1 **Steep declines in sightings of manta rays and devilrays (Mobulidae) in**

2 **southern Mozambique**

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8

9 **Abstract**

10 Mobulid rays are one of the most vulnerable chondrichthyan groups due to their low

11 population growth rates and high susceptibility to fisheries. While estimates of human-

12 induced mortality are lacking, sighting trend data can provide an index of their status. We

13 recorded underwater sightings data of *Mobula alfredi*, *M. birostris* and *M. kuhlii* over a 14-

14 year period in southern Mozambique. Generalised linear models were used to standardise

15 sightings and adjust for influences other than time. Standardised sightings of the three

16 species, individually, declined by >90%. Declines in sightings were driven primarily by a rapid

17 decrease between 2003–2007, although the declines continued to 2016. While

18 environmental variables did influence sightings, they did not explain this steep decline over

19 time. Increasing mortality from fisheries is likely to have played a significant role in the

20 declining sightings of these vulnerable species.

21

24

Introduction

Anthropogenic activities have impacted marine species faster than those found on land (Myers & Worm, 2003; McCauley et al., 2015). Shark and ray populations have, in particular, suffered pronounced declines (Dulvy et al., 2014a). Many chondrichthyan species are relatively large and long-lived, with a density-dependent rate of population increase, leaving them particularly vulnerable to human-induced pressures (Musick et al., 2000; Dulvy et al., 2014a). One in four chondrichthyans is now threatened with extinction, largely due to over-exploitation by directed fisheries and high incidental catches in other fisheries (Dulvy et al., 2014a).

Mobulid rays are a group of eight species, all medium to large pelagic rays feeding on zooplankton and small nekton that, as a genus, have a global distribution in tropical and warm-temperate oceans (Couturier et al., 2012; Last et al., 2016). Female mobulids generally reach maturity at a large size, do not immediately reproduce once reaching maturity, have a long gestation period and usually produce a single large offspring, and have a resting period between pregnancies (Rambahiniarison et al. submitted; Notarbartolo-Di-Sciara, 1988; Marshall & Bennett, 2010). This reproductive strategy results in some of the lowest population growth rates found among elasmobranchs (Dulvy et al., 2014b; Pardo et al., 2016). Mobulid rays are among the most vulnerable to over-exploitation of all marine species, and the human threat to these species has become increasingly obvious (Dulvy et al., 2014b; Croll et al., 2015; Lawson et al., 2017). All mobulids have been listed on CITES Appendix II and CMS Appendices I & II between 2013 and 2016.

48 Mobulids are caught in directed harpoon, hook and gillnet fisheries (Camhi et al., 2009;

49 Acebes & Tull, 2016), with the largest targeted fisheries reported from Sri Lanka, Indonesia,

50 India and the Philippines (Couturier et al., 2012; Croll et al., 2015). Target fisheries are often

51 driven by the export of gill rakers, which are valuable in some markets, fetching USD\$130 for

52 *Mobula kuhlii* and ~USD\$350 for *M. birostris* in China (Zeng et al., 2016). Mobulids are also

53 taken as bycatch, particularly in driftnets and purse-seine nets targeting tuna (White et al.,

54 2006; Hall & Roman, 2013; Francis & Jones, 2016). Quantifying these catches and assessing

55 their sustainability has been hampered by a lack of species-specific landing data and poor

56 monitoring of bycatch (White et al., 2006; Lack & Sant, 2009; Couturier et al., 2012).

57 Anecdotal evidence suggests that a decline in mobulid sightings has occurred in some areas

58 in response to increased mobulid fisheries catches (Ward-Paige, Davis & Worm, 2013). Manta

59 ray gill rakers in Chinese markets have decreased from 30% to 11% occupancy among mobulid

60 gill rakers over the past years, suggesting resource exhaustion, although this may also be a

61 result of better protection (Zeng et al., 2016).

62

63 In the absence of mortality and effort estimates from fisheries, sighting indices of free-

64 swimming animals are also useful in conservation assessment, although biases in survey effort

65 need to be considered when interpreting these results (Witt et al., 2012; Rohner et al., 2013).

66 The Inhambane province in southern Mozambique has been an important site for manta ray

67 research over the past decade (Marshall, Compagno & Bennett, 2009; Marshall, Dudgeon &

68 Bennett, 2011), as it contains Africa's largest populations of both reef manta rays *M. alfredi*

69 (Krefft, 1868) and giant manta rays *M. birostris* (Walbaum, 1792). Anecdotal evidence

70 suggests that manta rays are rarely seen outside this hotspot area in the Inhambane province.

71   The area has recently become a popular destination for dive tourists (Tibiriçá et al., 2011;

72   Venables et al., 2017).

73

74   The focal species in this study are Kuhl's devilray *Mobula kuhlii* (Müller & Henle 1841), a

75   relatively small inshore species measuring up to ~1.35 m disc width (DW; White et al., 2006;

76   Last et al., 2016), *M. alfredi* which grow to ~5.5 m DW, and the largest mobulid species, *M.*

77   *birostris*, growing to ~7.0 m DW (Marshall, Compagno & Bennett, 2009; Last et al., 2016). Both

78   manta ray species are listed as "Vulnerable" on the IUCN Red List, while *M. kuhlii* is "Data

79   Deficient" (Bizzarro et al., 2009; Marshall et al., 2011a,b). Manta rays in southern

80   Mozambique are usually seen by divers at cleaning stations on rocky reefs, which are also

81   important sites for social behaviours (Marshall & Bennett, 2010; Marshall, Dudgeon &

82   Bennett, 2011). Manta rays spend up to 8 h day^{-1} at these sites with a mean of 119 min day^{-1}

83   (Marshall, 2008). Devilrays are, in contrast, most often seen swimming in the water column

84   and encounter times with divers are generally short, although they have also recently been

85   seen cleaning for extended periods at other locations (Murie & Marshall, 2016). Until

86   recently, the two species of manta ray were assigned to the genus *Manta*, but recent DNA

87   analyses indicate that this genus should not be considered separate to *Mobula* (Last et al.,

88   2016). Following this taxonomic revision, but acknowledging the broad use of manta rays as

89   common names, we refer to the family or all three species here as "mobulids", to *M. kuhlii* as

90   "devilrays", and to the reef manta and giant manta ray taken together as "manta rays"

91   throughout this work.

92

93   Mobulids in Mozambique are caught offshore in tuna purse-seine nets (Romanov, 2002;

94   Amande et al., 2008; Poisson et al., 2014) and in gillnets set along the coast (Fig. 1). Gillnet

95   use has been increasing in Mozambique since the cessation of conflict in 1992 (Rohner et al.

96   submitted; WWF Eastern African Marine Ecoregion, 2004), and nets have been actively

97   distributed by fisheries officials in some areas to move fishing effort away from inshore

98   nursery habitats (Leeney, 2017). Fisheries-related mortalities of reef manta rays have been

99   previously estimated at 20–50 individuals per year in coastal fisheries in the Inhambane

100 province (Marshall, Dudgeon & Bennett, 2011), and there are extensive but unquantified

101 catches of devilrays (Fig. 1).

