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Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique

A. D. Marshall · C. L. Dudgeon · M. B. Bennett

Abstract The size and structure of a photographically identified population of reef manta ray, *Manta alfredi*, were examined at aggregation sites over a four-year period in southern Mozambique. The use and standardisation of photo-ID techniques was examined as a minimally-intrusive means to study this species. Using these techniques, we report on the size, structure and seasonality of this population of *M. alfredi*. In total, 449 individuals were identified during this time period, 40.5% of which were re-sighted on at least one occasion. The longest period between re-sighting events was 1,252 days. During the study period, annual population size estimates for *M. alfredi* ranged from 149 to 454 individuals. The superpopulation size estimate for the entire study period was 802 individuals, the first reported for *M. alfredi* at a monitored aggregation site. A highly significant sex bias was evident with a female:male ratio of 3.55:1. The majority of rays (89.9% males; 49.7% females) were considered mature, with most individuals between 3.0 and 4.9 m in disc width. *Manta alfredi* were observed at the study sites in each month of the calendar year. The maximum number of individual rays seen per dive was 30. Large numbers of rays (20 + per dive) were seen in the months of November, December and January, which coincide with the breeding season. Natural markings were unique to individuals and did not change substantially with time, which provided further support for their use in the identification of individual *M. alfredi* over multiple years. Multiple re-sightings of individual *M. alfredi* suggest that many individuals in this population exhibit site fidelity to the examined aggregation sites. As target subsistence fishing for *M. alfredi* exists along the Mozambican coastline, management efforts to monitor and prevent overexploitation at these critical habitats should be a priority.

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Introduction

The status of pelagic elasmobranch megafauna remains unclear, as the vast geographic areas that these species inhabit and the corridors through which they travel are largely unexplored (Amorim et al. 2000; Sims et al. 2000; Martin 2007). Subtropical hotspots have been identified worldwide as areas rich in species density and diversity (Worm et al. 2005), with aggregation sites for pelagic megafauna often present and conspicuous (Stevens 2007). These aggregation sites offer some of the best opportunities to gather data on species whose population sizes or distributions are otherwise unclear or unknown, a fact that ultimately hampers the assessment and management of their populations and fisheries (Bonfil 2002; Baum et al. 2003).

Manta rays are the largest batoid fishes in the world and are pelagic planktivores with wide-ranging distributions throughout most of the world's tropic and subtropic oceans (Last and Stevens 2009; Marshall et al. 2009). These large rays are most commonly found in productive coastal areas

and are commonly encountered by divers around island groups, shallow bays, tidal channels and offshore seamounts and pinnacles (Dewar et al. 2008; Luiz et al. 2009; Marshall et al. 2009). Although manta rays are conspicuous and often easy to approach, specific information is lacking on their population sizes, population structure and demography, and movement patterns.

Mark and re-capture studies using conventional tagging methods are not well suited to manta rays, as the required effort in the field would be high, equipment expensive, and extensive physical tagging may disturb the population under investigation (Minta and Mangel 1989; Kohler and Turner 2001; Castro and Rosa 2005). Additionally, tag-fouling and tag-shedding present fundamental problems (Kohler and Turner 2001; Feldheim et al. 2002a) for the studies of long-lived elasmobranch species, where collection of data over extended periods of time is desirable.

As an alternative to tagging, visual sight–re-sight techniques using natural markings or scars present a non-intrusive and potentially more accurate way to collect similar data (Pollock et al. 1974; Hiby and Hammond 1989; Evans and Hammond 2004). Photo-identification (photo-ID) has become an increasingly common and accepted technique, with several aquatic studies having confirmed its accuracy as a research tool (Würsig and Jefferson 1990; Stevick et al. 2001; Auger-Methe and Whitehead 2007). While research using photographic sight–re-sight techniques on elasmobranchs is still in its infancy, photo-ID studies to date have examined a suite of species using distinctive markings, natural spot patterning, dorsal fin shape and scars (Sims et al. 2000; Castro and Rosa 2005; Porcher 2005; Domeier and Nasby-Lucas 2006; Dudgeon et al. 2008). Photo-ID cannot always be used, as many shark and ray species lack suitable natural markings (Castro and Rosa 2005; Porcher 2005; Meekan et al. 2006); however, for suitable candidates, this non-intrusive technique provides an effective, low-cost alternative to conventional marker tagging and may be particularly appropriate when examining vulnerable species or populations (Bansemer and Bennett 2008). Species that are good candidates for photo-ID often possess one or more common characteristics: relatively small number of animals in a population or group; distinctive and persistent markings present in a high proportion of individuals; individuals large in overall size; and in many cases, concern over a species conservation status precludes more invasive studies.

Manta rays have natural markings on their ventral surface from birth (Beebe and Tee-Van 1941; Marshall et al. 2008) that allow for individual identification (Deakos 2010; Kitchen-Wheeler 2010; Marshall and Bennett 2010a). The elaborate spot patterns, patches and shading can easily be distinguished underwater and post hoc from photographs. Although a comprehensive long-term study is absent from the scientific literature, the longevity of these markings has been reported from the photo-ID studies of manta rays at monitored aggregation sites around the world (Homma et al. 1999; Rubin 2002). Such studies have revealed that these patterns remain unchanged over time periods of at least 20 years and suggest that these natural markings may be used with confidence in photo-ID studies.

In 2009, Marshall et al. published a revision of the genus *Manta*, which is currently comprised of two species, *Manta alfredi* and *Manta birostris*. Limited information exists at the population level on either species of *Manta*, despite their wide-ranging distributions across the globe. This study aims to promote the use and standardisation of minimally intrusive photo-ID techniques for *M. alfredi* as a means to study populations at aggregation sites. Methods for the application of this technique are discussed and used to report on the size, structure and seasonality of a photographically identified population of *M. alfredi* in southern Mozambique. Photographic sight–re-sight data are then used to estimate apparent survival and capture probabilities and annual and superpopulation sizes.

Methods

A population of *M. alfredi* off the coast of Inhambane, Mozambique, was assessed over a four-year period from May 2003 to April 2007. The primary field site for this study was a 250-m^2 rocky reef with associated corals in 20–25 m of water, located approximately 20 km south of the Inhambane harbour in southern Mozambique (22.5°S, 300°E) (Fig. 1). A second, narrow, reef plateau in approximately 25–32 m of water, located 8 km south of the harbour, was also monitored when conditions were calm. Water temperatures at these sites fluctuated both daily and seasonally reaching as high as 30°C and as low as 16°C. The two monitored reefs supported three and two major cleaning stations for *M. alfredi*, respectively, with *M. alfredi* using both sites year-round. Field seasons, organised by breeding season rather than calendar year, started in the month of May and ended the following April. Field seasons were completed in 2003–2004, 2004–2005, 2005–2006 and 2006–2007 (henceforth referred to as Year 1, Year 2, Year 3 and Year 4).

