REPORT

Population dynamics of the reef manta ray *Manta alfredi* in eastern Australia

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Abstract The reef manta ray *Manta alfredi* aggregates at several sites along the east coast of Australia. Photographic identification and mark–recapture methods were used to report on the site affinity, size and structure of this population of *M. alfredi*. A total of 716 individuals were identified in 1982–2012, including 636 at Lady Elliot Island (LEI), southern Great Barrier Reef. Over 60 % of individuals identified were resighted at least once during the study period. Multiple resightings within and among years imply a high degree of site affinity by individuals to aggregation sites. One individual was sighted 11 times at LEI over a 30-yr period. The sex ratio of this population was significantly biased towards females (1.2:1 female-to-male ratio), and females were more commonly resighted than males. Robust design population models were used to estimate the population size of the winter aggregation at LEI over a 4-yr period. The models estimated up to 456 (95 % CI 399–535) *M. alfredi* individuals in the population within one winter season and a high annual apparent survival. This study demonstrated that waters around LEI form a key aggregation site for a large portion of the *M. alfredi* population in east Australian waters.

Keywords Program MARK · Photographic identification · Aggregation · Abundance · Survival · Site affinity

Introduction

Effective assessment of a species' status and conservation requires detailed information on its biology, ecology and threats (e.g., IUCN 2001). Reliable abundance estimates are essential to the study of population dynamics and to underpin conservation biology (Caughley and Gunn 1996; He and

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Gaston 2000). Obtaining these estimates is often problematic, especially for wide-ranging species that are difficult to observe and sample. These challenges are acute for large oceanic animals such as elasmobranchs that are able to travel vast distances and remain submerged. Knowledge on their population dynamics is often limited due to a lack of information on their habitat use within the geographical areas they occupy and traverse (Stevens 2010). For such species, predictable aggregations at specific sites provide unique opportunities to assess population sizes, distribution patterns and, potentially, movement patterns of these otherwise elusive fishes (e.g., Dudgeon et al. 2008; Bansemer and Bennett 2009; Holmberg et al. 2009).

The reef manta ray *Manta alfredi* has a circumglobal distribution in tropical and subtropical waters and is resident in coastal areas (Marshall et al. 2009). Individuals exhibit affinities for particular sites over many years where they often form predictable seasonal aggregations (e.g., Dewar et al. 2008; Marshall et al. 2011a). These aggregations leave the species vulnerable to targeted fisheries. The rising demand for mobulid products in Asia has led to increasing targeted fisheries for *Manta* and *Mobula* species in several parts of the world (Couturier et al. 2012), and local *M. alfredi* populations have declined in some fished areas (Marshall et al. 2011b; Rohner et al. 2013). The species is vulnerable to localise fishing pressure because of its conservative life history strategy (i.e. slow growth, late age at maturity and low fecundity) and because connectivity between geographically distinct subpopulations is likely to be limited (Couturier et al. 2012). Despite growing scientific interest in *M. alfredi* and the species being listed as Vulnerable on the IUCN Red List of Threatened Species (Marshall et al. 2011b) and on Appendix II of the CITES (CITES 2013), information on the status of the global population, as well as many local subpopulations, is limited.

Photo-identification (photo-ID) of individuals, using natural markings and/or scarring patterns on the body, provides an effective, minimally invasive method of collecting sight–resight (capture–recapture) data for population modelling (Marshall and Pierce 2012). Individual *M. alfredi* can be identified from the unique skin pigmentation patterns on their ventral surface (e.g., Marshall et al. 2011a). These markings are present from birth (Marshall et al. 2008) and remain unchanged for >30 yrs (Marshall et al. 2011b). The use of photo-ID techniques on *M. alfredi* has already provided information on the ecology, population structure and behaviour of the species (e.g., Marshall and Bennett 2010a; Deakos 2012). It has also enabled population size estimates at several key aggregation sites. Deakos et al. (2011) estimated that up to 230 individuals were resident off Maui Island, Hawaii, within a 3-month sampling period. Marshall et al. (2011a) estimated that the

annual population of *M. alfredi* off Tofo beach, Mozambique, was 149–454 individuals, with a superpopulation (i.e. total number of individuals in the population over the study period, assuming no mortality) of 890 individuals in 2003–2007. A population size of 537 individuals was estimated around North Male Atoll in the Maldives (Kitchen-Wheeler et al. 2012). Assessment of population dynamics through a combination of mark–recapture modelling and photo-ID data can provide valuable information for the conservation and management of a species. Reliable population estimates require appropriate sampling regimes (Pollock et al. 1990), which should be considered prior to data collection and meet appropriate model assumptions.

Manta alfredi individuals travel seasonally and aggregate at several tropical and subtropical coral and rocky reefs along the east coast of Australia (Couturier et al. 2011). Here, we use photo-ID to investigate the population structure (size distribution and sex ratio), resighting rate, movements between aggregation sites and individual longevity within the *M. alfredi* population in eastern Australia. We applied mark–recapture methods over a 4-yr intensive survey at the key aggregation site of Lady Elliot Island (LEI) reef to estimate the population size, survival rate and emigration of both males and females. We used Pollock's robust design (Pollock et al. 1990) as this model allows for temporary emigration and heterogeneity in capture probabilities and thus provides the best estimates of abundance for each surveyed period. This is the first study to use this modelling approach to estimate the population size of *M. alfredi* during a seasonal aggregation.

Methods

Study site

Photographs of the ventral surface of manta rays were collected year round by the authors, dive instructors and recreational divers at manta ray aggregation sites along the east coast of Australia in 2007–2012 (Fig. 1). The primary sampling sites were Heron Island, LEI, North Stradbroke Island (NSI), Byron Bay and the Solitary Islands (Fig. 1). All sites have shallow coral or rocky reefs (5–25 m depth) where manta rays are commonly observed near the surface and around cleaning stations (Couturier et al. 2011). Most of the data collection was opportunistic, and thus, sampling effort was unequal across years and sites (Table 1). Photographs taken before 2007 were obtained for LEI and NSI sites.

