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

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Abstract	<p>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, <i>Manta birostris</i>, 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 <math>183 \pm 136</math> 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.</p>	
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2 **Movements and site fidelity of the giant manta ray,**  
3 ***Manta birostris*, in the Komodo Marine Park, Indonesia**

4 **Heidi Dewar · Peter Mous · Michael Domeier ·**  
5 **Andreas Muljadi · Jos Pet · Jeff Whitty**

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9 in near-shore tropical habitats, little published information  
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11 manta ray, *Manta birostris*, and what factors influence visi-  
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shifts. The long-term fidelity indicates that marine-pro- 38  
tected areas centered around aggregation sites could help 39  
protect this species from overexploitation. 40

41 **Introduction**

The giant manta ray (*Manta birostris*; Donndorff 1798) is a 42  
monogeneric species in the subfamily Mobulinae (Family 43  
Myliobatidae) that consists of the devil rays. The giant 44  
manta is the largest of all rays reaching a disc width of up to 45  
6.7 m and 1,400 kg weight (Last and Stevens 1994). Like 46  
the largest whales and sharks, manta rays are filter feeders. 47  
They and the other members of the subfamily funnel water 48  
and prey into their mouths using their distinctive cephalic 49  
lobes. Prey is then filtered from the water by modified gill 50  
rakers. The giant mantas are often observed feeding in 51  
surge channels (Wilson et al. 2001), on surface slicks, or 52  
near lights at night that act to concentrate prey. Like the 53  
largest filter feeding shark (the whale shark), manta rays 54  
occur worldwide in tropical and subtropical waters 55  
(Bigelow and Schroeder 1953; Last and Stevens 1994; 56  
Compagno 1999). While mantas are observed primarily in 57

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58 near-shore environments, they are also reported at sea-  
59 mounts and are even encountered far from shore in the open  
60 sea.

61 Some of the best information available on distribution  
62 patterns within the mantas' broad geographic range comes  
63 from photo identification studies that have recorded the  
64 occurrence of photographically identified individuals over  
65 time. Based on this and other research, local residence pat-  
66 terns appear to be site dependent. In certain regions, the  
67 same individual mantas are observed repeatedly over long  
68 time periods (e.g., in Yap, Hawaii and Bora Bora) whereas  
69 in others (e.g., New Zealand, Australia, Mexico, Africa,  
70 Ecuador, and Southern Japan) their occurrence is seasonal  
71 (Homma et al. 1997; Duffy and Abbott 2003; S. Fish, per-  
72 sonal communication; P. Ajhia, personal communication;  
73 S. Walker, personal communication). When mantas are  
74 sighted on multiple occasions, they are often returning to  
75 the same feeding and cleaning stations (Homma et al.  
76 1997). While these studies have provided important  
77 insights into manta behavior, they are limited temporally  
78 and spatially to periods when divers or snorkelers are in the  
79 water. Also, exactly what factors influence residence pat-  
80 terns between and within different regions is unknown.

81 Although not the target of large-scale fisheries, giant  
82 mantas are captured incidentally and/or taken in regional  
83 fisheries through much of their range (Garcia and Hall  
84 1997; Alava et al. 2002; Dewar 2002; Romanov 2002; Fuj-  
85 ita 2006; White et al. 2006). Concerns about overexploita-  
86 tion resulted in the listing of the giant manta as threatened  
87 through part of its range by the IUCN World Conservation  
88 Union (Marshall et al. 2006). Although scientific studies  
89 and exact population estimates are lacking, a decline in  
90 manta sightings has been noted in a number of locations  
91 including Japan, French Polynesia, and Mexico (Homma  
92 et al. 1997; Marshall et al. 2006). While elasmobranchs are  
93 generally considered highly susceptible to over fishing due  
94 to their natural history (Musick 1999; Musick et al. 2000),  
95 mantas are likely even at greater risk given their very low  
96 reproductive rates (one or two pups per year), generally  
97 small population sizes and potentially limited distributions  
98 (Marshall et al. 2006).

99 An additional challenge to the management and conser-  
100 vation of manta rays is the lack of published data on basic  
101 life history information. The lack of publications is due, in  
102 part, to the fact that no industrial fishery for mantas exists  
103 and there has been little systematic collection of data. The  
104 vast majority of publications simply report on sightings in  
105 regional species lists (Smith and Smith 1963; Santos et al.  
106 1997). Information on growth rates, gestation period, age at  
107 sexual maturity and reproductive rates is scarce (Bigelow  
108 and Schroeder 1953; White et al. 2006). The results from  
109 only one of the photo identification studies mentioned  
110 above have been published (Homma et al. 1997).

We report on the movements of giant manta rays deter- 111  
mined using an acoustic hydrophone array established in 112  
the Komodo National Park, Indonesia. There are a number 113  
of sites within the Komodo Marine Park where mantas are 114  
regularly observed although it was not clear whether these 115  
mantas were transient or resident and what factors influ- 116  
enced local patterns of occurrence. There was considerable 117  
interest in these questions for two reasons. First, local dive 118  
operators were interested in developing manta-based eco- 119  
tourism, and it was important to obtain baseline informa- 120  
tion on the local population as well as to identify visitation 121  
patterns to maximize the success of the program. Second, in 122  
two villages just east of Komodo (Lamalera and Lamakera) 123  
there is a directed manta fishery causing concern that the 124  
mantas in the park may be impacted. The objectives of this 125  
study were to determine whether the mantas in the park 126  
were resident, and to identify temporal and spatial move- 127  
ment patterns and their relation to environmental condi- 128  
tions. In addition to the value of this study to the local 129  
manta population, results may also provide insights into 130  
patterns observed in other locations. 131