102

103 Here, we assessed sightings trends of devilrays and manta rays in the Inhambane province, in

104 southern Mozambique, over a 14-year period. We have previously assessed sightings trends

105 of manta rays in southern Mozambique over a shorter time-frame (Rohner et al., 2013), but

106 the perception of continued declines prompted a re-analysis and expansion of scope. We

107 lengthened the time-series of observations from 9 to 14 years, increasing the number of

108 survey dives available for analysis from 855 to 2,524, and have included *M. kuhlii* sightings for

109 the first time. Mobulids are largely planktivores (Rohner et al. in press; Couturier et al., 2012),

110 and their sightings are likely to be influenced by environmental factors that can influence both

111 their movements and food sources on a short time-scale (Richardson, 2008). We thus

112 standardised sightings with generalised linear models (GLM) to account for environmentally-

113 driven variability in sightings. Sightings of all three mobulid species declined steeply, most

114 likely because of unsustainable catches.

115

116 **Methods**

117 *Surveys*

5

118   Sighting data of *Mobula kuhlii, M. birostris* and *M. alfredi* were collected during research dives

119   in the Inhambane province in the south of Mozambique. A complete dataset was available

120   for analysis from 2,524 survey dives conducted over 14 years between 2003 and 2016. The

121   majority of dives (90%, n = 2,262) were conducted from Praia do Tofo (23.85° S, 35.54°E), with

122   an additional 9% of dives (n = 221) from the Bazaruto Archipelago, and 41 dives from

123   elsewhere in the Inhambane region. Effort was uneven among years, with fewer surveys

124   conducted early in the study (Sup. Fig. 1). We partially accounted for this temporal bias by

125   applying a Generalised Linear Model (GLM), and tested the annual number of surveys as a

126   predictor in the models, though it was not retained in the final models (see below). Dive sites

127   in the Praia do Tofo area, with the majority of surveys, were spread over a ~40 km length of

128   coast, with additional dives at locations ~200 km north (Bazaruto) and ~90 km south (Zàvora).

129   Dives lasted between 2–78 minutes (mean ± sd = 40.5 ± 8.6 min), with 97% of surveys lasting

130   between 20–60 min. Each manta ray was identified from the natural markings on their ventral

131   side (Marshall, Dudgeon & Bennett, 2011; Marshall & Pierce, 2012), and individually counted,

132   while the number of devilrays was counted or sometimes estimated for the largest schools.

133   Raw sightings data were plotted as the number of individuals per survey over time, and also

134   as a binomial presence or absence plot, with a loess smoother (Cleveland, Grosse & Shyu,

135   1992), to examine the temporal trend. Using the individual identification data from *M. alfredi*

136   and *M. birostris*, respectively, we also used two additional indices: (1) the number of

137   individual rays sighted per year, by species; and (2) a simple residency index, measured as the

138   number of manta ray encounters (where an individual was identified) divided by the number

139   of unique individuals, per year. For the latter, a value of one would mean that each manta ray

140   was seen only once in that year. We plotted those indices with a gam smoother trendline and

141   confidence intervals (CI) in grey, which mean that if a horizontal line can be drawn through

142   the CI the relationship is not significant, and also added a linear regression to calculate

143   significance. Field work involved visual observations and photographic identification and was

144   carried out under Mozambique's Administração Nacional das Áreas de Conservação permit

145   number 13 for work within the Bazaruto Archipelago National Park. No permit was required

146   for work outside the park. No animals were restrained, captured or killed.

147

148   Sightings were standardised by including a suite of predictor variables (Table 1) in a GLM

149   constructed in R (R Development Core Team, 2008). Three temporal predictors were used:

150   year of observation, to test for a long-term trend in sightings; day of year, to adjust for

151   seasonality; and time of day, to investigate diel variation. The number of surveys per year was

152   included to account for variation in the annual sample size over the 14-year study. While

153   multiple dive sites were surveyed over this period, disparity in effort led us to categorise dive

154   sites as either 'deep' (22-32 m mean depth, most of which featured manta cleaning stations)

155   or 'shallow' reefs (10 - 18 m mean depth). Moon illumination data were downloaded from

156   NASA's Horizon website (http://ssd.jpl.nasa.gov/horizons.cgi) for the survey area, as moon

157   phase can influence the presence or behaviour of marine fishes (Agenbag et al., 2003; Jaine

158   et al., 2012; Rohner et al., 2013). Observers recorded weather conditions in four categories

159   (sunny, partial overcast (0–50% cloud cover), overcast (51–100% cloud cover), or raining) to

160   test for atmospheric influences on sightings, and surface swell to adjust for surface water

161   conditions. Current direction and strength can influence the cleaning behaviour of mantas

162   (Rohner et al., 2013) and were included in the models. The sightability of animals at these

163   sites can be influenced by underwater visibility (Williams et al., 2017), so observers estimated

164   horizontal visibility on each dive. Water temperature can influence mobulid sightings (Jaine

165   et al., 2012) so we measured the temperature at depth using dive computers and downloaded

166   8-day mean sea surface temperature data at 4 km resolution from off Praia do Tofo from

167   NASA's MODIS Aqua satellite (http://modis.gsfc.nasa.gov) using the R package 'xtractomatic'.

168   We also measured water temperatures every 30 min with a logger (HoboWare) at depth over

169   a 19-month period from three reefs off Praia do Tofo. We use this time-series to illustrate the

170   high variability in temperature at this site, and calculated daily amplitude to show frequent

171   cold water intrusions throughout the year (Sup. Fig. 2). As a general index for food availability,

172   observers recorded plankton densities in four categories: none, when no plankton was visible;

173   green, when phytoplankton was visible; some zooplankton, when the zooplankton density

174   was low; and dense zooplankton, when zooplankton density was high. Surface chlorophyll *a*

175   concentration (Chl-*a*) data were extracted for off Praia do Tofo at an 8-day mean and 4 km

176   resolution from NASA's MODIS Aqua satellite. Minor interpolation was applied for missing

177   dates (0.2 % for SST and 5.8% for Chl-*a*). Tidal range and time from high tide can affect

178   sightings of manta rays (Jaine et al., 2012; Rohner et al., 2013), so these were also included

179   as potential predictors. Raw data are available in supplementary table 1.

180

181   *Modelling*

182   Negative binomial generalised linear models (GLM) with natural splines were constructed in

183   R, with sightings as the response and the suite of variables listed above as predictors. A step-

184   wise AIC function was used to evaluate the best predictors in each model using a penalty

185   factor (k) of 2. A dropterm function with a χ^2-test was also used to select significant predictors

186   for the final model (Venables & Ripley, 2002). The deviance explained for each predictor was

187   calculated from an ANOVA of the final model. In the model output figures, the y-axis is a

188   relative scale, so that a y-value of zero is the mean effect of the adjusted predictor on the

189   response, a positive y- value indicates a positive effect on the response, and a negative y-

190   value indicates a negative effect on the response. If a horizontal line can be placed between

191   the 95% confidence limits (dotted lines), this implies that the relationship between the

192   response and the predictor is not significant. These lines tend to diverge near the extremes

193   of the range for continuous predictors because of fewer observations. To assess the trends in

194   sightings over time, we fitted a line through annual model estimates based on modal

195   (categorical predictors) and median (continuous predictors) input values. A negative

196   exponential fitted best for all species. We then estimated the percentage change from the

197   first to last years from these lines of best fit and used an ANOVA to calculate significance.

