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Sex biased individual variation in movement patterns of a highly mobile, near-shore marine planktivore, the reef manta ray *Mobula alfredi*

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Abstract

We examined individual variation and the role of sex on the movements of the reef manta ray *Mobula alfredi*. Specifically, we analysed several movement metrics using 6 years of nightly observations (1 January 2009–31 December 2014) of 118 individually identifiable manta rays at two discrete but spatially proximate sites, locally known as Manta Heaven and Manta Village, 15 km apart on the west side of the island of Hawaii, USA. Males were slightly more often (33.5%, model fitted mean, $P < 0.05$) observed than females at Manta Heaven, but females were much more often (156.4%, model fitted mean, $P < 0.05$) observed at Manta Village. Movement patterns among individuals varied greatly, but the level of variation was similar between sexes. Some animals, mainly females, displayed more resident patterns, whereas other, more mobile, animals moved between sites more frequently and had longer gaps between sightings. We did not detect discrete behavioural groups; rather, individuals varied along a continuous spectrum from many observations and high affinity to few observations and low fidelity to survey locations. These complex and variable movement patterns observed at the individual level, between sexes and between two nearby sites, in Hawaii's manta rays highlight the need for finer scale considerations in conservation and management of highly mobile marine populations.

KEYWORDS
elasmobranchs, Hawaii, intrapopulation variation, residency, site affinity

1 | INTRODUCTION

In many animals, movement patterns vary as a function of intrinsic factors such as life history stage, sex and health, as well as extrinsic environmental conditions (Costa *et al*., 2012; Shaw, 2016; Switzer, 1993). Movements may serve to maximise feeding opportunities, ensure reproductive success when optimal feeding and breeding areas are distant from each other, avoid concentrations of predators, adjust to ambient abiotic conditions and satisfy energetic demands (Costa *et al*., 2012; Domeier & Nasby-lucas, 2008; Greenwood, 1980). Given these diverse functions, patterns of movement vary considerably among species. For example, members of some elasmobranch species tend to limit their movements to a small area (Knip *et al*., 2012a; Papastamatiou *et al*., 2010), whereas other species migrate but can also have spatially and temporally predictable aggregations (Domeier & Nasby-lucas, 2008; Macena & Hazin, 2016). However, like many marine animals (Quinn & Brodeur, 1991), elasmobranch species often fall between these extremes of the continuum, showing more complex and variable movement patterns. Information on these movement patterns can assist in the conservation of the species, in such aspects of fishery management, by-catch reduction and optimising the size and placement of marine reserves (Braccini *et al*., 2016). Traditionally, movement studies sought to characterise entire populations but the growing recognition of variation in behaviour among individuals within populations (Mittelbach *et al.*, 2014) highlights the need for finer-scale information for mobile marine fishes (Hammerschlag-Peyer & Layman, 2010).

Sharks and rays display a wide range of intraspecific variation in behaviours, including movement patterns. For example, a broadnose seven-gill shark *Notorynchus cepedianus* (Péron 1807) population in Tasmania consists of coastal and offshore dwellers with different diets, demonstrating considerable intrapopulation resource partitioning (Abrantes & Barnett, 2011). Additionally, tiger sharks *Galeocerdo cuvier* Péron & LeSueur 1822 could be grouped based on the time they spent occupying distinct depth ranges (Vaudo *et al.*, 2014). Many sharks and rays exhibit feeding site fidelity (Jaine *et al.*, 2012; Knip *et al.*, 2012a, 2012b; Vianna *et al.*, 2013), aggregating when food is abundant. However, if the individuals composing the aggregation change, the observed group size may underestimate the total number of animals that use the location.

The movement patterns of males and females differ in many elasmobranchs. For example, females may migrate to specific nursery grounds to give birth or lay eggs in species such as lemon sharks *Negaprion brevirostris* (Poey 1868) (Feldheim *et al.*, 2014) and bonnethead sharks *Sphyrna tiburo* (L. 1758) (Chapman *et al.*, 2015; Portnoy *et al.*, 2015). At finer scales, male and female sharks and rays may segregate spatially or temporally (Stehfest *et al.*, 2014; Wearmouth & Sims, 2008) and both maturity and sex can affect movements (Bansemer & Bennett, 2011). Male and female sharks may also differ in hunting tactics, such as white sharks *Carcharodon carcharias* (L. 1758) (Towner *et al.*, 2016) and *N. cepedianus* (Stehfest *et al.*, 2015).