## 132 **Materials and methods**

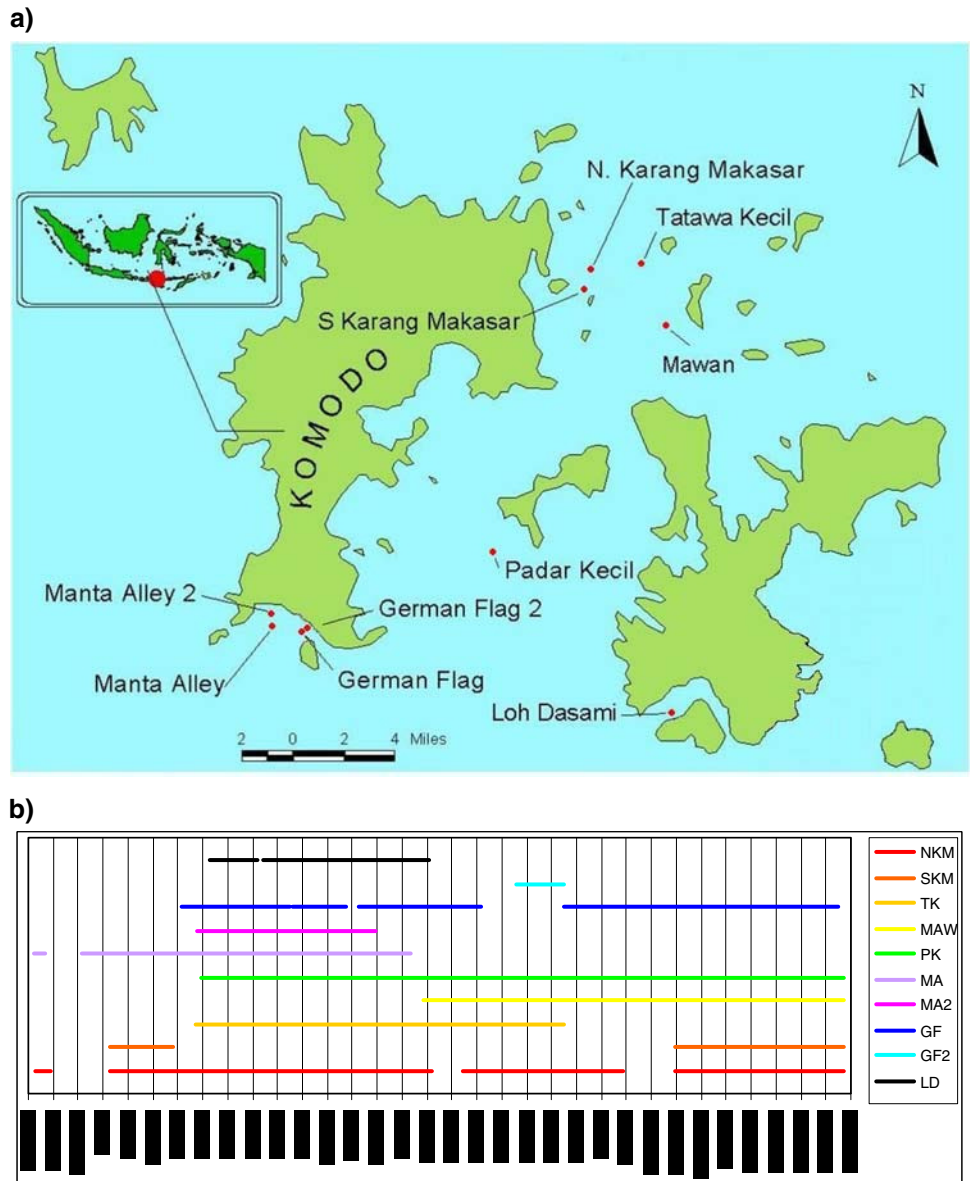
### 133 **Tag deployments**

The mantas were tagged with a V16-6H acoustic transmit- 134  
ter (Vemco V16, Nova Scotia Canada) in a shark casing. 135  
Each tag transmitted a unique code allowing individual ani- 136  
mals to be identified. The tags were secured to the mantas 137  
using large nylon darts that were attached to the tag using 138  
300-lb test monofilament line and stainless steal crimps. 139  
Two different dart types were used. White nylon darts with 140  
two anchoring barbs (Prince and Goodyear 2006) were 141  
used in the first deployment. Black nylon darts with eight 142  
barbs (Domeier et al. 2005) were used in the second and 143  
third deployments. The darts were inserted near the trailing 144  
edge of the wing, at the margin between the wing and the 145  
axial musculature with a modified spear gun. When the 146  
mantas were tagged, their size was estimated and the 147  
behavior of the animal as well as that of the other mantas in 148  
the area was noted. 149

### 150 **Acoustic array**

The acoustic array consisted of Vemco, VR2 omni-direc- 151  
tional hydrophones. The hydrophones were suspended at 152  
depths from 8 to 25 m using plastic fishing floats that were 153  
secured to the bottom with large screws or sand bags 154  
depending on the bottom substrate. The tag ID code and 155  
time were logged when tagged mantas were detected by the 156  
hydrophones. 157

**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



158 Over the course of the study, ten receivers were placed  
 159 in seven different locations for varying periods of time  
 160 (Fig. 1) including one hydrophone each at Padar Kecil  
 161 (PK), Mawan (MW), Loh Dasami (LD) and Tatawa Kecil  
 162 (TK) and two each at Karang Makasar (KM), Manta Alley  
 163 (MA) and German Flag (GF) (for color figure see online  
 164 version). Working from north to south, TK is a small, steep,  
 165 isolated rocky island with substantial coral coverage. KM is  
 166 located near a small sandy island away from distinctive  
 167 structures and is characterized by a very gradually sloping  
 168 coral rubble field with a few isolated coral heads. MW is a  
 169 small island to the East of Komodo with a broad fringing  
 170 reef that is exposed to strong tidal currents. PK is near an  
 171 isolated rocky island in the channel between Komodo and  
 172 Rinca Islands. The sites at GF and MA are in the same gen-  
 173 eral area approximately 1.8 km apart, at the south shore of