Population size estimates were generated for LEI (24°07′S 152°42′E), the southernmost coral cay of the Great Barrier Reef, where *M. alfredi* is sighted year round with a peak aggregation during cooler months (Couturier

Fig. 1 Locations of monitored sites in eastern Australia
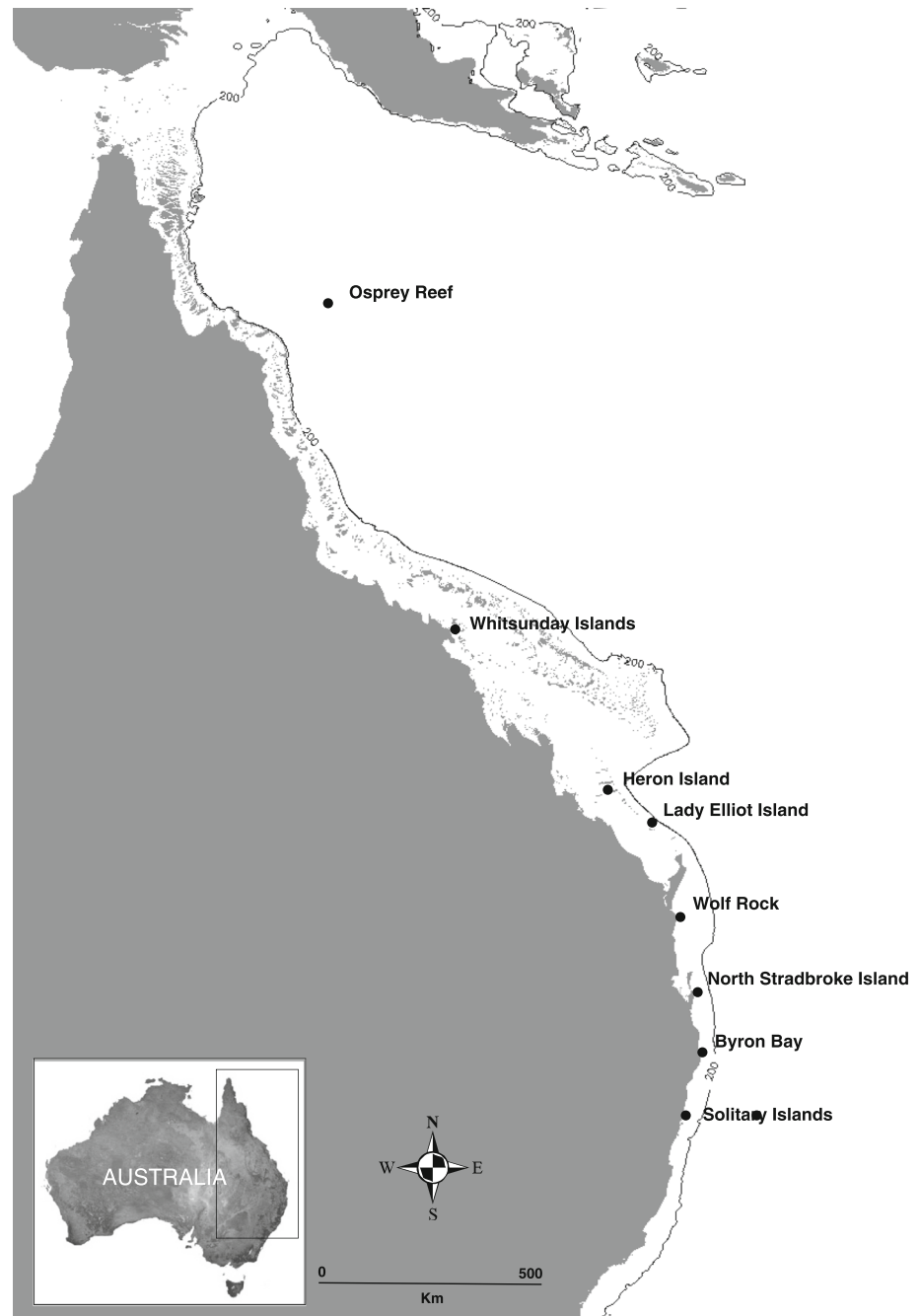
et al. 2011; Jaine et al. 2012). Specific photo-ID surveys were conducted at this site during June of each year between 2009 and 2012 to meet sampling design requirements for the application of population models (Table 1). The primary dive site, Lighthouse Bommie (9–15 m depth), is located off the western side of the island and has a sandy substrate with several large scattered coral bommies of ∼2–8 m maximum width and 0.5–2.5 m height, spread across an area of about 100 m × 50 m. This dive site is readily accessible and is a key cleaning station for *M. alfredi* (Jaine et al. 2012).

Photo-ID and laser photogrammetry

Photo-ID procedures followed those in Couturier et al. (2011). Population characteristics extracted from the database included longevity, mean number of sightings, site affinity, sex ratio and size structure among different sites (Table 1).

Two parallel laser pointers were mounted 20 cm (2010) or 50 cm apart (2011–2012) on an underwater camera housing using a custom-made aluminium frame (based on Deakos 2010). Projected laser beams were visible on the

Table 1 Summary of analyses applied to photo-identification data

Analysis	Site	Data	No. manta individuals	Effort type	Observers	Period
Resightings	EA (all sites)	Sight-resight, ID, sex	716	Opportunistic + surveys	Authors + community	1982–June 2012
Site affinity	LEI	Sight-resight, ID, sex, location	636	Opportunistic + surveys	Authors + community	1982–June 2012
Movements among sites	EA (all sites)	Sight-resight, ID, location	96	Opportunistic + surveys	Authors + community	1982–June 2012
Sex ratio and maturity	EA (all sites)	Sex, sighting, ID, location	716	Opportunistic + surveys	Authors + community	1982–June 2012
Sex ratio and maturity	LEI	Sex, sighting, ID, location	636	Opportunistic + surveys	Authors + community	1982–June 2012
Body size	LEI, NSI	ID, laser photogrammetry	75	Opportunistic	Authors	April 2010–June 2012
Minimum population size	LEI	ID, sight-resight, sex, location, date	621	Opportunistic + surveys	Authors + community	June 2009–June 2012
Robust design: population survival, temporary emigration, abundance estimate	LEI	ID, sight-resight, sex, location, date	430	Surveys	Authors	June 2009, June 2010, June 2011, June 2012

EA East Australia, *LEI* Lady Elliot Island, *NSI* North Stradbroke Island

body of the photographed manta ray, allowing extrapolation of its size (Fig. 2). Size estimations were determined using only images in which the photographed surface of the ray was near perpendicular to the axis of the laser projections and camera (Fig. 2).