Photographs and measurements

During each encounter with *M. alfredi*, a picture of the ventral surface of the ray was taken and, if possible, one was also taken of the dorsal surface and any other identifying characteristics/markings (Fig. 2a–h). The sex of the animal was determined through the presence or absence of
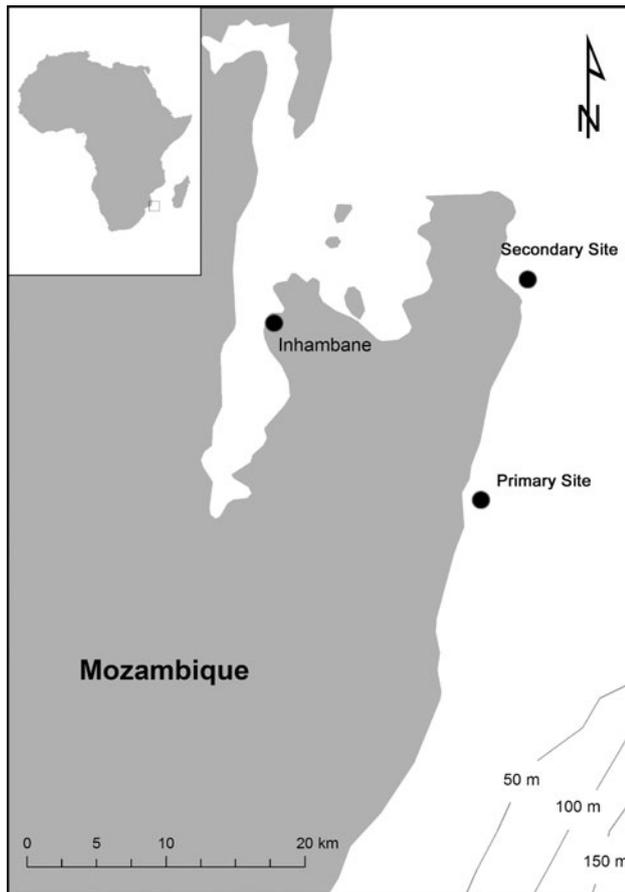
Fig. 1 Location of study sites off the coast of southern Mozambique

male reproductive organs (claspers) located on the pelvic fins (Fig. 2c, e). Male reproductive state was assessed through visual examination of the claspers following Walker (2005) (Fig. 2c, d) and is outlined in detail in Marshall and Bennett (2010a). Female reproductive status was assessed through pregnancy, i.e. observations of distended abdominal cavities (Fig. 2f) and reproductive scars (Marshall and Bennett 2010a).

Once the appropriate pictures were taken, a size estimate of the animal was obtained in the field. Size estimates were achieved using one of three methods. Disc width (DW), the distance between the tips of the pectoral fins, was often estimated based on known lengths of divers swimming immediately above or below the animal as it hovered above the reef while being cleaned by cleaner fish. Between 2003 and 2005, estimates were also periodically made using a measuring tape. Manta alfredi did not respond well to this technique. Instead of attempting to measure the entire animal, measurements were rather taken from the midline of the manta ray to the tip of one of the pectoral fins and doubled for total DW estimates. This method was found to slightly decrease the margin of error inherent in measuring such a large and flighty animal underwater. Starting in the

2006 field season, a custom-made bracket, supporting two fixed lasers projecting parallel beams of light (50 cm apart), was attached to an underwater camera housing. When photographs of the dorsal or ventral surface of a ray were taken, two small red dots, 50 cm apart, were visible in the resulting image (Fig. 2a) allowing the size of the ray to be extrapolated (as per Bansemer and Bennett 2008, 2009; Deakos 2010; Rohner et al. 2011). As a range of methods were used to estimate disc width, size classes were used rather than exact measurements. Based on the smallest and largest individuals encountered, four size class bins were used for this study: <3 m DW, 3.0–3.9 m DW, 4.0–4.9 m DW and >5 m DW.

Identifying marks

Distinctive and highly variable patterns of spots, patches and shading on *M. alfredi's* ventral surface (Fig. 2b–f, h) were used to distinguish one individual from another. Images of the natural markings were captured with underwater still cameras and on rare occasion with video cameras, with or without an artificial light source. Although natural markings on *M. alfredi* often occurred across the majority of its ventral surface, it was considered appropriate to standardise an area of the body for photographic identification and comparison. For this study, the standardised region was defined as a rectangle-shaped area extending posteriorly from the anterior margins of the anterior gill slits to, and including, the pelvic fins (Fig. 2b). Some individuals lacked natural markings either in between the gill slits or centrally on the abdomen, and thus, both regions were ultimately chosen for standardisation. The standardised area selected was easy to define, showed the sex of the animal, was not distorted by the degree of pectoral fin flexion and most importantly consistently had the most unique and distinctive patterns of any area on the ventral surface. At least one good-quality image of this area was required for the positive identification of each manta ray.

The majority of the *M. alfredi* observed (>75%) had distinctive injuries to their bodies or fins (Fig. 2g, h) that were attributed to boat strikes, fishing-related injuries and predominantly shark attacks (Marshall and Bennett 2010b). The presence or absence of a scar or bite mark (Fig. 3) or the natural markings on the dorsal surface was often used as a secondary check to confirm the identification or re-sighting of an individual whose ventral surface had already been matched.

Comparison of images

Identification and comparison of images were made by eye by a single individual. All photographs were divided into smaller more manageable groups for comparison to the
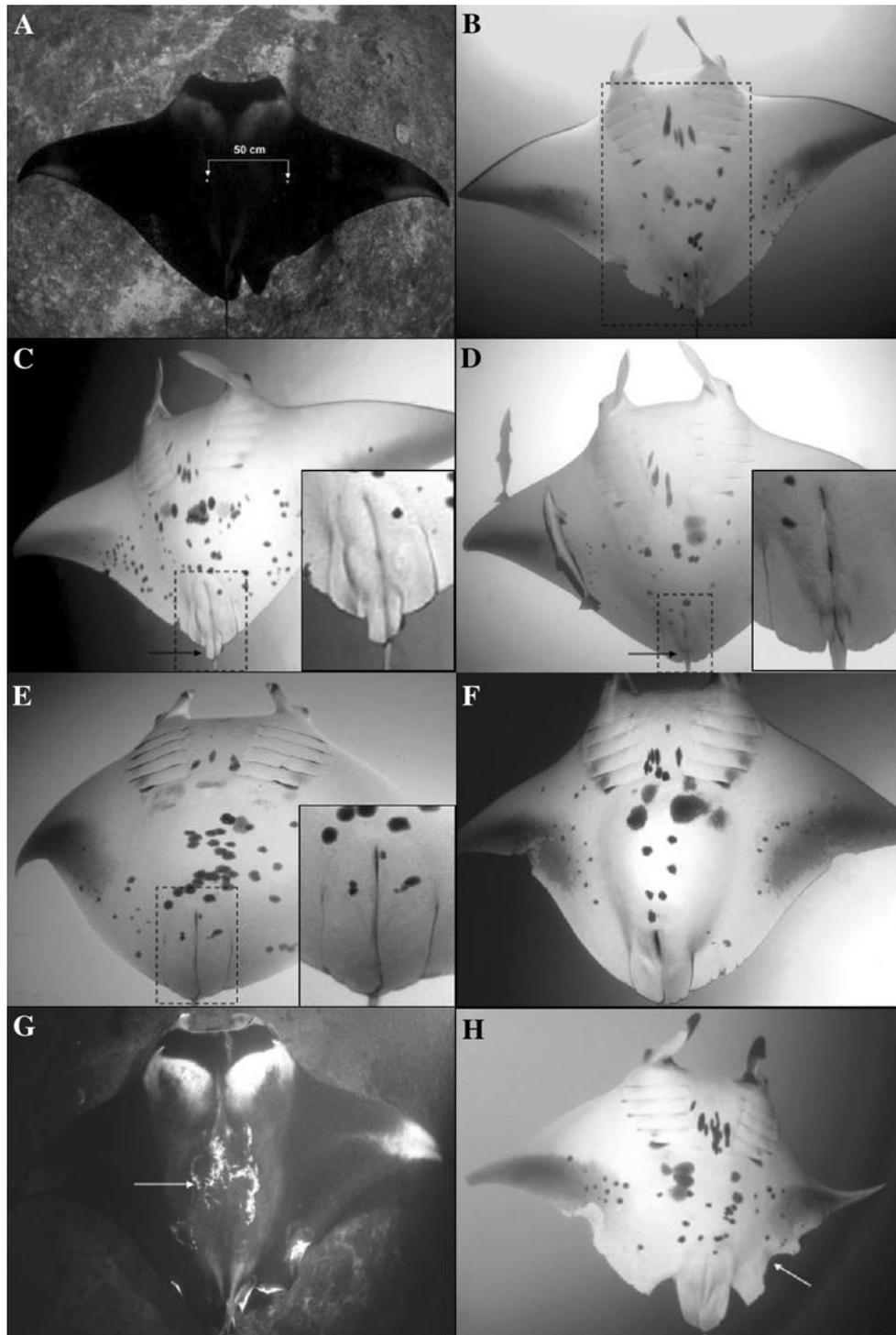
Fig. 2 Distinctive markings on *Manta alfredi*: **a** dorsal surface with laser spots indicating a 50-cm distance; **b** ventral spot patterning showing standardised area for ID shots; **c** a mature male with *boxed area* showing enlarged claspers; **d** an immature male with *boxed area* showing juvenile claspers; **e** a female with *boxed area* showing pelvic fins; **f** pregnant female; **g** *natural markings* and *bite mark* scars on the dorsal surface; **h** distinctive *bite marks* from sharks on the body of a female ray

