.296	0.0005	***

Table 3.2. Mantel tests of correlation in association strengths between months. Test statistics based on Pearson's product-moment correlation (9999 permutations). Test for all months uses partial mantel test. Significance values: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

3.4.5. Effect of behavioural heterogeneity on social network position

Variation in weighted degree (observed coefficient of variation over all individuals: 0.595, mean of permutations: 0.256, $p = 0$) and variation in betweenness centrality (observed coefficient of variation over all individuals: 4.36, mean of permutations: 0.95, $p = 0$) were much higher than expected if manta rays had random social associations, showing that individuals varied strongly in their social network positions. Overall levels of clustering (observed value: 0.904, mean of permutations: 0.882, $p = 0$) were also higher than expected, suggesting that individuals formed conserved social groups. Table 3.3 shows results of linear models of behavioural influences on social network positions. Individuals that made many short distance movements (within spatial communities) and those that made more long distance (between spatial community) movements had more social affiliations (higher weighted degree), than expected ($p = 0$ and $p < 0.001$, respectively), while individuals that had higher levels of area fidelity and those that made more long distance movements were more central (higher

betweenness centrality) to the overall social network ($p = 0.035$ and $p = 0.018$, respectively; see Figure 3.3B). These results suggest that more mobile individuals had an important role in connecting social communities and that social structuring was not purely a product of spatial segregation. We found no effect of phenotype or individual behavioural variability on local clustering. Males had stronger social affiliations compared to females than expected, but the high standard errors suggested that this was due to one or two individuals biasing results. Sex had no effect on clustering or betweenness centrality and body size had no effect on any social network metric.

A. Weighted Degree	Estimate (observed model)	Std. Error (observed model)	t value (observed model)	Mean of estimates (rands)	P value (rands)	Significance level
<i>(Intercept)</i>	-39.02	64.65	-0.603	127.90	>0.999	***
Area Fidelity	-1.765	2.179	-0.81	-2.254	0.377	-
<i>Movements < 3km</i>	<i>0.696</i>	<i>0.161</i>	<i>4.334</i>	<i>0.039</i>	<i>0</i>	***
<i>Movements > 20km</i>	<i>13.71</i>	<i>3.81</i>	<i>3.599</i>	<i>3.889</i>	<i><0.001</i>	***
<i>Sex (male)</i>	<i>18.45</i>	<i>19.78</i>	<i>0.933</i>	<i>-8.933</i>	<i>0.036</i>	.
Disc width	25.46	18.37	1.386	7.024	0.091	-
B. Betweenness log (x+1) transformed	Estimate (observed model)	Std. Error (observed model)	t value (observed model)	Mean of estimates (rands)	P value (rands)	Significance level
<i>(Intercept)</i>	6.444	9.324	0.691	8.355	0.940	.
<i>Area Fidelity</i>	<i>-1.868</i>	<i>0.314</i>	<i>-5.946</i>	<i>-1.939</i>	<i>0.035</i>	.
<i>Movements < 3km</i>	<i>-0.005</i>	<i>0.023</i>	<i>-0.227</i>	<i>-0.006</i>	<i>0.362</i>	-
<i>Movements > 20km</i>	<i>-1.711</i>	<i>0.549</i>	<i>-3.115</i>	<i>-1.853</i>	<i>0.018</i>	*
<i>Sex (male)</i>	<i>-4.121</i>	<i>2.853</i>	<i>-1.445</i>	<i>-4.514</i>	<i>0.144</i>	-
Disc width	-3.448	2.649	-1.302	-3.399	0.552	-
C. Local clustering	Estimate (observed model)	Std. Error (observed model)	t value (observed model)	Mean of estimates (rands)	P value (rands)	Significance level
<i>(Intercept)</i>	8.393	9.355	0.897	8.395	0.536	-
Area Fidelity	-1.927	0.315	-6.112	-1.927	0.655	-
<i>Movements < 3km</i>	<i>-0.008</i>	<i>0.023</i>	<i>-0.327</i>	<i>-0.008</i>	<i>0.140</i>	-
<i>Movements > 20km</i>	<i>-1.942</i>	<i>0.551</i>	<i>-3.524</i>	<i>-1.943</i>	<i>0.258</i>	-
<i>Sex (male)</i>	<i>-4.475</i>	<i>2.862</i>	<i>-1.564</i>	<i>-4.479</i>	<i>0.356</i>	-
Disc width	-3.555	2.658	-1.337	-3.559	0.290	-

Table 3.3. Influence of behavioural/phenotypic variability on social network metrics (overall social network). a) weighted degree; b) betweenness centrality; c) local clustering. Statistics from empirical networks compared to random networks. Significance values: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. 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, i.e. a value of 0.975 or above is significant at the standard 0.05 level) (Farine 2017). Significant influences on individual network metrics are indicated in bold italics. rands = randomizations.

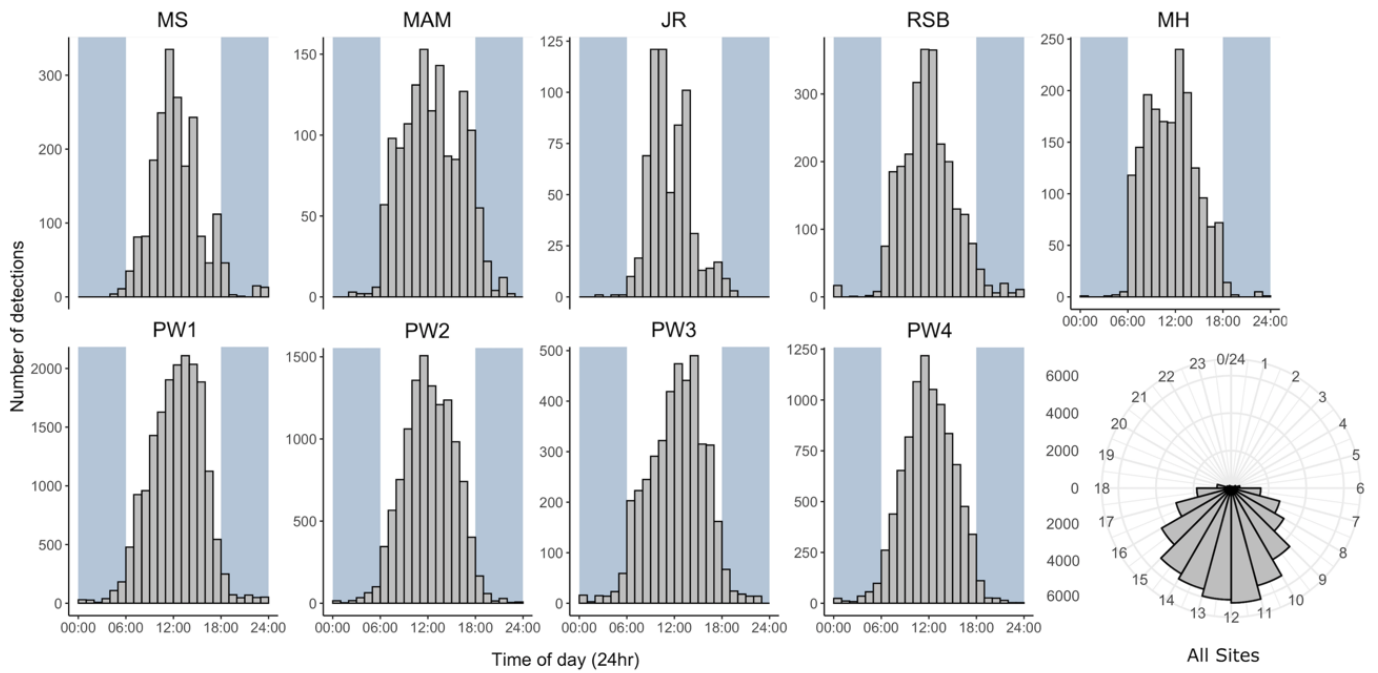


Figure 3.5. Total reef manta ray detections by hour of day at each site. Shading indicates night-time hours; note that y-axis scales are variable. MS: Manta Sandy; MAM: Mambarayup reef; JR: Juan’s reef; RSB: Rob’s Secret Bommie; MH: Manta Heaven; PW: Pulau Wai. Circular plot shows total detections over all sites.

3.5. Discussion

3.5.1. Summary of results

We found that *M. alfredi* in the Dampier Strait region of Raja Ampat form spatially assorted social communities through dyadic social affiliations. This social structuring was temporally stable over a period of at least several weeks, despite frequent movement of some individuals between the two main communities. It was consistent in the first two months of the study (and in the overall social network), although community structuring appeared to break down in month three. The different result in month three was likely due to the seasonal northward movement of *M. alfredi* in Raja Ampat in April-June (Setyawan et al. 2018), meaning that fewer individuals were detected, especially at the Southern Pulau Wai aggregation area. This is also likely to have increased interactions between individuals that were part of separate social communities in months one and two. We suggest that these patterns result from variation between individuals in their movements, habitat use and site fidelity. Individuals varied strongly in their movement behaviour, with some individuals regularly moving distances of >20km, while others stayed around a single aggregation area throughout the study period. These differences are likely to have strong impacts on social interactions and the dynamics of social structuring. Individuals with high levels of site attachment were more likely to be

clustered together, while those that made longer distance movements regularly appeared to be important in connecting different social communities. While individuals displaying both these behaviour types would be likely to be detected frequently (and therefore be recorded together more frequently), the method we used to calculate social affiliations and community structuring controls for differences in detection rates. We can thus be confident that the dynamics of social relationships between rays are impacted by variability in their behaviour. Social stability over extended periods is relatively common in animals traditionally viewed as highly social species, such as birds, primates and cetaceans (Lusseau et al. 2006; Kasper et al. 2009; Shizuka et al. 2014; St Clair et al. 2015; Titcomb et al. 2015). Our results add to growing evidence that wild elasmobranch populations can show long-term preferred associations. Similar patterns have been recorded in coral reef-associated elasmobranchs in other near-pristine locations (Mourier et al. 2012; Jacoby et al. 2016; Mourier et al. 2019; Papastamatiou et al. 2020). These patterns may represent natural states of population structuring. More broadly, our study improves understanding of the behavioural ecology of *M. alfredi*, specifically fission-fusion dynamics, social behaviour and information transfer. It has implications for aspects of the species' population biology that depend on social connectivity and dynamics, such as disease spread and gene flow (Salathé and Jones 2010; Croft et al. 2016), as well for conservation management.

3.5.2. Movements and habitat use

Residency to the whole study area was in the middle range of previous studies on *M. alfredi* (Clark 2010; Setyawan et al. 2020; Peel et al. 2019; Andrzejczek et al. 2020). Most recorded movements were within aggregation areas, but there were sufficient movements between these areas to suggest a high level of connectivity within the Dampier Strait. We provide support for previous research suggesting that social structuring in *M. alfredi* depends on fission-fusion group dynamics (Perryman et al. 2019). Our results showed that many individuals preferentially returned to the same reef locations during daylight hours, leaving these areas at night. This appeared to drive spatial assortment of different social communities. Fission-fusion dynamics are likely driven by daytime availability of cleaning services and social interactions (Stevens 2016; Perryman et al. 2019), combined with foraging opportunities in deeper waters at night (Couturier et al. 2013; Burgess et al. 2016). Though our results could be biased by increased reef noise at night masking tag detections (How & de Lestang 2012; Kessel et al. 2015), they are in broad agreement with several other studies that recorded *M. alfredi* at cleaning stations more frequently during the day (Clark 2010; Deakos et al. 2011; Couturier et al. 2018; Setyawan et al. 2018; Peel et al. 2019). Our results also suggest a high level of connectivity between several manta ray aggregation areas within the Dampier Strait. Understanding of broader-scale (i.e.

metapopulation level) connectivity and social dynamics was beyond the scope of this study, but would be an intriguing future research direction. Although several individuals were detected infrequently, gaps in detections were not usually longer than 1-2 weeks. This suggests that most tagged individuals stayed in areas adjacent to the study area during the short monitoring period, likely within Raja Ampat (Setyawan et al. 2018). The deep waters surrounding Raja Ampat may act as a barrier to *M. alfredi* movements (Deakos et al. 2011; Peel et al. 2019).

3.5.3. Individual behavioural heterogeneity

We found that individual rays varied strongly in overall levels of regional residency, location fidelity and movements; some individuals were more mobile, making frequent movements of >20km; others, though detected frequently, were only recorded making short movements. These differences appeared to affect social network positions. Highly mobile individuals had stronger affiliations and were more central to the overall social network, suggesting that social structuring was not purely a product of spatial segregation between communities. Results did not appear to be biased by differences in the detection ranges of the various tag types, as there was no difference of frequency of detections by tag type. Variability between individual *M. alfredi* in movements and habitat use has been recorded elsewhere (Peel et al. 2019; Andrzejczek et al. 2020; Venables et al. 2020) and may be a general feature of the species' behavioural ecology. Reef manta rays may be partial migrators, with some individuals moving regularly between aggregation areas (Papastamatiou et al. 2013; Chapman et al. 2015; Andrzejczek et al. 2019) while others remain resident to limited home ranges (Clark 2010; Venables et al. 2020). Unlike previous studies (Perryman et al. 2019; Peel et al. 2019), here we found that behavioural heterogeneity did not appear to be linked to phenotypic differences (i.e. in sex or maturity status). Though results could be biased by the low number of individuals tagged, they suggest that there is no hard-wired variability between physical phenotypes (e.g. differences in mobility between sexes; Bonnin et al. 2019), and indicate that consistent behavioural phenotypes or social personalities may exist.

Behavioural heterogeneity is likely to occur both between and *within* individuals. Group compositions may be affected by availability of food resources, cleaning services or social incentives that can change rapidly. Subtle differences between sites (water depth, availability of cleaning stations, cleaner fish density) and daily or seasonal variation in current flows, zooplankton availability, density and social behaviour of conspecifics, or anthropogenic disturbance, may all drive variability in behaviour and social structuring, especially if rays differ in motivation such as hunger or desire to reproduce. Alternatively, changes within individuals may occur seasonally or during ontogeny, affecting their

social behaviour and gregariousness. Differences in swimming ability, threat from predation, or experience in foraging offshore, for example, might cause juvenile rays to remain in certain areas (Pate et al. 2020; Setyawan et al. 2020; Werner 2020). Individuals may also alter their movements and habitat use depending on resource availability or reproductive periodicity (Wearmouth and Sims 2008). Perryman et al. (2019) suggested that mature female *M. alfredi* may be territorial at preferred cleaning station locations. It is plausible that sexually receptive females may change their movement behaviour to attract or avoid mates. Further research might examine environmental effects on manta ray movement dynamics in the context of social relationships/behaviours and individual personalities (Jacoby et al. 2014; Finger et al. 2018).

3.5.4. Cleaning stations as social information hubs

Understanding the impact of social information on behavioural decision-making is key to understanding group-living. Information transfer during conspecific interactions is important in linking individual behaviour to population- and community-level dynamics (Sueur et al. 2011). Spatial distributions, including community-level structuring may arise through social information sharing combined with density-dependent intraspecific competition (Seppänen et al. 2007; Papastamatiou et al. 2018a). Ecological models predict that greater foraging success among social foragers when prey are unpredictably and ephemerally distributed (e.g. Boyd et al. 2016; Kirchner et al. 2018). Our results suggest that information sharing may be an important aspect of social structuring in *M. alfredi*. Cleaning stations and local surroundings appear to act as focal points for some social and reproductive behaviours (Stevens et al. 2018; Perryman et al. 2019; Perryman 2020). Familiar individuals that use common locations are likely to gain foraging advantages by interacting socially rather than randomly searching for prey (Papastamatiou et al. 2020). By grouping at cleaning stations, it is possible that manta rays can communicate information on food patch locations, or recognise others with better current information to preferentially associate with and follow them to these locations. Further research on collective feeding and the potential for communication and cooperation (e.g. Stevens 2016; Stevens et al. 2018; Perryman et al. 2021) between manta rays; in the context of social network structuring (e.g. Van Doorn and Taborsky 2012; Marcoux and Lusseau 2013), is justified.

3.5.5. Conservation implications

Due to multiple global threats to manta rays throughout their range, it is vital that detailed management strategies are developed (Stewart et al. 2018). Here we provide information on the behavioural ecology of *M. alfredi* that may be used to aid regional conservation and management

efforts. Our study found patterns of movements at scales between several to tens of kilometres, fine-scale habitat use and high levels of residency to the Dampier Strait area of Raja Ampat, suggesting that this is a critical habitat for *M. alfredi*. The spatial assortment of social communities suggests that within Raja Ampat, there are distinct social units that are likely to be at differential risk of disturbance because of their ties to particular locations. This is important information because the marine tourism industry in Raja Ampat is focused around a central hub which contains several manta ray aggregation areas, while the rest of the archipelago is much less impacted by tourism. We suggest adopting a multi-faceted approach to protect manta rays and their associated habitats through spatial management measures with a focus on social connectivity. Our main findings (community-level social structure lasting weeks, regional residency, local site attachment and individual behavioural heterogeneity) suggest locally oriented management measures are likely to be effective in Raja Ampat. Here, the management of *M. alfredi* should be focused first on protecting aggregation areas (including cleaning and feeding sites) in the Dampier Strait area. We recommend some modifications and improvements to existing protocols that should help to mitigate disturbance from local tourism. For example, as cleaning stations appear to function as focal points for *M. alfredi* social interactions, we recommend periodic, alternating closures of dive sites at these locations during the manta ray season and stricter protocols in areas surrounding them, such as restrictions on boat speeds and diver/snorkeller numbers. Divers should be strongly discouraged from interfering with manta rays' natural cleaning and social behaviours, especially by approaching them too closely, through the implementation and enforcement of diver/snorkeller codes of conduct. This will help to minimise disturbance to manta rays while preserving high quality dive experiences for tourists, ensuring sustainability of eco-tourism in the region and benefits to the local economy (O'Malley et al. 2013; Venables et al. 2016). While local management measures are recommended here, protection of wider areas through which manta and other mobulid rays are known to move is still critically important (Germanov & Marshall 2014; Braun et al. 2015; Lewis et al. 2015; Armstrong et al. 2019; Peel et al. 2020; Putra et al. 2020). Regional- and national-level protections in Indonesia since 2014 (MMAF No.4/KEPMEN-KP/2014) appear to have been successful in reducing fisheries impact on manta rays (Booth et al. 2020) and are likely to be vital for long-term population genetic viability and survival of these species.

3.5.6. Future directions

Network-based studies provide excellent frameworks for holistic understanding of ecological processes, enabling predictions of the response of elasmobranch populations to disturbance and the use of appropriate conservation measures (Wilson et al. 2014; Mourier et al. 2018). To provide

appropriate information for manta ray population management, future studies should focus on attaining larger sample sizes and recording the dynamics of social affiliations over longer time periods and larger spatial scales (at which metapopulation structuring exists). This was unfortunately beyond the scope of this study. The data we collected on 27 individuals over three months provides an important insight into the dynamics of short-term social relationships, but is not sufficient to draw strong conclusions on social organisation of *M. alfredi* populations over the longer-term (though see Perryman et al. 2019). Research on long-term social dynamics should aim to show whether groups of *M. alfredi* demonstrate multi-year social stability (e.g. Papastamatiou et al. 2020), and if social relationships are maintained while manta rays move to different locations. If confirmed, this would provide stronger evidence for the importance of sociality to manta ray populations than has been reported so far. Such research would also be useful to understand any ongoing effects of human activities on manta ray populations, in Raja Ampat and elsewhere. Unlike reef sharks which display long-term residency to central habitat locations (Papastamatiou et al. 2018a; 2018b), *M. alfredi* in Raja Ampat and other locations aggregate seasonally in different areas (Setyawan et al. 2018). Setyawan et al. (2020) reported that the *M. alfredi* population in Raja Ampat is structured into at least four demographically inferred subpopulations, with limited exchange of individuals between these. Future research should aim to quantify and link long-term data on social and genetic and connectivity across the archipelago. Our research suggests that certain *M. alfredi* individuals are more resident/less mobile than others. Mobile individuals may be crucial to the overall integrity of social networks and wider metapopulation structuring and this should be investigated further using network-based analyses.

The rapid development of tagging technologies, including miniaturization and combined sensors (e.g. Wilson et al. 2015) will facilitate more comprehensive analyses of *M. alfredi* social interactions in the future, including effects of behavioural heterogeneity on social structuring. Complementary approaches, for example using animal-borne cameras (e.g. Stewart et al. 2019) or accelerometers (e.g. Kadar et al. 2019) may shed light on how and why social behaviours occur, for example whether these only occur at specific reef sites during the day or also at night or in deeper waters. Contact network data, such as that from proximity loggers, could be used to confirm the accuracy with which PAT truly captures social affiliations (Jacoby et al. 2016; Mourier et al. 2017b). The development of methods to weight social affiliations by the spatio-temporal scale at which they occur would be particularly useful, due to difficulty controlling for gradually weaker effects of locational preferences with distance. More biologically appropriate edge weights may be achieved by calculation of generalized affiliation indices (Perryman et al. 2019) that control for spatial variability before performing randomisations, or by

combining movement and social networks in multi-layer network analyses (Mourier et al. 2019). The use of appropriate randomisation procedures is essential to test biologically relevant hypotheses that separate the influence of social and spatial preferences, and determine the size of these effects (Spiegel et al. 2016; Farine et al. 2017; Franks et al. 2020; Farine and Carter 2020; Weiss et al. 2021). These are non-trivial issues for which consensus on solutions pertaining to various data types (focal individuals or groups, direct observations or automated data) is still lacking, though recent research (e.g. Spiegel et al. 2016; Perryman et al. 2019; Farine and Carter 2020) offers a range of solutions that may be adapted to a variety of animal systems and study designs.

3.6. References

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3.7. Appendix

Individual Data			Deployment			Overall data				Movements				Habitat use			Social network metrics		
Tag ID (type)	Sex	DW (m)	Tagging date	Site tag-ged	Last detection	No. detect-ions	No. days detec-ted	Track days	Total move distance (km)	<500m	>500m ; <3km	>20km	Mean speed (km/h)	Area fidelity score	No. sites visited	Resid-ency index	Degree	Between-ness centrality	Local cluster-ing
3304 (V9)	F	3.25	16/02/19 11:06	MS	29/04/19 14:28	1667	22	72.1	110.35	82	1	4	2.14	3.04	8	0.31	78	24	0.891
12473 (V13)	M	2.5	12/02/19 09:50	PW	13/05/19 21:05	6683	50	90.5	41.18	410	0	0	2.44	21.94	4	0.55	319	38	0.922
12476 (V13)	F	2.25	09/02/19 09:20	MR	05/04/19 12:12	542	15	55.1	32.92	26	8	1	2.12	2.75	8	0.27	76	1	0.902
12478 (V13)	F	3.75	28/02/19 12:10	PW	02/04/19 11:05	2771	31	33.0	18	181	0	0	1.94	12.99	4	0.94	147	15	0.998
12479 (V13)	F	4.25	09/02/19 09:15	MR	05/03/19 13:28	480	7	24.2	1.21	20	0	0	4.55	2.31	6	0.29	88	1	0.873
12480 (V13)	M	2.25	10/02/19 13:02	PW	13/02/19 09:31	99	3	2.8	0.72	4	0	0	2.66	0.29	3	1.00	28	0	0.993
12481 (V13)	M	3.75	16/02/19 10:38	MS	08/05/19 12:25	267	27	81.1	11.36	16	8	0	1.27	5.69	5	0.33	91	0	0.967
12482 (V13)	F	4	28/02/19 12:00	PW	10/05/19 17:07	937	23	71.2	158.22	35	12	6	1.46	0.58	9	0.32	207	27	0.895
12483 (V13)	F	3.25	12/02/19 10:05	PW	28/05/19 21:22	3563	41	105	232.08	190	0	9	2.12	14.09	6	0.39	360	56	0.873
12484 (V13)	F	3.75	12/02/19 11:30	PW	18/04/19 07:42	3698	52	64.6	15.29	205	0	0	2.36	19.34	4	0.80	278	9	0.924
12485 (V13)	M	3.25	12/02/19 11:45	PW	23/03/19 14:59	1112	16	39.1	2.83	44	0	0	1.54	5.20	6	0.41	160	0	0.883
12486 (V13)	M	2.75	24/02/19 11:45	RSB	06/04/19 18:27	1124	27	41.3	91.42	58	12	3	1.99	2.00	9	0.65	162	15	0.875
12487 (V13)	F	3.25	22/02/19 11:00	MS	25/05/19 16:15	854	35	92.2	28.68	46	9	0	3.92	13.77	4	0.38	94	0	0.966
12488 (V13)	F	2.75	09/02/19 09:25	MR	26/03/19 19:00	582	10	35.3	100.22	26	4	4	3.44	0.58	8	0.28	114	0	0.899
28041 (V16)	M	3	13/02/18 13:21	Unk.	20/05/19 19:13	4567	23	88.2	10.35	150	0	1	2.43	10.98	6	0.26	269	14.5	0.928
28046 (V16)	M	2.75	18/02/18 07:45	Unk.	25/02/19 18:48	247	4	3.6	0.72	6	0	0	6.18	1.15	3	1.00	40	0	0.985
28051 (V16)	F	3.75	23/01/19 10:28	Unk.	06/05/19 08:00	3434	34	86.0	33.43	185	0	2	2.12	14.18	7	0.40	226	0	0.912
28054 (V16)	F	3.5	23/01/19 14:10	Unk.	20/04/19 18:13	283	15	68.1	54.69	8	7	2	1.26	2.02	8	0.22	131	2	0.93
28055 (V16)	M	3.75	23/01/19 14:03	Unk.	18/05/19 10:27	4270	53	97.0	251.89	149	56	8	2.01	8.74	9	0.55	347	133	0.867
28057 (V16)	M	2.75	24/01/19 13:43	Unk.	19/04/19 06:38	2448	59	69.0	70.53	7	135	0	1.98	26.02	5	0.86	106	5	0.985
28058 (V16)	F	3.5	23/01/19 10:35	Unk.	15/03/19 16:54	561	17	35.0	20.82	4	35	0	2.42	4.58	5	0.49	62	0	0.97

28063 (V16)	M	3	23/01/19 14:05	Unk.	17/05/19 18:17	207	14	98.1	74.01	7	6	4	1.57	1.53	8	0.14	121	0	0.891
28065 (V16)	F	3.5	18/02/18 09:53	Unk.	10/05/19 23:22	5049	37	90.6	138.35	183	0	5	2.74	9.52	6	0.41	179	0	0.935
28067 (V16)	F	3.25	18/02/18 09:55	Unk.	05/05/19 17:44	5789	49	84.3	115.95	297	2	4	2.08	19.05	9	0.58	344	90.5	0.874
28069 (V16)	F	3.75	18/02/18 10:05	Unk.	10/04/19 20:34	637	5	60.4	73.12	25	0	3	2.73	1.32	6	0.08	85	0	0.885

Table A3.1. Summary of acoustic tag data from deployments on reef manta rays *Mobula alfredi* in Raja Ampat, West Papua (individuals in bold were included in dynamic network analysis). Unk. = unknown.

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Chapter IV. Reef manta ray cephalic lobe movements are modulated during social and inter-specific interactions

4.1. Abstract

Reef manta rays (*Mobula alfredi*) are social elasmobranchs that have structured societies and actively interact with preferred social partners. Being able to detect cues and signals produced by conspecifics is vital in enabling social behaviour. Many elasmobranch species communicate via body and fin postures, but it is not yet known if or how mobulid rays communicate or respond to cues produced by conspecifics. These rays have specialized cephalic lobes that are highly flexible and used in feeding, but may have other functions such as gestural communication. In this study we developed a standardized method to assess manta ray behavior in the wild via focal sampling and frame-by-frame video analysis. From observations recorded at cleaning stations in Raja Ampat, West Papua, we described various types of cephalic lobe positioning and movements made by free-ranging *M. alfredi* and investigated these in different behavioral contexts. We found that cephalic lobe curls were modulated when approaching both conspecifics and human divers, as well as during interactions with cleaner fish, suggesting that these lobes may be used in sensing water movements, olfactory sensing, and/or gestural communication. Cephalic lobes were moved independently of one another, but we found no evidence of individual laterality. The lack of chemosensory capacity on the lobes suggests that gestural communication is the most likely function, but further research is required to determine this. These results are informative in understanding the function of manta ray social interactions and add to our growing understanding of elasmobranchs' sophisticated social behavior.

4.2. Introduction

Sharks and rays (Chondrichthyes, Elasmobranchii) are increasingly found to be social animals. Though many species are primarily solitary, others aggregate in groups and school cohesively together (Klimley and Nelson 1981; Hart et al. 2006; Reyier et al. 2008; Jacoby et al. 2012; Loiseau et al. 2016; Duffy and Tindale 2018). Several of these species are known to choose social partners and form distinct social units, both in captive conditions (Guttridge et al. 2009; Jacoby et al. 2010) and the wild (Mourier et al. 2012; Perryman et al. 2019; Lieber et al. 2020). Sharks can also learn from each other (Guttridge et al. 2013; Vila Pouca et al. 2020), form social hierarchies (Gordon 1993; Pratt and Carrier 2001) and have distinct individual personalities (Jacoby et al. 2014; Byrnes and Brown 2016; Finger et

al. 2016, 2017), which may produce heterogeneity in gregariousness and social behaviour. Reef manta rays (*Mobula alfredi*) are large and mobile pelagic elasmobranchs that form groups in near-shore, shallow water habitats (Marshall et al. 2009). Mobulid rays have large brains compared to other elasmobranchs, with a highly developed telencephalon and central nucleus (Nishida 1990) suggesting high levels of cognitive ability and propensity for 'social intelligence' (Ari 2011). In Raja Ampat, West Papua, *M. alfredi* form relationships with preferred social partners that can last up to several weeks (Perryman et al. 2019). Social gathering is known to occur at cleaning station sites (Stevens 2016) that may function as focal points for daily fission-fusion of groups of rays (Perryman et al. 2019). Several studies have recorded potential social behaviours in manta rays including collective feeding, 'courtship trains', following, and copying at cleaning stations (Marshall 2008; Deakos et al. 2011; Gadig and Neto 2014; Stevens 2016; Stewart et al. 2016; Stevens et al. 2018; Perryman et al. 2019).

