Eat-clean-repeat: reef manta rays (*Mobula alfredi*) undertake repetitive feeding-cleaning cycles at an aggregation site in Seychelles

Rachel J. Newsome[1,2]*, Henriette M. V. Grimmel[2],
Dillys K. Pouponeau[2], Ellie E. Moulinie[2], Amy A. Andre[2]
and Robert W. Bullock[2,3]

[1]Physiology, Ecology and Conservation Laboratory, Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute and Environmental and Conservation Sciences, Murdoch University, Perth, WA, Australia, [2]Save Our Seas Foundation – D'Arros Research Centre, Geneva, Switzerland, [3]Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University, Townsville, QLD, Australia

To maximise energy efficiency, manta ray (*Mobula alfredi*, *M. birostris*) foraging and cleaning behaviours are thought to often be mutually exclusive, whereby individuals will only forage when prey density thresholds are met and will only clean when foraging is too energetically costly (i.e., thresholds are not met). Here, snorkel surveys and remote camera cleaning station footage show reef manta rays (*M. alfredi*) undertaking repetitive and short-term movements between surface-feeding and cleaning station visits around D'Arros Island, Seychelles. These observations demonstrate that foraging and cleaning behaviours are not mutually exclusive even when prey densities are high. At D'Arros Island, the proximity of cleaning stations to highly productive foraging areas may afford individuals the opportunity to undertake non-foraging activity without incurring significant energy loss from the shifts in behaviour. These data inform a more nuanced understanding of this species' use of key habitats.

KEYWORDS

energy expenditure, behaviour, manta ray, activity regime, habitat use

1 Introduction

Manta rays (Myliobatidae, Bonaparte 1838) (*Mobula alfredi*, *M. birostris*) are planktivorous ectotherms with a circum-global distribution in tropical and sub-tropical waters (Lawson et al., 2019). As planktivorous species, manta rays must often cope with the boom-and-bust characteristic nature of oligotrophic environments (i.e., Papastamatiou and Lowe, 2005; Papastamatiou et al., 2007), whereby sporadic foraging opportunities may be followed by periods of starvation (Rohner et al., 2017). In response to their patchily

distributed prey resource (Folt and Burns, 1999; Srokosz et al., 2003), manta rays often form predictable aggregations at known locations ("aggregation sites") often associated with high prey availability (Couturier et al., 2011; Armstrong et al., 2016; Harris et al., 2020; Harris and Stevens, 2021). Understanding the function of these aggregation sites is important for mobulid conservation (Palacios et al., 2023). Importantly, foraging opportunities are not wholly responsible for animal presence, with cleaning station visitation (O'Shea et al., 2010; Jaine et al., 2012), socialisation and/or mating opportunities (Stevens et al., 2018) and predator avoidance (Germanov et al., 2019) also known to be drivers.

Different behaviours have different energetic consequences to the individual (e.g., Kacelnik and Houston, 1984; Houston, 1995; Christian et al., 1997; Williams et al., 2006) and current understanding suggests that, in response to this, different behaviours (particularly foraging and cleaning) are often mutually exclusive, triggered by differing conditions and generally occurring at different times (O'Shea et al., 2010; Barr and Abelson, 2019; Weeks et al., 2015). For example, the slow swimming speed associated with filter-feeding is thought to be energetically costly (Alexander, 1990; but see Paig-Tran et al., 2011), and as a result, it is only energetically efficient for manta rays to forage when prey densities reach a threshold that outweighs the energetic costs of filter-feeding (Armstrong et al., 2016; Armstrong et al. 2021b). It even appears that different fine-scale local environmental conditions preferentially drive foraging behaviour and cleaning station visitation within aggregation sites around the world (e.g., Dewar et al., 2008; Jaine et al., 2012; Couturier et al., 2018; Harris and Stevens, 2021). While specific local conditions, such as tidal height and range, may be strongly associated with certain behaviours (e.g., foraging, cleaning), it does not restrict these behaviours from being undertaken under other conditions and cleaning and/or foraging may very well occur outside of these constraints within the same aggregation site, albeit less-frequently (e.g., Jaine et al., 2012; Harris and Stevens, 2021; Harris et al. 2021).

