

Large marine protected areas can safeguard highly mobile species: Manta rays in Komodo National Park, Indonesia

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Background. The reef manta ray (*Mobula alfredi*) is a globally threatened species and an iconic tourist attraction for divers and snorkelers in Komodo National Park (NP), Indonesia. Komodo NP, established in 1980 has functioned as the longest running protected area for manta rays worldwide. Yet, there are no population level studies investigating manta ray demographics and habitat use within the park. Further, characterization of existing threats to manta rays within the park is also limited.

Methods. This study uses a long-term (July 2004 – March 2018) library of photo-identification data coupled with observer reports to investigate manta ray demographics and habitat use within the park at four sites frequented by tour operators: Cauldron – CL, Karang Makassar – KM, Mawan – MW, and Manta Alley – MA. Residency and movements of manta rays were investigated with maximum likelihood analyses and Markov movement models.

Results. A total of 1,104 individual manta rays were identified over this period. Most individual manta rays displayed a higher affinity to specific sites. The highest re-sighting probabilities came from the comparatively remote MA, located south of Komodo Island. Although the two sites in the central park, KM and MW, are only ~5 km apart, individual manta rays still displayed affinity to each site. There was some exchange of individuals between MA and the two central sites (~35.5 km apart), particularly seasonal, but more manta rays traveled from the south to the central area than vice versa. Female manta rays were more mobile than males. Similar demographic groups used KM, MW, and MA for foraging, cleaning, cruising, or courtship activities. The northern site, CL, had a higher proportion of immature manta rays present, which displayed a higher prevalence of foraging activity than observed at the other sites. Fishing gear-related injuries were noted on 56 individuals (~5%), and predatory injuries were present on 32 individuals (~3%). Tourism within the park increased over the study period, with a combined 34% more dive boats at KM and MW from 2014 to 2017, indicating the need to assess tourism carrying capacity at sites important to manta rays and implement measures to minimize disturbance to the species.

Discussion. Overall, the large marine conservation zone of the Komodo National Park appears to have safeguarded several distinct critical habitats for manta rays that encompass all key stages of the manta ray life cycle and accommodates seasonal manta ray movements. Further research into their long-range

movements, connectivity, and identifying and protecting other critical aggregation areas within the region is vital to secure the recovery of the species.

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Abstract

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Introduction

Even highly mobile marine megafauna species often spend a disproportionate amount of time in and return to specific sites within their broad range (e.g., Baird *et al.*, 2008; Bowen & Karl, 2007; Dewar *et al.*, 2008; Graham *et al.*, 2016; Rooker *et al.*, 2008). Identifying and protecting these habitats should be prioritized to maximize population recovery for threatened species (Chapman *et al.*, 2015; Heupel *et al.*, 2007; Hueter *et al.*, 2005; Martins *et al.*, 2018; Norse, 2005; Speed *et al.*, 2010), particularly ecologically sensitive areas like nursery grounds, adult reproductive areas, and feeding grounds. It is also important to maintain protected movement corridors between such sites (Hooker *et al.*, 2011).

Manta rays (*Mobula alfredi* – Krefft, 1868; *M. birostris* – Walbaum, 1792) are long-lived, to at an estimated 45 years (Marshall *et al.*, 2019, 2020), with low fecundity of approximately one offspring every two years (Deakos *et al.*, 2012; Marshall and Bennet, 2010), resulting in low population growth rates, estimated as maximum intrinsic rate of population

increase (r_{\max}), of 0.166 or less per year (Dulvy *et al.*, 2014; Rambahiniarison *et al.*, 2018). Both species are threatened with extinction (Marshall *et al.*, 2019, 2020) due to declining population trends (Dulvy *et al.*, 2014; Ward-Paige *et al.*, 2013), and consequently are listed in Appendix II of the Convention on the International Trade of Endangered Species (CITES) and Appendices I and II of the Convention on the Conservation of Migratory Species (CMS). The demand for *Mobula* spp branchial gill plates, used in the Asian medicinal markets, incentivizes fishers to target manta rays and this trade has become the most significant contributor to manta ray population declines globally (Marshall *et al.*, 2019, 2020; O'Malley *et al.*, 2017; Stewart *et al.*, 2018).

Manta rays were heavily fished in Indonesia, which ranked within the top five mobulid fisheries nations (Heinrichs *et al.*, 2011). The Komodo National Park (NP), formally established in 1980, primarily as a conservation zone for the endemic Komodo dragon (*Varanus komodoensis*) (Erdmann, 2004a), coincidentally also served as the first refuge for *Mobula alfredi* (hereafter referred to as manta rays, as only this species is considered in this work). The first study on *M. alfredi* within Komodo NP (Dewar *et al.*, 2008) predated the taxonomic split from *M. birostris* (Marshall *et al.*, 2009) and investigated their movements within the area (October 2000 – June 2003). Passive acoustic telemetry employed between September 2000 and May 2003 identified regular use of specific areas and connectivity of manta ray sites within the park. These were welcome findings at a time when manta ray fisheries were active through the Lesser Sunda region (Heinrichs *et al.*, 2011; Lewis *et al.*, 2015; White *et al.*, 2006), as the park was seen to be affording the resident manta ray population an increased level of protection from fishers. The Komodo NP has subsequently been touted as a successful example of a beneficial Marine Protected Area (MPA) for manta rays (Rigby *et al.*, 2019).

In 2014, both manta species were formally protected by bans on directed fisheries in Indonesia throughout the entire exclusive economic zone (an area of over 6 million km²; Ministry of Marine Affairs and Fisheries, 2014). The nation-wide legislative protection of manta rays was adopted after these species were listed on the aforementioned conservation conventions, but the Indonesian government was also incentivized to protect the valuable manta ray tourism industry in the country, estimated to be over 10.6 million per year (Mustika *et al.*, 2020; O'Malley *et al.*, 2013). However, the species are still subject to bycatch and illegal directed fisheries (Booth *et al.*, 2020; Croll *et al.*, 2016), particularly in movement corridors (Germanov & Marshall, 2014; Lewis *et al.*, 2015). Designated conservation zones, such as the Komodo National Park (NP) and the Nusa Penida Marine Protected Area (MPA), offer an additional layer of protection due to general fishing restrictions and increased levels of compliance monitoring including from the tourism sector.

In the current study, we expand on earlier research in the Komodo NP (Dewar *et al.*, 2008; Germanov & Marshall, 2014) using a 14-year photo-identification library to investigate population-level habitat use of manta rays. Our study goals are to assess: (1) site affinity and movement, (2) population structure, (3) behavior, and (4) potential threats to manta rays to help identify specific management needs within the Komodo NP.

Materials & Methods

Study Area

The Komodo National Park (Komodo NP; Figure1) covers 1,817 km² of land and sea (Erdmann, 2004b). This area lies east of Bali and Borneo and west of Papua and contains high

levels of endemic terrestrial species and is on the southern side of the Flores Sea “Marine Wallace line” (Barber *et al.*, 2000). This is a complex oceanographic region (Komodo NP marine area = 1,214 km²) characterized by three large main islands (Komodo, Rinca, and Padar) and additional smaller islands within the park boundary totaling 603 km² of terrestrial habitat (Erdmann, 2004b). The three large islands create the large shallow (≤ 100 m), Lintah Strait, through the park’s center. The park boundaries are flanked by Sape Strait, another large, slightly deeper ($\sim 100 - 200$ m) strait to the west of Komodo Island, a narrow passage to the east of Rinca Island (Molo Strait), and deep water (> 800 m) basins to the north and south (Figure 1). Water exchange through the park is driven by strong tidal flow currents (up to ~ 15 km/h in the Lintah Strait), with water from the Indian Ocean flowing north through the straits on the incoming tide and water from the Pacific Ocean flowing south on the outgoing tide (Erdmann, 2004c) via the Indonesian Throughflow (ITF). Upwelling to the south of the Lesser Sunda region is strongest from June through October, coinciding with the south-east monsoon, active May – October, and serves to enrich the waters in southern Komodo NP during this time of year (Ningsih *et al.*, 2013). Nutrient-rich waters flow throughout the straits, particularly with spring tides. This trend is reversed during the inverse north-west monsoon period (November – April), with nutrient-rich water flowing through Komodo NP from the Flores Sea located to the north.

We focused our analyses on four main sites within the Komodo NP (from north to south: Cauldron – CL, Karang Makassar – KM, Mawan – MW, Manta Alley – MA) based on the consistent manta ray sightings at these locations and, hence, regular visitation by tourism operators which facilitated both research and citizen science contributions (Table 1). Three of these sites, KM, MW, and MA, were included in a previous acoustic telemetry study of manta ray movements within the park (Dewar *et al.*, 2008). Cauldron, the previously undescribed site, located in the north area of the park, is a shallow channel (< 25 m) between two islands with complex bathymetric structure and strongly affected by tidal currents. Located in the central area of the park, adjacent to a sandy island with a fringing reef, KM refers to a gently sloping shallow (< 18 m deep) rubble field that runs ~ 1.5 km north to south, with patchy reef and coral heads where manta rays clean (i.e., cleaning stations; see Germanov *et al.*, 2019a for a more detailed description). The island MW, ~ 5 km to the east of KM, has a shallow ‘cleaning station’ at 5 m on a sandy slope from three down to 20 m on its south-eastern tip. Shallow rubble reefs also serve as cleaning stations to the north and south of MW’s sandy slope, covering an overall distance of ~ 0.7 km. Strong tidal currents affect both these central sites (i.e., KM and MW). Approximately 35.5 km in a straight-line distance from KM is MA, in south-west Komodo NP. This site encompasses several rocky islands in a large bay lined with steep cliff walls and rocky shorelines. Several channel formations are exposed to surge and strong tidal current flows on the islands’ northernmost side, where manta rays clean and cruise. To the east and west of the islands are sloping reefs (to ~ 35 m), with several manta ray cleaning stations.

Data Collection and Processing

Data collection, including citizen science, contributed data, validation and processing, followed the procedures described in Germanov *et al.* (2019). Data on manta ray sightings (date, time, location, and identifying ventral photographs of manta rays) logged by observers and the public were accessed from the online database ‘Manta Matcher’ Wildbook (www.mantamatcher.org, Supplementary Figure 1). Approximately 20 trained observers contributed manta ray data from 2013–18. Briefly, their training included details of how to take manta ray identification photographs, identify sex, maturity and behavior, estimate size, and how

to record injuries and entanglements with fishing gear, along with other data collection relevant to effective manta ray management in the region, such as the number of dive boats present on-site (Germanov *et al.*, 2019a). Photo contributions from the public were encouraged through educational presentations, informative dive briefings, and awareness materials about ‘Manta Matcher’ (i.e., posters and infographics) displayed at local dive centers and within ‘liveaboard’ dive boats.

All identifying photographs were manually matched to an ID catalog, with the assistance of an automated pattern matching algorithm (Germanov & Marshall, 2014; Town *et al.*, 2013) or external software (‘MantaUtil,’ Winstanley, 2016). The lead author independently validated the sighting records included in the study. Manta ray sex was assigned based on the absence (female) or presence (male) of claspers, and maturity status was assigned based on clasper size in males or the presence of a pregnancy bulge or pectoral fin mating scars in females. This methodology avoids a default of classifying females as immature in the absence of maturity indicators and accurate size estimates; instead, their maturity status was classed as “unknown” (Marshall and Bennett, 2010; Marshall *et al.*, 2011). Behavior was classified into four mutually exclusive categories: foraging, cleaning, cruising, and courtship. Two additional non-exclusive behavior categories, foraging/cleaning and courtship/cleaning, were used when more than one behavior was observed for an individual manta ray within a single dive. Further details on behavioral categorization are provided in Germanov *et al.* (2019a).

The use of Manta Matcher also facilitated the identification of manta ray movements between geographical regions, such as re-sightings between Komodo NP and the Nusa Penida MPA. Sightings of all individuals are publicly available at www.mantamatcher.org. Identification numbers for the most re-sighted individuals and those making long-range movements are provided in the results section. These identification numbers can be input into the online database's search function to reveal full sighting histories for the individual manta rays.

Statistical Analyses

The core sightings records used for statistical analyses (outlined below) were collected between January 2013 and April 2018. Annual logged sightings records exceeded 400 across those years, with near year-round coverage for the three of the four main sites considered here. Data from 2018 were excluded from seasonal analyses, as year-round survey effort was not available, and from CL (all years) as there were relatively few records. Logged trained observer dives were used as a proxy for survey effort, assigned as per dive, as dive time was not recorded before 2016 (Supplementary Figure 2). However, dive times set by dive operators are a maximum of 60 minutes and the means of available dive times (post-2016) across sites were relatively consistent (58.3 ± 7.1 min). Since most dive operators complete two or more dives per day at the remote site MA (i.e., effectively doubling daily effort compared to other sites, E. Germanov, pers. obs.), we have presented total mean monthly sightings as a more appropriate comparison between MA and KM/MW as the number of hours and daily dives logged was not regularly available from public data.

Pearson's product-moment correlations, using the `cor.test` function of the R statistical software (R Core Team, 2018), were used to investigate the relationship between the annual number of survey days and the number of sightings. The `chisq.test` function (R Core Team, 2018) was used to test whether the numbers of individuals and sightings differed between males and females at KM, MW, MA and CL. Sex ratio data for each site were compared using chi-squared (χ^2) goodness of fit tests (one-dimensional contingency table), while sex ratios and behavior

frequencies between the sites were compared using a multiple-dimensional contingency table (vassarstats.net, 2020). To facilitate χ^2 testing for behavior, where counts were less than five per site, the data were condensed into four categories (i.e., foraging/cleaning was reclassified to foraging, and courtship/ cleaning was reclassified to courtship). Data from CL were excluded from χ^2 testing for behavior, and data from both CL and MW were excluded from χ^2 testing for seasonality in foraging, as the counts were less than five for several categories. A Fisher's Exact Probability Test was used for 2x2 contingency tables if counts were less than five. The Yates' continuity correction was applied to tests where there was one degree of freedom.