In group-living and social species, interactions between group members provide opportunities for individuals to obtain information that can improve their decision-making in ways that enhance their survival or reproductive fitness. Information may be obtained passively via various cues. For example, fish can use olfactory cues to recognize kin (Olsén et al. 1992) and social partners (Ward and Webster 2007). Schooling fish respond to visual and mechanosensory cues from the movement of neighbours (Pitcher et al. 1976; Berdahl et al. 2013; Pita et al. 2016), with benefits to navigation and collective responses to opportunities or threats (Couzin and Krause 2003; Couzin et al. 2005; Sumpter 2005). In addition, information may pass between individuals in a more directed fashion. Communication signals are evolved acts or structures that carry information about the sender (e.g. their sex, identity, group affiliation, location, condition or motivation) or referential information about the environment (e.g. predator presence, direction of food sources) (Otte 1974; Searcy et al. 2005; Griffiths and Ward 2011), and elicit a behavioural response in a receiver, with positive fitness consequences for both parties (Bradbury and Vehrencamp 1998; Smith and Harper 2003; Laidre and Johnstone 2013). There is evidence that some neural mechanisms for social communication in tetrapods, including vocal and gestural signalling, originated in fishes (Bass & Chagnaud 2012). Signalling in teleost fish is well studied in various behavioural contexts, including social interactions, territoriality and sexual selection (Almeida et al. 2005; Butler and Maruska 2016; Macario et al. 2017). The transfer of social and ecological information is known to be important for establishment of social hierarchies (e.g. Franz et al. 2015), social learning (e.g. Clarin et al. 2014), and leader-follower behaviour (e.g. Brent et al. 2015) in a range of species.

How animals produce, process and act on socially transmitted information is shaped by evolution (Endler et al. 1992, Römer et al. 2010) according to their morphology, the acuteness of their sensory functions and the environment they inhabit (Hauser 1997). Elasmobranchs have multiple acute senses (Hueter et al. 2004; Hart et al. 2006) that allow them to respond to a range of cues. For example, the lateral line mechanosensory system (Maruska 2001; Coombs et al. 2012) and olfactory senses (Meredith and Kajiura 2010; Yopak et al. 2012) are important in detecting and locating prey, but may also be involved in information transfer between individuals (e.g. pheromones may be used to advertise reproductive status) (Hueter et al. 2004; Pratt et al. 2005). Breaching or slapping of the water surface, observed in mobulid rays and some shark species (Klimley 1996; Sims et al. 2000; Sperone et al. 2010; Marshall and Bennett 2010; Curtis et al. 2011; Medeiros et al. 2015; Stevens 2016; Johnston et al. 2018) could be a form hydrodynamic signalling (Butler and Maruska 2016). Elasmobranchs are also sensitive to low-frequency sound and electrical cues (Hueter et al. 2004) but are unable to broadcast vocal or electrical signals. Their vision, however, appears to be important in communication at close quarters (Hart et al. 2006; Martin 2007). Elasmobranch visual systems are well-developed, with adaptations including mobile pupils that increase image resolution in bright environments, duplex retinas, and colour vision in batoid species (Hart et al. 2004; Van Eyk et al. 2011; Theiss et al. 2007; Lisney et al. 2012; Hart et al. 2020). Mobulid and other pelagic rays have larger eyes than their benthic relatives (Lisney and Collins 2007; Cunha et al. 2016) and manta rays can respond to visual cues at up to 30m distance (Ari and Correia 2008). Moreover, elasmobranchs use a range of visually received fin and whole-body movements and distinct postures as signals or cues during competitive and courtship interactions (Gordon 1993; Pratt and Carrier 2001; Martin 2007; Sperone et al. 2010; Findlay et al. 2016). These are also used during interactions with cleaner fish (Sazima and Moura 2000; Oliver et al. 2011), and in warning displays during encounters with humans (Johnson and Nelson 1973; Martin 2007). As a social species, reef manta rays may also communicate gesturally, potentially via movements including belly-flaring (Stewart et al. 2016) and head bobbing (RJYP and ADM, pers. obs.).

Paired cephalic lobes, hydrostatic organs with complex musculature (Mulvany and Motta 2013), positioned on the side of the head, are a distinct feature of the mobulid rays. These are specialized for feeding on zooplankton or small fishes (Notarbartolo Di Sciara 1987; McEachran et al. 1996) and functionally separated from the pectoral fins, that are used for swimming (Mulvany and Motta 2013; Fish et al 2018). Their evolution may have enabled some batoid rays, including mobulids, to switch to oscillatory swimming and a pelagic lifestyle (Mulvany and Motta 2013). While the fins of most pelagic elasmobranchs are immobile and inflexible, restricting their ability to make gestures (Barlow 1996; Hart et al. 2006), mobulid cephalic lobes are highly flexible. In reef manta rays they are large, reaching

11.13% of disc widths (Marshall et al. 2009). They can be moved independently of each other, and extended vertically and horizontally in various ways, including to a completely rolled position (Notarbartolo-di-Sciara and Hillyer 1989; Mulvany and Motta 2013) (see Figure 1). Due to the paired nature of these lobes, it is possible that right-left laterality influences their movement. Cerebral lateralization and behavioural laterality are known to occur in a range of fish species (Bisazza & Brown 2011), including manta rays which are known to have strong right-left laterality in mating behaviour (Marshall 2008).

Like other muscular hydrostatic organs, such as elephant trunks, cephalic lobes may have a variety of uses (Kier and Smith 1985). Chu and Wen (1979) described lateral line canals on the ventral sides of manta ray cephalic lobes that suggest they are used in detecting water movements or sensing prey during filter feeding. It is unlikely that cephalic lobes are used in sensing electrical signals, because they appear to lack Ampullae of Lorenzini (Mulvany and Motta 2013). As pelagic filter-feeders, mobulids probably do not require electrosensory pores to detect prey, since zooplankton form distinct visible patches and can also be detected by smell (Folt and Burns 1999). There is currently no evidence for gustatory receptors on cephalic lobes, but lobe movements may help to direct water flow to the nostrils, aiding olfaction. Tactile use of cephalic lobes has been recorded during courtship and other social interactions (Stevens 2016; RJYP pers. obs.) and free-ranging manta rays often open cephalic lobes when approaching cleaning stations, suggesting use in mechanosensation or signalling. In captive studies, manta rays have been observed to make unusual cephalic lobe movements in response to an underwater mirror (Ari and D'Agostino 2016), likely in attempts to interact socially with their reflection (Stewart et al. 2017), rather than as self-directed behaviour.

Due to their frequent social interactions, large brains and tolerance of human observers, manta rays are an excellent candidate species to investigate elasmobranch social behaviours in the wild. Here we made use of our well-established field site in Raja Ampat, West Papua, to study manta social interactions at cleaning stations. Observing the body positions and gestures they perform at these sites may help to understand if cephalic lobes are used in sensory reception or communication. Here we describe and quantify the movement and positioning of cephalic lobes in various contexts, but following Rendall et al. (2009), we do not imply any informational content or attempt to ascertain their meaning. Rather we segregate instances and non-instances of various swimming and cleaning behaviours, and social or inter-specific interactions, and compare cephalic lobes movements and positioning between these contexts. We hypothesized that differences in behavioural context (swimming/cleaning, conspecific interactions, interactions with cleaner fish/humans) might cause

manta rays to modify the frequency and duration of their cephalic lobe movements, as individuals would be more likely to benefit from gestural communication in these situations. We tested whether individuals of different sex, size, colour morph and maturity status differed in their cephalic lobe movements, and whether there was population- or individual-level laterality in the movement of the paired lobes. We hypothesized that phenotypic differences may occur due to variability in individual motivation to interact socially, and that laterality may influence lobe movements. We also considered the impact of several abiotic factors, including current strength, turbidity and site location. We hypothesized that these may affect cephalic lobe movements by direct mechanical forces acting on lobes or illustrate how lobes are used in non-social contexts.

4.3. Methods

4.3.1. Research location and environmental data

Behavioural observations were recorded in the Dampier Strait region of Raja Ampat, West Papua, between November 2014 and April 2018. Data were recorded during 36 SCUBA dives at two cleaning station sites, 'MS' and 'RSB' in the Dampier Strait region of Raja Ampat, West Papua (see Figure 4.1 for map of study area). Manta Sandy (MS) is an area of sandy substrate approximately 150m² and 10-16m depth, comprising two large 'bommies' (rocks covered in coral structures) approximately 9m apart, and multiple other small rocks with coral growth. Rob's Secret Bommie (RSB) was a similar habitat, being an area of sandy bottom of approximately 100m² at 16-20m depth, containing with one large and one smaller bommie approximately 12m apart, and several other small rocks with coral growth (see supplementary videos). Fish species observed to clean manta rays at these sites included *Labroides dimidiatus*, *Chaetodon kleinii* and *Thalassoma lunare*. MS was a popular dive site attracting large numbers of dive tourists daily, while RSB was rarely visited by divers other than the research team. Environmental variables recorded for each dive included time of day, weather, tidal phase, sea state, in-situ current strength and direction, in-situ water temperature and clarity, number of divers and number of manta rays in-water (see appendix for further details). These conditions varied significantly at various timescales but were not limiting factors in when we conducted dives. Weather was classified as 'sunny', 'cloudy', 'rainy', 'windy', or any combination of the above. Tidal phase was estimated from Admiralty predictions for Saonek, West Papua (Tideschart West Papua). Sea state was estimated according to the Douglas Sea Scale (Owens 1982). Current strength was estimated as follows; 'none': no water movement noticeable; 'slight': not difficult to swim against; 'moderate': difficult to swim against for extended periods; 'strong': impossible to swim against. Current direction

was estimated by reference to a compass underwater. Water clarity was estimated by the horizontal visibility of objects at known distances underwater.

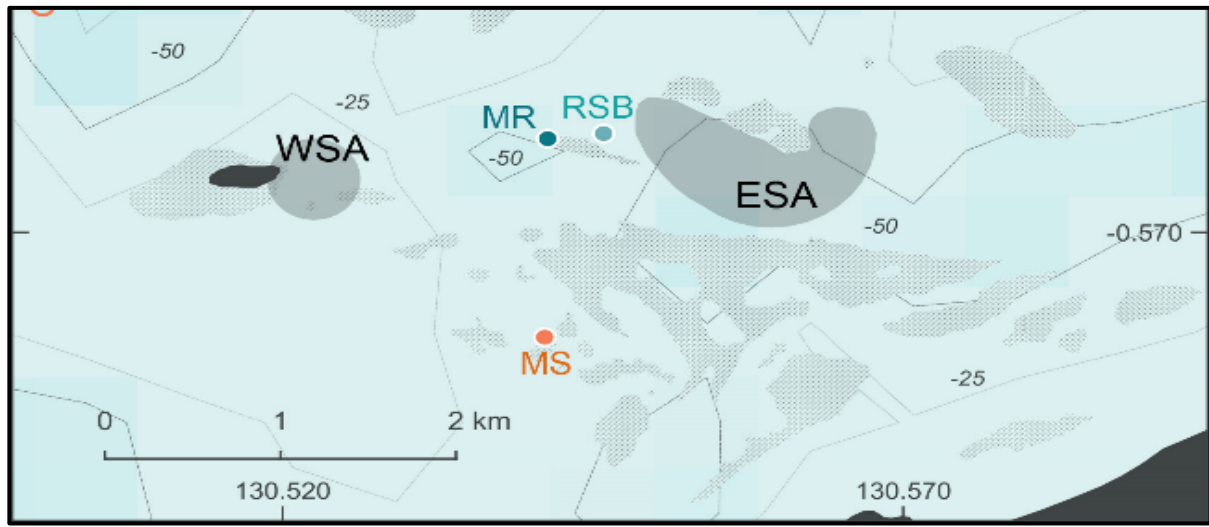


Figure 4.1. Map of manta ray aggregation sites in study area. Shows the two cleaning stations where all data were obtained: 'Manta Sandy' (MS); and 'Rob's Secret Bommie' (RSB).

4.3.2. Recording individuals and phenotypes

Individual reef manta rays were identified by photographs of their ventral surface, through their unique, lifelong spot patterns (Pierce et al. 2018), and photographic records of each encounter were stored in an online database (www.MantaMatcher.org). Phenotypic traits recorded for each focal individual included: sex, maturity, colour morph and estimated size (disc-width). Two distinct colour morphs were defined: 'normal' and 'melanistic' (see Venables et al. 2019). Rays were sexed by clasper presence/absence. Sexual maturity and activity were estimated using evidence from female pregnancies and mating scars, and male clasper size/calcification, as in Marshall and Bennett (2010). Disc-width (DW) was estimated visually in situ by comparing manta rays to coral bommies of known size. Female size-at-maturity in the population is estimated to be 3-3.5m DW (Perryman et al. 2019), similar to in Hawaii and Australia (Deakos et al. 2011, Couturier et al. 2014). Therefore, females with estimated DW ≥ 3.5 m were considered mature, and females with DW ≤ 3 m were considered immature. Any individuals between these sizes were recorded as 'unknown maturity'.

4.3.3. Design of observations

Continuous focal animal sampling (Altmann, 1974) was used to record single individuals' movements and social interactions (hereafter referred to as 'focal follows') during filmed encounters. Manta rays were filmed by a single observer using an underwater camera (GoPro Hero3 or Sony RX100 I).

Observers recorded video whilst kneeling or lying on the sand approximately 10m from the cleaning station (CS). Human observers did not approach manta rays closely, nor enter the main CS area. All manta-human interactions closer than 5m were initiated by manta rays. No video data were recorded during the first five minutes of dives in order to allow the manta rays to become accustomed to researcher presence. The first manta ray to arrive and enter the CS area after this time was chosen as the focal individual (i.e. rays already on the station were not chosen). Focal follows of individual mantas continued for as long as they remained at the CS, or until the observer was obliged to leave. If an individual moved out of clear view of the camera, the observer would try to reposition themselves, without moving close to the manta, to continue the focal follow. Five minutes after a focal individual had left the CS, the next individual to arrive became the new focal animal. Focal follow videos ranged in length from 6-32 minutes, but for data analysis, all videos were cut to exactly five minutes length.

4.3.4. Recording manta ray behaviours

We defined ethograms and calculated activity budgets using BORIS Version 7.4.11 (Friard and Gamba, 2016). A single researcher scored all video recordings. To check for any observer bias, a second researcher also analysed eight recordings, and only minor disagreements were found. General (non-cephalic lobe) behaviour, biotic stimuli, and cephalic lobe (CL) movements were recorded separately on different viewings of the same focal follow video. All behaviours were recorded as 'state events', with a 'start' and 'stop' time that allowed us to analyse their duration (see Table 4.1 for ethogram of all behaviours recorded, and see appendix table A4.2 for video examples of behaviour and cephalic lobe movements). Focal rays could be recorded performing more than one behaviour at once, though certain behaviours could not be recorded at the same time (see 'Excluded behaviours'). The number of manta rays present was recorded continuously throughout each focal follow.

General movement behaviours were divided into 'meander-cleaning' (e.g. videos 2-5), 'hover-cleaning' (e.g. videos 6-7) and 'travelling' (e.g. videos 8-9), and these were mutually exclusive. Cleaning was defined as when a manta swam through the cleaning station slowly, whilst being attended by cleaner fish. Meander-cleaning was recorded when manta moved around the reef during cleaning, while hover-cleaning was recorded if the manta ray remained in roughly the same position in the water column, often above a large coral bommie. 'Travelling' was defined as when a manta ray swam in the water column directly towards or away from a cleaning station, was not cleaning, and its movement was clearly in a single direction. Biotic stimuli, including social, cleaner fish and human interactions were also recorded and were not mutually exclusive from general movement behaviours.

Manta rays are known to regularly initiate close human encounters, and the presence of humans at cleaning stations is likely to affect their other behaviours. The number of humans present at a cleaning station throughout each dive was therefore recorded and CL movements were analysed in relation to this. 'Human interactions' were recorded when focal rays swam to within 5m of a human observer (e.g. videos 17-22). This proximity was chosen because it was noticed during preliminary observations that manta rays often modified their swimming or cephalic movements at this distance from an observer. Because all observations took place at cleaning stations, manta rays regularly interacted with cleaner fish, and their cephalic lobe movements may have been affected by this. A 'cleaner fish interaction' was recorded whenever an individual *C. kleinii*, *T. lunare* or *L. dimidiatus* approached within 1m of the focal ray's cephalic lobes (e.g. videos 4 and 7). Social interactions were recorded when two or more manta rays were within four body lengths' distance and made similar movements concurrently or with a slight time lag or appeared to respond to another individual's behaviour whilst in visual contact. These included 'leading'- where a focal individual swam in front of another individual/s (e.g. videos 9-11), 'following'- where a focal individual swam behind another individual/s (e.g. videos 12-13 and 24), and 'facing'- where a focal individual interacted socially with another individual/s, but was not 'following' or 'leading' (e.g. videos 14-16 and 26). The chosen proximity of four body lengths was based on observations of multiple interactions (RJYP pers. obs.) and the likely visual range of manta rays in clear waters, but it is important to note that rays were often within this proximity and not recorded as socially interacting (e.g. video 7).

Cephalic lobe movements/positions were recorded as 'uncurled', 'tip-curved', 'half-curved' or 'rolled-up' (see Table 4.1 and Figure 4.2), with each individual lobe scored separately and from the manta ray's perspective. Any lobe movements that did not fit here were categorized as 'other'. These included those that did not correspond with the listed positions, i.e. a very quick flicking motion, or a waving lateral motion. When the whole head and both CLs were movements vertically upward or downward, this was termed "bobbing". Manta rays were recorded as 'out of sight' (with no other data recorded), when they were briefly out of view of the camera, either from being too far away, obstructed from view, or when the videographer briefly pointed the camera elsewhere. When the CLs were out of sight and the focal individual still visible, "Cephalics OOS" was scored.

Type	Behavioural state (sub-categories)	Description	Excluded behaviours
General behaviour	Cleaning (Meandering) (Hovering)	In the vicinity of a cleaning station, attended to periodically by cleaner fish, not travelling. Swimming around or circling the cleaning station area Staying in the same position in the water column by gentle beats of pectoral fins	Travelling Hovering, Travelling Meandering, Travelling
General behaviour	Travelling	Moving directly towards, or away from, a cleaning station area, not cleaning.	Cleaning (meandering, hovering)
Biotic stimuli	Social interaction (Leading) (Following) (Facing)	Within four body lengths of another manta ray and performing the same type of movement in synchrony, or clear response to behaviour of another individual Swam in front of another ray/rays that copied the focal individuals' movements and swam with a similar trajectory Swam behind another ray/rays and copied its movements with a similar trajectory Any social interaction where not leading or following (e.g. swimming towards another individual head on, swimming alongside)	
Biotic stimuli	No. manta rays present	Count of the number of manta rays (other than the focal individual) present at the cleaning station at all times (not only during social interactions)	
Biotic stimuli	Cleaner fish interaction	Cleaner fish came within 1m of head of manta ray	
Biotic stimuli	Human Interaction	Manta ray approaches human to within 5m	
Cephalic lobe movement* *	Uncurled Tip curled Half-curved Rolled up Other	Lobe/s fully extended without any curling Lobe/s fully extended with just the terminal part curled Lobe/s rolled into a 'U' shape Lobe/s completely rolled up Any unusual movement or position lobe/s were held in	
Other behaviour	Courtship	Any of seven stages described in Stevens (2016)	Cleaning, Travelling, Human interaction
Other behaviour	Bobbing	Vertical movement of the whole head and both cephalic lobes	
Out of sight	Out of sight (OOS)	Whole manta ray out of sight	All behaviours
Out of sight	Cephalic lobes out of sight (CsOOS)	Cephalic lobes out of sight or hard to see due to poor water clarity	All cephalic lobe movements

Table 4.1. Ethogram of main whole-body movements and biotic stimuli recorded. Excluded behaviours could not occur at the same time as the given behaviour.

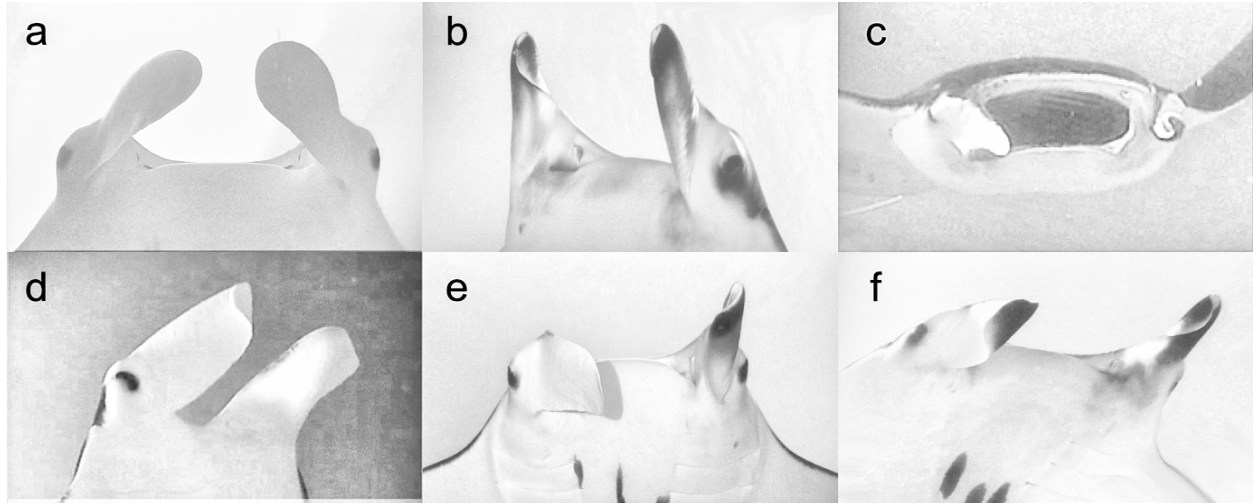


Figure 4.2. Cephalic lobe positions. a) both CLs uncurled; b) both CLs rolled up; c) left CL half-curved, right CL tip curled; d) left CL uncurled, right CL tip curled; e) left CL rolled up, right CL uncurled; f) left CL uncurled, right CL tip curled.

4.3.5. Data processing and analysis

We converted BORIS event ‘start’ and ‘stop’ times (rounded to the nearest second) for each category of behavioural state to a string of length 300s, describing changes from one second to the next, with strings for different behaviours corresponding in time to the others. Following Martin and Bateson (1986), we conducted separate analyses on the *frequency* of cephalic lobe (hereafter CL) movements and the *duration* of CL position holds. *Frequency* data were simple counts of CL movements. *Duration* data were proportional data indicating the number of seconds a focal ray held CLs in each of the recorded positions divided by the number of seconds it was recorded in each behavioural state. Because duration data were recorded at a continuous temporal scale, and their total components summed to 1, they required fitting to Beta or Dirichlet distributions (Hijazi and Jernigan 2009, Douma and Weedon 2019) to avoid inappropriate inference. Additionally, because zero and one values were present, and these may not be fit appropriately to Beta or Dirichlet distributions, we transformed proportions to non-integer values as follows: $p^* = \frac{p(n-1)+\frac{1}{C}}{n}$, where p is the proportion of a category, n the total number of observations in the dataset, and C the number of categories (Maier, 2014).

4.3.6. Effect of predictor variables on cephalic lobe movements

We modelled frequencies and durations of CL movements as a function of the various environmental, phenotypic and behavioural state covariates. To do this, we ran Poisson (*frequency* data) and Beta/Dirichlet (*duration* data) GLMMs using the ‘glmmTMB’ (Brooks et al. 2017) and ‘DirichReg’ (Maier, 2014) packages in R (R Core Team 2019). Our models accounted for non-independence of

observations due to simultaneous assessment of the effects of covariates on the relative contribution of multiple predictor variables to multiple response variables (Gueorguieva et al. 2008, Brooks et al. 2017). For environmental and phenotypic effects, we pooled all types of CL curl together (i.e. we considered all types of CL curl as equivalent) because here we were interested in whether lobe movements were modulated by factors unrelated to signalling or sensing (e.g. currents might cause involuntary CL movements). These initial models (Models 1 and 2, appendix) included all environmental and phenotypic variables as fixed covariates and were simplified by comparing all possible models using the `dropterm` function of the MASS package (Venables and Ripley 2002) (which maintains marginality between models) and retaining only significant covariates. Simplified model fits included ‘Number of manta rays’ (*frequency* data), ‘Current strength’, ‘Water clarity’ and ‘Site’ (*duration* data). To calculate the effect of general movement behaviour and biotic stimuli on CL movements, we modelled each type of CL curl separately as a function of each of the behavioural state variables using Poisson multinomial regression for frequency data (Model 3, appendix) and a Dirichlet regression for duration data (Model 4, appendix), including significant environmental and phenotypic predictors from previous analyses as fixed covariates. Dirichlet regression is a multivariate generalization of Beta regression to cases where proportional data are distributed over more than two categories (Camargo et al. 2012). In all models, ‘Lobe side’ was included as a fixed factor to investigate laterality, and ‘individual ID’ was included as a random grouping variable (to account for the dependency among observations of the same individual). We calculated the significance of random effects using likelihood ratio tests. For Poisson GLMMs, the log of ‘observation length’ was included as an offset term to account for differences in the amount of time focal rays were visible due to ‘out-of-sight’ time. For Beta and Dirichlet models this was not necessary because response variables were proportions of the length of observation intervals, however in Dirichlet models the precision was modelled as a function of observation length, according to Douma and Weedon (2019). Poisson GLMM outputs were deviation coded to compare the effects of different levels of each predictor variable to a grand mean over all levels. Estimated coefficients from Poisson models are reported on a multinomial log scale, and estimated coefficients from Dirichlet models are reported on a multinomial logit scale, with precision reported on a log scale. All models are described in full in the Appendix.

4.3.7. Markov chain transition analysis

To calculate the difference in probability of changing CL position or social behaviour according to different levels of behavioural state variables (see Table 4.1), we assumed that all behavioural data strings of 300s length were Markov sequences, where the probability of the n^{th} state is only dependent on the probability of the previous $n-1^{\text{th}}$. We applied Sandland’s (1976) method to determine

independence of two Markov chains, where one of these is considered to be a response and the other a covariate to that response. The method defines a combination of both chains, namely $Z(n)$, with f_{ij} as the count of the number of observations where $Z(n)$ goes from state i to state j in one step. We then compared this count value with our expected, estimated transition matrix p_{ij} . This comparison $\sum_i \sum_j (f_{ij} - f_i p_{ij})^2 / f_i p_{ij}$ is distributed asymptotically as a chi-square variate with $\sum_i (s_i - 1)$ degrees of freedom, where s_i is the number of j for which $p_{ij} > 0$ (Billingsley 1961). We used the *msm* package (Jackson 2011) in R, to first censor any state recorded as OOS (out of sight) and remove any missing data in the covariates. We then initialized a crude Q-matrix to state which transitions occurred and denoted any transitions that were not present as 0. We then used the *msm* function to estimate baseline transition intensities and the effect of covariates (baseline for comparison set to mean of covariates), separately for each behavioural state variable of interest. In some cases, there were computational issues resulting in non-convergence of models, probably due to the limited number of observations of particular transitions. For this reason, we only used data from the left CL side as a response, rather than the combined position of both lobes, and we were unable to consider the behavioural states ‘cleaner fish within 1m’, ‘human within 5m’ and ‘general movement behaviour’ as response variables.

4.4. Results

4.4.1. Basic behavioural data

Sample intervals were analysed from a total of 53 focal follow videos of 42 unique individual manta rays. From these, reef manta rays were visible for a total of 9604s (60.4% of total recorded time). A total of 9,860 behavioural events were recorded in these videos (mean 132 per focal follow). A total of 1157 cephalic lobe movement events were recorded (mean 21.8 per focal follow). The amount of time and % of total visible time focal rays spent in the different behavioural states was as follows: ‘meander-cleaning’ (7562s, 78.7%); ‘hover-cleaning’ (1109s, 11.5%); travelling (933s, 9.7%), social interactions (5104s, 53.1%), broken down as follows: ‘facing’ (2751s, 26.8%); ‘following’ (1647s, 17.1%); ‘leading’ (886s, 9.2%); interactions with humans within 5m (1615s, 16.8%); and interactions with cleaner fish within 1m (3382s, 35.2%). Cephalic lobes (CLs) were in visible positions for a total of 7499s (mean 141.49s, SD 46.48s per focal follow, 78.08% of total visible time). A total of 1157 CL movements (both lobe sides) were made (mean of one per 6.48s recorded time for both lobes), with a slightly higher number of movements made with the right CL. The five different types of lobe curl recorded varied substantially in frequency and duration (see Table 4.2). ‘Uncurled’ was the most

common, performed a total of 526 times (once per 14.26s), and held in this position for 68-70% of the time (mean over all individuals for both lobes), with mean durations of ~20s. ‘Tip-curled’ were almost as frequent (total 470 movements, one per 15.96s) but these were typically of short durations (mean ~6s). The ‘rolled-up’ type was performed much less frequently (total 67 movements, one per 111.93s), but lobes were usually held in this position for long durations (mean ~25s). ‘Half-curved’ and ‘other’ movement types were infrequent and brief.

	Uncurled		Tip-curled		Rolled up		Half-curved		Other		Total	
Lobe side	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
Total length of CL position holds (s)	5219	5094	1333	1466	815	840	96	55	36	44	7499	7499
Frequency of CL movements	253	273	228	242	33	34	28	24	23	19	565	592
Mean length of CL position holds (s)	20.6	18.7	5.9	6.1	24.7	24.7	3.4	2.3	1.6	2.3	13.3	12.7

Table 4.2. Frequency and duration of the main cephalic lobe movement types for all individuals and behavioural contexts.