The way an animal uses energy in its environment and how conditions influence the energetic costs of foraging and locomotion can be reconstructed from an animals' energy landscape (Shepard and Lambertucci, 2013). Requirements modulated through energy landscapes can provide explanation to an individual's habitat use, distribution, and migration pathways (Wilson et al., 2012; Shepard and Lambertucci, 2013). Given the disproportionate risk of extinction in large elasmobranchs and shifting global conditions affecting energy balance (Lawson et al., 2019), it is therefore increasingly relevant to develop a more nuanced understanding of energetics and habitat use in these species.

Here, observations are reported of reef manta rays (*M. alfredi*) around D'Arros Island, Seychelles undertaking frequent cycles between surface foraging and cleaning behaviours. To the best of our knowledge, these data suggest definitively for the first time that foraging and cleaning behaviours are not always mutually exclusive in reef manta rays. This has implications for our understanding of reef manta energetics as well as the functioning of key reef manta ray aggregation sites.

2 Methods

D'Arros Island (5°24.9'S, 53°17.9'E) is a 2 km long by 1 km wide coral sand cay, situated within the Amirantes Island Group, Seychelles (Figure 1). D'Arros is encompassed by a recently gazetted 'Zone 1' marine protected area (MPA) that affords the site "high biodiversity protection" (Official Gazette No 34 – Ministry of Agriculture, Climate Change and Environment, 2020). The surrounding reefs provide habitat for over 400 individual reef manta rays (Grimmel, *unpublished data*) that make use of productive foraging areas and cleaning stations year-round with seasonally driven peaks in their presence around the island (Peel et al., 2019, 2020).

2.1 Cleaning stations

The coastal reefs north of D'Arros Island host several cleaning stations, two of which have been identified and are monitored with stationary cameras set at fixed locations at ~ 20 m depth ("MantaCam"). These two stations are situated to the north of D'Arros Island approximately 150 m apart along a west-east axis and are located within 10 meters from the start of the reef crest, where the reef steeply slopes from ~3 m to ~ 20 m depth. As individual manta rays can be identified from unique ventral markings (Beebe and Tee-Van, 1941; Marshall et al., 2008), cameras face upwards to capture images of the ventral surface of reef manta rays as they use the cleaning site. GoPro Hero 8 and 9 cameras (GoPro Incorporation, California, United States of America) with Voltaic 75V always-on external batteries (Voltaic Systems, New York, United States of America) are housed inside waterproof casings and take pictures on timelapse every 10 seconds during daylight hours (0630-1830 or 0600-1800, depending on season). Cameras are changed regularly to ensure near continuous coverage of the sites. Data from each station is downloaded and processed by identifying individual mantas using the station against an ID database of all known individuals within the wider Seychelles archipelago (Seychelles Manta Ray Project). To distinguish between cleaning behaviours and cleaning station visitation for socialization (or other behaviours), cleaning was identified when cleaner wrasse were observed interacting with the individual. Date and timestamps for each sighting are recorded. Any individual that stayed at the station for a prolonged period had the entire duration of that visit noted down.