Disc length (DL) was measured from photographs using Image J.1.45s (Java 1.6.0_20). For comparison, conventional disc width (DW) measurements (Francis 2006) were estimated using the equation of Deakos (2010).

$$DW(mm) = 1.9576 \times DL(mm) + 469.13$$

Since parallax may still be present in some photos, individuals were separated into four 0.5-m size classes ranging from smallest (2.5 m DW) to largest (4.5 m DW) individuals.

The sex of individuals was determined by the presence or absence of claspers. Male maturity was assessed visually with individuals classified as 'immature', 'subadult' and 'mature' based on length and apparent thickness of the claspers, and observable clasper gland structure (Marshall and Bennett 2010a). Maturity of individual females could only be confirmed if a pregnancy was observed, and was presumed when a female was seen engaged in a courtship train or had reproductive mating scars on the left pectoral fin (Marshall and Bennett 2010a). Courtship behaviour, pregnancies and mating scars were monitored opportunistically throughout the study period through direct observations, video sequences and photographs. Female maturity was also assessed based on disc width estimates observed in Hawaii (Deakos 2012), where females ≥3.5 m DW were considered mature. Sex ratio data were analysed using a binomial test with a significant level of $p < 0.05$.

Fig. 2 Photographs showing projected green laser spots, 50 cm apart, on the ventral side of an individual *M. alfredi*

Population size estimate at LEI

Sampling design

Intensive photographic surveys were conducted by the authors during the peak aggregation of *M. alfredi* at LEI in 4 primary periods: June 2009, 2010, 2011 and 2012 (Table 1). Each primary period comprised 2 weeks of data collection, with surveys conducted twice daily for 50–60 min on SCUBA. Of the 104 dives at LEI (25 in

2009, 25 in 2010, 27 in 2011 and 27 in 2012), 101 were at Lighthouse Bommie. Each survey had one or two teams of 2–4 divers swimming a standard circuit. Differences in number of divers per dive were not considered to affect sampling success as manta rays are large and conspicuous, and all divers present at the same dive site saw the same individuals. Each dive team was allocated to opposite ends of the dive site to minimise possible effects of divers on manta ray behaviour. Similarly, recreational divers were briefed before each dive to minimise their impact on manta ray behaviour. All daily data were pooled to obtain the total number of identified individual rays per day.

Robust design

Annual population sizes of *M. alfredi* aggregating at LEI in winter from 2009 to 2012 were estimated using Pollock's robust design (RD) (Pollock et al. 1990; Kendall et al. 1995, 1997; see Electronic Supplementary Material, ESM) applied in program MARKv6.1 (White and Burnham 1999). The four winter seasons were designated as primary sampling periods separated by 1-yr time intervals (i.e. June 2009, June 2010, June 2011 and June 2012). During each of the primary periods, the population was sampled in secondary sampling periods consisting in daily sampling during the 2 weeks (see ESM). Days with ≤2 individuals 'captured' within secondary periods were removed from the data set as small sample size limits the ability of the model to assess temporary emigration and abundance. Several assumptions are inherent in the application of the robust design model to this species: (1) all manta rays possess unique markings that do not change over time; (2) survival rate among primary periods is equal for all manta rays of each sex; (3) the *M. alfredi* population is closed from additions (i.e. immigration and birth) and deletions (i.e. emigration and death) within each primary period.

Annual apparent survival φ between primary periods was modelled as constant over time $\varphi(\cdot)$, varying annually $\varphi(t)$ and with sex effects $\varphi(\text{sex})$, $\varphi(\text{sex} + t)$. The effect of temporary emigration on abundance estimates was assessed using the Markovian model γ' and γ'' and the random model γ ($\gamma' = \gamma''$) (see ESM). The temporary emigration estimate is the probability of individuals present in the population being unavailable for capture in a certain period (Kendall et al. 1997). The influence of temporary emigration for both types of model was examined as time varying (t), constant over time ($\cdot$) and with and without sex effect (sex), (sex). No temporary emigration $\gamma(0)$ models were included in the candidate model set (Kendall 2012). Due to the negligible effect of photo-ID techniques on manta ray behaviour, capture p and recapture c probabilities were assumed to be equal at all time ($p = c$) and were modelled as constant ($\cdot$) or time varying within secondary periods (t), with and without sex effects (sex), (sex + t). Some parameters can be poorly estimated near the probability boundaries of 0 and 1 due to data sparseness. Data cloning procedures were applied to selected models to help identify parameters that did not appear to be estimated as values were close to one of the boundaries (Cooch and White 2012). Akaike's information criterion for small sample sizes (AICc) was used to assess model support, where the smaller AICc value indicates better model fit to the data (Burnham and Anderson 2004). Abundance estimates and standard errors were averaged across models adjusted using normalised Akaike weights (White et al. 2001).

Results

Occurrence and resightings

A total of 716 *M. alfredi* individuals were identified along the east Australian coastline out of 2,168 reported encounters for which there was a photographic image suitable for identification purposes between 1982 and 2012. Of these, 636 individuals out of 1,828 encounters were sighted at least once at LEI, including 82 individuals also sighted at another location (i.e. Byron Bay, NSI and/or Heron Island). There were 80 individuals that were only sighted at locations other than LEI (i.e. Osprey Reef, Whitsunday Islands, Heron Island, Wolf Rock, NSI, Byron Bay and Solitary Islands; Fig. 1). Of the 716 individuals identified, 63 % were re-sighted at least once. The maximum number of sightings for the same individual was 20 (all at LEI between 2007 and 2012). Of the 636 individuals identified at LEI, 66 % were resighted at least once within the study period and 62 % were resighted at least once at that same site. A maximum of 32 different individuals were identified within one dive at LEI. The longest period between first and last sighting events was 30 yrs for a male photographed at LEI in 1982 (visibly mature at the time) and resighted 10 times at the same site in 2007–2012 (Table 2; Fig. 3).

Overall, 621 individuals were identified at LEI between June 2009 and June 2012 including 430 in the June surveys of 2009, 2010, 2011 and 2012 combined. A minimum of 110 and a maximum of 244 individuals were sighted in any one June survey (Fig. 4). Of the 430 individuals, 62 % were only seen in a single survey, 16 % were sighted in at least two consecutive surveys, while 22 % were seen at least twice but were absent in one or two of the surveys.