Residency and Movement Analyses

Following the habitat use definitions set by Chapman *et al.*, (2015), we reserve the use of the term 'residency' to refer to the generally uninterrupted occupation of a limited area by an individual for a defined length of time; and 'site fidelity' as the return of an individual to a site after a periodic absence of greater or equal duration to the residency period. Presence-only sightings data precludes discerning whether these same site visitations are true site fidelity or, at least for some individuals, movements within a large home range. In this case, the term 'site affinity' is more appropriate to describe the same site re-sightings (Couturier *et al.*, 2011; Jaine *et al.*, 2014). This term is also more appropriate in instances where there is high variability in site use between individuals and at least some individuals use several sites to a similar extent (see Germanov *et al.*, 2019a).

We compared daily manta ray re-sighting data against residency models to investigate residency patterns using a modified maximum likelihood approach, following Germanov *et al.* (2019). We excluded CL data from analyses, as sighting records at this site were sparse compared to those at KM, MW, and MA (Table 1). Lagged Identification Rate (LIR), defined as the probability of re-identifying an individual after a given time lag (Whitehead 2001), was calculated using the 'Movement Analyses' module of the program SOCPROG 2.8 (Whitehead, 2009). Empirical results were compared to model closed and open populations scenarios to estimate movement parameters (Table 2 and Supplementary Table 1). We evaluated emigration, immigration, re-immigration, and mortality in the various open population models. The lowest quasi-Akaike information criterion (QAIC) value, accounting for the over-dispersion of the data, determined the model that best fit the residency characteristics for each site (Whitehead, 2007). We estimated the probability of re-sightings in other sites using 'within/between' LIR analysis to test for population-level mixing between sites. Model fits were bootstrapped 1,000 times to generate standard errors (SE).

The annual transition probabilities between sites, i.e., the likelihood of an individual manta ray moving from one area to another within a year, were calculated using a parameterized Markov movement model (Tables 3 and 4; Whitehead, 2009). This model includes a hypothetical 'outside' area (i.e., leaving the study site/s). Movements between the three core sites (KM, MW, MA) were investigated by grouping KM and MW as a collective 'central' site and investigating movements to and from MA in the south. Optimized values of transition probabilities were bootstrapped 1,000 times to generate SE, and the maximum number of evaluations was set to 10,000. Mortality, including permanent emigration from all core sites, was considered in the model.

Ethics Statement

This study was conducted under permits issued by the Indonesian Ministry of Research and Technology (Permit #458/SIP/FRP/E5/Dit. KI/XII/2015; Permit Extension#11/TKPIPA/E5/Dit. KI/XI/2016 and #86/EXT/SIP/FRP/E5/Dit.KI/XI/2017) and the Komodo National Park (#SI.1432/BTNK-1/2016). This study was carried out in accordance with the approval of the Animal Ethics Committee, Murdoch University (R2781/15). Photographic and sighting data were collected opportunistically by the public and contributed to a public online repository (www.mantamatcher.org) developed explicitly to facilitate citizen science contributions to manta ray research.

Results

Sightings and Survey Effort

We identified 1,104 individual manta rays from 4,163 sightings (after excluding 765 daily re-sightings of the same individuals) across 791 unique dates (from 7 July 2004 to 31 March 2018) within the Komodo NP (Table 1). Sighting records for four sites within the park, Cauldron (CL), Karang Makassar (KM), Mawan (MW), and Manta Alley (MA), and within core survey years (2013 – 2018) represented ~ 94.7% ($n = 3,941$) of total sightings (Table 1). Sightings records prior to 2013 ($n = 177$) included 139 individuals. Annual manta ray sightings varied across study years (Table 1) and were positively correlated with survey effort ($r = 0.94$, $p = 0.002$). There were >400 sightings logged on Manta Matcher in each of the core years. Data submissions to Manta Matcher gradually increased over the study period with increased awareness of the citizen science program within the dive community, surpassing data collected solely by trained observers in 2014 (Supplementary Figure 1).

A total of 1,085 individual manta rays were identified from data collected during the core study years (January 2013 to April 2018) within the Komodo NP. Data collected from the three core study sites KM, MW, MA, yielded 1,061 individual manta rays. Of these individuals, 749 were sighted in KM, 535 in MW, and 376 in MA. Data collected from CL yielded 48 individuals, of which 22 were not sighted elsewhere, and two were sighted at all the other three sites. A further 45 individual manta rays also had sighting records in sites other than the above four sites, of which two had no other records elsewhere. Considering KM, MW, and MA sites combined (i.e., the three sites with substantial sighting records), the discovery curves of newly discovered individuals and the days elapsed showed a steep rise until approximately 685 individuals after 860 d (Figure 2). The curve continued to increase at a slightly lower rate until the end of the study period (1,061 individuals after 1,913 d) (Figure 3). Neither the combined discovery curve nor any of the site-specific discovery curves approached an asymptote. Gaps in the discovery curves indicate periods in which no new individuals were identified due to survey gaps during these periods.

Sightings across seasons and years

Sightings rates averaged (mean \pm 1 SE) 760 ± 130 sightings/year from 2013 – 2017, and January – March of 2018 had 188 sighting records. The highest number of sighting records was from 2017 ($n = 1,198$), with the second-highest number from 2014 ($n = 838$; Table 1). However, survey effort by trained observers was lower in 2015 and 2016 (Supplementary Figure 1). Monthly mean sightings varied among years (Figures 3A). There was an overall increase in

sightings from 2013 to 2017 across the sites, with the largest increase observed at MW. Sightings per dive recorded solely by trained observers varied modestly for sites among years, except for KM, where there was a ~two-fold increase in sightings per dive during 2015 and 2016 (Supplementary Figure 2A). Sightings per dive by trained observers also varied across months and sites (Supplementary Figure 2B), following similar trends to the sightings overall, with fewer sightings for the central sites (MW and KM) in August and September (Figure 3B). While trained observers recorded higher sighting rates for MA mid-year, data were not available for December–February and in June, prohibiting us from commenting on seasonality trends based on these data alone.

Population Structure

The overall sex ratio of males (507) to females (498) in Komodo NP did not differ significantly from 1:1 ($\chi^2_1 = 0.1$, $p = 0.777$), with the sex of 56 individuals remaining unknown. Likewise, the sex ratio did not differ significantly from 1:1 at any of the three main sites: KM (0.92:1, $\chi^2_1 = 1.4$, $p = 0.234$), MW (0.97:1, $\chi^2_1 = 0.2$, $p = 0.692$) or MA (0.9:1, $\chi^2_1 = 1.0$, $p = 0.319$) (Figure 4). While there were more males than females (23 vs. 16, with nine unknown individuals) identified at CL, this difference was not significant ($\chi^2_1 = 1.3$, $p = 0.262$). There was no significant association between site and sex for individuals ($\chi^2_2 = 0.3$, $p = 0.851$) at the three main sites.

Approximately 90% (454) of the males were sexually mature, with ~ 11% (50) of males remaining immature within the five core study years. An additional 11 immature males were identified at CL and not sighted at other sites. Altogether, 96 individuals (all males) or 9% of all individuals were immature at some point throughout the study, with 39 reaching maturity over this period. Females are more difficult to assign a maturity status without accurate size estimates, which the study lacked, and for 290 females representing ~27% of individuals, the maturity status was unknown. Considering KM, MW and MA combined, at least 43% (212) of the females were sexually mature, and just under half of those (92, 18% of females) were pregnant during the study period. Overall, the maturity status of males and females was comparable among all sites for individuals (Figure 4; $\chi^2_3 = 1.2$, $p = 0.742$).

However, looking at maturity status alone (i.e., excluding sex), there was a relationship between the site and maturity status of individuals ($\chi^2_3 = 78.7$, $p < 0.0001$), with relatively more immature than mature males sighted at CL (38% vs. 21%; Figure 4). Notably, of the manta rays identified at CL sighted more than once (range: 2 – 11 sightings), eight out of 17 individuals (47%) were immature males, with two maturing during the study (Supplementary Figure 4). All females except one encountered more than once at CL were of unknown maturity status. In contrast, all manta rays (females = 6 and males = 5; Supplementary Figure 3) with recorded long-range movements between Komodo NP and Nusa Penida MPA were mature, with estimated sizes ranging from 2.25 – 4 m for the six individuals with size data reported.

Residency and Movement

From 2013 – 2018, the majority (768; 72%) of manta rays were encountered more than once within KM, MW, and MA (Supplementary Figure 5). Of these individuals, 48 (5%) were sighted >10 times, with up to a maximum of 21 sightings per individual. The mean re-sightings per individual were 3.6 ± 0.1 , and 598 manta rays (56%) were re-sighted across multiple years (Figure 5). Considering all available data (2008 – 2018), the longest time between the initial and most current re-sighting for an individual (INKNP0154A) was 13.4 years. Further, using all

available data (2004 – 2018) on long-range movements to Nusa Penida MPA, the days between recaptures in the different regions for the 11 individuals varied widely (range: 33 – 1,550 d), averaging 391.4 ± 77.7 d. In addition to sightings within the Komodo NP, 11 (1%) individual manta rays sighted within the Komodo NP were also sighted within the Nusa Penida MPA on 89 separate days (including pre-2013 data; Supplementary Figure 3).

Interchange between sites

We recorded 104 (9.8%) individuals in all three core sites, and 275 (25.9%) were recorded in one of the central areas (either KM or MW) and MA in the south. We recorded 961 (91%) individuals in the park's central sites and an additional 100 (9%) individuals exclusively at MA. The Markov movement model showed that each individual's re-sighting probability was highest within rather than between sites (0.39 at KM, 0.59 at MW, and 0.58 at MA; Table 3A). However, there was a relatively high probability of movement from KM to MW (0.37 ± 0.16) or vice versa (0.29 ± 0.17), indicating sizeable interchange between the two adjacent central sites (~5 km apart). When these two central sites were grouped for analysis (Table 3B), there was a substantial probability of re-sighting within the central area (0.87), with less, yet considerable re-sightings (0.53) at MA. Further, the movement between central sites and MA was asymmetric, with far less movement from central sites to MA (0.11 ± 0.04) than vice versa (0.47 ± 0.11). More movement to the central sites from other 'outside' sites was modeled (0.11 ± 0.20) than from 'outside' sites to MA (0.000 ± 0.02). Notably, the model's maximum number of iterations was exceeded for these analyses, suggesting that the estimated SEs are inaccurate and larger than expected (H. Whitehead, Dalhousie University, pers. comm.). While excluded from movement analyses due to the smaller sample size, we observed that 40% of individuals sighted at CL were also sighted at central sites, and 13% at MA.

We tested for full interchange between sites using LIR analysis (Figure 6). A 'within/ between' analysis between just KM and MW did not support full interchange even within the central area (Supplementary Figure 6), as the curves for re-sightings within the same or different sites did not converge during the study period, indicating some level of site affinity to exist. LIRs were thus run for each site independently.

Site-specific analyses

The best-fit re-sighting model for all three sites was Model H (Table 1), a model which includes emigration and re-immigration with mortality. Mortality (which includes permanent emigration) was considered negligible for all sites and analyses (≤ 0.045). The LIRs within the two central sites were similar and much lower (~half) than those at MA, indicating that individuals have a higher probability of re-sightings at MA than either KM or MW (Figure 7). Model H scenarios provide estimates for the time individuals spend within (residence time in) and out (residence time out) of an area. Individuals stayed approximately twice as long at MA (1.6 ± 12.9 d) than at MW (0.8 ± 0.3 d), although there was high variability in residence time among individuals. The estimated time that individuals spent outside of these three sites ranged between 5.8 – 6.9 d. Overall, the results for MA indicated more variability between individuals' residence time than at MW and KM (Supplementary Table 2).

Sex-linked analyses

There were significantly more sightings of females (2,016) to males (1,672) ($\chi^2_1 = 32.1$, $p < 0.0001$). This was the trend observed at KM, MW, and MA, with KM having the highest female sightings (57%) compared to males (43%) ($\chi^2_1 = 35.1$, $p < 0.0001$). In contrast, the comparatively fewer (103) sightings at CL were biased towards males (66% vs. 34% females, $\chi^2_1 = 9.8$, $p = 0.002$). Likewise to the population structural differences outlined above, there was no significant association between site and sex for sightings ($\chi^2_2 = 4.9$, $p = 0.087$) at the three main sites. However, when CL was included in the analysis, an association was detected ($\chi^2_3 = 21.5$, $p < 0.0001$). Exploration into potential sex-linked differences in site use showed no substantial differences in LIRs between the sexes for KM, MW, or MA (Supplementary Figure 7, Supplementary Table 1). Movement analyses indicated that females tended to move more from central sites to MA, and from 'outside' to the central sites, than males (Table 4), suggesting that there might be some sex-linked differences in site use. Adequate data was not available to perform LIR or movement analyses with sightings at CL.

Behavior

Manta rays were observed foraging, cleaning, cruising, and engaging in courtship at KM, MW, and MA ($n = 2,306$, Figure 8A). There was a significant association between behavior and site ($\chi^2_6 = 202.1$, $p < 0.001$), with MW having the highest proportion of cleaning behavior (74%), while CL had the lowest (6%). More cleaning was observed at KM (53%) than MA (39%). Overall, few observations of mixed behaviors (i.e., cleaning and courtship = 20; cleaning and foraging = 1) were made for individuals within a single survey dive. Courtship behavior was observed at all sites except CL. Courtship activity took place throughout the year, although the number of recorded events and individuals engaged in courtship varied (Figure 8B). Cruising behavior was frequently observed at CL (74%) and, to a lesser extent, MA (45%). Both locations have strong currents flowing through narrow channels where manta rays are commonly observed swimming into the current, but not necessarily foraging or cleaning. Foraging observations differed between the study sites. There were fewer foraging records for individuals at MW (1%) than at other sites, especially CL, where foraging records were higher than elsewhere (20%). The highest number of individuals foraging at one time (up to 30 individual identifications in one day, $n = 3$) were recorded at KM during the NW monsoon.

