ORIGINAL PAPER

Movements and site fidelity of the giant manta ray, *Manta birostris,* in the Komodo Marine Park, Indonesia

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Abstract Despite their large size and frequent occurrence in near-shore tropical habitats, little published information is available on the movements and behaviors of the giant manta ray, *Manta birostris,* and what factors influence visitation patterns. To examine the movements of manta rays in the Komodo Marine Park, Indonesia, an acoustic array was installed at up to seven sites in the park between 2000 and 2003. A total of 41 acoustic tags were deployed in three separate deployments in 2000, 2001 and 2002. Mantas were recorded in the park for up to 526 days with an average duration of 183 ± 136 days, when mantas made from 3 to 303 individual visits to different sites (median 58 visits). There was a clear preference for three sites that comprised over 90% of manta activity. The most popular site (German Flag) was off the southern tip of Komodo Island in an area with a high degree of bathymetric structure. Examination of the longest records suggests some site preference with 5 of 7 individuals spending greater than 90% of their time at the location where they were tagged. Using a general linear model it was possible to examine the effects of daytime, lunar phase, aggregation site, season and tidal phase on visitation patterns. The vast majority of visits were recorded during daylight hours at all sites. The strongest effects of both the lunar and tidal phase were apparent in the northern sites with the most visits occurring when tidal intensity was the greatest during full and new moons. The strongest seasonal pattern was observed in the south where no mantas were recorded during the first quarter in any year. This coincides with an increase in temperature and reduction of productivity in this region associated with monsoonal shifts. The long-term fidelity indicates that marine-protected areas centered around aggregation sites could help protect this species from overexploitation.

Communicated by R. J. Thompson.

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Introduction

The giant manta ray (*Manta birostris;* Donndorff 1798) is a monogeneric species in the Family Mobulidae that consists of the devil rays. The giant manta is the largest of all rays reaching a disc width of up to 6.7 m and 1,400 kg weight (Last and Stevens 1994). Like the largest whales and sharks, manta rays are filter feeders. They and the other members of the subfamily funnel water and prey into their mouths using their distinctive cephalic lobes. Prey is then filtered from the water by modified gill rakers. The giant mantas are often observed feeding in surge channels (Wilson et al. 2001), on surface slicks, or near lights at night that act to concentrate prey. Like the largest filter feeding shark (the whale shark), manta rays occur worldwide in tropical and subtropical waters (Bigelow and Schroeder 1953; Last and Stevens 1994; Compagno 1999). While

mantas are observed primarily in near-shore environments, they are also reported at seamounts and are even encountered far from shore in the open sea.

Some of the best information available on distribution patterns within the mantas' broad geographic range comes from photo identification studies that have recorded the occurrence of photographically identified individuals over time. Based on this and other research, local residence patterns appear to be site dependent. In certain regions, the same individual mantas are observed repeatedly over long time periods (e.g., in Yap, Hawaii and Bora Bora) whereas in others (e.g., New Zealand, parts of Australia, Baja California, Mexico, Africa, Ecuador, and Southern Japan) their occurrence is seasonal (Homma et al. 1997; Duffy and Abbott 2003; S. Fish, personal communication; P. Ajhia, personal communication; S. Walker, personal communication). When mantas are sighted on multiple occasions, they are often returning to the same feeding and cleaning stations (Homma et al. 1997). While these studies have provided important insights into manta behavior, they are limited temporally and spatially to periods when divers or snorkelers are in the water. Also, this method has not revealed what factors influence residence patterns.

Although not the target of large-scale fisheries, giant mantas are captured incidentally and/or taken in regional fisheries through much of their range (Garcia and Hall 1997; Alava et al. 2002; Dewar 2002; Romanov 2002; Fujita 2006; White et al. 2006). Concerns about overexploitation resulted in the listing of the giant manta as near threatened through part of its range by the IUCN World Conservation Union (Marshall et al. 2006). Although scientific studies and exact population estimates are lacking, a decline in manta sightings has been noted in a number of locations including Japan, French Polynesia, and Mexico (Homma et al. 1997; Marshall et al. 2006). While elasmobranchs are generally considered highly susceptible to over fishing due to their natural history (Musick 1999; Musick et al. 2000), mantas are likely even at greater risk given their very low reproductive rates (one or two pups per year), generally small population sizes and potentially limited distributions (Marshall et al. 2006).

An additional challenge to the management and conservation of manta rays is the lack of published data on basic life history information. The lack of publications is due, in part, to the fact that no industrial fishery for mantas exists and there has been little systematic collection of data. The vast majority of publications simply report on sightings in regional species lists (Smith and Smith 1963; Santos et al. 1997). Information on growth rates, gestation period, age at sexual maturity and reproductive rates is scarce (Bigelow and Schroeder 1953; White et al. 2006). The results from only one of the photo identification studies mentioned above have been published (Homma et al. 1997).

We report on the movements of giant manta rays determined using an acoustic hydrophone array established in the Komodo National Park, Indonesia. There are a number of sites within the Komodo Marine Park where mantas are regularly observed, although it was not clear whether these mantas were transient or resident and what factors influenced local patterns of occurrence. There was considerable interest in these questions for two reasons. First, local dive operators were interested in developing manta-based ecotourism, and it was important to obtain baseline information on the local population as well as to identify visitation patterns to maximize the success of the program. Second, in two villages just east of Komodo (Lamalera and Lamakera) there is a directed manta fishery causing concern that the mantas in the park may be impacted. The objectives of this study were to determine whether the mantas in the park were resident, and to identify temporal and spatial movement patterns and their relation to environmental conditions. In addition to the value of this study to the local manta population, results could also provide insights into patterns observed in other locations.

Materials and methods

Tag deployments

The mantas were tagged with a V16-6H acoustic transmitter (Vemco V16, Nova Scotia Canada) in a shark casing. Each tag transmitted a unique code allowing individual animals to be identified. The tags were secured to the mantas using large nylon darts that were attached to the tag using 300-lb test monofilament line and stainless steal crimps. Two different dart types were used. White nylon darts with two anchoring barbs (Prince and Goodyear 2006) were used in the first deployment. Black nylon darts with eight barbs (Domeier et al. 2005) were used in the second and third deployments. The darts were inserted near the trailing edge of the wing, at the margin between the wing and the axial musculature with a modified spear gun. When the mantas were tagged, their size was estimated and the behavior of the animal as well as that of the other mantas in the area was noted.

Acoustic array

The acoustic array consisted of Vemco, VR2 omni-directional hydrophones. The hydrophones were suspended at depths from 8 to 25 m using plastic fishing floats that were secured to the bottom with large screws or sand bags depending on the bottom substrate. The tag ID code and time were logged when tagged mantas were detected by the hydrophones.