198

199   **Results**

200   *Raw sightings trends*

201   *Mobula kuhlii* had the highest mean sightings (1.31 $\pm$ 8.4 SD individuals per survey) and largest

202   groups, with up to 200 individuals seen on a dive. A mean of 1.1 ($\pm$ 2.75 SD) *M. alfredi* were

203   seen per survey, with a maximum of 29. A mean of 0.2 ($\pm$ 0.75 SD) *M. birostris* were observed,

204   with a maximum of 13 individuals on a single dive. Sightings were variable but declined over

205   time in all three species, with the most pronounced decline in *M. alfredi* (Fig. 2). In addition

206   to raw sightings numbers, binary presence also declined for all three species (Fig. 2). For

207   example, *M. alfredi* were seen on at least half of all dives until late 2007, but from late 2011

208   to 2016 they were seen on less than a quarter of all dives. *Mobula kuhlii* presence was

209   recorded on less than half the dives over the study, but their group size was often large which

210   increased their total sighting numbers.

211

212   *Overall model*

213   The GLMs explained 39.6% of the total variance for *M. alfredi* sightings, 25.8% for *M. kuhlii*

214   and 20.1% for *M. birostris*. The final GLM for *M. kuhlii* retained 10 predictors including year,

215   day of year, underwater visibility, current strength and direction, reef depth, underwater

216   temperature, plankton observations, weather, and surface swell (Fig. 3). Year was the most

217   significant predictor (p<0.0001) for *M. kuhlii* sightings, accounting for 12.7% of the variance.

218   Underwater temperature was also important, with a high significance (p<0.0001), explaining

219   2.1% of the variance (Table 2).

220

221   The final GLM for *M. birostris* retained nine predictors including year, day of year, time of day,

222   underwater visibility, current strength and direction, reef depth, moon illumination, and SST

223   (Fig. 4). Year was the most significant predictor (p<0.0001), accounting for 9.1% of the total

224   variance, while day of year was also significant (p<0.0001) and accounted for 4.9% of the

225   variance (Table 2).

226

227   The final GLM for *M. alfredi* retained nine predictors including year, day of year, time of day,

228   underwater visibility, current direction, underwater temperature, Chl-*a* concentration,

229   plankton observations, and the tidal range (Fig. 5). Year was the most significant predictor

230   (p<0.0001), accounting for 33.9% of the total variance. Current direction, underwater

231   visibility, and day of year were also highly significant (p<0.0001) (Table 2).

232

233   *Temporal trends in sightings*

234   Predictive models based on the final GLMs showed that adjusted sightings declined

235   significantly over time for all species. Modelled sightings of *M. kuhlii* declined by 98.8%, *M.*

236   *birostris* by 94.2%, and *M. alfredi* by 98% between 2003 and 2016. *Mobula birostris* were seen

237   more frequently in the middle of the year (Fig. 4), the cooler months in Mozambique, while

238   *M. alfredi* were seen more at the start and end of the year (Fig. 5). *Mobula kuhlii* had a low

239   peak in sightings around ~September (Fig. 3). The time of surveys was significant for manta

240   rays, with fewer sightings recorded in afternoons, but had no effect on *M. kuhlii* sightings.

241

242   *Environmental influence on sightings*

243   Temporal factors were the most influential in all three GLMs, but sightings were also affected

244   by environmental parameters. Underwater visibility had varied influence on sightings among

245   the species, with more devilrays seen in better visibility (Fig. 3) and more manta rays seen in

246   lower visibility (Figs. 4,5). Similarly, fewer manta rays were seen in southerly or "other"

247   current directions (Figs. 4,5), while "other" currents yielded the highest sightings of devilrays

248   (Fig. 3). Warmer water at depth correlated with lower devilray sightings, while this predictor

249   was significant but ambiguous in its effect for *M. alfredi*. Water temperature at depth had a

250   seasonal signal, but was also characterised by numerous cold water intrusions throughout the

251   year (Sup. Fig. 2). *Mobula kuhlii* and *M. birostris* were both sighted more frequently on deep

252   reefs. More *M. alfredi* were seen in either green water (i.e. high concentrations of

253   phytoplankton) or when a high density of zooplankton was recorded, but these parameters

254   had the opposite influence on devilray sightings. Surface predictors such as weather and swell

255   were only significant for *M. kuhlii* sightings, with no clear trend (Fig. 3). Sea surface

256   temperature was retained for *M. birostris*, with an increasing trend for warmer SST. However,

257   underwater temperature was not significant and was not retained (Fig. 4). Moon illumination

258   was significant for *M. birostris* but its relationship with sightings was ambiguous. Similarly,

259   Chl-*a* concentration was retained in the *M. alfredi* model, but was not significant and without

260   a clear trend (Fig. 5). Fewer *M. alfredi* were sighted when the tidal range was higher.

261

262   *Residency influences on sightings*

263   The residency index (sightings/individuals) decreased for *M. alfredi* over the course of the

264   study, from a maximum of 1.47 in 2004 to a minimum of 1.0 in 2016 (lm F = 16.5, p = 0.0016;

265   Fig. 6a). The number of individual *M. alfredi* identified per year also broadly decreased over

266   time, with a maximum of 208 in 2004 and a minimum of 19 in 2016 (Fig. 6b), although this

267   relationship was only marginally significant (lm F = 4.7, p = 0.05). *Mobula birostris* had no clear

268   trend in either the residency index (lm F = 0.18, p = 0.68) or the number of individuals

269   identified each year (lm F = 0.16, p = 0.69; Fig. 6c,d).

270

271   **Discussion**

272

273   Sightings of all three mobulid species declined precipitously over the 14-year study period,

274   with modelled sightings of devilrays declining by 98.8%, reef manta rays by 98%, and giant

275   manta rays by 94.2%. The downward trends present in the raw sightings data persisted once

276   a suite of temporal and environmental variables was accounted for by the GLMs. Short-term

277   environmental fluctuations did not explain this longer-term decline. Models explained

278   between 20–40% of the variation in sightings, indicating that while environmental predictors

279   were important, other parameters – not considered here – also played a significant role. The

280   most influential predictor in all three species was the year of observation, underlining the

281   clear declining temporal trend in sightings. This decline is alarming for mobulids in south-

282   eastern Africa because the Inhambane province hosts Africa's largest identified populations

283   of manta rays (Marshall, Dudgeon & Bennett, 2011) and is the only known hotspot for these

284   species in the region.

285

286   We think that the most likely explanation for this decline in sightings is an increase in

287   mortalities in fisheries. The use of large-mesh gillnets, often extending from near the beach

288   to ~500 m offshore, has significantly increased off the Inhambane coast in recent years

289   (Rohner et al. in review). While landings from these artisanal fisheries are presently

290   unquantified along this remote coast, the gillnet fishery poses a clear threat to marine

291   megafauna in this region. Considering the small population size for *Mobula alfredi* (~800

292   individuals; Marshall, Dudgeon & Bennett, 2011) and *M. birostris* (~600 individuals; Marshall,

293   2008), and the low population growth rates of manta rays and devilrays (Dulvy et al., 2014b),

294   even a small number of individuals taken per year could conceivably result in a steep

295   population decline. While increasing gillnet use may be the primary threat, the lack of regional

296   data on mobulid catches in offshore fisheries is also a concern.