Sex ratio and maturity

Of the 716 individuals identified across all sites, 377 (53 %) were females, 302 (42 %) were males, with a

Table 2 Sighting records for *M. alfredi* individuals photographed prior to 2007

Manta ID	Sex	First sighting	Site	Maturity status	Last sighting	Site	Maturity status	Years between 1st and last sighting	No. of resighting	Locations resighted
#002	F	02/2005	NSI	Unknown	17/06/2012	LEI	Unknown	7	6	LEI
#012	F	07/04/2004	LEI	Unknown	29/06/2012	LEI	Unknown	8	19	LEI
#069	F	11/03/2003	NSI	Unknown	1/02/2012	NSI	Unknown	9	4	LEI and NSI
#084	M	30/09/2006	NSI	Immature	26/06/2012	LEI	Mature	6	8	LEI and NSI
#134	M	1982	LEI	Mature	20/06/2012	LEI	Mature	30	10	LEI
#274	M	11/03/2003	NSI	Mature	29/06/2012	LEI	Mature	9	11	LEI and NSI
#320	F	07/09/2004	LEI	Unknown	26/06/2012	LEI	Unknown	8	2	LEI
#430	M	04/04/1993	NSI	Immature	3/03/2012	NSI	Mature	19	2	LEI and NSI

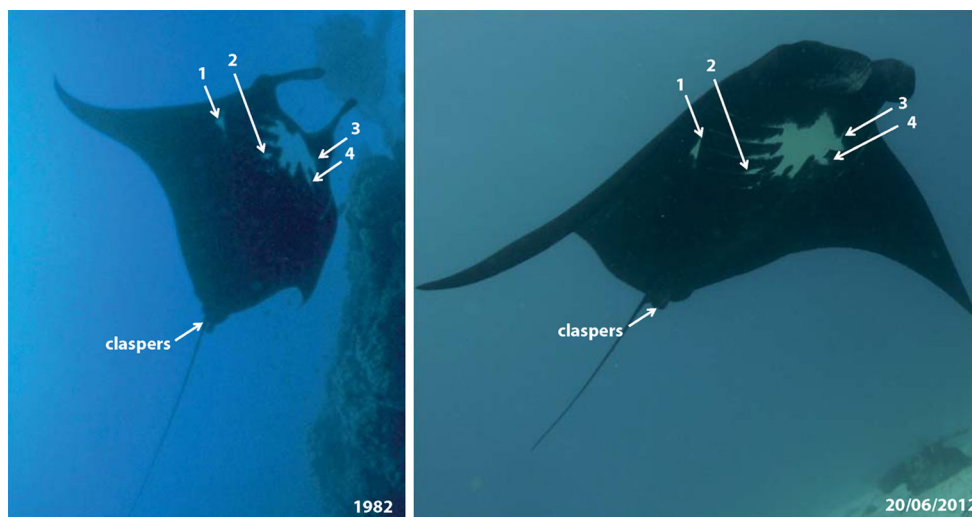*LEI* Lady Elliot Island, *NSI* North Stradbroke Island, *M* Male, *F* Female

Fig. 3 Photo-ID of individual male #134 at LEI in 1982 (month unknown, photographed by Peter Ross Allen, Aqua-Photo Pty Ltd) and June 2012 (last sighting). *Numbers* and *arrows* show different matching marking sets used to identify this individual; these remained unchanged over time

female-biased sex ratio of 1.2:1 ($p < 0.05$; proportion female = 0.56, 95 % CI 0.52–0.59), and 37 (5 %) could not be sexed. Of all males identified, 74 % were mature, 6 % were subadults and 20 % were immature. Considering pregnancies, presence of mating scars and observations of courtship behaviour as indicators of maturity, 18 % of the females identified were mature and 10 % confirmed to be pregnant at least once. Out of the 22 observations of courtship behaviour at LEI, 13 were in June–August, 5 in October–November and 1 in March. At NSI, 9 courtship behaviours were observed from October to March. One occurrence of courtship behaviour was reported at Osprey Reef in June 2009. A total of 16 identified females bore mating scars on their left pectoral fin, of which 4 had fresh red abrasions indicative of recent mating: 2 were seen in September 2010 at LEI, 1 in June 2012 at LEI and 1 in

December 2008 at NSI. Mating scars were not observed on the right pectoral fin.

Of the 450 resightings across all sites, 262 (58 %) were females, 177 (39 %) were males, and 11 (2 %) could not be sexed. Individual females were significantly more likely to be resighted than males, with 69 % of the total number of females resighted at least once in contrast to 59 % of all males ($\chi^2 = 16.46$, $df = 1$, $p < 0.05$). The mean number of sightings per individual was 3.4 for females and 2.8 for males. For resighted males, 73 % were mature, 5 % were subadults, and 21 % were immature.

Of the 636 individuals identified at LEI between 2007 and 2012, 340 (53 %) were females, and 269 (42 %) males, with a female-biased sex ratio of 1.3:1 ($p < 0.05$; proportion females = 0.56, 95 % CI 0.52–0.60), and 27 (4 %) could not be sexed. Of the males identified at LEI, 74 %

were mature, 7 % were subadults and 19 % were immature. Of the 395 individuals resighted at LEI, 60 % were females and 38 % males. Females were resighted more than males at LEI, with 69 % of the females resighted at least once in contrast to 57 % of the males identified ($\chi^2 = 18.19$, $df = 1$, $p > 0.05$). The mean number of sightings per individual at LEI was 3.3 for females and 2.7 for males.

Of the 621 individuals identified at LEI between June 2009 and June 2012, 331 (53 %) were females, 265 (43 %) were males and 25 (4 %) could not be sexed. Out of the 430 individuals sighted at LEI during the four intensive surveys, 252 (59 %) were females and 178 (41 %) were males (Fig. 4). Females were more likely to be resighted within and among primary periods than males (Figs. 4, 5).