4.4.2. Environmental and phenotypic effects on cephalic lobe movements

The movement of CLs was modified by several environmental and phenotypic variables. Lobes were moved more frequently when a larger number of manta rays were present at the dive site (estimate 0.051, SE 0.023, $p = 0.025$), and there were highly significant differences between individuals in frequency of lobe movements (groups 41, variance: 0.2, SD: 0.44, $p < 0.001$), but no other environmental or phenotypic variables had an effect on this. For duration data, lobes were held in curled positions for longer during running currents (estimates for current strength compared to base level ‘no current’: ‘slight’= 0.962, SE 0.28, $p < 0.001$; ‘moderate’= 1.049, SE 0.295, $p < 0.001$) (Figure 4.3a), and when water clarity was moderate (estimates for visibility compared to base level ‘5-10m’: ‘10-15m’= 0.911, SE 0.328, $p = 0.005$; ‘15-20m’= -0.018, SE 0.369, $p = 0.962$) (Figure 4.3b). Effects differed between the two cleaning station sites studied (estimate for ‘Site RSB’ compared to base level ‘Site MS’= 0.614, SE 0.235, z value 2.61, $p = 0.009$) (Figure 4.3a). Individuals varied strongly in the duration of their CL movements (variance: 0.389, SD: 0.624, $p < 0.001$). No other environmental or phenotypic variables had significant effects on CL movement durations (e.g. estimate for ‘males’ compared to base level ‘females’= -0.203, SE 0.328, $p = 0.536$), estimate for ‘mature individuals’ compared to base level ‘juveniles’= -0.077, SE 0.288, $p = 0.788$).

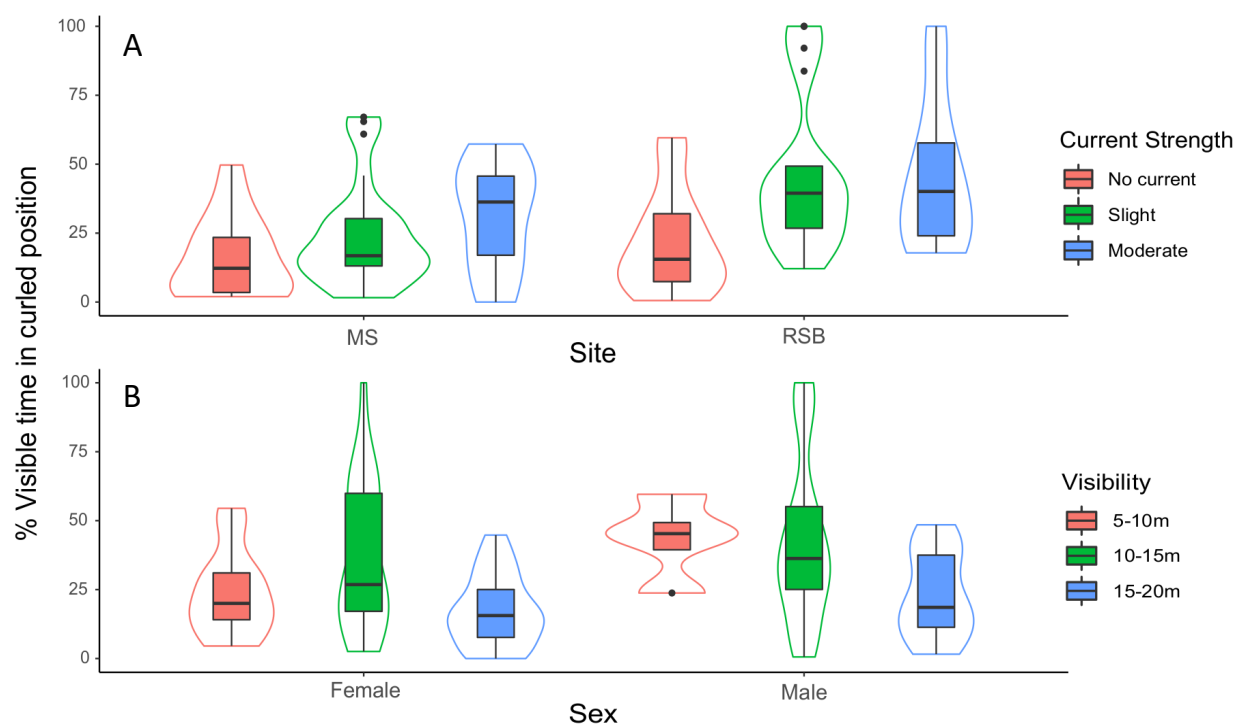


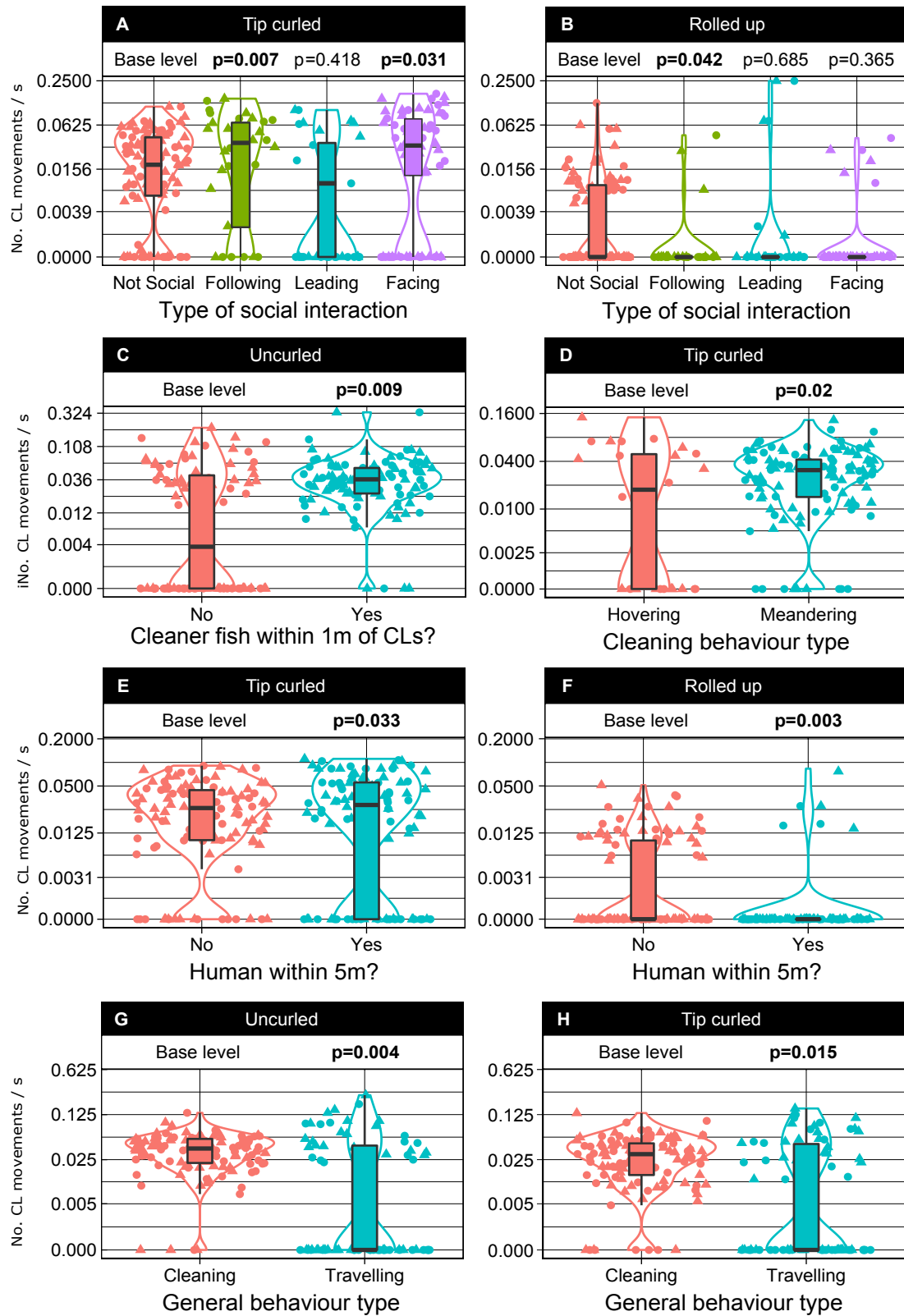
Figure 4.3. Environmental and phenotypic predictors of cephalic lobe curls. Percentage time manta rays spent with cephalic lobes curled (all curl types). Panel A shows the influence of current strength at each site. Panel B shows the influence of visibility (water clarity) on males and females. Box plots: thick black lines represent medians, boxes encompass the inter- quartile ranges, whiskers extend to the most extreme data points within 1.5× the interquartile range outside the box, dots show data points beyond the whiskers. Violin plots show probability density of data. Significant differences (indicated as * < 0.05 , ** < 0.01 , *** < 0.001) were as follows: Site- MS:RSB*; Current strength- no current: slight***, no current: moderate***, slight: moderate (no difference); Sex- female: male (no difference); Visibility- 5-10m:10-15m**, 5-10m:15-20m (no difference), 10-15m:15-20m (no difference).

4.4.3. Effect of behavioural context on cephalic lobe movements

The frequency of CL movements and duration of position holds varied considerably according to behavioural context (see Figure 4.4 for plots of significant effects, and Supplementary Table A4.1 for all results). During social interactions with conspecifics, manta rays curled lobe tips more frequently when following (estimate: 0.361, $p = 0.007$) and 'facing' (estimate: 0.285, $p = 0.031$) another individual, and held lobes in the tip curled position for longer when facing another (estimate: 0.315, $p = 0.039$) compared to non-social contexts. They also rolled lobes less frequently (estimate: -0.888, $p = 0.042$) and held lobes in the rolled position for less time (estimate: -0.466, $p = 0.038$) when following, but for more time when leading (estimate: 0.512, $p = 0.027$) compared to non-social contexts. The number of other individuals present during social interactions appeared to have little effect on lobe movements, however, and uncurling of CLs was not more or less frequent during social interactions compared to

when manta rays were not interacting socially. When cleaner fish were within 1m of their heads, manta rays uncurled CLs (estimate: 0.255, $p = 0.009$) and curled lobe tips (estimate: 0.316, $p = 0.053$) more often, and held lobes in the rolled position for less time (estimate: -0.393, $p = 0.016$) compared to the uncurled position. Focal rays also curled lobe tips more often (estimate: 0.282, $p = 0.033$) and rolled lobes less often (estimate: -0.805, $p = 0.003$) when within 5m of a human observer, but there was no effect of human presence on the length of time lobes were held in different positions.

Comparing general movement behaviours, manta rays uncurled CLs (0.511, $p = 0.004$) and curled lobe tips (estimate: 0.34, $p = 0.015$) more often when cleaning than when travelling. Lobe tips were also held in the tip curled position for longer (estimate: 0.147, $p = 0.041$) and in the rolled position for less time (-0.571, $p = 0.001$) when cleaning than travelling. Whilst cleaning, manta rays curled lobe tips more frequently (0.319, $p = 0.02$) and held lobes with tip curled for longer when swimming around the cleaning station ('meandering') (estimate: 0.664, $p = 0.003$) than when hovering. 'Half-curl' and 'other' types of cephalic movement were recorded infrequently compared other CL movements. We found no evidence that half-curls were modulated by any of the behavioural situations observed in this study, while 'other' curls were only modulated by the number of rays present at cleaning stations, being more frequent when two or more other individuals were present compared to when observed rays were alone (estimate: 0.781, $p = 0.045$). Individual ID was included in each model as a random effect and was highly significant (variance: 0.18-0.246, SD: 0.444-0.496, $p < 0.001$) in all cases, indicating that individual rays vary in their use of CLs. Lobe side ('right' or 'left') was non-significant in all cases suggesting a lack of laterality at the population level.



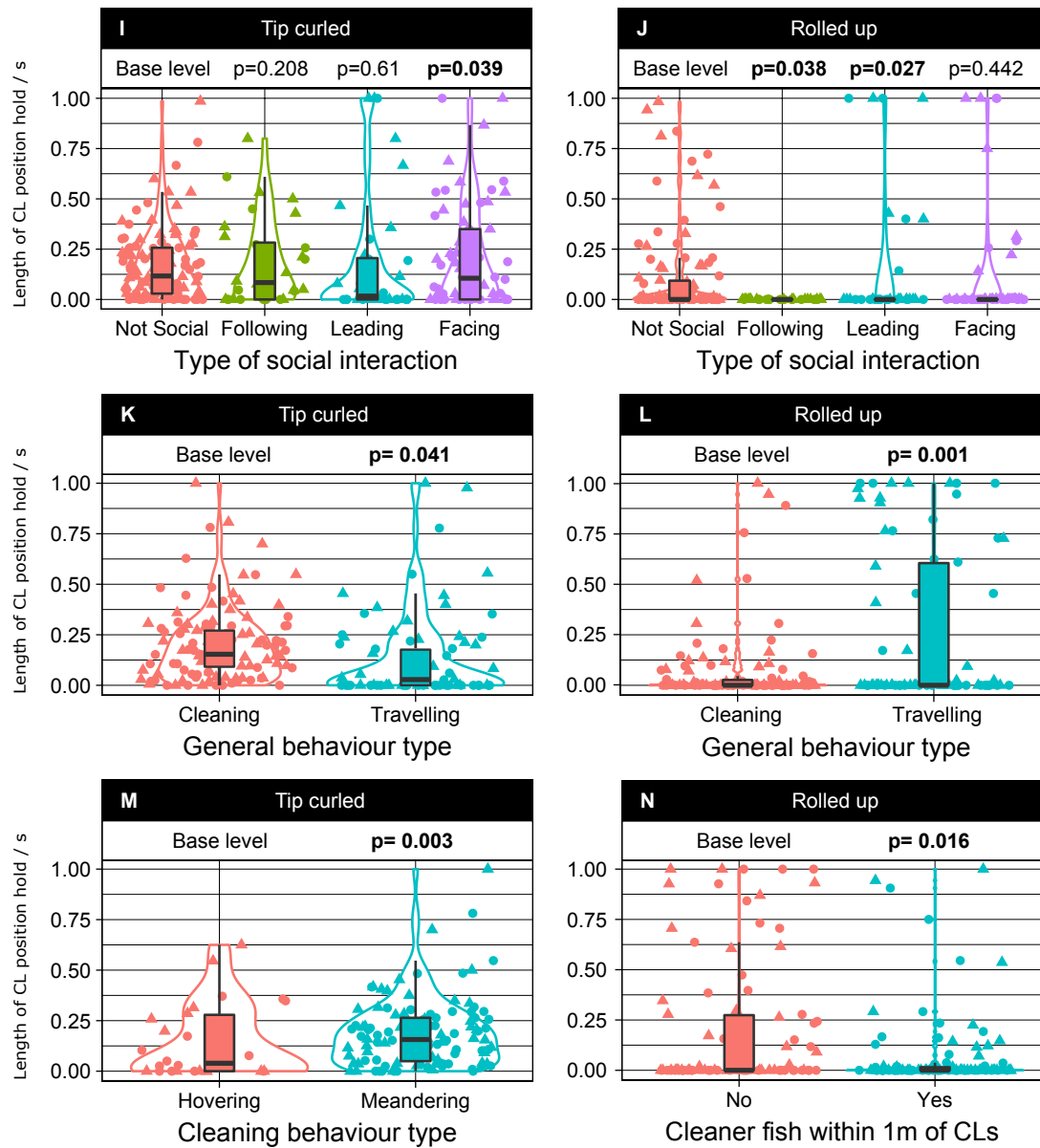


Figure 4.4. Frequency and duration of CL movements in relation to behaviour. Plots with significant effects for uncurled, tip curled and rolled positions included. For frequency data (panels A-H), the y axis shows the number of CL movements for each individual, divided by the amount of time lobes were visible during the given behavioural state. For duration data (panels I-N), the y axis shows the length of time in which lobes were held in each position divided by the amount of time that lobes were visible during the given behavioural state. 'Half-curved' and 'other' position types were not included due to insufficient data. For boxplots, thick black lines represent medians, boxes encompass interquartile ranges, whiskers extend to the most extreme data points within $1.5 \times$ the interquartile range outside the box. Violin plots show probability density of data. All data points shown, circles represent 'left' and triangles represent 'right' lobe sides.

4.4.4. Markov transition intensities

Markov transition intensities describing changes in social behaviour and cephalic lobe position are illustrated in Figure 4.5. For social interactions (Figure 4.5A), manta rays were more than six times (632%) as likely to transition from non-social behaviour to 'facing' social behaviour when travelling compared to 'hover-cleaning' (baseline transition probability (BTP) = 0.0048; 95% confidence level= 0.0034-0.0068; multiplier with covariate (xC) = 6.319, range= 1.38-28.93; significant at 95% confidence level), and around 70% less likely to transition from 'facing' to 'leading' when 'meander-cleaning' compared to 'hover-cleaning' (BTP= 0.0043; 95% confidence level= 0.0008-0.022; xC= 0.298, range= 0.094-0.946; significant at 95% confidence level). These results suggest that social behaviours were typically initiated by individuals arriving at cleaning stations, approaching rays that were already present. When cleaner fish were within 1m of their cephalic lobes, MRs were around 50% less likely to transition from non-social behaviour to 'facing' social behaviour (BTP= 0.0051; 95% confidence level= 0.0037-0.0071; xC= 0.506, range= 0.26-0.988; significant at 95% confidence level), around 83% less likely to transition from 'leading' social behaviour to non-social behaviour (BTP 0.0069; 95% confidence level= 0.0028-0.017; xC= 0.172, range= 0.094-0.946; significant at 95% confidence level), and around 50% less likely to transition from 'facing' social behaviour to non-social behaviour (BTP= 0.0126; xC= 0.493, range= 0.222-1.097; near-significant at 95% level). These results suggest that, when being attended to by cleaner fish, manta rays typically did not initiate or change their social behaviour. The sex of the focal manta ray, number of manta rays at the cleaning station, and whether or not human observers were within 5m all had no effect on change in the focal rays' social state (no significant difference in transition probabilities between any social state at the different levels of these covariates).

For cephalic lobe movement transitions (Figure 4.5B), MRs were around 65% less likely to curl the cephalic tip from an uncurled position when travelling compared to 'hover-cleaning' (BTP= 0.027; 95% confidence level= 0.022-0.032; xC= 0.351, range= 0.141-0.873; significant at 95% confidence level), around 42% less likely to uncurl the cephalic lobe from the tip-curved position when 'meander-cleaning' compared to 'hover-cleaning' (BTP= 0.121; 95% confidence level= 0.100-0.145; xC= 0.585, range= 0.35-0.976; significant at 95% confidence level), and around 59% less likely to do this when travelling compared to 'hover-cleaning' (BTP= 0.121; 95% confidence level= 0.100-0.145; xC= 0.414, range= 0.165-1.041; near-significant at 95% confidence level). They were around 81% less likely to curl cephalic tips from the 'rolled-up' position when 'meander-cleaning' (BTP= 0.023; 95% confidence level= 0.012-0.044; xC= 0.188, range= 0.038-0.91; significant at 95% confidence level), and around 90% less likely to do this when travelling (BTP= 0.023; 95% confidence level= 0.012-0.044; xC= 0.097,

range= 0.013-0.72; significant at 95% confidence level), compared to 'hover-cleaning'. Results suggest that tip curl-uncurl movements are made most frequently when manta rays are already cleaning, whilst lobes are kept in 'rolled-up' positions when travelling or moving around cleaning station sites. We found no effect of social behaviour type on the transition probabilities between the various cephalic lobe states. However, we were unable to test any transitions from, or to, the 'rolled-up' cephalic lobe state, because manta rays never rolled up lobes when following other individuals so we could not calculate baseline probabilities.

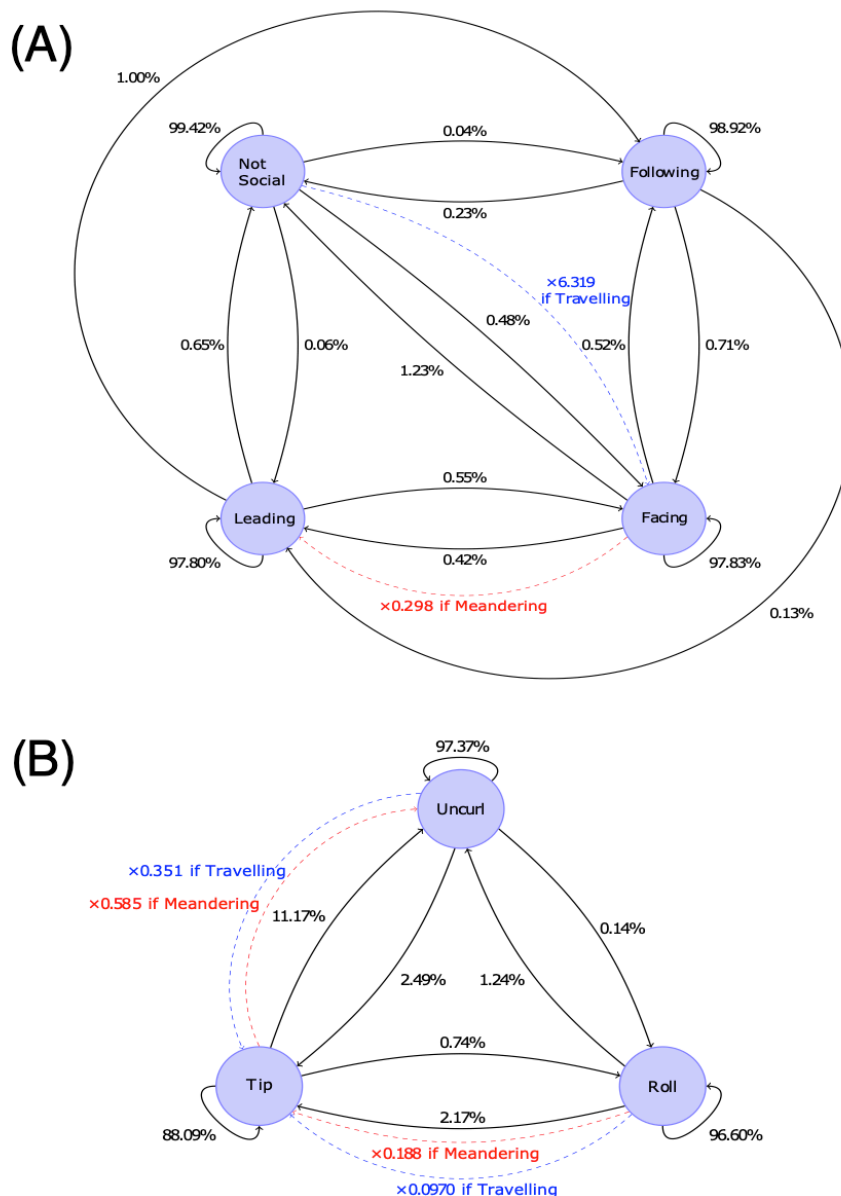


Figure 4.5. Transition flow diagrams of behavioural state switching. Showing (A) probability of changing social behaviour type per second and (B) probability of changing cephalic lobe position per second, during baseline general behaviour 'Hovering', with significant differences to 'Meandering' and 'Travelling' indicated.

4.5. Discussion

Signalling and sensory reception of cues may facilitate inter-specific and intra-specific interactions, including social behaviours, that are increasingly reported in elasmobranchs. This study investigated the movement and positioning of cephalic lobes (CLs) by reef manta rays at cleaning stations in Raja Ampat, Indonesia. We described and quantified the various types of CL movements made and compared the behavioural and environmental contexts in which they occurred. Overall, we recorded a high level of flexibility in the movement of CLs in different situations. This is likely to reflect that these lobes have a variety of uses and versatility in function. Muscular-hydrostatic mechanisms of support (Kier & Smith 1985) enable a remarkable diversity and complexity of movement in a range of species that possess such organs (e.g. Witmer et al. 1999; Gilbert et al. 2007; Kier & Stella 2007). These organs allow intricacy of deformation and fine movement precision (see Kier 2012 for review), which may be useful in gestural communication, sensing of water movements or other sensory functions in manta rays. If cephalic lobes are used in a variety of ways, then these are likely to overlap (e.g. feeding rays may also interact socially and communicate), making interpretation of behavioural data in an uncontrolled wild environment difficult. However, the fine temporal detail and precise nature of our recordings allowed us to record a number of interesting results and suggest possible uses according to behavioural context. Our results show that the various lobe movement types were observed at different rates, and for different durations depending on social context (i.e. the focal individual's physical position during social interactions), and the presence of cleaner fish or humans. We therefore suggest that manta rays modulated their CL movements according to behavioural context, and that CLs may be used in gestural communication and/or sensory reception. CLs were typically held in rolled positions when travelling, whereas uncurling of lobes and tip curls occurred more often during cleaning, particularly when rays were moving around the cleaning station area.

Environmental conditions affected CL movements, with curled lobe positions being held for longer during stronger currents and in more turbid waters. These results suggest streamlining was an important factor influencing cephalic lobe positioning, and also that signalling and sensory reception may have been reduced during these conditions. Closing of the large terminal mouth and rolling of lobes is known to occur during 'cruising' behaviour (Jaine et al. 2012). There were no broad demographic influences of sex, maturity or body size on CL movements, but there was significant variation between individuals. CLs were usually moved independently and the lobe closest to a potential subject/stimulus appeared to be moved more often, though we were not able to confirm this quantitatively due to difficulty in ascertaining the exact position of subject/s in relation to CL

positioning. A caveat to our results is that some of the environmental variates that we recorded may have been correlated (e.g. current strength/turbidity) and this may have led to bias due to multicollinearity, so further studies incorporating more robust methods of environmental data collection and design of observations under blocked or crossed environmental conditions are advised. Though reef manta rays have been shown to exhibit strong lateralized mating behaviour (Marshall and Bennett 2010), we found no evidence for population-level laterality in the use of CLs. Regarding the nature of social interactions, Markov analyses showed that focal rays did not typically change their social behaviour type during the length of focal follow that we recorded. Our analyses did suggest that social behaviours were often initiated as manta rays approached cleaning stations (focal rays were much more likely to transition from non-social to 'facing' social behaviour when travelling), and that cleaning and social behaviours occurred simultaneously. However, we found that when being actively cleaned, rays were unlikely to transition to social behaviour, so likely prioritise being cleaned in this situation.

Partial curling of the CL tip appeared to be particularly affected by the context of social or intraspecific interaction. 'Tip curls' were more common when 'following' behind and 'facing' another ray, less common when 'leading' others, and were generally increased when more manta rays were present at cleaning stations- suggesting a role in social sensory reception and/or gestural signalling. On some occasions, cephalic movements were slow and constituted a change in overall lobe position (e.g. videos 1-3, 10-13, 15, 17, 19, 21, 26), which could be indicative of a role in sensory reception. Markov transition and frequency-based analyses suggested that tip-curl and lobe uncurl positions were particularly influenced by the presence of cleaner fish close to CLs. The use of mechanoreception is used by many fish species to sense the movement and proximity of schoolmates, and as mechanosensory receptors extend onto the ventral surface of cephalic lobes of mobulid rays (Chu and Wen 1979), these lobes could play an important role in detecting fine-scale water movements. Deliberate, gradual movement and positioning of cephalic lobes could increase the ability of rays to sense fine water movements or vibrations produced by cleaner fish or conspecifics, by altering pressure gradients on either side of these thin organs. Variable CL movement and positioning could also facilitate olfactory sensing, for example uncurling of cephalic lobes is likely to increase water flow towards the nostrils and may expose the olfactory bulbs for use in chemoreception. However, cephalic tip movements were also often rapid, and repeated several times in quick succession when interacting closely with con- or hetero-specifics (e.g. videos 6, 7, 13, 14). Though we were not able to empirically test the function of this, or any other type of lobe movement, we tentatively suggest that such movements could point to a role in attracting the attention of other animals and eliciting a behavioural

response. For example, tip curls could alert other individuals to the presence, identity or motivation of the focal individual, or encourage following by conspecifics, a behaviour that is known to be common in this species and other elasmobranchs.

For gestural signalling using CLs to occur between manta rays, our research shows that a receiver would need to be able to visually resolve movement of a signaller's lobes at distances of 5-15m (typical interaction distance at cleaning stations- RJYP pers. obs.). This seems likely, considering our current knowledge of vision in large pelagic rays (Hart et al. 2006; Cunha et al. 2016; Lisney and Collins 2007; Ari and Correia 2008), and because our observations took place in bright and clear waters with good horizontal visibility (typically 10-25m). The contrasting dark and light coloration on mobulid CLs (Notarbartolo-di-Sciara 1987) may provide a visual reference aiding gestural signalling. In support of the social communication hypothesis, lobe curls were often associated with exaggerated whole-body movements, including short bursts of acceleration, belly-flaring and head bobbing, especially when manta rays were interacting closely with other rays or humans (e.g. videos 14, 19, 22, 23).

If manta rays use gestural signals, these may have become "ritualized" (Tinbergen 1952) via a co-evolutionary route from behavioural cues that were originally non-communicative but informative aspects of the signaller (Lorenz 1966; Dawkins and Krebs 1978; Laidre and Johnstone 2013). It is possible, therefore, that the flexibility and range of CL movements, as described in this study, may have enabled co-option in their use from prey manipulation to a role in signalling or sensory reception, or from gestural movements directed at cleaner fish (widespread among elasmobranchs) to socially communicative gestures between rays. Likewise, rolling of CLs could be an informative cue that became used as a signal. During cruising or travelling behaviours, rolled positions are most likely adopted for streamlining (Notarbartolo-di-Sciara et al. 1987; McEachran et al. 1996) and these could potentially be used by other manta rays as an indication of an individual's intention to move away from a cleaning station. Rolling of lobes was increased when focal individuals led social trains, suggesting that this may elicit following behaviour. Gestural signalling among manta rays might enable assortative grouping by phenotype (Perryman et al. 2019), formation of 'courtship trains' (Stevens 2016) or the occurrence of collective behaviours (RJYP in prep.), in conjunction with other potentially communicative behaviours such as fin-slapping or breaching (which may be used to attract mates, or indicate food availability) (Marshall et al. 2009; Stevens 2016; Perryman et al. 2019). In Raja Ampat, *M. alfredi* typically feed in groups of 5-20 individuals on zooplankton, a locally abundant but ephemerally distributed food source (Andersen et al. 1993). Sharing of information on foraging patch location and quality may occur in manta rays (Stevens 2016), and gestural communication at cleaning

stations, which appear to be used as ‘gathering points’ for socially familiar individuals (Perryman et al. 2019) might facilitate this. Manta rays appear to be inquisitive animals, and during this study we found that some individuals regularly approached divers, with tip-curls more frequent and rolling of CLs less frequent during these close human encounters. These differences in CL movements could indicate interest in or signalling directed at humans, sensory inspection, or could be involuntary movements, perhaps caused by heightened stress or excitement during encounters with humans. Tip-curl movements were recorded at similar average frequencies during conspecific interactions and manta ray-human interactions, suggesting that they had similar function in both of these situations. A caveat here is that while we were able to precisely record CL movements, it was more difficult to precisely define the start and end points of some general movement or social behaviours. Interactions with humans were usually easier to delimit temporally than social interactions, that often occurred whilst manta rays engaged in other behaviours (e.g. cleaning). Therefore, our records of CL movements during different behavioural contexts may not be directly comparable. We also recorded differences in cephalic movements between study sites. As one of the most obvious differences between the study sites was the visitation rate by dive tourists (boats and divers), that could indicate different levels of habituation to human presence, which may affect natural social behaviour.