2.2 Surface-feeding

Reef manta ray surface-feeding behaviour was monitored via survey, whereby a small vessel patrolled the coastal areas (within 1 km from shore) of D'Arros, completing a full circumference of the island. During these surveys, the vessel completed a distance of approximately 7 km around the island at a maximum speed of 8 knots, with the skipper and at least two snorkelers locating manta
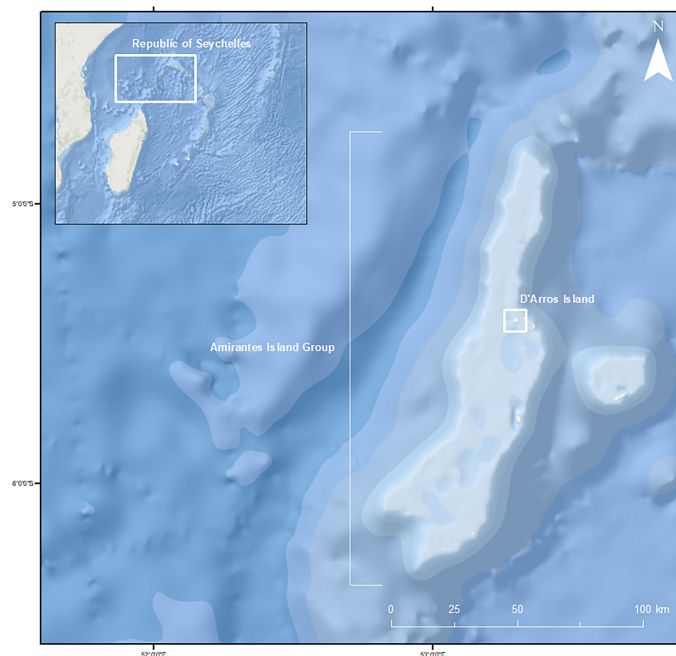
FIGURE 1
D'Arros Island (5°24.9'S, 53°17.9'E) situated within the Amirantes island group of the Seychelles archipelago. Manta survey efforts contained to shallower water depths around the perimeter of the island (within 1 km). Two cleaning stations are situated along the northern edge of the island. Exact locations are not disclosed to protect key habitats of the species. Basemap source: Esri®.

rays. On survey days described here, surveys were undertaken by three or four snorkelers (excluding the skipper) for a duration of approximately three hours. While individuals may be located along the entire survey area, during the surveys identified here individuals were predominantly located along the 2 km stretch north of D'Arros, intersecting where the two cleaning stations are located. The closest proximity of surface-feeding individuals to cleaning stations was approximately 20 m, when individuals were located directly above the cleaning stations. Manta rays located from aboard the vessel were followed via snorkel to collect photo identification of their ventral surface using GoPro Hero 9, 11 or 12. Footage was cross-referenced with the ID database to identify and pinpoint timestamps for each individual when they were surface-feeding. Surface-feeding was identified as when cephalic lobes unfurled and individuals' mouth was open.

2.3 Feeding-cleaning cycles

Repetitive movements, grouped as total numbers of behavioural transits (one-way movements from surface-feeding to cleaning station use or vice versa) as well as feeding-cleaning cycles (feeding, cleaning and back to feeding or vice versa), were quantified from survey and camera data. Behavioural transits were quantified over a maximum of 1-hour periods whereby an individual that was observed surface-feeding (or cleaning) must be observed undertaking the other behaviour within 1-hour of the initial observation. Feeding-cleaning cycles were quantified over a maximum of 2-hour periods whereby an individual had to be observed surface-feeding (or cleaning), transit to

the other behaviour, and then return to the original behaviour within the 2-hour period. This timeframe was based on survey duration and the time-period over which the majority of reef manta rays were observed surface-feeding. Individuals that cycled or transitioned between behaviours but outside of these parameters were not included.

3 Results

Across four survey days during November and December 2023, 11 identified individual reef manta rays undertook repetitive behavioural transits and feeding-cleaning cycles (Table 1). A total of 27 transits (μ = 2.45 ± 0.78 S.D) and 15 cycles (1.36 ± 0.5) were undertaken, with cycles ranging from 11 to 102 min (66 ± 29) in duration (Table 1). Here, duration of cycles is the total time taken for the individual to move from one behaviour (e.g., cleaning) to another (e.g., feeding) and then return again to the original behaviour (e.g., cleaning). Median time taken for an individual to transit between behaviours was 28 minutes (μ = 29.48 ± 17.75 S.D). SC-MA-0014 undertook the quickest transits between behaviours with a mean of 8.33 ± 5.44 minutes. SC-MA-0101 undertook the longest transits with a mean of 48.5 ± 2.5 minutes (Table 1).

Cleaning-only behaviour was the most commonly seen behaviour across the four survey days. The second most common behaviour was feeding-cleaning cycles except on 18 December where feeding-only was the second most common behaviour. The 21 November (n=23) had the highest proportion of individuals undertaking both feeding and cleaning behaviours (56.5%) and

TABLE 1 Metadata table of individual reef manta rays (*Mobula alfredi*) that undertook movements between surface-feeding and cleaning behaviours.