Komodo island where there are a series of rocky islands 174  
 and a rocky shoreline with a large degree of structure. LD is 175  
 situated in a horseshoe-shaped bay in the South of Rinca 176  
 Island that has rocky shores and little reef formation. All 177  
 locations were those where mantas had been observed by 178  
 the park rangers and The Nature Conservancy (TNC) staff 179  
 on multiple occasions. 180

Range test 181

Range tests were conducted at GF. A tag was placed in the 182  
 water and hung over the side of the vessel as the boat 183  
 drifted by the receiver with the tidal current. The precise 184  
 time and location of the boat were documented using a 185  
 GPS. These were then linked to the time-stamped data 186  
 recorded on the receiver. 187



## 188 Temperature records

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

## 196 Data analysis

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

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

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

coincide with the approximate time of sunrise and sunset 222  
through out the year). To examine the impact of both the 223  
tidal intensity and phase, two additional variables were 224  
examined. Moon phase (variable MOON) was included at 225  
three qualitative levels: ‘new’ (<10% illuminated), ‘half’ 226  
(10–90% illuminated) and ‘full’ (>90% illuminated). The 227  
% illumination was obtained from the United States Naval 228  
Observatory Astronomical Applications Department ([http://](http://aa.usno.navy.mil/data/docs/MoonPhase) 229  
[aa.usno.navy.mil/data/docs/MoonPhase](http://aa.usno.navy.mil/data/docs/MoonPhase)). Tidal phase (vari- 230  
able TIDE) was categorized as ‘rising’, ‘slack’, or ‘falling’. 231  
Tidal height data were taken from tide tables for Bima (ca. 232  
80 km to the East of Komodo National Park), the nearest 233  
location for which data are published. The tidal height data 234  
were offset with +1 h for north Komodo and with +2.5 h for 235  
south Komodo to align the table with observed current pat- 236  
terns. Because the effects of MONTH, DAY, MOON and 237  
TIDE may differ between aggregation areas, second order 238  
interactions of these variables with AA were also included. 239

The likelihood of recording a manta ray and number of 240  
hits or visits will likely depend on the number of tags and 241  
hydrophones in a particular area. This was accounted for by 242  
including sampling effort (SEFF) in the GLM; defined as 243  
the product of the number of active hydrophones at a partic- 244  
ular site and the number of deployed tags. In later analyses, 245  
SEFF was used to derive the number-of-hits per unit 246  
sampling effort (HUE, analogous to catch-per-unit-effort). 247  
In the GLM, however, SEFF was included as an independ- 248  
ent variable along with the other independent variables 249  
described above. 250

The binomial dependent variable in the GLM, here 251  
abbreviated as PRSNT, has a value of one if a manta ray 252  
was detected (‘present’), and zero when no mantas were 253  
detected (‘absent’). ‘Presence’ was evaluated per calendar 254  
day (24 h) per level of each of the qualitative variables. For 255  
example, if the hydrophones at MA recorded a series of hits 256  
during rising tide at daytime, but none during slack at 257  
daytime, then the dataset for that calendar day and that 258

**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

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

## 265 Visual surveys

266 To assess the acoustic results and obtain additional infor-  
 267 mation on manta abundance, a team of six observers made  
 268 61 trips to the three main sites (north and south Komodo  
 269 and PK) from May 2001 to June 2003, between 8:30 and  
 270 15:00. The survey team slowly cruised each site by boat at  
 271 a maximum speed of ca. 10 km h<sup>-1</sup> counting mantas swim-  
 272 ming at and below the surface when visible. When mantas  
 273 were observed the team reduced speed to better estimate the  
 274 group size. It took 5–30 min to search each site and verify  
 275 the presence of mantas.

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

## 284 Results

### 285 Tag deployments

286 A total of 41 tags were deployed during three deployment  
 287 periods, eight in October 2000, 15 in April 2001 and 18 in  
 288 May 2002 (Table 2). Deployments occurred at various sites  
 289 throughout the park near the location of the receivers. The  
 290 average estimated wingspan of tagged mantas was 3.6 ±  
 291 0.8 m (range 1.8–5 m).

### 292 Receivers

293 Acoustic monitoring of manta rays was conducted from  
 294 October 2000 to June 2003 (Fig. 1b). Due to a number of  
 295 problems coverage was not constant. Problems included  
 296 receiver loss (likely to fishermen), flooding, and battery  
 297 malfunction. The main sites, including GF (70%), MA  
 298 (92%), PK (78%) and KM (86%), or north Komodo, were  
 299 covered for at least 70% of the study. The more remote  
 300 sites had less coverage; MW (51%), TK (45%) and LD  
 301 (26%).

302 The range test at GF revealed that tags could be detected  
 303 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. 304 305

Sites had differing amounts of manta activity (Table 3) 306 with no mantas recorded at LD. The highest number of 307 mantas was recorded at KM ( $n = 27$ ) with only slightly 308 fewer at MA ( $n = 24$ ) and GF ( $n = 24$ ), 20 of these manta 309 were recorded at both GF and MA. Fewer mantas were 310

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

Location	# Mantas	Total hits	Corrected hits	Days mantas detected	Corrected days	Corrected 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)

311 documented at PK ( $n = 14$ ), TK ( $n = 3$ ) and MAW ( $n = 7$ ).  
 312 Despite the fact that a receiver was not installed at GF  
 313 until the second deployments, it had the highest number  
 314 of raw and corrected hits and days with 43% of the cor-  
 315 rected days at this site. The second most popular site was  
 316 KM (30% of corrected days) followed by MA (18%) and  
 317 PK (7%). MAW and TK had 1% or less of the total  
 318 corrected days.