Fig. 1 a Map showing Komodo Island, Indonesia and the locations of receivers around the Island. **b** The time a given hydrophone was in the water
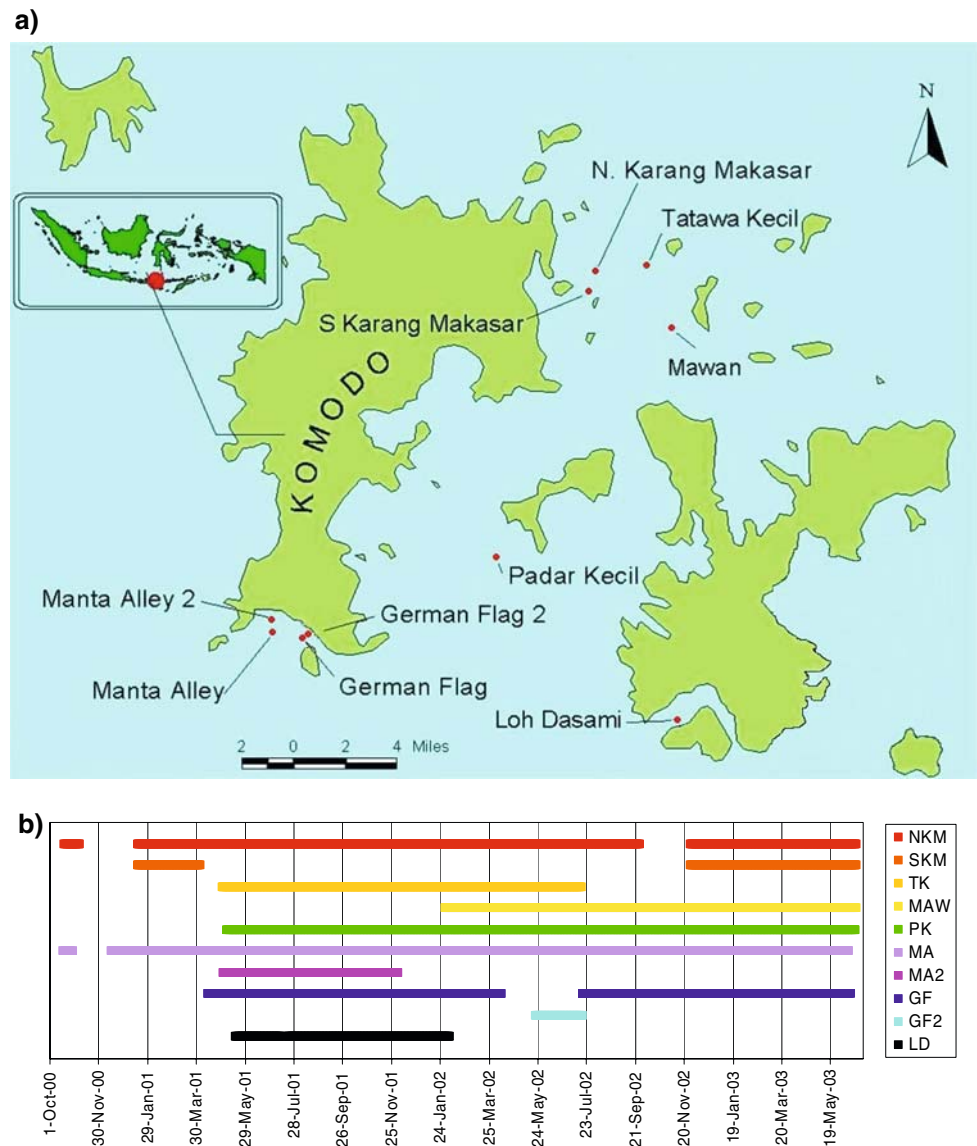
Over the course of the study, ten receivers were placed in seven different locations for varying periods of time (Fig. 1) including one hydrophone each at Padar Kecil (PK), Mawan (MW), Loh Dasami (LD) and Tatawa Kecil (TK) and two each at Karang Makasar (KM), Manta Alley (MA) and German Flag (GF) (for color figure see online version). Working from north to south, TK is a small, steep, isolated rocky island with substantial coral coverage. KM is located near a small sandy island away from distinctive structures and is characterized by a very gradually sloping coral rubble field with a few isolated coral heads. MW is a small island to the east of Komodo with a broad fringing reef that is exposed to strong tidal currents. PK is near an isolated rocky island in the channel between Komodo and Rinca Islands. The sites at GF and MA are in the same general area approximately 1.8 km apart, at the south shore of

Komodo island where there are a series of rocky islands and a rocky shoreline with a large degree of structure. LD is situated in a horseshoe-shaped bay in the south of Rinca Island that has rocky shores and little reef formation. All locations were those where mantas had been observed by the park rangers and The Nature Conservancy (TNC) staff on multiple occasions.

Range test

Range tests were conducted at GF. A tag was placed in the water and hung over the side of the vessel as the boat drifted by the receiver with the tidal current. The precise time and location of the boat were documented using a GPS. These were then linked to the time-stamped data recorded on the receiver.

Temperature records

Ambient water temperature was recorded at KM and MA every 10 min using Onset Computer Tidbits (Onset, Bourne, MA, USA). These were secured to the hydrophones and downloaded at the same time as the hydrophones. Additional temperature records were obtained from other concurrent studies in the park using the same temperature loggers.

Data analysis

To characterize visitation patterns, visits to a given site were calculated from individual time-stamped data records (termed hits). A hit was considered part of a given visit if it occurred within in a 24-h period at the same receiver. The duration of each visit and the interval between visits was calculated.

To examine the effects of location, time of day, time of year, moon phase and tides on manta occurrence a generalized linear model (GLM) (McCullagh and Nelder 1989) was constructed, using partial likelihood ratios for hypothesis testing (SAS Institute Inc. 1993). Applying a binomial error and logit link function, the GLM estimates the likelihood that one or more tagged manta rays are recorded in dependence of a range of variables (Table 1). This analysis likelihood, which varies between 0 and 1, is an indicator for the presence of manta rays. Analyses were restricted to hydrophone recordings from the dominant north and south aggregation areas (variable AA): north Komodo included KM and south Komodo both GF and MA. The other sites were not included because hydrophone deployment was less frequent, and the number of hits per unit recording effort was far lower.

For analyses, recordings were categorized into calendar months (variable MONTH) and into daytime (6 a.m.–6 p.m.) and nighttime (6 p.m.–6 a.m.) (variable DAY)

(these times coincide with the approximate time of sunrise and sunset through out the year). To examine the impact of both the tidal intensity and phase, two additional variables were examined. Moon phase (variable MOON) was included at three qualitative levels: 'new' (<10% illuminated), 'half' (10–90% illuminated) and 'full' (>90% illuminated). The % illumination was obtained from the United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/docs/MoonPhase). Tidal phase (variable TIDE) was categorized as 'rising', 'slack', or 'falling'. Tidal height data were taken from tide tables for Bima (ca. 80 km to the East of Komodo National Park), the nearest location for which data are published. The tidal height data were offset with +1 h for north Komodo and with +2.5 h for south Komodo to align the table with observed current patterns. Because the effects of MONTH, DAY, MOON and TIDE may differ between aggregation areas, second order interactions of these variables with AA were also included.

The likelihood of recording a manta ray and number of hits or visits will likely depend on the number of tags and hydrophones in a particular area. This was accounted for by including sampling effort (SEFF) in the GLM; defined as the product of the number of active hydrophones at a particular site and the number of deployed tags. In later analyses, SEFF was used to derive the number-of-hits per unit sampling effort (HUE, analogous to catch-per-unit-effort). In the GLM, however, SEFF was included as an independent variable along with the other independent variables described above.

The binomial dependent variable in the GLM, here abbreviated as PRSNT, has a value of one if a manta ray was detected ('present'), and zero when no mantas were detected ('absent'). 'Presence' was evaluated per calendar day (24 h) per level of each of the qualitative variables. For example, if the hydrophones at MA recorded a series of hits during rising tide at daytime, but none during slack at daytime, then the dataset for that calendar day and that

Table 1 Summary of independent variables used in the GLM analysis

Independent variable	Type	Description	Values
SEFF	Continuous	Sampling effort, a product of the number of hydrophones and the number of deployed tags	On average the two sites had 2 hydrophones while 30 tags were deployed. SEFF averaged 54 (minimum 4, maximum 164)
AA	Qualitative	Aggregation area	North Komodo, South Komodo
MONTH	Qualitative	Calendar month	1–12 (January–December)
DAY	Qualitative	Identifies recordings made during daytime or nighttime	Daytime (6 a.m.–6 p.m.), nighttime (6 p.m.–6 a.m.)
MOON	Qualitative	Illumination of the moon	New (<10% illuminated), half (10–90% illuminated) and full (>90% illuminated)
TIDE	Qualitative	Daily variation in tidal currents	Falling, slack, rising

aggregation area has one record with PRSNT = 1, DAY = 'daytime' and TIDE = 'rising' and one record with PRSNT = 0, DAY = 'daytime' and TIDE = 'slack'. Both records would have the same values for SEFF, AA, MONTH, and MOON. The analysis was done with PROC GENMOD in SAS 9.1 (SAS Institute Inc., Cary, NC).