Size distribution

Disc width estimates of 75 *M. alfredi* were pooled for 2010–2012 (54 females and 21 males). Most individuals
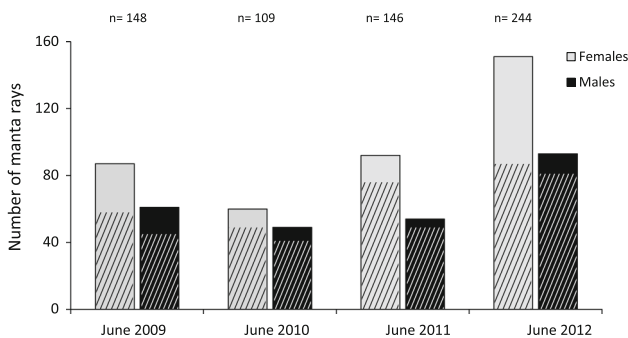

Fig. 4 Number of female (*grey bars*) and male (*black bars*) *M. alfredi* sighted during intensive June surveys in 2009–2012. *Hatched* areas represent the number of individuals sighted only once within the sampling period for each sex
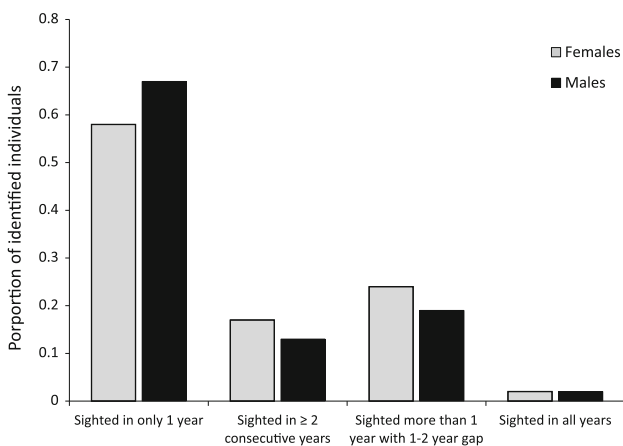

Fig. 5 Proportion of female (*grey bars*, $n = 252$) and male (*black bars*, $n = 178$) *M. alfredi* identified at LEI over the 4-yr intensive survey (June months of 2009–2012) with different sighting intervals among sampling years

were 3–4 m DW ($n = 62$), 5 individuals were <3 m DW (2 females, 3 males: all immature), and 8 were >4 m DW (all females) (Fig. 6). The vast majority of males (81 %) were 3–3.5 m DW, with 16 of 17 males classified as mature within this size class. Only one mature male was 3.5–4 m DW. The majority of females (56 %) were 3.5–4 m DW. Based on the assumption that *M. alfredi* in Australia reaches maturity at ∼3.5 m DW (Deakos 2012), 70 % of the females would be mature.

Movements

A total of 96 (13 % of 716 individuals) *M. alfredi* were sighted at more than one site along the east coast of Australia, including 83 individuals seen at two different sites and 13 at three different locations (Table 3). One manta ray was sighted at both LEI and North-West Solitary Island, in the Solitary Islands Marine Park, 650 km apart, within a 6-month period.

Population modelling and abundance estimates

A total of 15 out of the 17 RD selected models demonstrated information-theoretic support (Table 4). Models including constant apparent survival were best supported (Table 4: sum of Akaike weights for $\varphi(\cdot) = 0.66$), and this parameter was estimated close to the upper boundary [1] in the three most parsimonious models. Data cloning procedures showed that this parameter was being estimated by the models but could not be maximised away from the boundary due to data sparseness (low capture), and thus, no meaningful standard error and confidence interval were reported. Models incorporating random temporary emigration were better supported than Markovian models (Table 4: sum of Akaike weights for $\gamma = 0.82$), and thus, the probability for an individual to be absent at a certain period was independent of its presence
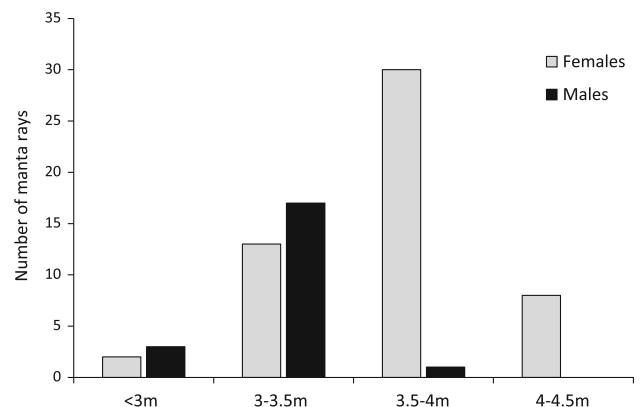

Fig. 6 Distribution of disc width for female (*grey bars*, $n = 54$) and male (*black bars*, $n = 21$) *M. alfredi* pooled for 2010–2012

Table 3 Number of individuals sighted at more than one location

	LEI and NSI	LEI and Byron Bay	LEI and HI	NSI and Byron Bay	LEI and North-West Solitary Island	LEI, NSI and Byron Bay	HI, LEI and NSI
Total	56	12	1	12	1	12	1
Male	21	5	0	5		6	
Female	33	5	1	7	1	6	1
Unsexed	2	2					

LEI Lady Elliot Island, *NSI* North Stradbroke Island, *HI* Heron Island

Table 4 Model selection for the robust design ($n = 17$) models used to estimate population size, survival and capture probability parameters for females and males

Model	AICc	ΔAICc	AICc weights	Model likelihood	No. of parameters
$\varphi(\cdot)\gamma(\text{sex})p = c(\text{sex} + t)$	1,111.391	0.000	0.551	1.000	65
$\varphi(\text{sex})\gamma(\text{sex})p = c(\text{sex} + t)$	1,113.745	2.354	0.170	0.308	66
$\varphi(\cdot)\gamma''(\text{sex})\gamma'(\text{sex})p = c(\text{sex} + t)$	1,115.942	4.550	0.057	0.103	67
$\varphi(\text{sex} + t)\gamma(0)p = c(\text{sex} + t)$	1,116.347	4.955	0.046	0.084	66
$\varphi(\cdot)\gamma(\cdot)p = c(\text{sex} + t)$	1,116.459	5.068	0.044	0.079	64
$\varphi(\text{sex})\gamma(\cdot)p = c(\text{sex} + t)$	1,117.452	6.060	0.027	0.048	65
$\varphi(\text{sex} + t)\gamma''(\text{sex} + t)\gamma'(\text{sex} + t)p = c(\text{sex} + t)$	1,117.891	6.499	0.021	0.039	68
$\varphi(\text{sex} + t)\gamma(\text{sex} + t)p = c(\text{sex} + t)$	1,118.298	6.906	0.017	0.032	68
$\varphi(\text{sex})\gamma''(\text{sex})\gamma'(\text{sex})p = c(\text{sex} + t)$	1,118.301	6.910	0.017	0.032	68
$\varphi(\text{sex})\gamma(0)p = c(\text{sex} + t)$	1,118.336	6.944	0.017	0.031	64
$\varphi(\text{sex} + t)\gamma(\text{sex})p = c(\text{sex} + t)$	1,118.340	6.948	0.017	0.031	68
$\varphi(\cdot)\gamma(0)p = c(\text{sex} + t)$	1,120.735	9.343	0.005	0.009	63
$\varphi(\text{sex})\gamma(\text{t})p = c(\text{sex} + t)$	1,121.684	10.293	0.003	0.006	67
$\varphi(\text{sex} + t)\gamma''(\text{sex})\gamma'(\text{sex})p = c(\text{sex} + t)$	1,122.862	11.470	0.002	0.003	70
$\varphi(\cdot)\gamma(\text{sex})p = c(t)$	1,140.838	29.447	0.000	0.000	61
$\varphi(\cdot)\gamma(\cdot)p = c(t)$	1,146.287	34.895	0.000	0.000	55
$\varphi(\cdot)\gamma(\text{sex})p = c(\text{sex})$	1,199.858	88.467	0.000	0.000	20

