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# Fine-scale oceanographic drivers of reef manta ray (*Mobula alfredi*) visitation patterns at a feeding aggregation site

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1 **Fine-scale oceanographic drivers of reef manta ray (*Mobula alfredi*) visitation patterns at a**  
2 **feeding aggregation site**

3 **Running head:**

4 Drivers of reef manta ray visitation patterns

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**21 Abstract**

22 Globally, reef manta rays (*Mobula alfredi*) are in decline and are particularly vulnerable to  
23 exploitation and disturbance at aggregation sites. Here, passive acoustic telemetry and a suite  
24 of advanced oceanographic technologies were used for the first time to investigate the fine-  
25 scale (5-min) influence of oceanographic drivers on the visitation patterns of 19 tagged *M.*  
26 *alfredi* to a feeding aggregation site at Egmont Atoll in the Chagos Archipelago. Boosted  
27 regression trees indicate that tag detection probability increased with the intrusion of cold-  
28 water bores propagating up the atoll slope through the narrow lagoon inlet during flood tide,  
29 potentially transporting zooplankton from the thermocline. Tag detection probability also  
30 increased with warmer near-surface temperature close to low tide, with near-surface  
31 currents flowing offshore, and with high levels of backscatter (a proxy of zooplankton  
32 biomass). These combinations of processes support the proposition that zooplankton carried  
33 from the thermocline into the lagoon during the flood may be pumped back out through the  
34 narrow inlet during an ebb tide. These conditions provide temporally limited feeding  
35 opportunities for *M. alfredi*, which are tied on the tides. Results also provide some evidence  
36 of the presence of Langmuir Circulation, which transports and concentrates zooplankton, and  
37 may partly explain why *M. alfredi* occasionally remained at the feeding location for longer  
38 than that two hours. Identification of these correlations provides unique insight into the  
39 dynamic synthesis of fine-scale oceanographic processes which are likely to influence the  
40 foraging ecology of *M. alfredi* at Egmont Atoll, and elsewhere throughout their range.

41

42 **Keywords:** Acoustic telemetry, boosted regression trees, foraging ecology, internal waves,  
43 cold-water bores, Langmuir Circulation.

## 44 Introduction

45 Reef manta rays (*Mobula alfredi*) are large zooplanktivorous elasmobranchs of the  
46 family Mobulidae (Hosegood *et al.*, 2020; Marshall *et al.*, 2009; White *et al.*, 2017). The  
47 global population is widely distributed in highly fragmented subpopulations throughout  
48 tropical and sub-tropical waters of the Indo-West Pacific Oceans (Couturier *et al.*, 2012;  
49 Marshall *et al.*, 2019). Subpopulations appear to have limited home ranges, typically centred  
50 around coral reef ecosystems (McCauley *et al.*, 2014; Kessel *et al.*, 2017; Couturier *et al.*, 2018;  
51 Setyawan *et al.*, 2018). Aggregation behaviour is characteristic of the species, whereby  
52 subpopulations will concentrate the majority of their activities at certain 'hotspot' locations  
53 (Couturier *et al.*, 2018; Setyawan *et al.*, 2018; Harris *et al.*, 2020). These aggregations  
54 typically occur within particular discrete habitats (Stevens, 2016; Harris *et al.*, 2020) such as  
55 cleaning stations (O'Shea *et al.*, 2010), and locations where they engaged in social (Stevens,  
56 2016; Perryman *et al.*, 2019) or reproductive activities (Stevens *et al.*, 2018). Large feeding  
57 aggregations also occur, and are often associated with the species' reliance on dense  
58 assemblages of prey (Armstrong *et al.*, 2016) in a largely oligotrophic environment (Morel *et*  
59 *al.*, 2010).

60 Extensive targeted and bycatch fisheries of *M. alfredi*, driven in part for their gill  
61 plates [pre-branchial appendages, used to filter their zooplankton prey from the water (Paig-  
62 Tran *et al.*, 2013), which are utilised in the Asian medicinal trade (O'Malley *et al.*, 2017)], has  
63 led to dramatic subpopulation declines in recent decades (Couturier *et al.*, 2013; Lawson *et*  
64 *al.*, 2017; Rohner *et al.*, 2017; Marshall *et al.*, 2019). Population recovery from such  
65 exploitation is hindered by their conservative life-history traits; the species are slow-growing,

66 late to mature and only have a few offspring in their lifetime (Dulvy *et al.*, 2014; Stevens,  
67 2016).