There were several other limitations to our study that may be addressed by future research on manta ray social and inter-species interactions. We did not investigate behavioural responses to potential signalling, or fitness consequences of CL movements, so we cannot confirm that gestural communication occurs. We were limited by observing manta rays for short periods and relying on individual focal follows. This was largely due to the mobile nature of manta rays and the difficulty in following their movements in the marine environment, which made the simultaneous recording of multiple individuals difficult. Further research is therefore required to demonstrate receiver responses to gestural signals and provide insight into the ecological functions of sharing information. This may be facilitated by advances in mini-ROV technology (e.g. Raoult et al. 2020), remote or animal-borne cameras (e.g. Stewart et al. 2016), and 360° camera traps (e.g. Campbell et al. 2018), or multi-camera rigs, which would allow simultaneous recording of fine-scale behavioural data on multiple individuals. Extension of the Markov chain analysis presented here could allow more detailed analysis of social and communication dynamics within social networks. Further studies on social behaviour and communication in manta rays will likely improve our understanding in several areas (e.g. feeding and reproductive ecology, movements, impact of dive-tourism) of relevance to elasmobranch conservation.

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4.7. Appendix

4.7.1. Models for data analysis

Model 1:

$$\begin{aligned} Nmoves_{ij} &\sim \text{Poisson}(\mu_{ij}) \\ E(Nmoves_{ij}) &= \mu_{ij} \\ \log(\mu_{ij}) &= NMantaRays + ID_i + LobeSide_j + \text{offset}(\log(ObsLength))_{ij} \\ ID_i &\sim N(0, \sigma^2_{ID}) \end{aligned}$$

(Poisson regression with log link function, where $Nmoves_{ij}$ = number of CL movements by individual i on lobe side j , $\text{offset}(\log(ObsLength))_{ij}$ = an offset term to account for the variation in observation lengths)

Model 2:

$$\begin{aligned} Ppos_{ij} &\sim \text{Beta}(\pi_{ij}) \\ E(Ppos_{ij}) &= \pi_{ij} \\ (\pi_{ij}) &= Site_{ij} + CurrentStrength_{ij} + WaterClarity_{ij} + ID_i + LobeSide_j \\ ID_i &\sim N(0, \sigma^2_{ID}) \end{aligned}$$

(Beta regression with logit link function, where $Ppos_{ij}$ = proportion of time spent with cephalic lobes curled/uncurled by individual i on lobe side j)

Model 3:

$$\begin{aligned} Ncurls_{ijk} &\sim \text{Poisson}(\mu_{ijk}) \\ E(Nmoves_{ijk}) &= \mu_{ijk} \\ \log(\mu_{ijk}) &= ID_i + State_j + LobeSide_{ij} + \text{offset}(\log \log(ObsLength))_{ij} + NMantaRays_{ijk} \\ ID_i &\sim N(0, \sigma^2_{ID}) \end{aligned}$$

where $Ncurls_{ijk}$ = number of CL movements of type k by individual i (included as random effect) during behavioural state level j (models run separately for each behavioural state), for CL movement types k ($Nmoves_{ij1}, \dots, Nmoves_{ij5}$), and $ObsLength$ = the length of time spent in each behavioural state.

Model 4:

$$\begin{aligned}
 p_{ijk} &\sim \text{Dirichlet}(\alpha_{ijk}) \\
 (\alpha_{ijk}) &= \beta_{ijk} + State_j + LobeSide_{ij} + Site_{ijk} + CurrentStrength_{ijk} + WaterClarity_{ijk} \\
 &\quad + \phi(ObsLength_{ijk}) \\
 \beta_{ijk} &\sim \text{Normal}(\mu_{\beta(jk)}, \sigma^2_i)
 \end{aligned}$$

where the observed vector of the proportions $p_{ijk} = p_{ij1}, \dots, p_{ij5}$, was fit for each CL movement type k during behavioural state level j (models run separately for each behavioural state). β_{ijk} specifies inclusion of individual i as a random grouping variable, with precision modelled as a function of observation length, using the “alternative” parametrization of Douma and Weedon (2019).

	Frequency of CL movements (GLMM, compared to Grand mean of all positions)					Duration of CL movements (Dirichlet regression), “alternative” parametrization (base=Uncurl)				
	Lobe Position (frequency data)					Lobe Position (duration data)				
Behavioural context	Uncurl	Tip	Roll	Half	Other	Uncurl	Tip	Roll	Half	Other
SocialType Intercept (Follow:NotSocial)	1.379	1.272	-0.556	-0.882	-1.213	1.888	-1.069	-1.668	-1.864	-1.91
2.5% CI	-0.27	-0.012	-1.853	-0.62	-0.304	-0.352	-0.739	-0.908	-0.595	-0.564
Estimate	0.139	0.361	-0.888	0.131	0.462	0.255	-0.289	-0.466	-0.152	-0.122
97.5% CI	0.548	0.689	0.078	0.882	1.229	0.762	0.161	0.024	0.29	0.32
P value	0.506	0.007*	0.042*	0.733	0.237	0.091	0.208	0.038*	0.5	0.59
SocialType (Lead:NotSocial)										
2.5% CI	-0.478	-0.862	-0.727	-1.375	-1.053	-0.569	-0.551	-0.314	-0.373	-0.299
Estimate	0.087	-0.252	0.19	-0.178	0.153	-0.134	-0.114	0.512	0.057	0.132
97.5% CI	0.652	0.358	1.106	1.019	1.36	0.3	0.323	0.954	0.488	0.563
P value	0.763	0.418	0.685	0.771	0.803	0.544	0.61	0.027*	0.794	0.548
SocialType (Facing:NotSocial)										
2.5% CI	-0.2	-0.071	-0.896	-1.084	-0.271	-0.379	-0.159	-0.487	-0.392	-0.347
Estimate	0.127	0.285	-0.283	-0.363	0.373	-0.021	0.315	-0.137	-0.044	0
97.5% CI	0.455	0.721	0.329	0.357	1.017	0.338	0.748	0.212	0.304	0.348
P value	0.445	0.031*	0.365	0.323	0.256	0.91	0.039*	0.442	0.806	0.999
Howmany Intercept (Alone: 1 other)	1.418	1.313	-0.69	-0.863	-1.178	1.704	-0.621	-1.421	-1.608	-1.678
2.5% CI	-0.344	-0.405	-0.24	-0.624	-0.525	-0.231	-0.323	-0.178	-0.222	-0.17
Estimate	-0.072	-0.126	0.221	-0.086	0.062	-0.072	0.004	0.135	0.102	0.145
97.5% CI	0.201	0.153	0.681	0.452	0.65	0.192	0.267	0.301	0.418	0.479
P value	0.607	0.376	0.348	0.755	0.835	0.621	0.578	0.421	0.672	0.61
Howmany (Alone: ≥2 others)										
2.5% CI	-0.221	-0.155	-2.133	-1.382	0.016	-0.442	-0.629	0.078	-0.411	-0.177
Estimate	0.247	0.314	-0.96	-0.381	0.781	-0.161	-0.318	0.371	-0.116	0.215
97.5% CI	0.714	0.784	0.212	0.619	1.545	0.108	-0.016	0.581	0.125	0.532
P value	0.301	0.19	0.108	0.455	0.045*	0.392	0.128	0.218	0.351	0.417
Howmany (1 other: ≥2 others)										
2.5% CI	-0.183	-0.066	-2.387	-1.362	-0.136	-0.19	-0.337	0.412	-0.237	-0.182
Estimate	0.318	0.44	-1.181	-0.296	0.718	0.104	-0.091	0.789	0.172	0.235
97.5% CI	0.819	0.946	0.025	0.77	1.573	0.307	0.077	1.141	0.351	0.481
P value	0.214	0.088	0.055	0.587	0.099	0.421	0.162	0.083*	0.615	0.521
Fish:NoFish										
Intercept	1.228	1.228	0.081	-1.269	-1.269	1.796	-1.184	-1.387	-1.809	-1.81
2.5% CI	-0.057	-0.096	-0.509	-0.23	-0.429	-0.252	-0.129	-0.714	-0.358	-0.385
Estimate	0.255	0.316	0.052	0.436	0.245	0.069	0.193	-0.393	-0.041	-0.068
97.5% CI	0.567	0.631	0.597	1.102	0.92	0.39	0.515	-0.073	0.277	0.25
P value	0.009*	0.053	0.301	0.2	0.476	0.672	0.239	0.016*	0.801	0.677
Human:NoHuman										
Intercept	1.419	1.221	-0.49	-0.931	-1.218	2.048	-1.092	-1.909	-2.022	-2.026
2.5% CI	-0.219	0.023	-1.349	-0.426	-0.095	-0.356	-0.271	-0.385	-0.262	-0.25
Estimate	0.038	0.282	-0.805	0.07	0.415	-0.047	0.031	-0.081	0.04	0.052
97.5% CI	0.295	0.54	-0.26	0.567	0.925	0.262	0.332	0.222	0.343	0.354
P value	0.772	0.033*	0.003**	0.781	0.111	0.767	0.84	0.599	0.793	0.737
Travel:Clean										
Intercept	1.475	1.341	-0.921	-0.856	-1.039	1.719	-0.836	-1.606	-1.706	-1.734
2.5% CI	-1.073	-0.961	0.335	-1.19	-1.015	-0.538	-0.499	0.22	-0.175	-0.157
Estimate	-0.511	-0.34	0.126	-0.42	-0.238	-0.189	-0.147	0.571	0.172	0.189
97.5% CI	0.083	0.11	0.277	0.35	0.539	0.161	0.204	0.921	0.518	0.535
P value	0.004*	0.015*	0.523	0.285	0.548	0.29	0.041*	0.001**	0.331	0.285

Hover:Meander										
Intercept	1.545	1.421	-0.352	-1.163	-1.451	2.469	-1.842	-2.273	-2.461	-2.493
2.5% CI	-0.341	-0.731	-0.005	-1.217	-1.441	-0.61	-1.11	-0.542	-0.609	-0.608
Estimate	0.07	-0.319	0.662	-0.349	-0.464	-0.156	-0.664	-0.091	-0.157	-0.157
97.5% CI	0.48	0.077	1.329	0.519	0.514	0.298	-0.221	0.359	0.294	0.294
P value	0.739	0.02*	0.052	0.43	0.352	0.5	0.003**	0.691	0.494	0.495

Table A4.1. Estimates from Poisson and Dirichlet regression models. Showing differences in cephalic lobe movements according to behavioural context. All significant effects indicated in greyed out boxes. All models with same heading (SocialType, Howmany, Fish:NoFish, Human:NoHuman, Travel:Clean, Hover:Meander) were run separately.

Video # Date Location	Behavioural context*	Cephalic Lobe (CL) movements* (side, type, transitions)	Description
Video 1. 20150304 RSB	Travelling	Left: Roll up > Uncurl Right: Roll up > Uncurl	The focal manta ray (typical morph female) swims towards the cleaning station and uncurls both cephalic lobes at the same time when it is approximately 10m away from the main coral bommie.
Video 2. 20150304 RSB	Meander-cleaning, human interaction, social interaction (leading, following)	Manta 1. Left: Uncurl Right: Tip curl Manta 2. Left: Uncurl Right: Tip curl > Uncurl	Two manta rays (both typical morph females) swim past small coral structures in front of the observer. Both hold the right cephalic lobe (which is closest to the observer) with the tip curled whilst doing this and uncurl the lobe again whilst swimming towards the main coral bommie.
Video 3. 20141231 RSB	Meandering, interaction with cleaner fish, interaction with human	Left: Uncurl > Tip curl > Half-curl Right: Uncurl	The focal manta ray (melanistic morph male) is hover-cleaning, then meander-cleaning, very close to the videographer. As the manta turns a Klein's butterflyfish (cleaner fish) swims in front of the rays' head, and the ray curls it's left CL tip and then holds it in the half-curved position.
Video 4. 20150126 RSB	Meander-cleaning, cleaner fish interaction	Left: Tip curl > Other > Tip curl Right: Tip curl	Focal manta ray (typical morph female) is hover-cleaning with several cleaner fish attending it. Both CL tips are curled. As a fish swims close to the left CL, the manta flicks this lobe towards it, whilst keeping it in the tip-curved position.
Video 5. 20150103 RSB	Meander-cleaning, human interaction	Left: Uncurl Right: Uncurl	Example of 'meander-cleaning' behaviour. The focal manta ray (melanistic morph female) swims in circles around cleaning station. The cephalic lobes are uncured and are not moved from this position.
Video 6. 20150108 RSB	Hover-cleaning	Left: Uncurl > Tip curl > Uncurl > Tip curl Right: Uncurl	Example of 'hover-cleaning' behaviour. The focal manta ray (melanistic morph male) uses strong current to hover directly above coral bommie of cleaning station. Several movements of left CL to/from uncured position to/from tip curled position.
Video 7. 20150223 MS	Hover-cleaning, cleaner fish interaction	Left: Uncurl > Tip curl > Uncurl > Tip curl > Uncurl > Tip curl Right: Uncurl	The focal individual (melanistic morph male) makes many rapid curls of both CLs (mostly tip curls) whilst hover-cleaning. Two other individuals are at the cleaning station, but the focal individual does not appear to interact with them.

		Right: Uncurl > Half-curl > Uncurl > Tip curl > Uncurl > Tip curl > Uncurl > Tip curl > Uncurl > Tip curl	
Video 8. 20150114 MS	Travelling, human interaction	Left: Roll up Right: Roll up	Example of travelling behaviour. The focal manta ray (typical morph female) swims away from cleaning station, over several divers. Both cephalic lobes are held in the rolled-up position.
Video 9. 20150227 MS	Social interaction (leading), travelling	Left: Uncurl > Roll up Right: Uncurl > Tip curl > Roll up	The focal manta ray (typical morph female) briefly leads another individual (typical morph female), but then rolls up both CLs before leaving the cleaning station area. The right CL is held for a short time in the tip curled position. The other individual stays at the cleaning station.
Video 10. 20150223 RSB	Social interaction (leading), human interaction	Left: Roll up > Uncurl Right: Roll up	The focal manta ray (typical morph female) leads chain of 2 males (one melanistic, one typical morph), with both CLs in rolled position. As the focal ray passes by the observer, she opens the left CL (closest to observer) and holds it in this position.
Video 11. 20150227 MS	Social interaction (leading), meander-cleaning	Left: Uncurl Right: Tip curl > Roll up	Focal manta ray (typical morph female) leads another female whilst meander-cleaning, rolling the left CL as it swims, with the right CL remaining uncurled.
Video 12. 20150304 RSB	Social interaction (following), meander-cleaning	Left: Uncurl > tip curl Right: Uncurl	Focal manta ray (melanistic morph male) male manta ray follows a typical morph female whilst meander-cleaning. The focal individual places its left CL close to the typical morph's pelvic area, curling the tip of the lobe as it does this. Possible sensory inspection.
Video 13. 20150109 RSB	Meander- cleaning, social interaction (following)	Left: Uncurl > Half-curl > Uncurl > Tip curl Right: Tip curl > Uncurl	Focal individual (typical morph male) is hover-cleaning and curls the left CL twice (half-curl and tip curl) as he begins to follow the leading ray. The Right CL tip is uncurled from the tip curled position before leaving the cleaning station. The leading individual also curls its left CL tip just before being followed.
Video 14. 20150127 RSB	Social interaction (facing), Meander-cleaning	Left: Uncurl > Tip curl > Uncurl > Half-curl > Uncurl > Tip curl > Uncurl > Tip curl > Uncurl Right: Tip curl > Uncurl	Focal manta ray (typical morph male) approaches the cleaning station from right of frame, whilst another individual (unknown sex) approaches behind the cleaning station from the left side of frame. Focal individual makes successive rapid curls of left CL tip while in visual range of the other individual, and changes position in water column to swim over the other individual.
Video 15. 20150129 RSB	Social interaction (facing), meander-cleaning	Left: Uncurl Right: Uncurl > Tip curl > Uncurl	Focal individual (typical morph female in center of frame), meander-cleans close to the cleaning station coral bommie. As another individual (typical morph male to bottom left of frame) approaches the bommie, the focal individual curls the right CL tip and holds in this position for several seconds, until

			the male passes by. The focal individual then uncurls this lobe again.
Video 16. 20150302 MS	Social Interaction (facing), meander-cleaning	Manta ray 2. Left: Uncurl Right: Uncurl > Tip curl > Uncurl Manta ray 2: Left: Uncurl > Tip curl Right: Uncurl	Three mantas are on the cleaning station in a train with cephalic lobes uncured, whilst a human is also in the middle of the cleaning station area. Manta 1 (typical morph male) is on the left side of the frame, facing manta 2 (typical morph female) on the right side of the frame, both are behind another typical morph female (center). The two rays closest to the observer both curl the tip of the CL that is closest to one another; for manta 1 this is the right CL and for manta 2 this is the left CL.
Video 17. 20150306 RSB	Human interaction	Left: Roll up > Uncurl Right: Roll up > Half-curl > Roll up	The focal manta ray (typical morph male) approaches human observer whilst swimming away from the cleaning station, with both CLs rolled up. As it approaches to within approx. 5-10m of the observer, it first uncurls its left CL and then partially uncurls the right CL as it passes the observer, before rolling the right CL up again.
Video 18. 20150123 RSB	Human interaction, travelling	Left: Uncurl > Tip curl > Uncurl Right: Uncurl > Tip curl > Uncurled	The focal manta ray (melanistic morph female) passes very close to observer, and briefly curls the left CL tip, and then the right CL tip straight afterwards, as it passes the camera. Both lobes are uncured again immediately.
Video 19. 20150120 RSB	Meander- cleaning, Human interaction, Travelling	Left: Uncurl > Tip curl > Uncurl Right: Uncurl	The focal manta ray (melanistic morph male) is meander-cleaning, and drifts close to the human observer and another diver. It curls the left CL tip, before uncurling this again and accelerating away from the cleaning station.
Video 20. 20150103 RSB	Human interaction	Left: Uncurl > Tip Curl > Uncurl Right: Uncurl > Tip curl > Uncurl > Tip curl > Uncurl > Tip	The focal manta ray (typical morph male) is meander-cleaning, circling around close to the cleaning station, passing a diver several times within 5-10m. Each time the tip of the CL closest to the diver is curled briefly as the manta ray passes by (seemingly when in visual range of the diver).
Video 21. 20150226 RSB	Social interaction (facing), human interaction	Left: Uncurl > Half-curl > Uncurl Right: Uncurl	Three typical morph female manta rays are on the cleaning station. The focal individual (on left side of frame) approaches another individual head on with both cephalic lobes uncured but turns right towards the videographer and approaches within 1m. During this interaction, the tip of the left CL is curled to the half-curved position, before being uncured again.
Video 22. 20150108 RSB	Human interaction	Left: Uncurl Right: Uncurl > Other > Uncurl	The focal individual (melanistic morph male) approaches human divers off the cleaning station with both cephalic lobes uncured. One diver makes hand motions and the manta swims upward in an exaggerated body movement, and makes an unusual movement of the right CL, drawing it backwards towards the face, before uncurling it again.

Video 23. 20150109 RSB	Hover-cleaning, Human interaction	Left: Uncurl > Tip curl > Roll up Right: Uncurl > Tip curl > Roll up	Focal manta ray (typical morph male in background at start of clip) is hover-cleaning with both cephalic lobes rolled up, before drifting towards divers in the foreground, whilst uncurling and curling the tip of both CLs at the same time. The ray then rolls both lobes up at the same time as it accelerates and turns just in front of a diver in an exaggerated whole-body movement.
Video 24. 20150223 RSB	Social interaction (following)	Left: Uncurl Right: Uncurl	The focal individual (melanistic morph male) hovers over a smaller typical morph male, both following behind a typical morph female. The focal individual deliberately touches the back of the other male with its cephalic lobes, mainly the left cephalic lobe. The smaller male quickly swims away after the female, with the focal individual following behind.
Video 25. 20150226 RSB	Social interaction (courtship initiation)	Left: Uncurl > Roll up Right: Uncurl > Roll up	The focal individual (melanistic morph male) attempts to engage a typical morph female in courtship by approaching from behind and positioning himself on top of the female. Both CLs are rolled up just prior to touching the dorsal surface of the female. The female then flips backwards, separating herself from the male, and swims away.
Video 26. 20150220 RSB	Social interaction (facing)	Manta ray 1: Left: Uncurl > Tip curl > Uncurl Right: Uncurl Manta ray 2: Left: Uncurl Right: Uncurl > Tip curl > Uncurl	Two typical morph mantas (manta 1- male on left of frame, manta 2- female on right) approach each other belly to belly, with CLs uncured. Both curl the tips of the CL closest to the other individual during this interaction (the left CL for manta 1, and the right CL for manta 2), and then uncurl these lobes afterwards.

Table A4.2. Details of supplementary video clips. Showing examples of various behavioural contexts and cephalic lobe movements/positions outlined in the main text. *All behaviour contexts and cephalic lobe positions are for focal individuals unless otherwise stated in the description.

Chapter V. Investigating manta ray collective movements via drone surveys

5.1. Abstract

Obtaining data on the movement and natural behaviour of mobile, free-ranging species of marine megafauna is a considerable challenge, but this data is urgently required to manage and conserve populations. For animals that live in groups, collective behaviours are often vital to survival and reproduction. Reef manta rays (*Mobula alfredi*) form structured social groups in shallow-water habitats where they also regularly come into contact with humans. Research on how groups of manta rays form and behave in the wild is required to understand their natural behaviour and monitor their ongoing population health, including how disturbance by humans affects them. New technologies offer the potential to observe and perform rapid assessments of group-based behaviour in remote areas. Here we conduct drone-based aerial surveys on groups of reef manta rays in Raja Ampat, West Papua, to understand group-based behaviours which have not previously been studied quantitatively in manta rays. The techniques used are applicable to a range of wild elasmobranch and other marine species. We found that *M. alfredi* showed unique patterns of collective behaviour, including differences between sexes, and high levels of local attraction, especially in larger groups. The behaviour (relative positioning and alignment) of individuals during group interactions was flexible and strongly dependent on situational context (e.g. foraging, 'swarming' or courtship), as well as group size and phenotypic structure. 'Following' behaviour was common in surface waters, suggesting that rays frequently engaged in courtship initiation, but this behaviour might have other social functions. Our results suggests that manta rays adjust rules of interaction depending on local environmental and social conditions. Further studies on manta ray movement behaviour should therefore consider utilising models of collective motion to capture group-level processes that are not apparent at the individual level. Tracking data on tagged individuals in isolation from broader group structures should be interpreted with caution.

5.2. Introduction

A fundamental feature of animal group-living is that individuals influence and respond to the behaviour of conspecifics by interacting with them (Krause et al. 2002). Social interactions are a key part of the overall environment that animals experience, with behavioural decisions made through a balance of habitat factors, internal motivations and density-dependent social forces (Lima and Dill

1990; Manning and Dawkins 1998; Stephens 2008; Farine et al. 2014). Group structural patterns often vary considerably over time and space due to the response of heterogeneous individuals to changes in local conditions (Herbert-Read et al. 2013; Jolles et al. 2020). Understanding the relative and collective movements of individuals within groups is important, because these are major units in which many fitness-related activities, such as foraging, reproduction and predation occur, and on which conservation activities are focused (Snijders et al. 2017). Aggregated individuals constantly assess their social environment, along with private information (within a collective context) (Dall et al. 2005), in order to make optimal behavioural decisions that minimize predation risk or disturbance, increase their movement and foraging efficiency, and optimize their access to potential mates and suitable habitats (Miller et al. 2013; Marras et al. 2015). Thus, structural and behavioural changes at the group level reflect how individual animals balance the costs and benefits of group-living (Ginelli et al. 2015; MacGregor, Herbert-Read and Ioannou 2020).

Once an individual has joined a group, decisions on how to interact with others are in large part governed by simple, self-organising rules (e.g. attraction to and alignment with others, positive and negative feedback, response thresholds) (Bonabeau 1997; Camazine et al. 2003; Sumpter 2006; Silk et al. 2014). These rules can drive complex collective behaviours where cohesion in movements and consensus in group decision-making emerge without any centralised control or leadership (Radakov; 1973; Camazine et al. 2003; Couzin & Krause 2003; Sumpter 2006; Petit & Bon 2010). Responsiveness to neighbour behaviour can allow groups to solve problems beyond the capacity of individuals, known as 'swarm intelligence' (Krause et al. 2010; Ioannou 2017a), and enable individuals to realise the fitness benefits of group membership (Couzin et al. 2005; Aplin et al. 2014). For example, in schooling fish, alignment in orientation and speed enables the rapid propagation of information gathered over a wide spatial range, without direct costs to individuals associated with directly sampling their environment. This can improve collective navigation by averaging of errors in the detection of oceanographic gradients and dampening responses to small fluctuations in conditions (Pitcher and Parrish 1993; Couzin & Krause 2003; Ioannou et al. 2011; Berdahl et al. 2018). Couzin et al. (2002) defined four stable collective movement states typical in schooling fish ('swarm-like', 'torus', 'dynamic parallel swimming' and 'highly parallel directional alignment') that occur interchangeably depending on the relative alignment and angular momentum of individuals, due to changes in interaction rules regarding the size of 'zones of orientation'.

For example, collective motion similar to the 'torus' formation appears to occur during manta ray mass-feeding events in the Maldives where plankton densities are particularly high (Stevens 2016).

The ability of groups to change patterns of collective structuring may be important in allowing individuals to maximise fitness as conditions change (Schaerf et al. 2017; Kent 2019). There is increasing evidence that behavioural adjustments by individuals promote efficient transfer of information, collective responsiveness and evasion from predators within fish shoals (Gerlotto et al.; 2006; Marras et al. 2012; Rieucau et al. 2016b).

In homogenous groups, individual animals often have similar needs and motivations, and respond in similar ways to local conditions (Conradt and Roper (2005). Because of this, cohesion and consensus during collective movement may be easily maintained. The inherent complexity and flexibility of many social systems, however, stems largely from the heterogeneity of individuals within groups, both in their phenotypic characteristics (e.g. in biomechanics, bioenergetics, neuroendocrinology and cognitive abilities) and their internal states (e.g. hunger, knowledge, position within social hierarchy) (Petit & Bon 2010; Hansen et al. 2016; Zafeiris & Viscsek 2017; Jolles et al. 2020; MacGregor et al. 2020). Selectively maintained phenotypic variation is a key feature of animal social systems that drives the behavioural capacity of individuals and can be an intermediary mechanism regulating collective behaviour (Jolles et al. 2020). Differences between individuals will affect how they balance the relative costs and benefits of grouping in response to dynamic local conditions, and potentially the 'rules of interaction' that they follow (Herbert-Read et al. 2011; Farine et al. 2014; Herbert Read et al. 2017; Schaerf et al. 2017; Jolles et al. 2017; Kent 2019). This can drive complexity in social and collective behaviour through a variety of hierarchical and whole-group effects, including leader-follower polymorphisms (Aplin et al. 2014; Webster 2016), within-group assortment (Krause et al. 2000; Killen et al. 2017) and group-level fission-fusion dynamics (King 2010; Sueur et al. 2011; Silk et al. 2014).

These hierarchical and whole-group effects are more common amongst heterogenous groups living in variable environments and are likely to shift as a function of group size, phenotypic composition and behavioural motivation (Sueur et al. 2011; Jolles et al. 2020). Individuals may behave according to 'quorum' rules, responding only when they observe a threshold number of others perform a particular behaviour (Ward et al. 2008; Sumpter and Pratt 2009). Group behaviours will depend on the 'consensus costs' individuals are willing to pay to forgo their preferred action (Conradt and Roper 2003) and the fine-structure of social relationships within groups. For example, some individuals may possess attributes or personalities (Brown & Irving 2014; Aplin et al. 2014) that make them more or less attractive to groupmates, affecting their ability to initiate group movement (King et al. 2009; King 2010; Petit and Bon 2010). Where conflict in movement preferences occurs, this may drive fission-fusion dynamics (Sueur et al. 2011; Silk et al. 2014). Individuals with weaker social tendencies may

exert ‘pulling power’ on others, while those with stronger motivation to be social can provide cohesion and promote stability in group structuring (Aplin et al. 2014; Ioannou et al. 2015). For example, sex differences are known to be a significant driver of leadership in wild elasmobranch populations (Jacoby et al. 2016; Fernandez-Garcia et al. in review) and these appear to be important to courtship, foraging and navigation. Effective group actions often depend on a high level of consensus between individuals, though when this is present they may be driven by only a small percentage of individuals changing their behaviour (Couzin et al. 2005). Research into the processes by which leaders and followers emerge is critical to understanding collective decision-making and the evolution, function and persistence of social units in various contexts (Couzin et al. 2005; King et al. 2009; King 2010; Tóth & Griggio 2011; Wang et al. 2016; Webster 2016; Jolles et al. 2020).

