Deep-water feeding and behavioral plasticity in *Manta birostris* revealed by archival tags and submersible observations

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26 **Abstract**

27 Foraging drives many fundamental aspects of ecology, and an understanding of foraging

28 behavior aids in the conservation of threatened species by identifying critical habitats and

29 spatial patterns relevant to management. The world's largest ray, the oceanic manta

30 (*Manta birostris*) is poorly studied and threatened globally by targeted fisheries and

31 incidental capture. Very little information is available on the natural history, ecology and

32 behavior of the species, complicating management efforts. This study provides the first

33 data on the diving behavior of the species based on data returned from six tagged

34 individuals, and an opportunistic observation from a submersible of a manta foraging at

35 depth. Pop-off archival satellite tags deployed on mantas at the Revillagigedo

36 Archipelago, Mexico recorded seasonal shifts in diving behavior, likely related to

37 changes in the location and availability of zooplankton prey. Across seasons, mantas

38 spent a large proportion of their time centered around the upper limit of the thermocline,

39 where zooplankton often aggregate. Tag data reveal a gradual activity shift from surface

40 waters to 100–150 m across the tagging period, possibly indicating a change in foraging

41 behavior from targeting surface-associated zooplankton to vertical migrators. The depth

42 ranges accessed by mantas in this study carry variable bycatch risks from different

43 fishing gear types. Consequently, region-specific data on diving behavior can help inform

44 local management strategies that reduce or mitigate bycatch of this vulnerable species.

45 *Keywords*: *Manta birostris*; Mobulidae; Foraging ecology; Deep scattering layer; Diving

46 behavior

47

48

1. Introduction

Foraging behavior is a fundamentally important aspect of animal ecology. How, when and where species feed drives competition (Menge, 1972), reproductive success (Suryan et al., 2000), spatial ecology and distribution (Friedlaender et al., 2006), and can also influence evolutionary patterns such as speciation through niche separation (Pastene et al., 2007; Poortvliet et al., 2015). Understanding the foraging ecology of threatened species will aid in their conservation and management as feeding behavior often determines critical habitat use and spatial patterns that are important in preventing or mitigating targeted or incidental capture and other human impacts (James et al., 2006).

The oceanic manta ray (*Manta birostris*), distributed circumglobally in tropical and subtropical warm seas, is the largest and most highly derived member of the devil ray family (Mobulidae) (Compagno, 1999; McEachran and Aschliman, 2004). Compared to its smaller congener, the reef manta ray (*Manta alfredi*), it inhabits colder, pelagic, upwelled regions in association with seamounts and oceanic islands, and is the least well-known member of the genus (Marshall et al., 2009; Kashiwagi et al., 2011). Oceanic manta rays, and in some areas reef mantas, are threatened globally by fisheries. The species is landed in targeted fisheries in countries such as Indonesia, Philippines, Mozambique, Peru, and previously Mexico; taken as non-discarded bycatch in Sri Lanka, India, and a variety of other small-scale artisanal fisheries; and caught frequently but discarded in purse seine tuna fisheries globally, with a high presumed post-release mortality rate (Croll et al., 2015). While reliable fisheries landing data or population trends are unavailable, the demographic characteristics of mantas make them highly susceptible to fisheries impacts (Dulvy et al., 2014). Large-scale studies suggest family-

72 wide declines for mobulid rays globally (Ward-Paige et al., 2013), and several studies

73 indicate severe declines in local manta populations based on catch rates or sighting

74 frequency (Lewis et al., 2015; White et al., 2015). Improving our understanding of the

75 ecology and critical habitat use of manta rays will help facilitate effective management.

76 Major knowledge gaps exist in our understanding of population connectivity and stock

77 structure in oceanic manta rays, which impacts the scale at which management action is

78 implemented; and the habitat use and diving behavior of the species, which may

79 determine individuals' susceptibility to incidental capture in various fishing methods such

80 as gill nets and purse seines.

81 Most studies of manta rays have focused on descriptive morphology and natural history

82 observations in near-surface environments. As a result of the recent division of the genus

83 into two distinct species (Marshall et al., 2009), many previous research findings

84 attributed to oceanic mantas are now correctly recognized as describing aspects of the

85 biology of the reef manta ray. As such, fundamental biological and ecological

86 information for oceanic mantas is rare. Graham et al. (2012) reported on the horizontal

87 movements of tagged oceanic mantas in the Gulf of Mexico, although tagged individuals

88 may have belonged to a third, undescribed Caribbean species (*Manta* sp. cf. *birostris*;

89 Marshall et al., 2009). While many planktivores are highly mobile and often undertake

90 long-distance migrations related to foraging (Corkeron and Connor, 1999; Skomal et al.,

91 2009), neither manta species has been shown to follow this trend, with recent data

92 suggesting patterns of residency in both species (Deakos et al., 2011; Braun et al., 2014;

93 Stewart et al., 2016). However, there are several recorded long-distance movements in

94 both species of manta of over 400 km, which may be relevant to aspects of the species'

95   life history or critical habitat use (Rubin et al., 2008; Germanov and Marshall, 2014;

96   Hearn et al., 2014).

97   A more robust body of literature is available for the reef manta ray than the oceanic

98   manta, and the diving and foraging patterns of other mobulids may provide insight into

99   the most likely strategies exhibited by oceanic manta rays. Feeding on near-surface

100   aggregations of zooplankton is commonly observed in a variety of mobulids

101   (Notarbartolo di Sciara, 1988; Jaine et al., 2012; Paig-Tran et al., 2013). Some species

102   also presumably forage in deep-water habitats, including prolific dives by *Mobula*

103   *tarapacana* to access dense aggregations of bathypelagic fishes (Thorrold et al., 2014)

104   and movements between shallow reef habitats and deep, offshore pelagic habitats by

105   *Manta alfredi* (Braun et al., 2014). Additional studies suggest that deep nighttime dives

106   made by reef manta rays may provide access to vertically migrating zooplankton entering

107   the epipelagic zone (Anderson et al., 2011; Braun et al., 2014).