#### 319 Tag activity

320 Tag activity is summarized in Table 2 and Fig. 2. Of the 41  
 321 tags, all but 6 were recorded by a receiver at least once. Tag  
 322 transmissions were detected for periods up to 526 days  
 323 (average  $183 \pm 136$ ). An individual manta made from 3 to  
 324 303 visits (median 58 visits). The median number of hits  
 325 per visit was 8 (maximum 209) and 23% of all visits con-  
 326 sisted of only one hit. The median visit duration calculated  
 327 for each individual manta ranged from 8 min to 6.7 h with a  
 328 median over all mantas of 2 h. The longest visits were close  
 329 to 24 h, although this was uncommon and only 8 (0.4%)  
 330 visits were longer than 20 h. The number of days on which  
 331 hits were received for the individual mantas ranged from 3  
 332 to 171 (median 42). The percentage of days of a given  
 333 deployment on which hits were received from a given tag  
 334 ranged from 0.7 to 75% (median 20.6%).

#### 335 Manta movements

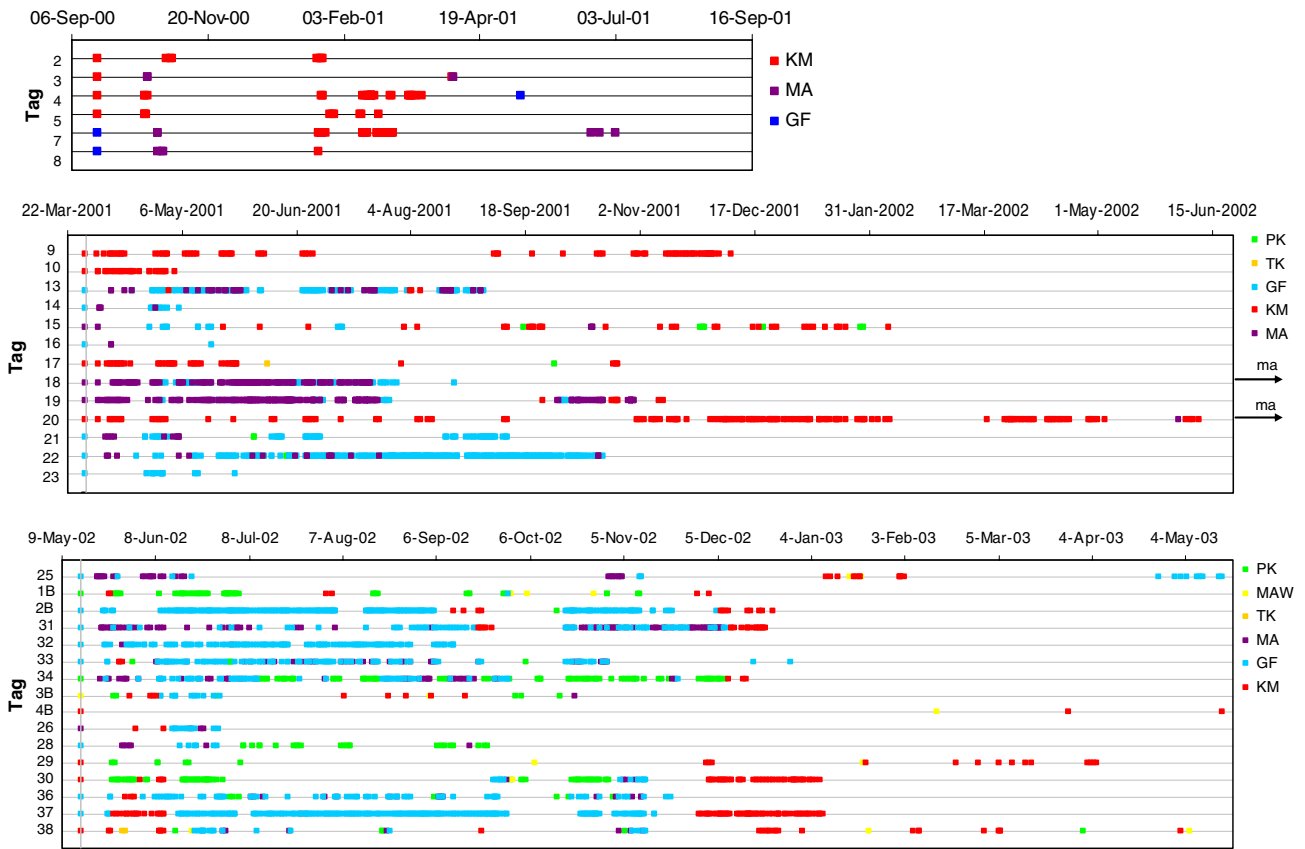
336 The visits for all the 35 mantas are shown in Fig. 2 (for  
 337 color figure see online version). Given the variability and  
 338 complexity of patterns both within and across individuals  
 339 two approaches were taken to quantify patterns. First, the  
 340 timing of visits and movement between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

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

quent visits than to 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 con-  
 secutive visits was 44 days).