Data on the movements, behaviour and spatial ecology of wild elasmobranchs has always been difficult to collect but is urgently required to develop sound conservation and management plans (Anderson & Gaston 2013; Dulvy et al. 2014; Dulvy et al. 2017; Brewster et al. 2018; Stewart et al. 2018). Collective behaviour is well understood among lab-reared fish in experimental conditions (e.g. Ward et al. 2008; Katz et al. 2011; Ward et al. 2011; Tunstrøm et al. 2013; Schaerf et al. 2017; Herbert-Read et al. 2017; Ioannou et al. 2017b; Kent 2019), but few studies have explicitly quantified collective movement patterns in free-ranging fish. Behavioural studies often rely on diver operated or baited cameras, which are unlikely to record natural behaviours (e.g. Bond et al. 2012; Papastamatiou et al. 2009; Rizzari et al. 2014). Recent technological advances, however, promise new insight into elasmobranch spatial ecology and collective behaviour (King et al. 2018). In particular, small unmanned aerial vehicles (UAVs or quadcopter ‘drones’) are a cheap and efficient way to observe marine megafauna species, including sharks and rays (Colefax et al. 2018; Rieucou et al. 2018; Raoult et al. 2018; Kelaher et al. 2019; Tagliafico et al. 2020; Butcher et al. 2021). Applications include monitoring of population size and density, determining presence of particular rare or cryptic species, observation of fine-scale movements and rarely observed behaviours (social, mating, group/collective behaviours), and collection of samples (e.g. Geoghegan et al. 2018). Drones enable detailed observations of the natural behaviour of whole groups of animals in remote locations, even when individuals interact at considerable distances (e.g. Torres et al. 2018), without disturbance created by divers or in-water equipment. Drones can hover directly above phenomena of interest at low altitudes, allowing collection of data at fine spatial resolutions, and accurate locational information through inbuilt GPS. Coupled with high-definition cameras that allow accurate recording of habitat variability, they can be used to generate tracks of a focal individual's habitat use (e.g. Raoult et al. 2018). Alternatively, they can record the behaviour of whole groups of animals (Kiszka et al. 2016;

Hodgson et al. 2018). For example, video footage recorded from drones may be used to quantify swimming alignment, nearest-neighbour distances and movement velocities of elasmobranchs (Rieucau et al. 2018; Butcher et al. 2021). Recent advances in animal tracking software and computer processing power permit the quantification of the relative movements of large numbers of individuals and characterisation of ‘rules of interaction’ in large groups (Lukeman et al. 2010; Katz et al. 2011; Herbert-Read et al. 2017; Kent 2019). Using such methods, it is now possible to perform detailed quantitative analyses of the collective movement of elasmobranch groups in their natural environment.

Reef manta rays (*Mobula alfredi*) are highly mobile pelagic species that aggregate in surface waters of coastal regions during daylight hours and interact socially during activities such as feeding, cleaning and courtship (Deakos 2010; Stevens 2016). This makes them highly amenable to aerial monitoring but also vulnerable to several anthropogenic impacts, including illegal fishing, unregulated dive tourism and coastal development. *M. alfredi* are known to have active social preferences between individuals that are linked to individual habitat preferences, phenotypic assortment and fission-fusion dynamics (Perryman et al. 2019). Feeding sites and cleaning ‘stations’ appear to function as social ‘gathering points’ (Stevens 2016; Perryman et al. 2019) and are important for courtship behaviours (Marshall & Bennett 2010; Stevens 2016). Quantifying manta rays’ natural social behaviour is inherently difficult, but research on their aggregations and group-based behaviours may be used to assess their ongoing conservation status and plan for sustainable ecotourism activities (Venables et al. 2016; Lawson et al. 2017; Stewart et al. 2018). To our knowledge, no drone-based studies have yet been completed on these species.

As a critical habitat for a substantial *M. alfredi* population, the Raja Ampat archipelago in West Papua, Indonesia is a high priority area for conservation. Currently, manta rays are abundant in this area and well protected from illegal fishing, but tourism in the region has increased substantially in the past decade and is likely to affect the species’ distributions and natural behaviours. Understanding manta ray group movements and behaviours will provide insight into their foraging and courtship, the nature and function of their social interactions and how these drive higher-order social structuring (Perryman et al. 2019). Like some other elasmobranchs (Sims et al. 2000; Guttridge et al. 2012; Gallagher et al. 2014), manta rays move in socially interactive formations. We do not yet understand, however, how these movements are driven by adjustments in alignment or speed, or how individual heterogeneity and variable environmental conditions affect emergent collective behaviours. This knowledge will be important to understand the natural behaviour of manta rays in the wild, assess the impact of human

entry to their habitats and design conservation strategies that mitigate the impacts of tourism (e.g. disturbance from boat traffic or divers) on their populations.

In this study we use drones to investigate the collective movement of reef manta rays during foraging, ‘swarming’ and courtship behaviours. We examined differences between sexes and colour morphs, and the influence of body size, group size and group structural patterns on individual movements. We empirically quantify the extent to which this social elasmobranch modulates its collective behaviour according to the position and behaviour of conspecifics, identify differences in movement characteristics by phenotype and assess the rules that individuals adopt when interacting (and heterogeneity in these). We discuss the importance of leadership in structuring manta ray social groups and implications for conservation.

Our aims were to:

- Monitor the size and composition of groups of manta rays across multiple aggregation sites.
- Describe and quantify patterns of individual and collective movement.
- Quantify behavioural heterogeneity by phenotype and its impact on collective movement.
- Understand possible impacts of human activities on manta ray collective behaviour.

Based on prior knowledge of *M. alfredi* and other species’ behaviour, we hypothesized that:

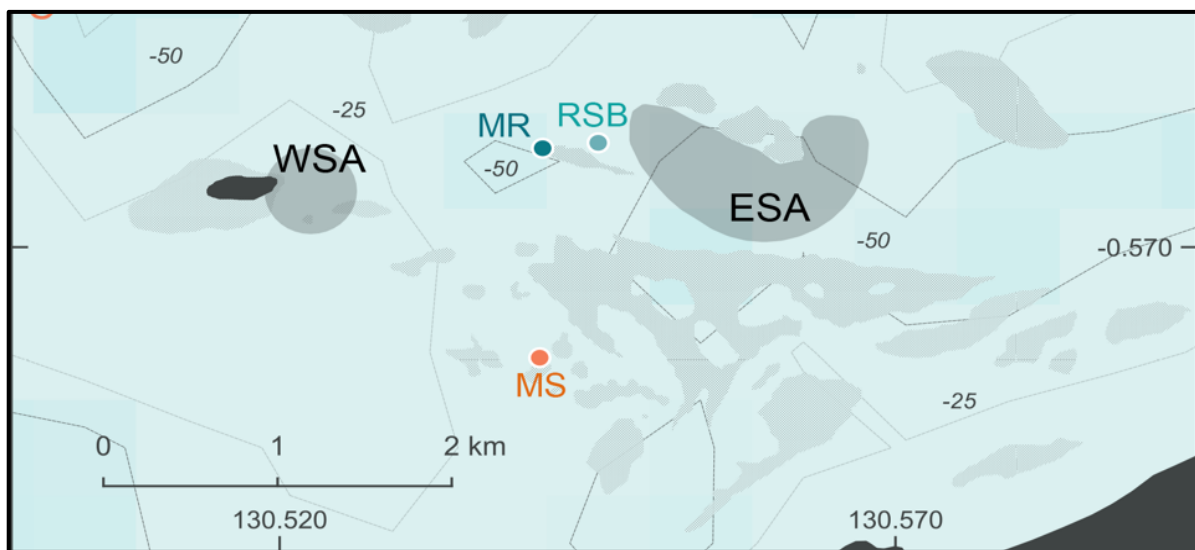
- Simple rules of interaction would govern manta ray interactions with conspecifics.
- Manta rays would adjust rules of interaction depending on local environmental and social conditions, affecting emergent collective behaviours
- Differences between the sexes would affect patterns of collective motion during ‘following’ behaviour, but not affect other types of behaviour (e.g. foraging behaviour).
- Collective behaviours would be impacted by disturbance from boats and divers/snorkellers.

5.3. Methods

5.3.1. Location and sampling methods

The study area in Raja Ampat, West Papua is a shallow-water marine environment with a high amount of bathymetric structure, including areas of coral reef, seagrass beds and sandy bottom, among small islands and sandbanks. Manta rays are commonly encountered here from November to April each year at known feeding aggregation and cleaning station sites, which range in water depth from ~5-50m (see Map 1). Diving and other tourism activities (boating, snorkelling), as well as local subsistence

fishing occur throughout the area during the day. Drone surveys were carried out on 80 different days between 1 October 2017 and 30th May 2019, at times between 08:00-18:00h, at locations where manta rays were commonly observed (known feeding and cleaning aggregation sites), using either a DJI Phantom III Advanced or a DJI Mavic Pro UAV quadcopter drone (www.dji.com). Both drones contained an onboard camera, GPS, compass and tri-axis gimbal allowing for flights at consistent speed and altitude, and stable video recording at an adjustable angle between 45° and 90° to the water surface. Cameras recorded 1920 × 1080 or 2706 × 1520 pixel video at 24 frames/s, in the wide field of view setting, for the duration of all survey flights. Drone surveys were conducted at known *M. alfredi* aggregation sites and designed to record the collective behaviour of groups of individuals.



Map 1. Map of the location of our study sites in Dampier Strait, Raja Ampat. The majority of drone surveys were performed at shallow-water cleaning station sites (MR= Manta Ridge, RSB= Rob's Secret Bommie, MS= Manta Sandy), or in feeding areas (ESA, WSA).

5.3.2. Drone survey protocol

Survey flights were launched from one of several islands, sandbanks, built wooden structures or from a small speedboat, close to known aggregation sites. Surveys began with 'search' phase and progressed to 'behavioural observation' phase if a group of manta rays was detected. On reaching a known aggregation site, the drone was flown slowly over it whilst filming at 90° angle to the water surface, for at least 30 seconds. This length of time was deemed sufficient to detect manta rays due to the shallow water habitat at most aggregation sites and high contrast of manta rays' dorsal colouration against the reef or sandy substrate. If no manta rays were observed, the search would continue with the drone being flown to the next known aggregation site. If manta rays were observed, the drone was positioned directly above a chosen group of rays (typically the largest group visible) at

a height of 40-80m (lower if the group was small, higher if the group was large and dispersed), with the camera facing straight down (important to avoid parallax issues and to accurately record the relative size of each ray), and the drone hovering in a stationary position (though movement of manta rays out of shot necessitated the occasional adjustment of drone position). Filming of the group then commenced, with at least 10 minutes of continuous video recorded, unless remaining battery levels in the drone were insufficient to allow this. At the end of each 'behavioural observation' phase, we lowered the altitude of the drone to approx. 20-30m and filmed each individual ray in turn. This allowed us to more accurately record data on the sex and colour morph of individual rays.

5.3.3. Monitoring of manta rays via aerial surveys

Flight and wildlife observation data were collected from DJI flight and video file metadata, and by visual inspection of recorded videos. For each survey we recorded the location of all behavioural observations, the time of day (start, end and mid-point time of drone flight) and the number of manta rays visible during this time. We recorded various environmental conditions, including weather, water temperature and sea state during surveys, using methods outlined in Perryman et al. (2019). Surveys were not performed during strong winds or rainy conditions. There was considerable variation in current conditions and bathymetry within and between sites. Sea state/wave conditions were usually calm (0 or 1, and never above 3 on the Douglas Sea Scale) (Owens 1982), ensuring that manta rays were clearly visible to depths of ~5-10m. As a measure of potential disturbance to the behaviour of manta rays from dive tourism, we recorded the presence of boats (within ~250m and within ~50m of manta rays) and human divers/snorkellers (within ~50m and ~10m of manta rays). Notable other species (e.g. sharks, mobulid rays, dolphins, dugongs) that might influence manta ray behaviour were also recorded. GPS tracks were recorded through the DJI GO app on a smartphone and saved for later analysis.

5.3.4. Tracking manta ray movements

To quantify the relative movement of manta rays in groups and investigate collective behaviours, including the 'rules of interaction' they adopted, we tracked and analysed the position and movement of all rays from 46 groups of 2 or more individuals. Because occasional movement of the drone was necessary to track moving groups, it was not usually possible to analyse full 10-minute movement tracks continuously. Rather tracking was recorded on multiple shorter sections extracted from each video clips (typically 30-120 seconds in length, 107 clips in total), and data from separate sections of the same video clip was combined for analysis, considering the combined data as a single independent

sample. Care was taken to ensure that individuals were marked with the same identification number in the separate sections. In all clips used for tracking analysis, the majority of individuals present at the aggregation site (counted during prior search) were clearly visible, the camera was filming straight down at a 90° angle to the water surface, and there was no movement of the drone or the frame of recording. We used VirtualDub 1.10 (Lee 2010) to convert each video section into stacks of multiple .jpeg image files (one per frame) and scaled all image files to 1920 x 1080 pixels, assigning a number to each individual ray in the first image file. We then uploaded all image stacks to Imagej (Rasband 1997-2002), for tracking with the 'manual tracking' plugin. To do this we manually positioned the mouse cursor over the head of a manta ray and followed its movement as the sequence of images progressed, using mouse autoclicker software (FastClicker; <http://murgaa.com>) to record x and y coordinates throughout the sequence of images (each click recorded a pair of coordinates). We then exported all coordinates to Microsoft Excel and repeated the process for each individual ray in the group. In total, we recorded coordinates over 82,105 video frames, which contained 5 hours, 58 minutes and 43 seconds of behavioural observations for all focal individuals. Coordinates were used to calculate various measures, of individual movement within groups and of whole-group movement characteristics.

5.3.5. Recording individual characteristics

Phenotypic characteristics for all individual rays were estimated as far as possible from observation of original video recordings. Distinct colour morph variants ('melanistic' and 'typical') (Venables et al. 2019) were recognised by their dorsal colouration and the presence or absence of white shoulder bars (see Figure 5.1). Mature male rays were identified by the presence of calcified claspers, and mature female rays were identified by evidence from wing scars and pregnancies (as in Perryman et al. 2019), from sections of video after the behavioural observation phase, where the height of the drone was lowered to <20m to provide higher resolution imaging of individual rays. Despite this method, it was not possible to reliably identify the sex or maturity status of many individual rays. We instead recorded and ranked the relative size of each individual (from sections of video clips where the height of the drone was not lowered), using this as a proxy for maturity, and used size comparisons within each observation to estimate sex. To measure the size of rays, we used the ruler in ImageJ to measure body length (in pixels) from the edge of the upper jaw to the trailing edge of pelvic fins, in image frames where the body was at the water surface, close to the centre of the frame (this minimised errors from distortion due to bending of the body surface or parallax issues). Though disc width (DW) is typically used to measure manta ray body size, body length (BL) is proportional to DW in manta rays (Deakos 2010b) and was considered more reliable here because pectoral fins are bent during swimming,

whereas the body is rarely flexed lengthways. Mature male reef manta rays in Raja Ampat are known to range from 2.25-3.75m DW, mature females range from 2.5-4.5m DW, and immature males are not larger than 2.75m (Perryman et al. 2019). We therefore considered rays that both lacked visible claspers and were >125% the size of the smallest identified mature male (i.e. larger than 2.75m) in each clip as mature females. We also estimated all rays that were <60% the size of the largest identified mature male (i.e. smaller than 2.25m), or <50% the size of the largest individual, as immature (assuming that females reach sexual maturity at larger size than males). All remaining rays, and those for which body size could not be estimated (due to not being at the surface or centre of frame) were recorded as sex or maturity status 'unknown'. From a total of 46 observed groups, 303 behavioural observations of manta rays were performed. It was not possible to identify distinct individual rays, so we could not determine how many of these were repeat observations of the same individuals. Our observations included 170 on 'melanistic morph' rays, 133 on 'typical morph' rays. 106 observations were of male rays (all from direct inspection of their claspers), 117 were of female rays (38 from pregnancies or wing scars, 81 from size comparison), while 80 observations were recorded as 'unknown sex'. Observations of 195 rays were recorded as mature adults, with 13 juvenile observations, and 95 recorded as 'unknown maturity'.

5.3.6. Group 'behaviour types'

To investigate potential differences between various collective behaviours that manta rays might perform, we provisionally divided our recordings into three group 'behaviour types'. These were defined based on what the movement characteristics of the majority of individuals visible were, over the majority of the observation time, and included 'feeding': when manta rays swam with cephalic lobes open, often with their upper jaw out of the water (Stevens 2016), in areas that were known as feeding sites (Perryman et al. 2019), either at a consistent heading angle (often in the opposite direction to local currents) or with repeated $\sim 180^\circ$ turns (typically occurring in weaker current conditions) (Stevens 2016); 'following': a polarized state where manta rays led or followed behind another individual/s, and emulated their speed and heading angle (often similar to the courtship initiation behaviour described in Stevens, 2016); or 'swarming': when manta rays swam without any clear directional heading, and did not appear to interact socially except for slight directional changes when encountering conspecifics, that did not comprise following (Tunstrøm et al. 2013; Calovi et al. 2014). Though these categorisations were based on subjective interpretation and did not always capture the behaviour of all individuals in a group, it was desirable to attempt to subset the data in such a way that might bring out differences in collective behaviour, which could then be confirmed by quantitative analysis. For 'feeding' rays, we recorded coordinates over 16,731 frames for 88

individuals in 17 groups, equivalent to 1 hour, 10 mins and 4 seconds of individual tracking data. For ‘following/chasing’ rays, we recorded coordinates over 43,184 frames, for 128 individuals in 15 groups, equivalent to 3 hours, 18 mins and 40 seconds of individual tracking data. For ‘swarming’ rays, we recorded coordinates over 22,190 frames, for 86 individuals in 15 groups, equivalent to 1 hour, 29 mins and 57 seconds of individual tracking data.

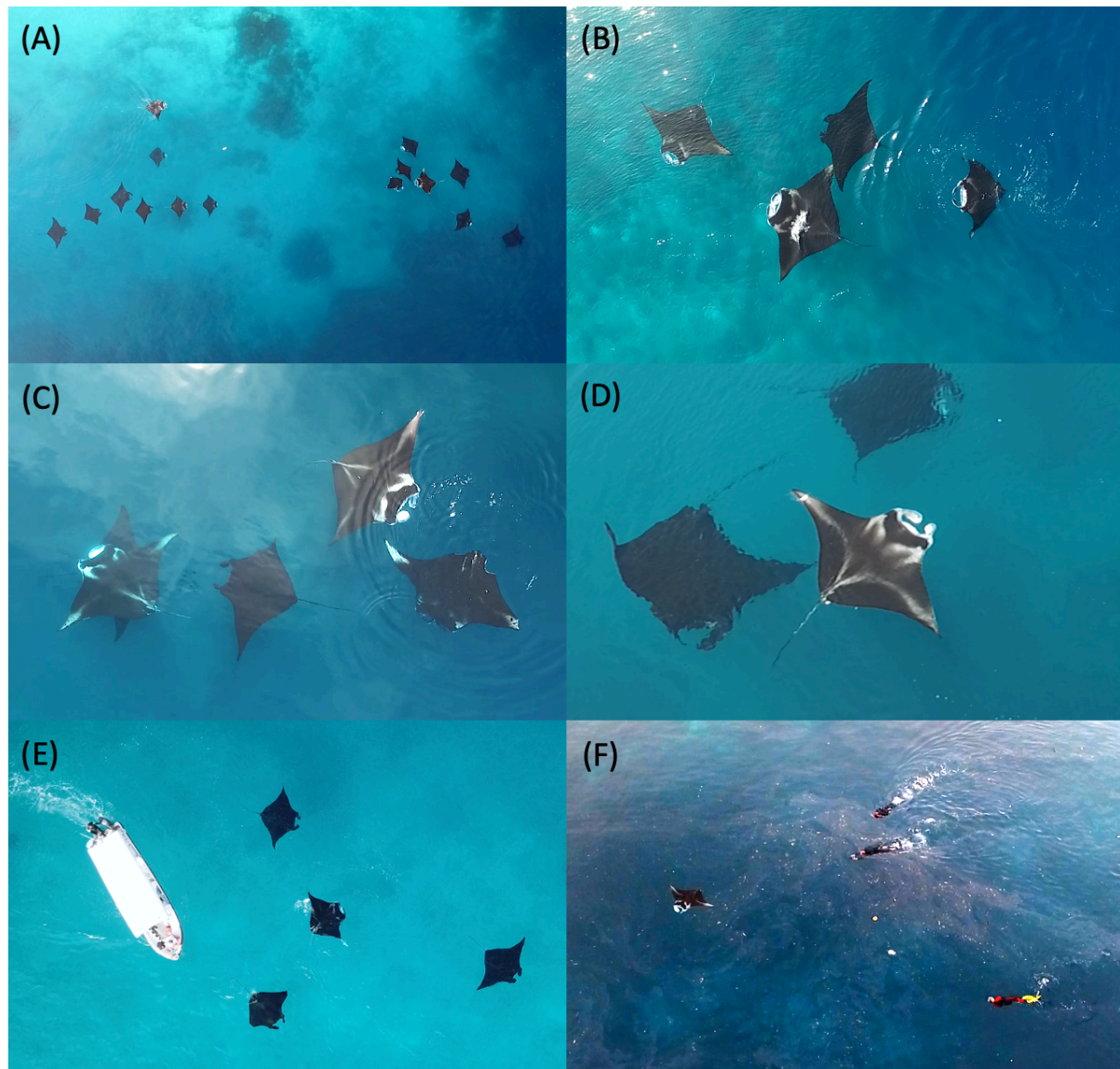


Figure 5.1. Images of manta rays captured during drone surveys. (A) image from typical altitude of behavioural observations (~60m) showing division of larger group in two ‘subgroups’; (B) surface feeding behaviour (three typical morph, one melanistic morph manta rays); (C) image from typical altitude for phenotypic data recording (~15m), showing identification of female rays by wing scars; (D) identification of male typical morph manta ray by claspers; (E) disturbance of group of three melanistic morph and one typical morph manta rays by boat; (F) disturbance of manta ray by human snorkellers.

5.3.7. Correcting for height differences

Because of the large variation in group sizes recorded, to fit all rays into the frame, videos were recorded at different heights. These differences had to be corrected if results from tracking of groups of rays were not to be biased. Therefore, following completion of tracking from all video observations and estimation of relative body sizes of all manta rays in each video, we scaled all coordinates according to the mean body length recorded for all individuals in each video. This ensured that relative positions, alignment and speed could be compared between all observations, with distances between rays recorded in 'mean body lengths', which is biologically appropriate where individuals vary in size. However, this correction did not take into account differences in mean body sizes of each group and therefore assumed that all groups had the same average individual size, which would have introduced some bias, but this was likely to be minor compared to the bias that would occur if height differences were not corrected.

5.3.8. Individual movement and leadership within groups

To understand group-based movements and local rules of interaction, we utilised methods provided in sections S1.2, S1.3 and S1.5 of the supplementary material of Schaerf et al. (2017) to illustrate patterns of individual positioning and alignment as a function of relative partner position and calculate basic measures of individual locomotion, group configuration, speed and relative alignment. We produced density heat plots from the perspective of a given focal individual by centring each individual at the origin and rotating it so that its direction of travel was parallel to the positive x-axis, then recording the positions of neighbouring fish relative to it and repeating this for each frame and each individual in turn (i.e. each individual was considered as the focal individual in turn). These illustrated the probability of observing groupmates at particular (x, y) coordinates, relative to the focal individual. We used similar methods to create alignment heat plots showing both the mean relative directions of motion of partners at given (x, y) coordinates (illustrated with arrows) and a measure of the degree of focus of all the relative directions of motion observed for partners at given (x, y) coordinates (on a scale of 0, indicating high angular variance, to 1, indicating perfect alignment about the mean). We drew additional heat plots to show differences in following behaviour by sex, because initial results showed that individuals were most responsive to the position and alignment of others during this behaviour type and because following behaviours are an important aspect of courtship in manta rays. We expected to find differences between the sexes in the patterns and rules of interaction used during following behaviour. To investigate differences between individuals related to leadership, we first calculated the coordinates of the centroid by averaging all X and Y coordinates together. We then

calculated the mean direction of travel of the centroid and rotated all individuals to be facing the same direction. Individuals were then ranked (i.e. leaders were given a rank of 1, 2nd in line were given a rank of 2, 3rd in line were given a rank of 3...etc.), with ranks proportional to the size of the group.

5.3.9. Calculating group speed and polarization

We used coordinate data from behavioural tracks to calculate measures of speed and alignment as in Schaerf et al. 2017, and these were used in additional regression-based analyses. The mean speed of all individuals in a group (hereafter ‘mean speed’) was taken as a measure of whole group movement. For individual alignment measurements, we first smoothed all x, y coordinate data using a Savitsky-Golay filter (over 29 data points) in MS Excel. We calculated the arctangent (angle of direction of travel, in radians) for each individual over 5 frames and calculated group polarization in heading direction for each video frame as the square-root of the summed sum-of-squares of the cosine and sine values for each arctangent value, divided by the number of individuals in the group, i.e. $\frac{\sqrt{\sum \cos^2 + \sum \sin^2}}{N}$. For this a value of 1 would indicate that individuals were perfectly aligned, while a value of 0 would indicate that individuals were completely out of alignment. We then took the mean of polarization values from all frames in an observation as a measure of ‘group polarization’ in heading angle. Individual-based values for alignment to the mean group heading were calculated as the numerical distance of the mean arctangent value for each individual over all frames in an observation from the mean of means over all individuals.

5.3.10. Regression-based analyses

To determine factors influencing individual and collective movements, and quantify local rules of interaction, we quantitatively analysed the effect of various characteristics of individuals and local conditions on individual movement speeds and alignment of focal individuals relative to groupmates. We also quantitatively analysed the effect of several group-based characteristics and local condition variables on the two group-based movement measures (mean speed, group polarization). Data exploration was carried out following the protocol described in Zuur, Leno & Elphick (2010). All models were validated by checks of residual and other diagnostic plots (QQ plots, Cullen-Frey graphs) using the *fitdistrplus* package in R. Assumptions were verified by plotting residuals versus fitted values, for each covariate in the model and each covariate not in the model. Distributions for individual speed movement measures were non-normally distributed, right skewed and fit best to the Gamma distribution. For group-based measures, similar diagnostic plots and comparison of distribution fits indicated that fitting both measures to the normal distribution was appropriate.

To test effects on individual speed and alignment, we constructed Gamma generalized linear mixed models (GLMMs) with a log link function, using the 'glmmTMB' package (Brooks et al. 2017) in R (R Core Team 2019). The log link ensures positive fitted values. We modelled each individual's speed (continuous variable) as a function of their deviation from the mean group heading (continuous variable), and included sex (categorical variable with three levels including 'unknown sex'), colour morph (categorical variable with two levels), within group size rank (continuous variable), group behaviour (categorical variable with three levels), group size (continuous variable), location (categorical variable with five levels), current strength (categorical variable with two levels) and boat/diver presence (categorical variable with two levels) as fixed covariates. Because our individual-based movement measures consist of observations of multiple individual manta rays within groups, we included the observation ID (Video #) as a random intercept to model the dependency structure among observations of individuals in the same group.

To test effects on collective speed and alignment, we constructed Gaussian generalized linear models in R. We modelled the mean speed of all individuals in a group (continuous variable) as a function of group polarization (continuous variable), and included group size (continuous variable), group sex ratio (continuous variable), group behaviour (categorical variable with three levels), location (categorical variable with five levels), current strength (categorical with two levels) and boat/diver presence (categorical variable with two levels) as fixed covariates. For these group-based models, we included 'Date x Site' as a random intercept to model the dependency structure among observations of groups at the same site on the same day. Results for location were compared to a grand mean over all levels of this variable, whereas pairwise comparisons between levels were used for other categorical variables.

5.4. Results

5.4.1. Basic data on drone surveys

We analysed movement tracks from a total 303 individual reef manta rays in 46 groups, from drone surveys on 27 different days, at 5 different known aggregation sites. Group sizes ranged from 2-21 individuals (mean 6.72). 117 individuals were recorded as females, 106 as males, and 80 of unknown sex. 195 individuals were recorded as mature adults, 13 as juveniles, and 95 of unknown maturity status. 33 groups contained both females and males, with 4 being comprised of only females, 3 only males, and 6 of unknown sex composition. 15 groups (116 individuals) were recorded as performing 'following' behaviour, 15 groups (91 individuals) were recorded as performing 'feeding' behaviour,

and 16 groups (96 individuals) were recorded as performing 'swarming' behaviour. 7 of our observations had humans or boats within 50m of the group of rays. 30 surveys were in calm current conditions, and 16 were in moving current conditions (stronger than $\sim 0.2\text{m/s}$).

5.4.2. Phenotypic differences in size and speed

Female reef manta rays were on average around 20-25% larger than males (IQ ranges, females: 60-66 pixels, males: 48.5-53.5 pixels), which was consistent with previous studies utilising in-water size estimation methods for manta rays in Raja Ampat (Perryman et al. 2019). Average swimming speeds for both sexes were similar (mean speed, females: 23.9 pixels/s, males: 26.5 pixels/s) but males swam much faster than females in relation to their body size (female mean speed: 0.391 body lengths/second (BL/s), IQ range: 0.238-0.532, male mean speed: 0.532 BL/s, IQ range: 0.34-0.683 (estimated regression parameter (est.) 0.174, SE= 0.063, $p= 0.006$; Table 5.1). For additional analyses we used speed relative to body size (measured in BL/s), because this measurement was not biased by correction for any difference in drone height between observations. In general, smaller individuals swam faster in relation to their body size (est. 0.016, SE= 0.008, $p= 0.038$; Table 5.1). The distinct colour morph types ('typical' and 'melanistic') swam at similar speeds (est. 0.073, SE= 0.047, $p= 0.121$; Table 5.1).