108   Here we report on the diving and foraging behavior of oceanic manta rays at the

109   Revillagigedo Archipelago, a remote, pelagic archipelago in Pacific Mexico. We

110   observed a coupling of surface and deep-water feeding areas and seasonal variation in

111   diving behavior related to variation in thermocline depth. In addition we provide video

112   evidence of daytime foraging at depth, in dense aggregations of zooplankton in close

113   proximity to the sea floor. These data provide the first insights into diving patterns and

114   habitat use of oceanic manta rays in pelagic environments.

115

116   **2. Materials and methods**

117   *2.1. Archival tag deployments*

118 We deployed miniPAT tags (Wildlife Computers, Redmond, WA, USA) on oceanic

119 manta rays at San Benedicto Island (The Boiler) on April 7th, 2014 (female: $n = 3$; male:

120 $n = 1$) and at Socorro Island (Cabo Pearce) on April 8th, 2014 (male: $n = 1$). We

121 programmed miniPAT tags to detach and begin transmitting archived data after 180 days.

122 Previously, we had deployed PAT Mk-10 tags (Wildlife Computers) on oceanic mantas

123 at Roca Partida and San Benedicto (The Boiler) on November 12th and 13th, 2003,

124 respectively ($n = 2$, sexes unknown). We programmed those Mk-10 tags to detach and

125 begin transmitting after 60 and 150 days. Both tag models collect data on temperature,

126 depth and light level at 5-second (miniPAT) and 5-minute (Mk-10) intervals, and

127 subsequently transmit temperature and depth data histograms binned into preset intervals,

128 as well as partial time-series data at coarse intervals via satellite after the tags detach. We

129 programmed miniPATs to bin depth and temperature data in 6-hour intervals starting at

130 midnight in Baja California Sur (GMT-6). We considered the combined 18:00–00:00 and

131 00:00–06:00 bins to represent nighttime hours, and the combined 06:00–12:00 and

132 12:00–18:00 bins to represent daytime hours. We programmed Mk-10 tags to bin data in

133 12-hour intervals starting at 00:00 and 12:00. We used PERMANOVAs (on 2014 data

134 only; 'adonis' function in the R package 'vegan') to compare nighttime and daytime

135 diving behavior between months. We considered the effect of month, night/day, and the

136 interaction of these two terms on both depth and temperature distributions using the

137 equation:

138   Response variable ~ month + time of day + month:time of day

139   where the response variable was either depth or temperature. We ordinated the binned

140   depth and temperature data for plotting purposes using a non-parametric

141   multidimensional scaling ('metaMDS' function in the R package 'vegan').

142   MiniPAT tags also collect, and report via satellite, data on the temperature and depth of

143   the mixed layer. Archived temperature and depth samples are used to keep a running

144   estimate of the mixed layer temperature. Subsequent samples are considered to be taken

145   from within the mixed layer if the temperature reading is $+/- 0.5$ °C from the current

146   estimate, and the depth is less than 200 m. The tag will automatically update its estimate

147   of the mixed layer temperature if it encounters the surface, or if it detects water that is

148   well mixed within 50 m of the surface. The surface is defined as any depth reading

149   between 0 and 5 m. The water is considered well mixed if a change of depth of greater

150   than 15 m is observed with a corresponding change in temperature of less than 0.05 °C

151   (Wildlife Computers, pers. comm.). For example, if the tag records a sea surface

152   temperature (SST) of 18 °C, this is initially set as the mixed layer temperature. If the tag

153   then encounters a water temperature of 16 °C at 5 m depth, which extends to 20 m depth

154   or greater, the mixed layer temperature is reset to 16 °C. The transmitted data include the

155   range of SST readings observed, the range of the estimated mixed layer temperatures, the

156   time spent within mixed layers, and the deepest depth recorded within the layer, over the

157   6-hour period. We only considered mixed layer depth records where the maximum diving

158   depth of the tag exceeded the mixed layer depth for the same 6-hour period, and we

159   interpreted the base of the mixed layer as the top of the thermocline. We sorted mixed

160   layer depth records into bins with the same bounds as the diving histograms in order to

161   directly compare histograms of the two datasets. We converted frequency histograms of

162   mixed layer depths into percentages and overlaid them on diving histograms at a 0.1x

163   scale to create an inset (see Fig. 1). Not every 6-hour diving histogram period had a

164   corresponding mixed layer depth due to gaps in satellite-transmitted data. We selected all

165   of the diving histogram data that had a mixed layer depth from the same time period and

166   the same tag, and determined the percentage of time spent in the depth bin containing the

167   base of the mixed layer. We conducted all analyses using R version 3.2.3 (R Core Team,

168   2015). We reported horizontal movements recorded by miniPAT tags in (Stewart et al.,

169   2016).

170   Tagging methods were carried out in accordance with protocol S12116 approved by the

171   University of California, San Diego Institutional Animal Care and Use Committee.

172

173   *2.2. Submersible observations*

174   During the *Televisa–Por el Planeta* expedition, project scientists made submersible dives

175   around the islands of Roca Partida, San Benedicto and Socorro from March 6 to March

176   30, 2014 to survey the benthic assemblages of the Revillagigedo Archipelago. Over the

177   25 days, 34 submersible dives were conducted at Socorro Island (Bahia UNAM, $n = 1$;

178   Cabo Pearce, $n = 11$; and Punta Tosca, $n = 10$), San Benedicto Island (The Canyon, $n =$

179   10), and Roca Partida ($n = 2$). During each dive, researchers recorded high-definition

180   video to facilitate benthic and pelagic species identification and analysis of bottom fauna

181   and substrate composition.