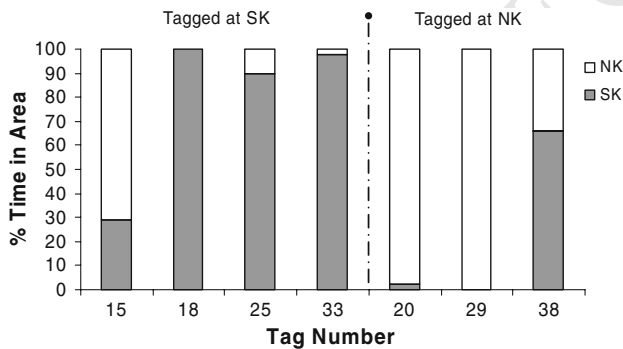
While some mantas visited only one site for weeks at a  
 time, there was considerable movement among sites and  
 most mantas visited more than one site. The most com-  
 mon movements were between the two closest sites off  
 south Komodo, MA and GF ( $n = 376$ ) and 155 of these  
 occurred within 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 vis-  
 its 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 aver-  
 age 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% ( $\pm 4\%$ ) of the corrected days (days corrected  
 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 corrected 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

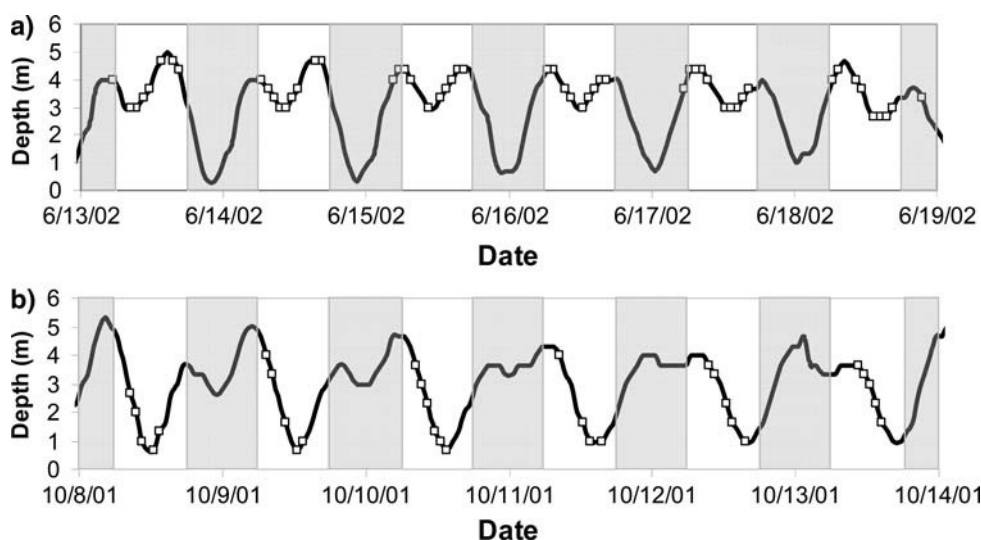
385 Effects of place, time, daylight, moon phase and tides:

386 The GLM explained 36% of the total deviance, using 34  
 387 degrees of freedom. All main effects and all interactions  
 388 with AA are summarized in Table 4 and were significant  
 389 ( $P < 0.01$ ). The GLM that included second order interactions  
 390 was less parsimonious than the first model (97 degrees  
 391 of freedom vs. 34 degrees of freedom) and explained only

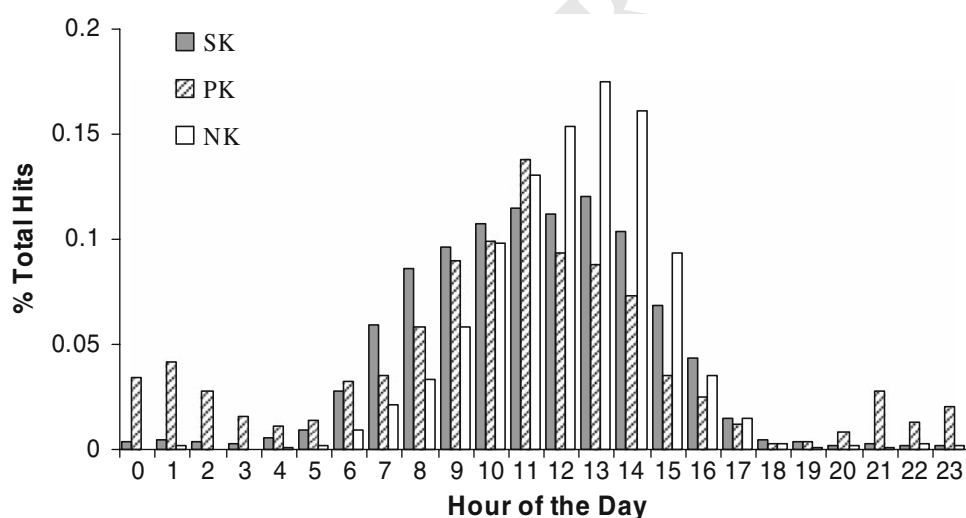
slightly more of the total deviance (38 vs. 36%). The more 392  
 parsimonious model comprising the main effects and sec- 393  
 ond order interactions with AA was unlikely to have missed 394  
 major effects. Consequently, this model was used to 395



**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 throughout the day



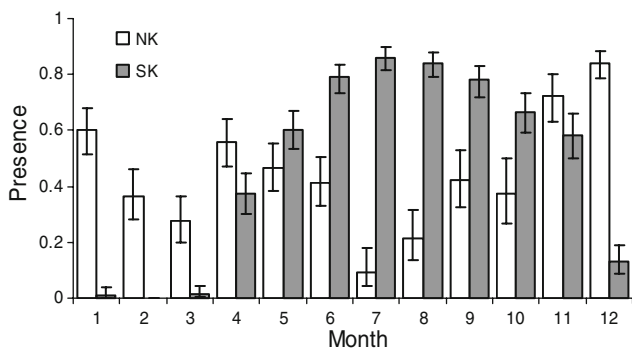
396 describe patterns, standardized for SEFF = 60. The GLM  
397 used 10,512 records, 1,974 indicating presence of tagged  
398 manta rays.