or absence at the previous sampling period. Random temporary emigration varying between sexes had more support than constant ($\cdot$), time varying (t) or no temporary emigration (0) [Table 4: sum of Akaike weights for $\gamma(\text{sex}) = 0.73$]. The best-fit model indicated that females were more likely to be temporarily emigrant than males between primary periods ($\gamma_{\text{female}} = 0.32 \pm 0.06$, $\gamma_{\text{male}} = 0$). Temporary emigration parameters for males could not be maximised away from the [0] boundary due to data sparseness.

Time-varying capture probability with a sex effect was supported by all 15 informative RD models (Table 4). This is attributed to the high variation in *M. alfredi* sightings between secondary samples (Fig. 7). These models also strongly supported differences in capture probabilities between males and females (Table 4: sum of Akaike weight = 1). Although both sexes followed the same trend within each primary period, females had higher capture probability than males at all times, with differences between female and male probability values varying between 0.005 and 0.11 (Fig. 7).

Little variation in abundance estimates was attributed to model selection for males and females for primary periods (Table 5). Weighted abundance estimates showed an increase in population size and that females were more abundant than males during the first and second primary periods, and then lower during the third and fourth periods, although 95 % CI for male estimates encompassed the female values (Table 5).

Separate models excluding sex differentiation were run to obtain overall population abundance estimates for each June survey. The best-fit model had most of the AIC weighting $[\varphi(\cdot)\gamma(\cdot)p = c(t)$; Akaike weight = 0.95] and abundance estimates from this model varied between 256 and 456 individuals for the June surveys (Tables 4, 5).

Discussion

Seasonal aggregations of *M. alfredi* have been documented across their range (e.g., Dewar et al. 2008; Anderson et al. 2011; Deakos et al. 2011; Marshall et al. 2011a). Although
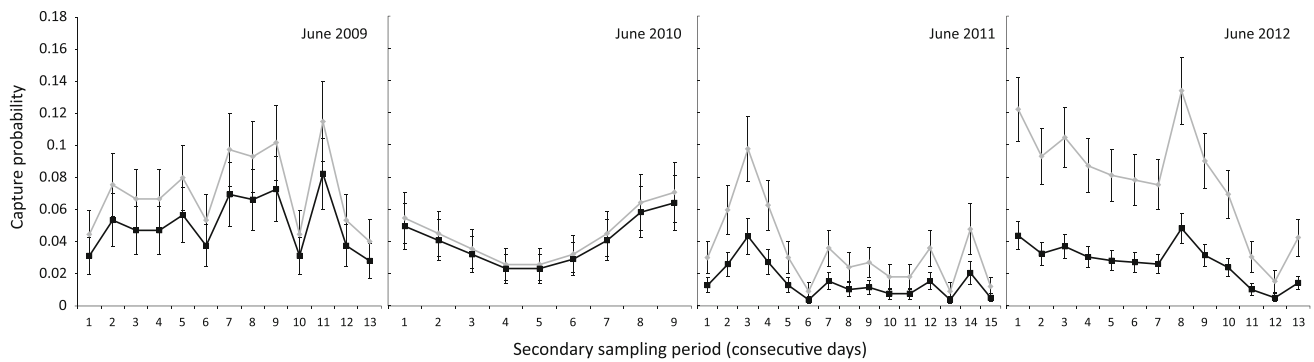
Fig. 7 Capture probabilities for secondary sampling periods for female (*grey line*) and male (*black line*) *M. alfredi* at LEI, taken from the best-fit model $\varphi(\cdot)\gamma(\text{sex})p = c(\text{sex} + t)$. Standard errors are shown

Table 5 Population size estimates of female and male *M. alfredi*; weighted average across 17 robust design (RD), overall population size estimates from best-fit model $\varphi(\cdot)\gamma(\cdot)p = c(t)$ and total number of individuals identified at LEI using photo-ID between June 2009 and 2012

Sex	Method	Year	Weighted average	Uncond. SE	95 % CI	% variation
Female	RD	2009	140	15	110–169	0
		2010	183	38	109–257	10.48
		2011	229	36	158–300	15.05
		2012	230	17	196–264	5.43
	Photo-ID	2009–2012	331			
Male	RD	2009	121	21	80–163	0
		2010	150	31	90–211	3.04
		2011	264	60	147–382	3.37
		2012	301	45	214–389	6.17
	Photo-ID	2009–2012	265			
Overall	RD	2009	256	24	219–314	
		2010	321	46	248–432	
		2011	454	58	361–589	
		2012	456	34	399–535	
	Photo-ID	2009–2012	621			

Uncond. SE standard error estimate that is unconditional on a particular model, *CI* confidence interval for the weighted average estimate based on the logit transformation, *% variation* variation in the estimate attributable to the model uncertainty

these predictable aggregations are not likely to represent entire regional populations, they nonetheless provide unique opportunities to investigate subpopulation dynamics. Using photo-ID, we have provided detailed information on the population dynamics of *M. alfredi* in eastern Australia, as well as the first population size estimates for this species in Australia. Females were sighted more frequently, and site visitation patterns varied between sexes. As individuals use multiple aggregation sites within east Australian waters and adequate sampling effort could not be achieved at all monitored sites (Couturier et al. 2011), it was not possible to estimate the total population size of *M. alfredi* for the entire area. The boundaries separating *M. alfredi* subpopulations and the interconnectivity with

neighbouring regions are currently unknown. The focus for assessing population size was thus on manta rays that use waters around LEI, the most important known aggregation site in eastern Australia.

Photo-ID validation

The availability of photographs of *M. alfredi* from the 1980s provides supporting evidence on the longevity of *M. alfredi* (Marshall et al. 2011b), with one individual photographed 30 yrs apart. Moreover, this photographic record indicates that retention of ventral body surface pigmentation extends over long period of times, including for melanistic (i.e. dark-coloured skin) manta rays.