Manta rays (Mobulidae) are large, highly mobile planktivores with two recognised species, recently reclassified into the genus *Mobula* Rafinesque 1810 (White *et al.*, 2018). The pelagic manta ray *Mobula birostris* (Walbaum 1792) primarily occupies the open ocean (Marshall *et al.*, 2009) whereas the smaller reef manta ray *Mobula alfredi* (Krefft 1868) displays more limited movements, though some individuals exchange between neighbouring populations (Germanov & Marshall, 2014). *Mobula alfredi* also exhibit site affinity and are commonly re-sighted throughout the year at certain locations (Anderson *et al.*, 2011; Braun *et al.*, 2015; Clark, 2010; Couturier *et al.*, 2011; Jaine *et al.*, 2012; Marshall *et al.*, 2011). Individuals can be identified by unique spot patterns on their ventral surface (Marshall *et al.*, 2011; Town *et al.*, 2013), facilitating research into their movements and behaviour without the need to handle and mark them. Data such as these can reveal distinct movement patterns by individuals and groups within populations and may also assist management in assessing critical habitats and determining appropriate conservation measures, such as the size of marine reserves.

In this study, we analysed nightly sightings of individual *M. alfredi* at two sites *c.* 15 km apart over 6 years to assess variation among individuals and between males and females in site affinity and movement. We hypothesised that sex ratio and overall abundance will vary seasonally and that movement patterns would vary among individuals and between sexes. We also hypothesised that based on movement metrics, we would identify distinct behavioural types including groups of more resident and transient individuals.

2 | METHODS

2.1 | Data collection

Near Kailua-Kona, Hawaii, USA, manta rays are sighted by scuba divers and snorkelers almost every night at two discrete sites, locally known as Manta Village, at Kaukalaelae Point (19.640° N, 155.997° W) and Manta Heaven, in Makako Bay (19.736° N, 156.054° W; Figure 1). Manta Heaven is located *c.* 15 km north of Manta Village. At these sites, dive operators illuminate the water column from the surface and the ocean floor (*c.* 10 m), attracting dense patches of zooplankton on which manta rays fed. The average sea surface temperatures during this study ranged from a low of *c.* 24.5°C in March to *c.* 27°C in October (United States National Oceanic and Atmospheric Administration data; www.pifsc.noaa.gov/west_hawaii_iea/sea_surface_temperatures.php).

The manta ray identification project began in 1991 in Kailua-Kona, Hawaii, by the Manta Pacific Research Foundation (MPRF; www.mantapacific.org). Manta rays have unique patterns of spots on their ventral side which, in conjunction with other distinctive features such as injury to fins and scrape marks, allow them to be reliably identified (Deakos, 2012; Germanov & Marshall, 2014; Town *et al.*, 2013). Using this approach, photos and videos from divers were used to build a regional photo-identification catalogue. Individual manta rays have been identified from the Kona coast area, mostly *M. alfredi*, observed during night dives at Manta Heaven and Manta Village. Mantas were sexed by the presence or absence of claspers in the images or videos; the data analysed here included 66 males and 52 females.

Mobula alfredi observations were recorded at Manta Heaven and Manta Village from 1 January 2009–31 December 2014 by Ocean Wings Hawaii, Inc. (www.mantarayadvocates.com). Throughout this time, data were collected at Manta Heaven on 2017 (92%) nights and at Manta Village on 1702 (78%) nights. Dives typically began immediately following sunset (*c.* 18:00 hours) and lasted *c.* 1 h. During these dives, the manta rays repeatedly came very close to the divers (<1 m) who are on the bottom and thus can look up and record the ventral spotting patterns. Moreover, the manta rays are typically present throughout the dive within *c.* 10 m of the lights (*i.e.*, not at the periphery), thus the probability of a manta ray being present but not seen is very small.