Date	Individual ID	Sex	Maturity	Size class	Surface-feeding (timeframes)	MantaCam West (timeframes)	MantaCam East (timeframes)	Behavioural Transits	Feeding-Cleaning Cycles
14-Nov-23	SC-MA-0298	M	Immature	2	1009-1017, 1140-1144, 1232-1235	–	1104-1112, 1341	2	1
21-Nov-23	SC-MA-0006	M	Mature	3	0900-0901, 1056-1058	1009-1011	1014, 1033-1047, 1126	2	1
21-Nov-23	SC-MA-0100	F	Mature	4	0917-0921, 0928-0929, 1054	0929-0931, 1043-1047	0847-0849, 0941, 1126	4	2
21-Nov-23	SC-MA-0101	F	Mature	4	916	0824-0825, 1009-1011, 1028-1042, 1135-1139, 1306	1002-1009, 1011-1013, 1015-1023, 1141-1154, 1221-1230, 1253-1303	2	1
21-Nov-23	SC-MA-0092	M	Mature	3	0821-0843, 0903-0905, 1026	–	0642-0639, 0938, 0956—0959	2	1
21-Nov-23	SC-MA-0014	F	Mature	3	0842-0846, 0857-0905, 0914	0931-0952	0851-0853, 1427-1430	3	2
21-Nov-23	SC-MA-0321	F	Immature	2	0820-0840, 1056-1057	–	0956-0959, 1121-1125	2	1
21-Nov-23	SC-MA-0281	M	Immature	2	0920, 1055-1058	1135, 1154	0832-0837, 1008, 1154-1158, 1612-1638	4	2
21-Nov-23	SC-MA-0267	F	Immature	1	0905-0916, 1058-1106	1034, 1154, 1434, 1539	1154-1158, 1318-1322, 1434-1442, 1526-1539	2	2
18-Dec-23	SC-MA-0007	F	Mature	4	0824, 0909-0912, 0915-0916, 0947, 1046-1052	–	0916-0920	2	1
19-Dec-23	SC-MA-00461	M	*NA*	*NA*	0928-0930, 0936-0943, 1100-1112, 1130-1136, 1148-1157	1002	0955-0958	2	1

Surface-feeding timeframes are based on how long the individual is in one video. MantaCam timeframes are based on the first and last timestamp for individuals photographed at that cleaning station. Where timeframes consist of a single time, the individual was at the cleaning station or video footage from snorkel surveys were of the individual < 1 minute. This does not necessarily represent the amount of time the individual was feeding or cleaning in the area but instead reflects either the snorkeller moving to a different individual or limitations in MantaCam camera angle. To account for variability in individual wingspan (wingtip to wingtip) estimation based off stereo video, individuals were classed into binned estimates of their wingspan: (1) 2-2.5 m, (2) 2.6-3 m, (3) 3-3.5 m, (4) 3.6-4 m and (5) 4+ m.

feeding-cleaning cycles (34.8%). The 18 December (n=10) had the lowest proportion of individuals exhibiting both behaviours (14.3%) and feeding-cleaning cycles (7%), with an equal representation of cleaning-only and feeding-only behaviours (42.9% for both). Most individuals (excluding SC-MA-0298, -0092, -0321 and -0007), not only undertook repetitive movements between surface-feeding and cleaning behaviours but also repetitively moved between visiting each of the two cleaning stations (Table 1).

4 Discussion

An individual's capacity to minimise energy expenditure (i.e. cost of locomotion) and maximise energy gain through foraging has

direct (e.g., body condition, mortality) (du Plessis et al., 2012; Giles et al., 2020) and indirect (e.g., reproductive success) (Ballard et al., 2010; Jeanniard-du-Dot et al., 2017; Jeanniard du Dot et al., 2018) consequences on fitness and survival. According to optimal foraging theory, animals must maximise energy acquisition by obtaining as much energy as possible through foraging in a given period of time (Schoener, 1971; Norberg, 1977, 2021). Under this assumption, when conditions favour foraging (e.g., plankton densities exceed a threshold), manta rays will exclusively forage in order to meet energetic demands and will not expend energy undertaking other behaviours elsewhere (see O'Shea et al., 2010; Barr and Abelson, 2019). Findings here, however, demonstrate short-term cycles between surface-feeding and cleaning station use in reef manta rays at a Seychelles aggregation site for the first

