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ARTICLE *in* MARINE BIOLOGY · SEPTEMBER 2014

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Reliance of mobile species on sensitive habitats: a case study of manta rays (*Manta alfredi*) and lagoons

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Received: 10 December 2013 / Accepted: 14 June 2014
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Abstract Quantifying the ecological importance of individual habitats to highly mobile animals is challenging because patterns of habitat reliance for these taxa are complex and difficult to observe. We investigated the importance of lagoons to the manta ray, *Manta alfredi*, a wide-ranging and vulnerable species in a less-disturbed atoll ecosystem. Lagoons are highly sensitive to anthropogenic disturbance and are known to be ecologically important to a wide variety of mobile species. We used a novel combination of research tools to examine the reliance of *M. alfredi* on lagoon habitats. Stable isotope analysis was

used to assay the recent energetic importance of lagoons to *M. alfredi*; high-resolution tracking data provided information about how *M. alfredi* utilised lagoonal habitats over long and short time periods; acoustic cameras logged patterns of animal entrances and departures from lagoons; and photo identification/laser photogrammetry provided some insight into why they may be using this habitat. *M. alfredi* showed strong evidence of energetic dependence on lagoon resources during the course of the study and spent long periods of residence within lagoons or frequently transited into them from elsewhere. While within lagoons, they demonstrated affinities for particular structural features within this habitat and showed evidence of temporal patterning in habitat utilization. This work sheds light on how and why *M. alfredi* uses lagoons and raises questions about how this use may be altered in disturbed settings. More generally, these observations contribute to our knowledge of how to assess the ecological importance of particular habitats situated within the broader home range of mobile consumers.

Communicated by C. Harrod.

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Electronic supplementary material The online version of this article (doi:10.1007/s00227-014-2478-7) contains supplementary material, which is available to authorized users.

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Introduction

Mobile animals have been heavily impacted by anthropogenic activity in both terrestrial (e.g., wolves, mountain lion, African wild dog) and marine settings (e.g., whales, sharks, tuna) (Noss et al. 1996; Myers and Worm 2003; Terborgh and Estes 2010). Because they range across multiple habitats and even regularly traverse political jurisdictions, mobile animals are often at high risk of encountering and deleteriously interacting with humans (Woodroffe and Ginsberg 1998) and it is challenging to manage threats to such species in these spatially expansive regions using tools from conventional conservation policy (Techera and Klein 2011). It is sometimes assumed that anthropogenic effects that are confined to discrete habitats have little effect on mobile animals (as opposed to sessile or low-vagility taxa) because these taxa have the capacity to transit out of these affected habitats and concentrate activities in less perturbed habitats within their home range (Debinski and Holt 2000). Such assumptions would be erroneous, however, in instances where impacted habitats are disproportionately important to a mobile species. Thus, an important part of understanding how human pressure affects mobile species requires determining how mobile taxa use and rely upon the various habitats that they may traverse. This task is made difficult, however, because detailed descriptions of the habitat dependency patterns of mobile fauna are often lacking (Block et al. 2001, 2011; Ferraroli et al. 2004; James et al. 2005), particularly in marine settings where mobile study subjects are especially difficult to observe and enumerate (McCauley et al. 2012b).

Here, we use a diverse set of tools to construct a comprehensive description of the ecological dependency of the large, mobile, and vulnerable manta ray (*Manta alfredi*) on a particularly sensitive habitat—atoll lagoon ecosystems (Amereson and Shelton 1976; Collen et al. 2009). *Manta alfredi* and other mobulids are capable of long-range movements (e.g., >100 km; Homma et al. 1997; Dewar et al. 2008; Luiz et al. 2009; Couturier et al. 2011; Graham et al. 2012; Braun et al. 2014) and have been observed in a variety of marine habitats, including lagoons. There is little available information, however, on the relative importance of specific habitats to manta rays and no information, to our knowledge, on their potential utilization of lagoons. *Manta alfredi* is classified by the IUCN as a Vulnerable species (Marshall et al. 2011a, b). There is uncertainty about how anthropogenic pressures (e.g., coastal development, harvesting) are affecting this species and where the majority of these negative interactions are occurring. The sheltered and readily accessible waters of lagoons are areas of concentrated and elevated human activity (e.g., fishing, boat traffic, pollution) (Blumenthal et al. 2010) and as such may be high-risk habitat for manta rays. Other highly mobile marine consumers are known to be

ecologically linked to lagoons in important ways; e.g., reef sharks (Economakis and Lobel 1998; Papastamatiou et al. 2009a); sea turtles (Mendonca and Ehrhart 1982); spinner dolphins (Karczmarski et al. 2005). The hypothesized uses of this vulnerable habitat by these particular species include suggestions that lagoons serve as thermal refuges, nursery or resting habitat, predator refuges, or that they provide valuable foraging opportunities. Determining how often and for what purposes *Manta alfredi* utilizes lagoons would help evaluate whether targeted management actions are necessary to protect them in these sensitive habitats.

In this study, we used Palmyra Atoll—a remote coral reef ecosystem—to investigate how *M. alfredi* uses and relies upon lagoon habitats. While the lagoons of Palmyra were heavily altered between 1940 and 1945 during military occupation of the atoll (Collen et al. 2009), their relative insulation from disturbance in the last six decades, the steady breakdown of military-era anthropogenic modifications, and the atoll's current status as a wildlife reserve have helped the lagoons become an important refuge for many large marine fish (McCauley et al. 2010; Papastamatiou et al. 2010). As such, they provide an excellent opportunity to study how *M. alfredi* uses lagoon habitats in the absence of human activity and to assess the importance of carefully managed lagoons to this species. At Palmyra, we endeavored to determine: (1) what proportion of its resources *M. alfredi* draws from lagoons during the time frame of our study; (2) how *M. alfredi* uses space (vertically and horizontally) in lagoons; (3) if these patterns vary between individuals and across temporal/physical boundaries; and (4) which sizes and sexes of *M. alfredi* are the most frequent users of this habitat. We used four main tools to answer these questions at Palmyra: stable isotopes, active and passive animal tracking, acoustic imaging, and photo identification/laser photogrammetry. To our knowledge, these diverse research methods have never been utilized together in a single study and they collectively contribute an integrative view of *M. alfredi* reliance on lagoons. The temporal scope of these data collection methods varied from 1 month to >1 year, necessitating that we focus on short-term facets of the relationship between *M. alfredi* and lagoon use. Our aim was not to provide a cross-seasonal portrait of habitat utilisation within lagoons, but rather to provide a snapshot assessment of the importance of these spatially discrete habitats for this wide-ranging species.