Injury Rates

Predatory injuries, i.e., bite marks, were present on 32 (~3%) individuals. Fifty-six individuals (~5%) had cephalic fin, pectoral fin, or fishing line injuries. Nine individuals had more than one injury. The breakdown of injuries was: 13 individuals with hook and line entanglements and 30 and 26 truncations or disfigurements to the cephalic fins and pectoral fins, respectively. We noted six injured pregnant individuals during the study period.

Boating Activity

The two central sites, KM and MW, are the closest to the population center at Labuan Bajo on Flores Island (Figure 1), from where most diving/ snorkeling tours operate. Based on observer logs, these sites saw a combined 34% increase in the number of tour boats recorded from 2014 to 2017. This increase was greater at MW than at KM, with the daily average of boats at MW increasing from 1.8 in 2014 to 3.4 in 2017 (81% increase), while at KM, boats increased from 5.8 in 2014 to 7.7 in 2017 (33% increase). The number of boats on-site during July or

August were 102% (12.3 boats) and 50% higher (4.1 boats) than the September – June average for KM and MW, respectively (Figure 9B). Records for CL and MA were sparse and were not available year-round. However, for comparative purposes, and to establish a baseline, from 2014 – 2017 inclusive, the daily mean and median numbers of boats at CL were 2.6 ± 0.3 and 2 (range: 1–14), respectively ($n = 57$). While the number of boats is much lower than those of the central sites, the daily numbers in August 2017 were well above average (i.e., 10 and 14 boats), suggesting that a significant increase in tourism is also occurring at this site. Based on limited records ($n = 27$), it appears that the daily mean (1.9 ± 0.2) and median (2; range: 1–4) boat numbers at MA have remained relatively stable over time.

Discussion

Komodo National Park hosts one of the largest populations of reef manta rays globally (Germanov *et al.*, 2019a), highlighting the importance of Komodo NP as a manta ray refuge during Indonesia's transition from manta fishing to non-consumptive use through tourism. New identifications were common throughout the study, with a steadily increasing discovery curve indicating 1,100 as a minimum number of manta rays using the Komodo NP that will likely increase with continued effort. The present study is the first to report on the Komodo NP manta rays at a population level and characterize demographics. While individual rays are highly mobile (Germanov & Marshall, 2014) and around 1% of individuals have been re-sighted ~ 450 km away at the Nusa Penida MPA, they show distinct site affinity within the Komodo NP. Manta rays were commonly sighted at four sites in the park: Cauldron (CL), Karang Makassar (KM), Mawan (MW), and Manta Alley (MA). Site-use differed between demographic groups with mature individuals frequenting the reefs for cleaning and the initiation of courtship activity and immature males frequenting sites with more foraging activity observations. The heterogeneity of site use indicates that management requirements need to be tailored to prevent disruption to manta ray behaviors.

Habitats for a range of manta ray demographics and behaviors

All manta ray demographic groups were represented within Komodo NP. The three core sites, KM, MW, and MA were all dominated by mature manta rays and had similar demographic profiles. Komodo NP's manta rays had an equal ratio of males to females overall, in contrast to many other well-studied populations (Germanov *et al.*, 2019a). However, the observed bias towards mature males over females might be attributed to the difficulty in assigning maturity to females in the absence of accurate size estimates and visual maturity indicators (i.e., mating wing scars or pregnancy bulge). At sites where mature manta rays were prevalent (i.e., KM, MW and MA) cleaning was generally the most observed behavior, and courtship activity was only observed at these sites. These observations are like those from Manta Point in the Nusa Penida MPA, where the site is used predominantly for cleaning, social activity, and courtship (Germanov *et al.*, 2019a), as well as observations at adjacent reefs within Raja Ampat that were deemed to be "courtship supersites" (Setyawan *et al.*, 2020). Our findings support the idea that cleaning stations act as lekking sites (i.e., aggregation areas where courtship and mate competition take place; Deakos *et al.*, 2011; Stevens, 2016).

On the other hand, more immature male rays and fewer mature female rays were observed at CL, where the demographic and behavioral profiles differed substantially from the three other main sites. Used primarily as a foraging site by immature manta rays, CL possibly

serves as a nursery for these individuals (Germanov *et al.*, 2019a; Heupel *et al.*, 2007; Martins *et al.*, 2018; McCauley *et al.*, 2014; Setyawan *et al.*, 2020; Stevens, 2016). Elasmobranch nurseries are habitats where yearlings are disproportionately sighted compared to adults and are used for extended periods and across years (Heupel *et al.*, 2007). These habitats likely provide substantial benefits to maturing young, such as nutrition, temperature regulation, and predator avoidance (Heupel *et al.*, 2019).

Long-term observations of immature males within Komodo NP revealed that 50 (52%) did not reach maturity within the five core study years, whereas 39 did (40%). Thus far, the age of maturity for male manta rays reported ranges from 3 to 13 years, depending on the study location (Stewart *et al.*, 2018). Our observations suggest that the age of maturity for male manta rays in Komodo NP might be closer to those reported for Mozambique (3–6 yrs.; Marshall *et al.*, 2011) and Japan (4–9 yrs.; Kashiwagi, 2014) than reported for the Maldives (9–13 yrs; Stevens, 2016). However, the lack of size data to classify immature individuals as yearlings precludes more detailed analyses on the age of maturity.

Fewer immature individuals were recorded in Komodo NP ($n = 96$, 8.7%) compared to the other studied regional aggregation, Nusa Penida MPA ($n = 123$; 19.7%, Germanov *et al.*, 2019). This discrepancy in the identified immature individuals in Komodo NP could indicate insufficient survey effort at CL and at other sites not regularly visited by tour operators (e.g., German Flag) that may be important to immature individuals. Dewar *et al.* (2008) reported that German Flag had the highest visitation rates of any other sites investigated, including data on immature individuals as small as 1.8 m. Further, individuals were commonly observed feeding at German Flag (Dewar *et al.*, 2008). Like observations at other manta ray feeding grounds in Indonesia (Germanov *et al.*, 2019a; Setyawan *et al.*, 2020) and elsewhere (Stevens, 2016; Peel *et al.*, 2019a), it is likely that immature individuals also disproportionately use German Flag rather than nearby cleaning stations at MA. This is because immature manta rays would have lower cleaning requirements because of their generally lower parasite loads (Treasurer, 2002). While the present study lacks sighting data at German Flag, the habitat use patterns of frequently sighted immature individuals (≥ 10 sightings) from other study sites within Komodo NP and Nusa Penida MPA show that when younger, some individuals have higher site affinity than when they are older (Germanov *et al.*, 2019a).

Demographic influences on site use and movements

Population demographics, particularly age- and sex-linked differences in movements, appear to influence fine-scale habitat use in manta rays (Deakos *et al.*, 2001; van Duinkerken, 2011; Germanov *et al.*, 2019a; Perryman *et al.*, 2019; Stevens, 2016). However, in Komodo NP, unlike in the nearest studied aggregation, Nusa Penida MPA (Germanov *et al.*, 2019a), the Lagged Identification Rates - LIRs did not differ between the sexes. Similarly, Couturier *et al.* (2018) did not consider sex a significant predictor of manta ray visitation rates to Lady Elliot Island in Australia. However, movement analysis suggests that females within the Komodo NP are slightly more mobile, and females may have ranged ‘outside’ the study sites more than males. In contrast, studies elsewhere report that males are more mobile than females (Deakos *et al.*, 2011; van Duinkerken, 2011; Germanov *et al.*, 2019a; Perryman *et al.*, 2019; Stevens, 2016). However, sex-biased dispersal does not appear to be the sole factor in the long-range movements from Komodo NP to the Nusa Penida MPA, as individuals of both sexes were documented moving between these locations (Germanov & Marshall, 2014).

Once mature, it appears that individuals shifted to a more mobile lifestyle, characterized by increased movements between nearby sites in Komodo NP, Nusa Penida MPA (Germanov *et al.*, 2019a), and elsewhere (Peel *et al.*, 2019a). Within the Nusa Penida MPA (Germanov *et al.*, 2019a), we suggested that age-linked shifts in site use were linked to prey availability and prey density (Armstrong *et al.*, 2016). Thus, a lower prey density might be able to sustain immature or smaller individuals, whereas larger individuals might need to forage primarily offshore to meet their greater energy demands (Lawson *et al.*, 2019; Nøttestad *et al.*, 1999). Another potential explanation for age-linked shifts in site use is the formation of social structures between individuals, which appear to be demographically influenced in manta rays (Perryman *et al.*, 2019) and other elasmobranchs (Heupel and Simpfendorfer, 2005; Guttridge *et al.*, 2011).

Manta ray site use underscores MPA effectiveness

Hundreds of manta rays were re-sighted within the Komodo NP and displayed a high degree of site affinity to distinct locations. While the results from our study indicate that connectivity exists throughout the park, within/between analysis did not align with a fully mixed population. Further, affinity within the park was not uniform, and manta rays displayed higher affinity to MA in the south than to sites centrally located in the park (MW, KW), highlighting the importance of MPAs to be large enough to encompass as key aggregation sites (Peñaherrera-Palma *et al.*, 2020). These observations parallel the conclusions of an earlier acoustic telemetry study using sighting-independent monitoring and indicate that residency trends were conserved for over a decade (Dewar *et al.*, 2008). Long-term and high site affinity trends are reported for manta rays elsewhere in Indonesia (Germanov *et al.*, 2019; Perryman *et al.*, 2019) and globally (Andrzejaczek *et al.*, 2020; Couturier *et al.*, 2018; van Duinkerken, 2011; Peel *et al.*, 2019; Venables *et al.*, 2020). Together, these similar findings across the years and geographies indicate that large conservation zones, such as the Komodo NP, that encompass critical habitats and complete demographics can effectively afford long-term protection to manta populations (Stewart *et al.*, 2016).

Estimations of residence time in and out of sites were most variable for MA, potentially a reflection of differential site use by a specific demographic, e.g., males being more mobile than females (van Duinkerken, 2011), mature individuals being more mobile than juveniles (Germanov *et al.*, 2019a; Peel *et al.*, 2019a), or social groups (Perryman *et al.*, 2019). Notably, Dewar *et al.* (2008) also reported frequent observations of manta rays feeding at German Flag, a site directly adjacent to MA (~1.8 km away). The present study lacked information from German Flag but, based on the results from Dewar *et al.* (2008), it is possible that sustained foraging opportunities at this site contributed to the higher residency at MA, particularly as in the previous study, 20 out of 24 individuals (83.3%) recorded at German Flag were also recorded at MA.

There was higher interchange (i.e., immigration and emigration) between the two nearby central sites (~4.5 km apart) than elsewhere, indicating substantial connectivity between the individuals using these locations. More individuals were identified from the two central sites, but these individuals had a lower probability of being re-sighted (lower LIR) than those observed at MA. Further, the resident times in central sites were also shorter than those observed at MA, albeit with less variability. These observations could be explained by repeated movements of individuals between the two central sites. Indeed, grouping KM and MW for movement analysis indicated that most movements were within this central area rather than to MA in the south. However, a certain degree of structure was still maintained. Conversely, nearly half of the individuals moved northward from MA to the central area of the park. A further notable

percentage (~11%) of movements to the central sites were from ‘outside’ areas. These outside areas might include CL, or other manta ray aggregation areas, such as the Nusa Penida MPA, where there is documented exchange (Germanov & Marshall, 2014; Conservation International Indonesia, 2016).

One notable difference between the present and the previous acoustic telemetry study (Dewar *et al.*, 2008) is that MW in central Komodo NP contained an important cleaning station that was visited by half of the region’s known individuals. In contrast, few visitations to this site were previously reported despite >1-year receiver deployment. Further, the northern site CL was not previously investigated, and this is the first time this manta ray habitat is formally reported on, indicating that long-term, population-level studies are valuable for capturing habitat use information that might otherwise be missed by short-term sampling a small representation of the population. Population doubling times for *M. alfredi* have not been estimated; however, estimates for *M. birostris* indicate long population doubling times of ~15 – 87 years (Rambahiniarison *et al.*, 2018), and the estimated generation length for both species is 29 years (Marshall *et al.*, 2019, 2020). Thus, long-term, ongoing studies are crucial to ensure current MPA management and protection strategies are sufficient and effective and provide data to answer key questions on population dynamics.

Environmental influence on seasonal movements

The Komodo NP is uniquely located in an area of several oceanographic features (i.e., mixing of waters from the Pacific Ocean via the Indonesian Throughflow (ITF) and the Indian Ocean, tidal mixing, and productive upwelling) which are likely to provide highly productive waters year-round for manta rays (Ningsih *et al.*, 2013). The local productivity and in turn zooplankton availability in the region shifts in response to these broader regional oceanographic processes. Densely concentrated prey makes for prime feeding grounds to support the many manta rays that use the Komodo NP (Armstrong *et al.*, 2016), and manta ray site use and movements between sites are likely influenced by prey availability (Anderson *et al.*, 2011; Harris *et al.*, 2020). For example, in Mozambique higher manta ray numbers were seen at cleaning stations when prey was locally abundant, indicating that manta rays preferentially visit cleaning stations on reefs close to where they are feeding (Rohner *et al.*, 2013). In Komodo NP, the seasonal shifts in the prevailing winds, precipitation, and sea temperature, broadly referred to as the north-west and south-east monsoons, coincide with manta ray visitations increasing in the south during the south-east monsoon and in the central region during the north-west monsoon (Dewar *et al.*, 2008; present study). Seasonal-associated shifts in manta ray abundance also occur elsewhere (Anderson *et al.*, 2011; Couturier *et al.*, 2018; Peel *et al.*, 2019; Setyawan *et al.*, 2018), and it appears that Komodo NP is large enough area to accommodate seasonal manta ray movements in this region of Indonesia.