Visual surveys

To assess the acoustic results and obtain additional information on manta abundance, a team of six observers made 61 trips to the three main sites (north and south Komodo and PK) from May 2001 to June 2003, between 8:30 and 15:00. The survey team slowly cruised each site by boat at a maximum speed of ca. 10 km h^{-1} counting mantas swimming at and below the surface when visible. When mantas were observed the team reduced speed to better estimate the group size. It took 5–30 min to search each site and verify the presence of mantas.

To compare the acoustic and visual survey results, hits were aggregated over both north and south Komodo and only daytime hits were used. Numbers of hits per area per day were adjusted for SEFF. The correlation between the adjusted number of hits and results from the visual surveys was assessed through a non-parametric test for association (Spearman's coefficient of rank correlation, Sokal and Rohlf 1995).

Results

Tag deployments

A total of 41 tags were deployed during three deployment periods, eight in October 2000, 15 in April 2001 and 18 in May 2002 (Table 2). Deployments occurred at various sites throughout the park near the location of the receivers. The average estimated wingspan of tagged mantas was 3.6 ± 0.8 m (range 1.8–5 m).

Receivers

Acoustic monitoring of manta rays was conducted from October 2000 to June 2003 (Fig. 1b). Due to a number of problems coverage was not constant. Problems included receiver loss (likely to fishermen), flooding, and battery malfunction. The main sites, including GF (70%), MA (92%), PK (78%) and KM (86%), or north Komodo, were covered for at least 70% of the study. The more remote sites had less coverage; MW (51%), TK (45%) and LD (26%).

The range test at GF revealed that tags could be detected only 10s of meters from the receiver. The spacing of posi-

Table 2 Summary of tag deployments including the location (Padar Kecil = PK, Mawan = MW, Karang Makasar = KM, Manta Alley = MA, German Flag = GF) and date of tagging, the days between the tagging date and when the manta was last recorded, the total number of visits and the days a manta was recorded

Tag #	Location	Date	Days	Visits	Days
2	KM	10/16/00	101	8	7
4	KM	10/16/00	208	26	21
5	KM	10/16/00	162	9	8
3	KM	10/17/00	178	4	4
7	GF	10/19/00	266	28	21
8	GF	10/19/00	98	5	5
9	KM	4/2/01	250	71	66
10	KM	4/3/01	31	24	21
13	GF	4/3/01	151	132	86
14	GF	4/3/01	32	13	10
15	MA	4/3/01	311	53	51
16	GF	4/3/01	48	3	3
17	KM	4/3/01	207	40	36
18	MA	4/3/01	519	165	96
19	MA	4/3/01	222	168	109
20	KM	4/3/01	526	152	131
21	GF	4/3/01	161	60	44
22	GF	4/3/01	198	208	139
23	GF	4/3/01	54	12	9
25	GF	5/19/02	362	57	44
1B	PK	5/20/02	202	63	41
2B	GF	5/20/02	216	207	125
31	GF	5/20/02	215	159	120
32	GF	5/20/02	116	111	81
33	GF	5/20/02	367	132	92
34	PK	5/20/02	216	170	126
3C	MAW	5/23/02	155	29	27
4B	KM	5/23/02	383	4	4
26	MA	5/23/02	37	16	14
28	GF	5/23/02	123	36	32
29	KM	5/23/02	346	24	23
30	KM	5/23/02	229	144	85
36	GF	5/23/02	196	91	74
37	GF	5/23/02	230	278	171
38	KM	5/23/02	348	57	42

Six mantas (two from each deployment year) that were never recorded are not included in the table

tions obtained with the GPS during the range test did not allow for greater accuracy.

Sites had differing amounts of manta activity (Table 3) with no mantas recorded at LD. The highest number of mantas was recorded at KM (n = 27) with only slightly fewer at MA (n = 24) and GF (n = 24), 20 of these manta were recorded at both GF and MA. Fewer mantas were

Table 3 Summary of the number of manta rays that visited each site, the total and adjusted hits, and the total and adjusted days and % of total adjusted days on which mantas were recorded

Location	# Mantas	Total hits	Adjusted hits	Days mantas detected	Adjusted days	Adjusted days (%)
GF	24	14,975	384	958	26.8	0.43
KM	27	9,265	314	521	18.8	0.30
MA	24	4,729	124	419	11.2	0.18
PK	14	2,941	72	185	4.5	0.07
MW	7	54	1	15	0.4	0.01
TK	3	152	4	4	0.1	0.00
LD	0	0	0	0	0	0

The data for the two hydrophones at each of GF, MA, and KM were are combined in this table. (Padar Kecil = PK, Mawan = MW, Karang Makasar = KM, Manta Alley = MA, German Flag = GF, Loh Dasami = LD, Tatawa Kecil = TK)

documented at PK ($n = 14$), TK ($n = 3$) and MAW ($n = 7$). Despite the fact that a receiver was not installed at GF until the second deployment, it had the highest number of raw and adjusted hits and days with 43% of the adjusted days at this site. The second most popular site was KM (30% of adjusted days) followed by MA (18%) and PK (7%). MAW and TK had 1% or less of the total adjusted days.

Tag activity

Tag activity is summarized in Table 2 and Fig. 2. Of the 41 tags, all but 6 were recorded by a receiver at least once. Tag transmitions were detected for periods up to 526 days (average 183 ± 136). An individual manta made from 3 to 303 visits (median 58 visits). The median number of hits per visit was 8 (maximum 209) and 23% of all visits consisted of only one hit. The median visit duration calculated for each individual manta ranged from 8 min to 6.7 h with a median over all mantas of 2 h. The longest visits were close to 24 h, although this was uncommon and only 8 (0.4%) visits were longer than 20 h. The number of days on which hits were received for the individual mantas ranged from 3 to 171 (median 42). The percentage of days of a given deployment on which hits were received from a given tag ranged from 0.7 to 75% (median 20.6%).

Manta movements

The visits for all the 35 mantas are shown in Fig. 2 (for color figure see online version). Given the variability and complexity of patterns both within and across individuals two approaches were taken to quantify patterns. First, the timing of visits and movement between sites were quantified. Second, the GLM was used to examine the influence of environmental conditions comparing the north (KM) and south (MA and GF combined) areas.

An examination of successive visits reveals that it was more common for mantas to visit the same site in subse-

quent visits than move to a different site. The majority of subsequent visits (81%) were at the same site. Some mantas were documented at the same site for many consecutive days. For example manta # 20 missed only 6 out of 83 days at KM and manta #22 missed only 7 days out of 113 at GF. When not on consecutive days, the median time between visits was 4 days with a maximum of 335 days (across all tags the median value of the maximum time between consecutive visits was 44 days).