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

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

seasonal pattern appeared the reverse of that in the south, 415  
although animals were present in all months. The move- 416  
ments of some individuals suggested that mantas might 417  
move from south to north late in the year. In 2002 six man- 418  
tas (25, 2B, 31, 30, 37 and 38) left southern Komodo in 419  
November and December and arrived at northern Komodo 420  
from 1 to 59 days later; two additional manta rays (1B and 421  
34) left PK for north Komodo around the same time. These 422  
mantas remained at the northern sites for up to 50 days 423  
before leaving although one animal (38) was recorded 424  
infrequently through May. This pattern was not observed in 425  
2001 indicating the potential for inter-annual differences. 426

MOON and TIDES affected visits at both north and 427  
south Komodo but were strongest in the north (Fig. 7). For 428  
MOON at north Komodo, manta ray abundance was higher 429  
when currents are strongest during full and new moons. 430  
The GLM includes all visits over a 24-h period; an exami- 431  
nation of nighttime visits alone reveals a different pattern. 432  
Around the full moon in south Komodo the number of 433



**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

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

439 Visual surveys

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

447 Temperature

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

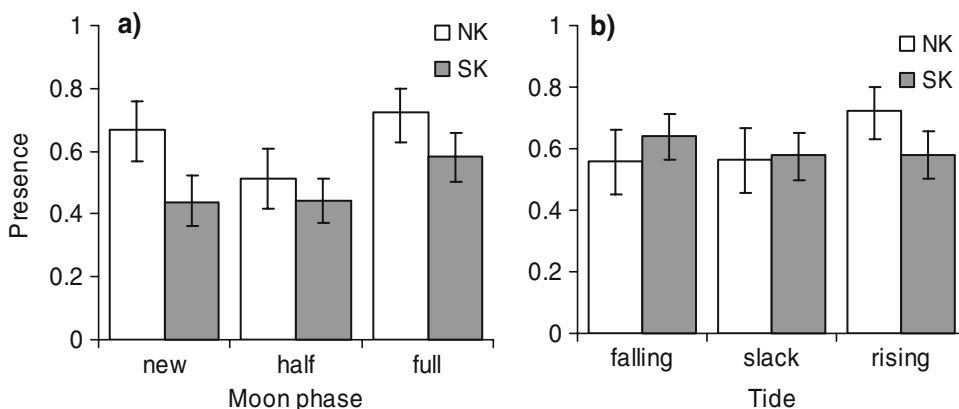
was less, from 23.9 to 29.4°C, and the lowest temperatures 454  
 were recorded in both the first and third quarter. The tem- 455  
 peratures that the mantas encountered varied with location 456  
 (Fig. 8). In the south 83% of hits occurred from 25 to 27°C 457  
 degrees (range 22 to 28°C). In the north 91% of hits 458  
 occurred from 26 to 28°C (range 24–29°C). 459

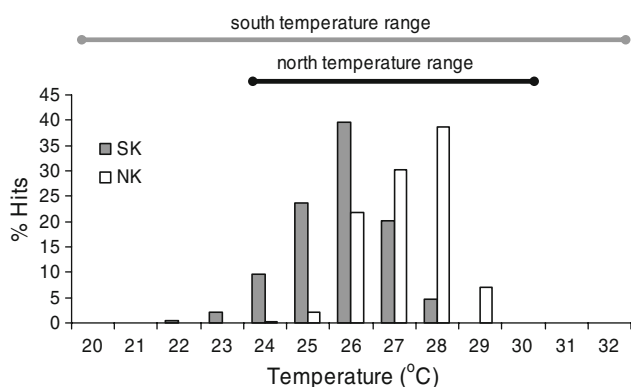
**Discussion and conclusions** 460

The acoustic array in the Komodo Marine Park, Indonesia 461  
 enabled near continuous monitoring of manta activity at the 462  
 sites throughout the park where mantas were most com- 463  
 monly observed. By collecting data over multiple years it 464  
 was possible to examine visitation patterns over various 465  
 time scales providing insights into the influence of time of 466  
 day, tides, lunar phase, and season. Here we present the 467  
 most comprehensive analysis of manta ray movements pub- 468  
 lished to date. 469

Acoustic arrays have proven a valuable tool in this and 470  
 other studies (Klimley and Halloway 1999; Sundstrom 471  
 et al. 2001; Voegeli et al. 2001; Heupel and Simpfendorfer 472  
 2005) and are ideal for species that return to predictable 473  
 locations. There are however limitations. First, it is not pos- 474  
 sible to determine where a tagged animal is when it is not 475  
 recorded or to distinguish between animals leaving the 476  
 study area and tag shedding. Second, the receiver range is 477  
 limited in near-shore habitats such as those frequented by 478  
 the mantas in the Komodo Marine Park where snapping 479  
 shrimp and bubbles associated with strong regional currents 480  
 limited the range of receivers (Voegeli et al. 2001). Recep- 481  
 tion range was particularly low in the south, nonetheless, 482  
 these receivers collected the most data. The high number of 483  
 detections at GF in particular may result from its location 484  
 between Komodo Island and a second, small island that 485  
 serve as a bottle neck. In addition, foraging mantas were 486  
 observed to repeat the same route, which would increase 487  
 the probability of detection. While estimates of manta pre- 488  
 sence are undoubtedly conservative at all sites, the agree- 489

**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

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

492 Manta rays in the park exhibited considerable site fidelity  
493 and demonstrated some individual preference for certain  
494 areas. Mantas returned to the same site almost daily for up to  
495 3 months and visited sporadically for up to 2 years. Mantas  
496 with the longest records (>300 days), appeared to prefer cer-  
497 tain areas, and were recorded most often near the tagging  
498 location. While most mantas with longer records visited at  
499 least two areas, movements between areas were somewhat  
500 limited. Thus, while there is clearly exchange between sites,  
501 there may be residency patterns within the park.