master photo-ID database on the basis of gender and occasionally distinctive marks/scars, state of maturity or size. New images were cropped and the brightness or contrast of images was often adjusted to enhance the natural markings. Random subsets of the image database (including re-sighted images) were checked by two independent observers; no errors or incorrect identifications were discovered.
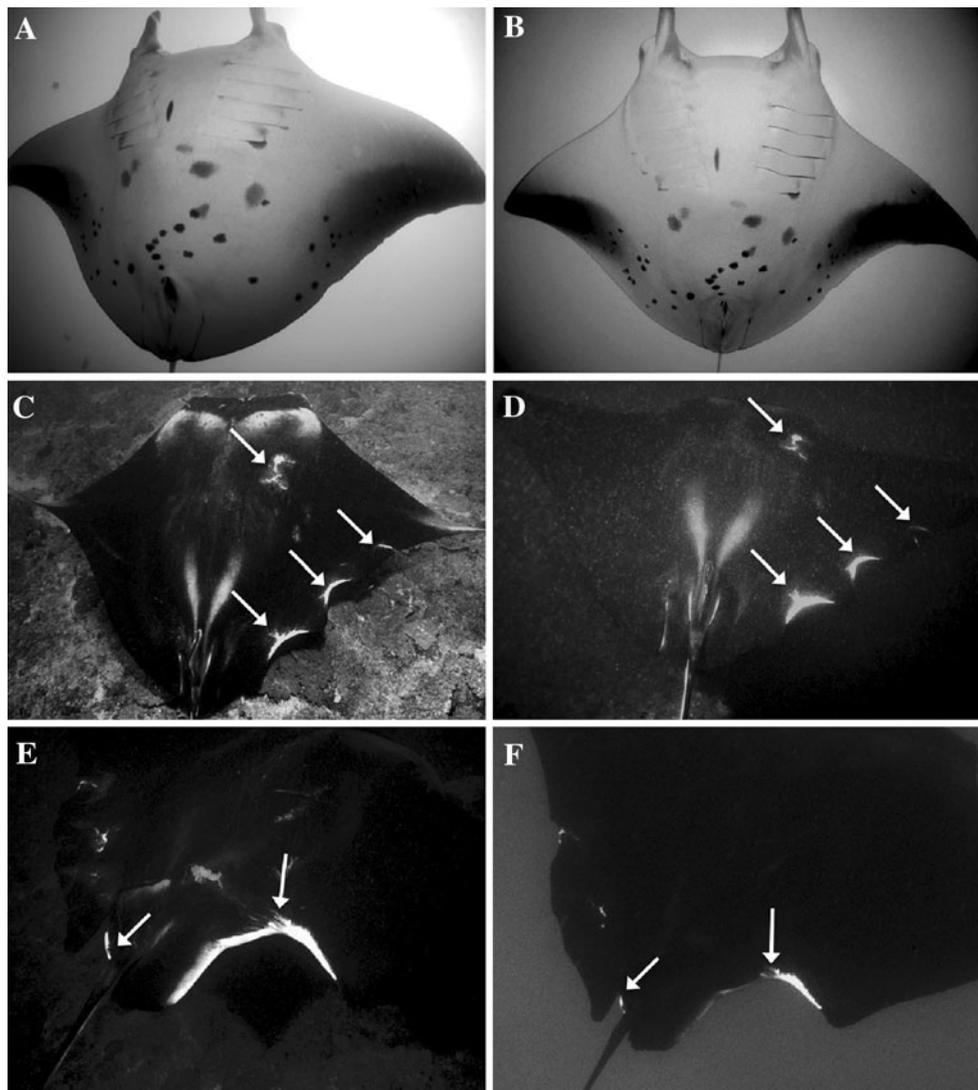
Fig. 3 An example of *unchanged spot patterning* and *bite marks* in re-sighted individuals. Photo-ID of individual #081 in: **a** May 2003; **b** January 2007. Colouration, prominent scarring and *bite marks* on the dorsal surface of individual #009 in: **c** August 2003; **d** November 2006. *Bite marks* of individual #018 in: **e** 2003; **f** 2006

Identifications and re-sightings

For each reef, divers swam in a uni-directional fashion along specific transect routes that bounded all monitored cleaning stations. The total number of individuals counted along a transect route was recorded and later compared with the total number individuals identified from photographic images or video footage taken during that survey. The total number of individuals identified or counted per minute of a dive was also determined.

New identifications were plotted over time in a discovery curve to show the rate at which newly identified individuals were recruited into the population database. Re-sighting events were defined as the positive identification of a previously known individual more than 24 h after it had most recently been seen. Re-sighting events were tracked over time at both reefs and other dive sites along the coastline.

Seasonality

Weather and practical constraints prohibited even sampling throughout and between years. The dive transects were made in the morning or the early afternoon; however, the timings of the launches varied from day to day. While conditions at the study site allowed for dives to be made independent of tide state, current strength and water temperature, large swell, strong wind and the availability of light often restricted dive transect opportunities.

To examine seasonal trends, both the total number of rays and the total number of photographically identifiable rays seen per minute of observational dive time (transect time) were calculated for each dive and then pooled by calendar month. Data were combined for the entire four-year sampling period and the means were compared across calendar months. For November, December and January, there were 4 years of data combined; for May, October and February, 3 years; for July, August, September, March and April, 2 years; and June was represented by a single year's data. The primary approach, referred to as sighting per unit effort (SPUE), offered the most realistic indication of manta ray abundance at the study sites for each month of the year as it reflected the total number of *M. alfredi* counted along the transect. The latter approach, identifications per unit effort (IPUE), represented the minimum number of rays seen on the transect reef per dive without the possibility of recounts.

Statistical analysis

Chi-square (χ^2) analysis was used to compare sex ratio data. Yates' correction factor was applied to all chi-square tests where there was one degree of freedom. Seasonal SPUE and IPUE data were examined using the Kruskal–Wallis one-way analysis of variance (ANOVA) on ranks as data were non-normal and could not be normalised. An all-pairwise (Dunn's method) was used as the post hoc test. Significance was accepted at $p < 0.05$. Analyses were conducted using Sigmastat (SigmaStat® S.P.S.S.).

Population size

A mark–re-capture approach was used to obtain population size estimates for *M. alfredi* at the monitored aggregation sites. Encounter histories for individual manta rays comprised four events between October 2003 and March 2007, where each event corresponded to pooled sighting data across the defined six-month mating period from October to March (Marshall and Bennett 2010a). Due to the low numbers of males in the data set, males and females were pooled for all analyses. As the assumption of population closure between sampling intervals (births, deaths, immigration and emigration; Otis et al. 1978) is likely to have been violated, open population models were implemented. Initially, Cormack–Jolly–Seber (CJS) models were used to assess overdispersion in the data and estimate survival between sampling years and re-capture probabilities for each year (Cormack 1964; Jolly 1965; Seber 1970). Schwarz and Arnason's parameterisation of the Jolly–Seber (JS) model (Schwarz and Arnason 1996) was then used to estimate seasonal population sizes and the superpopulation size, defined, respectively, as the number of individuals

visiting the study area each mating season (annually) and the total number of individuals visiting the study area over the duration of the study.