While a few mantas visited only one site for weeks at a time, there was considerable movement among sites and most mantas visited more than one site. The most common movements were between the two closest sites off south Komodo, MA and GF ($n = 376$) and 155 of these occurred within a single day. Movements between the three main areas (PK, north and south Komodo) occurred less frequently ($n = 145$). Of the 21 animals with more than 6 months of data and greater than 10 visits, 19 visited at least two areas and nine were recorded in all three areas (PK, north and south Komodo). The interval between visits to different areas increased with distance. The average time between south Komodo and PK ($n = 45$) was 6.6 days (min = 0.45 days), between north Komodo and PK ($n = 30$) was 14 days (min = 0.6 days) and between north and south Komodo ($n = 47$) was 25 days (min = 0.7 days). Only two movements between the three main areas (both between south Komodo and PK) were documented on the same calendar day. Note that the average time between areas is substantially longer than the minimum values.

To explore site preference, seven mantas tagged at south ($n = 4$; tag #15, 18, 25, 33) and north ($n = 3$; tag #29, 20, 38) Komodo with more than 300 days of data and 25 visits were examined. A period of 300 days spans the seasonal variations (see below). Five of the seven mantas spent on average 97% (± 4%) of the adjusted days (days adjusted for SEFF) at the tagging location whereas the remaining two spent 29 and 34% of the days at the tagging location (Figs. 2, 3).
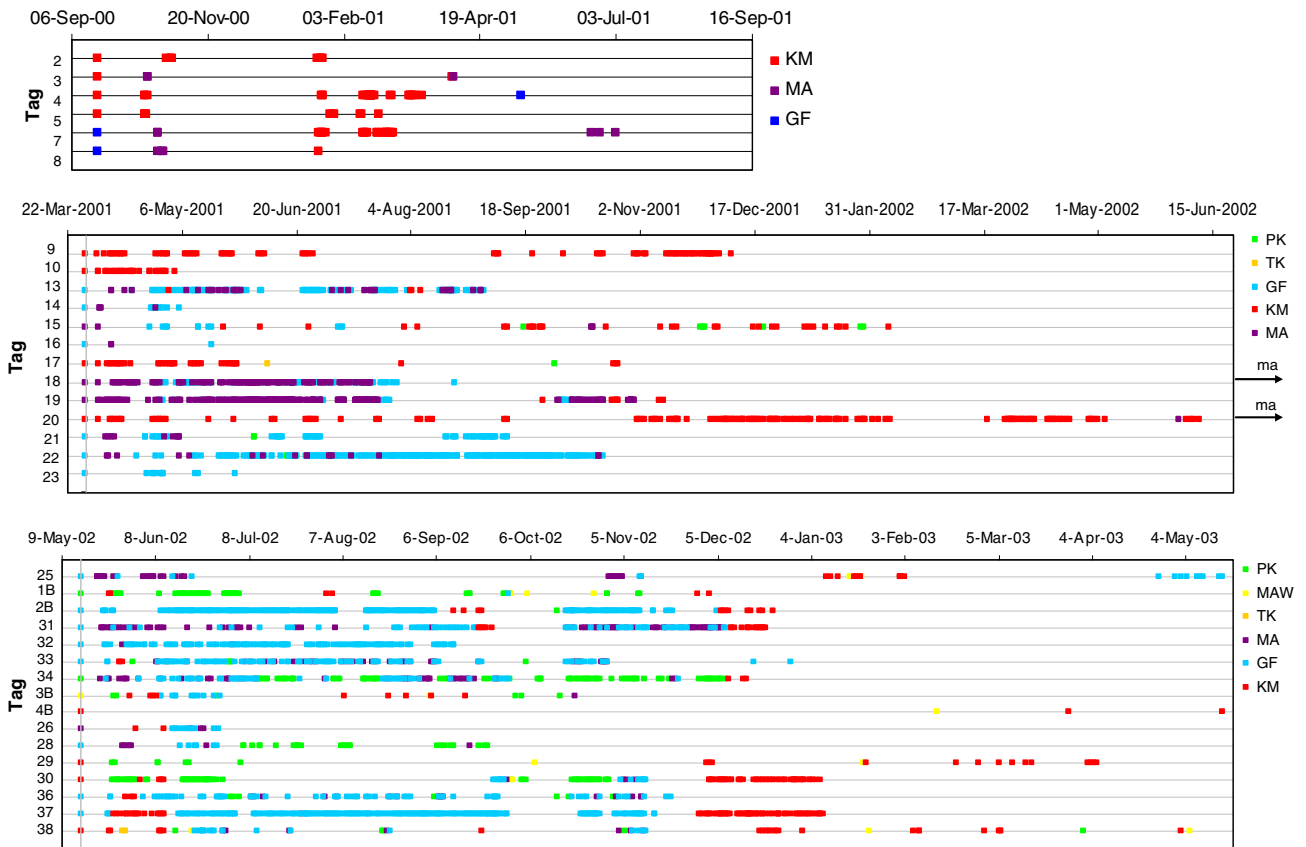
Fig. 2 The visitation patterns for all 35 mantas recorded by the acoustic array with the specific location of each visit color coded. Data are separated by the three deployment years. For deployment 2, the *arrows* indicate that for two tags additional recording were made after June 15th at the sites indicated
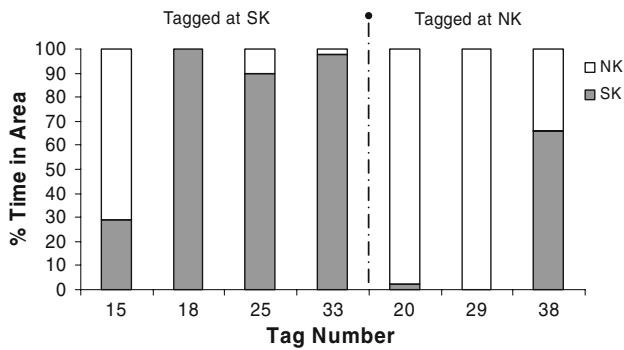
Fig. 3 The adjusted days at north Komodo (*NK*) and south Komodo (*SK*) are shown for seven mantas with deployment durations of greater than 300 days and more than 25 visits

Table 4 Results from the Generalized Linear Model (Type I analysis, SAS Institute Inc. 1993)

| Source	Deviance	df	Chi-Squared	P
Intercept	10,155			
SEFF	9,701	1	454	<.0001
AA	9,668	1	33	<.0001
MONTH	9,044	11	624	<.0001
AA × MONTH	8,081	11	963	<.0001
MOON	8,015	2	66	<.0001
AA × MOON	8,000	2	15	0.0005
DAY	6,568	1	1,431	<.0001
AA × DAY	6,535	1	34	<.0001
TIDE	6,517	2	17	0.0002
AA × TIDE	6,475	2	432	<.0001

Shown are the source of deviance (McCullagh and Nelder 1989), the amount of deviance that remains after including the variable, the Chi-Square statistic for estimating significance of the source, and the *P*-value of Chi-Square

## Effects of place, time, daylight, moon phase and tides

The GLM explained 36% of the total deviance, using 34 degrees of freedom. All main effects and all interactions with AA are summarized in Table 4 and were significant ($P < 0.01$). The GLM that included second order interactions was less parsimonious than the first model (97 degrees of freedom vs. 34 degrees of freedom) and explained only slightly more of the total deviance (38 vs. 36%). The more parsimonious model comprising the main effects and second order interactions with AA was unlikely to have missed major effects. Consequently, this model was used to