2.2 | Data analysis

To determine whether *M. alfredi* abundance or sex ratio varied throughout the year, we counted the male and female individuals seen at least once in each month at each site. A χ^2-test was used to determine if the sex ratio differed between sites. Monthly occurrences of individuals at each site were used instead of total observations to reduce the number of non-independent observations because individuals were often seen on consecutive days. For each site, a generalised

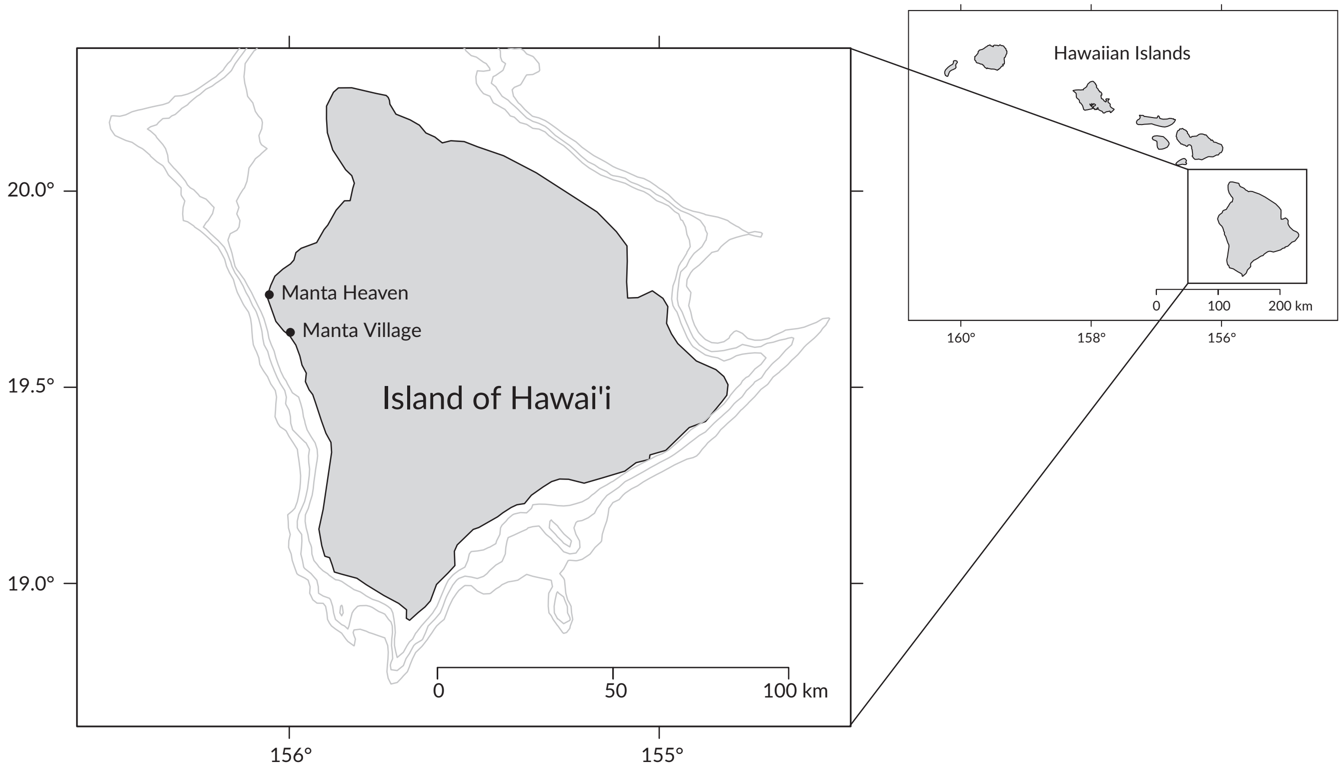

FIGURE 1 Map of study locations Manta Heaven and Manta Village. Grey lines indicate bathymetry contours at 1000, 1500 and 2000 m

linear model with a Poisson distribution was used to examine the effects of month and sex and their interaction, on the count of unique individuals present (glm function in the stats pack; R Core Team, 2018). A *post hoc* multiple comparison test was then used to further examine differences among groups for significant models (lsmeans function in the lsmeans package in R; Lenth, 2016). The model fitted means and 95% CI were plotted for sex and month for each site.

To explore sex-specific variation in movement patterns, we derived three metrics from the data for each individual: the total number of observations throughout the study period, the number of days between the first and last sighting and the total number of moves from one site to the other in either direction. We used three generalised linear models with a Poisson distribution to test for differences between males and females for each metric (response variables) and the model fitted means and 95% confidence intervals were plotted for each model. All statistical analyses were performed in R (R Core Team, 2017).