The estimation of demographic parameters using open models is based on several assumptions. These include (1) all individuals possess unique markings and these are stable over time; (2) sampling is instantaneous relative to the survival interval, and each release is made immediately after the sample; (3) all individuals have the same probability of capture; (4) all marked individuals have the same probability of survival. The third assumption refers to only marked individuals for the CJS models and both marked and unmarked individuals for the JS models. The first and second assumptions were addressed by assessing the photo-ID tagging methodology and by appropriate pooling of sighting data for analyses with respect to sampling interval, i.e. each sampling occasion was pooled over 6 months, while the survival interval between sampling events was 12 months. The third and fourth assumptions for the CJS model were addressed by conducting goodness-of-fit (GOF) tests implemented in program U-Care (Choquet et al. 2005).

Data analysis and model selection were carried out using the CJS and POPAN options in program MARK version 4.3 (White and Burnham 1999). For the CJS analyses, apparent survival (φ—i.e. animal is alive and available for re-capture) and re-capture probability (p) were held constant over time (.) or varied with sampling interval (t), resulting in a total of four candidate models that were assessed. The JS model provides estimates for the following parameters: apparent survival (φ), initial capture and re-capture probability (p), permanent entry into the population (β) and initial population size (N). Apparent survival and permanent entry were both modelled as constant (.) or variable over time (t). To eliminate any confounding in the estimation of population size, re-capture probability was modelled either as constant over time or was allowed to vary with sampling interval where the first and last intervals were held constant at the value of 1 (Schwarz and Arnason 1996). In total, eight JS models were fitted using the logit link function for φ and p, the identity link function for N and the multinomial logit link function for β to constrain the set of parameters to $\beta \leq 1$ (White and Burnham 1999).

Overdispersion of the data was assessed using program RELEASE (implemented through MARK), and the variance inflation factor $\hat{c}$ was calculated by dividing the combined Test 2 and Test 3 chi-square statistic by the degrees of freedom (White and Burnham 1999). Model support was assessed using the Quasi-likelihood Akaike's Information Criterion, adjusted for $\hat{c}$ and for small sample sizes (QAICc), where a smaller value of QAICc indicates better fit of the model to the data. However, differences

between QAICc values of less than 2 indicate approximately equal support of candidate models. Parameter estimates and associated errors were obtained through model averaging across normalised Akaike weights to account for model variation in the precision of the estimates (Burnham and Anderson 2002).

Results

Effort & photo-ID

In total, 265.50 h over a four-year period were spent underwater at the field sites. In the first year, 27.75 h of effort were completed at the field sites; in the second, third and fourth seasons, 77.25, 73.5, and 87 h, respectively, were spent carrying out underwater transects. A total of 3,524 slide and 765 digital images of *M. alfredi*, including those captured from video, were taken at the two study reefs during the study. During the four-year study, over 90% of the images taken of the ventral surface of *M. alfredi* were of suitable quality for positive identification, with 43% of images capturing the entire ventral surface of the individual.

Natural markings on *M. alfredi* were highly varied between all individuals (Fig. 2b–f, h) but were not affected by sex or ontogeny. The intensity of an animal's colouration sometimes appeared to change over time, with natural markings often darkening with age. The presence or shape of natural markings in the standardised area of all re-sighted individuals, however, did not alter during the study period (Fig. 3a, b). Natural markings near to the margins of the pectoral fins were sometimes obscured or altered where manta rays had sustained injuries from sharks or fishing equipment including scratches, scaring or missing flesh. With the exception of additional trauma to areas already containing bite marks or scars, all bite marks maintained their integrity throughout the study period (Fig. 3c–f). Even in cases where fresh scars or bite marks healed, there was still evidence of the original bite wound in re-sighted individuals (Marshall and Bennett 2010b).

Occurrence and re-sightings

New individuals were steadily identified throughout the study period (Fig. 4), with 449 individual *M. alfredi* ultimately identified between 2003 and 2007. A total of 852 individual encounters were made at the two study reefs. Despite these numerous observations, *M. alfredi* was absent from the transect areas on the study reefs on 91 of the 354 dives. The maximum number of *M. alfredi* seen during a transect dive was 30 individuals. The mean number of individuals observed along a transect was 4.81.
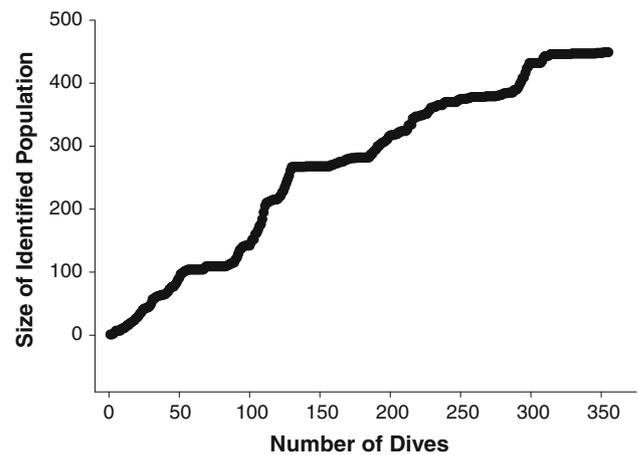
Fig. 4 Discovery curve illustrating the steady rise in total number of identified individuals over the study period

However, if calculated only for the days when conditions were optimal and at least one individual was present, the mean number of individuals sighted during surveys of the study reefs was 6.47.

One hundred and eighty-two (40.5%) of the 449 identified individuals were re-sighted on at least one occasion, with a total of 403 re-sighting events made during the study. In the first two years, the number of newly identified rays exceeded re-sighted rays, but in years 3 and 4, the number of re-sighted individuals exceeded new identifications (Fig. 5). Of the identified individuals, 327 were sighted only within the initial year of identification. Eighty-seven and 27 individuals were seen in a total of two and three of the 4 years, respectively, and only eight individuals were seen in all 4 years of the study period. The maximum number of re-sights for an identified ray in the observed population was 12, while the mean number of re-sights was 2.21. The longest period between re-sighting events was 1,252 days.
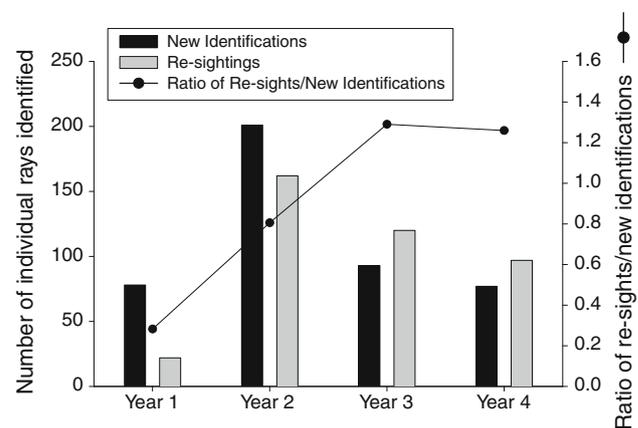
Fig. 5 Total number of individuals identified and total number of re-sights in each of the years of the study and the ratio of re-sights/new identification plotted over the 4 years

Sex ratios and size distribution

Of the total individuals identified, 78% were female and 22% were male, indicating a female-biased population ($\chi^2 = 140.31$, $df = 1$, $p < 0.0001$) that was maintained for all years of the study (ratios of 1:3.2, 1:5.4, 1:4.9, 1:10.7; chi-square for each year $p < 0.0001$) (Fig. 6).

Of the 99 males identified, 89.9% were mature, while 3 and 7.1% were classified as subadult and immature, respectively. Using pregnancy as an indicator of maturity, 17.1% of the females identified were classified as mature. However, with 42.9% of the identified females bearing visible reproductive scaring on their pectoral fins from mating (Marshall and Bennett 2010a), it was considered likely that at least 49.7% of females were mature.