Fig. 4 *Solid line* shows the tidal depth over two different 6-day periods at south Komodo. The *points* indicate visits at either German Flag or Manta Alley on those days rounded to the nearest hour. The *shaded bars* indicate the time between 6 p.m. and 6 a.m.
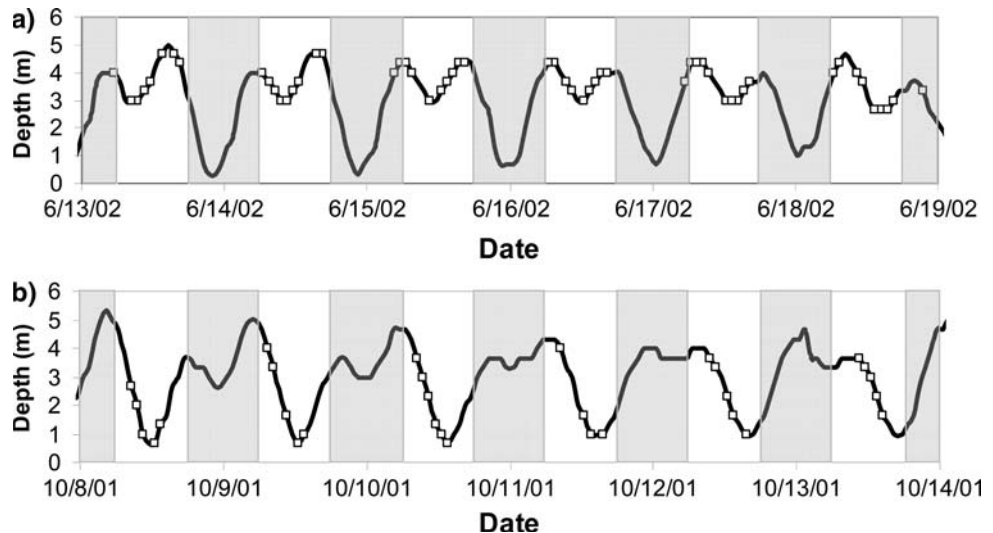
Fig. 5 Percent of total hits at north Komodo (*NK*), south Komodo (*SK*) and Padir Kecil (*PK*) that occurred in a given hour through out the day
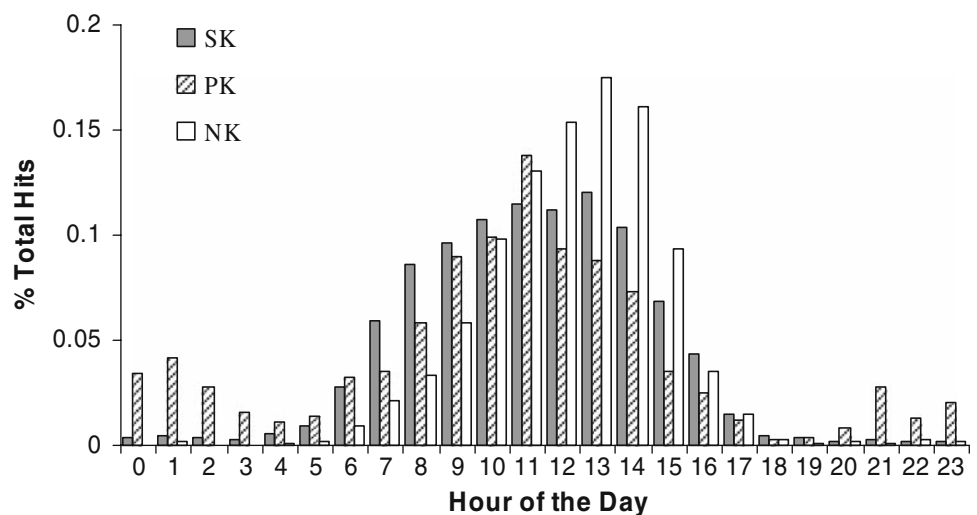
describe patterns, standardized for SEFF = 60. The GLM used 10,512 records, 1,974 indicating presence of tagged manta rays.

The effects of the interaction of AA and DAY were particularly strong (Table 4). Figure 4 shows hits in relation to both time of day and the tidal cycle, note that most hits are recorded during the day in south Komodo even at different tidal phases. Figure 5 shows the compiled hits per hour at PK, south and north Komodo over a 24-h period (note, only north and south Komodo were included in the GLM). The number of hits gradually increased during the morning and then decreased again prior to sunset with a peak shifted slightly later at north Komodo. The percent of nighttime hits varied across locations and was highest at PK (north Komodo = 1%, south Komodo = 4%, and PK = 22%).

The second strongest interaction was between AA and MONTH. In the south, the most visits occurred from April to July and then declined until December after which no mantas were recorded until March (Fig. 6). In the north, the

seasonal pattern appeared the reverse of that in the south, although animals were present in all months. The movements of some individuals suggested that mantas might move from south to north late in the year. In 2002 six mantas (25, 2B, 31, 30, 37 and 38) left south Komodo in November and December and arrived at north Komodo from 1 to 59 days later; two additional manta rays (1B and 34) left PK for north Komodo around the same time. These mantas remained at the northern sites for up to 50 days before leaving although one animal (38) was recorded infrequently through May. This pattern was not observed in 2001 indicating the potential for inter-annual differences.

MOON and TIDES affected visits at both north and south Komodo but were strongest in the north (Fig. 7). For MOON at north Komodo, manta ray abundance was higher when currents were strongest during full and new moons. The GLM includes all visits, day and night; an examination of nighttime visits alone reveals a different pattern. Around the full moon in south Komodo the number of nighttime

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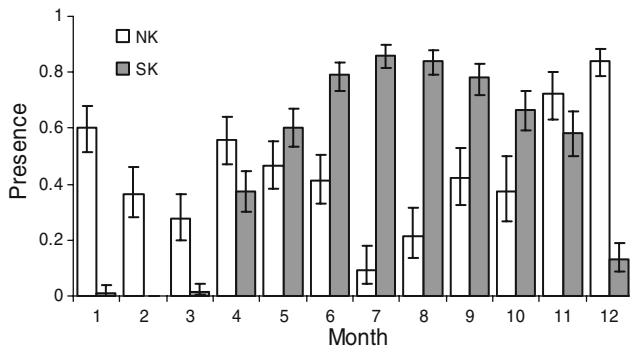
Fig. 6 Model results showing monthly variation in presence of tagged manta rays in north Komodo (*NK*) and south Komodo (*SK*). Error bars are 95% confidence limits of the model estimates

visits doubled from 10% (±1) to 20% (±1) of the total visits. No similar increase in nighttime visits was observed at the other sites. The effect of TIDES was also more pronounced in north with more visits during the rising than the falling tide (Fig. 7).

Visual surveys

During the visual surveys, the number of manta rays counted varied between 0 and 83, averaging 8.3. The adjusted number of visits from the acoustic receivers varied between 0 and 3.6 per day, averaging 0.24. The value of Spearman's coefficient comparing the number of adjusted hits and observed mantas was positive and significant (Spearman's coefficient = 0.3. $n = 61$, $P < 0.05$).

Temperature

Temperatures varied with season, tidal cycles and across sites. The highest (32.8°C) and lowest (20.2°C) temperatures were recorded in south Komodo, which also had the most notable seasonal pattern with maximum temperatures observed in the first quarter and the lowest values in the third quarter of the year. In the north the temperature range

was less, from 23.9 to 29.4°C, and the lowest temperatures were recorded in both the first and third quarter. The temperatures that the mantas encountered varied with location (Fig. 8). In the south 83% of hits occurred from 25 to 27°C degrees (range 22 to 28°C). In the north 91% of hits occurred from 26 to 28°C (range 24–29°C).

Discussion and conclusions

The acoustic array in the Komodo Marine Park, Indonesia enabled near continuous monitoring of manta activity at the sites throughout the park where mantas were most commonly observed. By collecting data over multiple years it was possible to examine visitation patterns over various time scales providing insights into the influence of time of day, tides, lunar phase, and season. Here we present the most comprehensive analysis of manta ray movements published to date.