Fine-scale oceanographic conditions, bathymetry, and tidal currents appear to affect MA and the central sites/CL differently, likely influencing prey availability and seasonal variations in manta ray site use (Peel *et al.*, 2020). The southern site, MA, faces the Indian ocean and adjacent deep basins and is more directly exposed to the south-east monsoon seasonal upwelling (Ningsih *et al.*, 2013). The resulting increase in local productivity at this site coincides with increased manta ray sightings in the south-east monsoon. Further, tidal current and phase had a lesser effect on visitations in MA (Dewar *et al.*, 2008), presumably because nutrient availability in the south is less dependent on tidal transport. Tidal transport is likely the primary way nutrients and prey are delivered to the central sites (KM and MW), which are sheltered from direct Indian

Ocean exposure by the large Komodo, Padar, and Rinca islands. In line with this phenomenon, Dewar *et al.* (2008) found that on the spring tides (i.e., during a full and new moon), when currents and tidal transport are highest, manta ray visitations to KM and neighboring sites increased.

Tidal transport of nutrients into the central area would hypothetically occur year-round, allowing for regular foraging opportunities and for manta rays to use the central area year-round. In Germanov *et al.*, (2019b), we noted foraging behavior under specific tidal conditions on the north-west section of KM. However, we were recorded fewer feeding events during the south-east monsoon at this location. During the north-west monsoon, when we would expect productivity to be high in the park's central area, we recorded mass feeding events of up to 30 individuals. Interestingly, ~12 km to the north of KM, the site CL appears to support feeding for some individuals during the south-east monsoon season, when productivity in the north is generally lower. This site is essentially a channel between two islands where tidal current flows, and potentially plankton, is concentrated, providing feeding opportunities for what appears to be primarily a specific demographic of individuals (i.e., immature individuals). Thus, prey availability sustaining optimal foraging conditions for manta rays is likely a factor of seasonal influences on productivity, tidal delivery, and specific topographical features that concentrate prey.

Previously, Dewar *et al.* (2008) noted that temperature was a predictor for manta ray visitations to sites within Komodo NP, with most site visits ($\geq 83\%$) occurring between 25 and 28°C, with no visitations above 29°C. However, thermal thresholds alone are unlikely to be responsible for the observed temperature preference. While manta rays exhibited temperature preferences in other locations, optimal temperatures varied considerably from location to location: $\geq 21^\circ\text{C}$ in southern Mozambique (Rohner *et al.*, 2013), between 21 and 24°C at Lady Elliot Island, Eastern Australia (Jaine *et al.*, 2012), 28°C in the Amirante Islands, Seychelles (Peel *et al.*, 2019), and within the full temperature range of the Red Sea (21.6 – 34.2°C) (Braun *et al.*, 2014). Similar to the association between productivity and temperature at Lady Elliot Island (Couturier *et al.*, 2018), the optimal temperatures for manta ray visitations observed within the Komodo NP are more likely a reflection of the increased localized productivity from deep, cold water upwelling (Putra *et al.*, 2020). Seasonal weather patterns largely govern upwelling in the region (Ningsih *et al.*, 2013), with the times and areas of increased productivity aligning with seasonal trends in manta ray abundance.

It is vital to continue to investigate local environmental drivers specific to each manta ray aggregation area. Amassing data on these different areas worldwide indicates that environmental predictors for manta ray abundance vary, and unique local factors likely dictate when conditions are most optimal for foraging and cleaning (Barr & Abelson 2019; Jane *et al.*, 2012). To predict manta ray site use in other sites within the park and within the region, we could monitor these large-scale shifts in oceanographic conditions with remote sensing of sea surface temperature and surface chlorophyll-*a* concentration (Dewar *et al.*, 2008; Jaine *et al.*, 2012; Harris *et al.*, 2020; Putra *et al.*, 2020).

Komodo NP is crucial to regional population recovery

Since its inception, Komodo NP has likely acted as a refuge for reef mantas for 30 years before declaring nationwide manta ray protection. There may now be spillover from aggregations within the park that could repopulate depleted areas throughout the Lesser Sunda region. Until recently, manta rays were actively targeted in fisheries <400 km to the east and

west of the Komodo NP (White *et al.*, 2006; Heinrichs *et al.*, 2011; Lewis *et al.*, 2015), which suggests that additional adjacent aggregations might exist, or might become more apparent as populations recover (Pierszalowski *et al.*, 2016; Salton *et al.*, 2021). Long-range movements from Komodo NP to Nusa Penida MPA and elsewhere in the Lesser Sunda region (Germanov & Marshall, 2014; Conservation International Indonesia, 2016), coupled with the lower individual re-sighting rates and site-specific LIRs (i.e., higher degree of transience) in Komodo NP compared to previous reports elsewhere in Indonesia (Germanov *et al.*, 2019a; Perryman *et al.*, 2019), indicate a degree of dispersal from the park's studied aggregations. However, we did not extensively survey some large areas of the Komodo NP, such as the north of Komodo Island, Padar Island, and the east of Rinca Island. Thus, other manta ray high-use areas are probable within the park boundaries (Conservation International Indonesia, 2016), requiring additional research within the Komodo NP.

Links between different populations enable the exchange of genetic diversity (Bonfil *et al.* 2005; Skomal *et al.* 2009), bolstering the resilience of populations and ecosystems (Oliver *et al.*, 2015; Sgrò *et al.*, 2011). These processes are likely occurring with adjacent proposed manta ray subpopulations in the Raja Ampat MPA, which show limited exchange (Setyawan *et al.*, 2020). Interchange of Komodo's manta rays might also be occurring with aggregations in locations where there were historic manta fisheries or elsewhere where studies are not yet completed at adjacent islands in the archipelago, such as Sumba and Rote. Connectivity of the Lesser Sunda region with further Indonesian aggregations, such as Raja Ampat, West Papua and Sangalaki, East Kalimantan is less likely as they are further than the currently known movement range for *M. alfredi* (~500 km). Additionally, deep basins can be barriers to movement between Lesser Sunda and Raja Ampat (Deakos *et al.*, 2011; Peel *et al.*, 2020). In contrast, the interchange along the shallow continental shelf with northern Australia might be more likely (Armstrong *et al.*, 2020). Thus, it is vital to mitigate threats outside of the Komodo NP, particularly in potential movement corridors. Telemetry tracking studies would provide more information on movement corridors throughout the region, connectivity between conservation zones, and highlight any seasonality trends in long-range movements. Genetic analyses can be used in tandem with telemetry to provide information on population connectivity throughout Indonesia and neighboring countries like Australia, where exchange might occur (Venables *et al.*, 2020).

Local Threats

Growing tourism

Identifying key habitats and presence/absence trends can improve the tourism experience by increasing the chances of encounters with manta rays (Barr & Abelson, 2019; Dewar *et al.*, 2008; O'Malley *et al.*, 2013). However, it is essential to consider that mass gatherings of manta rays may coincide with crucial feeding, cleaning, social or reproductive events, where minimal disturbance to natural behavior is necessary (Armstrong *et al.*, 2016, Germanov *et al.*, 2019a; Stevens, 2016, Weeks *et al.*, 2015). The rapid increase in marine tourism at manta ray sites in Indonesia (Germanov *et al.*, 2019a), and a major (~ 14-fold) increase in tourism in the Komodo NP (Komodo NP, pers. comm.), underscores the need for effective tourism management to avoid potential negative impacts (i.e., reviewed by Stewart *et al.*, 2018; Trave *et al.*, 2017; Tyne *et al.*, 2014). Further, overcrowding can reduce the quality of the experience and tourist satisfaction (Mustika *et al.*, 2020; Ziegler *et al.*, 2012). Tourism in the Komodo NP has greatly increased since the Dewar *et al.* (2008) study, which aimed to improve the understanding of the spatial

distribution of manta rays residing in the Komodo NP and help establish a viable manta ray tourism industry. Additional information is now needed to guide management better to regulate the rapidly expanding marine tourism in the park and prevent undue pressure on the manta rays in this critical habitat (e.g. Division of Boating and Ocean Recreation, 2016; Germanov *et al.*, 2019a; Kasmidi & Gunadharma, 2017; Venables *et al.*, 2016). To combat the rising pressure from tourism, in September 2019, the Komodo NP began to trial limitations on the number of boats and divers/ snorkelers allowed in the water simultaneously at the popular manta ray aggregation site Karang Makassar. While regulations on appropriate marine conduct within the park are socialized with operators, the consequences against infringements remain minimal.

Tourism boats regularly visit manta ray sites carrying between 10 and 35 divers/snorkelers per day (Komodo Diver Operators Community, pers. comm.). The central area manta rays sites are the most accessible year-round and receive the bulk of visits, which increased by 34% percent within five years. Thus, manta rays with greater site affinity to the central area are at risk of chronic disturbance - especially KM, which is repeatedly used by most identified manta rays. In September 2019, the Komodo NP authority introduced daily limits on the number of boats and people allowed to visit KM to 32 boats carrying a maximum of ten divers (Komodo National Park, pers. comm.) to cap diver interactions with manta rays. However, at the time of writing, the other manta ray aggregation sites remain without restrictions, and it is foreseeable that caps on KM will displace tourism pressure to nearby MW.

The cleaning station at MW is especially small and has lower tourism carrying capacity than KM or MA. Divers commonly overcrowded this area during the peak tourist season (July and August; E Germanov, pers. obs). Further, tourism boats dropping off and picking up divers commonly drive over the shallow reef housing cleaning stations creating noise pollution, which startles cleaning rays (E Germanov, pers. ob). Excessive divers on the site could substantially reduce the quality or length of cleaning station visits by manta rays, similar to the disturbance of feeding rays by swimmers elsewhere (Garrud, 2016; Gómez-García *et al.*, 2021; Venables *et al.*, 2016). Cleaning provides manta rays with a vital health service (i.e., removing parasites and facilitating wound healing), and its disruption could affect individual fitness (O'Shea *et al.*, 2010). Further, cleaning stations likely serve as hubs for significant behavioral interactions, such as courtship, and thus reduced visitations might have population-wide implications (Perryman *et al.*, 2019; Stevens, 2016; Stewart *et al.*, 2018). More divers visiting these reefs also increase the risk of habitat destruction by poor diving techniques (Trave *et al.*, 2017). Increased boat traffic in manta ray feeding aggregation areas likely also increase the risk of boat strikes and propeller injuries (McGregor *et al.*, 2019).

In the north of Komodo NP, tourism at CL also appears to be on the rise. This site is generally accessible year-round, and continued use of this site by as many as ten or more boats at a time (> 100 divers/snorkelers), without strict adherence to best practice codes of conduct, will likely have a substantial impact on foraging manta rays (Garrud 2016; Venables *et al.*, 2016). The narrow channel at CL also serves as a passage for boats and this general boat traffic further increases the pressure on manta rays in the area.

Continued monitoring of boat and tourist numbers at all sites is necessary to advise managers. Carrying capacity estimates for boats and divers/snorkellers for all popular manta ray sites, restrictions on boat speed and minimum distances to foraging manta rays, and known cleaning stations are strongly recommended to minimize disturbance to the manta rays and to ensure the safety of divers/snorkelers. Further, marked zones of no entry for divers can discourage entry into known cleaning stations. General best practice codes of conduct explicitly

developed for SCUBA diving, and snorkeling with manta rays are available online (Marine Megafauna Foundation Indonesia, 2018; Manta Trust, 2018), as well as an example of detailed guidelines for activities at a manta ray cleaning station in Raja Ampat, Indonesia (Kasmidi & Gunadharma, 2017). Consideration should be given as to how these codes of best practice could be implemented effectively in the Komodo NP.

Impacts from fisheries and natural predators

Fishing activities continue to threaten manta ray populations in Indonesia to some extent (Germanov *et al.*, 2019a), even if only by sub-lethal injuries (Stewart *et al.*, 2018). Fewer individuals were recorded with fishing gear injuries within the Komodo NP than in the neighboring Nusa Penda MPA (5% vs. 14%; Germanov *et al.*, 2019a) or Hawaii (10%; Deakos *et al.*, 2011) but had more than the Ningaloo Coast World Heritage Area (~1%; McGregor *et al.*, 2019). A better understanding of manta ray site use and limiting fisheries to specific gear types in high-use areas and along movement corridors would enhance conservation measures (Graham *et al.*, 2016). While all the current study sites in the Komodo NP are within no-take fishing zones, in practice it is logistically prohibitive to strictly enforce these regulations, and non-compliance is common (E. Germanov, pers. obs.; Dive Operators Community of Komodo, pers. comm.).

Approximately 3% of manta rays had predatory injuries compared to 5% with fishing gear injuries. The potential predators in this region include grey reef sharks *Carcharhinus amblyrhynchos*, silvertip sharks *C. albimarginatus*, Java sharks *C. amboinensis*, bull sharks *C. leucas*, oceanic whitetip *C. longimanus*, dusky sharks *C. obscurus*, tiger sharks *Galeocerdo cuvier*, great hammerhead *Sphyrna mokarran*, and bluntnose sixgill *Hexanchus griseus* (White *et al.*, 2006), similar to those proposed for manta rays in Mozambique (Marshall & Bennet, 2010). Of those mentioned above, divers regularly encounter only grey reef sharks and, less commonly, silvertip sharks. Thus, manta rays in this region might be less exposed to predators than in other locations across their range (Marshall & Bennet, 2010). However, it should be noted that anthropogenic and predator injuries observe and count only those individuals who have survived the encounters and do not provide a full indication of the number of individuals impacted. Modeled mortality rates were very low (~ 0), similar to those of the Nusa Penida MPA, suggesting that mortality due to fisheries or natural predators is low for the manta rays sighted in the Komodo NP. In addition, these analyses cannot discern between true mortality or permanent immigration.