Materials and methods

Study area

Palmyra Atoll (5°53'N, 162°05'W) is located in the Northern Line Islands of the central Pacific Ocean. The atoll's

lagoons and surrounding waters have been protected as a US National Wildlife Refuge since 2001, and the take of all marine organisms is prohibited within the refuge. Palmyra hosts only a low-impact research station. The atoll has three main lagoon basins: West, Center (3.37 km², area of both basins combined), and East (1.12 km²) lagoon. West and Center lagoons are functionally similar with negligible physical separation between basins and so were grouped as West-Center lagoon hereafter. West-Center and East lagoon are largely separated from each other by a man-made causeway (constructed in 1943) with six narrow breaks (3–22 m wide, each of variable depth) (Collen et al. 2009). West-Center lagoon is directly connected to the open ocean by a channel that is a maximum of approximately 80 m wide and 8 m deep. Other much shallower and smaller reef passages provide additional, albeit less significant open ocean connections in both lagoon basins. Depths in West-Center and East lagoons do not exceed 60 m and 50 m, respectively (NOAA 2006).

Energetic reliance of *M. alfredi* on lagoons

We used stable isotopes to investigate the energetic dependency of *M. alfredi* on lagoon habitats. We assumed that manta rays feed on plankton in either of two source environments: lagoons or offshore waters. We collected zooplankton samples from surface waters in both of these source locations [lagoon $n = 12$; offshore (i.e., 1–5 km offshore of forereef) $n = 21$] using a 50- μm plankton net, with catch samples post-filtered through 250- μm sieves. Isotope ratios of nitrogen ($n = 33$), carbon ($n = 33$), and sulfur ($n = 19$) were measured in lagoon and offshore zooplankton samples. We then similarly analyzed muscle tissue collected from *M. alfredi* using biopsy poles in the lagoon ($n = 5$), the main channel connecting the lagoon to offshore waters ($n = 15$), and in offshore waters (2–5 km offshore of forereef, $n = 6$). Isotope samples were collected at multiple time points from September 2007 to August 2011 and multiple locations, but were pooled for analysis. We used two-source Bayesian isotope mixing models (mixSIR v.1.0.4) to estimate the probable contribution of lagoon and offshore zooplankton to the diet of (1) manta rays sampled inside the lagoons and in the lagoon channel and (2) manta rays sampled offshore (Moore and Semmens 2008; see Appendix S1 for details of mixing model). Relationships between manta rays' isotope signatures (lagoon + channel manta rays only) and their size (disk width) and sex were examined for individuals for which these data were available.

Spatial utilization of lagoon habitats by *M. alfredi*

We used active acoustic tracking to determine how manta rays spatially utilize lagoon habitats. *M. alfredi* ($n = 11$)

were tagged and tracked with V16 acoustic transmitters (Vemco, Nova Scotia, Canada) in West-Center and East lagoon from June 6, 2009, to August 9, 2009. Tagged manta rays were detected using a directional hydrophone (Vemco VR110) connected to an acoustic receiver (Vemco VR100). Continuous tracking of manta rays was conducted by following tagged individuals in a small vessel and recording their positions with GPS every 5 min. During tracking, we maintained an estimated 5–25 m distance behind tagged subjects, but before recording their location, we would direct the boat into the last position occupied by the animal at the end of each sampling interval. Manta ray movement and behavior did not appear to be influenced by the presence of the vessel at these distances. Manta rays were tracked continuously during daytime and nighttime hours. If an animal was lost or departed the lagoon, tracking was resumed upon subsequent detection. Although manta rays did not display any observable differences in behavior directly after tagging, we omitted the first 30 min of tracking data to conservatively account for the possible influence of tagging stress on their movement. All track analysis was performed in ArcGIS version 10 and ArcView version 3.3 (Esri, CA, USA) using the Animal Movement Analyst Extension (Hooge and Eichenlaub 2000). Although some animals were tracked offshore, all tracking and associated analysis reported upon herein refer to properties of *M. alfredi* movement within Palmyra's lagoon system where the majority of active tracking took place.

As a complement to active acoustic tracking, we tagged 18 *M. alfredi* with V13 acoustic transmitters (Vemco, Nova Scotia, Canada) and monitored their locations using an array of 58 VR2W acoustic receivers positioned inside and outside the lagoon (i.e., on the forereef). For complete details of the array see Papastamatiou et al. (2010) and Pedersen and Weng (2013). Passive acoustic tags were deployed between September 2010 and August 2011 and were monitored continuously until the cessation of detections.

Below, we describe five types of data gathered from active and passive tracking data used to characterize the spatial utilization of lagoons by manta rays.

Activity space size To estimate the size of the activity space of manta rays actively tracked within the lagoons, we calculated kernel utilization distributions (KUDs) for all active-tracked individuals (Seaman and Powell 1996, Fig. S1). We report both 50 % KUD (i.e., core activity space) and 95 % KUD (i.e., total activity space) of these animals. Because only within-lagoon movement data were used to calculate these KUDs, these metrics exclusively describe the size of manta ray activity space inside lagoons.