Site affinity and movements

Over 88 % of rays recorded between Osprey Reef and South Solitary Island were sighted at least once at LEI, and individuals revisited this same site multiple times over long periods. Dive sites at LEI are accessed almost daily, which may help explain the large numbers of manta rays sighted and resighted at LEI between 2007 and 2012 (Couturier et al. 2011; Jaine et al. 2012). Nonetheless, occurrence of manta rays comparable to those seen at LEI, e.g., over 30 individuals sighted in one dive or 80 rays seen feeding at the surface (Jaine et al. 2012), has not been observed or reported at any other location in eastern Australia. It is possible, however, that there are similar aggregations along the coastline that have yet to be identified. *M. alfredi* presence at LEI may be related to seasonal food availability in the area. The island is located near the continental shelf edge where the Capricorn Eddy supplies nutrient-rich waters to the neighbouring reefs via upwelling (Weeks et al. 2010). This oceanographic process could be the source of a pulse in zooplankton productivity within this region (Jaine et al. 2012). Findings of the current study, together with those from previous research (Couturier et al. 2011; Jaine et al. 2012), demonstrate that waters off LEI provide an important seasonal habitat for what appears to be a large proportion of the *M. alfredi* population in eastern Australia.

Over 66 % of identified individuals were seen more than once at LEI. These results are comparable with those of Hawaii, where over 70 % of identified rays revisited the same site within the 5-yr study period (Deakos et al. 2011). *M. alfredi* showed greater site affinity at LEI than in Mozambique and the Maldives. Over 40 % of identified individuals in Mozambique were resighted at least once in the study area over a 4-yr period (Marshall et al. 2011a), and 36 % of the identified individuals at North Male Atoll revisited the same site over a 9-yr period (Kitchen-Wheeler et al. 2012). *M. alfredi* exhibit site affinity for several locations within a certain range, with individuals travelling seasonally up to 270 km in the Maldives (Anderson et al. 2011), 400 km in Japan (Marshall et al. 2011b) and up to 650 km in eastern Australia (this study). These recurrent movements indicate that subpopulations occupy large areas that include several key aggregation sites. Long-term resighting records of individuals at these key sites combined with strong site affinity suggest that *M. alfredi* subpopulations are unlikely to overlap with other geographically distant subpopulations (e.g., Australia and the Maldives). Interestingly, no population overlap was detected between Maui and Hawai'i Islands, two aggregation sites for *M. alfredi* only 49 km apart, even though both sites were intensively monitored for over 10 yrs (Deakos et al. 2011). These sites are separated by a 2,000-m deep channel, which

suggests movements of individuals between subpopulations might be restricted by bathymetric features and/or regional circulation (Deakos et al. 2011). The possibility exists, however, that geographically adjacent subpopulations to the present study area have a degree of connectivity, and this should be assessed through analysis of manta ray image databases from different localities, such as waters off Fiji, New Caledonia and western Australia, and by the application of molecular genetics approaches (e.g., Dudgeon et al. 2012; Kashiwagi et al. 2012).

Population structure

Size range and size at maturity (3.0–3.5 m) for males in eastern Australia are in agreement with estimates generated from Hawaiian to Mozambican reef manta ray populations (Marshall and Bennett 2010a; Deakos 2012). It is not possible to determine female sexual maturity without an indicator of mating activity, and thus, only 18 % of the identified females were considered mature. However, direct size measurements showed that 70 % of the females examined were larger than the size at maturity (≥3.5 m) reported by Deakos (2012) and within the size range (3.0–4.5 m) estimated for mature females by Kitchen-Wheeler et al. (2012). This might not be representative of the whole population but suggests that the majority of females are likely to be mature.

Females were significantly more prevalent than males at LEI (and in eastern Australian waters as a whole, although these data are strongly influenced by the LEI sightings) with a 1.3:1 female:male ratio. Although more pronounced than in eastern Australia, female-biased sex ratios were also observed in the Maldives (1.8:1) (Kitchen-Wheeler et al. 2012) and Mozambique (3.5:1) (Marshall et al. 2011a). By contrast, the *M. alfredi* population at Maui Island had no significant bias (Deakos et al. 2011). Reasons behind sex-biased habitat use in manta rays are unclear but could be related to behavioural strategies. A strong female-biased sex ratio in Mozambique, in addition to higher site affinity by females, suggests that this area is a refuge habitat for females and may be an important breeding and/or pupping site for *M. alfredi* (Marshall et al. 2011a). Molecular genetic analyses on several elasmobranch species suggest greater levels of philopatry in females than males (e.g., Schrey and Heist 2003; Blower et al. 2012). Male *M. alfredi* may also roam more than females, which return more regularly to a natal or pupping site. Courtship behaviours and mating scars observed at LEI suggest that this site is important for social interaction and mating activities. However, the lack of small *M. alfredi* (<2 m DW) indicates that females are unlikely to give birth at this site.

The smallest free-swimming *M. alfredi* reported in the literature measured 1.2–1.5 m DW (Marshall and Bennett

2010a). We found only one individual <2 m DW at NSI in March 2011 over our 4-yr study. Few small individuals were also reported in Hawaii, Mozambique and the Maldives (Deakos et al. 2011; Marshall et al. 2011a; Kitchen-Wheeler et al. 2012). The rare occurrence of small individuals (<2 m) at major aggregation sites may reflect the low reproductive rate of the species. It may also suggest size-based segregation in *M. alfredi* populations, with different habitats used by neonates and young-of-year. Many other elasmobranch species give birth in nursery areas where food resources are plentiful and neonate survival is thought to be enhanced due to lower predation pressure (Feldheim et al. 2002; Heupel et al. 2007; Bansemer and Bennett 2011), but it is unknown whether this is the case in manta rays.