297

298   Manta rays are long-distance swimmers and deep-divers (Jaine et al., 2014; Braun et al., 2015;

299   Stewart et al., 2016), although their consistent cleaning behaviour does makes them easier

300   to survey underwater than most other large marine species. However, our field survey data

301   have biases that must be acknowledged. Research dives only covered a small proportion of

302   the day and a small fraction of the total habitat available to these rays. Sightings-independent

303   methods, such as acoustic or satellite telemetry, have frequently shown that visual surveys

304   miss a proportion of the individuals that are present (MacNeil et al., 2008; Cagua et al., 2015).

305   It is also possible that over the 14-year survey period, mobulids have shifted to using different

306   reefs along the coast, or deeper reefs outside the depth limits of our surveys. The high

307   significance in the decline over time in our basic residency index for *M. alfredi* supports this

308   hypothesis. Potential drivers of a change in habitat use, such as marine tourism (Venables et

309   al., 2016) were not investigated here, but should be considered for future studies. Along with

310   a decline in residency, the number of individual *M. alfredi* identified per year also decreased,

311   suggesting that mortality or permanent emigration is an important driver. We did not find a

312   clear trend in the residency of *M. birostris*.

313

314   While temporal variables were the primary influence on sightings of all species, the GLMs also

315   revealed some interesting relationships with other predictors. Lower visibility was associated

316   with higher manta ray sightings, but fewer devilray sightings. This is likely because devilrays

317   have a higher probability of being sighted in clearer water, as they often swim high in the

318   water column. This is similar to results on turtle sightings on the same reef systems, as turtles

319   need to swim to the surface to breathe (Williams et al., 2017). Manta rays, in contrast, are

320   generally associated with cleaning stations that are specifically surveyed by the research

321   team, partially negating the influence of visibility. More devilrays were seen in cooler water

322   temperatures at depth, but during the warmer months at the start and end of the year. This

323   apparent disparity could in fact indicate that devilray presence is associated with upwelling

324   events, which occur throughout the year and create daily amplitudes of up to 11°C (Sup. Fig.

325   2). Sightings of *M. alfredi* were lower in cold water (<21°C), but plateaued in warmer water.

326   This is a similar result to that demonstrated for *M. alfredi* in Australia, which had a

327   pronounced peak at ~22°C when foraging and a general increase in sightings with warmer

328   water (Jaine et al., 2012). The lack of a relationship between water temperature and *M.

329   birostris* sightings may reflect their broad temperature tolerance, with *M. birostris* extending

330   further into temperate areas than *M. alfredi* (Marshall, Compagno & Bennett, 2009). *Mobula

331   kuhlii* and *M. birostris* were seen more on deep reefs, as expected for all three species.

332

333   Previously, we reported an 88% decline in *M. alfredi* sightings and no clear trend for *M.*

334   *birostris* sightings within the same study area over a shorter time-frame (Rohner et al., 2013).

335   Here, we increased our previous time-series data for manta rays by 5 years (2003–2011

336   previously vs. 2003–2016 here) and by nearly tripling the number of survey dives (855 vs.

337   2,524). Some relationships between manta ray sightings and predictors remained stable,

338   indicating that these are likely to be reliable associations. For example, *M. alfredi* were

339   consistently seen more when water was >21°C, and during the warmer months at the start

340   and end of the year. The decreasing trend of *M. alfredi* sightings continued over time,

341   resulting in a total decline going from 88% to 98% over the longer time-series. *Mobula*

342   *birostris* sightings had no significant trend between 2003–2011, but this enlarged data-series

343   shows a steep decline over this longer study period. The lack of observable trend in the earlier

344   assessment was influenced by a short-lived increase in sightings in 2009, underlining the need

345   for long-term observations to assess trends in mobulid sightings.

346

347   Mozambique is a signatory to both CMS, on which all mobulids are recommended for

348   protection, and CITES which promotes sustainable international trade. While international

349   trade in mobulid products is not known to be a driver of contemporary catches in

350   Mozambique, it is a major driver globally (Lawson et al., 2017). Although improved data on

351   catches are required to confirm our hypothesis that mobulid stocks are being rapidly depleted

352   by fisheries, we argue that precautionary management is required for these species. There is

353   a strong economic argument (Tibiriçá et al., 2011; Venables et al., 2017) and conservation

354   imperative to implement legislative protection for mobulids in Mozambique.

355

356   **Acknowledgements**

364

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524 **Table 1.** Predictors used in the GLMs for *Mobula kuhlii*, *M. alfredi* and *M. birostris*, with an explanation, the type of predictor, the units and

525 mean ± standard deviation.

Predictor	Explanation	Type	Units	Mean ± SD
Year	Year of observation	Continuous	yr	
Day of year	Day of observation	Continuous	d	
Time of day	Time of day	Continuous	hh	10.3 ± 1.78
Surveys per year	Number of surveys per year	Continuous	count	269.4 ± 125.4
Reef depth	Type of reef	Categorical	m	Shallow or deep
Weather conditions	Weather conditions at the surface	Categorical	levels: sunny, <50% cloud cover, overcast, rain	
Moon illumination	Proportion of moon disc illuminated	Continuous	Proportion	0.5 ± 0.36
Underwater temperature	Temperature at depth	Continuous	°C	24.3 ± 2.15
SST	Satellite-derived 8-d mean surface temperature	Continuous	°C	26.3 ± 1.77
Chl-*a* concentration	Satellite-derived 8-d mean chlorophyll *a* concentration	Continuous	mg m-3	0.3 ± 0.39
Plankton observations	Visual assessment of plankton at depth	Categorical	levels: none, green, some zooplankton, dense zooplankton	
Underwater visibility	Underwater horizontal visibility	Continuous	m	12.7 ± 5.96
Current direction	Dominant direction of current at depth	Categorical	levels: northward, southward, other, no current	
Current strength	Current strength at depth	Categorical	levels: none, light, medium, strong	
Surface swell	Ocean swell at the surface	Categorical	Levels 1 to 5: flat, minimal, light, medium, strong, heavy	
Tidal range	Difference between high and low tide	Continuous	m	2.4 ± 0.39
Time from high tide	Time from the nearest high tide	Continuous	min	52.9 ± 222.3

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528 **Table 2**. Model outputs showing the variance explained and the p-values for each predictor

529 retained in the final GLMs for *Mobula kuhlii, M. birostris* and *M. alfredi*.