To further investigate the degree to which individual movement variation occurred and if discrete behavioural patterns were evident, we calculated the encounter rate of individuals at each site, measured as the total number of days observed divided by the total number of days surveyed. A value of 0.0 at a given site indicates that it was never observed there and a value of 1.0 indicates that the individual was observed every day that the site was surveyed. The encounter rate of individuals for each site was plotted against each other with a 1:1 line for reference. Observations on the line would indicate that the individual was observed with equal frequency at each site. Values close to an axis indicate individuals that were mostly observed at the location corresponding to that axis.

3 | RESULTS

Over the 6 years of this study there were a total of 25444 observations of 118 different *M. alfredi*, with more observations at Manta Heaven than at Manta Village (19841 *vs.* 5603; binomial test, $P < 0.05$). Of the individuals observed, 66 were male and 52 were female; this ratio of 1.27:1 did not differ significantly from 1:1 ($\chi^2 = 1.661$, $df = 1$, $P > 0.05$). On average, females were sighted more often but the difference was not significant (Mean ± SD = 261 ± 313 times *vs.* 180 ± 236 times for males, Wilcoxon signed rank test, $W = 1496$, $P > 0.05$). Of the 118 *M. alfredi*, 39 were detected on over 10% of all nights in the study area, including 15 individuals that were detected on over 25% of the nights and one on over 56% of the nights.

The 19841 observations at Manta Heaven included 111 individuals: 64 males, observed 11026 times and 47 females observed 8815 times. Generalised linear model results revealed significant differences in number of individuals across months ($\chi^2 = 47.9$, $df = 11$, $P < 0.05$) and between sexes ($\chi^2 = 58.7$, $df = 1$, $P < 0.05$). There was no significant interaction between month and sex, meaning that the number of males and females did not change significantly across months. *Post hoc* multiple comparison tests revealed that there were more males (model fitted mean ± SE = 22.7 ± 0.56) than females (model fitted

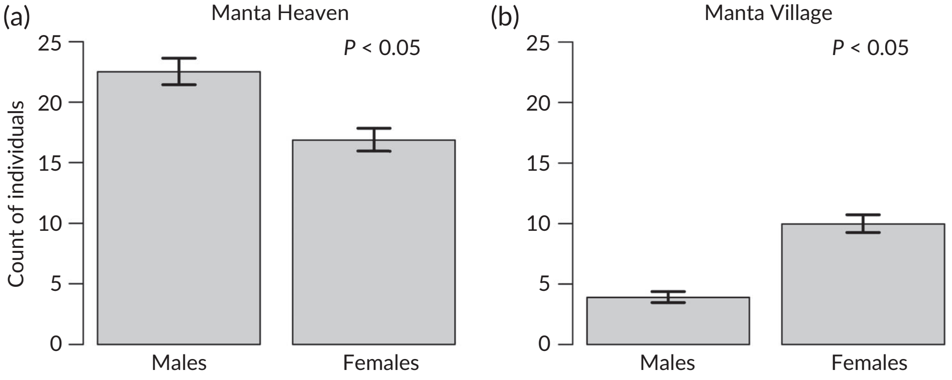

FIGURE 2 (a) Generalised linear model fitted mean (±95% CI) values for the unique number of male and female manta rays detected at Manta Heaven and (b) Manta Village

mean ± SE = 17.0 ± 0.49, $P < 0.05$; Figure 2a). Most individuals were seen in April and July and the fewest were seen in January (Figure 3a).

At Manta Village, 5603 observations were made of 71 individuals: 36 males and 35 females. Males were observed 872 times and females were observed 4731 times. Generalised linear model results revealed that month (χ^2 = 24.9, *df* = 11, $P < 0.05$) and sex (χ^2 = 200 *df* = 1, $P < 0.05$) significantly influenced the number of individuals seen at this site. There was no significant interaction between month and sex meaning that the number of males and females did not differ across months. *Post hoc* tests revealed that females (model fitted mean ± SE = 10.1 0.37) were significantly more likely to be observed than males (model fitted mean ± SE = 3.9 ± 0.44, $P < 0.05$; Figure 2b). At Manta Village the highest number of individuals were seen in August and the fewest in January (Figure 3b).