Of the 403 re-sighting events, 91.8% of the re-sights were of female rays and 8.2% were of males. There was a significant difference in the re-sightability of males and females ($\chi^2 = 7.66$, $df = 1$, $p = 0.006$), with 45.7% of the total 350 identified female manta rays re-sighted on at least one occasion as opposed to only 22.2% of the 99 male individuals identified. The maximum number of re-sighting events for any individual between 2003 and 2007 was 4 times for males and 12 times for females, while the mean number of re-sighting events was 1.50 for male rays and 2.21 for female rays.

Only seven (1.6%) individuals in the identified population were less than 3 m DW, with most individuals sized in the three- or four-meter-size class ranges. Only four (0.9%) individuals, all females, were over 5 m DW. When analysed by sex, the vast majority of the females (85.7%) were between 4.0 and 4.9 m in disc width, while in contrast, the majority of males (56.6%) were sized between 3.0 and 3.9 m DW.

Seasonality

Manta alfredi was present during all months of the calendar year (Fig. 7). Due mainly to field conditions, dive effort was not consistent throughout the study. Transect effort, however, was consistent, as dive routes were standardised and dive profiles were generally similar. The maximum number of rays seen per dive during the study period was 30 individuals, with the months of November, December and January the only ones where an excess of 20 rays were seen during a single dive.

A Kruskal–Wallis one-way ANOVA on ranks demonstrated a significant difference among months in the median values of manta rays seen per minute of dive time (SPUE) ($p < 0.001$). The post hoc all-pairwise comparison, however, only revealed significant differences between the months of May, August, November, December and January and the month of March ($p < 0.05$) (Fig. 7a) A Kruskal–Wallis one-way ANOVA on ranks also revealed a significant difference in the median values of identified individuals seen per minute of dive time (IPUE) ($p < 0.001$), with the post hoc all-pairwise comparison this time showing significant differences between the months of November, December and January and the months of March and June ($p < 0.05$) (Fig. 7b).

Population size estimates

The combined goodness-of-fit testing (Test 2 & Test 3) for the full time-dependent CJS model showed a poor fit to the

Fig. 6 Number of male and female rays observed in each year. Numbers across the *top* indicate total number of individuals observed that year, ***indicates significance to the $p < 0.001$ level of sex ratio bias
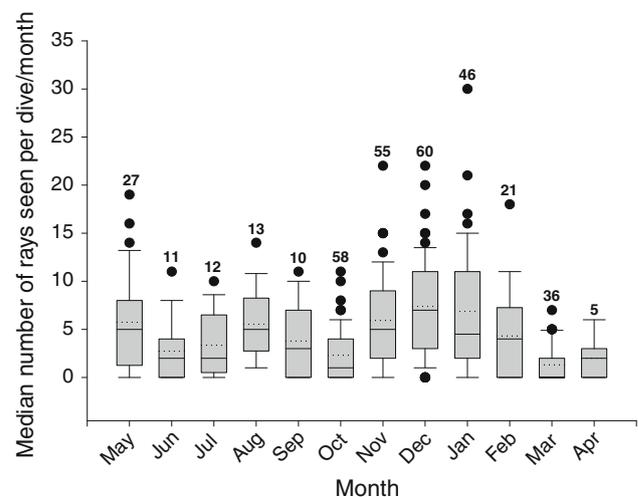
Fig. 7 Inter-month comparison of the seasonality of *Manta alfredi*: SPUE median number of rays seen per minute of dive effort/month (all years). Box plots graphically represent non-normalised data, with the *box* itself representing the 25 and 75% confidence intervals (CI) and the whiskers representing the 5 and 95% CI. Median values are reflected by the box plots but the mean is also displayed by the *dotted line*. Outliers are indicated by *solid dots* with the numbers directly over them indicating the number of sampling events (dive transects) for each month over the four-year study period

data ($\chi^2 = 16.53$, $df = 4$, $p = 0.002$) indicating overdispersion. The resulting model outputs for the CJS and JS models were adjusted with $\hat{c} = 4.13$. The one-sided test for transience was highly significant ($p < 0.001$). However, no significant heterogeneity was found for the expected time of first reencounter for new and re-sighted individuals (Test 3.SM: $p = 0.801$), nor was there any statistical support for trap-dependent behaviour (Test 2.CT: $p = 0.767$).

All four CJS models demonstrated information theoretic support with three models showing equal support for most parsimonious model (Δ QAICc. <2). There was overall greater support from the model selection for time constant over time-variant survival (sum of QAICc weights: $\varphi(.) = 0.75$). Model averaging for constant survival from the two most parsimonious models yielded an estimate of 0.683 ($\pm$0.147 SE). Model support was similar for time-constant or time-varied re-capture probabilities (sum of QAICc weights: $p(.) = 0.56$, $p(t) = 0.44$). Re-capture probabilities were averaged across the three most parsimonious models and showed a strong decrease between the first and second seasons ($p_1 = 0.528 \pm 0.188$ SE, $p_2 = 0.388 \pm 0.126$ SE, $p_3 = 0.378 \pm 0.122$ SE). Variation due to the model was high for all re-capture probabilities though more pronounced in the first season (% model variation: $p_1 = 40.05$, $p_2 = 18.50$, $p_3 = 23.01$).

The JS model list comprised seven models, of which three models showed equal support for the most parsimonious model (Δ QAICc < 2). Parameter values were only averaged for the two models with constant re-capture probability due to the inflated variation in parameter estimates due to inclusion of the model that includes fixed capture probability parameters (Table 1). There were inestimable parameters for the model $\varphi(t)p(.)\beta(t)N$, and therefore, this model was excluded from the final list. The survival and re-capture probability estimates were similar to those for the CJS model with overlapping error margins

(Table 2). There was very strong model support for permanent entry to vary over time (sum of QAICc weights = 1.00), which was primarily driven by a pulse in the second mating season that then dropped off in the third and fourth seasons (Table 2). Annual population size estimates for *M. alfredi* ranged from 149 to 454 and reflected the variation in the probability of permanent entry, with an increase in numbers between the first and second sampling occasions and then a levelling off in the third and fourth seasons (Table 2). The superpopulation size estimates, i.e. the number of manta rays visiting the study area over the duration of the study, was 802 (SE = 106, % model variation = 10.82%).

Discussion

Photographic identification

This study demonstrates that natural ventral markings coupled with body scars can be confidently used as unique identifiers of individual *M. alfredi* during discrete study periods at aggregation sites. The applicability of the photo-ID technique for *M. alfredi* over long time scales (e.g. lifespan of the animal, and from birth to maturity) still needs to be established. However, the long-term viability of these markings for individual recognition is likely, as these natural marks do not appear to change with age or alter dramatically with time, as is reported in some elasmobranch species such as *Stegostoma fasciatum* (leopard shark) or *Galeocerdo cuvier* (tiger shark) (Last and Stevens 2009).