time. At D'Arros, high-use cleaning stations adjacent to the northern reef slopes coincide with areas of preferred feeding (Peel et al., 2024). The reefs on the northern shores have a steeper topographic relief relative to the south, potentially driving greater upwellings of plankton and influencing observed spatial patterns in feeding at the site. Similarly, the steeper reef slopes around the north of D'Arros make for more pronounced deep reef patches that act as quality cleaning stations. The proximity of these cleaning stations to highly productive foraging areas may mean that cleaning activity can be undertaken without significant loss of energy or that intermittent cleaning confers other benefits to the individual. Cleaning stations play an important role in manta ray fitness, offering an important location for socialisation and potentially improving social learning, predator avoidance and contribute to foraging efficiency through collective feeding events (Perryman et al., 2019). As a result, manta rays are thought to preferentially select cleaning stations with hard coral substrate and specific cleaner wrasse species with these 'quality' cleaning stations contributing to a spatial map the individuals possess of their landscape (Armstrong et al. 2021a). Here, reef manta rays most commonly exhibited cleaning behaviours, whether these were cleaning-only or cleaning alongside feeding behaviours. While cleaning may very well be the most common behaviour over surveyed days, cleaning stations are consistently monitored by remote camera across the entire day whereas surveys are limited to the survey period (~3 hours). Therefore, it is possible that an animal that was only observed cleaning also surface-fed but was not identified during the survey. Regardless, functional cleaning and foraging habitat in close proximity may benefit not just foraging success but also sociability in this population whereby interrupted or unsuccessful cleaning events can be returned to after a brief foraging 'break'. Such quality cleaning sites occurring in concert with productive foraging areas may play an important role in selection of key high-use habitats.

Observations here offer a unique perspective into the energy landscape of D'Arros Island reef manta rays where the seascape hosts opportunities to undertake multiple behaviours simultaneously without suffering an apparent net energy loss through reduced foraging opportunities. Energy landscapes are dynamic, varying in space and time (Masello et al., 2017) and so these observations may be situational even within the D'Arros Island aggregation site as both localised and broad-scale environmental conditions influence energetic costs of behaviour for the population. It should be noted that the need to maximize foraging activity, as according to optimal foraging theory, may not be applicable to all populations of manta ray. Some populations live in highly productive environments where they do not suffer the energetic knife edge associated with oligotrophic conditions (see Papastamatiou and Lowe, 2005; Papastamatiou et al., 2007). For populations where feeding to satiation is not favoured, repetitive and simultaneous cycles between foraging and cleaning events may offer a unique opportunity to undertake a multitude of behaviours

without a net energy loss. Regardless of the potential circumstantial nature of these feeding-cleaning cycles, the data presented here offers important consideration for conservation of key aggregation sites of vulnerable species.

While other aggregation sites suggest feeding and cleaning behaviours may present closer to mutual exclusivity in manta rays (O'Shea et al., 2010; Barr and Abelson, 2019), specific habitats, such as D'Arros, may provide for alternative energetic strategies. D'Arros is not the only site that may offer habitat characteristics that afford multiple behaviours occurring simultaneously. Manta rays in aggregation sites within Raja Ampat, Indonesia, use the habitat for foraging and cleaning, though repetitive feeding-cleaning cycles have not been formally identified at these sites (Setyawan et al., 2020). Areas such as these may be important for both social behaviour and energy acquisition through foraging. Continuous effort should be made into identifying habitat where individuals undertake multiple key behaviours simultaneously and can be done using non-invasive techniques (e.g., remote camera as used in this study, drones as discussed in Setyawan et al., 2020). Increasing anthropogenic pressure at manta ray aggregation sites, particularly cleaning stations (Tratalos and Austin, 2001; Murray et al., 2020), could have ongoing consequences for the capacity of individuals to meet their energy demands if these areas coincide with highly productive foraging areas. Defining the function and overlap in important cleaning, feeding or socialisation areas is therefore imperative to the long-term conservation of these species.