182

183   **3. Results**

184   *3.1. Archival tagging*

185   Both of the PAT Mk-10 tags deployed in 2003, and four of the five miniPAT tags

186   deployed in 2014 (female: $n = 2$; male: $n = 2$) reported and transmitted data. The PAT

187   Mk-10 tags both detached after 11 days, while the four miniPAT tags detached after 181,

188   184, 186 and 189 days. The distribution of depths accessed by animals tagged in 2014

189   varied across months, with a general trend of a greater proportion of time spent deeper as

190   the tagging period progressed from April to September (Fig. 1A). PAT Mk-10

191   deployments are summarized in Fig. 1B. Both depth and temperature utilization were

192   significantly different between night and day and between months, and the interaction of

193   those effects was also statistically significant ($p < 0.001$ in all cases). After the depth and

194   temperature data are ordinated, the months of April–June and August–September form

195   distinctive clusters, with no overlap between those groups on the ordination axis 1

196   (NMDS1; supplementary Figs. S1 and S2 in the online Appendix). This multidimensional

197   separation is highlighted by the differences in diving behavior between the months of

198   April–June and August–September, with April–June showing a greater proportion of time

199   spent at the surface, and August-September showing a greater proportion of time spent in

200   deeper water (Fig. 1A). July appears to be an intermediate month, overlapping with both

201   the April–June cluster and August–September cluster in NMDS1 for diving data

202   (supplementary Fig. S1), but clustering with August–September on the temperature data

203   ordination (supplementary Fig. S2). For both depth and temperature data, the ordinated

204   centroids of night and day bins are well separated both within months and for all months

205   combined (supplementary Figs. S1 and S2).

206   There were 741 out of 1,367 diving histograms that had an associated mixed layer depth

207   record from the same time, date and tag. Tagged mantas spent, on average, 11.33–21.64

208   percent of their time in the depth bins containing the base of the mixed layer (also

209   interpreted as the start of the thermocline) during daytime hours, and 9.65–21.24 percent

210   during nighttime hours per month. These data are reported by month in Table 1.

211   The tag deployments in November 2003 summarized diving data into very different

212   histogram bins than the 2014 tag deployments and recorded data during 12-hour periods

213   that covered daytime and nighttime hours approximately evenly (midnight to noon and

214   noon to midnight). The November 2003 diving data indicate that mantas spent on average

215   over 90% of their time in the top 100 m of the water column. Furthermore, the proportion

216   of time spent in the 0–10 m, 10–50 m, and 50–100 m bins in 2003 are more similar to the

217   months of April–June than to July–September 2014, although we emphasize that these

218   data sources are not directly comparable due to the differences in temporal and depth

219   binning.

220

221   *3.2. Submersible observations*

222   On March 29th, 2014 at 11:22 AM, M. Hoyos recorded an oceanic manta ray foraging on

223   a thick layer of zooplankton at 130–140 m depth (Fig. 2 and supplementary Video 1 in

224   the online Appendix) off of Cabo Pearce (Socorro Island) (Fig. 3). The manta had its

225   cephalic fins fully extended, its mouth open, and its oral cavity expanded. Furthermore, it

226   was making continuous somersaults through the zooplankton layer at depth, consistent

227   with feeding strategies observed in both members of the *Manta* genus (Couturier et al.,

228   2012). We identified mysid shrimp (Mysidae), euphausiids (Euphausiacea), and copepods

229   (Calanoida) in the zooplankton layer, as well as a variety of other unidentifiable

230   zooplanktors. We note that visual identification was challenging from the video,

231 especially in differentiating between mysids and euphausiids. The zooplankton layer was

232 approximately 10 m above the sea floor (supplementary Video 2 in the online Appendix).

233

234 **4. Discussion**

235 Based on our results, oceanic manta rays demonstrate a high degree of plasticity in the

236 depths they access throughout the year, and we posit that this is driven primarily by shifts

237 in prey location and foraging behaviors. The most consistent pattern across the six

238 months of diving data in 2014 was the close relationship between mixed layer depths and

239 the depth ranges most frequently accessed by mantas. As the tag-recorded mixed layer

240 depths shift from month to month, the most commonly accessed depths closely match

241 these changes (Fig. 1). Zooplankton density is often greatest at the thermocline, which

242 begins at the base of the mixed layer (Sameoto, 1984, 1986). This aggregation of

243 zooplankton within the thermocline can be made up of zooplankton that remains within

244 the thermocline day and night, or vertical migrators that enter the thermocline only at

245 night (Sameoto, 1986). We speculate that oceanic mantas are foraging on zooplankton

246 within the thermocline throughout the year, both during the day and night, and may be

247 using the thermocline as a cue to identify regions of high zooplankton density where

248 foraging efficiency can be maximized (Pelletier et al., 2012).

249 In April and May, nighttime depth utilization closely resembled daytime behavior, while

250 from June through September tagged individuals accessed deeper waters at night. While

251 studies reporting on the seasonal density and distribution of zooplankton in this region

252 are sparse in the literature, the available data (Blackburn et al., 1970) indicate that the

253 input of vertical migrators into the top 200 m of the water column is minimal in April and

254   May, but increases from June to September and throughout the rest of the year. This

255   could explain the shift to deeper nighttime diving from June onwards in our tag data, as

256   mantas increasingly access portions of the deep scattering layer at its shallow extreme.