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	M. kuhlii		*M. birostris*		*M. alfredi*	
	Variance (%)	p (χ^2)	Variance (%)	p ($\chi^{2)}$)	Variance (%)	p (χ^2)
Year	12.7	<0.0001	9.1	<0.0001	33.9	<0.0001
Day of year	0.9	0.016518	4.9	<0.0001	1.0	<0.0001
Underwater visibility	1.4	0.002349	0.6	0.038225	1.1	<0.0001
Current direction	1.0	0.038349	0.9	0.026168	2.2	<0.0001
Current strength	1.6	0.003886	0.6	0.115711		
Reef depth	0.5	0.044791	0.1	0.423935		
Underwater temperature	2.1	<0.0001			0.0	0.80132
Plankton observations	1.5	0.005658			0.6	0.01182
Weather	1.8	0.001132				
Surface swell	2.3	0.001601				
Time of day			2.0	<0.0001	0.3	0.06806
Moon illumination			1.0	0.006055		
SST			0.9	0.008499		
Chl-*a* concentration					0.1	0.26538
Tidal range					0.4	0.02837
Sum	25.8		20.1		39.6	

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536   **Fig. 1.** Mobulids caught in gillnets in the Inhambane province of Mozambique, with (a) and

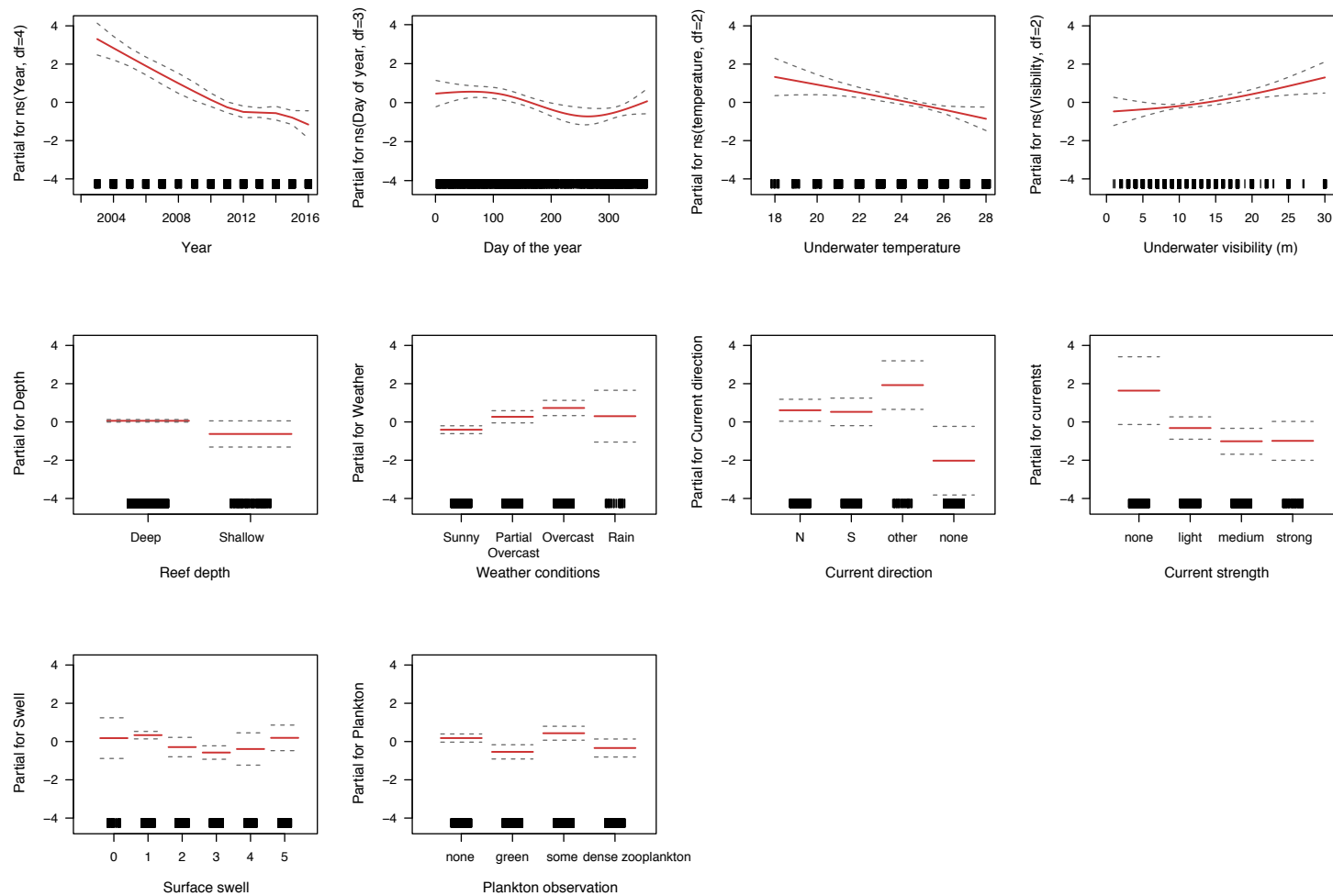537   (b) *M. alfredi* and (c) and (d) *M. kuhlii*.

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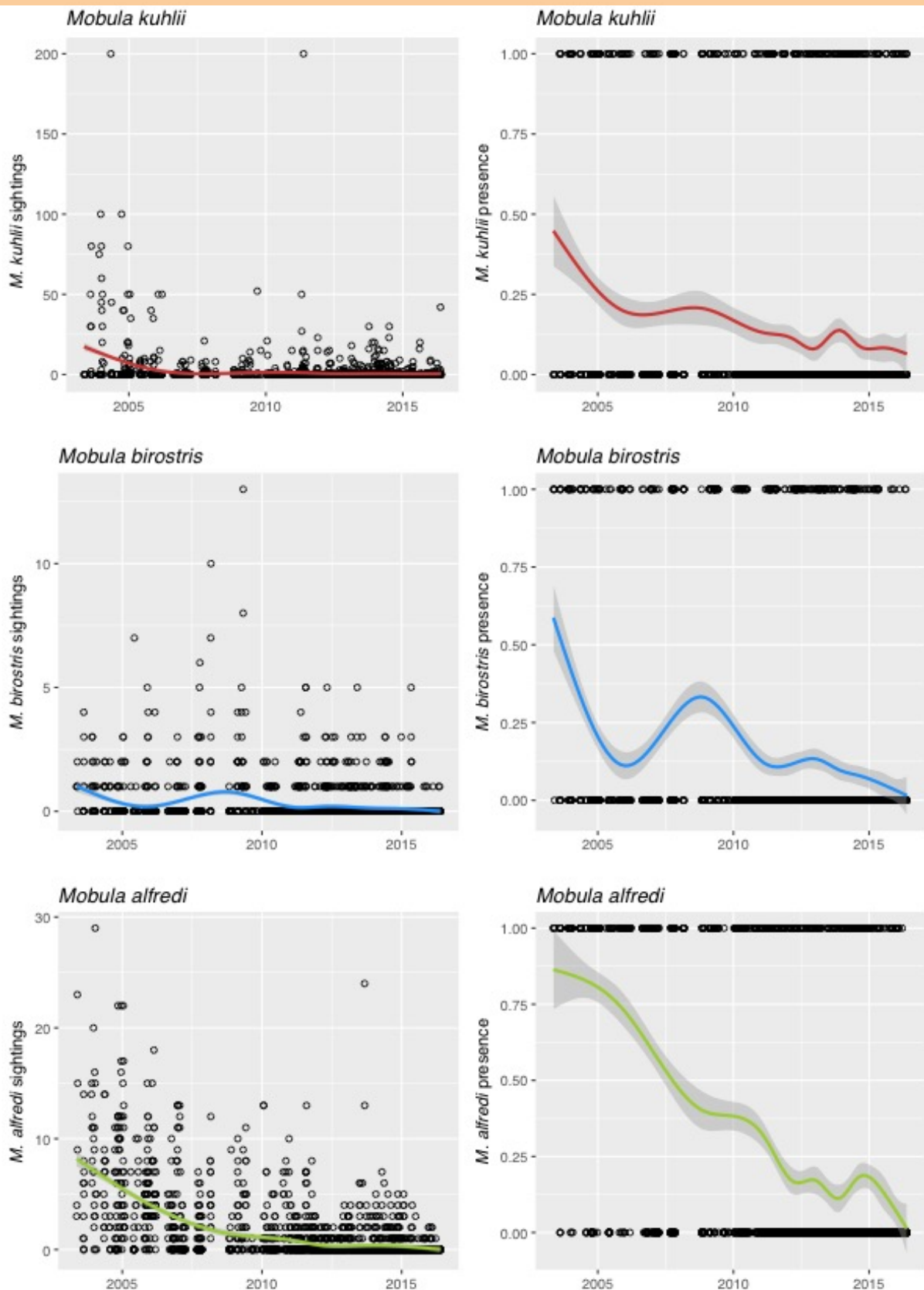
Fig. 2. Raw, unadjusted sightings (left panels) and binomial presence (right panels) over time