5.4.3. Collective positioning and alignment

Over all observations, we found that there was a high probability of finding partner rays within approximately 1-2 body lengths (BLs) ($\sim 40\text{-}80$ pixels) of a given focal individual, and gradually decreasing probability with distance from it. The highest position probabilities were in front or behind, rather than to either side, at approximately 0.5-1.5 BLs distance ($\pm 20\text{-}60$ pixels on the x axis) (Figure 5.2a). On average, the direction of motion of focal individuals and their groupmates were well aligned in wide areas behind the focal individual (Figure 5.2b), approximately where $x < -30$ pixels and $-75 \text{ pixels} < y < 60 \text{ pixels}$, and in front of the focal individual, approximately where $x > 25$ pixels and $-60 \text{ pixels} < y < 40 \text{ pixels}$. Observed relative directions of motion were slightly more focussed (exhibited less variance) about the mean in these same regions. There was a high probability of alignment over the full extent of the x axis, and where $-150 \text{ pixels} < y < 100 \text{ pixels}$, although rays moving directly behind or in front of the focal individual ($-50 \text{ pixels} < y < 50 \text{ pixels}$) were most likely to be aligned directionally. Rays moving behind were likely to be inclined directionally towards the focal individual, whereas rays moving in front were likely to be inclined away from the focal individual. Similar patterns of positioning and alignment in groups occurred, but were accentuated (higher probability of being in

front or behind than to the side, stronger directional alignment) in large groups of 10 or more individuals (Figures 5.3b, 5.3d). Ten individuals or more was considered as a large group because around half of the observations of individuals took place in groups with this number of individuals or more. Smaller groups tended to be more dispersed than larger groups, with neighbours less likely to be found close to a given focal ray (in the area from ~25-60 pixels, in all directions), and more likely to be found in the areas approximately 60-120 pixels (1.5-3 BLs) in front or behind a given focal ray, to the left side if behind, and to the right side if in front (Figure 5.3a). Alignment in smaller groups was mainly focused towards the positive x axis in areas approximately 2 BLs in front or behind a given focal ray, but there was little directional alignment to the sides or at distances < 2.5 BL (~100 pixels) (Figure 5.3c).

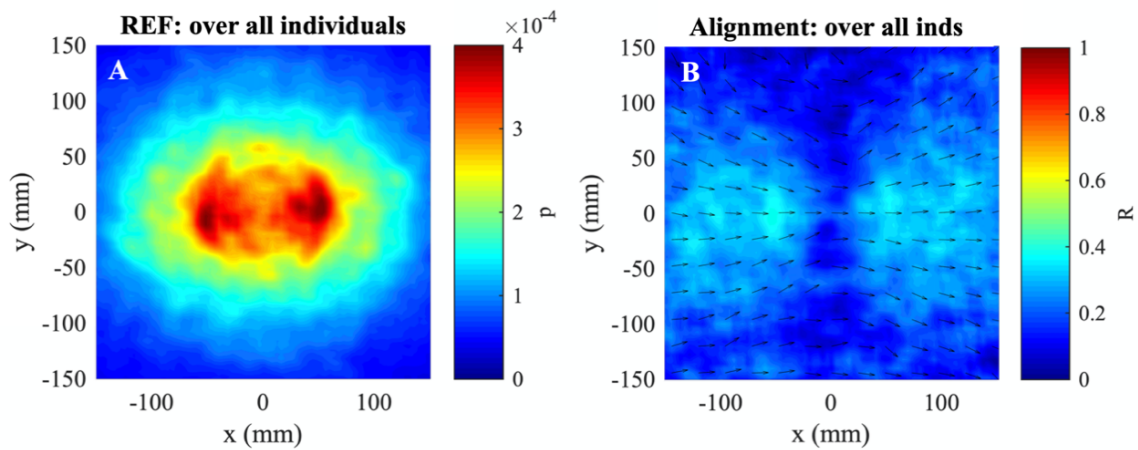


Figure 5.2. Relative positions and alignment of manta rays over all observations. Panel A: relative frequency (estimated probability p) of partner manta rays occupying particular (x, y) coordinates relative to a given focal manta ray located at the origin and travelling parallel to the positive x-axis. Warmer colours in heatplots denote higher relative frequencies of partner fish. Panel B: Mean relative direction of motion (arrows) and associated R values of partner manta rays based on their location relative to a given focal manta ray located at the origin and travelling parallel to the positive x- axis. R is a measure of the focus of all observed relative directions of motion within a particular observation, represented by the colour scale from 0 (greatest variance) to 1 (greatest focus about the mean). mm = pixels. 1 body length = ~40 pixels, depending on individual.

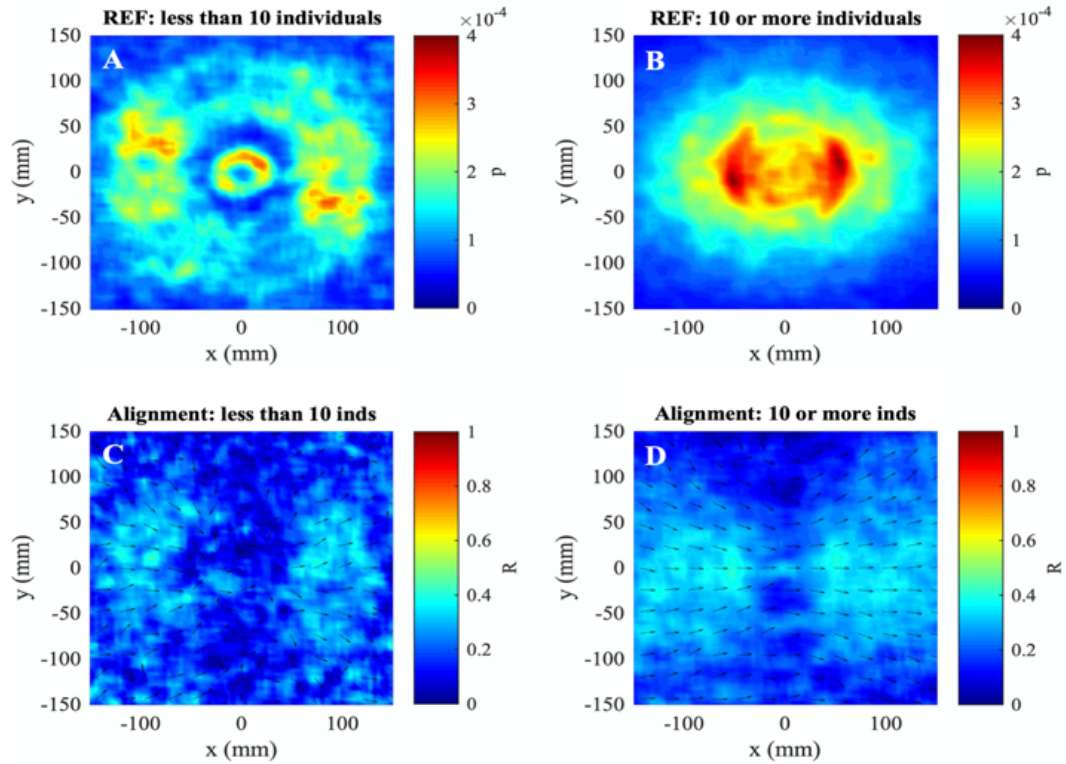


Figure 5.3. Relative positions and alignment of manta rays by group size. All coordinates show partner positions (Panels A and B) or alignment (Panels C and D) relative to a given focal individual, comparing groups of less than 10 individuals (Panel A, C), to groups of 10 or more individuals (Panels B, D). Heatplots constructed in the same way as Figure 5.2. mm = pixels; 1 body length = ~40 pixels, depending on individual.

There was no significant difference between group sizes for ‘following’ (mean 7.8 ± 2.96 individuals, 95% CI), ‘feeding’ groups (mean 6.27 ± 2.9 individuals), and swarming’ (mean 6.13 ± 1.25 individuals). As expected, there were clear differences in the relative positioning and alignment of reef manta rays within groups performing these different types of behaviour, confirming our qualitative classification of these behaviours. ‘Feeding’ and ‘swarming’ groups were more dispersed, though during feeding rays were likely to come very close together (within 0.5 BLs) (Figure 5.4a), with a strong mean focus of alignment in this small area, and some alignment behind and in front of a given focal ray (Figure 5.4D).

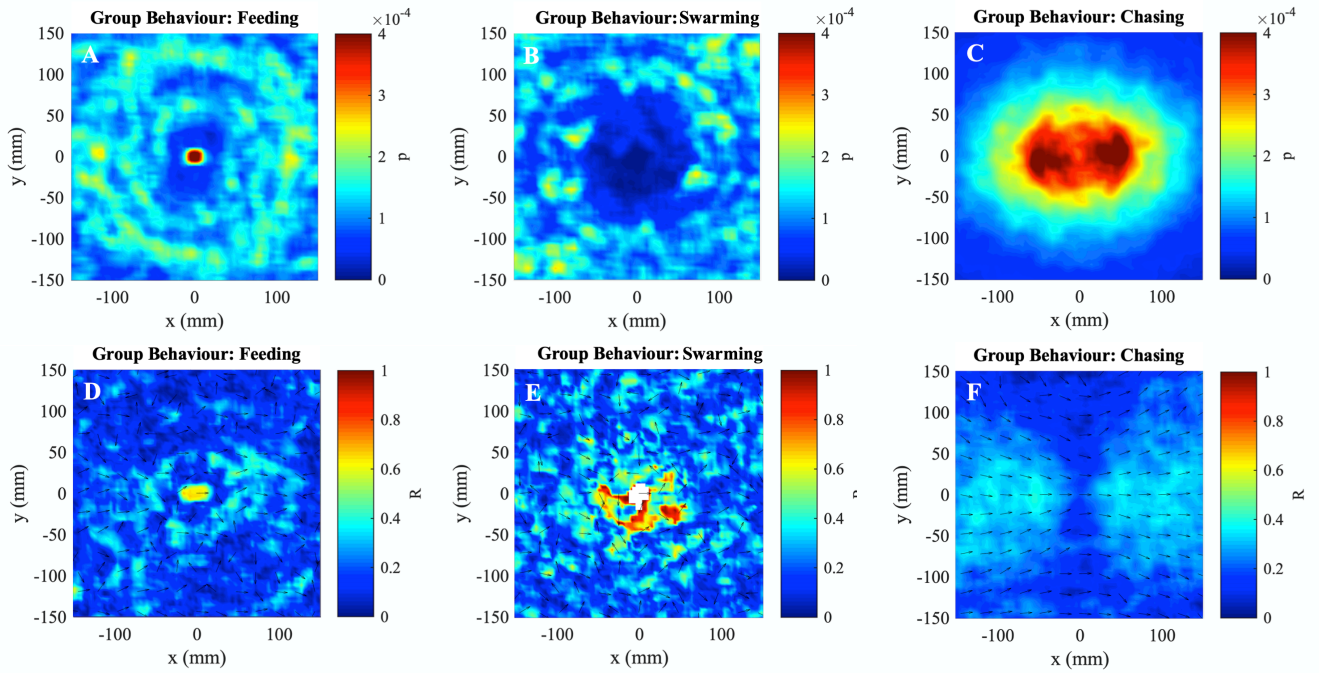


Figure 5.4. Relative positions and alignment of manta rays by collective behaviour type. All coordinates show partner positions (Panels A-C) or alignment (Panels D-F) relative to a given focal individual, comparing groups performing different types of behaviour: feeding (Panels A, D), swarming (Panels B, E), chasing (Panels C, F). Heatplots constructed in the same way as Figure 5.2. mm = pixels; 1 body length = ~40 pixels, depending on individual.

In ‘swarming’ groups, rays were unlikely to be found within 2 BLs (closer than 80 pixels on both the x and y axes), and more likely to be further away from a given focal individual in any direction (Figure 5.4b). These groups did not appear to be aligned in any direction (Figure 4E). Groups of ‘following’ rays were positioned (Figure 5.4c) and aligned (Figure 5.4f) similarly to the overall data (see above). In ‘following’ groups, female reef manta rays were likely to be found within 1BL of each other (50 pixels) at all angles from the focal individual. Male rays were most likely to be directly behind a given focal female (Figure 5B), and females were most likely to be directly in front of a given focal male (Figure 5.5c) (approximately 0.5-2 BLs in front/behind, $\pm$ 20-80 pixels on the x axis), and within one body length to the side ($\pm$ < 50 pixels on the y axis). Males were also more likely to be found in front or behind of each other than to the side, at a range of distances from a given focal individual (Figure 5.5d). However male rays were also likely to be in front of a given focal female (at approximately 1 BL (40 pixels on x axis), Figure 5.5b), and likewise females were likely to be behind a given focal male (at approximately 1BL distance (-50 pixels) on the x axis, Figure 5.5c). Males were as or more likely to be observed at this distance in front of a female than in front of other males. Alignment during ‘following’ behaviour was focused in the areas of highest neighbour density, with similar patterns for same-sex following behaviour (alignment along the x axis, up to $\sim$ $\pm$ 50 pixels on the y axis). Patterns of collective

behaviour here appear to be consistent with known ‘courtship initiation’ behaviour in reef manta rays, where a single (occasionally multiple) female/s will elicit following by multiple male rays. The multiple points at which males were more likely to be found directly behind other males (Figure 5.5d) suggests following in a train pattern. The close association (Figure 5.5a) and strong alignment (Figure 5.5e) of different females suggests that females were regularly within social contact during courtship events. Males appeared to approach and align with females from the left side (Figure 5.5f), which is consistent with studies showing behavioural lateralisation in mating behaviour (wing scars from male bites to female pectoral fins are almost always on the left side). This may also be partly due to females being more likely to turn to the left when being followed by males, which is suggested by Figure 5.5g.

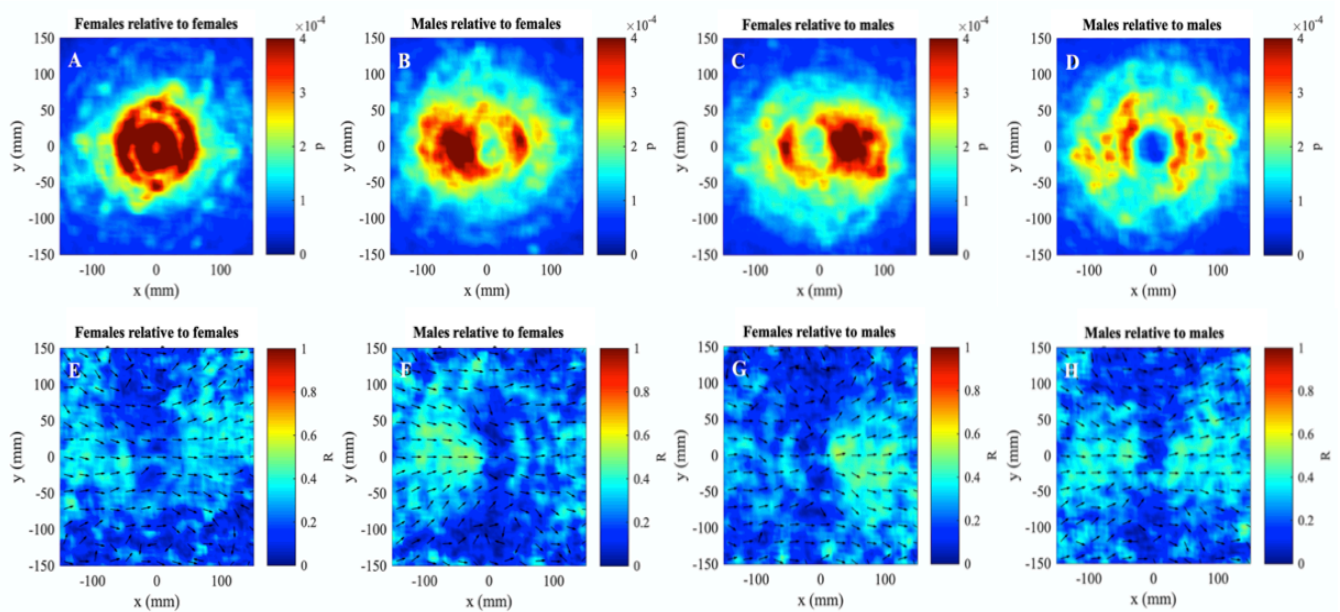


Figure 5.5. Relative positions and alignment of females and males during ‘following’. Coordinates show partner positions or alignment relative to a given focal individual. Plots constructed in the same way as Figure 5.2. mm = pixels; 1 body length = ~40 pixels, depending on individual.

5.4.4. Individual speed and alignment

Results in Tables 5.1 and 5.2 show the effect of various measures and environmental variables on individual swimming speeds and alignment of individuals (compared to the group as a whole). Manta rays swam more slowly when human divers or boats were close by (est. -0.413, SE= 0.114, $p < 0.001$, Table 5.1), and during moving currents (est. -0.51, SE= 0.134, $p < 0.001$, Table 5.1). Males (est. 0.174, SE= 0.063, $p = 0.006$, Table 5.1) and unknown sex (est. 0.218, SE= 0.071, $p = 0.002$, Table 5.1) individuals both swam faster than females relative to their body size, and smaller individuals swam faster than larger individuals (est. 0.016, SE= 0.054, $p = 0.008$, Table 5.1) relative to their body size. Swimming

speeds were also modulated according to alignment with groupmates and according to whole group behaviour. Individuals that were less well aligned with the average heading of their groupmates swam faster than those that were more aligned (est.= 0.141, SE= 0.054, $p < 0.001$, Table 5.1; est. -1.993, SE= 0.45, $p < 0.001$, Table 5.2; $R=0.3$, $p < 0.001$, Figure 5.6A). This effect was stronger for females ($R= 0.45$, $p < 0.001$, Figure 5.6B), who swam more slowly on average when involved in ‘following’ behaviour (mean 0.317 $\pm$ 0.047 BL/s, 95% CI) than during ‘feeding’ (mean 0.416 $\pm$ 0.083 BL/s, 95% CI) or ‘swarming’ (mean 0.458 $\pm$ 0.042 BL/s, 95% CI) behaviours. This appeared to be mainly due to females swimming slowly when well aligned with the direction of their groupmates during ‘following’ ($R= 0.33$, $p= 0.017$, Figure 5.7A) and ‘feeding’ ($R= 0.62$, $p= 0.001$, Figure 5.7B), but not ‘swarming’ ($R= 0.19$, $p= 0.26$, Figure 5.7C). Males swam at similar speeds during ‘following’ (mean 0.514 $\pm$ 0.064 BL/s, 95% CI) and ‘feeding’ (mean 0.514 $\pm$ 0.077 BL/s, 95% CI), and slightly faster during ‘swarming’ (mean 0.587 $\pm$ 0.082 BL/s, 95% CI), but did not appear to modulate their speed based on their alignment with groupmates (see Figure 6c). Individuals that spent more time in leading positions swam slower than individuals that were in following positions (est. 0.21, SE= 0.103, $p= 0.043$, Table 5.1). The group’s location (site), and size (number of rays) had no apparent effect on individual swim speeds. Individual alignment in relation to groupmates was not affected by any individual phenotypic characteristics, environmental variables (except for human/boat presence: estimate 0.407, SE= 0.212, $p= 0.05$), or group-based characteristics, except that individuals were aligned much more strongly during ‘following’ than during ‘feeding’ (Est. 0.553, SE= 0.195, $p= 0.005$, Table 5.2) or ‘swarming’ (Est. 0.539, SE= 0.192, $p= 0.005$, Table 5.2) behaviour.

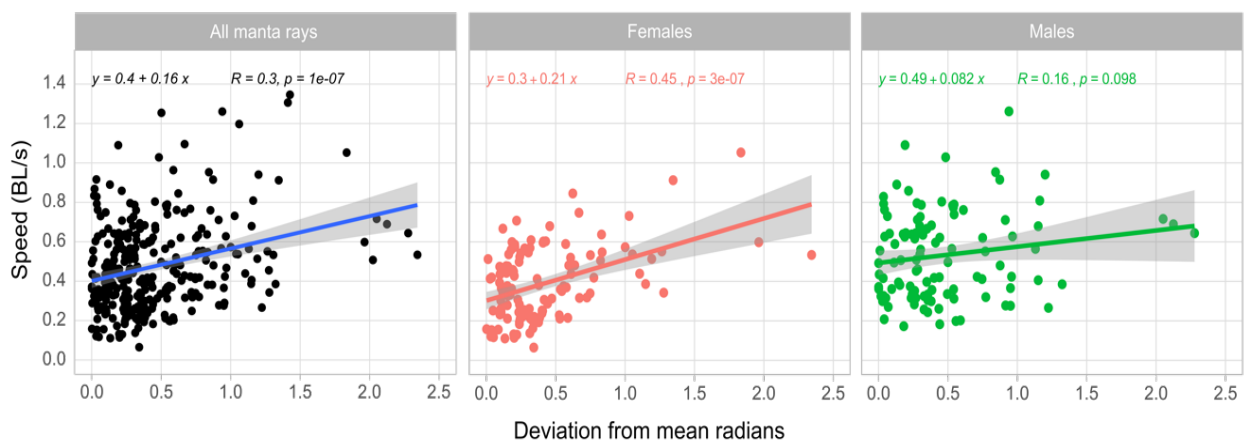


Figure 5.6. Linear models showing individual reef manta ray swim speeds. Speeds in body length/s (average over whole observation) as a function of individual deviation from the mean direction of travel for all rays in the group (average over whole observation). Speed was increased with deviation from group direction, but this effect is stronger for females than males.

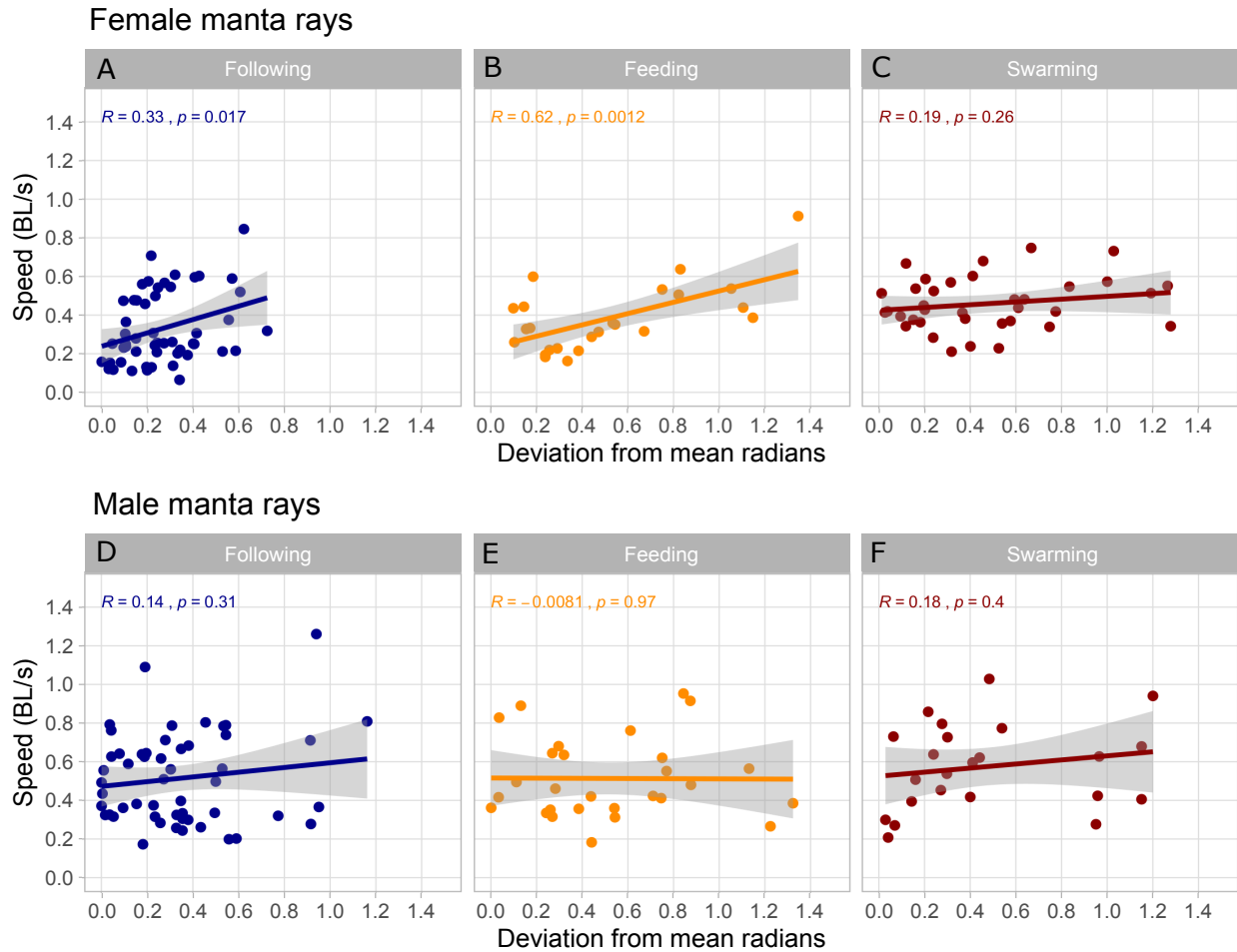


Figure 5.7. Linear models showing swim speeds during different behaviour types. Speeds in body lengths/s (average over whole observation) as a function of individual deviation from the mean direction of travel for all rays in the group (average over whole observation), for female (upper panels) and male (lower panels) reef manta rays during ‘following’ (Panels A, D), ‘feeding’ (Panels B, E) and swarming (Panels C, F).

5.4.5. Group-based measures of collective structuring

Results in Tables 5.3 and 5.4 show the relative effects of various group-based measures. We found a highly significant negative correlation between group size and group polarization (Estimate from GLMM = -0.017, SE= 0.004, $p < 0.001$; Table 5.4), with larger groups being less well aligned than smaller groups (see Figure 5.8A for linear model). Group size did not appear to affect average movement speeds (see Figure 5.8B for linear model). Similar to results for individual movement and alignment, we found that group polarization and average movement speeds were negatively correlated with each other (estimates from GLMM with polarisation/average speed as response variable: -0.28/-0.476, SE= 0.105/0.179, $p = 0.008$; Table 5.3/Table 5.4) (see Figure 5.8C for linear model).

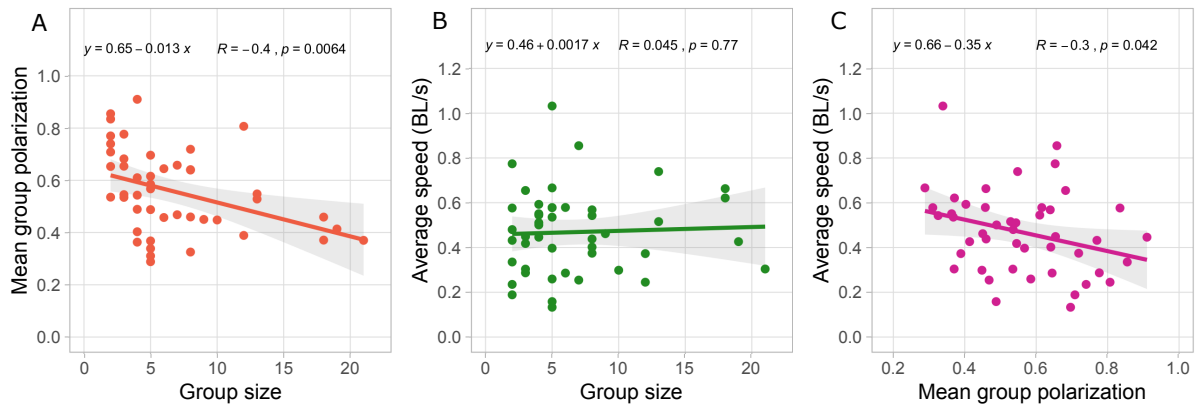


Figure 5.8. Linear models showing relationships between three whole group measures. Panel A: group size (no. individuals) relative to polarisation of individuals within group (mean over whole observation, 0= completely out of alignment, 1= completely aligned); Panel B: group size relative to average speed of all individuals (mean over whole observation); Panel C: polarisation of individuals within group relative to average speed of all individuals. Larger groups are less polarized than smaller groups, but individuals swim at similar speeds regardless of group size. More polarized groups have higher average speeds.

High polarization values were mainly observed in small ‘following’ and ‘feeding’ groups (see Figure 5.9). ‘Following’ groups were more polarized on average than ‘feeding’ (Estimate from GLMM = 0.134, SE= 0.053, $p = 0.011$) or ‘swarming’ (Est.= 0.134, SE= 0.051, $p = 0.008$) groups, but there was no difference in polarization between ‘feeding’ and ‘swarming’ groups. Polarization appeared to decrease with group size at a similar rate in ‘following’ groups ($R = -0.62$, $p = 0.014$, Figure 5.9A), and ‘feeding’ groups ($R = -0.5$, $p = 0.058$, Figure 5.9B). This negative relationship might be expected if there was heterogeneity in the response of individuals to the movement of groupmates, making consensus in collective movement harder to achieve in larger groups. Polarization was lower in small ‘swarming’ groups and did not appear to be affected by group size ($R = 0.041$, $p = 0.88$, Figure 5.9C), suggesting that ‘swarming’ manta rays were less responsive to the movement of others. Polarization was also higher when human divers or boats were close by (estimate= 0.103, SE= 0.051, $p = 0.043$) and during moving currents (estimate= 0.111, SE= 0.055, $p = 0.046$), suggesting that anthropogenic disturbance and local conditions affect the relative position of individual (probably due to hydrodynamic effects or facing into current when feeding). Polarization and average movement speeds were similar at most sites, except for ‘Manta Ridge’ (where current strengths were usually higher). Here groups were more polarized and moved faster than the average over all sites (polarization est.= 0.099, SE= 0.034, $p = 0.004$; Av. speed est.= 0.145, SE= 0.043, $p < 0.001$). Average swimming speeds were most strongly affected by group sex ratio, with groups that had a higher proportion of females swimming slower (in relation to body size) than those that had a higher proportion of males. This was unsurprising given the effect of sex on individual movement speeds described above. We found no effect of group size, group behaviour type, current conditions or diver/boat presence on group average swim speeds.