257   Despite the differences in histogram bins between 2003 and 2014 tag deployments, based

258   on the similarity of the November 2003 diving data to those of the months of April

259   through June in 2014, it is possible that the deeper diving behavior of mantas is restricted

260   to the summer months, while individuals spend more time in near-surface waters from

261   November through June. However, this inference carries the obvious limitation that these

262   two sets of tags were deployed more than ten years apart, and inter-annual variability in

263   local and regional oceanography may be responsible for the change in depth distribution

264   from September (2014) to November (2003) rather than seasonal patterns in diving

265   behavior.

266   During April and May, tagged mantas spent over 15% of their time on average (night and

267   day combined) in the top meter of the water column. This time spent immediately at the

268   surface could be attributed to either surface feeding (Notarbartolo di Sciara, 1988; Paig-

269   Tran et al., 2013) or basking behavior (Notarbartolo di Sciara, 1987; Canese et al., 2011;

270   Thorrold et al., 2014) both frequently observed in mobulids. *M. tarapacana* accessing

271   depths of up to 1,800 m and temperatures lower than 5 °C frequently basked for extended

272   periods at the surface before and after deep dives, presumably to recover body

273   temperatures after long periods in cold water (Thorrold et al., 2014). Our diving data, on

274   the other hand, show that tagged mantas spent more time at the surface in months with

275   less deep diving behavior, and less time at the surface in months with more deep diving

276   behavior. If mantas were basking at the surface after exposure to colder water

277 temperatures, we would expect basking and deep dives to occur concurrently. Further,

278 mantas spent a large portion of their time at the surface in these months both during the

279 night and day, whereas *M. tarapacana* only exhibited basking behavior during daytime

280 hours. It is possible that oceanic mantas in this study did not require active

281 thermoregulation in the form of basking because they rarely accessed waters colder than

282 15 °C. Instead, we posit that the surface time represents foraging behavior on surface

283 zooplankton, which is often observed at the Revillagigedo Archipelago (Rubin et al.,

284 unpublished data). The shift throughout the tagging period away from surface activity

285 and towards deeper diving suggests that mantas may have switched from surface feeding

286 to foraging on the deep scattering layer as the nighttime influx of vertical migrators

287 became more regular or the density of zooplankton increased. If our interpretations of the

288 observed diving behavior are correct, the mantas tagged in this study exhibited three

289 distinct foraging patterns that shifted across seasons: foraging (i) at the surface; (ii) in the

290 thermocline; and (iii) on vertical migrators at depths over 100 m. This demonstrates a

291 high degree of behavioral plasticity to account for the shifts in location and/or abundance

292 of prey resources.

293 The major limitation of the present study and all other attempts to infer behavior from

294 tag-recorded diving data is the lack of direct behavioral observations. Without direct

295 observations, we are limited to interpreting diving data in relation to covariates that we

296 expect to be meaningful, such as zooplankton location and density. These interpretations

297 are further hindered by the paucity of zooplankton time-series data in the region and lack

298 of zooplankton data collected during the tagging period, both of which are unsurprising

299 given the remoteness of the study site and difficulty in conducting fieldwork there. Our

300 observations could be supported by future research examining the isotopic signatures of

301 putative sources (e.g. surface zooplankton, deep scattering layer zooplankton, etc.) and

302 the relative contribution of these sources to manta tissue isotopic signatures at the islands

303 (e.g. Couturier et al., 2013; McCauley et al., 2014).

304 Given the absence of direct observations during the tagging period, the opportunistic

305 submersible observation described here is of significant value. While oceanic manta rays,

306 and a variety of other mobulid rays, have been observed feeding on zooplankton in

307 surface and near-surface waters (Notarbartolo di Sciara, 1988; Paig-Tran et al., 2013) and

308 presumably recorded feeding in bathypelagic zones (Thorrold et al., 2014), this is the first

309 direct observation of a mobulid ray foraging at depth. During the submersible

310 observation, the manta ray made continuous barrel rolls, apparently circling repeatedly

311 through the densest area of zooplankton. The morphological adaptations of mobulid gill

312 plates that facilitate cross-flow filtration allow them to retain a variety of particle sizes,

313 even those smaller than the filter pores (Paig-Tran et al., 2013). This mechanism may

314 enable mantas to efficiently feed on mixed zooplankton assemblages such as the one we

315 observed, where prey items range in size from larger mysids and euphausiids to much

316 smaller calanoid copepods. While barrel-rolling behavior is observed frequently in near-

317 surface waters, our observation confirms that this foraging strategy is also exhibited at

318 depth. Diving to depths of 100–150 m, which would include the observed manta feeding

319 at 130–140 m, made up on average only 5–10% of daytime water column use during the

320 tagging period. This suggests that either (i) the observed behavior represented

321 opportunistic or infrequent foraging; or (ii) this type of behavior is more frequent in

322 March and earlier months when no tag data were collected. We do not believe this was an

323 observation of foraging on zooplankton within the thermocline, as the mixed layer depth

324 rarely exceeded 80 m and never 100 m. Thus, this represents a fourth feeding strategy:

325 daytime foraging on epipelagic scattering layers or aggregations of zooplankton.