The results from the current study indicate that the ventral markings on *M. alfredi* should also be suitable to examine small- and large-scale movement patterns between aggregation sites. Future photo-ID studies on

Table 1 Model selection for the Cormack–Jolly–Seber (CJS) models and Jolly–Seber (JS) models of survival (φ), capture probability (p) and permanent entry (β) probabilities

Model	QAICc	Δ QAICc	QAICc weight	Model likelihood	No. parameters
(i) CJS					
$\Phi(.)p(t)$	163.65	0.00	0.38727	1.000	4
$\Phi(.)p(.)$	163.77	0.13	0.36348	0.937	2
$\Phi(t)p(.)$	164.99	1.34	0.19802	0.511	4
$\Phi(t)p(t)$	167.69	4.05	0.05123	0.132	6
(ii) JS					
$\Phi(.)p(.)\beta(t)$	177.89	0.00	0.51395	1.000	6
$\Phi(t)p(.)\beta(t)$	179.14	1.25	0.27536	0.536	8
$\Phi(t)p(t)\beta(t)$	179.74	1.85	0.20378	0.397	9
$\Phi(.)p(.)\beta(.)$	187.89	10.00	0.00346	0.007	4
$\Phi(.)p(t)\beta(t)$	187.91	10.03	0.00342	0.007	8
$\Phi(t)p(t)\beta(.)$	197.87	19.98	0.00002	0.000	8
$\Phi(.)p(t)\beta(.)$	200.98	23.10	0.00000	0.000	6

QAICc Quasi Akaike information criterion for small samples ($\hat{c} = 4.13$); *ΔQAICc* difference in the QAICc of a model from the minimum QAICc model; *QAICc weight* Akaike weight

Table 2 Parameter estimates from the Jolly–Seber model, averaged across the two most parsimonious models based on QAICc weights

Parameter	Year	Estimate	SE	% variation
Φ	04–05	0.737	0.229	47.87
	05–06	0.601	0.134	8.87
	06–07	0.605	0.144	7.39
p	All	0.436	0.120	0.41
β	03–04	0.217		
	04–05	0.501	0.096	4.48
	05–06	0.127	0.096	2.59
	06–07	0.155	0.065	0.98
N	03–04	149	55	0.32
	04–05	454	131	0.11
	05–06	360	99	0.64
	06–07	324	101	1.77

Parameter: φ survival, p = re-capture probability, β permanent entry, N derived annual population estimate; *Year* 6-month sampling period spanning October–March from 2003 to 2007; *SE* standard error that is unconditional on a particular model; *% variation* variation in the estimate attributable to model uncertainty

M. alfredi would benefit by using the natural markings contained within the standardised ventral area defined in this study (see Fig. 2b) to facilitate global comparisons of individuals. Although automated computer programs have been used for comparing natural markings within various species of elasmobranchs (e.g. whale sharks and grey nurse sharks) (Arzoumanian et al. 2005; Van Tienhoven et al. 2007), the presence of many obvious identifying marks on *M. alfredi* made identification by eye manageable and efficient, with far less data waste than is typically associated with automated programs (Kitchen-Wheeler 2010). However, the study of larger populations, comparisons (cross-matching) of different populations or a global database would benefit from the use of a comprehensively designed, computer-based imaging program that is capable of dealing with large volumes of images.

Most notably, the results of this study indicate the viability of natural markings to examine the size, structure, seasonality and behaviour of *M. alfredi* populations in the wild, as individuals were easily 're-captured' through re-sighting events. *Manta alfredi* were present on the monitored reefs in southern Mozambique throughout the calendar year in all 4 years of the study. However, there was a degree of seasonality in regard to their presence at these sites. Based on daily counts, which factored in dive effort, slightly more *M. alfredi* were present on the study reefs from November to January. These data correspond to trends in seasonal catches of *M. alfredi* in the bather protection nets in Kwazulu-Natal, South Africa, approximately 900 km farther south, where 48.6% of the total number of *M. alfredi* landed per year were caught between

the months of November and February (Young 2001). As the mating and birthing season for *M. alfredi* roughly correspond to this timeframe (Marshall and Bennett 2010a), the increase in sightings along the coast may be related to reproductive behaviour or parturition, although higher sightings during the Austral summer may equally be related to environmental factors or food availability.

A strong sex bias in the observed population in southern Mozambique was revealed during this study, with females outnumbering males 3.5:1. Re-sighting data show that females are not only more prevalent in the area but were re-sighted more commonly than males. Sexual biases occur at the population level in many species of elasmobranches in space and time (Springer 1967; Klimley 1987; Anderson and Pyle 2003). Whale sharks (*R. typus*), for instance, show male-biased ratios at particular aggregation sites (Meekan et al. 2006; Graham and Roberts 2007), whereas nurse sharks (*G. cirratum*) and grey nurse sharks (*C. taurus*) in contrast exhibit a strong female bias at certain monitored aggregation sites (Castro and Rosa 2005; Bansemer and Bennett 2009). Other elasmobranch species have shown almost complete sexual segregation outside of mating seasons (Lessa et al. 1986). A strong sex bias has not been formally reported previously for an identified population of *M. alfredi*, and in Japan, 20 years of photo-ID work (Homma et al. 1999; Ito 2000) revealed significantly similar sex ratios of 1♀:1.1♂ ($n = 101$) in the total identified population of *M. alfredi*. While reports of *M. alfredi* captures in bather protection nets in South Africa have shown a slight bias towards females, with sex ratios of 1.25♀:1♂ (Young 2001), this ratio is not nearly as pronounced as the one reported in the present study (3.55♀:1♂). Such a significant female bias in the population composition along the southern coast of Mozambique may suggest that this is area is an important breeding or birthing site for this species, with female rays showing more residency to the area within and between years (Marshall and Bennett 2010a).

With only a few studies worldwide using photography to identify individual *M. alfredi* at aggregation sites, trends in abundance and distribution of this species remain largely unknown. This situation is hampering the assessment of their conservation status as well as the implementation of management programmes. Currently, regional population sizes are unclear, and the extent of mixing between neighbouring populations is unknown. The number of catalogued individuals at monitored aggregation sites appears to vary quite dramatically from region to region, despite the effort or duration of the study period. Some long-term monitoring and photo-ID studies, such as the one in the Yaeyama Islands, Japan, which spans three decades, have only identified approximately 300 individuals (Homma et al. 1999; Takashi Ito, pers. comm.). Similarly, long-term monitoring around the island of Yap has lead to

the registration of only 100 individuals over the last 20 years (Bill Acker, pers. comm.). In contrast, a study in the Maldivian Islands has registered a record of 1,442 individual *M. alfredi* in only a six-year period (Kitchen-Wheeler 2010). As it stands, the coastline off southern Mozambique boasts the second largest identified population of *M. alfredi* in the world, although projected population numbers are still relatively low in absolute terms.

The calculation of annual and superpopulation sizes at monitored aggregation sites through long-term photo-ID studies will significantly enhance the knowledge of the ecology and conservation status of *M. alfredi*. The precise and unbiased estimation of demographic parameters from the mark–re-capture modelling requires, however, that a number of key assumptions are met. The challenges of sampling highly mobile pelagic megafauna in the marine environment make these criteria difficult to fulfil in some cases. One of the most critical assumptions for mark–re-capture modelling is that marks are not lost or overlooked. Any bias due to violation of this assumption is likely to result in the underestimation of re-capture probabilities and an overestimation of abundance estimates (Pollock et al. 1990). This study supports other studies on *M. alfredi*, which have demonstrated that the natural ventral markings on individuals do not change over short periods of time (Homma et al. 1999; Deakos 2010; Kitchen-Wheeler 2010); therefore, any resulting positive bias in abundance estimates is likely to be minimal. Further, as the photo-ID method is unobtrusive and does not require the capture of individuals to mark them, there should be no trap-dependent behaviour demonstrated by the manta rays. It is therefore suggested that future studies on *M. alfredi* employ a similar methodology to the one presented in this study.

The second requirement for a successful mark–re-capture study is instantaneous sampling. Although sampling was conducted over a series of 6 months within each sampling year, this period is short in comparison with the survival interval (12 months) and is unlikely to result in bias of estimates (Pollock et al. 1990). The goodness-of-fit testing showed that the assumption of equal survivorship among marked individuals was also unlikely to be violated. However, there was statistical support for individual variation in capture probabilities and transience within the marked population in this study. Individual heterogeneity may be due to several reasons such as behavioural differences of age cohorts or differing amounts of time spent by individuals within the study area (Buckland 1990). While the specific influences on the observed differences in re-sighting patterns between individuals were not investigated during the present study, several possible contributing factors have been identified. With respect to *M. alfredi* in Mozambique, it is possible that individual female rays may

show higher site fidelity to the area during years they give birth or mate (e.g. most typically every 2–3 years; Marshall and Bennett 2010a). Individuals may also show greater site fidelity when they are injured from shark attacks and may opt to stay in the region so as to regularly visit cleaning stations and promote wound healing. While the factors influencing individual sightability are likely to differ between study populations, use of the photo-ID methodology outlined here allows the concurrent evaluation of scars and reproductive status that could assist in the interpretation of modelling results (Bansemer and Bennett 2009).