Habitat utilization We used selection indices to quantify the preference of active-tracked manta rays for different habitat types within the lagoons. We used bathymetric

maps (NOAA 2006) and satellite imagery to partition lagoon space that was physically accessible to manta rays into seven discrete types: deep water, ledges, subsurface mounts, subsurface mount borders, coastal subtidal flats, terrace coastline, and coral flats (see Appendix S2 and Fig. S2 for details). We tested the null hypothesis that individual manta rays used a habitat type within the lagoons in proportion to its availability using a chi-square goodness-of-fit test (Morrissey and Gruber 1993). Percent utilization of the different parts of lagoons was defined as: number of tracking points within a given lagoon habitat type/total number of points recorded. We restricted this analysis to the area within the confines of an individual's 95 % KUD. Percent availability of the seven lagoon habitat types was thus calculated as: area that each habitat type occupied within the 95 % KUD/total 95 % KUD area. If the null hypothesis was rejected for an animal's habitat utilization, we employed the modified Strauss linear index of food selection ($L = r_i - p_i$) to quantify lagoon habitat type selection; where L is the habitat type selection value, r_i is the percent use of habitat type and p_i is the percent availability of the habitat type (Morrissey and Gruber 1993). Positive selection values (L) for a particular habitat type indicate selection, negative values indicate avoidance, and zero values indicate random use of that habitat type.

Depth To characterize vertical movement behavior, we fitted two of the eleven tagged animals with acoustic tags (Vemco V16P) that included a built-in pressure/depth sensor (max. depth rating 136 m). One individual was depth-tagged in each of the West-Center and East lagoons. In situ testing of the tags prior to deployment indicated that instrument sensitivity limits required that all depth values 0–5 m be binned together. Depth data were recorded during active follows with position every 5 min.

Diel changes in lagoon utilization To quantify diel changes in manta ray space use, we analyzed differences in activity space size and depth profiles across periods of daytime (0620–1930 h) and nighttime (1930–0620 h); boundaries were determined using defined cutoffs for dawn and dusk.

Movement patterns between different marine habitats

To examine rates and patterns of *M. alfredi* movement between the lagoon and offshore environment, we used a dual-frequency identification sonar (DIDSON 300; Sound Metrics Corp., WA, USA) to detect manta rays as they passed through the main channel that connects Palmyra's West-Center lagoon to offshore habitats (Fig. S3). The device uses sonar to generate high-resolution digital images of animals traveling within the instrument's sensor field (Belcher et al. 2002). The unit was installed in the midpoint of the channel at 3 m depth and set to visualize a 41.7-m³

section of water extending across the width of the channel. While range limitations prevented us from monitoring the entire channel width using the DIDSON, the area visualized was sufficiently large so as to provide an accurate depiction of animal movement through this key inter-habitat transit zone. The DIDSON recorded footage for approximately 9.5 h per session and was operated nearly continuously from July 2, 2009, to July 29, 2009, and as such provides provisional insight into *M. alfredi* utilization of the lagoons during this 1-month period. We calculated the number of manta rays m⁻³ min⁻¹ in the view area of the instrument as well as the directionality of animal movement (i.e., traveling into or out of the lagoons). We were unable to differentiate individuals among the animals that were detected. From these data, we compared the total number of sightings of manta rays entering and exiting the lagoons during four diel periods (dawn, day, dusk, night) and four tidal periods (ebb, flow, high slack, low slack); see Appendix S4 for period definitions.

Characteristics of the *M. alfredi* population using lagoon habitats

We used photo identification and laser photogrammetry to gather preliminary demographic information on the population of *M. alfredi* utilizing the lagoons at Palmyra, as well as to investigate longer term patterns of manta ray site fidelity to these lagoons. Images were taken using a camera coupled with paired, calibrated lasers during haphazardly conducted underwater surveys of lagoon, channel, and offshore habitats from June 7, 2010, to September 7, 2010. From each photographic record, we attempted to record the size (disk width), sex, and when possible, identity of each animal (from distinct dorsal and ventral patterning) (Deakos 2010; Fig. S4). The mean size of animals sighted in channel and offshore environments was compared against those observed within the lagoons.

Statistical analysis

Comparisons of focal properties of *M. alfredi* ecology were made using two-way parametric (Student's *t* tests: East vs. West-Center lagoons 50 and 95 % KUD size, stable isotope comparisons) and nonparametric comparisons [Wilcoxon tests: diel 50 % and 95 % KUD size (paired), diel depths, and manta ray size]. Parametric statistics were applied only in instances where the assumptions of these parametric tests (e.g., normality) were met by the data. In instances where multiple points of comparison were required (DIDSON diel and tidal comparisons), data were analyzed using nonparametric Kruskal–Wallis tests with post hoc Holm's sequential Bonferroni corrections. Linear regressions were used to examine the relationships between the isotopic

signatures of manta rays and their size. All tests were performed using the statistical software R (R Development Core Team 2013).

Results

Energetic reliance of *M. alfredi* on lagoons

Zooplankton collected in lagoon and offshore environments were isotopically distinct from one another both in terms of $\delta^{15}\text{N}$ ($t_{30.3} = 3.8$, $P < 0.001$) and $\delta^{34}\text{S}$ ($t_{11.3} = 5.2$, $P < 0.001$), however discrimination was more pronounced between these two sources with respect to $\delta^{34}\text{S}$ (Fig. 1a). No significant differences were observed for $\delta^{13}\text{C}$ ($t_{15.3} = 1.3$, $P = 0.20$). Consequently, data for $\delta^{13}\text{C}$ were not admitted into our mixing model or our considerations of patterns of *M. alfredi* energetic reliance; i.e., the analysis was run as a two source (lagoon and offshore plankton), two isotope ($\delta^{15}\text{N}$, $\delta^{34}\text{S}$ only) model.