326 Tag-recorded diving data, an opportunistic observation from a submersible, and personal

327 observations by the authors of mantas surface-feeding suggest that manta rays are

328 accessing prey resources in a variety of different habitats at the islands by employing

329 several foraging strategies. The horizontal movement data from tags deployed in 2014,

330 along with stable isotope and genetic analyses, indicate that oceanic manta rays at the

331 Revillagigedo Archipelago exhibit philopatry and remain resident to a restricted

332 geographic region surrounding the archipelago (Stewart et al., 2016). This is in contrast

333 to other large marine vertebrates, including planktivores, that inhabit similar oceanic

334 habitats and often undertake extensive migrations between breeding and foraging grounds

335 (Corkeron and Connor, 1999; Hueter et al., 2013; Thorrold et al., 2014). In the Tropical

336 Eastern Pacific near the Revillagigedo Archipelago, the standing stock of zooplankton in

337 the upper 200 m remains largely consistent throughout the year (Blackburn et al., 1970),

338 potentially providing a year-round food source and contributing to the observed

339 philopatry by making long-distance movements to access prey unnecessary. However,

340 accessing this year-round food supply may require frequent changes in diving behavior

341 and habitat use in order to target resources that shift seasonally in vertical distribution.

342 These shifts in diving behavior and vertical habitat use may also be related to horizontal,

343 onshore–offshore movements across the study period. However, due to the substantial

344 uncertainty in light-based geolocation from this type of archival tag (in many cases

345 estimated locations have an error radius of 50–100 km), it was not possible for us to

346   separate nearshore and pelagic diving patterns. However, acoustic tagging data from the

347   islands (Rubin, unpublished data) demonstrate that mantas generally leave the near-shore

348   habitats during late afternoon and nighttime hours, presumably entering more offshore,

349   pelagic habitats. This may explain the differences between daytime and nighttime diving

350   patterns in some months, as mantas may need to move into deeper waters to access

351   vertically migrating zooplankton at night. Recent improvements to tagging technology,

352   such as the addition of Fastloc GPS that has an accuracy on the scale of tens of meters

353   (Dujon et al., 2014), could help determine the horizontal component of seasonal shifts in

354   diving behavior in future studies.

355   Oceanic manta rays are threatened by both targeted fisheries and incidental bycatch, and

356   the conservative reproductive strategy of the species makes populations extremely

357   susceptible to fisheries-induced declines (Dulvy et al., 2014; White et al., 2015).

358   Understanding spatial and temporal changes in habitat use can help prevent bycatch of

359   the species, as the various fishing gears and strategies that incidentally capture mantas

360   target different depth ranges. For example, the population of mantas studied here would

361   be far more susceptible to surface-set gill nets, one of the primary gear types associated

362   with manta and mobula bycatch (Couturier et al., 2012), between April and June than

363   between July and September. Similarly, bycatch of mantas in midwater trawls from 50 to

364   150 m, observed in the Peruvian Merluza fishery (S. Rojas Perea, pers. comm.), would be

365   much more likely to occur during months in which mantas are more frequently accessing

366   those depths. Consequently, region-specific data on diving behavior can help inform local

367   management strategies designed to reduce or mitigate bycatch of this vulnerable species.

368   At the Revillagigedo Archipelago, the high density of recreational dive boats present

369   from November through June may present additional threats to the manta population.

370   Many dive operators use down-lines to provide easy descents to dive sites, and mantas

371   occasionally become entangled in these lines as well as lines connected to divers' surface

372   marker buoys, causing severe injuries (E.M. Hoyos-Padilla, pers. obs.). Our data indicate

373   that mantas spend a large proportion of their time near the surface, where they are likely

374   most susceptible to entanglement in these down lines, from April to June, and perhaps

375   starting again in November. Personal observations by the authors further indicate that

376   mantas are present in near-surface waters from November through June. Additional

377   tagging data across the entire year would help determine the relative threat of

378   entanglements to mantas in different seasons.

379   Marine science is increasingly dominated by data collected by remote instrumentation,

380   from global-level environmental data to individual-level movement data such as those

381   presented here. As these data become removed from direct observations, it can be

382   challenging to interpret them in an ecological or behavioral context. Tagging data in

383   marine systems, in particular, have the limitation of showing us where an animal goes,

384   but not what it is doing. Direct observations of behavior that is unusual or that takes place

385   in hard-to-reach environments aid in the interpretation of remotely-sensed data and allow

386   us to, in effect, ground-truth our assumptions about how marine species are using various

387   habitats. Improvements and breakthroughs in technology such as accelerometers and

388   photographic and video imaging built into animal-mounted tags can improve our

389   understanding of marine ecology and individual behaviors. In the case of oceanic manta

390   rays, future work employing both novel and existing technology, such as short-

391   deployment animal-mounted cameras, will provide a better understanding of habitat use,

392   foraging and natural history of the species.

393

394   **Acknowledgements**

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References

Anderson, R.C., Adam, M.S., Goes, J.I., 2011. From monsoons to mantas: seasonal distribution of *Manta alfredi* in the Maldives. Fish. Oceanogr. 20, 104–113.

Blackburn, M., Laurs, R.M., Owen, R.W., Zeiyzschel, B., 1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. Mar. Biol. 7, 14–31.

Braun, C.D., Skomal, G.B., Thorrold, S.R., Berumen, M.L., 2014. Diving behavior of the reef manta ray links coral reefs with adjacent deep pelagic habitats. PLoS One 9, e88170.

Canese, S., Cardinali, A., Romeo, T., Giusti, M., Salvati, E., Angiolillo, M., Greco, S., 2011. Diving behavior of the giant devil ray in the Mediterranean Sea. Endanger. Species Res. 14, 171–176.

Compagno, L., 1999. Systematics and body form. In: Hamlett, W.C. (Ed.), Sharks, Skates and Rays: The Biology of Elasmobranch Fishes. Johns Hopkins University Press, Baltimore, pp. 1–42.

Corkeron, P.J., Connor, R.C., 1999. Why do baleen whales migrate? Mar. Mammal Sci. 15, 1228–1245.