68 *Mobula alfredi* are particularly vulnerable to exploitation and changes in climate at  
69 feeding aggregation sites. For example, anthropogenic disturbance may reduce individual *M.*  
70 *alfredi* fitness by driving them away from productive feeding areas (Venables *et al.*, 2016;  
71 Murray *et al.*, 2019), which has been highlighted as a major conservation concern for the  
72 species (Murray *et al.*, 2019; Harris *et al.*, 2020). Feeding behaviour may also be disrupted by  
73 enhanced stratification driven by rising sea surface temperatures, which can decrease marine  
74 phytoplankton (Roxy *et al.*, 2016), and with it zooplankton biomass (Richardson, 2008).

75 Studies which investigate *M. alfredi* aggregation behaviour have associated their  
76 occurrence with various broadscale physical factors, such as wind speed, moon phase, sea  
77 surface temperature, and tidal phase (Dewar *et al.*, 2008; Jaine *et al.*, 2012; Couturier *et al.*,  
78 2018; Peel *et al.*, 2019b). However, the fine-scale changes in the oceanographic environment  
79 that potentially drive feeding aggregations have yet to be investigated.

80 Situated in the central Indian Ocean, the Chagos Archipelago (Figure 1) has been  
81 uninhabited for many decades (excluding Diego Garcia Atoll) (Sheppard *et al.*, 2012). Due to  
82 the lack of human influence, such as coastal development and anthropogenic pollution, the  
83 region is considered virtually pristine (Readman *et al.*, 2013). Owing to the region's unique  
84 marine environment, a no-take marine protected area (MPA), which encompasses the entire  
85 exclusive economic zone (EEZ) (640,000km<sup>2</sup>) except for a 3nm exclusion around the boundary  
86 of Diego Garcia Atoll, was established in 2010 (Sheppard *et al.*, 2012). The archipelago  
87 supports a subpopulation of *M. alfredi* which is largely undocumented due to the remoteness  
88 of the location and strict protective measures; as is the region's physical oceanographic

89 environment (Hosegood *et al.*, 2019). Broadscale studies conducted in the region indicated  
90 that Egmont Atoll, situated in the southwest of the archipelago, provides key habitats for this  
91 *M. alfredi* subpopulation (Harris, 2019; Andrzejczek *et al.*, 2020). Feeding *M. alfredi* are  
92 regularly observed around the atoll (Harris, 2019); behaviour which is thought to be  
93 associated with shallow bathymetry, low current speeds, and cooler sea surface temperatures  
94 (Jaine *et al.*, 2012; Armstrong *et al.*, 2016; Couturier *et al.*, 2018; Harris, 2019; Peel *et al.*,  
95 2019b). Together, these factors may act to induce upwelling of nutrients, increasing primary  
96 and secondary production (McManus *et al.*, 2005). Furthermore, currents interacting with  
97 topography may aggregate zooplankton (Genin *et al.*, 2005), resulting in highly productive  
98 feeding grounds for a range of species, including *M. alfredi* (Hosegood *et al.*, 2019).

99         Field observations have identified an *M. alfredi* feeding aggregation ‘hotspot’ at the  
100 north of Egmont Atoll (Harris and Stevens, unpublished data). However, *M. alfredi* feeding  
101 activity can be dramatically different from one day to another, with little apparent change in  
102 broadscale oceanographic conditions (Harris, 2019). Therefore, a greater understanding of  
103 how *M. alfredi* respond to fine-scale environmental drivers is needed. Here, passive acoustic  
104 telemetry and *in situ* oceanographic monitoring is used to investigate *M. alfredi* activity at  
105 Egmont Atoll, and assess what physical factors drive fine-scale (5-min) visitation patterns at  
106 the observed feeding aggregation hotspot. This study aims to enhance the current  
107 understanding of *M. alfredi* foraging ecology by providing detailed insight into their fine-scale  
108 movement patterns in response to natural changes in their oceanographic environment.