Median values of the posterior distribution of model outputs (indicative of the most probable contribution of source prey) suggested that the population of manta rays that we sampled inside the lagoons and in the channel leading into the lagoons took the majority of their plankton prey (approximately 82 %) from the lagoons and a smaller fraction (approximately 18 %) from offshore sources (Fig. 1b). Comparison of the isotopic values of manta rays sampled inside the lagoons and those sampled in offshore environments revealed significant differences in their $\delta^{34}\text{S}$ signatures—with offshore manta rays aligning more strongly with the $\delta^{34}\text{S}$ value of offshore plankton ($t_{7.2} = -3.9$, $P < 0.01$; Fig. 1a). There were, however, no significant differences between the $\delta^{15}\text{N}$ of lagoon and offshore manta rays ($t_{8.9} = 0.69$, $P = 0.5$). Regression analyses suggested that the variance in $\delta^{15}\text{N}$ (adjusted $R^2 = -0.06$, $df = 15$, $P = 0.83$) or $\delta^{34}\text{S}$ (adjusted $R^2 = 0.05$, $df = 16$, $P = 0.18$) could not be explained by manta ray size (disk width). While the mean $\delta^{34}\text{S}$ of female manta rays ($\bar{X} = 16.58$, $\text{SD} = 0.85$) was higher than that of males ($\bar{X} = 15.85$, $\text{SD} = 0.75$), this difference was not statistically significant ($t_{15.7} = 1.9$, $P = 0.07$).

Spatial utilization of lagoon habitats by *M. alfredi*

A total of 352 h of data were collected on manta ray movement using active acoustic tracking (Fig. 2; see Table S1 for the duration of tracks of individual animals). While animals were tagged and tracked in both lagoons, we recorded no movements between these two lagoon basins. Seven of the eight manta rays tracked in West-Center lagoon moved beyond the lagoon system into offshore waters. Of the individuals that travelled offshore, all but one was relocated

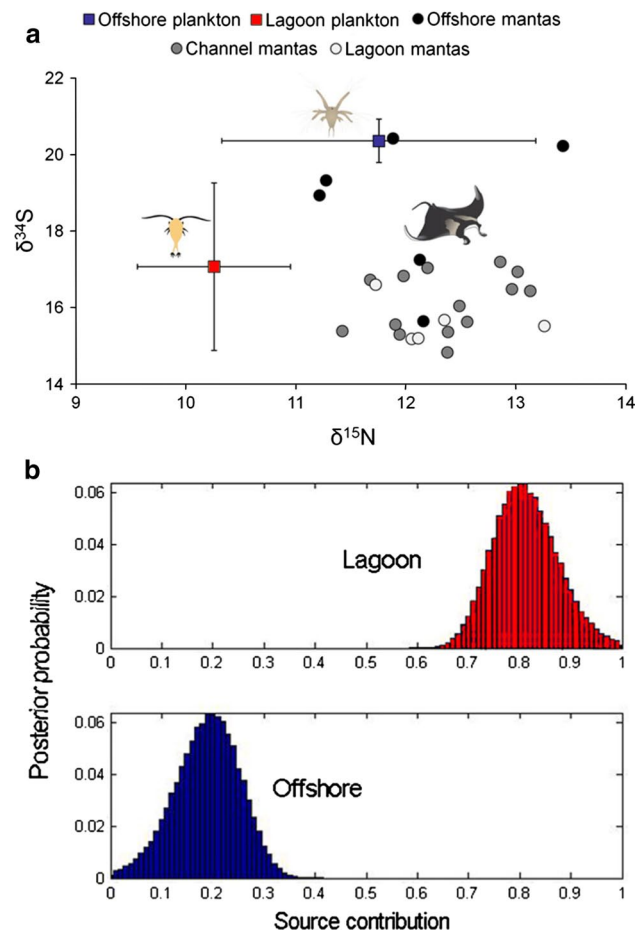


Fig. 1 Plot of **a** $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ of zooplankton collected in lagoon (red) and offshore (blue) waters. The isotopic composition (both $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$) of zooplankton from these two sources was significantly different. Isotopic signatures from *M. alfredi* biopsied in the lagoons (white), main channel (gray), and offshore (black) are compared against these zooplankton sources upon which they might feed. Values are plotted without trophic adjustment. Posterior probability distributions generated by Bayesian isotope mixing models **b** depict model predictions of the reliance of sampled manta rays on a given zooplankton source. Higher values indicate source contributions that are more likely

and tracked within the lagoons days later. The one West-Center lagoon individual that did not transit offshore (the smallest individual in our study, ~1.2 m) was detected in West-Center lagoon during every instance that it was searched for over the course of this study period. All tagged animals in East lagoon were relocated in this lagoon basin during all subsequent checks (up to 52 days after tagging), suggesting that they rarely or never traveled offshore during the duration of this study.

Results from our passive tracking data show similar patterns to those observed during active tracking (Fig. S5). Of the fifteen manta rays tagged and passively tracked in the West-Center lagoon and the main channel,