Couturier, L.I.E., Marshall, A.D., Jaine, F.R.A., Kashiwagi, T., Pierce, S.J., Townsend, K.A., Weeks, S.J., Bennett, M.B., Richardson, A.J., 2012. Biology, ecology and conservation of the Mobulidae. J. Fish Biol. 80, 1075–1119.

Couturier, L.I.E., Rohner, C.A., Richardson, A.J., Marshall, A.D., Jaine, F.R.A., Bennett, M.B., Townsend, K.A., Weeks, S.J., Nichols, P.D., 2013. Stable isotope and signature fatty acid analyses suggest reef manta rays feed on demersal zooplankton. PLoS One 8, e77152.

Croll, D.A., Dewar, H., Dulvy, N.K., Fernando, D., Francis, M.P., Galvan-Magana, F., Hall, M., Heinrichs, S., Marshall, A., McCauley, D., Newton, K.M., Notarbartolo-Di-Sciara, G., O'Malley, M., O'Sullivan, J., Poortvliet, M., Roman, M., Stevens, G., Tershy, B.R., White, W.T., 2015. Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. Aquat. Conserv.: Mar. Freshw. Ecosyst. doi:10.1002/aqc.2591.

Deakos, M.H., Baker, J.D., Bejder, L., 2011. Characteristics of a manta ray *Manta alfredi* population off Maui, Hawaii, and implications for management. Mar. Ecol. Prog. Ser. 429, 245–260.

Dujon, A.M., Lindstrom, R.T., Hays, G.C., 2014. The accuracy of Fastloc-GPS locations and implications for animal tracking. Methods Ecol. Evol. 5, 1162–1169.

Dulvy, N.K., Pardo, S.A., Simpfendorfer, C.A., Carlson, J.K., 2014. Diagnosing the dangerous demography of manta rays using life history theory. PeerJ 2, e400.

Friedlaender, A.S., Halpin, P.N., Qian, S.S., Lawson, G.L., Wiebe, P.H., Thiele, D., Read, A.J., 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. Mar. Ecol. Prog. Ser. 317, 297–310.

Germanov, E.S., Marshall, A.D., 2014. Running the gauntlet: regional movement patterns of *Manta alfredi* through a complex of parks and fisheries. PLoS One 9, e110071.

Graham, R.T., Witt, M.J., Castellanos, D.W., Remolina, F., Maxwell, S., Godley, B.J., Hawkes, L.A., 2012. Satellite tracking of manta rays highlights challenges to their conservation. PLoS One 7, e36834.

459 Hearn, A.R., Acuna, D., Ketchum, J.T., Penaherrera, C., Green, J., Marshall, A.,
460   Guerrero, M., Shillinger, G., 2014. Elasmobranchs of the Galapagos Marine
461   Reserve. In: Denkinger, J., Vinueza, L. (Eds.), The Galapagos Marine Reserve: A
462   Dynamic Social-Ecological System. Springer, New York, pp. 23–59.
463 Hueter, R.E., Tyminski, J.P., de la Parra, R., 2013. Horizontal movements, migration
464   patterns, and population structure of whale sharks in the Gulf of Mexico and
465   northwestern Caribbean sea. PLoS One 8, e71883.
466 Jaine, F.R., Couturier, L.I.E., Weeks, S.J., Townsend, K.A., Bennett, M.B., Fiora, K.,
467   Richardson, A.J., 2012. When giants turn up: sighting trends, environmental
468   influences and habitat use of the manta ray *Manta alfredi* at a coral reef. PLoS One
469   7, e46170.
470 James, M.C., Sherrill-Mix, S.A., Martin, K., Myers, R.A., 2006. Canadian waters provide
471   critical foraging habitat for leatherback sea turtles. Biol. Conserv. 133, 347–357.
472 Kashiwagi, T., Marshall, A.D., Bennett, M.B., Ovenden, J.R., 2011. Habitat segregation
473   and mosaic sympatry of the two species of manta ray in the Indian and Pacific
474   Oceans: *Manta alfredi* and *M. birostris* – CORRIGENDUM. Mar. Biodivers. Rec. 4,
475   e86. doi:10.1017/S1755267211000881.
476 Lewis, S.A., Nanen, S., Dharmadi, F., O'Malley, M.P., Campbell, S.J., Yusuf, M.,
477   Sianipar, A., 2015. Assessing Indonesian manta and devil ray populations through
478   historical landings and fishing community interviews. PeerJ PrePrints 3, e1642.
479 Marshall, A.D., Compagno, L.J.V., Bennett, M.B., 2009. Redescription of the genus
480   *Manta* with resurrection of *Manta alfredi*. Zootaxa 28, 1–28.
481 McCauley, D.J., DeSalles, P.A., Young, H.S., Papastamatiou, Y.P., Caselle, J.E., Deakos,
482   M.H., Gardner, J.P.A., Garton, D.W., Collen, J.D., Micheli, F., 2014. Reliance of
483   mobile species on sensitive habitats: a case study of manta rays (*Manta alfredi*) and
484   lagoons. Mar. Biol. 161, 1987–1998.
485 McEachran, J., Aschliman, N., 2004. Phylogeny of Batoidea. In: Carrier, J., Musick, J.,
486   Heithaus, M. (Eds.), Biology of Sharks and Their Relatives. CRC Press, New York,
487   pp. 79–113.
488 Menge, B.A., 1972. Competition for food between two intertidal starfish species and its
489   effect on body size and feeding. Ecology 53, 635–644.
490 Notarbartolo di Sciara, G., 1987. A revisionary study of the genus *Mobula* Rafinesque,
491   1810 (Chondrichthyes: Mobulidae) with the description of a new species. Zool. J.
492   Linn. Soc. 91, 1–91.
493 Notarbartolo di Sciara, G., 1988. Natural history of the rays of the genus *Mobula* in the
494   Gulf of California. Fish. Bull. 86, 45–66.
495 Paig-Tran, E.W.M., Kleinteich, T., Summers, A.P., 2013. The filter pads and filtration
496   mechanisms of the devil rays: variation at macro and microscopic scales. J.
497   Morphol. 274, 1026–1043.
498 Pastene, L.A., Goto, M., Kanda, N., Zerbini, A.N., Kerem, D., Watanabe, K., Bessho, Y.,
499   Hasegawa, M., Nielsen, R., Larsen, F., Palsbøll, P.J., 2007. Radiation and speciation
500   of pelagic organisms during periods of global warming: the case of the common
501   minke whale, *Balaenoptera acutorostrata*. Mol. Ecol. 16, 1481–1495.
502 Pelletier, L., Kato, A., Chiaradia, A., Ropert-Coudert, Y., 2012. Can thermoclines be a
503   cue to prey distribution for marine top predators? A case study with little penguins.
504   PLoS One 7, 4–8.