## 109 **Methods**

### 110 *Study site*

111 The Chagos Archipelago is comprised of seven atolls, several large submerged banks and  
112 more than 60 low lying islands, located at the southernmost end of the Lakshadweep–  
113 Maldives–Chagos ridge; 450km south of the Maldives (Sheppard *et al.*, 2012) (Figure 1).  
114 Egmont Atoll’s geomorphology is typical of an atoll with an interior lagoon system which is  
115 separated from the open ocean by reef crests and flats, with narrow connecting channel  
116 systems (Woodroffe and Biribo, 2011). During six expeditions, between January 2015 and  
117 December 2019 (Harris and Stevens, unpublished data), the authors repeatedly observed  
118 aggregations of *M. alfredi* engaged in feeding activity at a site called Manta Alley (Figure 1).  
119 At this foraging hotspot, using in-water observations (Figure 2) and ROVs, *M. alfredi* were  
120 recorded feeding at the surface and down to a depth of 120 m (Harris and Stevens,  
121 unpublished data; Diaz and Foster, unpublished data). Manta Alley is located 100 m north of  
122 Egmont Atoll’s northeast rim, where two narrow (<350 m) passages are situated. From the  
123 shallow lagoon passages (<5 m), the topography slopes steeply down (up to 47°) before  
124 reaching a 50 m wide plateau 80 m from the lagoon, with a depth of 65-71 m. On the seaward  
125 side, there is a narrow ridge which inclines steeply (up to 39°) to a height of approximately 10  
126 m, followed by another sharp slope down to >100m (Robinson and Hosegood *et al.*,  
127 unpublished data) (Figure 1).

#### 128 *Oceanographic Moorings*

129 Two instrumented oceanographic moorings were deployed in Manta Alley (Figure 1)  
130 from a research ship on 30<sup>th</sup> December 2019. Both moorings were positioned within Manta  
131 Alley. The first was a subsurface taut-line mooring deployed in 66 m, with the uppermost  
132 buoyancy element at a depth of 20 m. Temperature was measured by RBRSolo<sup>3</sup>T temperature  
133 sensors positioned at 2 m intervals from 4 m to 48 m above the seabed. In addition to the

134 temperature sensors, RBR Concerto conductivity-temperature-depth (CTD) sensors with a  
135 sampling interval of 5s were positioned at 2 m and 50 m above the bed. An acoustic receiver  
136 (see *acoustic receiver array* section below) was positioned approximately 7 m below the near-  
137 surface CTD, at 43 m above the bed. The second mooring, deployed 182 m southeast of the  
138 first, comprised an upward-facing Nortek Signature 500kHz acoustic Doppler current profiler  
139 (ADCP), mounted on a subsurface buoy 3 m above the seabed. Both moorings were recovered  
140 on 17<sup>th</sup> March 2020; however, the Nortek Signature 500kHz ADCP had ceased sampling on  
141 10<sup>th</sup> March 2020.

#### 142 *Acoustic tag deployment*

143 Tagging activities were carried out at Egmont Atoll between 19th November 2019 -  
144 3rd December 2019 while freediving. Twenty VEMCO V16-4x acoustic transmitter tags  
145 (Vemco Inc., Nova Scotia, Canada), each tethered to a titanium anchor (Wildlife Computers)  
146 with a small diameter cable, were deployed on the right dorsal musculature using a modified  
147 Hawaiian hand sling while swimming behind the *M. alfredi*. Each tag was set to operate at 69  
148 kHz and transmit a unique acoustic signal at random intervals between 30 and 90 seconds.  
149 Before being tagged, the ventral side of each *M. alfredi* was photographed to capture their  
150 unique spot pattern for identification purposes (Marshall and Pierce, 2012), and their sex and  
151 size class (a proxy of maturity status) were recorded (Stevens, 2016). Five of the twenty *M.*  
152 *alfredi* that were tagged were re-sighted at their tagging locations between three and 12 days  
153 after deployment. All five were observed to be engaged in normal feeding activities (Stevens,  
154 2016). All activities were approved by the University of Plymouth Animals in Science Ethics  
155 Committee under permit ETHICS-24-2019.