Data availability statement

Ethics statement

Author contributions

Investigation, Methodology, Writing – review & editing. RB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing, Supervision.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

References

Alexander, R. M. (1990). Size, speed and buoyancy adaptations in aquatic animals. *Am. Zoologist* 30, 189–196. doi: 10.1093/icb/30.1.189

Armstrong, A. O., Armstrong, A. J., Bennett, M. B., Richardson, A. J., Townsend, K. A., Everett, J. D., et al. (2021a). Mutualism promotes site selection in a large marine planktivore. *Ecol. Evol.* 11, 5606–5623. doi: 10.1002/ece3.7464

Armstrong, A. O., Armstrong, A. J., Jaine, F. R., Couturier, L. I., Fiora, K., Uribe-Palomino, J., et al. (2016). Prey density threshold and tidal influence on reef manta ray foraging at an aggregation site on the great barrier reef. *PloS One* 11, e0153393. doi: 10.1371/journal.pone.0153393

Armstrong, A. O., Stevens, G. M., Townsend, K. A., Murray, A., Bennett, M. B., Armstrong, A. J., et al. (2021b). Reef manta rays forage on tidally driven, high density zooplankton patches in Hanifaru Bay, Maldives. *Peerj* 9, e11992. doi: 10.7717/peerj.11992

Ballard, G., Dugger, K. M., Nur, N., and Ainley, D. G. (2010). Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Mar. Ecol. Prog. Ser.* 405, 287–302. doi: 10.3354/meps08514

Barr, Y., and Abelson, A. (2019). Feeding–cleaning trade-off: Manta ray "decision-making" as a conservation tool. *Front. Mar. Sci.* 6, 88. doi: 10.3389/fmars.2019.00088

Beebe, W., and Tee-Van, J. (1941). Eastern Pacific expeditions of the New York Zoological Society. XXVIII Fishes from the tropical eastern Pacific. Part 3: rays, mantas, and chimaeras. *Zool. Sci. Contrib. NY Zool. Soc.* 26, 245–280.

Christian, K. A., Baudinette, R., and Pamula, Y. (1997). Energetic costs of activity by lizards in the field. *Funct. Ecol.* 11, 392–397. doi: 10.1046/j.1365-2435.1997.00099.x

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

Couturier, L., Newman, P., Jaine, F., Bennett, M., Venables, W., Cagua, E., et al. (2018). Variation in occupancy and habitat use of *Mobula alfredi* at a major aggregation site. *Mar. Ecol. Prog. Ser.* 599, 125–145. doi: 10.3354/meps12610

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

du Plessis, K. L., Martin, R. O., Hockey, P. A., Cunningham, S. J., and Ridley, A. R. (2012). The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biol.* 18, 3063–3070. doi: 10.1111/j.1365-2486.2012.02778.x

Folt, C. L., and Burns, C. W. (1999). Biological drivers of zooplankton patchiness. *Trends Ecol. Evol.* 14, 300–305. doi: 10.1016/S0169-5347(99)01616-X

Germanov, E. S., Bejder, L., Chabanne, D. B., Dharmadi, D., Hendrawan, I. G., Marshall, A. D., et al. (2019). Contrasting habitat use and population dynamics of reef manta rays within the Nusa Penida marine protected area, Indonesia. *Front. Mar. Sci.* 215. doi: 10.3389/fmars.2019.00215

Giles, S. L., Harris, P., Rands, S. A., and Nicol, C. J. (2020). Foraging efficiency, social status and body condition in group-living horses and ponies. *Peerj* 8, e10305. doi: 10.7717/peerj.10305

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

Harris, J. L., McGregor, P. K., Oates, Y., and Stevens, G. M. (2020). Gone with the wind: Seasonal distribution and habitat use by the reef manta ray (*Mobula alfredi*) in the Maldives, implications for conservation. *Aquat. Conservation: Mar. Freshw. Ecosyst.* 30, 1649–1664. doi: 10.1002/aqc.3350