505 Poortvliet, M., Olsen, J.L., Croll, D.A., Bernardi, G., Newton, K., Kollias, S., O'Sullivan,
506   J., Fernando, D., Stevens, G., Galván Magaña, F., Seret, B., Wintner, S., Hoarau, G.,
507   2015. A dated molecular phylogeny of manta and devil rays (Mobulidae) based on
508   mitogenome and nuclear sequences. Mol. Phylogenet. Evol. 83, 72–85.
509 R Core Team, 2015. R: A Language and Environment for Statistical Computing. R
510   Foundation for Statistical Computing, Vienna, Austria. https://r-project.org.
511 Rubin, R., Kumli, K., Chilcott, G., 2008. Dive characteristics and movement patterns of
512   acoustic and satellite-tagged manta rays (*Manta birostris*) in the Revillagigedos
513   Islands of Mexico. Joint Meeting of Ichthyologists and Herpetologists, Montreal,
514   Canada, Abstract 0318. http://www.asih.org/meetingabstracts2008.
515 Sameoto, D.D., 1984. Vertical distribution of zooplankton biomass and species in
516   northeastern Baffin Bay related to temperature and salinity. Polar Biol. 2, 213–224.
517 Sameoto, D.D., 1986. Influence of the biological and physical environment on the
518   vertical distribution of mesozooplankton and micronekton in the eastern tropical
519   Pacific. Mar. Biol. 93, 263–279.
520 Skomal, G.B., Zeeman, S.I., Chisholm, J.H., Summers, E.L., Walsh, H.J., McMahon,
521   K.W., Thorrold, S.R., 2009. Transequatorial migrations by basking sharks in the
522   western Atlantic Ocean. Curr. Biol. 19, 1019–1022.
523 Stewart, J.D., Beale, C.S., Fernando, D., Sianipar, A.B., Burton, R.S., Semmens, B.X.,
524   Aburto-Oropeza, O., 2016. Spatial ecology and conservation of *Manta birostris* in
525   the Indo-Pacific. Biol. Conserv., doi:10.1016/j.biocon.2016.05.016.
526 Suryan, R.M., Irons, D.B., Benson, J., 2000. Prey switching and variable foraging
527   strategies of black-legged kittiwakes and the effect on reproductive success. Condor
528   102, 374–384.
529 Thorrold, S.R., Afonso, P., Fontes, J., Braun, C.D., Santos, R.S., Skomal, G.B., Berumen,
530   M.L., 2014. Extreme diving behaviour in devil rays links surface waters and the
531   deep ocean. Nat. Commun. 5, 4274. doi:10.1038/ncomms5274.
532 Ward-Paige, C.A., Davis, B., Worm, B., 2013. Global population trends and human use
533   patterns of *Manta* and *Mobula* rays. PLoS One 8, e74835.
534 White, E.R., Myers, M.C., Flemming, J.M., Baum, J.K., 2015. Shifting elasmobranch
535   community assemblage at Cocos Island − an isolated marine protected area.
536   Conserv. Biol. 29, 1186–1197.
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539 **Table 1.** Percentage of time spent by tagged mantas in the same depth bin as the base of

540 the mixed layer, which we considered a proxy for the location of the thermocline.

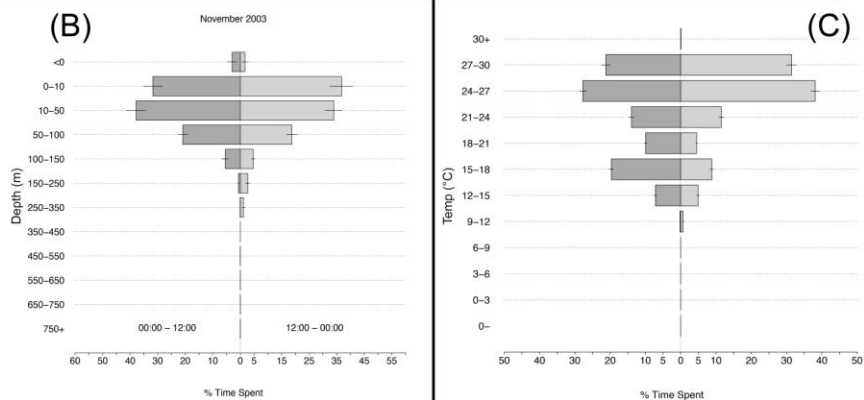| Month	% Time (Day)	SD (Day)	% Time (Night)	SD (Night)
April	13.01	8.13	15.29	8.95
May	11.33	6.87	9.65	6.66
June	11.51	6.78	10.46	6.66
July	19.60	10.34	18.25	8.59
August	19.80	8.34	16.80	9.51
September	21.64	10.12	21.24	8.95