502 Site fidelity has been reported in manta rays in other  
503 locations as well. Through photo identification manta rays  
504 have been documented to regularly return to specific feed-  
505 ing or cleaning stations over long time periods. An individ-  
506 ual manta studied in the Yaeyama Islands, Japan for  
507 example, was observed in the area for 15 years (Homma  
508 et al. 1997). Manta rays observed off the big island of  
509 Hawaii have been re-sighted over similarly long periods  
510 (T. Clark, personal communication). In Bora Bora, where  
511 studies started more recently, the same mantas have been  
512 observed returning to the same cleaning stations for over  
513 2 years (S. Walker, personal communication). In many  
514 locations it is also common for individuals to be  
515 documented only once (S. Walker, personal communica-  
516 tion; K. Yano, personal communication) raising the ques-  
517 tion as to whether some mantas are transient. This could  
518 explain some of the shorter records observed in this study  
519 although it is impossible to determine whether mantas left  
520 the area or lost their tags.

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

2001), or take advantage of a predictable food source 527  
(Klimley and Anderson 1996; Sims and Quayle 1998; Hey- 528  
man et al. 2001; Domeier and Nasby 2006; Graham et al. 529  
2006). Based on our observations, the mantas returned to 530  
the sites in the park for both feeding and cleaning. It is also 531  
possible, however, that these areas are important for repro- 532  
duction (males and females are observed in the park) and/or 533  
provide important refuge from predators such as killer 534  
whales and sharks which are known to attack manta rays 535  
(Homma et al. 1997). 536

537 While many of the manta rays in the park exhibited con-  
538 siderable site fidelity, there are protracted periods when  
539 they are not recorded at any receiver. It is not clear whether  
540 the animals are just outside the range of the array or have  
541 left the park. Similarly, manta rays in Bora Bora are not  
542 recorded for months at a time before returning although  
543 with only Photo ID this pattern is difficult to confirm (S.  
544 Walker, personal communication). Additional work using  
545 pop-up satellite archival tags and/or active telemetry  
546 (Arnold and Dewar 2001; Voegeli et al. 2001) would help  
547 to resolve movements of mantas when they are not detected  
548 by the receivers. 549

#### Diurnal pattern 549

550 The examination of diurnal patterns shows the highest tag  
551 activity at all sites during daylight hours. The time of  
552 arrival and departure coincides with the approximate time  
553 of sunrise and sunset, which changes little at these latitudes.  
554 One possible explanation for the diurnal pattern is that the  
555 mantas are moving offshore during the night possibly to  
556 feed on the deep scattering layer (DSL) when it approaches  
557 the surface (Tont 1975; Robinson and Gomez-Gutierrez  
558 1998). This could help to explain the slight shift to later  
559 hours at the northern site, which is farther from deeper  
560 water. There is evidence for off-shore movement and feed-  
561 ing on the DSL from other areas. Manta rays that were  
562 actively tracked off Japan moved offshore at night and then  
563 returned the following day (K. Yano, personal communica-  
564 tion). While this may occur in other regions as well no pub-  
565 lished accounts are available. Another member of the same  
566 family (*Mobula japonica*) feeds on crustaceans primarily at  
567 night when they come to the surface (D. A. Croll et al.,  
568 unpublished data). A number of other elasmobranchs  
569 including scalloped hammerheads, blacktip reef sharks and  
570 gray reef sharks are also observed to aggregate in near  
571 shore waters during the day and then disperse offshore at  
572 night (Klimley and Nelson 1984; Klimley et al. 1988; Eco-  
573 nomakis and Lobel 1998; Heupel and Simpfendorfer 2005).  
574 Other possible explanations for the diurnal pattern are that  
575 different sites are preferred at night or that activity is lower,  
576 reducing the potential of detecting animals. Clearly more  
577 work is needed to explain the diurnal pattern.

## 578 Foraging and tidal currents

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

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

609 Consistent with the apparent role of tidal currents in con-  
610 centrating resources, tidal phase and intensity impacted vis-  
611 its. More visits were documented at in north Komodo at the  
612 rising tide (when currents move from the south to the north)  
613 when the moon was new or full and tidal flux is greatest.  
614 Tidal currents in this area shift 180 degrees with each tidal  
615 change and can be up to 5 knots. In contrast, the influence  
616 of tidal current and phase was less pronounced in south  
617 Komodo. In this region the variation in strength and direc-  
618 tion of tidal currents is lower than in the north and therefore  
619 one might expect a less pronounced effect of lunar and tidal  
620 phase on visitation patterns. Furthermore, the southern part  
621 of the island has a more complex geography and bathyme-  
622 try, which may result in a more constant food supply that is  
623 less dependent on tidal strength or specific direction.