Limitations

We looked at hundreds of individuals' residency and movement patterns; however, our sighting-based approach was limited temporally and spatially to when and where divers are present in the water (i.e., by observer/photographer effort). For example, annual weather patterns influenced the results. Strong winds during December–February limit access to the north (CL) and central (KM, MW) sites, while there is limited access to the south (MA) during June–August. Environmental conditions consequently reduced survey effort. Further, the few manta ray sightings recorded from December–March for MA might also be an artifact of low sampling effort, as most boats do not travel to MA at that time. However, Dewar *et al.* (2008) also reported fewer manta visitations to MA during December–March via a sightings-independent acoustic telemetry approach. The few sighting records for German Flag, and none for Padar Kecil, which the previous study identified as important sites, results from insufficient sampling effort at these sites. Tourism operators rarely visit these sites because of sub-optimal environmental conditions

(e.g., swell and visibility). Nevertheless, the similarity in results between the present study and Dewar et al. (2008) validates the use of sightings data and a citizen science approach to make population-level observations. Dewar *et al.*, (2008) revealed that manta rays typically used habitats within Komodo NP during the day, indicating that our sightings-based sampling during the day nearby cleaning stations is an accurate record of site use.

Conclusions

This long-term study confirms that Komodo NP is (1) an essential habitat for manta rays with several documented high-affinity aggregation sites that individuals move within. (2) Different aggregation areas are used differently by immature individuals and adults. (3) Immature individuals generally showed affinity to foraging grounds, whereas adults used the same sites for foraging, cleaning, and reproductive behaviors. (4) Manta ray injuries from fisheries and, to a lesser extent, predation were readily observed, and by-catch in movement corridors outside of MPAs will continue to pressure these depleted populations. Tourism use of manta aggregation sites increased during the study timeframe requiring a science-based management strategy to be developed, implemented, monitored, and adapted to maintain these essential habitats from undue anthropogenic disturbance. Further, to be sustainable, national conservation strategies for manta rays need to account for the uneven financial benefits that manta tourism provides, as benefits need to reach the communities that still rely on fisheries (Mustika *et al.*, 2020). Nevertheless, it appears that Komodo NP has afforded manta rays some site-specific protection from directed fisheries before the nationwide manta ray fisheries ban in 2014. Komodo NP highlights the benefits of large MPAs as a conservation tool. After decades of fishing in surrounding areas, Komodo NP still retains large manta ray aggregations that allow for broad-scale recovery in Indonesia with careful ongoing management and threat mitigation.

Ongoing long-term monitoring is necessary to ensure management and protection strategies successfully safeguard manta rays going forward. To overall increase the current understanding of site use, movements, population demographics, and dynamics within the Komodo NP, we recommend expanding the survey area to other locations that tracking studies revealed manta rays occupy (e.g., German Flag and Padar; Dewar *et al.*, 2008; East Rinca and West Komodo; Conservation International Indonesia, 2016). Additional studies have the potential to reveal other aggregation sites important for courtship and yearlings. However, studies at additional sites will require a dedicated research program as they are less accessible/less visited by tourism operators, hence citizen science programs. Further, population abundance and survival remain to be estimated for the manta population in Komodo NP (Couturier *et al.*, 2014, Marshall *et al.*, 2011). An enhanced understanding of females' maturity status, pregnancy, and birthing rates is crucial for the regional manta ray population dynamics (Deakos, 2012; Marshall & Bennett, 2010). Longitudinal abundance estimates would also be useful in gauging the impact of tourism at cleaning stations, which has yet to be empirically assessed. Abundance estimates can then be correlated with the number of boats and divers in the water visiting cleaning stations. Further, studies enabling a better understanding of the environmental influences on prey density and foraging in the region will help inform manta population ecology (Anderson *et al.*, 2010; Armstrong *et al.*, 2016; Barr & Abelson, 2019; Dewar *et al.*, 2008; Jaine *et al.*, 2012; Harris *et al.*, 2020).

Acknowledgements

This study would not have been possible without the support of Dive Operators Community of Komodo, the local dive community, and many citizen scientists. Notably, we thank, D. Arriaga, J. Arriaga, M. Cobussen, S. Ecob, S. Geier, S. Inderbitzi, D. Keim, N. Longfellow, J. Marlow, F. Nompas, and for their photo contributions, data processing assistance, and overall dedication to Indonesia's manta rays. Further, we appreciate the data processing assistance provided by L. Auditore, R. Cooper L. Ellevog, and E. Sinderson, and other Marine Megafauna Foundation staff and volunteers. Wildbooks provided the use of the online database MantaMatcher.org. We thank G. Winstanley who provided the use of 'MantaUtil' for streamlined data processing. We thank H. Whitehead for the guidance he provided on the use of Markov movement models, M. Calver and R. Admiraal for statistical analysis assistance, D. Chabbane for SOCPROG use assistance and S. Venables for plotting using R and critical reading of the manuscript. Dharmadi contributed meaningful discussions towards country-wide implications for manta rays in Indonesia. He, unfortunately, passed before the final version of the article was completed but left a significant legacy for shark and ray conservation in Indonesia in his wake, including this study. Bathymetry information used in creating Figure 1 was available from GEBCO_2014 Grid, version 20150318; www.gebco.net. We thank members of the Faculty of Marine Sciences and Fisheries, Universitas Udayana, Bali, Indonesia for assisting in creating Figure 1. We are grateful for the study permit from the Indonesian Ministry of Research (Ristek Dikti) and from the Komodo National Park and the assistance of Park Rangers and staff, D. Indrisari, and Y. J. Hamzah. This paper represents HIMB and SOEST contribution numbers XXX and XXX, respectively.

References

- Anderson RC, Adam MS, Goes JI. 2011. From monsoons to mantas: seasonal distribution of *Manta alfredi* in the Maldives. *Fisheries Oceanography*, 20:104-113.
- Andrzejczek S, Chapple TK, Curnick DJ, Carlisle AB, Castleton M, Jacoby DM, Peel LR, Schallert RJ, Tickler DM, Block BA. 2020. Individual variation in residency and regional movements of reef manta rays *Mobula alfredi* in a large marine protected area. *Marine Ecology Progress Series*, 639:137-153.
- Armstrong AJ, Armstrong AO, Bennett MB, McGregor F, Abrantes KG, Barnett A, Richardson AJ, Townsend KA, Dudgeon CL. 2020. The geographic distribution of reef and oceanic manta rays (*Mobula alfredi* and *Mobula birostris*) in Australian coastal waters. *Journal of fish biology*, 96:835-840.
- Armstrong AO, Armstrong AJ, Jaine FR, Couturier LI, Fiora K, Uribe-Palomino J, Weeks SJ, Townsend KA, Bennett MB, Richardson AJ. 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.
- Baird RW, Gorgone AM, McSweeney DJ, Webster DL, Salden DR, Deakos MH, Ligon AD, Schorr GS, Barlow J, Mahaffy SD. 2008. False killer whales (*Pseudorca crassidens*) around the

903 main Hawaiian Islands: Long-term site fidelity, inter-island movements, and association patterns.
904 *Marine Mammal Science*, 24:591-612.

905 Barber PH, Palumbi SR, Erdmann MV, Moosa MK. 2000. A marine Wallace's line?. *Nature*,
906 406:692-693.

907 Barr Y, Abelson A. 2019. Feeding–Cleaning Trade off: Manta ray ‘decision making’ as a
908 conservation tool. *Frontiers in Marine Science*, 6:88.

909 Booth H, Pooley S, Clements T, Putra MIH, Lestari WP, Lewis S, Warwick L, Milner-Gulland
910 E. 2020. Assessing the impact of regulations on the use and trade of wildlife: An operational
911 framework, with a case study on manta rays. *Global Ecology and Conservation*, 22:e00953.

912 Bowen BW, Karl S. 2007. Population genetics and phylogeography of sea turtles. *Molecular*
913 *ecology*, 16:4886-4907.

914 Braun CD, Skomal GB, Thorrold SR, Berumen ML. 2014. Diving Behavior of the Reef Manta
915 Ray Links Coral Reefs with Adjacent Deep Pelagic Habitats. *PLoS One*, 9:e88170.

916 Chapman DD, Feldheim KA, Papastamatiou YP, Hueter RE. 2015. There and back again: a
917 review of residency and return migrations in sharks, with implications for population structure
918 and management. *Annual review of marine science*, 7:547-570.

919 Conservation International. 2016. *Laporan Program Kerjasama Tagging Satelit Pari Manta*.
920 Jakarta: Conservation International Indonesia.

921 Couturier LIE, Jaine FRA, Townsend KA, Weeks SJ, Richardson AJ, JBennett MB. 2011.
922 Distribution, site affinity and regional movements of the manta ray, *Manta alfredi* (Krefft, 1868),
923 along the east coast of Australia, *Marine and Freshwater Research*, 62:628.

924 Couturier L, Newman P, Jaine F, Bennett M, Venables W, Cagua E, Townsend K, Weeks S,
925 Richardson A. 2018. Variation in occupancy and habitat use of *Mobula alfredi* at a major
926 aggregation site. *Marine Ecology Progress Series*, 599:125-145.

927 Croll DA, Dewar H, Dulvy NK, Fernando D, Francis MP, Galván-Magaña F, Hall M, Heinrichs
928 S, Marshall A, Mccauley D. 2016. Vulnerabilities and fisheries impacts: the uncertain future of
929 manta and devil rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26:562-575.

930 Deakos MH. 2012. The reproductive ecology of resident manta rays (*Manta alfredi*) off Maui,
931 Hawaii, with an emphasis on body size. *Environmental Biology of Fishes*, 94:443-456.

932 Deakos MH, Baker JD, Bejder L. 2011. Characteristics of a manta ray *Manta alfredi* population
933 off Maui, Hawaii, and implications for management. *Marine Ecology Progress Series*, 429:245.

934 Dewar H, Mous P, Domeier M, Muljadi A, Pet J, Whitty JV. 2008. Movements and site fidelity
935 of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. *Marine Biology*,
936 155:121-133.

937 Division of Boating, and Ocean Recreation. 2016. Manta Viewing within the West Hawaii
938 Ocean Recreation Management Area: Introduction of Proposed Administrative Rules. Kona:
939 Department of Land and Natural resources. Available at:
940 <https://dlnr.hawaii.gov/dobor/files/2013/08/MantaDiveSitesManagementPlan-9.9.16.pdf>
941 (accessed January 2, 2019).

942 van Duinkerken, D. 2010. Movements and site fidelity of the reef manta ray, *Manta alfredi*,
943 along the coast of southern Mozambique. *Utrecht University*,

944 Dulvy NK, Pardo SA, Simpfendorfer CA, Carlson JK. 2014. Diagnosing the dangerous
945 demography of manta rays using life history theory. *PeerJ*, 2:e400.

946 Erdmann AM. 2004a. A History Guide to the Komodo National Park - Book 3: Management.
947 The Nature Conservancy Indonesia Coastal and Marine Program.

948 Erdmann AM . 2004b. A History Guide to the Komodo National Park - Book 1: Terrestrial. The
949 Nature Conservancy Indonesia Coastal and Marine Program.

950 Erdmann AM . 2004c. A Natural History Guide to the Komodo National Park - Book 2: Marine.
951 The Nature Conservancy Indonesia Coastal and Marine Program.

952 Germanov ES, Bejder L, Chabanne DBH, Dharmadi D, Hendrawan IG, Marshall AD, Pierce SJ,
953 van Keulen M, Loneragan NR. 2019a. Contrasting Habitat Use and Population Dynamics of
954 Reef Manta Rays Within the Nusa Penida Marine Protected Area, Indonesia. *Frontiers in Marine*
955 *Science*, 6:215.

956 Germanov ES, Marshall AD. 2014. Running the gauntlet: regional movement patterns of *Manta*
957 *alfredi* through a complex of parks and fisheries. *PLoS One*, 9:e110071.

958 Germanov ES, Marshall AD, Hendrawan IG, Admiraal R, Rohner CA, Argeswara J, Wulandari
959 R, Himawan MR, Loneragan NR. 2019b. Microplastics on the menu: Plastics pollute Indonesian
960 Manta Ray and Whale Shark feeding grounds. *Frontiers in Marine Science*, 6:679.

961 Graham F, Rynne P, Estevanez M, Luo J, Ault JS, Hammerschlag N. 2016. Use of marine
962 protected areas and exclusive economic zones in the subtropical western North Atlantic Ocean
963 by large highly mobile sharks. *Diversity and Distributions*, 22:534-546.

964 Guttridge TL, Gruber SH, DiBattista JD, Feldheim KA, Croft DP, Krause S, Krause J. 2011.
965 Assortative interactions and leadership in a free-ranging population of juvenile lemon shark
966 *Negaprion brevirostris*. *Marine Ecology Progress Series*, 423:235-245.

967 Harris JL, McGregor PK, Oates Y, Stevens GM. 2020. Gone with the wind: Seasonal
968 distribution and habitat use by the reef manta ray (*Mobula alfredi*) in the Maldives, implications
969 for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30:1649-1664.

970 Heinrichs S, O'Malley M, Medd H, Hilton P. 2011. Manta Ray of Hope 2011 Report: The Global
971 Threat to Manta and Mobula Rays.