Population dynamics from mark–recapture models

Survival

Although annual apparent survival of *M. alfredi* at LEI could not be assessed robustly, all models estimated this parameter to be near 1 in both sexes, suggesting little mortality and/or permanent emigration of individuals between years. This is biologically plausible as *M. alfredi* is not commercially fished in Australia and probably suffers low natural predation rates once mature. The high survival rate between years was thus not surprising as the sampled population comprised mostly large and mature individuals exhibiting strong site affinity for LEI. High survival estimates are also strongly supported by the long-term photo-ID sighting records showing that some individuals were regularly resighted at LEI over at least 6 yrs and up to 30 yrs. Higher rates of mortality likely occur at neonate and early juvenile life stage, as is common for many elasmobranchs (Cortés 2004). Given their apparent longevity and their expected low natural mortality, this 4-yr study represents a relatively short period in the lifespan of a reef manta ray. High survival rates between years were also found in the Maui subpopulation where *M. alfredi* is fully protected against commercial fishing and appears to have low exposure to predation pressure (Deakos et al. 2011). The annual apparent survival of the Mozambique population was estimated to vary between 0.6 and 0.7, which may be due to the local subpopulation sustaining a high fishing mortality (Marshall et al. 2011a). Further, >75 % of individuals identified at this location bore shark-inflicted injuries indicative of high predatory pressure on this population (Marshall and Bennett 2010b), especially when compared with the Hawaiian and east Australian subpopulations where 33 % (Deakos et al. 2011) and 23 % (LIE Couturier pers obs) of individuals have scars that result from shark predatory interactions,.

Abundance and temporary emigration

A minimum of 621 individuals were sighted at LEI in June 2009–June 2012, which is likely an underestimate of the true population size of individuals using LEI waters. In addition, the rare occurrence of individuals <2.5 m DW means that the sampled population excluded most immature individuals and only represented a portion of the true population. The largest annual number of *M. alfredi* estimated to visit LEI during winter was 456 individuals (95 % CI 399–535) for our last survey period in 2012, suggesting that not all individuals present in the sampled population use this habitat in winter. Limitations in the interpretation of RD abundance estimates, with regards to model assumptions, are discussed in the ESM. The total number of females identified between 2009 and 2012 was larger than the RD estimates in any given year, which suggests that the subpopulation of females visiting in winter represents only a portion of the available population. By contrast, the total number of males identified and the abundance estimate from RD models were similar in the last 2 yrs, which suggests that individual males are more likely to revisit the site every year. Temporary emigration estimates from the best-fit RD model indicated that females were more likely to be temporary emigrants than males (see ESM for temporary emigration estimate limitations). This further supports the assumption that not all the available female population visit LEI in winter and individual females have different visitation intervals than males. Courtship behaviours of *M. alfredi* were regularly observed in winter at LEI, suggesting mating occurs during these seasonal aggregations. Although *M. alfredi* can produce offspring every year, this species may have a 1- or 2-yr resting period between pregnancies (Marshall and Bennett 2010a). This biennial (or triennial) reproductive periodicity may explain why not all females visit LEI each winter, and individual females may have different visitation intervals. In *Carcharias taurus*, an elasmobranch with a biennial (or longer) reproductive periodicity, movement patterns are dependent upon whether a female is reproductively active or resting (Bansemer and Bennett 2011).

The RD models indicated an annual increase in abundance for both sexes from 2009 to 2012, which may indicate genuine growth of the subpopulation as *M. alfredi* is not exploited in Australian waters. Variations in abundance among years may also be influenced by fluctuations of broader environmental parameters that would affect seasonal visitation patterns at LEI (Jaine et al. 2012). However, this population increase pattern could also be, in part, an artefact due to year-on-year improvement in the ability of observers to recognise whether an individual manta ray had already been photographed within a single dive. With increased experience in the field, observers were less likely

to miss an individual ray when many rays were on site at one time. The effect of these different factors can only be assessed by extending the study across multiple years and controlling for sampling effort.

Comparison of trends in population sizes from this study with those from other subpopulations of *M. alfredi* is constrained by differences in sampling, modelling approaches and different environmental conditions. Deakos et al. (2011) reported an increase in the estimated population at a single site across several opportunistic sampling periods over 5 yrs, with the exception of the last period monitored. By contrast, Marshall et al. (2011a) showed a decrease in reef manta ray population size in Mozambique over the last three surveyed years. This decline may be linked to local anthropogenic pressures (Marshall et al. 2011a) or natural predation (Marshall and Bennett 2010a). Population estimates for *M. alfredi* in the Maldives from Kitchen-Wheeler et al. (2012) are difficult to interpret as the sampling design and analysis appear to violate assumptions of the models used, and the model selection process was not reported. Together, these studies suggest that subpopulations of *M. alfredi* generally number in the hundreds within defined areas across years. Rapid removal of individuals through fisheries or habitat loss at such aggregation sites may have a strong impact on the survival of these subpopulations due to slow fecundity and limited immigration in *M. alfredi*.

Capture probability

Probability of capture within and between each primary period showed strong variation between sampling days. It is unlikely that these results are biased by trap-dependent behaviour of individuals as photo-ID is a minimally invasive technique that generally does not interfere with the ray's activity (LIE Couturier pers ob). Within the primary period, variation in capture probability could reflect changes in the local environment as the daily abundance of individuals at LEI is influenced by temperature, wind speed, tide, local productivity and moon phase (Jaine et al. 2012). Differences in capture probability among primary periods could also be influenced by broader atmospheric and oceanographic processes associated with the El Niño Southern Oscillation, which influences the oceanography of the southern Great Barrier Reef (Weeks et al. 2010; Redondo-Rodriguez et al. 2012).

Aggregation sites as key habitats

Lady Elliot Island is an important aggregation site for *M. alfredi* in eastern Australia and provides a unique opportunity to study its population dynamics across seasons and among years. We showed that ∼456 individuals visited

this site within one winter season by application of a robust sampling design. The role that the environment plays in supporting the *M. alfredi* subpopulation at LEI is not fully understood. However, this site supports a substantial seasonal aggregation, which is likely to be a consequence of regional productivity events triggered by oceanic circulation patterns (Jaine et al. 2012). We showed here that this aggregation may also be linked with the reproductive ecology of the species and that a high proportion of the surveyed population was associated with this site for an extended period of time. Investigation of residency and site fidelity across seasons, as well as movement patterns outside the study area, will provide greater information on the role of LEI as a critical habitat for *M. alfredi*.

This study highlights the importance of aggregation sites as critical habitat for reef manta ray populations over extended periods. It also presents a robust sampling design that could be replicated at other aggregation sites to monitor local subpopulations. This is relevant to management, as localised anthropogenic pressures such as coastal development, unmanaged tourism and/or fisheries can have a direct impact on manta ray visitation patterns or population depletion (Marshall et al. 2011b). Considering the relatively low population size and high site affinity estimated for all monitored aggregations (i.e. Hawaii, Mozambique, the Maldives and LEI), it is appropriate that manta rays at these sites are protected from overexploitation and disturbances.

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