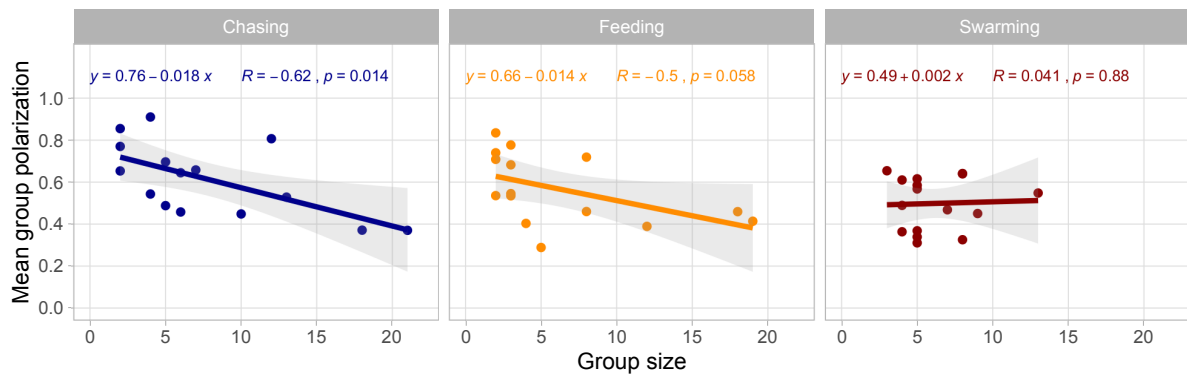


Figure 5.9. Polarization of individual headings within a group, by group size. Mean values given over whole observation. Results for groups performing different types of (collective) behaviour (chasing: $n = 15$, feeding, $n = 17$, swarming: $n = 15$) are shown in separate panels. Mean group polarization is represented on a scale from 0 (rays completely out of alignment) to 1 (rays completely aligned).

	Estimate	Std. Error	Z value	P-value
Intercept	-0.894	0.204	-4.372	< 0.001
Sex: male	0.174	0.063	2.763	0.006
Sex: unknown	0.218	0.071	3.056	0.002
Colour morph: typical	0.073	0.047	1.552	0.121
Size rank (within trial)	0.016	0.008	2.079	0.038
Leadership rank (within trial)	0.210	0.104	2.027	0.043
Group size	0.012	0.008	1.541	0.123
Angle (deviation from mean radians)	0.141	0.054	2.634	0.008
Following : Feeding	-0.273	0.123	-2.230	0.026
Following : Swarming	0.199	0.141	1.413	0.158
Feeding : Swarming	-0.075	0.117	-0.642	0.521
Site: ARB	-0.218	0.277	-0.788	0.430
Site: KR	-0.267	0.283	-0.943	0.346
Site: MR	0.199	0.192	1.034	0.301
Site: MS	-0.158	0.186	-0.848	0.396
Human/boat disturbance	-0.413	0.114	-3.624	< 0.001
Current (running)	-0.510	0.134	-3.804	< 0.001

Table 5.1. Output of model for individual speeds (BL/s). Presented results are estimated regression parameters, their standard errors, z-values and P-values. Bias from individuals within the same trial accounted for by including Video # as a random variable.

	Estimate	Std. Error	Z value	P-value
Intercept	-1.776	0.247	-7.196	< 0.001***
Sex: male	-0.216	0.151	-1.434	0.152
Sex: unknown	-0.313	0.167	-1.874	0.061
Colour morph: typical	0.084	0.110	0.763	0.445
Size rank (within trial)	0.028	0.019	1.450	0.147
Leadership rank (within trial)	0.097	0.077	1.210	0.236
Group size	-0.008	0.018	-0.434	0.664
Speed (BL/s)	-1.993	0.450	-4.428	<0.001***
Following : Feeding	0.553	0.195	2.840	0.005**
Following : Swarming	0.539	0.192	2.801	0.005**
Feeding : Swarming	-0.014	0.192	-0.073	0.942
Site: ARB	0.121	0.097	1.262	0.229
Site: KR	-0.263	0.221	-0.951	0.310
Site: MR	0.210	0.199	1.161	0.289
Site: MS	0.268	0.239	0.898	0.407
Human/boat disturbance	0.183	0.294	0.324	0.561
Current (running)	-0.222	0.334	-0.881	0.401

Table 5.2. Output of model for individual alignment (deviation from mean radians). Presented results are estimated regression parameters, their standard errors, z-values and P-values. Bias from trials at same site on same date accounted for by including SiteDate as a random variable.

	Estimate	Std. Error	Z value	P-value
Intercept	0.83	0.098	8.45	< 0.001***
Sex ratio	-0.09	0.067	-1.378	0.168
Mean speed	-0.28	0.105	-2.663	0.008**
Group size	-0.017	0.004	-4.717	< 0.001***
Human/boat disturbance	0.103	0.051	2.021	0.043*
Current (running)	0.111	0.055	1.993	0.046*
Site: ARB	-0.025	0.051	-0.494	0.621
Site: KR	-0.058	0.06	-0.959	0.33
Site: MR	0.099	0.034	2.91	0.004**
Site: MS	0.021	0.044	0.468	0.64
Site: PW	-0.036	0.061	-0.591	0.554
Following: Feeding	-0.134	0.053	-2.527	0.011**
Following : Swarming	-0.134	0.051	-2.629	0.009**
Feeding : Swarming	-0.000	0.061	-0.005	0.996

Table 5.3. Output of model for mean group polarization. Presented results are estimated regression parameters, their standard errors, z-values and P-values. Bias from trials at same site on same date accounted for by including SiteDate as a random variable.

	Estimate	Std. Error	Z value	P-value
Intercept	0.825	0.132	6.263	< 0.001***
Sex ratio (female)	-0.279	0.079	-3.545	< 0.001***
Mean group polarization	-0.476	0.179	-2.663	0.008**
Group size	-0.01	0.005	-1.745	0.081
Human/Boat disturbance	0.077	0.068	1.124	0.261
Current (running)	0.037	0.075	0.487	0.626
Site: ARB	0.017	0.067	0.253	0.8
Site: KR	-0.1	0.078	-1.281	0.2
Site: MR	0.145	0.043	3.358	< 0.001***
Site: MS	0.069	0.057	1.216	0.224
Site: PW	-0.13	0.078	-1.681	0.093
Following : Feeding	-0.036	0.074	-0.486	0.627
Following : Swarming	0.044	0.071	0.613	0.54
Feeding : Swarming	0.079	0.078	1.015	0.31

Table 5.4. Output of model for mean swim speeds within groups. Estimated regression parameters, standard errors, z-values and P-values. Bias from trials at same site on same date accounted for by including SiteDate as a random variable.

5.5. Discussion

We present the first quantitative analysis of patterns of collective movement in elasmobranchs, and of manta ray behaviour via drone surveys, revealing hitherto unknown features of the natural behaviour of *M. alfredi*. Groups of *M. alfredi* occupying surface waters in Raja Ampat, West Papua frequently performed socially interactive behaviours where they positioned themselves close to and in alignment with near-neighbours. *M. alfredi* showed unique patterns of collective behaviour, including differences between sexes, and high levels of local attraction. Patterns of collective movement were strongly context dependent. Group size, phenotypic structure and several other factors affected the relative movement and alignment of individuals, suggesting that manta rays adjust rules of interaction (e.g. the size and shape of zones of attraction, orientation and repulsion) depending on local environmental and social conditions (Schaerf et al. 2017). We suggest that this, along with inherent behavioural heterogeneity between individuals linked to their phenotypic characteristics (sex and size), leads to the emergence of a range of group-based behaviours (i.e. ‘swarming’, ‘following’ and ‘feeding’) in surface waters, with collective movements being driven by leader-follower behaviour. The negative correlation between speed and alignment/polarization (i.e. that individuals moved slower on average when moving cohesively) suggests that modulation of speed

might be a mechanism by which collective movements emerge, or alternatively that collective movement causes individuals to reduce their swim speeds. Our results suggest that manta rays are likely to be impacted by boat traffic and dive-tourism activities in areas adjacent to cleaning stations and feeding sites. These sites function as multi-purpose areas for a range of behaviours including social and collective interactions.

We found that many groups of manta rays maintained strong directional alignment typical of polarized collective schooling states (Couzin et al. 2002). However directionally aligned groups were typically elongated at a local scale with higher densities of neighbours and strongest alignment immediately in front or behind a focal individual rather than to the side (Figure 5.2), resulting in chain-like ‘following’ behaviour. These patterns of positioning and alignment clearly provided a strong signal to overall heatplots, perhaps due to the greater volume of data, but also probably because rays followed more consistent rules of interaction during this type of behaviour. In smaller groups and during ‘swarming’ behaviour, neighbours appeared to avoid being around 0.5-1.5 body lengths apart, whereas in larger groups neighbours were commonly found at this distance and were much more strongly aligned at close quarters. During ‘swarming’ and ‘feeding’ behaviour manta rays were relatively well dispersed (suggesting larger zones of repulsion) and did not adopt consistent neighbour positions, although for ‘feeding’ behaviour this result is likely to be because reef manta rays forage in several different ways depending on local zooplankton density and oceanographic conditions (Stevens 2016). The high observed probability of feeding in very close proximity to others (Figure 5.4a), for example, might indicate the common occurrence of ‘piggy-back’ or ‘chain’ feeding, whereas ‘ram’ feeding rays may prefer to stay at further distances from each other to ensure unobstructed flow of water to their mouths. The lack of directional alignment seen during ‘feeding’ and ‘swarming’ (Figures 5.3d, 5.3e) suggests that swarm-like (Couzin et al. 2002) or non-collective movement was also common. ‘Swarming’ behaviour may occur as a precursor to more complex collective behaviours when individuals are in the process of aggregating.

Observed patterns of collective movement may be emergent properties of social interactions, but are also likely to be influenced by physical properties of the local environment (such as currents and underlying habitat), as these may affect the efficiency of different types of movement (e.g. Strandburg-Peshkin et al. 2015, 2017). For example, ‘chain feeding’ may be a social activity that improves foraging success through interaction with known conspecifics but is also likely to occur due to being an efficient way to reduce drag whilst swimming. Similarly, differences in speed or positioning in feeding groups may be a consequence of restricted area searches or a tendency for animals to turn

more frequently when foraging, but could also indicate socially cooperative behaviours that enhance food acquisition (e.g. ‘cyclone feeding’, Stevens 2016). We did not record any collective movement similar to the ‘torus’ (Couzin et al. 2002) or ‘cyclone feeding’ formation, suggesting plankton availability or oceanographic conditions were not conducive to this in Raja Ampat. Unfortunately, it was not possible within the scope of this study to quantify how collective movements were affected by physical properties of the local environment. It is also important to point out that the depth of individuals during these different behaviours was not taken into account, and its contribution to variation in spatial positioning is therefore unknown. This may bias results, particularly if depth differences between individuals were larger during certain behaviour types.

Leader-follower behaviour in *M. alfredi* has been qualitatively described in several previous studies (e.g. Marshall and Bennett 2010; Deakos 2011; Stevens 2016; Stevens et al. 2018). It is known to occur during foraging and courtship. ‘Chain feeding’ seems to allow rays foraging together to feed more efficiently on prey that is capable of evading capture by solitary individuals. ‘Precopulatory chasing’ (often referred to as ‘mating train’ behaviour) is thought to involve the attraction of males to a sexually receptive female/s during a ‘courtship initiation’ phase, and sexual selection through male competition and female mate selection through ‘endurance’ behaviour. ‘Escorting’ of females by males over long time periods is also reported (Stevens 2018). Our observations suggest that ‘chain feeding’ and ‘precopulatory chasing’ are both common in surface waters, but also that these functional explanations are likely to be insufficient to fully explain leader-follower behaviour in *M. alfredi*. Leadership was shared between group members and the leading individual changed frequently, suggesting that group movements often occurred without being driven by particular dominant individuals (e.g. sexually receptive females). Female rays were more likely to lead groups, but both male and female rays were regularly positioned in front of groupmates. Females were often observed in close proximity to each other, while males were more dispersed from other males (Figure 5.5). Despite the large number and length of our observations, we did not observe any progression of following behaviour to the later stages of courtship described in Stevens (2018), and this has rarely been reported by other authors or underwater videographers.

In fish species that show peak neighbour densities and alignment along the y-axis (e.g. Ward et al. 2017; Schaerf et al. 2017), collective movements often protect from predation or enable gathering of environmental information (Ward et al. 2011; Ioannou et al. 2017b; Herbert-Read et al. 2017). Chain-like leader-follower behaviour in manta rays, however, suggests social benefits as well as known reproductive behaviours (Stevens et al. 2018). It is well recognised that high levels of alignment,

reduced neighbour distances and structural flexibility in collective movement are important features to promote efficient transfer of information in groups of fish (Gerlotto et al. 2006; Herbert-Read et al. 2011; Marras et al. 2012). Moving in this way may enable individual manta rays to more easily inspect their groupmates, and actively position themselves close to specific neighbours that they recognise and prefer to interact with. It may improve navigation, though navigating groups do not always rely on individuals at the front (Flack et al. 2013; Strandberg-Peshkin et al. 2015; Berdahl et al. 2018). In many ungulate species, for example, dominant individuals that drive overall group behaviour tend to remain in the middle or rear of a herd rather than at the front (e.g. Bourjade et al. 2015; Andrieu et al. 2016; Go et al. 2020).

Rather than being only a means of feeding or courtship, leader-follower behaviour may have broader importance to the cohesive movement and social behaviour of manta ray groups, enabling information transfer and potentially influencing the formation and persistence of preferred social relationships between individuals (Perryman et al. 2019). A plausible explanation for our combined results is that ‘chain feeding’, ‘precopulatory chasing’, and other movements involving leader-follower behaviour occur interchangeably according to local conditions, emerging passively as individuals aggregate and interact socially in increasing numbers (Ginnaw et al. 2020). This is likely to occur as a result of simple but flexible social interaction rules (e.g. attraction to and alignment with near-neighbours, increased speed when out of alignment, or possibly positive feedback as larger chains may attract additional rays). We found that manta rays in larger groups appeared to swim closer together and were more strongly aligned directionally, although group-level polarization was reduced with group size, especially when rays were feeding or following. This suggests that large groups were often divided into clusters of several individuals that moved cohesively but did not typically move as a collective whole. Actual swimming speeds were increased with group size, although this was likely to be partly an artefact of differences in swimming ability due to sexual dimorphism in body size and the larger numbers of males in large groups. However, our results also showed that individual rays decreased their speed relative to body size according to local conditions (when currents were moving and when humans or boats were present in the water nearby). Currents and human presence also appeared to affect group-level polarisation, but not group-level average movement speeds, suggesting that while individuals may respond independently to local conditions, these responses can produce structural changes in collective behaviour. Female rays also appeared to increase their speed the further out of alignment with groupmates they were, which males did not do. This may indicate that females are more reactive to the behaviour of groupmates than males, for example they may actively elicit following rather than being the subject of unwanted ‘chasing’.

Taken together, our results indicate that collective movement in manta rays is driven primarily by leader-follower behaviour, but that a high level of flexibility in the rules of interaction leading to this behaviour can produce different group-level responses. Highly social species with greater cognitive abilities often exhibit more flexibility in their collective behaviour because individuals are able to recognise differences that exist between themselves and their groupmates and use this information to guide their behavioural decisions (Couzin et al. 2005; Ward and Webster 2016; Viscek and Zafeiris 2012). Behavioural flexibility may enable manta rays to balance coordination of essential group-based behaviours with exploration and information-gathering (King et al. 2009; Johnstone and Manica 2011; Brown and Irving 2014) and develop new ways to solve collective problems (Sumpter 2005). It is likely to be a key factor driving fission-fusion dynamics of social groups in variable environments due to conflicts between individual preferences in the timing and direction of movements (Sueur et al. 2011). Understanding how and why collective behaviour in manta rays (which are highly mobile, migrate seasonally, potentially in groups) occurs may be crucial for their conservation (Westley et al. 2018), because this will enable predictions of when and where groups move. A clear result with practical conservation implications is that manta rays regularly perform collective behaviours in near-surface waters around cleaning and feeding sites. This is likely to put *M. alfredi* at risk of boat strikes and disturbance by divers and snorkellers at popular dive sites, because large collective groups are more likely to attract attention, particularly in areas that manta rays are known to frequent. Management measures should be implemented to protect *M. alfredi* from these threats. These might include drone-based monitoring to when animals are present (e.g. Barreto et al. 2021), mitigate human-wildlife conflict (e.g. Colefax et al. 2019) and set guidelines for ecotourism (e.g. Rieucan et al. 2018). In the future, improved battery technology may permit longer continuous flight durations to aid such projects in remote locations.

Drone-based surveys may provide an excellent way rapidly assess broad areas of potential elasmobranch habitat, track individual elasmobranchs and identify priority conservation areas, among other uses (Raoult et al. 2018; Rieucan et al. 2018; Kelaher et al. 2019; see Butcher et al. 2021 for review of utility of drones in elasmobranch research). Here we demonstrate that they can also be used to conduct detailed research on manta ray collective behaviour and fine-scale interactions. This suggests several possible further research directions, such as investigating transfer of information between individuals and responses to humans or natural predators (Butler et al. 2021), and the testing of simulation-based models of collective behaviour on wild populations (King et al. 2018). Models of collective motion (e.g. Bode et al. 2010; Herbert Read et al. 2011), collective decision-making (e.g. Farine et al. 2014; Ioannou et al. 2017) and other mechanisms of group coordination will be important to explain and predict the dispersal, spatial ecology and evolutionary dynamics of manta rays in a

changing marine environment, and develop appropriate conservation measures. Collective models should take into account the dynamic and ephemeral nature of manta rays' zooplanktonic food resources and the daily movement of rays between shallow and deep water (Couturier et al. 2013; Burgess et al. 2016), which are likely to strongly impact fission-fusion dynamics (Sueur et al. 2011; Silk et al. 2014). They might, for example, focus on understanding how socially interactive groups form in the mornings and break apart in the evenings, and on the potential impact of human disturbance to social and collective behaviours, as well as the importance of hysteresis effects whereby the existing collective state influences future collective behaviour (Couzin et al. 2002). Such models should incorporate failed initiations of leadership as well as occasions where strong follower behaviour is elicited (King 2010; Petit & Bon 2010), and if possible, attempt to incorporate individual personalities (Aplin et al. 2014; Jolles et al. 2017) and data on social relationships (Bode et al. 2010, Perryman et al. 2019). Frequency-dependent selection for leader-follower behaviour is known to be an important driver of distinct personalities and dominance-based relationships in animal groups (Aplin et al. 2014). Manta rays are often anecdotally described as having individual personalities and this may have significant effects on group behaviour (Jacoby et al. 2014; Byrnes and Brown 2016; Finger et al. 2018).

The inability of drones to identify manta rays and other elasmobranchs individually, however, is a major limitation compared to in-water surveys (Perryman, unpublished data). This hampered our interpretation of leader-follower interactions and prevented us from quantifying social interactions or other hierarchical interactions such as dominance-based relationships. Another drawback is that aerial drone surveys are limited to recording behaviour in surface water and shallow environments. While manta rays display collective and social behaviours at the surface that can be recorded easily, most elasmobranchs spend considerable time at greater depths, and this is likely to hamper efforts to understand their interactions. To improve studies of collective and social behaviour in manta rays, aerial observation might be combined with in-water observations (to record individual identities) and/or telemetry studies. For example, accelerometers (e.g. Kadar et al. 2019) or sensor tags could be used to record movement energetics and/or the inner biology/metabolism of individuals. Understanding the impact of individual's inner motivational states (Fischhoff et al. 2007) and various phenotypic characteristics (e.g. biomechanics, bioenergetics) may be important to determine how adjustments to rules of interaction occur during collective interactions. Tagging methods to study collective behaviour are, however, only likely to be effective in small, isolated or area-restricted populations, where it is feasible to tag a large proportion of individuals that are likely to form groups.

In summary, collective movement appears to be an important aspect of the biology of manta rays that is likely to affect all aspects of their life histories, as well as being vital to foraging and courtship. Further investigation of leader-follower polymorphisms and fission-fusion dynamics in manta ray groups, including the impact of between individual variation and within-individual behavioural flexibility is justified. Understanding of these processes should enable better assessment of manta rays' local vulnerability to environmental change and human disturbance, and the development of effective rules and restrictions for marine tourism operators, benefitting conservation in coastal, shallow water habitats, where the species are often vulnerable to human disturbance.

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Chapter VI. Summary, conservation implications and future directions

In the **General Introduction** (Chapter I) to this thesis I outline how knowledge of the natural behaviour of animals, including their social relationships, is essential for understanding their overall biology and ecology, including population dynamics and susceptibility to anthropogenic impacts. I describe how recent research on group-forming elasmobranchs supports the hypotheses that their populations are structured socially, and that social interactions are important to various aspects of their life history. I outline how reef manta rays' habitat use, foraging and courtship behaviour, their conservative demography and spatial distributions, are all likely to have been conducive to the evolution of social behaviour.

Given the above, my overarching aim was to provide a more comprehensive understanding of the behaviour of free-ranging reef manta rays through study of their sociality. I approached this by combining research in different but complementary disciplines (social network analysis, collective behaviour, ethology), taking advantage of multiple observational and analytical methods. Following Hinde's (1976) framework, I investigated social organisation at the population (surface structure) level, and the level of relationships between individuals. I also conducted detailed research on reef manta ray social interactions, including potential communication and patterns of collective movement. These different aspects are explored in each of my empirical data chapters, where I apply and develop methods that have been used previously in teleost fishes, marine mammals and sharks, in captive conditions and the wild (e.g. Mourier et al. 2012; Whitehead and James 2015; Jacoby et al. 2016; Schaerf et al. 2017; Kent 2019). I adapted my study design to deal with specific issues in observing and recording data on free-ranging manta rays, using specific knowledge of their behavioural ecology to form and test biologically relevant hypotheses. I present evidence that sociality is a fundamental aspect of *M. alfredi* behaviour that provides structure in the studied population. My results suggest that further study of free-ranging manta rays and other mobile elasmobranchs, and management of their populations, will benefit from a network-based approach. This should incorporate the interdependent behaviour of heterogeneous individuals in the context of their spatial ecology, including social interactions, group-based movements and information transfer.

6.1. Overview of findings

The major findings of my research, and their contribution to the field of elasmobranch behavioural ecology, are summarised below. These were: (i) that *M. alfredi* populations can be socially structured; (ii) that phenotypic assortment, habitat use and active social preferences are important drivers of social structuring; (iii) that individual movement and habitat use patterns are highly variable; (iv) that *M. alfredi* make frequent movements of their cephalic lobes during social interactions that are suggestive of gestural communication; and (v) that *M. alfredi* perform collective movements that are strongly context-dependent.

In **Chapter II**, using a large photographic dataset collected over several years in Raja Ampat, West Papua, I was able to confirm the hypothesis that reef manta rays have active social preferences. These were the result not only of spatiotemporal overlap due to passive aggregation with conspecifics, or behavioural differences between phenotypes, but of social familiarity between pairs of individuals. This result confirms that reef manta rays can recognise and remember previous interactions with conspecifics and use this knowledge to distinguish between and choose social partners. Social recognition and partner preference confer numerous fitness benefits in teleost fishes (Ward et al. 2003; Ward et al. 2007; Griffiths and Ward 2011) and marine mammals (Wiszniewski et al. 2010; Bruck 2013), such as increased efficiency of social information transfer, which we explored in Chapters VI and V. Analysis of lagged association rates suggested that associations between individuals lasted on average several days to weeks. Social affiliations were correlated with site use preferences and assorted by sex, occurring especially between females, with males tending to avoid repeated social interactions. These factors appeared to drive the structuring of the manta ray population into partially segregated communities.

Chapter III focused at the level of relationships between individual reef manta rays and associated dynamics in the context of their spatial ecology, through network analyses of their movements and social associations. Continuous data on the presence of 25 tagged individuals within an acoustic receiver array were obtained, and used to record residency events at, and rates of movement at multiple spatial scales (from ~200m to >20km) between, several aggregation sites in Raja Ampat. This enabled investigation of the impact of behavioural variability on social structuring. We found that individual reef manta rays varied strongly in their movements and levels of site attachment, and that network structural patterns were stable over time. As also shown in Chapter II, many appeared to repeatedly return to the same area of reef during daylight hours, over several days or weeks. Interestingly, individual variability was stronger than variability between physical phenotypes, and this

appeared to influence network structure, suggesting that *M. alfredi* may have varied personalities that affect their social relationships. As in other social species, some individuals may be territorial, so investigating dominance relationships may shed light on behavioural ecology.

That many of the main findings in Chapters II and III are consistent regarding social organization (including that social affiliations over several weeks drive community-level structuring, and that individuals vary in site attachment and movements), despite the different methods used, strengthens confidence in their accuracy regarding the studied population. It suggests that potential sources of bias, due to 'nuisance' sampling effects or other potentially confounding social effects (Farine and Carter 2020), did not affect our biological interpretation of results. Together, these findings imply that site attachment and fission-fusion dynamics in reef manta rays are important mechanisms affecting social structuring. They provide support for the hypotheses that manta rays preferentially occupy home ranges (Clark et al. 2010; Venables et al. 2020) in which they develop social relationships, driving the partial segregation of populations into social communities, and that behavioural phenotypes exist, with the potential for behavioural polymorphisms between sexes, or according to development. We showed that some individuals (particularly mature females) repeatedly attended particular cleaning stations or feeding sites but completely avoided similar areas of reef habitat nearby. Strong site attachment has been consistently reported in reef manta rays populations in other locations (Dewar et al. 2008; Peel et al. 2019; Andrzejczek et al. 2020; Venables et al. 2020); my research suggests this may occur at finer scales (<3km) than previously thought. Similar processes are likely to occur in other elasmobranch species. Recent evidence from reef sharks (Mourier 2012; Papastamatiou et al. 2020) suggests that these species are central point foragers that display high levels of locational philopatry that drives the segregation of social communities.

Following confirmation of the existence of social structuring and social relationships in the studied *M. alfredi* population, Chapters IV and V focused on the nature and context-dependency of underlying social interactions. The methodologies developed for these chapters might usefully be applied in future studies of manta ray social behaviour, or adapted to research on other elasmobranch species. Chapter IV provides a detailed investigation of the behaviour of reef manta rays during social interactions at cleaning stations, focusing on cephalic lobe movements. It shows that a range of complex movements are made that indicate likely gestural communication between rays at close quarters, and/or the use of these lobes in sensory reception. This suggests that interactions between *M. alfredi* at cleaning stations are important to the maintenance of social relationships, and that disturbance of natural behaviour in these locations will be detrimental to their survival and

reproduction. Chapter V described patterns of collective movement in *M. alfredi* groups. It demonstrated that drone-based observations can be used to study the relative movement and interactions of multiple wild elasmobranchs in fine detail and accurately record data on the size and constitution of social groups. Our results show that *M. alfredi* display unique patterns of collective behaviour that depend on local attraction and alignment, and that these patterns are strongly context-dependent. Following behaviour was important in structuring patterns of manta ray schooling. Movement speeds and the alignment of neighbouring individuals were influenced by several factors, including the sexual composition of groups, group size and disturbance by humans. Our results add to knowledge of how manta ray feeding and courtship behaviours occur, suggesting that collective movement is essential for those specific types of behaviour, though it is also likely to be important in the general movement behaviour and social interactions of manta rays. We suggest that social interactions and collective behaviours are important influences on *M. alfredi* aggregations, which is important knowledge for management (Stewart et al. 2018). As in other populations (Stevens 2016), *M. alfredi* in Raja Ampat performed multiple behaviours at cleaning stations; these sites may function as multi-purpose areas that are crucial to survival and reproduction, including as ‘meeting points’ for social interactions. Interacting socially is likely to be an adaptive mechanism driving the evolution of behaviour in manta rays, with significant implications for studies on their neurobiology, intelligence and communication. Our results suggest that complex information transfer may occur between manta rays during social interactions, and that social information is important to collective movements during foraging and courtship.

6.2. Conservation implications

The increased knowledge of sociality in manta rays provided in the thesis has important implications for their management. Manta ray populations already appear to be declining in several regions (Dulvy et al. 2014; Rohner et al. 2017; Marshall et al. 2018, 2019). The species’ highly conservative life history strategies, including, among elasmobranchs, extremely low fecundity and late maturation, means manta ray populations are unable to support any level of fishery exploitation (Stevens et al. 2016). Thus, a key priority for conservation is immediate protection of their populations in remaining strongholds. Regional and global scale conservation measures that protect manta rays from exploitation and illegal trade throughout their range are critically important. There is also an urgent need to identify critical habitats, levels of connectivity between these, and drivers of manta rays’ spatial aggregation and fine-scale habitat use at biologically appropriate spatiotemporal scales (Couturier et al. 2012; Dulvy et al. 2014; Lawson et al. 2017; Stewart et al. 2018). This thesis helps to fill some of these knowledge gaps, particularly on manta rays’ fine-scale movements and habitat use,

the structure and dynamics of their social interactions, and the likely importance of social and collective behaviours. Results suggest that, to design management strategies appropriate to spatial ecology and evolutionary dynamics (Kurvers et al. 2014), predict the impacts of exploitation by fisheries, and mitigate disturbance from marine ecotourism, a stronger focus on manta rays' social organisation and social behaviours is required. Local management measures that view groups as complex, dynamic structures resulting from social interactions between heterogeneous individuals are likely to be useful. As has been revealed in cetaceans, detailed studies on communication, social learning, societal organisation and intelligence can reveal unexpected aspects of species' social lives that have significant implications for conservation. For example, understanding sociality in cetaceans (e.g. communication, cooperative hunting, and community structuring) has been vital to the development of various practical, local conservation measures, such as restrictions on underwater noise, altered shipping routes and selective fishing methods (Reiss et al. 2006; Weilgart et al. 2007; Peterson et al. 2008; Zappes et al. 2011; Goetz et al. 2015; Wiener 2015; Frantzis et al. 2019; Wild et al. 2020). Information on social behaviour and intelligence in cetaceans has also been instrumental in raising of awareness, conservation fundraising and the general popularity of these species worldwide, and has been crucial to support for the 1986 moratorium on commercial whaling which has enabled some species recoveries (Lotze et al. 2011). We are already beginning to uncover unexpected insights into sociality in many elasmobranchs (e.g. Vila Pouca et al. 2020; Papastamatiou et al. 2020), some of which are presented in this thesis. Manta rays are prime candidates for a social elasmobranch species that could capture the attention of the public, promote investment in elasmobranch conservation and inspire future generations to care about sharks and rays (Perryman et al. 2018).