972 Heupel MR, Carlson JK, Simpfendorfer CA. 2007. Shark nursery areas: concepts, definition,
973 characterization and assumptions. *Marine Ecology Progress Series*, 337:287-297.

974 Heupel MR, Kanno S, Martins AP, Simpfendorfer CA. 2018. Advances in understanding the
975 roles and benefits of nursery areas for elasmobranch populations. *Marine and Freshwater*
976 *Research*, 70:897-907.

977 Heupel M, Simpfendorfer C. 2005. Quantitative analysis of aggregation behavior in juvenile
978 blacktip sharks. *Marine Biology*, 147:1239-1249.

979 Hooker SK, Cañadas A, Hyrenbach KD, Corrigan C, Polovina JJ, Reeves RR. 2011. Making
980 protected area networks effective for marine top predators. *Endangered Species Research*,
981 13:203-218.

982 Hueter R, Heupel M, Heist E, Keeney D. 2005. Evidence of philopatry in sharks and
983 implications for the management of shark fisheries. *Journal of Northwest Atlantic Fishery*
984 *Science*, 35:239-247.

985 Jaine FRA, Rohner CA, Weeks SJ, Couturier LIE, Bennett MB, Townsend KA, and Richardson
986 AJ. 2014. Movements and habitat use of reef manta rays off eastern Australia: offshore
987 excursions, deep diving and eddy affinity revealed by satellite telemetry. *Marine Ecology*
988 *Progress Series*, 510:73-86.

989 Jaine FRA, Couturier LIE, Weeks SJ, Townsend KA, Bennett MB, Fiora K, Richardson AJ.
990 2012. When Giants Turn Up: Sighting Trends, Environmental Influences and Habitat Use of the
991 Manta Ray *Manta alfredi* at a Coral Reef. *PLoS One*, 7:e4610.

992 Kashiwagi T. 2014. Conservation biology and genetics of the largest living rays: manta rays.
993 University of Queensland.

994 Kasmidi M, Gunadharma A. 2017. Diving in Manta Sandy? Here's What You Need to Know!
995 *Bird's Head Seascape*. Available at: <http://birdsheadseascape.com/diving/diving-manta-sandy-heres-need-know-meidiarti-kasmidi-nikka-amandra-gunadharma/> (accessed January 2, 2019).

997 Lewis SA, Setiasih N, Fahmi F, Dharmadi D, O'Malley MP, Campbell SJ, Yusuf M, Sianipar
998 AB. 2015. Assessing Indonesian manta and devil ray populations through historical landings and
999 fishing community interviews. *PeerJ PrePrints*.

1000 Marine Megafauna Foundation. 2018. Codes of Conduct. Yayasan Megafauna Laut. Available
1001 at: <https://mmfindonesia.wordpress.com/resources/>

1002 Manta Trust. 2018. How to Swim with Manta Rays. Manta Trust. Available at:
1003 <https://swimwithmantas.org/>

1004 Marshall AD, Bennett MB. 2010. Reproductive ecology of the reef manta ray *Manta alfredi* in
1005 southern Mozambique. *Journal of Fish biology*, 7:169-190.

- 1006 Marshall AD, Compagno LJV, Bennett MB. 2009. Redescription of the genus *Manta* with
1007 resurrection of *Manta alfredi* (Krefft, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae).
1008 *Zootaxa*, 2301:1-28.
- 1009 Marshall AD, Dudgeon CL, Bennett MB. 2011. Size and structure of a photographically
1010 identified population of manta rays *Manta alfredi* in southern Mozambique. *Marine Biology*,
1011 158:1111–1124.
- 1012 Marshall A, Barreto R, Carlson J, Fernando D, Fordham S, Francis M, Derrick D, Herman K,
1013 Jabado R, Liu K. 2020. *Mobula birostris*. *The IUCN Red List of Threatened Species 2020: e*.
1014 *T198921A68632946*.
- 1015 Marshall A, Barreto R, Carlson J, Fernando D, Fordham S, Francis M, Herman K, Jabado R, Liu
1016 K, Pacoureau N. 2019. *Mobula alfredi*. *The IUCN Red List of Threatened Species*:19.
- 1017 Martins A, Heupel M, Chin A, Simpfendorfer C. 2018. Batoid nurseries: definition, use and
1018 importance. *Marine Ecology Progress Series*, 595:253-267.
- 1019 McCauley DJ, DeSalles PA, Young HS, Papastamatiou YP, Caselle JE, Deakos MH, Gardner JP,
1020 Garton DW, Collen JD, Micheli F. 2014. Reliance of mobile species on sensitive habitats: a case
1021 study of manta rays (*Manta alfredi*) and lagoons. *Marine Biology*, 161:1987-1998.
- 1022 McGregor F, Richardson AJ, Armstrong AJ, Armstrong AO, Dudgeon CL. 2019. Rapid wound
1023 healing in a reef manta ray masks the extent of vessel strike. *PLoS One*, 14:e0225681.
- 1024 Ministry of Marine Affairs and Fisheries. 2014. *Keputusan Menteri Kelautan dan Perikanan*
1025 *Republik Indonesia No4/Kepmen-KP/2014 tentang Penetapan Status Perlindungan Penuh Ikan*
1026 *Pari Manta*. Jakarta: Ministry of Marine Affairs and Fisheries. Available at:
1027 [http://kkji.kp3k.kkp.go.id/index.php/dokumen/regulasi-hukum/keputusan-menteri/finish/14-](http://kkji.kp3k.kkp.go.id/index.php/dokumen/regulasi-hukum/keputusan-menteri/finish/14-keputusan-menteri/516-kepmen-kp-no-4-tahun-2014-tentang-penetapan-status-perlindungan-penuh-ikan-pari-manta)
1028 [keputusan-menteri/ 516- kepmen- kp- no- 4- tahun- 2014- tentang- penetapan- status-](http://kkji.kp3k.kkp.go.id/index.php/dokumen/regulasi-hukum/keputusan-menteri/finish/14-keputusan-menteri/516-kepmen-kp-no-4-tahun-2014-tentang-penetapan-status-perlindungan-penuh-ikan-pari-manta)
1029 [perlindungan- penuh-ikan-pari-manta](http://kkji.kp3k.kkp.go.id/index.php/dokumen/regulasi-hukum/keputusan-menteri/finish/14-keputusan-menteri/516-kepmen-kp-no-4-tahun-2014-tentang-penetapan-status-perlindungan-penuh-ikan-pari-manta) (accessed January 2, 2019).
- 1030 Mustika PLK, Ichsan M, Booth H. 2020. The economic value of shark and ray tourism in
1031 Indonesia and its role in delivering conservation outcomes. *Frontiers in Marine Science*, 7:261.
- 1032 Ningsih NS, Rakhmaputeri N, Harto AB. 2013. Upwelling variability along the southern coast of
1033 Bali and in Nusa Tenggara waters. *Ocean Science Journal*, 48:49-57.
- 1034 Norse E. 2005. Pelagic protected areas: the greatest parks challenge of the 21st century. *Parks*,
1035 15, 32-39.
- 1036 Nøttestad L, Giske J, Holst JC, Huse G. 1999. A length-based hypothesis for feeding migrations
1037 in pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 56:26-34.
- 1038 O'Malley MP, Lee-Brooks K, Medd HB. 2013. The Global Economic Impact of Manta Ray
1039 Watching Tourism. *PLoS One*, 8:e65051.

- 1040 Peel LR, Stevens GM, Daly R, Daly CAK, Lea JS, Clarke CR, Collin SP, Meekan MG. 2019.
1041 Movement and residency patterns of reef manta rays *Mobula alfredi* in the Amirante Islands,
1042 Seychelles. *Marine Ecology Progress Series*, 621:169-184.
- 1043 Peel LR, Stevens GM, Daly R, Keating Daly CA, Collin SP, Nogués J, Meekan MG. 2020.
1044 Regional movements of reef manta rays (*Mobula alfredi*) in Seychelles waters. *Frontiers in*
1045 *Marine Science*, 7:558.
- 1046 Peñaherrera-Palma C, Hobday A, Hearn A, Espinoza E, Shillinger G, Ketchum J, Klimley A,
1047 Frusher S, Fischer G, Semmens J. 2020. Assessing the efficacy of a marine reserve to protect
1048 sharks with differential habitat use.
- 1049 Perryman RJ, Venables SK, Tapilatu RF, Marshall AD, Brown C, Franks DW. 2019. Social
1050 preferences and network structure in a population of reef manta rays. *Behavioral Ecology and*
1051 *Sociobiology*, 73:1-18.
- 1052 Putra MIH, Setyawan E, Laglbauer BJ, Lewis S, Dharmadi D, Sianipar A, Ender I. 2020.
1053 Predicting mobulid ray distribution in coastal areas of Lesser Sunda Seascape: Implication for
1054 spatial and fisheries management. *Ocean & Coastal Management*, 198:105328.
- 1055 R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna: R
1056 Foundation for Statistical Computing. Available at: <https://www.R-project.org/>(accessed April
1057 1, 2018).
- 1058 Rambahiniarison J, Lamoste MJ, Rohner C, Murray R, Snow S, Labaja J, Araujo G, Ponzo A.
1059 2018. Life History, Growth, and Reproductive Biology of Four Mobulid Species in the Bohol
1060 Sea, Philippines. *Frontiers in Marine Science*, 5:269.
- 1061 Rigby CL, Simpfendorfer CA, Cornish A. 2019. A Practical Guide to the Effective Design and
1062 Management of MPAs for Sharks and Rays.
- 1063 Rohner CA, Pierce SJ, Marshall AD, Weeks SJ, Bennett MB, Richardson AJ. 2013. Trends in
1064 sightings and environmental influences on a coastal aggregation of manta rays and whale sharks.
1065 *Marine Ecology Progress Series*, 482:153-168.
- 1066 Rooker JR, Secor DH, De Metrio G, Schloesser R, Block BA, Neilson JD. 2008. Natal homing
1067 and connectivity in Atlantic bluefin tuna populations. *Science (New York, N.Y.)*, 322:742-744.
- 1068 Setyawan E, Erdmann MV, Lewis SA, Mambrasar R, Hasan AW, Templeton S, Beale CS,
1069 Sianipar AB, Shidqi R, Heuschkel H. 2020. Natural history of manta rays in the Bird's Head
1070 Seascape, Indonesia, with an analysis of the demography and spatial ecology of *Mobula alfredi*
1071 (Elasmobranchii: Mobulidae). *J Ocean Sci Found*, 36:49-83.
- 1072 Setyawan E, Sianipar AB, Erdmann MV, Fischer AM, Haddy JA, Beale CS, Lewis SA,
1073 Mambrasar R. 2018. Site fidelity and movement patterns of reef manta rays (*Mobula alfredi*):
1074 Mobulidae using passive acoustic telemetry in northern Raja Ampat, Indonesia. *Nature*
1075 *Conservation Research*, 3:1-15.

- 1076 Sgrò CM, Lowe AJ, Hoffmann AA. 2011. Building evolutionary resilience for conserving
1077 biodiversity under climate change. *Evolutionary applications*, 4:326-337.
- 1078 Speed CW, Field IC, Meekan MG, Bradshaw CJ. 2010. Complexities of coastal shark
1079 movements and their implications for management. *Marine Ecology Progress Series*, 408:275-
1080 293.
- 1081 Stevens GMW. 2016. Conservation and population ecology of Manta rays in the Maldives,
1082 University of York.
- 1083 Stewart JD, Beale CS, Fernando D, Sianipar AB, Burton RS, Semmens BX, Aburto-Oropeza O.
1084 2016. Spatial ecology and conservation of *Manta birostris* in the Indo-Pacific. *Biological*
1085 *Conservation*, 200:178-183.
- 1086 Stewart JD, Jaine FR, Armstrong AJ, Armstrong AO, Bennett MB, Burgess KB, Couturier LI,
1087 Croll DA, Cronin MR, Deakos M. 2018. Research priorities to support effective manta and devil
1088 ray conservation. *Frontiers in Marine Science*, 5:314.
- 1089 Town C, Marshall A, Sethasathien N. 2013. Manta Matcher: automated photographic
1090 identification of manta rays using keypoint features. *Ecology and evolution*, 3:1902-1914.
- 1091 Treasurer JW. 2002. A review of potential pathogens of sea lice and the application of cleaner
1092 fish in biological control. *Pest Management Science: formerly Pesticide Science*, 58:546-558.
- 1093 Venables SK, van Duinkerken DI, Rohner CA, Marshall AD. 2020. Habitat use and movement
1094 patterns of reef manta rays *Mobula alfredi* in southern Mozambique. *Marine Ecology Progress*
1095 *Series*, 634:99-114.
- 1096 Ward-Paige CA, Davis B, Worm B. 2013. Global Population Trends and Human Use Patterns of
1097 Manta and Mobula Rays. *PloS One*, 8:e74835.
- 1098 Winstanley, G.W. (2016). *MantaUtil: manta database utility*. Available:
1099 <http://www.pelagicon.com/software/mantautil/>. (accessed March 1, 2017).
- 1100 White WT, Giles J, Dharmadi, Potter IC. 2006. Data on the bycatch fishery and reproductive
1101 biology of mobulid rays (Myliobatiformes) in Indonesia. *Fisheries Research*, 82:65-73.
- 1102 Whitehead H. 2009. SOCPROG: Programs for analyzing social structure.
- 1103 Whitehead H. 2007. Selection of models of lagged identification rates and lagged association
1104 rates using AIC and QAIC. *Communications in Statistics—Simulation and Computation*®,
1105 36:1233-1246.
- 1106 Whitehead H. 2001. Analysis of animal movement using opportunistic individual identifications:
1107 application to sperm whales. *Ecology*, 82:1417-1432.
- 1108 VassarStats. 1998. *VassarStats: A Website for Statistical Computation*. USA. Available at:
1109 <http://vassarstats.net/> (accessed December 1, 2018).