for *Mobula kuhlii*, *Manta birostris* and *M. alfredi* (top to bottom).

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Figure 3. Model output for the *Mobula kuhlii* GLM, showing the relationship between sightings and all significant predictors. The rug plot along

the x-axis shows sampling effort and the dotted lines mark the 95% confidence intervals.

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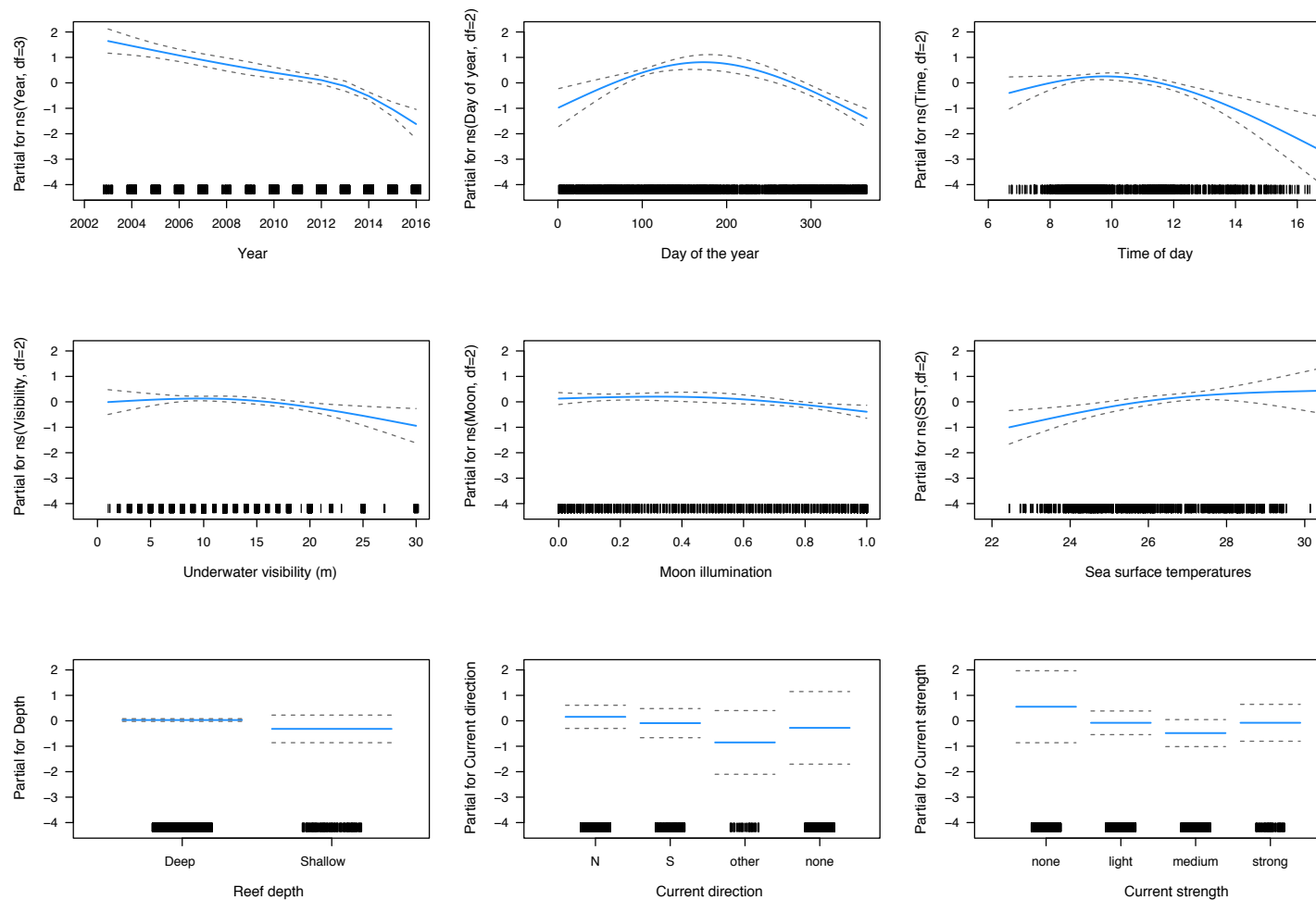
546