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542

Figure Captions
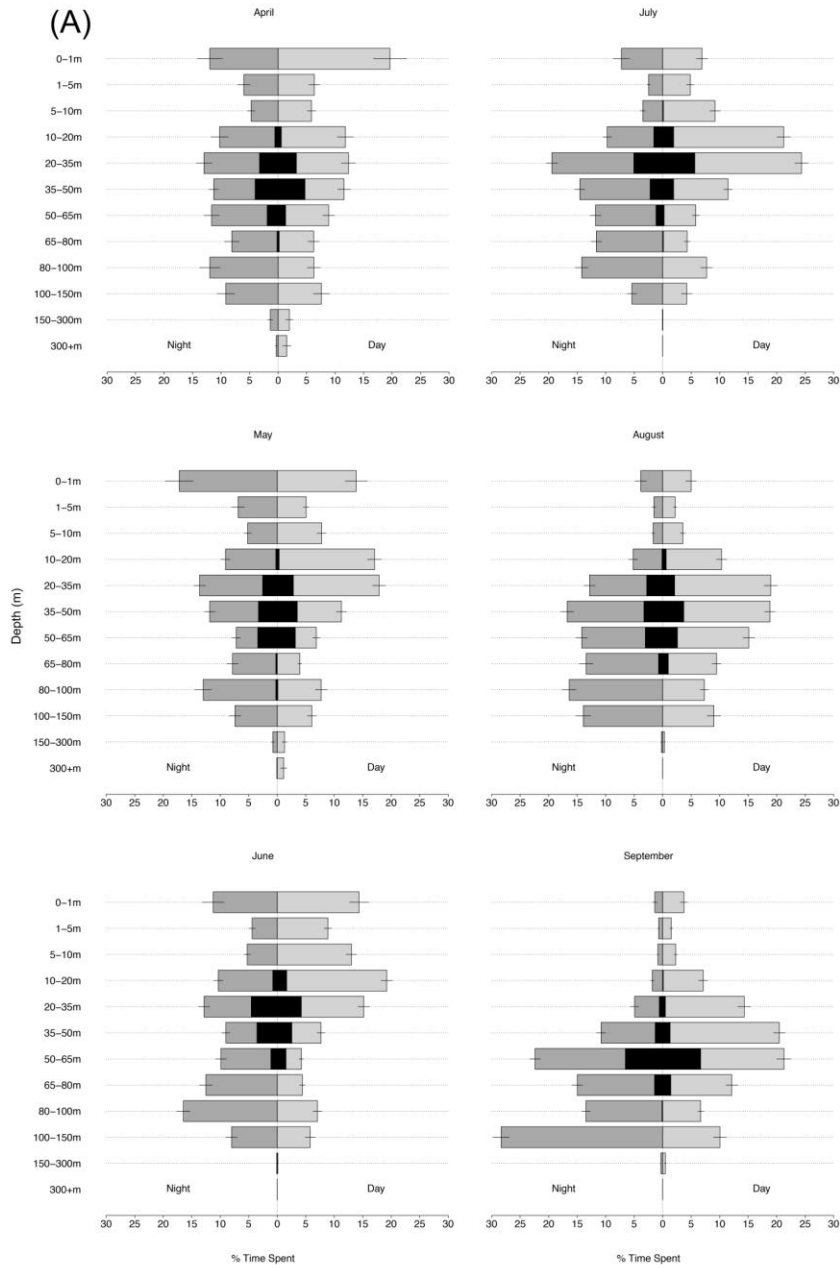
Fig. 1. (A) Depth distributions from four oceanic manta rays (combined) separated into nighttime and daytime periods, recorded by miniPAT tags deployed from April to September 2014 at the Revillagigedo Archipelago. Histogram bars represent mean values across all individuals in a given month, and error bars represent standard error. Inset black bars represent frequency histograms of mixed layer depth, separated into the same depth bins as diving data for ease of comparison. Mixed layer frequency histograms were converted to percentages and plotted as inset histograms at a 0.1x scale. For example, black bars at 5% represent 50% of mixed layer depth records in that binned depth range. (B) Depth distributions from two oceanic manta rays (combined) recorded by PAT Mk-10 tags deployed in November 2003 at the Revillagigedo Archipelago. (C) Temperature histograms recorded by miniPAT tags averaged across the entire tagging period (April to September 2014).

Fig. 2. (A) An oceanic manta ray performs barrel rolls to forage on zooplankton prey in an epipelagic scattering layer. Photo illustration created from three video frame grabs. Footage was captured from a submersible at 11:22 AM in 130–140 m depth. The full video is available as supplementary content in the online Appendix. (B) Close-up of prey in aggregation at the time of feeding, made up of mysid shrimp, calanoid copepods, euphausiids and other zooplankton. Video was taken on the *Televisa–Por el Planeta* expedition.

565 **Fig. 3.** A map of the Revillagigedo Archipelago with a detail on Cabo Pearce, on the

566 island of Socorro, where the deep-water foraging was observed from a submersible and

567 one PSAT was deployed. Additional tags were deployed at San Benedicto and Roca

568 Partida.

569

570

(A)

April | July

May | August

June | September

(B) November 2003 | (C)

571

572

573

ISLA SOCORRO

MEXICO

Revillagigedo Islands

San Benedicto

Roca Partida

SOCORRO

km

0   250   500

REVILLAGIGEDO ISLANDS

18.85°N

18.80°N

18.75°N

Cabo Pearce

111.05°W   111.0°W   110.95°W   110.90°W

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