624 The concentration of prey associated with tidal currents  
625 provides important forage for animals from diverse taxo-  
626 nomic groups and impacts the temporal and spatial patterns  
627 in feeding. In a comparison of marine birds with different  
628 prey preferences, the plankton feeder, Ancient Murrelets,  
629 were most active when tidal flow was the greatest (Holm


and Burger 2002). Dolphin foraging was most often 630  
observed in association with tidal fronts in a narrow estua- 631  
rine channel off Scotland (Mendes et al. 2002). The two 632  
filter feeding sharks also forage in tidal currents. Basking 633  
sharks feed in near-shore regions where strong tidal flows 634  
aggregate zooplankton, often near islands or headlands 635  
(Sims and Quayle 1998). Whale sharks position themselves 636  
to take advantage of tidal currents transporting material out 637  
of the lagoon on Ningaloo reef Australia (Wilson et al. 638  
2001). Similar to these other species, mantas appear to take 639  
advantage of the increase in prey density associated with 640  
the strong tidal currents around Komodo Island. 641

642 A second factor that varies along with tidal intensity is  
643 lunar illumination. The increase in nighttime visits during  
644 the full moon but not the new moon in south Komodo sug-  
645 gests that high light levels and not tidal intensity are associ-  
646 ated with the increase in visitation. This shift could be  
647 associated with an increase in foraging near-shore at higher  
648 light levels or a decrease in offshore foraging opportunities.  
649 During the full moon the DSL organisms remain deeper in  
650 the water column (Blaxter 1974) and overall predation on  
651 zooplankton has been shown to decrease as a result (Her-  
652 nández-León et al. 2001).

## Season 653

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

662 While it is difficult to identify the driving force behind  
663 the seasonal change in manta abundance, it is likely linked  
664 to seasonal environmental patterns. The shift in abundance  
665 corresponds to the monsoonal shift in the Indo-Pacific that  
666 influences both temperature and productivity. During the  
667 first quarter when no mantas were observed in south Kom-  
668 odo the Indian Equatorial Counter Current and north mon-  
669 soon are the driving processes (Tomczak and Godfrey  
670 1994). At this time there is a reduction in the net flow from  
671 the Pacific to the Indian Ocean that results in a drop in  
672 productivity and an average 3°C increase in temperature  
673 (Hahude and Gordon 1996). It was during this quarter that  
674 temperatures here exceeded 30°C, which is thought to be  
675 the upper thermal limit for manta rays (no mantas were  
676 recorded above 29°C in this study). Over the same period in  
677 north Komodo, waters are cool with poor visibility. From  
678 May to September when visitation in south Komodo is  
679 high, the South Equatorial Current and southeast monsoon  
680 are both fully developed which maximizes westward flow

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681 (Tomczak and Godfrey 1994) and results in a drop in tem- 732  
 682 perature and large increase in productivity (Hahude and 733  
 683 Gordon 1996). During this phase, the waters in the south 734  
 684 are cool and murky (visibility ca. 5 m) and rich in plankton. 735  
 685 Temperatures at in the north remained below 30°C and 736  
 686 mantas were seen here through out the year. 737

687 As mentioned above, seasonal shifts in manta distribu- 738  
 688 tions have been documented in a number of places and are 739  
 689 likely associated with temperature. In locations such as 740  
 690 New Zealand mantas are observed primarily in the austral 741  
 691 summer (Duffy and Abbott 2003). In the Gulf of California 742  
 692 mantas are observed in the Boreal summer (P. Ahjua, per- 743  
 693 sonal communication). In the Maldives seasonal shifts are 744  
 694 thought to be associated with the local monsoons, when 745  
 695 current directions reverse and mantas move from one side 746  
 696 of the Maldives to the other (Anderson 1996). In the Kom- 747  
 697 odo Marine Park the monsoons also impacted visitations 748  
 698 patterns although seasonality was site dependent. This sug- 749  
 699 gests that subtle shifts in distributions may be associated 750  
 700 with seasonal patterns and that in a location as diverse as 751  
 701 Indonesia it may not be necessary to move very far to find 752  
 702 suitable habitat. 753

### 703 Management implications

704 The predictability of the spatial distribution of manta rays 754  
 705 has important consequences for conservation and tourism 755  
 706 management. The information on patterns of occurrence 756  
 707 will assist dive operators in successfully planning manta 757  
 708 dives, maximizing the potential of this ecotourism resource. 758  
 709 For management and conservation, the high site fidelity and 759  
 710 ability to predict spatial patterns has two implications. First, 760  
 711 there is the potential for localized depletion or extirpation 761  
 712 once fishers start exploiting an aggregation site. On the 762  
 713 other hand, site-specific protection or marine protected 763  
 714 areas based around aggregations sites should have a direct 764  
 715 positive effect on local abundance. 765

716 In Komodo specifically, one of the key questions was 766  
 717 whether the boundaries of the park serve to protect the local 767  
 718 mantas from regional fisheries. Clearly, the park encom- 768  
 719 passes a number of sites that are important for manta rays, 769  
 720 and therefore the park provides some protection at least 770  
 721 during the day. Of concern however, is where the mantas 771  
 722 move when they are not within in the range of the receiver. 772  
 723 Tagged mantas were not detected for long periods, during 773  
 724 which they may have left the park. One of the greatest 774  
 725 potential threats are the fisheries in Lamalera and Lama- 775  
 726 kera, which are approximately 400 km from the park. 776  
 727 Manta ray migrations as far as 350 km have been docu- 777  
 728 mented (Homma et al. 1997) and longer migrations are 778  
 729 likely possible raising the possibility that mantas could 779  
 730 move into this region. In Lamakera it is estimated that 780  
 731 approximately 1,000 mantas are taken in the fishing season 781


732 from May through October (Dewar 2002). Mantas are also 733  
 734 taken in other locations throughout Indonesia although at 735  
 736 lower levels. Additional information on the larger-scale 737  
 738 movements of mantas and the pattern of fisheries is 739  
 739 required to better determine the management requirements. 740  
 740 As indicated above, mantas have the potential to be highly 741  
 741 susceptible to over fishing and vigilance is warranted. 742

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 750 and not the National Oceanographic and Atmospheric Administration. 750  
 751 Experiments were conducted in accordance with current laws in 751  
 752 Indonesia. 752

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