#### 156 *Acoustic receiver array*



157 An acoustic array of five VR2W-69 kHz omnidirectional acoustic receivers (Vemco Inc.,  
158 Nova Scotia, Canada) were deployed at depths ranging from 12 to 22 m below the sea surface  
159 on the reef flat close to the reef slope at sites corresponding to known *M. alfredi* aggregation  
160 areas around the outer rim of Egmont Atoll (Figure 1). Four of the receivers were suspended  
161 approximately 2 m above the seabed, while the fifth was attached to an oceanographic  
162 mooring 43 m above the seabed at the Manta Alley aggregation site. Acoustic tags were  
163 detected within approximately 160 m of the receivers: mean =  $162 \pm 31$  m (SD) as determined  
164 by range testing conducted following the method described by Lea (2017).

#### 165 *Acoustic tag analysis*

166 All tag detection data was imported into VUE software (version 2.6.2) and filtered for  
167 active tags. The False Detection Analyser (VUE version 2.6.2) was then used to identify false  
168 detections, whereby the ratio of short and long periods between detections is calculated from  
169 the time between detections on each receiver (Simpfendorfer *et al.*, 2015). Here, the default  
170 short to long periods of <30 min and >12 h, respectively were used (Simpfendorfer *et al.*,  
171 2015) and all detections suspected to be false were removed from analysis. The percentage  
172 of sightings at each location were then projected in ArcGIS 10.7.

173 To assess whether Egmont Atoll can be considered a key habitat, residency indices (RI)  
174 were calculated using the following form (Peel *et al.*, 2019b), allowing comparison of  
175 residency patterns at Egmont Atoll between *M. alfredi* regardless of differences in tracking  
176 periods (Daly *et al.*, 2014).

$$177 \quad RI(\%) = \frac{\text{Number of days detected}}{\text{Number of days between first and last detection}} \times 100$$

178 To assess the intensity at which locations were utilised, the amount of time each  
179 tagged *M. alfredi* spent within the detection range of each acoustic receivers was calculated  
180 using the VTrack R package (Campbell *et al.*, 2012) in R 3.5.2 (R Core Team, 2018). Briefly,  
181 each tag detection was classed as a resident or non-resident events. A resident event began  
182 when there were two or more successive detections (Nalesso *et al.*, 2019) at the same  
183 receiver within 60 minutes. Termination of the resident event occurred at the time of the last  
184 detection when there were no further detections within 60 minutes, or when the tag was  
185 detected at least twice at another receiver (Campbell *et al.*, 2012; Nalesso *et al.*, 2019).

#### 186 *Environmental Influences: Boosted regression trees*

187 Boosted regression trees (BRT) were used to investigate the relationship between  
188 environmental variables and the visitation patterns of tagged *M. alfredi* to the feeding  
189 aggregation site at Manta Alley. The modelling technique is based on two algorithms:  
190 regression trees models and boosting, which build and combine large numbers of relatively  
191 small trees by fitting each new tree to the residuals of the last (Elith *et al.*, 2008). Each tree is  
192 constructed through a series of binary splits of predictor variables (Hastie *et al.*, 2009), which  
193 occur based on the homogeneity of their relationship to the response variable (Colin *et al.*,  
194 2017). Multiple splits are tested, and partitioning occurs when the greatest improvement of  
195 homogeneity is found (Colin *et al.*, 2017). Advantages of this modelling technique include its  
196 ability to fit complex, non-linear relationships, model interactions between response  
197 variables (Elith *et al.*, 2008), and the appropriate data model does not require assumptions  
198 about the residuals of the model (Derville *et al.*, 2016).

199 Detection data was divided into a time-series of 5-min bins starting from 1<sup>st</sup> December  
200 2019 and ending on 10<sup>th</sup> March 2020. The BRT was then constructed with a binomial response

201 of present (1) or absent (0) within each 5-min bin. The final time-series contained 28654 x 5-  
202 min bins of presence and absence observations.