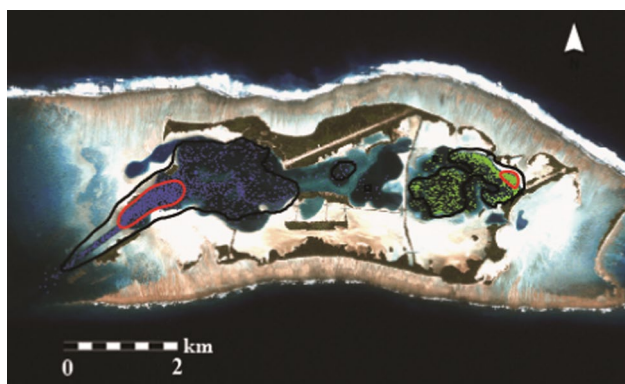
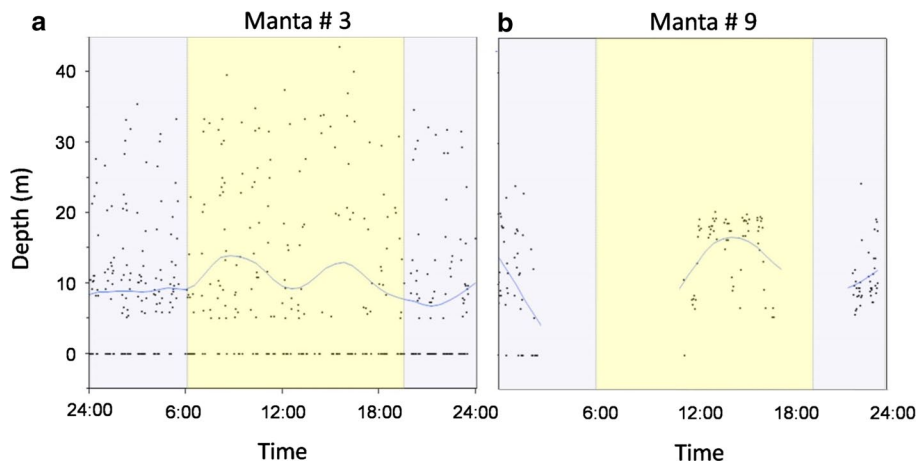


Fig. 2 Kernel utilization distributions (KUD) for all *M. alfredi* tracked at Palmyra Atoll in West-Center (blue points, $n = 7$) and East lagoons (green points, $n = 3$). Outer black contour = 95 % KUD, while inner red contour = 50 % KUD. Individual points indicate the spatial location of manta rays obtained every 5 min during active acoustic tracking

the majority of detections were from those locations. The percentage of all detections in West-Center lagoon and the main channel ranged from 88 to 100 %. Movements outside of the lagoons and into offshore areas (as detected by receivers on the forereef) were minimal. The percent of detections on the forereef for these same 15 animals ranged from 0 to 8.2 %. Of the 3 East lagoon animals, 100 % of all detections were made on East lagoon receivers (duration of detections and number of detections, respectively: 116, 90 and 12 days; 1,170, 383 and 373 detections).

Activity space size 50 % KUDs for manta rays ranged from 0.02 to 0.32 km² and 95 % KUDs ranged from 0.15 to 1.97 km² (Table S2). The mean 50 % KUD of West-Center lagoon manta rays was nearly three times larger than that of animals in East lagoon ($t_{6,1} = -3.20$, $P = 0.02$; Fig. 2). There was, however, no significant difference in the size of 95 % KUDs between West-Center lagoon and East lagoon manta rays ($t_{5,7} = 1.63$, $P = 0.16$; Fig. 2).

Fig. 3 Profile of lagoon depths used by *M. alfredi* tagged in the **a** East (Manta #3) and **b** West-Center (Manta #9) lagoon basins. A fitted average (blue line), along with daytime (yellow) and nighttime (gray) divisions are depicted



Habitat utilization Patterns of habitat utilization demonstrated by the animals tracked in the different lagoon basins revealed nuanced trends (Table S3). All three manta rays in East lagoon actively selected ledge habitats (Fig. S6a). This preference was best exemplified by two animals whose 50 % KUDs (core activity spaces) overlapped (43.9–86.4 % overlap) with ledge habitat and were confined to an area <200 m from this feature. By contrast, when manta rays in West-Center lagoon exhibited evidence of non-random habitat use, they actively avoided ledge habitats and selected deep water habitats (Fig. S6b).

Depth The individual fitted with a depth tag in East lagoon spent greater than 60 % of its time in the upper 10 m of the water column, approximately 30 % of its time between 10 and 30 m, and less than 8 % of its time at depths greater than 30 m (Fig. 3a). The second depth-tagged animal in West-Center lagoon spent approximately 40 % of its time in the upper 10 m of the water column and the rest of its time at depths between 10 and 30 m (Fig. 3b).

Diel changes in lagoon utilization Comparisons of mean 50 and 95 % KUDs generated exclusively from daytime and nighttime manta ray track data revealed no significant differences in activity space size as a function of diel period (50 % KUD: $V = 35$, $P = 0.49$; 95 % KUD: $V = 51$, $P = 0.12$; Table 1). Comparisons of mean daytime and nighttime depths revealed patterns which suggested that greater depths were used during the day for both animals with depth sensors in West-Center ($W = 4,229$, $P < 0.0001$; Table 1) and East lagoon ($W = 30,509$, $P = 0.06$; Table 1).

Movement patterns between different marine habitats

A total of 443 h of DIDSON data were collected and analyzed; 333 manta ray sightings were recorded in Palmyra's main channel during this 1 month of data collection (Fig. 4 and Video S1). Detection rates across the four selected diel periods (dawn, day, dusk, night; entrances and exits pooled) were significantly different ($\chi^2 = 9.61$, $df = 3$, $P = 0.02$;

Table 1 Influence of diel period on key factors of *M. alfredi* spatial ecology in lagoon habitats

All Mantas	Day	Night	Statistic
50 % KUD (km ²)	0.20 (±0.06)	0.11 (±0.03)	$V = 35, P = 0.49$
95 % KUD (km ²)	1.04 (±0.28)	0.50 (±0.12)	$V = 51, P = 0.12$
West-Center-Manta #9 depth (m)	15.2 (±0.6)	10.5 (±0.6)	$W = 4,228.5, P < 0.0001$
East-Manta #3 depth (m)	11.3 (±0.8)	8.4 (±0.6)	$W = 30,509, P = 0.06$

Values (mean ± SE) were averaged across all individuals (except for individuals carrying depth sensors)

Fig. 5), with this difference principally driven by a significant increase in transits recorded during the day than at dusk (post hoc comparison: $W = 454, P < 0.01$; no other post hoc comparisons revealed significant differences). There was no significant difference in the direction (in or out of the lagoons) of manta ray movement within each time period. Manta ray detection rates in the channel during the four tidal periods (ebb, flow, high slack, low slack; entrances and exits pooled) did not reveal any significant differences ($\chi^2 = 0.24, df = 3, P = 0.97$; Fig. S7).