Transience in the marked *M. alfredi* population in Mozambique was also considerable, with 75% of individuals identified during this study only seen in one sampling year. It should be remembered that dive transect effort was relatively low, with only small portions of the daylight hours available for monitoring. Of the 25% of animals that were sighted in more than one sampling year, 5% showed patterns of missing a year in between re-captures (suggestive of temporary emigration) while 20% were observed in subsequent years. It is thus likely that a portion of the population of *M. alfredi* may use the area more frequently than others. When individual heterogeneity in capture probabilities results in increased re-capture of some individuals, this tends to negatively bias population estimates. However, patterns of temporary emigration were also displayed by some individuals and these may cause a negative bias in survival estimates and a consequent positive bias in abundance estimates (Pollock et al. 1990). Of greater importance, though, is the primary underlying assumption for estimating population size from JS models: that there is equal catchability between marked and unmarked individuals (Schwarz and Arnason 1996). The evidence for individual heterogeneity and transience in the population of *M. alfredi* in southern Mozambique suggests that it is highly likely that this assumption is violated. As marked individuals have an inflated probability of being re-sighted over unmarked individuals, there is a resulting negative bias on population estimates (Pollock et al. 1990). Consequently, it is important to note that the JS population size estimates we obtained from this study most likely represent minimum estimates of the true population size at the monitored aggregation site in southern Mozambique.

The strong female bias at the monitored aggregation sites also inherently creates issues with attempts to generate abundance estimates that reflect total population numbers. Additionally, the infrequency with which juvenile individuals were sighted at the monitored aggregation sites also thwarts attempts to generate accurate abundance estimates for the region. Despite these limitations, the current data represent the first estimates of population size at a known aggregation site for *M. alfredi*, even if they

represent minimum estimates or are more representative of the abundance of breeding females.

As Jolly–Seber analyses cannot separate survival from emigration, the resulting survival estimates include both permanent and temporary emigration and low-level mortality. In general, mortality in elasmobranchs is likely to be highest during the juvenile stages (Cortés 2004). As the identified population of *M. alfredi* in southern Mozambique was comprised primarily of large, mature individuals, natural mortality should be relatively low. However, it is crucial to consider all potentially important factors when examining individual populations. For instance, attacks by predatory sharks were found to be relatively common in this region, with slightly over 75% of identified individuals affected (Marshall and Bennett 2010b). It remains unclear how these attacks affect the natural mortality of large, mature individuals, particularly with many individuals clearly surviving multiple encounters with sharks (Marshall and Bennett 2010b). However, particular consideration should be given to the fact that comparatively fewer numbers of male rays were observed in the present study. While this may be a behavioural difference such as differential habitat use or higher rates of permanent or temporary emigration, it may also be an artefact of high levels of mortality from predation due to the smaller overall disc width of male rays. The same could be said of fishing pressure along the coast, with male rays being disproportionally targeted by fishermen because of their smaller size and ease of capture and handling. While care should be made not to violate the assumptions of specific models, it is equally important to incorporate the unique behavioural nuances of specific populations when interpreting results so as to ultimately place the results in context. If applied correctly, the resulting data can be very informative, providing not only preliminary indications of abundance but revealing specific behavioural differences in subpopulations, allowing population trends to be monitored and providing baselines to assist in the conservation assessment of specific populations.

The aggregation sites identified in southern Mozambique presented an exceptional opportunity to study *M. alfredi* in the wild, as encounter rates were high, rays were present throughout the year, and individual were often re-sighted. Ultimately, over 40% of the identified individuals at the monitored study sites in southern Mozambique were re-sighted on at least one occasion, despite relatively low diving effort. In spite of this restricted effort, some individuals were re-sighted multiple times over several years. As such, it may be reasonable to infer that at least a proportion of the identified individuals exhibit a degree of site fidelity to this stretch of coastline as well as to critical habitats like the study reefs which host-specific cleaning stations for *M. alfredi*. Sharks and rays are often philopatric

to their natal nursery grounds and/or show site fidelity to aggregation sites, which may include mating grounds, feeding sites or cleaning stations (Morrissey and Gruber 1993; Klimley and Anderson 1996; Heupel and Hueter 2001; Sims et al. 2001; Feldheim et al. 2002b; Domeier and Nasby-Lucas 2006). Even though some individuals were seen in all years of the study, detailed movement patterns and habitat use remain unclear and would be a logical extension to this study. Additionally, the collection of longitudinal and within-season data would enable analyses with other types of models, such as the robust design model (Pollock et al. 1990; Kendall et al. 1995) that can be used to separate effects of survival and emigration for valid parameter estimation. Closed populations or those showing a high degree of site fidelity must be carefully managed as fishing impacts and other anthropogenic factors can have a more directed effect on the depletion of individuals in a specific region (Stevens et al. 2000; Heupel et al. 2006). Target subsistence fishing for *M. alfredi* exists at various locations along the coastline in southern Mozambique, with opportunistic monitoring estimates of 20–50 individuals killed per annum (from a 50-km area surrounding the study sites) (A. Marshall, unpublished data). Due to the low annual population size estimates of *M. alfredi* along the coastline and the suggested degree of site fidelity of some individuals, conservation and management efforts to monitor and prevent the overexploitation of *M. alfredi* should be an immediate priority.

References

Amorim AF, Arfelli CA, Castro JI (2000) Description of a juvenile megamouth shark, *Megachasma pelagios*, caught off Brazil. Environ Biol Fish 59:117–123

Anderson SD, Pyle P (2003) A temporal, sex-specific occurrence pattern among white sharks at the south Farallon Islands, California. Calif Fish Game 89:96–101

Arzoumanian Z, Holmberg J, Norman B (2005) An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. J Appl Ecol 42:999–1011

Auger-Methe M, Whitehead H (2007) The use of natural markings in studies of long-finned pilot whales (*Globicephala melas*). Mar Mamm Sci 23:77–93

Bansemer CS, Bennett MB (2008) Multi-year validation of photographic identification of grey nurse sharks, *Carcharias taurus*,

and applications for non-invasive conservation research. Mar Freshw Res 59:1–10

Bansemer CS, Bennett MB (2009) Reproductive periodicity, localised movements and behavioural segregation of pregnant *Carcharias taurus* at Wolf Rock, Southeast Queensland, Australia. Mar Ecol Prog Ser 374:215–227

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of the shark populations in the Northwest Atlantic. Science 299:389–392

Beebe W, Tee-Van J (1941) Eastern Pacific expeditions of the New York zoologicial society. XXVIII fishes from the tropical eastern pacific. Part 3: rays, mantas, and chimaeras. Zoologica 26:245–278

Bonfil R (2002) Trends and patterns in world and Asian elasmobranch fisheries. Elasmobranch biodiversity, conservation and management: proceedings of the international seminar and workshop, Sabah, Malaysia, July 1997. IUCN SSC Shark Specialist Group, IUCN, Gland, Switzerland, pp 15–24

Buckland ST (1990) Estimation of survival rates from sightings of individually identifiable whales. Rep Int Whal Comm Spec Issue 12:149–153

Burnham KP, Anderson DR (2002) Model selection and multimodal inference: a practical information-theoretic approach. Springer, New York

Castro ALF, Rosa RS (2005) Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol das Rocas biological reserve, Brazil. Environ Biol Fish 72:213–221

Choquet R, Reboulet AM, Lebreton JD, Gimenez O, Pradel R (2005) U-CARE 2.2 user's manual. CEFE, UMR 5175. CNRS, Montpellier