Of particular relevance to conservation is that several behavioural mechanisms that we report here, including grouping behaviour, sexual assortment and site philopatry (and increased public knowledge of these) will likely increase manta rays' susceptibility to several acute anthropogenic threats (Wearmouth and Sims 2008; Mucientes et al. 2009; Jacoby 2012) including target fishing (often performed via fleets of small boats equipped with modern engines and traditional harpoons; Dewar 2002; Lewis et al. 2015), marine debris (Croll et al. 2016; Germanov et al. 2018), and increasingly, unregulated dive tourism. Over the last two decades there has been a huge increase in demand for dive experiences with elasmobranch, including in areas where they have previously been exploited by fisheries, such as Raja Ampat. Dive tourism can be a major force for conservation of marine wildlife, particularly large charismatic species such as reef manta rays, which can act as 'flagship' or 'umbrella' species for protection of wider ecosystems (Perryman and Tapilatu 2018). Tourism operators can often offer alternative employment to fishing or other exploitative activities, creating a win-win

situation for local communities and wildlife, leading to a shift in focus to prioritise environmental protection from within local communities (Tongson and Dygico 2004; Masud et al. 2017). If not managed correctly, however, tourism may have harmful effects on wildlife (Trave et al. 2017). In Raja Ampat and other locations, scores of divers and snorkellers regularly attend aggregation sites during peak manta ray activity periods (O'Malley et al. 2013; Venables et al. 2016; Needham et al. 2017; RP pers. obs.). These people may disturb natural social behaviours, potentially affecting the social transfer of information and collective behaviours, which we explored in **Chapters IV and V**, though further research is required to effects of disturbance on social interactions. The rapid increase in numbers of tourists visiting Raja Ampat every year (King 2017) makes enabling sustainable tourism a pressing issue for the manta ray populations there.

Our results throughout this thesis suggest that locally oriented management measures may be effective in protecting *M. alfredi* in Raja Ampat. For local conservation of marine species and ecosystems, management within marine protected areas (MPAs) and MPA networks is increasingly recommended. These measures should be tailored to the needs of local wildlife and humans and can be combined well with the development of sustainable tourism (Masud et al. 2017). MPAs should generally be large enough to protect a significant portion of the home ranges of populations they aim to protect, which may be difficult in large, mobile species. For species like *M. alfredi*, however, that display philopatric behaviour, and aggregate seasonally at disproportionately high densities in specific locations (Peel et al. 2019), MPA networks may offer significant protection. The Raja Ampat Marine Park is currently divided into zones that vary in the level of protection provided to wildlife, and human activities permitted (Grantham et al. 2013), as are many other MPA networks. As manta rays are known to move seasonally at broad habitat scales, flexibility in MPA zonation that maximises protection of the population in high-use areas at different times of the year is recommended (Lea 2017). Protecting habitats during periods when manta ray groups aggregate according to food availability or reproductive and social activity may be particularly useful. The MPA network in Raja Ampat is well established and appears to be broadly effective in limiting human impacts on marine wildlife, while enabling local communities to benefit from marine resources (McLeod et al. 2009). The structure of local governance in Raja Ampat, including adherence to traditional practices (Boli et al. 2014), provides excellent opportunities for effective local management of manta rays. However, I recommend several improvements to mitigate disturbance of *M. alfredi*, which take inspiration from many of the findings of this thesis. These include stricter restrictions and regulations for diving or snorkelling operations in areas where manta rays are known to interact socially, no-go zones for boat traffic in these areas, temporary or seasonal closure of dive sites, and monitoring via local patrols. This

will help to protect manta rays' natural social behaviours, while preserving high quality dive experiences for tourists, ensuring sustainability of eco-tourism in the region, and benefits to the local economy (Tongson and Dygico 2004; O'Malley et al. 2013; Venables et al 2016; Atmodjo et al. 2017). These measures would not necessarily impact the operations of local tourism providers. For example, dive site closures during midday periods during the peak-time for manta ray aggregations could be designed to coincide with lunch breaks for dive tourists. Stricter regulations would likely lead to better coordination of operations by different providers and therefore less crowding and better experiences for guests. To effectively safeguard critical habitats, future research should aim to define other high-use areas for manta rays in different parts of the Raja Ampat archipelago.

Cleaning stations are well known to be used by manta rays for maintaining their health and healing wounds (Grutter 1999; Marshall 2009), but these areas are now known to provide important opportunities for reproductive and social interactions (Stevens et al. 2018; Perryman et al. 2019). Our results suggest that cleaning stations and other shallow reef sites function as multi-purpose areas for feeding, courtship and other behaviours that appear to be purely social (e.g. rays of same sex swimming together). We identified five priority locations within the Dampier Strait region where manta rays are likely to be disturbed by tourism ('Manta Sandy', 'Manta Ridge', Pulau Arborek, Pulau Wai and 'Blue Magic'); it is essential to rapidly protect these areas from habitat destruction or disturbance. Detailed protocols for interactions with manta rays have recently been proposed and implemented at one of the main aggregation sites ('Manta Sandy'), and appear to be well received by tourists, while providing employment for several local people. They include the designation of borders around the cleaning station there, which divers are asked to remain behind, and codes of conduct for diving and underwater photography. However, our research suggests that practical conservation measures should be expanded from a specific focus on known cleaning stations, to protection of wider aggregation areas around these sites. In Chapter V, we showed that manta rays interact socially and collectively, and perform courtship behaviours, in surface waters surrounding cleaning stations and feeding sites (approximately 30-40% of manta rays recorded via drone surveys in aggregation areas were located at or just below the water surface). Management measures should therefore be implemented to protect manta rays (and other species such as dugong and sea turtles) in the upper metres of the water column, where they are particularly vulnerable to boat strikes and human disturbance. We propose strict restrictions on boat speeds to <5 knots within 500m of dive sites, maximum group sizes of 10 divers, and that snorkellers should be divided into groups of 2-4 people, to facilitate safe, sustainable and enjoyable dive experiences. Another useful measure would be to restrict dive operations in areas where currents are running particularly strongly, which would help to

protect manta rays during feeding events, whilst at the same time improving diver safety. The use of reef hooks at manta ray cleaning stations and feeding sites should be banned to discourage diving with manta rays during strong currents. Dive resorts, conservation groups and local people in Raja Ampat should be encouraged to continue working together to design locally specific strategies, agree and enforce rules, and provide training to local staff in best practices for marine ecotourism.

6.3. Limitations and future directions

This thesis provides detailed information on the social structuring, spatial ecology and social and collective behaviour of *M. alfredi* in Raja Ampat, around which future research and conservation efforts may be developed and implemented. Findings are limited in their scope in space and time, and by the difficulties researchers still face in recording and evaluating the behaviour of these wild animals (some of which are outlined in the next section). Many important outstanding questions remain or have yet to be fully answered. To build on the contribution of this thesis, further research is required to: (i) reproduce and compare network-based studies in different populations; (ii) incorporate the dynamics of social connectivity in network modelling; (iii) assess the relationship between genetic structuring and social structuring; and (iv) further understand social and collective behaviours, and the impact of disturbance on these.

6.3.1. Reproducibility and extension of social network studies

A clear next step for research on the social nature of mobulid rays and other elasmobranchs would be to extend the type of network-based research presented here and elsewhere (e.g. Mourier et al. 2012; Jacoby et al. 2016; Lea 2017; Mourier et al. 2017a; Mourier and Planes 2021; Peel et al. 2019; Andrzejaczek et al. 2020; Papastamatiou et al. 2020) to various different populations, to examine the reproducibility of results and their wider implications for population and community ecology. If the patterns of social and collective structuring observed here are common in other populations of manta rays and other elasmobranchs, or to certain habitats or ecosystems, this would suggest that systematic conservation and management procedures may be applied successfully across multiple populations. Alternatively, if species and populations display high levels of organisational variability, then bespoke, locally-oriented conservation measures are likely to be more appropriate. To date, few researchers have attempted to compare social networks within or between species (Castles et al. 2014; Sosa et al. 2020). To make valid comparisons, it will be important to standardise research methodologies, for example the dimensions of acoustic receiver arrays, sampling methods used to construct networks, and how social connections are recorded (e.g. through proximity or directly observed interactions);

these have important effects on the precision/accuracy and properties of network samples. Agreement on the most appropriate way to test null models is also required. Recently, several authors have demonstrated problems in the robustness of commonly used pre-network and post-network randomisation techniques to both Type I and Type II errors, and thus in the reliability of published results (Franks et al. 2020; Puga-Gonzalez et al. 2020; Weiss et al. 2021). This thesis demonstrates the utility of several analytical approaches to this aspect of the social network analysis procedure. In Chapter II, generalized affiliation indices (GAIs) were used to control for confounding effects on observed social structure before conducting randomisations. In Chapter III, the GMMevents method developed by Psorakis et al. (2012, 2015) and Jacoby et al. (2016) was used to randomize data at the bipartite graph stage, allowing detection frequencies of individuals to be constrained. These approaches should be considered in future network-based analyses of elasmobranch social organisation. Farine and Carter's (2020) 'double permutation' method, which performs pre-network and post-network randomisations and accounts for the weaknesses of each is similarly promising. A further way to control for confounding variables is to include them within statistical dyadic or nodal models, which also appears to improve effect size calculations (Franks et al. 2020). Using standardized methods, it may be possible to compare populations, and research how individual species social networks are embedded within broader communities or ecosystems.

The extension and standardization of network analyses in elasmobranchs will depend largely on how social data are collected. Chapter II demonstrates the utility of photographic databases to the social network analysis of elasmobranchs, beyond their primary applications in population demography (Pierce et al. 2018). Photography-based research has been vital to social network studies of other marine species, such as cetaceans, and has the advantages that data collection is cheap and relatively simple. The now widespread availability of underwater photographic equipment, and concurrent increase in the popularity of underwater photography and videography among divers and hobbyists, provides opportunities to collect individual identification data (and examine social networks) on elasmobranchs at a scale unachievable for individual research projects (Ward-Paige et al. 2011; Araujo et al. 2017; Bargnesi et al. 2020). Videos recorded by citizen scientists can provide a useful way to collect fine-scale behavioural data. Successful co-ordination of citizen science initiatives is likely to provide future opportunities to collect data and perform detailed network studies on movements and social interactions over larger scales than previously attempted, especially in species that move widely such as pelagic sharks. This should allow increased research on metapopulation dynamics and trophic ecology that may provide crucial information for ecosystem-based management (Levin and Lubchenko 2008). Such research will, however, require increased collaboration and data-sharing

agreements between scientists at a regional and/or global scale (Stewart et al. 2018) to ensure comparability between studies. The development of online citizen science databases such as MantaMatcher (www.mantamatcher.org) or the whale shark wildbook (www.whaleshark.org) (Town et al. 2013, Berger-Wolf et al. 2017) in the past decade are a crucial step, but currently able to capture only a small portion of observations worldwide. Evidently network-based research on these wild animals will benefit hugely from better networking between the scientists studying them.

Automated methods of data collection have many advantages, as discussed in Chapter III. Telemetry-based network analyses may be particularly appropriate for species that are less amenable to direct observation, less predictable in their aggregations, or that occupy deeper or more offshore pelagic habitats than *M. alfredi*, including other mobulid species such as *M. birostris*, *M. mobular* and *M. tarapacana*. The cost and logistical difficulty of telemetry-based methods, however, may preclude their widespread use in some species or regions, in which case photographic methods are likely to be more useful. The limited number of technological systems available to track marine wildlife has already encouraged standardization of research questions and collaboration at local and regional scales (e.g. the Integrated Marine Observing System IMOS <https://imos.org.au/>, and the Ocean Tracking Network <http://oceantrackingnetwork.org/>) (Cooke et al. 2011; Lara-Lopez et al. 2016). This bodes well for future reproducibility and integration of network studies in marine wildlife conservation. Future developments will aid investigation into the causes and consequences of social structuring and connectivity in elasmobranchs, and help in examining the influence of different types of habitat or different levels of disturbance across populations and species. The use of large, densely clustered receiver arrays can enable the collection of accurate data on individual locations via the triangulation of transmitter signals from three or more receivers, with obvious benefits for the construction of social networks, but these are expensive, and therefore unlikely to capture the movement behaviour of highly mobile species.

Many ways of constructing, measuring and manipulating networks can offer interesting and valuable insights into elasmobranch behavioural ecology (Jacoby et al. 2012; Mourier et al. 2018), and we were not able to attempt some of these here for practical reasons or due to time constraints. More in-depth analysis of the importance of particular individuals in connecting networks would be of particular relevance to conservation. In some species, certain individuals occupy central positions, and have important roles in maintaining connectivity between social units, facilitating transmission processes. Removal of such individuals (e.g. by targeted fishing of larger individuals) may disproportionately affect a population's resilience or response to external pressures (e.g. changes in food availability or

emergence of novel diseases) (Bilgmann 2007). Further studies should attempt to model the impact of removal of individuals (including those most central to network structuring), and of social units on the connectivity of manta ray populations. Mourier et al. (2017) provide a useful example that could be adapted in various elasmobranch species. Another way to investigate individual roles within social communities would be to use egocentric networks that investigate social connections from the perspective of a focal individual. These may be constructed dynamically (e.g. Wilson et al. 2014) to track how an individual's social relationships change through its development. The use of such methods will undoubtedly aid assessment of commercial exploitation on elasmobranch populations and prediction of the effects of humans' increasing entry into their habitats (Jacoby et al. 2012; Gallagher and Huveneers 2018; Stewart et al. 2018).

Separating the influence of social preferences from spatial distributions is vital for a realistic understanding of the nature of animal sociality. While the analyses presented in Chapters II and III used a variety of methods to control for spatial influences, the social networks we constructed were based on inferring social associations by the 'gambit of the group', without detailed knowledge of the nature of those associations. To confirm that social processes are important, more detailed knowledge of social contact is desirable. Proximity logger tags enable the quantitative analysis of social contact rates, because they record whenever two tagged individuals are in close proximity with one another (e.g. Guttridge et al. 2010; Haulsee et al. 2016; Mourier et al. 2017b). If such tags were to be placed on a large number of individuals within a population, they would provide unprecedented opportunities to gather large quantities of detailed information on direct social interactions.

6.3.2. Dynamics of spatial and social connectivity

For conservation initiatives to be successful, accurate predictions of where, and for how long species aggregate, and validation of these predictions based on empirical observations are needed. Knowledge of changes in movements and habitat use, and their effects on social structuring over time, will be crucial for protecting manta ray populations in the future. In Chapters II and III, investigation of some aspects of the spatial and temporal dynamics of *M. alfredi* social organisation was attempted. In Chapter II, this was limited by sparse observations recorded through photographic identification of rays during SCUBA dives. Chapter III investigated the influence of spatial ecology on social relationships by constructing movement networks, but logistical and financial constraints meant this could only be examined in a small fraction of the habitat available over a short time period. Thus, we could not fully address the importance of social dynamics at spatial or time scales biologically appropriate to the life-history of manta rays. Further studies over seasonal or generational time

periods are required to elucidate this. These should include research into the spatial connectivity of habitats over time, the duration of social interactions and the temporal dynamics of social network topology. Improvements in tagging technology are likely to facilitate this in the near future.

Incorporating spatial dynamics within more extensive movement networks is an obvious next step. Using larger acoustic receiver arrays would allow collection of data on movements in and out of a range of habitat types, and testing of more specific hypotheses about how manta rays use their environment over larger spatial scales (e.g. whether habitat use changes seasonally or during development). Collection of movement data over extended periods might also enable better understanding and prediction of population dynamics related to changes in environmental conditions or seasonal variations in resource availability, and the impact of long-term anthropogenic pressures, such as climate change and fishery exploitation, at timescales appropriate to the species' life cycle. (Morales et al. 2010; Scharf et al. 2016). Greater ability to predict the impact of these external influences, and the susceptibility of populations to them, will be extremely valuable to conservation efforts. The use of dynamic, rather than static, social networks is particularly important if an aim is to capture changes in social structuring over time (e.g. diel cycles or seasonal processes), or transmission processes within a network context, especially where the relationship between edge weights and transmission probability is nonlinear (Farine 2018). Dynamic social networks can be produced in several ways. For example, time-ordered networks retain the order of interactions, and record chronological changes in network structure that are particularly useful in studying transmission processes. Time-aggregated networks combine data within defined time periods to show average changes in network structure that can be used to identify causes of change in network topology (Blonder et al. 2012), for example between seasons or during El Niño or La Niña years, or gradual changes over long time periods.

Studies that attempt to place the social structuring of animal societies within their overall behavioural ecology are likely to be especially useful for understanding social connectivity in a changing world. The recent application of multi-layer network analysis to studies of animal behaviour and ecology (Silk et al. 2018; Finn et al. 2019; Mourier et al. 2019) is promising, as it aims to more accurately represent intricate and multi-faceted social systems. Multi-layer networks enable quantification of complex processes within social systems that incorporate many types of social interactions that occur at different times and locations. They are made up of assemblages of various 'stacks' of network 'layers' connected horizontally (by intralayer edges representing connections such as social interactions among individuals or movements between habitats), and vertically (with each facet of layering

representing an ‘aspect’ of connection between these networks, such as temporal dynamics). They can take the form of multiplex networks that represent various types of interaction, or interconnected networks that connect different types of nodes. Mourier et al. (2019) outline an interconnected multilayer network approach that integrates movement networks and temporally dynamic social networks, thereby providing a novel and holistic framework for studying individual variability in social behaviour in the context of spatiotemporal connectivity. They use this to show how blacktip reef (*Carcharhinus melanopterus*) and grey reef (*Carcharhinus amblyrhynchos*) shark movements are connected to individual’s social relationships. Similar analyses could be undertaken in manta rays. Such modelling of dynamic processes is likely to offer broader insight into their long-term ecological and evolutionary effects (Kurvers et al. 2014). There are, of course, clear logistical and financial difficulties in performing analyses that incorporate multiple aspects of species or community ecology over extended periods, especially if these require monitoring of large numbers of individuals in inhospitable environments. Simpler and more easily replicable analyses may be more appropriate in many cases.

Alternatively, tracking the dynamics of social *interactions* using proximity loggers will allow the construction of contact networks through continuous recording of distances between pairs of tagged individuals (Ryder et al. 2012; Croft et al. 2016; Mourier et al. 2018). This method may be combined with use of biologging tags such as accelerometers or sensor tags (e.g. Andrzejczek et al. 2019; Kadar et al. 2019; Semmens et al. 2019; Watanabe et al. 2019) that record fine-scale physiological and behavioural data to better understand the types of behavioural interaction that occur and their causes or consequences. It would be particularly interesting to study behavioural interactions between individuals that we predict are likely to remain in social contact, such as sexual partners or individuals with similar habitat preferences, in these ways. Dynamic interaction networks could also be based on drone-based video observations, and used to study the impact of disturbance on fine-scale social structuring, using Markov methods (e.g. Wilson et al. 2014) similar to those described in Chapter IV. These methods would be useful in understanding mechanisms of collective behaviour and social information transfer, including how variation in individual behaviour drives group-level dynamics (Sumpter et al. 2010; Bonnell et al. 2020). This is likely to be useful in species that display high levels of individual behavioural variability. The use of animal-borne cameras to directly record videos of social behaviours without bias due to the presence of a human observer may provide an interesting alternative, perhaps enabling the construction of ego-centric networks from the perspective of a focal individual (Hays et al. 2015; Papastamatiou et al. 2018; Watanabe et al. 2019). The above methods have the potential to revolutionize our understanding of sociality in free-ranging elasmobranchs

(Jacoby 2012; Krause et al 2013). However, there are some difficulties here; they include the necessity of retrieving tags attached to animals before data can be obtained, and the large size of multi-sensor or camera tag equipment that must currently be attached to animals internally or externally via dart heads or toothed clamps (Jacoby 2012), which requires comprehensive animal welfare and ethical considerations. Improvements in tag miniaturization and non-invasive attachment methods (e.g. attachment via suction cups by free-divers) are promising, however. Here we demonstrate that the use of small V-9 or V-13 tags can provide similar detection data to larger V-16 tags that are typically attached to manta rays. Further developments in tagging research and its application to studies of elasmobranch behavioural ecology are likely to rely on increased collaboration between scientists working in a range of areas.

Further research into the spatiotemporal dynamics of sociality will help in identifying where and how elasmobranch populations are at risk from various anthropogenic activities, and prioritising the protection of certain populations or locations that may provide connectivity or refuge (Heupel et al. 2007; Cartamil et al. 2010; Bass et al. 2017). It will help us understand changes in metapopulation structuring, including the heterogeneous response of social units to disturbance (Snijders et al 2017) and allow a more holistic understanding of the dynamics of space use within populations and the importance of individual heterogeneity here (Jolles et al. 2020).

6.3.3. Social structuring and genetic relatedness

One area I was unable to investigate in this thesis was the potential influence of genetic relatedness on manta ray social relationships. Many species form social bonds with kin that improve their fitness. Like other elasmobranchs, manta rays do not appear to perform any parental care, and females typically give birth to just a single pup, suggesting that interactions between siblings may be uncommon, although these factors do not necessarily preclude affiliations with kin. There are several reasons to suppose that kin recognition might be adaptive in elasmobranchs. It is known to provide benefits such as reduced aggression (Olsén and Jäurvi 1997; Hamilton 1964) and enable cooperative behaviours in terrestrial species. It is a key factor structuring the societies of cetacean species that have evolved in similar conditions in the marine environment (Wisniewski et al. 2010; Mann et al. 2012; Reisinger et al. 2017). The partial segregation of elasmobranch populations into social communities (which appears to occur not only in manta rays but also in reef sharks and potentially other groups of wild elasmobranchs) suggests that selective pressures are likely to act differently on individuals depending on their social unit membership, leading to stratification in their survival and reproductive success. It is likely to be misleading to assess the evolution of elasmobranchs without

incorporating this heterogeneity (Lusseau et al 2007). For example, the targeting of groups of rays may result in the differential exploitation of social units by fisheries (Mucientes et al. 2009) potentially influencing survival of genotypes and thus species evolution. This would likely be exacerbated if individuals are assorted into social units by their levels of relatedness. An integration of fine-scale population genetic studies (e.g. using microsatellites or single-nucleotide polymorphisms) with social network research would allow these, and other similar areas, to be explored (Mourier and Planes 2021). A hypothesis suggested by some of our findings is that manta rays live in societies dominated by females that occupy home ranges, but in which the majority of gene flow occurs due to partial migration of some highly mobile individuals. This might be tested by combining social and movement network analyses with population genetic methods (Kurvers et al. 2014; Day et al. 2019; Schwanck et al. 2020). For large elasmobranchs such as manta rays, such studies may be facilitated by the development of tagging methods that simultaneously retain a small portion of animal tissue during the attachment of transmitters. An area of difficulty that we encountered during the course of this study, however, was the difficulty in obtaining permission to export tissue samples across international borders (in this case out of Indonesia). This situation may be resolved or ameliorated by improved dialogue between scientists and government officials. Future studies should consider the potential delays to research that might result from such logistical difficulties.

6.3.4. Social and collective behaviour

Our research on social and collective behaviour in manta rays suggests several future directions. It is clear that the collection of empirical behavioural data in the wild is crucial to a fuller and more realistic perspective on the behaviour of teleost and elasmobranch fishes (King et al. 2018; Kent 2019). Ethological studies should enable better understanding of manta rays' natural behaviour, and their local vulnerability to anthropogenic disturbance. They may be used to develop more effective rules and restrictions for marine tourism operators, benefitting conservation in coastal, shallow water habitats, where the species are most vulnerable to human exploitation.

Research in this field should incorporate variation between individuals, as well as within-individual behavioural flexibility. Consistent differences in the behaviour of individuals may be considered important aspects of individual personality (Bell et al. 2009; Carere and Locurto 2011). Several personality traits, such as boldness, stress reactivity and social network position, have been shown to vary within groups of elasmobranchs (Jacoby et al. 2014; Byrnes et al. 2016; Finger et al. 2017). Studies on manta ray personalities are promising because these animals are reported, anecdotally, to display highly variable behavioural characteristics such as inquisitiveness and playfulness. Consistent

individual variation in behaviour can be heritable in the wild (e.g. Brown et al. 2007; Ariyomo et al. 2013) and may have large impacts on both social (e.g. Jacoby et al. 2014) and collective structuring (e.g. Jolles et al. 2020). It may be possible to examine the repeatability of individual traits such as boldness in wild manta rays using methods similar to those employed in Chapter IV. These methods might similarly be used to investigate dominance relationships. Many fish species, including batoid elasmobranchs, are known to form dominance hierarchies, which are typically size-based (e.g. Wong et al. 2008; Ang and Manica 2010; Pini-Fitzsimmons 2017). Dominance is known to be an important mechanism controlling reproduction in fish, including courtship, sexual development and sequential hermaphroditism (Rodgers et al. 2007; Desjardins and Fernald 2008; Eason and LaManna 2011), and appears to occur during social interactions between manta rays at cleaning stations (RP, MC pers. obs.). Dominance hierarchies can be assessed using network-based methods similar to those used throughout this thesis, including interaction matrices, dominance indices and randomization procedures.

My results suggest that cleaning stations are critical areas for the aggregation of manta rays and are used as meeting points where social and collective behaviours emerge. Further research is required to elucidate the function of social behaviours during courtship and feeding, though we can draw some tentative conclusions. The results do not support the hypothesis that cleaning stations function as leks (Stevens 2016). Courtship behaviours that appear to involve sexual selection of males by females occurred at cleaning stations, but males did not aggregate together repeatedly in these locations—rather females were more likely to return daily to a particular station. Their presence appeared to attract mature males (that adopted more roving movements) to engage in courtship initiation behaviours. Male attraction to female-dominated areas may occur particularly when females are sexually receptive, but was seemingly also driven, to a large extent, by favourable current and feeding conditions.

Though our research quantified patterns of social behaviour and collective movement in *M. alfredi*, we were not able to study the function, development or evolution of these behaviours. Research here is obviously difficult in a large, long-lived and highly mobile species. Comparing the collective movement of wild manta rays under variable environmental conditions (e.g. presence of zooplankton prey or predators) within and between groups may be useful, however. It is likely that plasticity exists in rules of interaction that produce schooling and following behaviour (Schaerf et al. 2017; Kent 2019). Capturing this variation should be possible using aerial observations, and may provide insight into the function of collective behaviours. Including data on variable aspects of the environment would be

useful; for example, the construction of models that track movements of feeding manta rays in relation to the flow of water (and zooplankton) around them might enable more detailed analysis and interpretation of collective and cooperative feeding. Drone-based observations could be used to monitor breaching events, including the propagation of vibrational waves from these, which may be a method of communication between rays (Stevens 2016). Further investigation of information transfer in manta rays is warranted in light of our results. The use of remote cameras rather than human operated cameras is recommended, to avoid unnecessary observer bias.

A limitation in the research presented in this thesis is that it was necessarily based on real-world observations, with little or no control over the study environment. To deal with several issues related to this (including non-independence of individuals and autocorrelated time-series data), we used randomization procedures, including several types of permutation test and Markov modelling. These allowed us to control for various confounding effects that were likely to influence our empirical observations. Importantly, though, in testing for specific causes or consequences of sociality, we relied on our imagination and practical capacity to include all counterfactuals (aspects of what is possible or might have occurred) in the constraints we imposed on the randomisation procedure. To varying degrees, this restricts confidence in our interpretations in each of the empirical data chapters. To test whether communication between manta rays occurs, for example, it will be necessary to study the behavioural response of potential receivers of communication signals in a controlled environment. The use of manipulative experiments potentially offers an alternative route to understand social behaviour. This type of research has been attempted previously in semi-captive elasmobranchs (Guttridge et al. 2009), and the observational methods set out in Chapters IV and V provide an excellent starting point. Possibilities include using drone-based observations to record the collective reaction of groups of rays to a simulated predator (e.g. by playing noise through an underwater speaker). Studies of predator and prey interactions can provide important insights into the speed at which social information is transmitted, which may be important in understanding the function of collective schooling behaviour (Handegard et al. 2012). Studies attempting to elucidate cognitive abilities may be best approached in captive conditions (e.g. Ari and Correia 2008, Ari and D'Agostino 2016). Here it is important to carefully consider the relative ethical merits and demerits of housing manta rays in aquaria, and performing such experiments on captive or wild animals.

6.4. Concluding remarks

Conducting research on the behavioural and spatial ecology of pelagic elasmobranchs is a major challenge. Network-based and social analyses, however, can provide an essential framework in which individual behaviour can be understood in the context of broader population dynamics and susceptibility to anthropogenic threats. Recent advances in tracking and observational technologies offer the opportunity to collect the data on wild elasmobranchs required to assess their social structuring and social connectivity at appropriate spatiotemporal scales. This thesis combines research in multiple disciplines and has incorporated a range of analytical methods within a holistic framework. Its results broaden our understanding of the biology and ecology of a globally vulnerable species of manta ray, providing the first detailed investigation of social organisation in a batoid species. This thesis contributes substantially to knowledge of social processes and the behavioural ecology of manta rays and elasmobranchs in general. This new knowledge should be used to improve the design and implementation of management strategies for these species at a local and regional scale in Eastern Indonesia, and potentially other locations.

Many possible future research directions have been outlined in this **General Discussion**, advocating the use of different types of social network analysis, aerial observations and ethological studies to test specific hypotheses about the causes and consequences of social behaviour, and examine the reproducibility of these results between groups, populations and species. Expanding the use of social network analyses will enable the testing of biologically realistic predictions regarding the impact of changing environmental conditions and fisheries exploitation on elasmobranch populations. Further study of social and collective behaviours will be useful in identifying and mitigating the level of disturbance caused to manta rays by human activities. Studies of social behaviour and social organisation are increasingly seen as vital to understanding population viability and resilience to anthropogenic threats, and in explaining how environmental influences act at the level of the group. This knowledge will help to increase understanding of the drivers of spatial ecology for individuals, groups and populations, guide prioritisation of conservation efforts in critical and threatened habitats, and generate public support for conservation. Recent studies have begun to illuminate these topics in elasmobranchs, and my research throughout this thesis helps to edge open a window into manta rays' social lives. My hope is that the information provided here will be built on and used to help protect manta rays from the many threats they face.

6.5. References

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