Characteristics of *M. alfredi* population using lagoon habitats

We compiled a total of 107 *M. alfredi* photographs in the database; 69 were identified to be distinct individuals. Of these, 24 individuals were resighted on multiple occasions. In total, 12 individuals were resighted more than 2 months after their initial sighting.

Disk width of the 45 *M. alfredi* measured ranged from 1.88 to 3.39 m, with a mean size of 2.82 m (Fig. S8). Manta rays that were measured offshore and in the main channel ($n = 34$) were nearly 1.5 times larger than those sized within the lagoons ($n = 11; W = 0, P < 0.0001$). Sex determination of 60 *M. alfredi* revealed a sample slightly biased toward females (55 %).

Discussion

Manta alfredi provide a compelling demonstration of how a wide-ranging species may be ecologically reliant upon discrete habitats within its broader home range. This information contributes to our evolving understanding of the relative importance of the many habitats that a particular mobile species may traverse or otherwise interact with (Yong et al. 1998; James et al. 2005; McCauley et al. 2012c). Despite the overall capacity of *M. alfredi* and its congeners to traverse multiple marine habitats in a large geographic area (Homma et al. 1997; Dewar et al. 2008; Luiz et al. 2009; Couturier et al. 2011; Graham et al. 2012), our results suggest that a significant number of the *M. alfredi* in this study population at Palmyra Atoll appear to be intimately

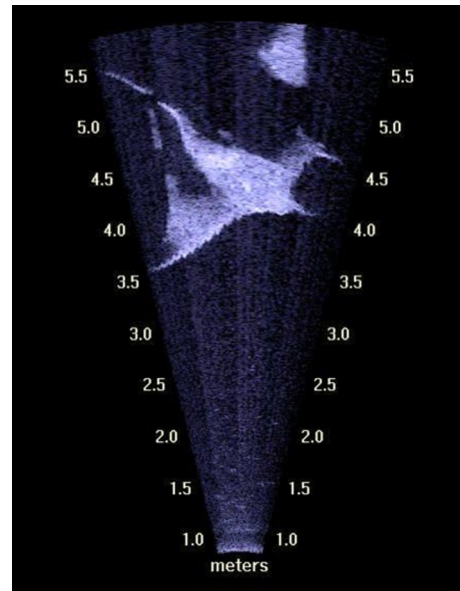


Fig. 4 Acoustic camera image of a 2.97-m *M. alfredi* traveling into the lagoons of Palmyra Atoll. High-resolution imaging data from this instrument permitted quantitative assessments to be made of the patterns by which manta rays entered and departed from lagoon habitats

connected in complex ways to very particular parts of this home range—in this case lagoons. We employed four different research tools to assess the energetic, spatial, and temporal dependence of *M. alfredi* on lagoons. The data gathered using some of these methods are relatively limited in temporal scope and consequently may provide a somewhat static view of the ecological dependency of *M. alfredi* on lagoons. More research will be required to determine whether seasonal migrations of *M. alfredi* or other sources of intra-annual variability in other attributes of their spatial ecology affect the nature of the interpretations we contribute here. Seasonal variation, however, is generally likely to be muted in this equatorial context. The behavioral connections we observe between *M. alfredi* and the lagoons of this remote and unfished atoll exhibit how this species associates with lagoons in the absence of intense human disturbance, and as such provide some insight into the baselines of spatial behavior that may be being perturbed in undetected ways in other more disturbed contexts.

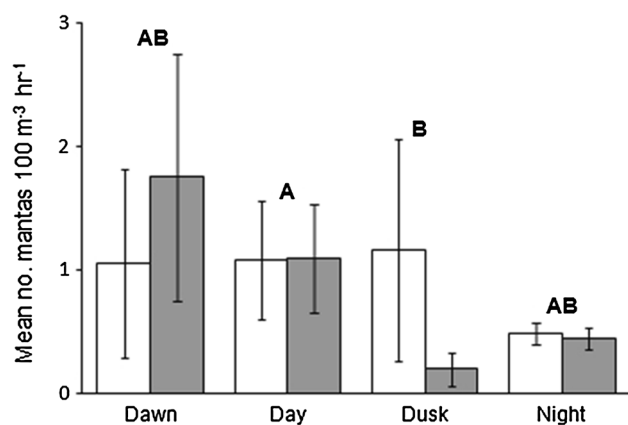


Fig. 5 Number of *M. alfredi* sighted by acoustic camera entering (white bars) and exiting (gray bars) the lagoon habitat at Palmyra Atoll over the course of four diel periods (mean \pm SE) during 1 month of data collection. Temporal periods marked with the same letters are not significantly different (after post hoc correction; entrances and exits pooled); there were no statistical differences between entrance and exit rates in any of these diel periods. See Appendix S4 for diel period definitions

Energetic reliance of *M. alfredi* on lagoons

The significant differences we observed in the nitrogen and sulfur stable isotope signals of lagoon and offshore zooplankton derive most likely from fundamental and persistent between-source differences in zooplankton community trophic level, nitrogen sourcing, and the influences of anaerobic conditions in Palmyra's lagoon basins on sulfur utilization (Peterson and Fry 1987; Gardner et al. 2011). $\delta^{34}\text{S}$ is especially useful as a discriminating agent for our purposes as it remains relatively homogenous in marine phytoplankton (ca. 20 ‰) over very large spatial scales, but is diagnostically different in the plankton of Palmyra's lagoons (Koch 2007). These observed isotopic source differences in nitrogen and sulfur allowed us to model the energetic dependency of *M. alfredi* on lagoon habitats (Fig. 1a). Model outputs suggest that a major proportion (~80 %) of the forage of the manta rays encountered in the lagoons and the main channel leading into the lagoons during the time scale of this study was derived from zooplankton of lagoonal origin (Fig. 1b). Complete isotopic turnover of the muscle of elasmobranch fishes has been estimated to take many months (Logan and Lutcvage 2010; Malpica-Cruz et al. 2012). These reported rates of muscle tissue turnover indicate that the isotopic signatures of these lagoon associated manta rays reflect reliance on lagoon resources commensurate with this period of turnover. Whether *M. alfredi* at this study site utilize plankton of lagoon origin at time scales greater than multiple months cannot be determined using these methods. The divergent isotopic signature of the manta rays sampled outside of the lagoons suggests that not all manta rays at Palmyra utilize