Cormack RM (1964) Models for capture-recapture. Biometrika 51:429–438

Cortés E (2004) Life history patterns, demography, and population dynamics. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, pp 449–469

Deakos MH (2010) Paired-laser photogrammetry as a simple and accurate system for measuring the body size of free-ranging manta rays *Manta alfredi*. Aquat Biol 10:1–10

Dewar H, Mous P, Domeier M, Muljadi A, Pet J, Whitty J (2008) Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. Mar Biol 155(2):121–133

Domeier M, Nasby-Lucas N (2006) Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island Mexico). Mar Biol 150:977–984

Dudgeon CL, Noad MJ, Lanyon JM (2008) Abundance and demography of a seasonal aggregation of zebra sharks *Stegostoma fasciatum*. Mar Ecol Prog Ser 368:269–281

Evans PGH, Hammond PS (2004) Monitoring cetaceans in European waters. Mamm Rev 34:131–156

Feldheim KA, Gruber SH, de Marignac JRC, Ashley MV (2002a) Genetic tagging to determine passive integrated transponder tag loss in lemon sharks. J Fish Biol 61:1309–1313

Feldheim KA, Gruber SH, Ashley MV (2002b) The breeding biology of lemon sharks at a tropical nursery lagoon. Proc R Soc Lond B 269:1655–1661

Graham R, Roberts CM (2007) Assessing the size, growth and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. Fish Res 84:71–80

Heupel MR, Hueter RE (2001) Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. In: Silbert JR, Nielsen JL (eds) Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers, Netherlands, pp 217–236

Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006) Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. Environ Biol Fish 76:47–67

Hiby AR, Hammond PS (1989) Survey techniques for estimating abundance of cetaceans. Rep Int Whal Comm 11:47–80

Homma K, Maruyama T, Itoh T, Ishihara H, Uchida S (1999) Biology of the manta ray, *Manta birostris* Walbaum. In: Seret B, Sire JY (eds) The proceedings of the 5th Indo-Pacific fish conference, Noumea, 1997. Soc. Fr. Ichtyol, Paris, pp 209–216

Ito T (2000) Manta swims as if he flapped the wings. Metamor Publishing, Tokyo

Jolly GM (1965) Explicit estimates from mark-recapture data with both death and immigration-stochastic models. Biometrika 52:225–247

Kendall WL, Pollock KH, Brownie C (1995) A likelihood-based approach to capture-recapture estimation of demographic parameters under the Robust Design. Biometrics 51:293–308

Kitchen-Wheeler A (2010) Visual identification of individual manta ray (*Manta alfredi*) in the Maldives Islands, Western Indian Ocean. Mar Biol Res. doi:10.1080/17451000903233763

Klimley AP (1987) The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. Environ Biol Fish 18:27–40

Klimley AP, Anderson SD (1996) Residency patterns of white sharks at the South Farallon Islands, California. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Charcharodon carcharias*. Academic Press Inc., San Diego, pp 309–316

Kohler NE, Turner PA (2001) Shark tagging: a review of conventional methods and studies. Environ Biol Fish 60:191–223

Last PR, Stevens JD (2009) Sharks and rays of Australia. CSIRO, Melbourne, pp 478–480

Lessa R, Vooren CM, Lahaye J (1986) Desenvolvimento e ciclo sexual das fémeas, migrações e fecundidade da viola *Rhinobatos horkelii* (Müller and Henle, 1841) do sul do Brasil. Atlântica Rio Grande 8:5–34

Luiz OJ Jr, Balboni AP, Kodja G, Andrade M, Marum H (2009) Seasonal occurrences of *Manta birostris* (Chondrichthyes: Mobulidae) in southeastern Brasil. Jpn J Ichthyol 56(1):96–99. doi:10.1007/s/0228-008-0060-3

Marshall AD, Bennett MB (2010a) Reproductive ecology of the reef manta ray (*Manta alfredi*) in southern Mozambique. J Fish Biol 77:169–190

Marshall AD, Bennett MB (2010b) The frequency and effect of shark-inflicted bite injuries to the reef manta ray (*Manta alfredi*). Afr J Mar Sci 32(3):573–580

Marshall AD, Pierce SJ, Bennett MB (2008) Morphological measurements of manta rays (*Manta birostris*) with a description of a foetus from the east coast of Southern Africa. Zootaxa 1717:24–30

Marshall AD, Compagno LJV, Bennett MB (2009) Redescription of the genus Manta with resurrection of Manta alfredi (Krefft, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae). Zootaxa 2301:1–28

Martin RA (2007) A review of the behavioural ecology of whale sharks (*Rhincodon typus*). Fish Res 84:10–16

Meekan MG, Bradshaw CJA, Press M, McLean C, Richards A, Quasnichka S, Taylor JG (2006) Population size and structure of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. Mar Ecol Prog Ser 319:275–285

Minta S, Mangel M (1989) A simple population estimate based on simulation for capture-recapture a capture-resight data. Ecology 70:1738–1751

Morrissey JF, Gruber SH (1993) Home range of juvenile lemon sharks, *Negaprion brevirostris*. Copeia 1993:425–434

Otis DL, Burnham KP, White GC (1978) Statistical inference for capture data on closed animal populations. Wildl Monogr 62:1–135

Pollock KH, Solomon DL, Robson DS (1974) Tests for mortality and recruitment in a K-sample tag-recapture experiment. Biometrics 30:77–87

Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical-inference for capture-re-capture experiments. Wildl Monogr 107:1–97

Porcher IF (2005) On the gestation period of the blackfin reef shark, *Carcharhinus melanopterus*, in waters off Moorea, French Polynesia. Mar Biol 146:1207–1211

Rohner CA, Richardson AJ, Marshall AM, Weeks SJ, Pierce SJ (2011) How big is the world's biggest fish? Measuring whale sharks with laser photogrammetry. J Fish Biol 78:378–385

Rubin R (2002) Manta rays: not all black and white. Shark Focus 15:4–5

Schwarz CJ, Arnason AN (1996) A general methodology for the analysis of open-model capture recapture experiments. Biometrics 52:860–873

Seber GAF (1970) Estimating time-specific survival and reporting rates for adult birds from band returns. Biometrika 57:313–318

Sims DW, Speedy CD, Fox AM (2000) Movements and growth of a female basking shark re-sighted after a three year period. J Mar Biol Ass UK 80:1141–1142

Sims DW, Nash JP, Morritt D (2001) Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Mar Biol 139:1165–1175

Springer S (1967) Social organisation of shark populations. In: Gilbert PW, Mathewson RF, Rall DP (eds) Sharks, skates and rays. Johns Hopkins Press, Baltimore, pp 149–174

Stevens JD (2007) Whale shark (*Rhincodon typus*) biology and ecology: a review of the primary literature. Fish Res 84:4–9

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57:476–494

Stevick PT, Palsbøll PJ, Smith TD, Bravington MV, Hammond PS (2001) Errors in identification using natural markings: rates, sources, and effects on capture–recapture estimates of abundance. Can J Fish Aquat Sci 58:1861–1870

Van Tienhoven AM, Den Hartog JE, Reijns RA, Peddemors VM (2007) A computer aided program for pattern-matching of natural marks on the spotted raggedtooth shark *Carcharias taurus*. J Appl Ecol 44:273–280

Walker TI (2005) Reproduction in fisheries science. In: Hamlett WC (ed) Reproductive biology and phylogeny of Chondrichthyes, vol 3. Science Publishers Inc., Enfield, pp 81–127

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Stud 46:120–138

Worm B, Sandow M, Oschlies A, Lotze HK, Myers RA (2005) Global patterns of predator diversity in the open oceans. Science 309:1365–1369

Würsig B, Jefferson T (1990) Methods of photo-identification for small cetaceans. Rep Int Whal Comm 12:43–52

Young N (2001) An analysis of the trends in by-catch of turtle species, angelsharks, and batoid species in the protective gillnets off Kwazulu-Natal, South Africa. Thesis, University of Reading