Acoustic arrays have proven a valuable tool in this and other studies (Klimley and Halloway 1999; Sundstrom et al. 2001; Voegeli et al. 2001; Heupel and Simpfendorfer 2005) and are ideal for species that return to predictable locations. There are however limitations. First, it is not possible to determine where a tagged animal is when it is not recorded or to distinguish between animals leaving the study area and tag shedding. Second, the receiver range is limited in near-shore habitats such as those frequented by the mantas in the Komodo Marine Park where snapping shrimp and bubbles associated with strong regional currents limited the range of receivers (Voegeli et al. 2001). Reception range was particularly low in the south, nonetheless, these receivers collected the most data. The high number of detections at GF in particular may result from its location between Komodo Island and a second, small island that serve as a bottle neck. In addition, foraging mantas were observed to repeat the same route, which would increase the probability of detection. While estimates of manta presence are undoubtedly conservative at all sites, the agreement

Fig. 7 Model results showing the difference in presence of tagged manta rays at north Komodo (*NK*) and south Komodo (*SK*) during **a** new moon, half moon and full moon recordings and **b** falling, slack and rising tide. These model estimates apply to the month November but are representative of all months. Error bars are 95% confidence limits of the model estimates
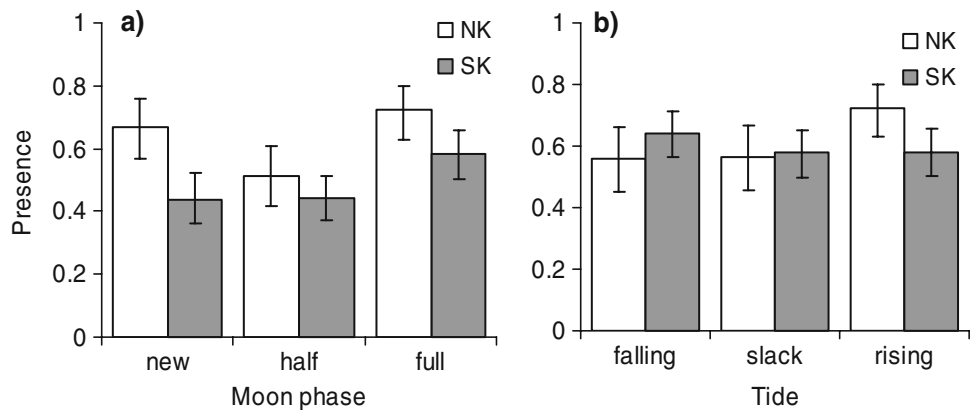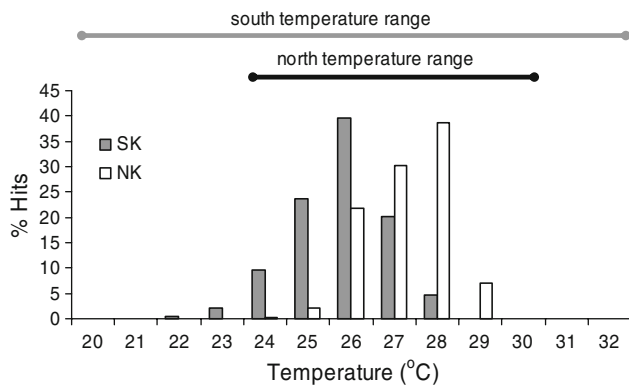
Fig. 8 The percentage of hits at a given temperature are shown at both north Komodo (*NK*) and south Komodo (*SK*). The temperature range at each site is also indicated

between visual and acoustic surveys suggests that the major trends were likely captured in this study.

Manta rays in the park exhibited considerable site fidelity and demonstrated some individual preference for certain areas. Mantas returned to the same site almost daily for up to 3 months and visited sporadically for up to 2 years. Mantas with the longest records (>300 days), appeared to prefer certain areas, and were recorded most often near the tagging location. While most mantas with longer records visited at least two areas, movements between areas were somewhat limited. Thus, while there is clearly exchange between sites, there may be residency patterns within the park.

Site fidelity has been reported in manta rays in other locations as well. Through photo identification manta rays have been documented to regularly return to specific feeding or cleaning stations over long time periods. An individual manta studied in the Yaeyama Islands, Japan for example, was observed in the area for 15 years (Homma et al. 1997). Manta rays observed off the big island of Hawaii have been re-sighted over similarly long periods (T. Clark, personal communication). In Bora Bora, where studies started more recently, the same mantas have been observed returning to the same cleaning stations for over 2 years (S. Walker, personal communication). In many locations it is also common for individuals to be documented only once (S. Walker, personal communication; K. Yano, personal communication) raising the question as to whether some mantas are transient. This could explain some of the shorter records observed in this study although it is impossible to determine whether mantas left the area or lost their tags.

Teleosts and sharks return to predictable locations for a range of reasons, to spawn or reproduce (Domeier and Colin 1997), using sites as landmarks along a migratory route (Klimley and Halloway 1999; Klimley et al. 1988), to visit cleaning stations (Homma et al. 1997), to take refuge (Klimley and Nelson 1984; Holland et al. 1993; Sims et al.

2001), or take advantage of a predictable food source (Klimley and Anderson 1996; Sims and Quayle 1998; Heyman et al. 2001; Domeier and Nasby 2006; Graham et al. 2006). Based on our observations, the mantas returned to the sites in the park for both feeding and cleaning. It is also possible, however, that these areas are important for reproduction (males and females are observed in the park) and/or provide important refuge from predators such as killer whales and sharks which are known to attack manta rays (Homma et al. 1997).

While many of the manta rays in the park exhibited considerable site fidelity, there are protracted periods when they are not recorded at any receiver. It is not clear whether the animals are just outside the range of the array or have left the park. Similarly, manta rays in Bora Bora are not recorded for months at a time before returning although with only Photo ID this pattern is difficult to confirm (S. Walker, personal communication). Additional work using pop-up satellite archival tags and/or active telemetry (Arnold and Dewar 2001; Voegeli et al. 2001) would help to resolve movements of mantas when they are not detected by the receivers.

Diurnal pattern

The examination of diurnal patterns shows the highest tag activity at all sites during daylight hours. The time of arrival and departure coincides with the approximate time of sunrise and sunset, which changes little at these latitudes. One possible explanation for the diurnal pattern is that the mantas are moving offshore during the night possibly to feed on the deep scattering layer (DSL) when it approaches the surface (Tont 1975; Robinson and Gomez-Gutierrez 1998). This could help to explain the slight shift to later hours at the northern site, which is farther from deeper water. There is evidence for off-shore movement and feeding on the DSL from other areas. Manta rays that were actively tracked off Japan moved offshore at night and then returned the following day (K. Yano, personal communication). While this may occur in other regions as well no published accounts are available. Another member of the same family (*Mobula japonica*) feeds on crustaceans primarily at night when they come to the surface (H. Dewar, personal observation). A number of other elasmobranchs including scalloped hammerheads, blacktip reef sharks and gray reef sharks are also observed to aggregate in near shore waters during the day and then disperse offshore at night (Klimley and Nelson 1984; Klimley et al. 1988; Economakis and Lobel 1998; Heupel and Simpfendorfer 2005). Other possible explanations for the diurnal pattern are that different sites are preferred at night or that activity is lower, reducing the potential of detecting animals. Clearly more work is needed to explain the diurnal pattern.