plankton resources in lagoons to the same degree or that lagoons are not used all at the same time. There are at least three explanations for this observed variation in *M. alfredi* isotopic signatures: (1) the individuals that look isotopically like offshore forage never feed in lagoons and represent individual variation in habitat/diet use; (2) these manta rays fed previously in the lagoons but have been consistently feeding offshore for many months; (3) these mantas just arrived to Palmyra and have not yet commenced feeding in the lagoons. We are unable to identify which of these mechanisms are contributing to the differences we observed using these non-lethal sampling methods.

Overall, the suggestion that many manta rays found in and near the lagoons draw a good portion of their energy from these lagoons is consistent with observations elsewhere that *M. alfredi* are reliant on zooplankton of demersal origin (Couturier et al. 2013).

Spatial utilization of lagoon habitats by *M. alfredi*

Residency in lagoons

Movement tracks, activity space locations, and animal relocations taken from telemetry data, as well as photo resighting records all indicate that considerable numbers of *M. alfredi* at Palmyra spend large portions of their time inside the lagoon system. Both active and passive tagged animals in East lagoon appeared to be largely or exclusively resident within this lagoon basin for months—if not longer. Manta rays tagged in West-Center lagoon made long stays within this lagoon, but with the exception of a single animal, all periodically traveled out of the lagoons into offshore/outer reef waters. Nearly, all of the West-Center lagoon animals that made these offshore excursions were subsequently relocated again within the lagoons, suggesting consistent patterns of lagoon usage. Passive tracking data again suggest prolonged utilization of Palmyra's lagoons (i.e., often >1 month). Feeding behaviors (e.g., open mouth swimming, back flips) were regularly exhibited by *M. alfredi* during these tracking and observation periods inside the lagoons, thus corroborating our isotopic evidence that these are important feeding zones. Our inability, however, to consistently record animal behavior using these data collection methods prevents us from estimating the proportion of time that *M. alfredi* divided between different activities while within the lagoons.

Spatial variation in habitat use

Data from active acoustic tracking of *M. alfredi* in Palmyra's lagoons provide detailed insight into their behavior and patterns of movement in this habitat. The total activity spaces (95 % KUDs) of manta rays when in lagoons extended over

large proportions of the available lagoon area. Two manta rays in East lagoon, for example, had 95 % KUD sizes that were greater than three quarters of the total area of the East lagoon basin. These total in-lagoon activity space areas are quite large relative to other large mobile species also found in this same habitat (Papastamatiou et al. 2009a). *Manta alfredi* showed distinct preferences and aversions for certain features inside lagoons, but these associations varied by lagoon basin (Table S3 and Fig. S6). This variability may stem from within habitat spatial heterogeneity in the factors that influence the quality and quantity of their planktonic prey (McCauley et al. 2012a) as well as the divergent hydrological properties of these different lagoon basins which may affect the physical delivery of plankton (Gardner et al. 2011; Papastamatiou et al. 2012).

Manta alfredi spent the majority of their time in the well-mixed surface layers (i.e., <10 m depth) of the lagoons (Fig. 3). At Palmyra, it is known that the deeper lagoon waters (10–50 m) become rapidly depleted in oxygen—with dysoxic/anoxic conditions occurring at >35 m depth (Gardner et al. 2011). Manta rays made limited movements into these deeper zones, suggesting that these conditions may impose some important constraints on their use of vertical space in lagoons. Preliminary comparisons between *M. alfredi* depth usage and primary productivity levels in Palmyra's lagoons provide anecdotal evidence that some of these patterns of vertical space use may be driven by prey abundance (Fig. S9).

Temporal variation in habitat use

Comparisons of the vertical and horizontal patterns of space use by *M. alfredi* in Palmyra's lagoons across time (i.e., day vs. night) provide insight into the temporal variability of their use of this habitat. Lack of difference in the daytime and nighttime KUD sizes of *M. alfredi* (Table 1) suggests that mantas are continuously using a large portion of the lagoons and that they may be foraging constantly. The absence of diel shifts in activity space size has been noted for other lagoon-using elasmobranchs (Papastamatiou et al. 2009a), but diel shifts have been recorded for certain other ray species (Matern et al. 2000; Cartamil et al. 2003). There were significant, albeit small differences between patterns of daytime and nighttime manta ray depth utilization (greater depths used during the day; Fig. 3; Table 1). Such vertical shifts may reflect tracking by *M. alfredi* of their planktonic prey. Plankton show strong diel patterns in their depth use, even within lagoons, and many epibenthic plankton are likely to rise higher into the water column at night (Madhupratap et al. 1991). Other studies of the behavior of manta rays have shown similar diel variation in space use that appear linked to the dynamics of plankton (Dewar et al. 2008; Clark 2010).