547 **Figure 4.** Model output for the *Mobula birostris* GLM, showing the relationship between sightings and all significant predictors. The rug plot
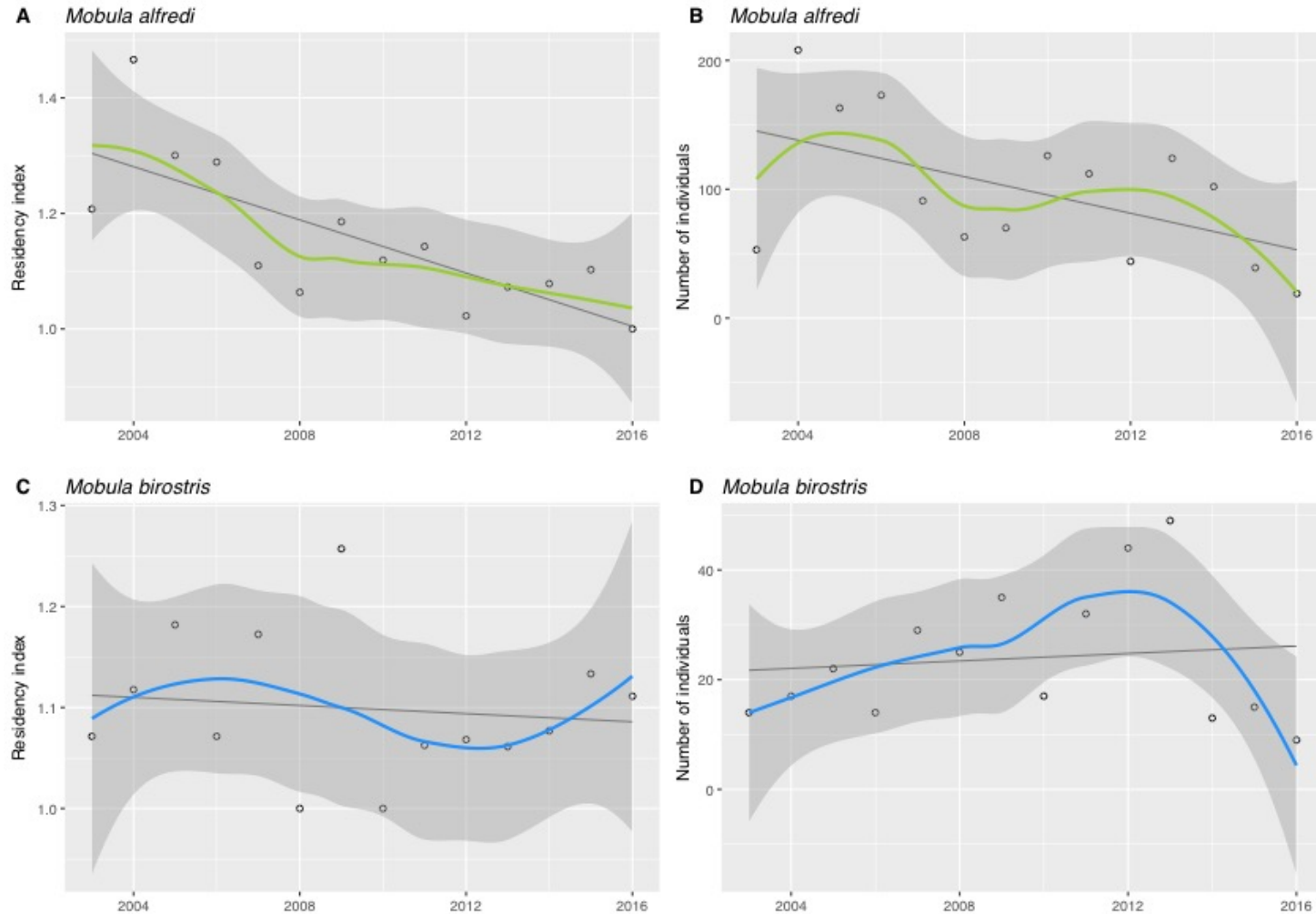
548 along the x-axis shows sampling effort and the dotted lines mark the 95% confidence intervals.

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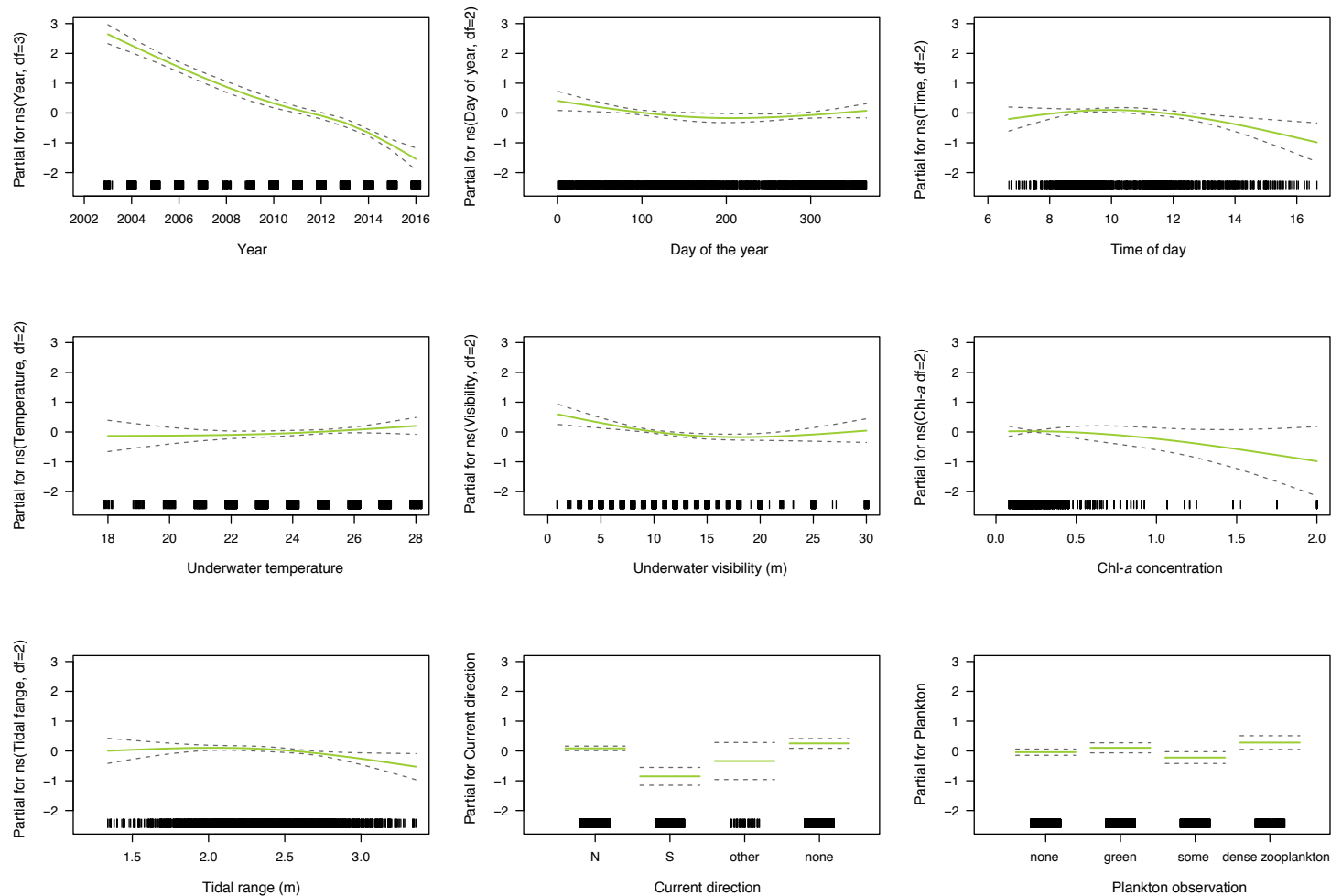
Figure 5. Model output for the *Mobula alfredi* GLM, showing the relationship between sightings and all significant predictors. The rug plot
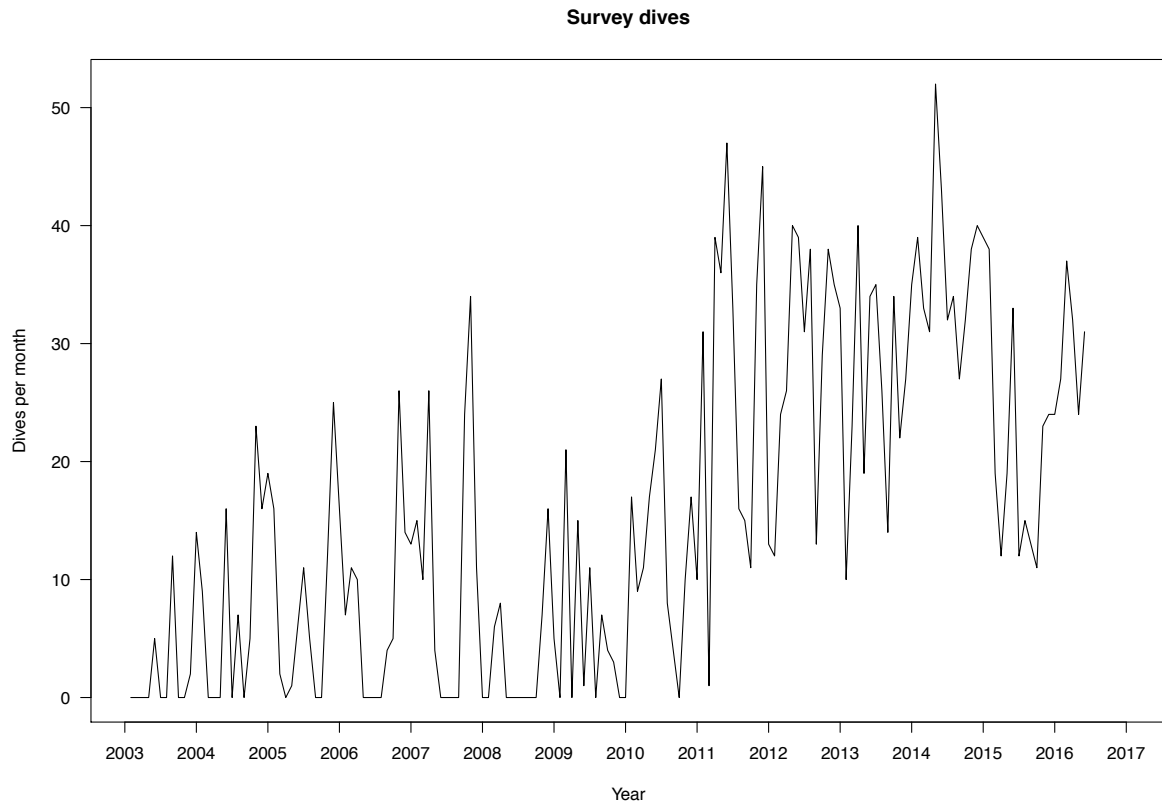
along the x-axis shows sampling effort and the dotted lines mark the 95% confidence intervals.