Table 1(on next page)

Individual manta rays, sightings, and survey days between July 2004 and April 2018.

Data are reported for Komodo National Park (KNP) overall, Cauldron (CL), Karang Makassar (KM), Mawan (MW), Manta Alley (MA), other sites within KNP and for manta rays sighted in KNP as well as in the Nusa Penida Marine Protected Area (NP MPA). Daily duplicates are removed (n = 755).

1

	All KNP	CL	KM	MW	MA	Other KNP	NP MPA
<i>Year</i>	Individuals						
<i>2004 – 12</i>	139	1	122	-	16	2	5
<i>2013</i>	308	3	186	58	103	3	4
<i>2014</i>	473	8	270	92	186	5	6
<i>2015</i>	371	5	192	127	102	2	7
<i>2016</i>	457	8	277	103	159	9	8
<i>2017</i>	688	34	354	348	116	24	4
<i>2018*</i>	167	1	103	72	-	1	1
<i>TOTAL</i>	1104	48	779	535	383	45	11
	Sightings						
<i>2004 – 12</i>	177	1	156	-	18	2	13
<i>2013</i>	463	3	246	67	144	3	19
<i>2014</i>	838	19	404	116	294	5	16
<i>2015</i>	535	11	229	147	146	2	13
<i>2016</i>	764	10	375	117	253	9	19
<i>2017</i>	1198	59	476	464	174	25	6
<i>2018*</i>	188	1	107	79	-	1	3
<i>TOTAL</i>	4163	104	1993	990	1029	47	89
	Survey days						
<i>2004 – 12</i>	73	1	66	-	8	2	13
<i>2013</i>	116	2	85	23	14	3	19
<i>2014</i>	150	12	94	39	39	3	15
<i>2015</i>	97	9	56	35	15	2	12
<i>2016</i>	114	7	77	33	21	9	18
<i>2017</i>	198	30	103	103	13	20	6
<i>2018*</i>	43	1	26	25	-	1	3
<i>TOTAL</i>	791	62	507	258	110	40	86

*To April only

- = no data available for this time

2

3

4

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Table 2 (on next page)

Residency model parameters and fits ($\Delta QAIC$) for individual manta ray sightings at Karang Makassar (KM), Mawan (MW), and Manta Alley (MA), Komodo National Park.

1

Study Sites		KM	MW	MA
Model	Model description	ΔQAIC	ΔQAIC	ΔQAIC
A	Closed ($1/a_1 = N$)	58178.48	13966.47	81.84
B	Closed ($a_1 = N$)	101.70	10.14	81.84
C	Emigration/mortality (a_1 =emigration rate; $1/a_2=N$)	15.77	4.83	11.90
D	Emigration/mortality ($a_1=N$; a_2 =mean residence)	15.77	4.83	11.90
E	Closed: emigration + re-immigration (a_1 =emigration rate; $a_2/(a_2+a_3)$ =proportion of population in study area at any time)	73.33	3.12	61.46
F	Emigration + re-immigration ($a_1=N$; a_2 =res time in; a_3 =res time out)	42.88	3.12	2.90
G	Emigration + re-immigration + mortality	1547.52	8.95	781.20
H	Emigration + re-immigration + mortality ($a_1=N$; a_2 =res time in; a_3 =res time out; a_4 =mort)	0	0	0

N = population

2

3

4

Table 3(on next page)

The estimated probability (± 1 SE) of re-sighting an individual manta ray in the same or another site.

Movement probabilities are presented for manta rays ($n = 1,061$) at (A) the three Komodo NP core sites Karang Makassar (KM), Mawan (MW), Manta Alley (MA) and additional ‘outside’ sites. (B) Sites grouped into central (KM + MW) and south (MA) regions.

1

	To:	KM	MW	MA	Outside
A) Core From:	KM	0.39	0.37 ± 0.16	0.13 ± 0.03	0.11 ± 0.07
	MW	0.29 ± 0.17	0.59	0.01 ± 0.02	0.02 ± 0.05
	MA	0.20 ± 0.97	0.23 ± 0.06	0.58	0.00 ± 0.03
	Outside	0.10 ± 0.06	0.12 ± 0.05	0.00 ± 0.03	0.79
	To:	Central	South	Outside	
B) Central, south From:	Central	0.87	0.11 ± 0.04		0.03 ± 0.20
	South	0.47 ± 0.11	0.53		0.03 ± 0.01
	Outside	0.11 ± 0.20	0.00 ± 0.02		0.89

2

Table 4(on next page)

The estimated probability (± 1 SE) of re-sighting an individual manta ray in the same or another site according to sex.

Movement probabilities are presented for (A) males and (B) females at core sites Karang Makassar (KM), Mawan (MW) and Manta Alley (MA), Komodo National Park.

1

From Area:	To Area:	KM	MW	MA	Outside
A) Males (<i>n</i> = 507)	KM	0.53	0.27 ± 0.15	0.11 ± 0.02	0.08 ± 0.05
	MW	0.32 ± 0.12	0.51	0.08 ± 0.02	0.10 ± 0.09
	MA	0.21 ± 0.07	0.15 ± 0.06	0.64	0.00 ± 0.00
	Outside	0.02 ± 0.02	0.02 ± 0.02	0.00 ± 0.00	0.96
B) Females (<i>n</i> = 498)	KM	0.43	0.28 ± 0.17	0.17 ± 0.05	0.11 ± 0.01
	MW	0.32 ± 0.18	0.41	0.15 ± 0.04	0.02 ± 0.05
	MA	0.23 ± 0.11	0.19 ± 0.10	0.58	0.00 ± 0.00
	Outside	0.15 ± 0.09	0.09 ± 0.04	0.00 ± 0.00	0.79

2

3

Figure 1

Location of study sites within the north (Cauldron – CL), central (Karang Makassar – KM, Mawan – MW), and south (Manta Alley – MA) regions of the Komodo National Park (NP), Lesser Sunda, Indonesia.

Core study sites (colored circles) and other popular SCUBA diving locations with infrequent manta ray sightings are marked as “other” sites (white circles). These locations include (from north to south): ‘Castle’ and ‘Crystal Rock’, ‘Lighthouse’, ‘Tatawa Besar’, ‘Tatawa Kecil’, ‘Batu Bolong’, ‘Siaba Besar’, and ‘German Flag’. The boundary of Komodo NP is marked is highlighted by an orange line. The figure was created using QGis v 2.18, 2016 and bathymetry information was obtained from: GEBCO_2014 Grid, version 20150318; www.gebco.net .

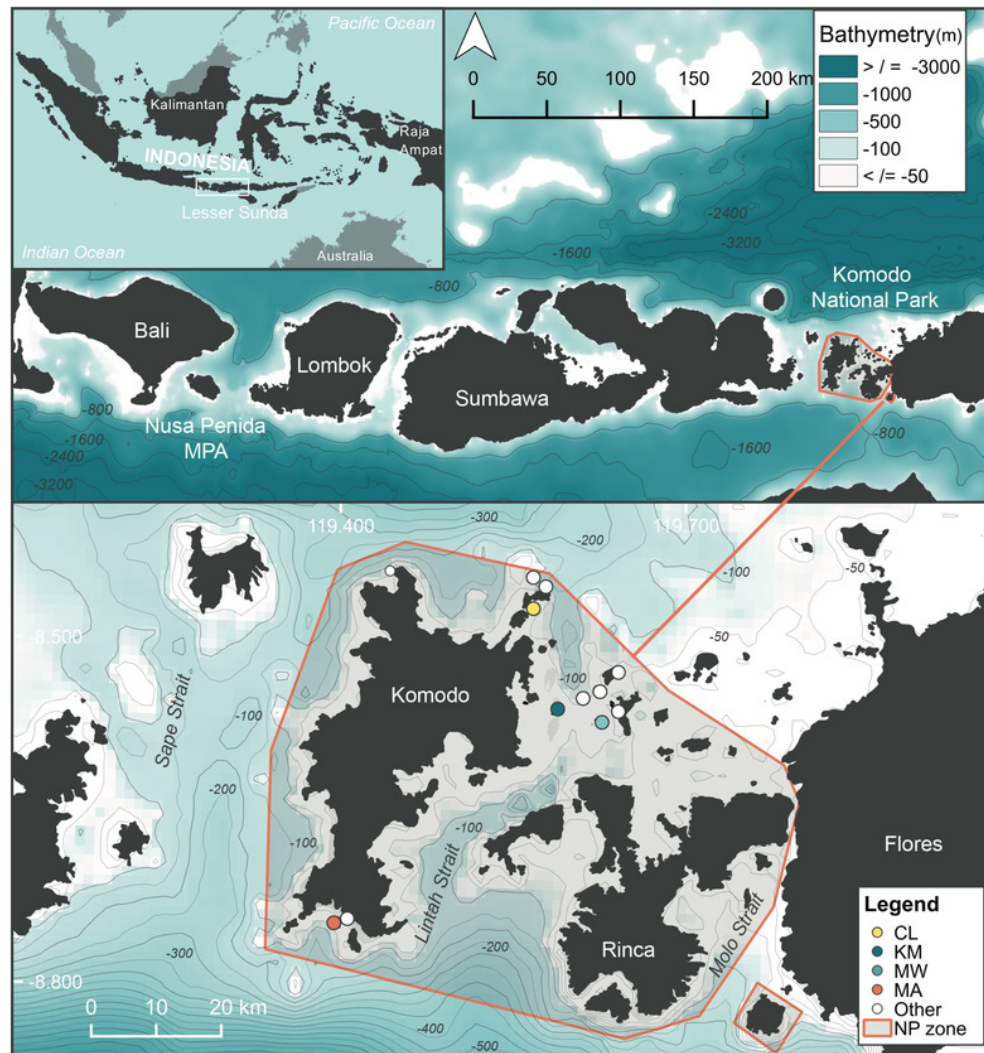


Figure 2

Discovery curves for newly-identified manta rays in Komodo National Park over time (in days) from January 2013 until April 2018.

Discovery curves are presented for the sites combined (Comb.) and separately for Karang Makassar (KM), Mawan (MW), and Manta Alley (MA). NS = number of survey days and NI = number of individuals.

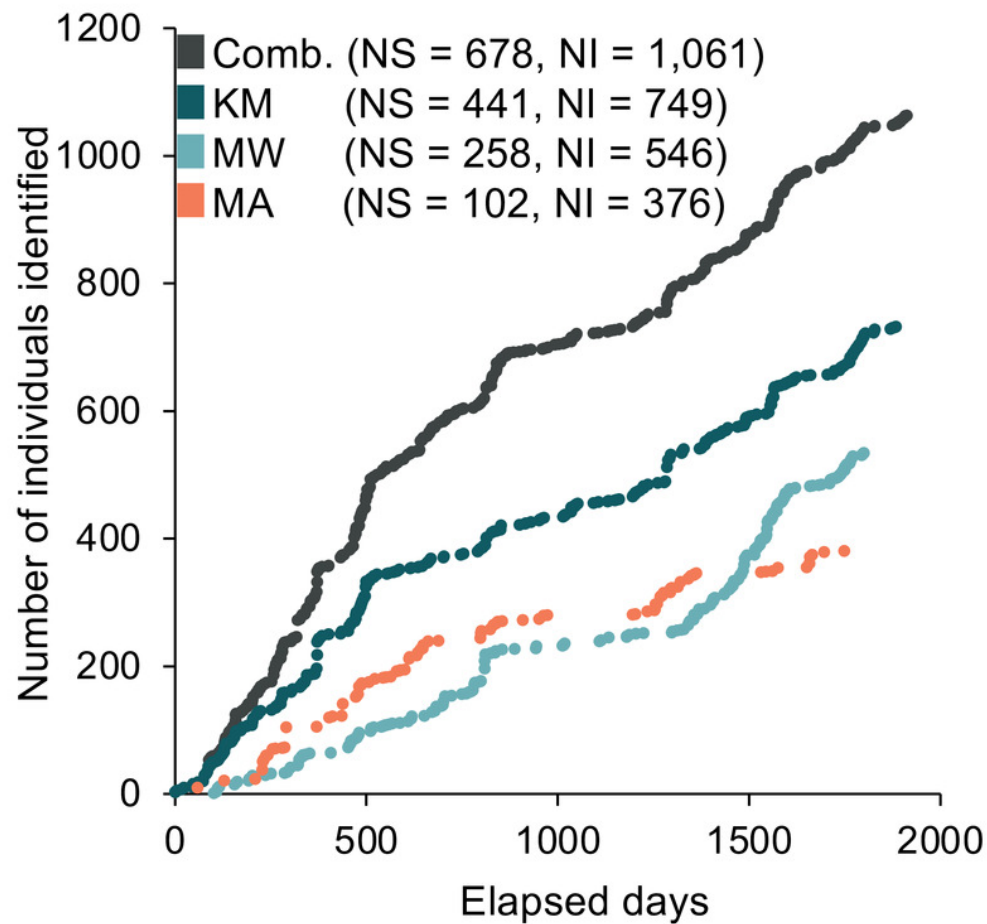


Figure 3

Total mean monthly sightings (± 1 SE) of identified manta rays for the Komodo National Park at Karang Makassar (KM), Mawan (MW) and Manta Alley (MA) from 2013-2017.

Data are presented as annual (A) and monthly (B) mean sightings per month. KM = 1,730 sightings, 415 days; MW = 911 sightings, 233 days; MA = 1,011 sightings, 102 days.