For all individuals, generalised linear models indicated that the total number of observations was higher for females (model fitted mean ± SE = 260.5 ± 2.24) than males (model fitted mean ± SE = 180.3 ± 1.65, $P < 0.05$; Figure 4a). The number of days from first to last observation was higher for females (model fitted mean ± SE = 1417.2 ± 5.22) than males (model fitted mean ± SE = 1275.6 ± 4.40, $P < 0.05$; Figure 4b) and females moved more often between sites (model fitted mean ± SE = 21.9 ± 0.65) than males (model fitted mean ± SE = 6.6 ± 0.32, $P < 0.05$; Figure 4c).

Individuals had variable encounter rates between sites (Figure 5). Fewer males were encountered at Manta Village (n = 35) and those observed there were not encountered often (mean = 13.2 days). Females at Manta Village were observed often (mean = 169.5 days) and showed affinity to that site (Figure 5). Manta Heaven had both males and females that were encountered often (n = 11 individuals with >500 days observed) and had many individuals with few observations (n = 25 individuals with <10 days observed; Figure 5). Individuals at Manta Heaven had the highest encounter rates (>0.4; Figure 5).

4 | DISCUSSION

This study revealed differences in individual movements, some of which were associated with sex, in a highly mobile, marine planktivore, *M. alfredi*. There was sex-biased segregation between feeding sites and considerable variation in movement patterns among individuals. The data also suggested that some *M. alfredi* displayed resident-

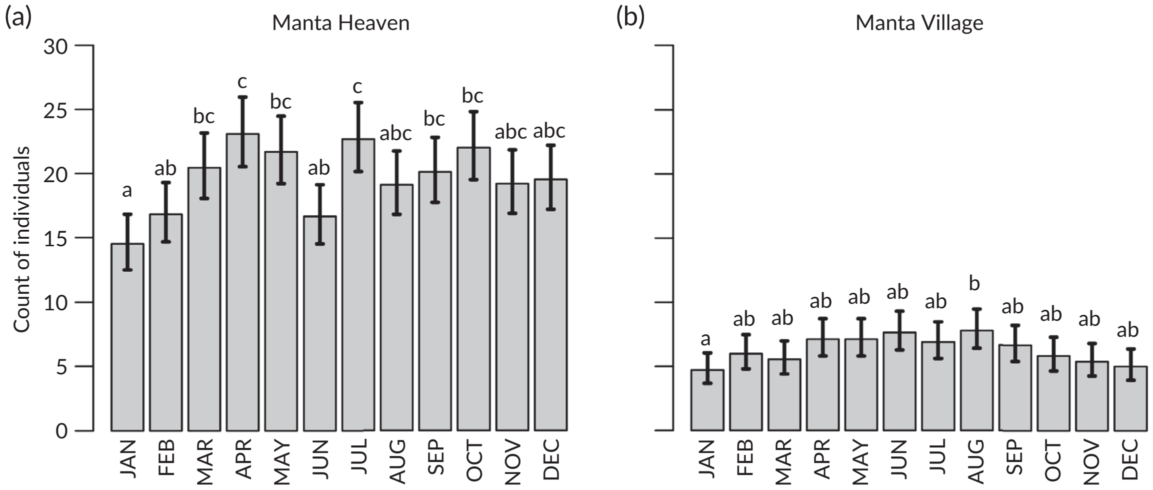

FIGURE 3 (a) Generalised linear model fitted mean (±95% CI) values for the unique number of individual manta rays seen each month at Manta Heaven and (b) Manta Village. Different lower-case letters indicate a significant difference across months ($P < 0.05$)