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

Houston, A. I. (1995). Energetic constraints and foraging efficiency. *Behav. Ecol.* 6, 393–396. doi: 10.1093/beheco/6.4.393

Jaine, F. R., Couturier, L. I., Weeks, S. J., Townsend, K. A., Bennett, M. B., Fiora, K., et al. (2012). When giants turn up: sighting trends, environmental influences and habitat use of the manta ray Manta alfredi at a coral reef. *PloS One* 7. doi: 10.1371/journal.pone.0046170

Jeanniard-du-Dot, T., Trites, A. W., Arnould, J. P., and Guinet, C. (2017). Reproductive success is energetically linked to foraging efficiency in Antarctic fur seals. *PloS One* 12, e0174001. doi: 10.1371/journal.pone.0174001

Jeanniard du Dot, T., Trites, A. W., Arnould, J. P. Y., Speakman, J. R., and Guinet, C. (2018). Trade-offs between foraging efficiency and pup feeding rate of lactating northern fur seals in a declining population. *Mar. Ecol. Prog. Ser.* 600, 207–222. doi: 10.3354/meps12638

Kacelnik, A., and Houston, A. I. (1984). Some effects of energy costs on foraging strategies. *Anim. Behav.* 32, 609–614. doi: 10.1016/S0003-3472(84)80298-5

Lawson, C. L., Halsey, L. G., Hays, G. C., Dudgeon, C. L., Payne, N. L., Bennett, M. B., et al. (2019). Powering ocean giants: the energetics of shark and ray megafauna. *Trends Ecol. Evol.* 34, 1009–1021. doi: 10.1016/j.tree.2019.07.001

Marshall, A. D., Pierce, S. J., and Bennett, M. B. (2008). Morphological measurements of manta rays (*Manta birostris*) with a description of a foetus from the east coast of Southern Africa. *Zootaxa* 1717, 24–30. doi: 10.11646/zootaxa.1717.1

Masello, J. F., Kato, A., Sommerfeld, J., Mattern, T., and Quillfeldt, P. (2017). How animals distribute themselves in space: variable energy landscapes. *Front. Zool.* 14. doi: 10.1186/s12983-017-0219-8

Murray, A., Garrud, E., Ender, I., Lee-Brooks, K., Atkins, R., Lynam, R., et al. (2020). Protecting the million-dollar mantas; creating an evidence-based code of conduct for

manta ray tourism interactions. *J. Ecotourism* 19, 132–147. doi: 10.1080/14724049.2019.1659802

Norberg, R. A. (1977). An ecological theory on foraging time and energetics and choice of optimal food-searching method. *J. Anim. Ecol.* 46, 511–529. doi: 10.2307/3827

Norberg, R.Å. (2021). To minimize foraging time, use high-efficiency, energy-expensive search and capture methods when food is abundant but low-efficiency, low-cost methods during food shortages. *Ecol. Evol.* 11, 16537–16546. doi: 10.1002/ece3.8204

O'Shea, O. R., Kingsford, M. J., and Seymour, J. (2010). Tide-related periodicity of manta rays and sharks to cleaning stations on a coral reef. *Mar. Freshw. Res.* 61, 65–73. doi: 10.1071/MF08301

Paig-Tran, E. M., Bizzarro, J. J., Strother, J. A., and Summers, A. P. (2011). Bottles as models: predicting the effects of varying swimming speed and morphology on size selectivity and filtering efficiency in fishes. *J. Exp. Biol.* 214, 1643–1654. doi: 10.1242/jeb.048702

Palacios, M. D., Stewart, J. D., Croll, D. A., Cronin, M. R., Trejo-Ramirez, A., Stevens, G. M. W., et al. (2023). Manta and devil ray aggregations: conservation challenges and developments in the field. *Front. Mar. Sci.* 10. doi: 10.3389/fmars.2023.1148234

Papastamatiou, Y. P., and Lowe, C. G. (2005). Variations in gastric acid secretion during periods of fasting between two species of shark. *Comp. Biochem. Physiol. Part A: Mol. Integr. Physiol.* 141, 210–214. doi: 10.1016/j.cbpb.2005.05.041