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Figure 6. The residency index and number of individuals sighted per year for *M. alfredi* (a,b) and *M. birostris* (c,d) with a gam-based trendline in colour with confidence intervals in grey, and a linear regression line in black.

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Survey dives

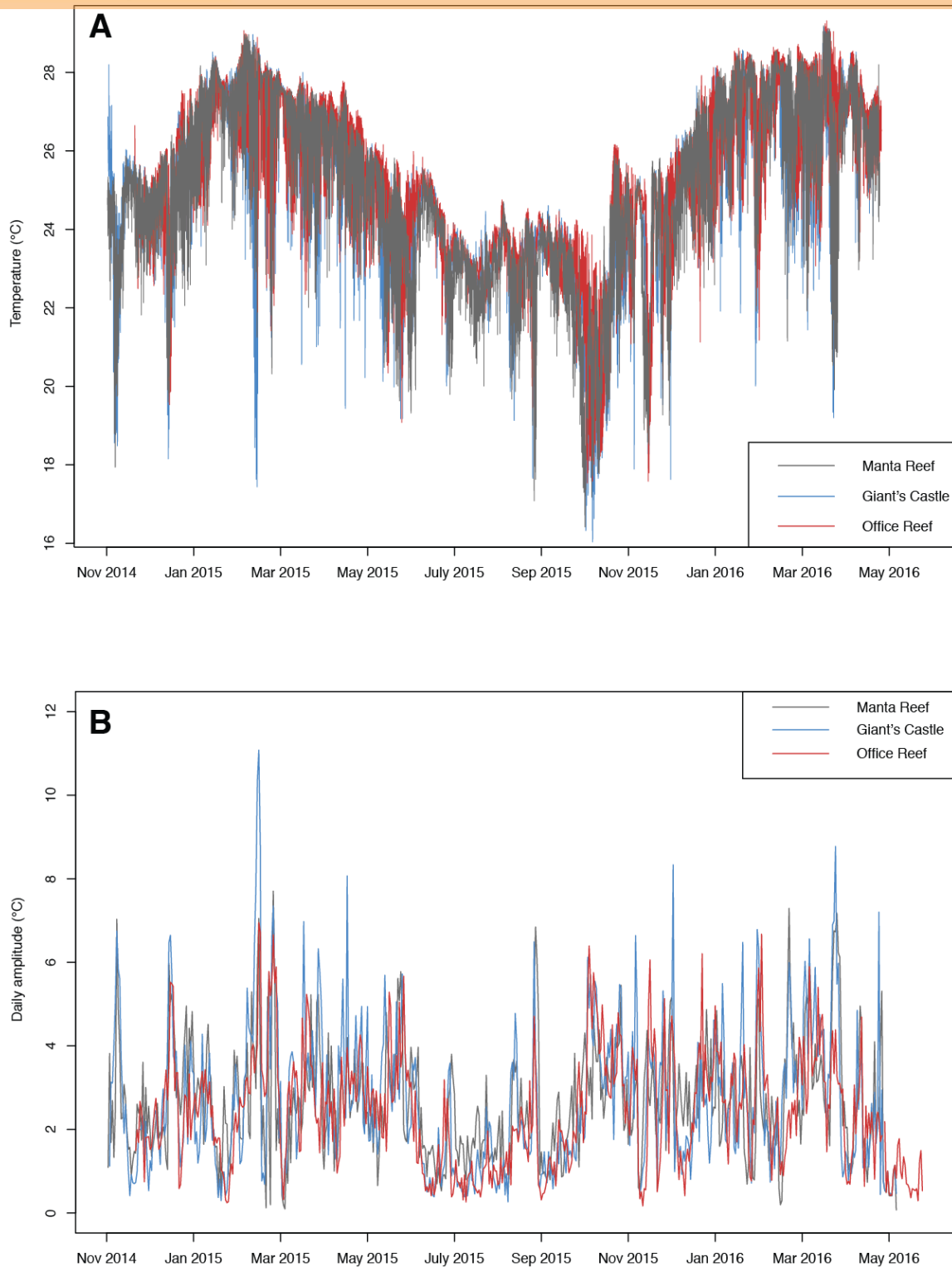555

556   **Supplementary Figure 1:** Survey effort showing dives per month between 2003–2016.

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Supplementary Figure 2: Underwater temperature plots from three reefs (Manta Reef 22 m

depth; Giant's Castle 28 m; Office Reef 24 m) off Praia do Tofo over a 19-month period, with

(A) time-series of temperature readings every 30 min; and (B) amplitude of temperature

variation over 24h periods.