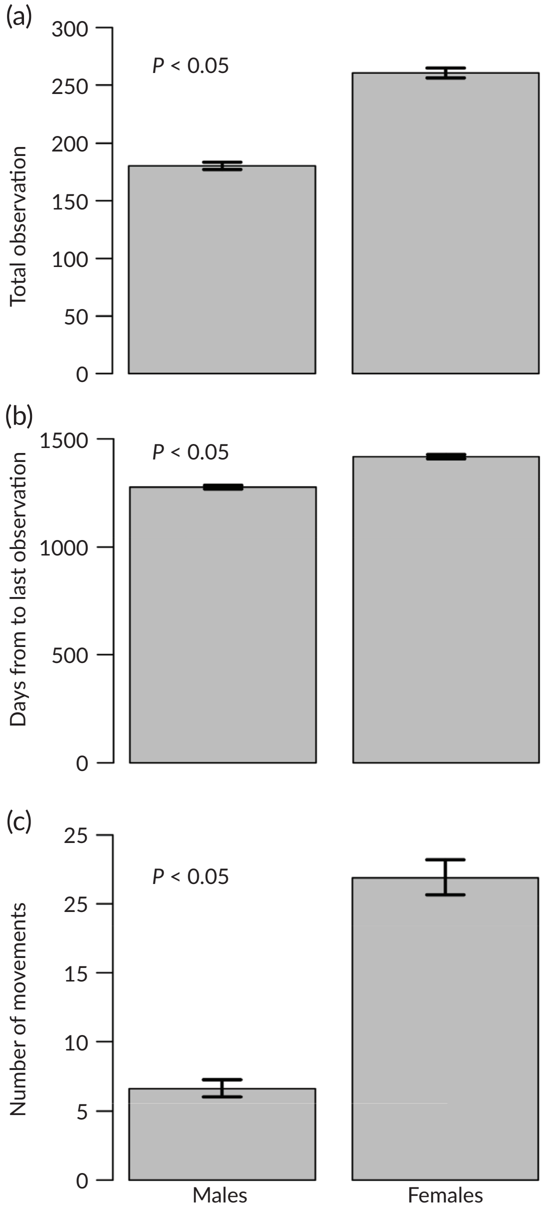

FIGURE 4 (a) Generalised linear model fitted mean (±95% CI) values between male and female manta rays for total observations, (b) days from first to last observation and (c) number of movements

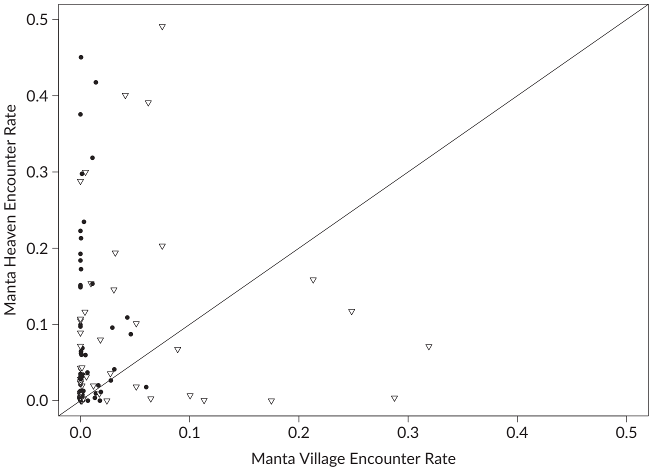

FIGURE 5 Encounter rates (number of days observed per number of days surveyed) for each individual male (●; n = 66) and female (▽; n = 52) observed at Manta Village (x-axis) and Manta Heaven (y-axis). Plotted line represents 1:1 encounter ratio, observations along the line would indicate that an individual was observed with equal frequency at each site

like behaviour due to their high frequencies of occurrence in a limited area over nearly the entire 6 years of observations.

Some results of this study are similar to the findings of Clark (2010), who used photo-identification, in addition to active and passive telemetry, to track the movements of Kona's manta rays. Clark (2010), using diver survey data, mostly from one site, concluded that Kona's *M. alfredi* display a high degree of resident behaviour, noting that 7 of 134 *M. alfredi* were detected often, on over 10% of surveys. The present study confirmed that trend and that it has been maintained over time at two sites, further supporting patterns of residency. We also observed seasonal changes in abundance, with higher *M. alfredi* abundance occurring in the northern hemisphere summer months (April to September) and fewer in the winter months, agreeing with (Clark, 2010). Seasonal peaks in frequency of observations superimposed on a patterns of year-round presence were also reported for the sicklefin devil ray, *Mobula tarapacana* (Philippi 1892) (Mendonça *et al*., 2018), but other mobulids show more distinct seasonal patterns of apparent abundance (Acebes & Tull, 2016; Anderson *et al*., 2011; Rohner *et al*., 2017; Stewart *et al*., 2017). For Kona's *M. alfredi* is unclear what drives this seasonal abundance. Clark (2010) found a correlation between *M. alfredi* and plankton abundance but did not observe any seasonal patterns of plankton abundance.