Papastamatiou, Y. P., Purkis, S. J., and Holland, K. N. (2007). The response of gastric pH and motility to fasting and feeding in free swimming blacktip reef sharks, *Carcharhinus melanopterus*. *J. Exp. Mar. Biol. Ecol.* 345, 129–140. doi: 10.1016/j.jembe.2007.02.006

Peel, L. R., Meekan, M. G., Daly, R., Keating, C. A., Collin, S. P., Nogues, J., et al. (2024). Remote hideaways: first insights into the population sizes, habitat use and residency of manta rays at aggregation areas in Seychelles. *Mar. Biol.* 171. doi: 10.1007/s00227-024-04405-6

Peel, L. R., Stevens, G. M., Daly, R., Daly, C. A. K., Lea, J. S., Clarke, C. R., et al. (2019). Movement and residency patterns of reef manta rays *Mobula alfredi* in the Amirante Islands, Seychelles. *Mar. Ecol. Prog. Ser.* 621, 169–184. doi: 10.3354/meps12995

Peel, L. R., Stevens, G. M., Daly, R., Keating Daly, C. A., Collin, S. P., Nogués, J., et al. (2020). Regional movements of reef manta rays (*Mobula alfredi*) in Seychelles waters. *Front. Mar. Sci.* 7, 558. doi: 10.3389/fmars.2020.00558

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

Rohner, C. A., Flam, A. L., Pierce, S. J., and Marshall, A. D. (2017). Steep declines in sightings of manta rays and devilrays (Mobulidae) in southern Mozambique. *PeerJ Preprints* 5, e3051v3051. doi: 10.7287/peerj.preprints.3051v1

Schoener, T. W. (1971). Theory of feeding strategies. *Annu. Rev. Ecol. systematics* 2, 369–404. doi: 10.1146/annurev.es.02.110171.002101

Setyawan, E., Erdmann, M. V., Lewis, S. A., Mambrasar, R., Hassan, A. W., Templeton, S., et al. (2020). Natural history of manta rays in the Bird's Head Seascape, Indonesia, with an analysis of the demography and spatial ecology of *Mobula alfredi* (Elasmobranchii: Mobulidae). *J. Ocean Sci. Foundation* 36, 49–83. doi: 10.5281/zenodo.4396260

Shepard, E. L., and Lambertucci, S. A. (2013). From daily movements to population distributions: weather affects competitive ability in a guild of soaring birds. *J. R. Soc. Interface* 10, 20130612. doi: 10.1098/rsif.2013.0612

Srokosz, M., Martin, A., and Fasham, M. (2003). On the role of biological dynamics in plankton patchiness at the mesoscale: An example from the eastern North Atlantic Ocean. *J. Mar. Res.* 61, 517–537. doi: 10.1357/002224003322384915

Stevens, G. M., Hawkins, J. P., and Roberts, C. M. (2018). Courtship and mating behaviour of manta rays Mobula alfredi and M. birostris in the Maldives. *J. Fish Biol.* 93, 344–359. doi: 10.1111/jfb.13768

Tratalos, J. A., and Austin, T. J. (2001). Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. *Biol. Conserv.* 102, 67–75. doi: 10.1016/S0006-3207(01)00085-4

Weeks, S. J., Magno-Canto, M. M., Jaine, F. R., Brodie, J., and Richardson, A. J. (2015). Unique sequence of events triggers manta ray feeding frenzy in the Southern Great Barrier Reef, Australia. *Remote Sens.* 7, 3138–3152. doi: 10.3390/rs70303138

Williams, R., Lusseau, D., and Hammond, P. S. (2006). Estimating relative energetic costs of human disturbance to killer whales (Orcinus orca). *Biol. Conserv.* 133, 301–311. doi: 10.1016/j.biocon.2006.06.010

Wilson, R. P., Quintana, F., and Hobson, V. J. (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. R. Soc. B: Biol. Sci.* 279, 975–980. doi: 10.1098/rspb.2011.1544