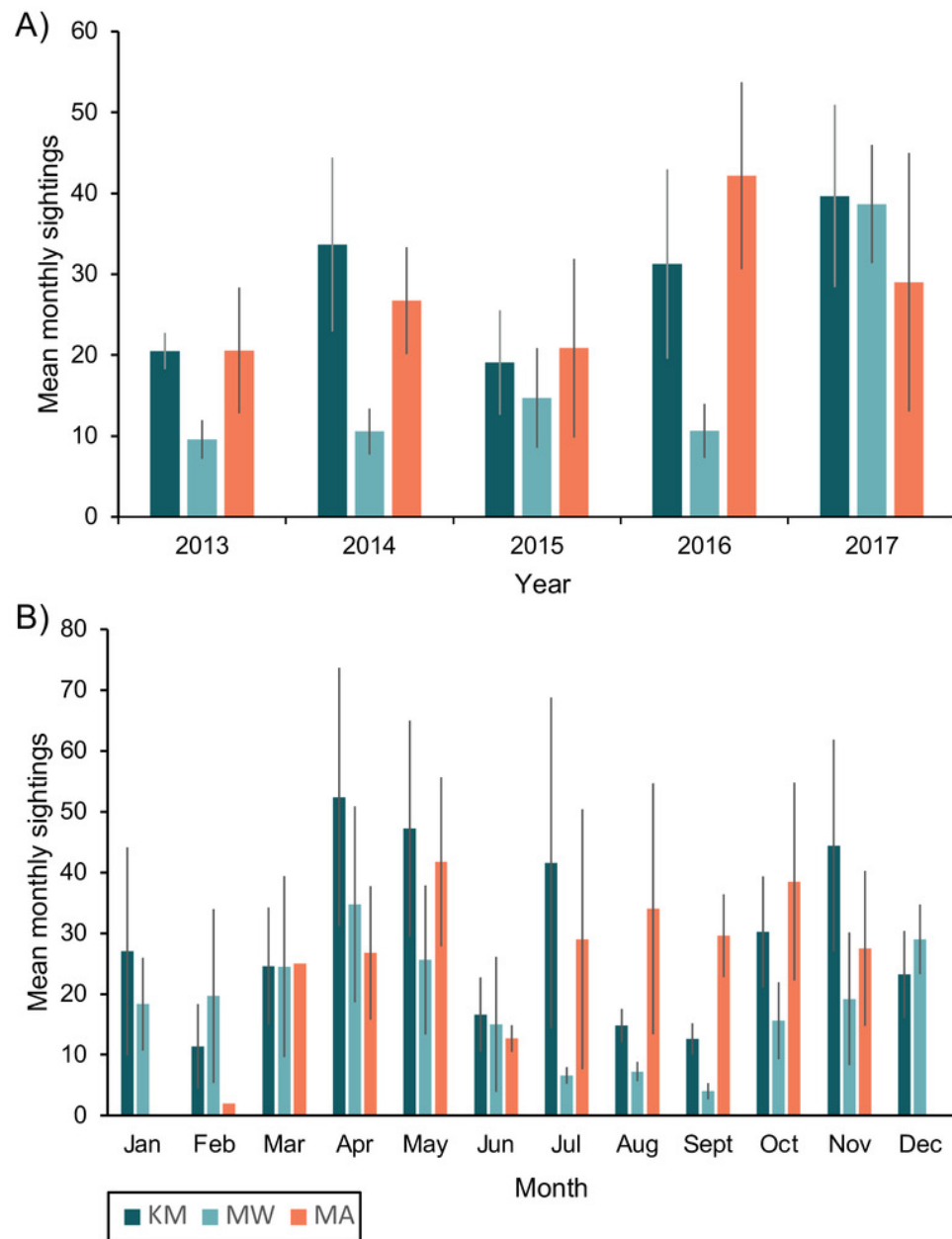


Figure 4

Population structure of manta rays in the Komodo National Park.

The number of individuals sighted in each site (from north to south): Cauldron (CL), Karang Makassar (KM), Mawan (MW) and Manta Alley (MA). The records are from January 2013 to April 2018.

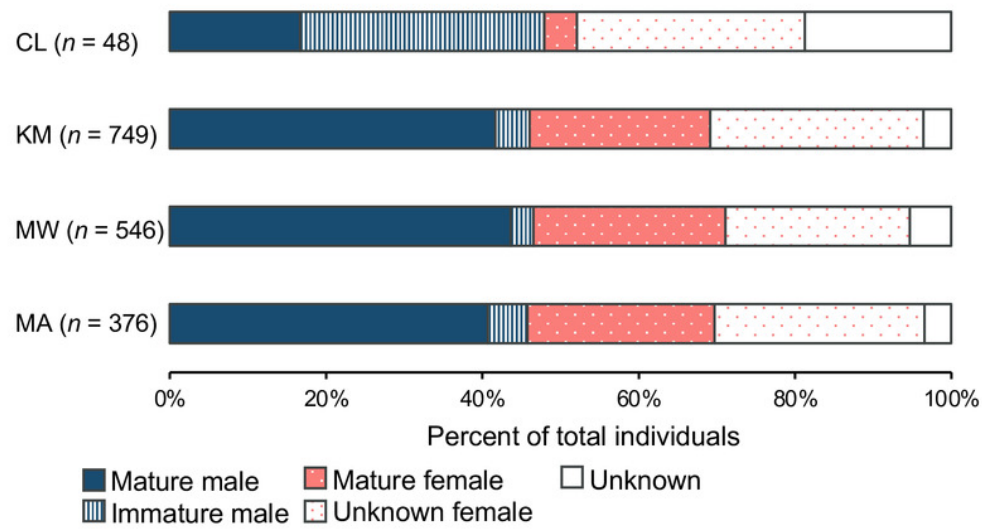


Figure 5

Individual manta (N = 1,061) ray sighting span (years) from the core study sites combined.

Core sites are Karang Makassar, Mawan and Manta Alley. The records are from January 2013 to April 2018.

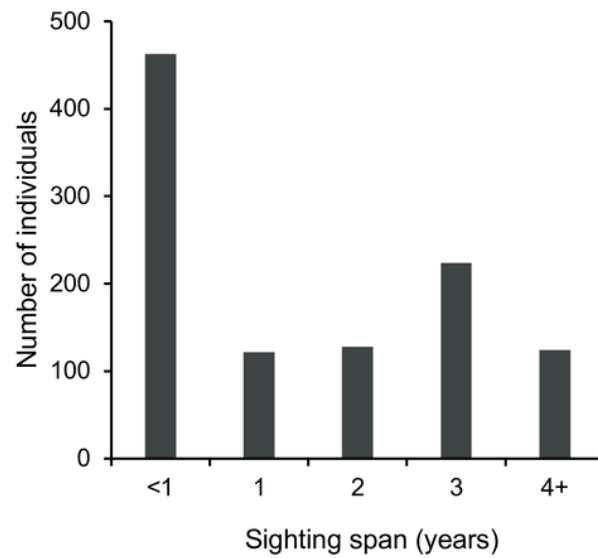


Figure 6

The probability of an individual manta ray being identified in the same or a different site within Komodo National Park over time (days).

Lagged Identification Rates (LIR) (\pm SE) were calculated with records from January 2013 to April 2018.

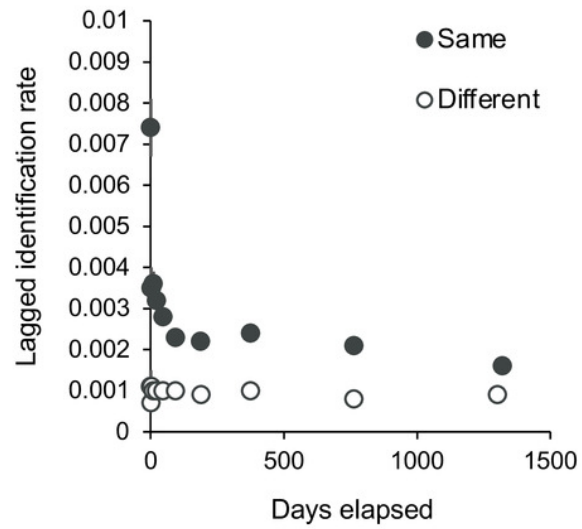


Figure 7

The probability of an individual manta ray being identified over time (days) within each of the three core sites.

Lagged Identification Rates (LIR) (\pm SE) for the three core study areas in Komodo NP: Karang Makassar (KM), Mawan (MW), and Manta Alley (MA), Komodo NP were calculated with records from January 2013 to April 2018. Best-fit LIR models (dotted lines) are shown for each site. Standard Errors (SE) are depicted as vertical lines for each data point.

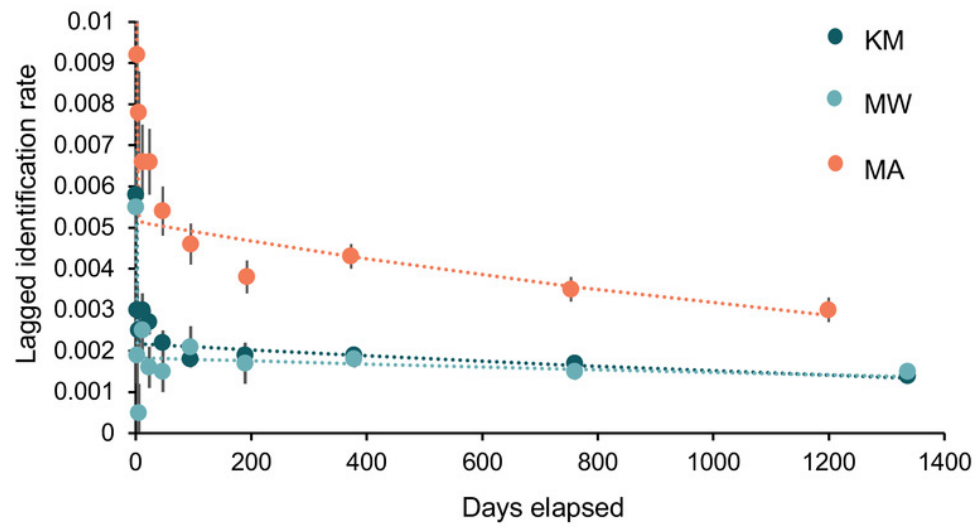


Figure 8

Manta ray behavioral habitat use and seasonality trends in the Komodo National Park.

(A) Manta ray behaviors at four sites: Cauldron (CL, $n = 49$), Karang Makassar (KM, $n = 1,067$), Mawan (MW, $n = 741$) and Manta Alley (MA, $n = 498$). The records are from January 2013 to April 2018. (B) The average identified manta rays engaging in courtship behavior on a daily basis broken down by month. The data recorded between 2013 and 2017 across sites KM, MW and MA and presented as the daily means (± 1 SE). The textured and solid backgrounds indicate the north-west monsoon (NW; November – April) and south-east monsoon (SE; May – October), respectively.

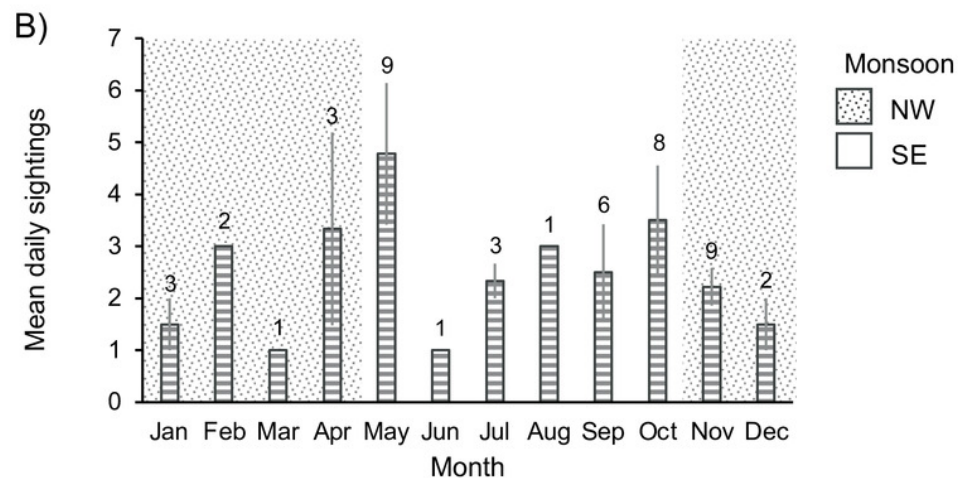
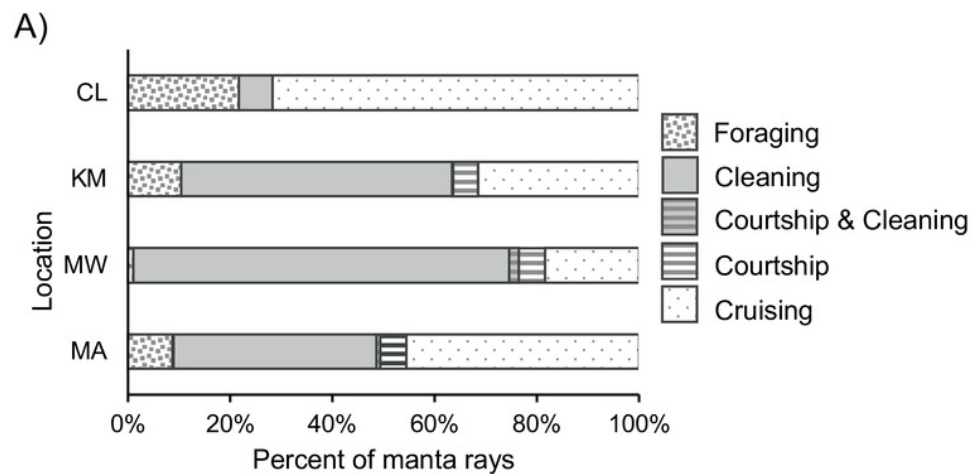


Figure 9

Monthly variation in the daily average (± 1 SE) number of boats present at Komodo National Park manta ray sites Karang Makassar (KM) and Mawan (MW).

The records are from 2014 and 2017.