The sex-ratio of individual *M. alfredi* observed monthly was consistent at each site but different between sites and agrees with other long-term manta ray population studies in that the sex-ratio remains constant throughout the year (Couturier *et al*., 2014; Kitchen-Wheeler *et al*., 2012; Marshall *et al*., 2011). Specifically, males were more common than females at Manta Heaven, whereas females were much more common than males at Manta Village, which was previously reported at the same sites (Clark, 2010). Thus, despite the relative proximity of the two sites (15 km), the patterns differed. Marshall *et al*. (2011) suggested that a high female-to-male ratio in manta rays may be due to breeding or pupping behaviours in the area, but our study lacked the size and maturity data needed to draw such a conclusion. Regardless, further research into sex-specific behavioural differences of *M. alfredi*, that examine movements coupled with other behaviours, are needed to draw reasonable conclusions about this high degree of sex-specific feeding site segregation.

The encounter rates of individuals at each site indicated that there were not discrete behavioural groups; that is, few individuals had similar encounter rates at each site. The continuum of movement behaviours we observed may be a consequence of the individual's size or age, which can influence dispersal and other behaviours in elasmobranchs (Abrantes & Barnett, 2011; Newman *et al*., 2012; Speed *et al*., 2010).

The patterns of movements varied considerably among individual *M. alfredi* and between sexes, indicating that the frequency of sightings, movements between sites and overall time spent in an area were not similar for all animals. Females were observed more often, observed over longer time periods and moved more frequently between sites than males. Most individuals (of both sexes) were seen infrequently and they may have been transients, moving widely, or more resident at sites other than those observed here. However, some individuals were seen moderately or very often and individuals tended to occur more often at one site than the other. Interestingly, females were re-sighted more often than males despite the similar number of each sex, which is consistent with other manta ray studies (Couturier *et al*., 2014; Kitchen-Wheeler *et al*., 2012). While sex-biased dispersal patterns are yet unknown for *M. alfredi* (Jaine *et al*., 2014), they do occur in other elasmobranchs (Chin *et al*., 2013; Phillips *et al*., 2017).

Several animals were sighted consistently and throughout the study period, suggesting that they were long-term residents of the Kona coast area. A similar pattern was observed in Atlantic stingrays *Hypanus sabinus* (Lesueur 1824); 85% of the individuals made seasonal migrations and the remainder resided year-round in an estuary (Ramsden *et al*., 2017), however, this may not be the case for Kona's *M. alfredi*. Based on the active tracking of nine tagged individuals along the Kona coast, it is thought that these *M. alfredi* show high affinity to the area, spending most of their time in small, 0.4–5.9 km^2, core areas with home ranges of the order 4.5–55.1 km^2 (Clark, 2010). Thus, perhaps more of Kona's *M. alfredi* occupy discrete, overlapping home ranges than could be inferred by results of the present study due to the limitation of observing only two proximate sites. Furthermore, the sites where our observations were made had bright lights to attract plankton and thus the behaviour of the manta rays may not be fully representative of other sites where aggregations occur without such attraction. Finally, it should be noted that harassment or even contact with the Kona manta rays is strictly prohibited and studies comparing their behaviour among sites might consider the extent to which humans might affect them.

Regardless of these possible sources of influence on the results reported here, we did not detect dramatic seasonal changes in abundance or discrete modes of behaviour, as have been seen in many studies of mobile marine animals. These data did not provide evidence for clusters that would be expected if there had been such modes (*e.g*., some animals seen often and others rarely, or some at both sites and others at a single site). Rather, there was a broad distribution of encounter rates, differing primarily between males and females and between locations. Thus, while such modes of behaviour may exist, they were not evident in these data.

The complexity and variation in movement patterns of highly mobile marine animals, at the individual level, has implications for their ecology and management (Bolnick *et al*., 2003; Hammerschlag-Peyer & Layman, 2010) which can be further complicated by sexual segregation (Mucientes *et al*., 2009). For animals that vary greatly in their degrees of movement, it is useful for conservation managers to know the proportion of individuals in those populations that use a specific area and why they use it (Egli & Babcock, 2004). For manta rays and other highly mobile marine animals, whose populations are suffering due to targeted fisheries and incidental by-catch (Lawson *et al*., 2017), knowledge about their behaviours on individual scales can greatly enhance their management and conservation, particularly at a regional scale (Stewart *et al*., 2018). This particular population is already protected but the information presented might, in a more general way, benefit conservation efforts in other places where they are less well-studied.

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AUTHOR CONTRIBUTIONS

J.B.A. helped design the study, analysed data and wrote the manuscript. J.M.S. analysed data and helped prepare the manuscript. M.S.W. collected the data. T.P.Q. helped design the study and prepare the manuscript.

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