Foraging and tidal currents

While the acoustic tags do not indicate when animals are feeding, insights into foraging were gained through visual observations and by examining visitation patterns. Foraging (when a manta's cephalic lobes are unfurled and their mouth is wide open) was common in the three main areas in the park. Mantas fed where prey appeared to be concentrated both in the water column, where visibility was very low, and on surface slicks. The concentration of prey is considered to be critical for filter feeders likely due to the energetic cost of feeding; foraging is observed in both basking sharks (Sims 1999) and fin whales (Clark et al. 2000) only above threshold prey density. Although it has not been directly measured, prey density appears to be important for mantas as well.

There are a number of factors that likely enhance prey densities in the Komodo Marine Park. (1) The strong tidal currents and complex bathymetry will enhance upwelling and increase primary productivity (Field and Gordon 1996; Kinkade et al. 1996). (2) The extreme tidal currents and convoluted shorelines create complex secondary circulations which results in convergence zones and tidal slicks that act to accumulate zooplankton (Sugimoto 1975). The site where the majority of visits were documented (GF) has a high degree of structure. (3) In addition, tidally forced internal waves and associated surface slicks transport entrained material, such as planktonic larvae, towards the shore likely bringing additional resources from off-shore waters (Shanks 1983). These processes will enhance the biomass of available prey in the park beyond that produced locally.

Consistent with the apparent role of tidal currents in concentrating resources, tidal phase and intensity impacted visits. More visits were documented at in north Komodo at the rising tide (when currents move from the south to the north) when the moon was new or full and tidal flux was greatest. Tidal currents in this area shift 180 degrees with each tidal change and can be up to 5 knots. In contrast, the influence of tidal current and phase was less pronounced in south Komodo. In this region the variation in strength and direction of tidal currents is lower than in the north and therefore one might expect a less pronounced effect of lunar and tidal phase on visitation patterns. Furthermore, the southern part of the island has a more complex geography and bathymetry, which may result in a more constant food supply that is less dependent on tidal strength or specific direction.

The concentration of prey associated with tidal currents provides important forage for animals from diverse taxonomic groups and impacts the temporal and spatial patterns in feeding. In a comparison of marine birds with different prey preferences, the plankton feeder, Ancient Murrelets, were most active when tidal flow was the greatest (Holm and Burger 2002). Dolphin foraging was most often observed in association with tidal fronts in a narrow estuarine channel off Scotland (Mendes et al. 2002). The two filter feeding sharks also forage in tidal currents. Basking sharks feed in near-shore regions where strong tidal flows aggregate zooplankton, often near islands or headlands (Sims and Quayle 1998). Whale sharks position themselves to take advantage of tidal currents transporting material out of the lagoon on Ningaloo Reef Australia (Wilson et al. 2001). Similar to these other species, mantas appear to take advantage of the increase in prey density associated with the strong tidal currents around Komodo Island.

A second factor that varies along with tidal intensity is lunar illumination. The increase in nighttime visits during the full moon but not the new moon in south Komodo suggests that high light levels and not tidal intensity are associated with the increase in visitation. This shift could be associated with an increase in foraging near-shore at higher light levels or a decrease in offshore foraging opportunities. During the full moon the DSL organisms remain deeper in the water column (Blaxter 1974) and overall predation on zooplankton has been shown to decrease as a result (Hernández-León et al. 2001).

Season

A distinct seasonal pattern was identified in both north and south Komodo. Mantas were most abundant in the south during the summer and in the north during the winter. While maximum abundances were reversed between the two sites, this pattern did not result solely from a shift from one site to another although there is some suggestion, at least for the 2002 deployments, that some mantas moved north after leaving south Komodo.

While it is difficult to identify the driving force behind the seasonal change in manta abundance, it is likely linked to seasonal environmental patterns. The shift in abundance corresponds to the monsoonal shift in the Indo-Pacific that influences both temperature and productivity. During the first quarter when no mantas were observed in south Komodo the Indian Equatorial Counter Current and north monsoon are the driving processes (Tomczak and Godfrey 1994). At this time there is a reduction in the net flow from the Pacific to the Indian Ocean that results in a drop in productivity and an average 3°C increase in temperature (Hahude and Gordon 1996). It was during this quarter that temperatures here exceeded 30°C, which is thought to be the upper thermal limit for manta rays (no mantas were recorded above 29°C in this study). Over the same period in north Komodo, waters are cool with poor visibility. From May to September when visitation in south Komodo is high, the South Equatorial Current and southeast monsoon are both fully developed which maximizes westward flow

(Tomczak and Godfrey 1994) and results in a drop in temperature and large increase in productivity (Hahude and Gordon 1996). During this phase, the waters in the south are cool and murky (visibility ca. 5 m) and rich in plankton. Temperatures in the north remained below 30°C and mantas were seen here throughout the year.

As mentioned above, seasonal shifts in manta distributions have been documented in a number of places and are likely associated with temperature. In locations such as New Zealand mantas are observed primarily in the austral summer (Duffy and Abbott 2003). In the Gulf of California, Mexico mantas are observed in the Boreal summer (P. Ahjua, personal communication). In the Maldives seasonal shifts are thought to be associated with the local monsoons, when current directions reverse and mantas move from one side of the Maldives to the other (Anderson 1996). In the Komodo Marine Park the monsoons also impacted visitations patterns although seasonality was site dependent. This suggests that subtle shifts in distributions may be associated with seasonal patterns and that in a location as diverse as Indonesia it may not be necessary to move very far to find suitable habitat.

Management implications

The predictability of the spatial distribution of manta rays has important consequences for conservation and tourism management. The information on patterns of occurrence will assist dive operators in successfully planning manta dives, maximizing the potential of this ecotourism resource. For management and conservation, the high site fidelity and ability to predict spatial patterns has two implications. First, there is the potential for localized depletion or extirpation once fishers start exploiting an aggregation site. On the other hand, site-specific protection or marine protected areas based around aggregations sites should have a direct positive effect on local abundance.

In Komodo specifically, one of the key questions was whether the boundaries of the park serve to protect the local mantas from regional fisheries. Clearly, the park encompasses a number of sites that are important for manta rays, and therefore the park provides some protection at least during the day. Of concern however, is where the mantas move when they are not within in the range of the receiver. Tagged mantas were not detected for long periods, during which they may have left the park. One of the greatest potential threats are the fisheries in Lamalera and Lamakera, which are approximately 400 km from the park. Manta ray migrations as far as 350 km have been documented (Homma et al. 1997) and longer migrations are likely possible raising the possibility that mantas could move into this region. In Lamakera it is estimated that approximately 1,000 mantas are taken in the fishing season

from May through October (Dewar 2002). Mantas are also taken in other locations throughout Indonesia although at lower levels. Additional information on the larger-scale movements of mantas and the pattern of fisheries is required to better determine the management requirements. As indicated above, mantas have the potential to be highly susceptible to over fishing and vigilance is warranted.