Movement patterns between different marine habitats

Our adaptation of acoustic imaging technology for the purposes of monitoring the entry and exit of *M. alfredi* into Palmyra's lagoons demonstrated that, at least during the duration of this study, the main channel into Palmyra's West-Center lagoon is a main transit corridor that is intensely used by animals moving between offshore and lagoon habitats (Figs. 5, S7, and Video S1). While this particular channel was heavily modified by military dredging, smaller natural channels or narrow reef passes likely provided similar historical access routes for manta rays to lagoon waters at Palmyra (Collen et al. 2009). Large natural channels are likely to serve as similarly important transit pathways into lagoons for *M. alfredi* in other atoll and island settings. Manta ray movement through the channel showed peaks during certain periods of the day (e.g., dawn and day; Fig. 5) but no correlation with tidal period (Fig. S7). Our active tracking of tagged West-Center lagoon animals showed no relationship between the timing of lagoon departure by tagged animals and time or tide, suggesting that either some other unmeasured factor is governing the timing of their departure or that it is simply randomly determined. Tides do regulate patterns of habitat use in other species of rays, particularly by shaping access to feeding grounds (Silliman and Gruber 1999; Vaudo and Heithaus 2012). The apparent lack of influence of tides on *M. alfredi* habitat use leaves them more closely aligned with other ray species that have relatively constant access to their prey (Cartamil et al. 2003).

Interpreting reasons for use of lagoons by *M. alfredi*

There are several possible explanations for why *M. alfredi* would select to use lagoons in the fashion we observed. Lagoons are generally more contained, and their surface waters can be less mobile and more productive than often oligotrophic, dynamic offshore surface waters (Delesalle and Sournia 1992; Le Borgne et al. 1997); as such, lagoons may provide reliable and easy to access foraging habitat for manta rays.

A second possible advantage of lagoon habitats is that they may provide a refuge for *M. alfredi* from large offshore predators (e.g., large sharks) that are known to lethally and sub-lethally attack manta rays (Marshall and Bennett 2010). The same deep water passages that permit *M. alfredi* to enter these lagoons are also used by some larger predators. Surveys of sharks, however, conducted inside the lagoons and on the outer forereef indicate that certain species of larger sharks that have been observed to attack manta rays (e.g., *Carcharhinus amblyrhynchos*, *C. galapagensis*; Marshall and Bennett 2010) are rarer inside the lagoons (McCauley et al. 2012c; McCauley

unpublished data; Papastamatiou et al. 2009b) potentially making this a safer habitat for *M. alfredi*.

A third, non-mutually exclusive explanation, is that lagoons may serve as important nursery habitat for *M. alfredi*. Measurements obtained using laser photogrammetry indicate that *M. alfredi* inside the lagoons were significantly smaller than those measured in the main channel/offshore waters of Palmyra and generally smaller than *M. alfredi* observed at other offshore sites (Deakos 2010; Marshall et al. 2011a, b; Fig. S8). This raises the possibility that lagoons may be particularly important habitats for younger *M. alfredi*. Many species of sharks and rays use protected waterways as nursery habitats (Heupel et al. 2007; Dale et al. 2011) and Palmyra's lagoons and sandflats appear to be used as nursery areas for other reef elasmobranchs (Papastamatiou et al. 2009a). Further investigation will be required to confirm the validity of these different hypotheses for lagoon use as well as to more rigorously explore other possible drivers that may attract manta rays to lagoons.

Conclusions

Resolving the nature of the often cryptic patterns of reliance that mobile animals have upon specific habitats within the landscapes and seascapes that they range across requires the use of a diverse suite of methods. In this study, by combining information gathered using tools that confer information on direct space use (animal tracking) with data from methods that reveal energetic connections to these mosaics of space (stable isotopes) with insight from technology that can quantitatively monitor patterns of habitat access (acoustic camera), and data about the individual composition of habitat users (photo recognition/laser photogrammetry)—we were able to construct a valuable understanding of how *M. alfredi* uses and relies upon lagoon habitats.

Conclusions drawn using methods that provide insight into the ecology of *M. alfredi* over relatively short periods (e.g., active acoustic tracking, acoustic imaging) were corroborated by the use of longer term data sources (e.g., passive acoustic tracking, isotope chemical tracking). Nevertheless, additional, longer-term datasets will need to be collected in order to build fully resolved descriptions of the importance of lagoons to *M. alfredi*. Our results also suggest that there is considerable ecological diversity within *M. alfredi* found at the same locality and more work will need to be conducted to build a clearer portrait of why certain manta rays appear to use lagoons rarely and how they make use of offshore/pelagic habitats. Future work will also be necessary to evaluate how generalizable our conclusions about the importance of lagoons to Palmyra's manta rays are to other systems where *M. alfredi* occurs and to determine

how *M. alfredi* behavior differs in lagoons that are fished or are otherwise heavily impacted by anthropogenic activity. There is considerable imperative to make these determinations. Lagoons the world over are habitats that have been particularly altered by anthropogenic disturbances including pollution, overfishing, dredging, water flow impedence, structural modification, and intensification of watercraft traffic (Amerson and Shelton 1976; Fagoonee 1990; Jacquet et al. 2006; Collen et al. 2009; Williams et al. 2011). The manta rays that do make use of lagoons are directly exposed to all of these threats and such disturbance may be blocking use of this apparently valuable habitat in impacted contexts.

This ability of mobile animals such as *M. alfredi* and its congeners to traverse large distances can easily draw attention away from the potential importance of particular habitats within these broader home ranges. We hope that this work illustrates that it is necessary to collect detailed information on how mobile species ecologically relate to specific habitats within these home ranges, regardless of how expansive they may be. Information of this kind will be needed in order to properly understand the ecology of this class of mobile consumers and to effectively manage their futures.

Acknowledgments We thank staff at The Nature Conservancy and US Fish and Wildlife Service for field support and research permission. Funding was provided by the National Science Foundation, Stanford University, the Woods Institute for the Environment, and the Marisla Foundation. We also thank Sound Metrics Corp. and VEMCO for invaluable technical assistance. For important contributions in the laboratory and field, we thank: A. Briggs, C. Burniske, A. Carlisle, R. Dunbar, M. DeGraff, E. Hoffman, A.M. Friedlander, T. Jen, D. Mucciarone, N. Wenner, and E. Wulczyn. This represents publication #0105 of the Palmyra Atoll Research Consortium.

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