References

Alava ERZ, Dolumbaló ER, Yaptinchay AA, Trono RB (2002) Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. In: Fowler SL, Reed TM, Dipper FA (eds) Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop. Sabah, Malaysia, July 1997, pp 132–148

Anderson C (1996) Manta tagging starts in the Maldives. Shark News 7:6

Arnold G, Dewar H (2001) Electronic tags in marine fisheries research: a 30-year perspective. In: Seibert J, Nielsen J (eds) Electronic tagging and tracking in marine fisheries. Kluwer , Dordrecht, pp 7–64

Bigelow HB, Schroeder WC (1953) Fishes of the Western North Atlantic. Part two: Sawfishes, Guitarfishes, Skates and Rays. Memoir Sears Foundation for Marine Research, Number 1. Yale University, New Haven, pp 481–515

Blaxter JHS (1974) The role of light in the vertical migration of fish—a review. In: Evans GC, Bainbridge R, Rackham O (eds) Light as an ecological factor, II. Blackwell, Oxford, pp 189–210

Clark CW, Croll DA, Acevedo A, Urban-Ramirez J (2000) Multi-modal surveys of fin whales in the Sea of Cortez, Mexico. J Acoust Soc Am 108:2539

Compagno LJV (1999) Checklist of living elasmobranchs. In: Hamlett WC (ed) Sharks, skates, and rays: the biology of elasmobranch fishes. John Hopkins University Press, Maryland, pp 471–498

Dewar H (2002) Preliminary report: manta ray harvest in Lamakera. Report to the World Wildlife Fund. http://www.tnc-seacmpa.org/downloads/alor%20-%20eBook.pdf

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. Bull Mar Sci 60:698–726

Domeier ML, Kiefer D, Nasby-Lucas N, Wagschal A, O'Brien F (2005) Tracking Pacific bluefin tuna (*Thunnus thynnis orientalis*) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface-temperature data from satellites with temperature data from tags on fish. Fish Bull 103:292–306

Domeier ML, Nasby N (2006) Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) in an eastern Pacific aggregation site (Guadalupe Island, Mexico). Mar Biol. doi:10.1007/s00227-006-0380-7

Duffy CAJ, Abbott D (2003) Sightings of mobulid rays from northern New Zealand, with confirmation of the occurrence of *Manta birostris*. NZ J Mar Freshwat Res 37:115–121

Economakis AE, Lobel PS (1998) Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. Environ Biol Fishes 51:129–139

Field AL, Gordon AL (1996) Tidal mixing structures in the Indonesia Seas. J Physic Oceanog 26:1924–1937

Fujita T (2006) A study of tuna bycatch using correspondence analysis. Masters Thesis University of California Los Angeles, California. 2006

Garcia MA, Hall MA (1997) Spatial and seasonal distribution of bycatch in the purse seine tuna fishery in the eastern Pacific Ocean. In: Fisheries Bycatch: Consequences and Management, Dearborn MI, Alaska Sea Grant Program Report 97–02, pp 46–49

Graham RT, Roberts CM, Smart JCR (2006) Diving behaviour of whale sharks in relation to a predictable food pulse. J R Soc Interface 3:109–116

Hahude AG, Gordon AL (1996) Thermocline stratification within the Indonesian Seas. J Geophys Res 101:12401–12409

Hernández-León S, Almeida C, Yebra L, Arístegui J, Fernández de Puelles ML, García-Braun J (2001) Zooplankton abundance in subtropical waters: is there a lunar cycle? Sci Mar 65:59–64

Heupel MR, Simpfendorfer CA (2005) Quantitative analysis of aggregation behavior in juvenile blacktip sharks. Mar Biol 147:1239–1249

Heyman WD, Graham RT, Kjerfve B, Johannes RE (2001) Whale sharks, *Rhincodon typus*, aggregate to feed on fish spawn in Belize. Mar Ecol Prog Ser 215:275–282

Holland KN, Wetherbee BM, Peterson JD, Lowe CG (1993) Movements and distribution of hammerhead shark pups on their natal grounds. Copeia 1993:495–502

Holm KJ, Burger AE (2002) Foraging behavior and resource partitioning by diving birds during winter in areas of strong tidal currents. Waterbirds 25:312–325

Homma K, Maruyama T, Itoh T, Ishihara H, Uchida S (1997) Biology of the manta ray, *Manta birostris*, Walbaum, in the Indo-Pacific. In: Séret B, Sire JY (eds) Proceedings of the 5th Indo-Pacific Fish Conference, Nouméa. Soc Fr Ichthyol, Paris, pp 209–216

Kinkade C, Marra J, Langdon C, Knudson C, Ilahude AG (1996) Monsoonal differences in phytoplankton biomass and production in the Indonesian Seas: tracing vertical mixing using temperature. Deep Sea Res I 44:581–592

Klimley AP, Nelson DR (1984) Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. Behav Ecol Sociobiol 15:45–54

Klimley AP, Butler SB, Nelson DR, Stull AT (1988) Diel movements of scalloped hammerhead sharks, *Sphyrna lewini*, to and from a seamount in the Gulf of California. J Fish Biol 33:751–761

Klimley AP, Anderson S (1996) Residency patterns of white sharks at the South Farallon Islands, California. In: Klimley AP, Ainly DG (eds) Great white sharks, the biology of Carcharodon carcharias. Academic Press, San Diego, pp 365–373

Klimley AP, Halloway CF (1999) School fidelity and homing synchronicity of yellowfin tuna, *Thunnus albacares*. Mar Biol 133:307–317

Last PR, Stevens JD (1994) Sharks and rays of Australia. CSIRO, Australia

Marshall A, Ishihara H, Dudley SFJ, Clark TB, Jorgensen S, Smith WD, Bizzarro JJ (2006) *Manta birostris*. In: IUCN 2006. 2006 IUCN Red List of Threatened Species. http://www.iucnredlist.org

McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman Hall, London

Mendes S, Turrell WR, Lutkebohle T, Thompson PM (2002) Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. Mar Ecol Prog Ser 239:221–229

Musick J A (1999) Ecology and conservation of long-lived marine animals. Am Fish Soc Symp 23:1–10

Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S (2000) Management of sharks and their relatives (Elasmobranchii). Fisheries 25:9–13

Prince ED, Goodyear CP (2006) Hypoxia-based habitat compression of tropical pelagic fishes. Fish Oceanogr 15:451–464

Robinson CJ, Gomez-Gutierrez J (1998) Daily vertical migration of dense deep scattering layers related to the shelf-break area along the northwest coast of Baja California, Mexico. J Plankton Res 20:1679–1697

Romanov EV (2002) Bycatch in the tuna purse-seine fisheries of the western Indian Ocean. Fish Bull 100:90–105

SAS Institute, Inc (1993) SAS/STAT Software: The GENMOD Procedure, Release 6.09 SAS Technical Report P–243. SAS Institute Inc. Cary, North Carolina

Santos RS, Porteiro FM, Barreiros JP (1997) Marine fishes of the Azores: annotated checklist and bibliography. Bull Univ Azores Supplement 1, p 244

Shanks AL (1983) Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar Ecol Prog Ser 13:311–315

Sims DW, Quayle VA (1998) Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature 393:460–464

Sims DW (1999) Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife edge? Proc R Soc Lond B 266:1437–1443

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

Smith JLB, Smith MM (1963) The fishes of Seychelles. Rhodes University, Grahamstown

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. W. H. Freeman, New York

Sugimoto T (1975) Effects of boundary geometries on tidal currents and tidal mixing. J Oceanogr Soc Jpn 31:1–14

Sundstrom LF, Gruber SH, Clermont SM, Correia JPS, de Marignac JRC, Morrissey JF, Lowrance CR, Thomassen L, Oliveira MT (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. Environ Biol Fishes 60:225–250

Tomczak M, Godfrey JS (1994) Regional oceanography: an introduction. Permagon, Tarrytown

Tont SA (1975) Deep scattering layers: patterns in the Pacific. CALCOFI Rep 18:112–117

Voegeli FA, Smale MJ, Webber DM, Andrade Y, O'Dor RK (2001) Ultrasonic telemetry, tracking, and automated monitoring technology for sharks. Environ Biol Fishes 60:267–281

White W, Giles J, Dharmadi, Potter I (2006) Data on the bycatch fishery and reproductive biology of mobulid rays (Myliobatiformes) in Indonesia. Fish Res 82:65–73

Wilson SG, Taylor JG, Pearce AF (2001) The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Niño/Southern Oscillation. Environ Biol Fishes 61:1–11