203         Nine predictor variables representing temperature (1-2), zooplankton biomass (3),  
204 ocean currents (4-8), and tide (9), all of which have been shown to influence *M. alfredi*  
205 occurrence (O'Shea *et al.*, 2010; Anderson *et al.*, 2011; Harris *et al.*, 2020) were selected for  
206 inclusion (Table 1). Temperature variables included: temperature at 2 m above the seabed  
207 (temp 2 m) (1), and 50 m above the seabed (temp 50 m) (2), sampled every 5s using RBR  
208 Concerto CTDs. Data were pooled into the same 5-min bins as the presence and absence data.  
209 The mean temperature for each 5-min bin was then calculated from the 60 data points. For  
210 zooplankton biomass (3), acoustic backscatter was used as a proxy. Data were taken from  
211 beam 1 of the Nortek Signature 500kHz ADCP, aligned with x positive and a centre frequency  
212 of 500kHz with a bandwidth of 25kHz and retrieved from the Nortek Average AD2CP file with  
213 a sample interval of 10 mins. The instrument has a vertical resolution of 2 m per bin, and the  
214 first 25 bins were taken for data processing (0.5-50.5 m range from the instrument). The  
215 vertical profile at each time step was filtered with a running median window with a length of  
216 3 and a maximum deviation of 1. These parameters were chosen based on observations in  
217 the data that any areas of amplified return (likely due to large targets which are not  
218 zooplankton) were constrained to the extent of a single bin due to the relatively large size of  
219 the 2 m bins when compared to the observed target size. A depth-mean value was then  
220 calculated for each time step and linearly interpolated into the 5-min bins. Ocean current data  
221 (4) included vertical velocity, for which a depth mean was calculated from the same average  
222 data and bin selection as backscatter, but with no filtering applied due to the low noise level  
223 in averaged velocity measurements. Data were then interpolated on to a 5-min time scale.  
224 Ocean current data also included the eastward (u) component at 8.5 m and 48.5 m above the

225 seabed, and northward (v) component 8.5 m and 48.5 m above the bed. Data were obtained  
226 from the Nortek Average AD2CP file, which provides a reading of component velocity at 10-  
227 min intervals; each reading covers a time period of 120 seconds and is composed of 48  
228 independent samples (0.4 Hz), giving an overall measurement uncertainty of  $<1 \text{ cm s}^{-1}$  for  
229 horizontal velocity measurements. Ten-min data were interpolated onto a 5-min timescale  
230 using linear sampling. Each variable is representative of a single 2 m depth bin, chosen to be  
231 safely out of the influence range for ringing and sidelobe interference (5.5m and 45.5 m from  
232 the transducer, respectively). Both u and v velocity components were then rotated clockwise  
233  $117^\circ$  relative to north, to align with the slope in Manta Alley (adjusted positive and negative  
234 directions, shown in Figure 3), resulting in the ocean current predictor variables: cross-shore  
235 current at 48.5 m above the bed (CS current (v) 48.5 m) (5), cross-shore current at 8.5 m above  
236 the bed (CS current (v) 8.5 m) (6), longshore current at 48.5 m above the bed (LS current (u)  
237 48.5 m) (7), and longshore current at 8.5 m above the bed (LS current (u) 8.5 m) (8). To  
238 estimate tidal phase, pressure data was taken from the lower RBR Concerto CTD (depth 64.1  
239 m) and converted to depth data using RSKTools inbuilt conversion function. Data were  
240 cleaned with a median filter and averaged with a running window (both size 501 points). The  
241 Matlab inbuilt find peaks function was then used and ran twice to pick out both high and low  
242 tides by inverting the data on one run. A 5.5 h minimum peak spacing was specified to further  
243 reduce susceptibility to noise, and the resulting data points were visually validated against  
244 the raw depth data. The variable time relative to high tide (9), was then calculated with high  
245 tide as zero and negative hours before (flood) and positive hours after (ebb) (Peel *et al.*,  
246 2019b).

247 All models were fitted using the `gbm.step()` function of the `dismo` R package (Hijmans  
248 *et al.*, 2017). Initial models were built to find suitable settings for four parameters: tree

249 complexity ( $tc$ ), which specifies the number of interactions that should be modelled, learning  
250 rate ( $lr$ ), which regulates the contribution of each tree to the growing model, bag fraction ( $bf$ ),  
251 which controls stochasticity by randomly selecting (without replacement) a specified subset  
252 of the data at each iteration and step size ( $ss$ ), which controls the number of trees which  
253 should be added at each iteration (Elith *et al.*, 2008). The following parameter settings were  
254 tested:  $tc = 1-6$ ,  $lr = 0.01, 0.005, 0.001$  and  $0.0001$ ,  $bf = 0.5, 0.7, 0.9$ ,  $ss = 25$  and  $50$ , resulting  
255 in 144 models.

256 Ten-fold cross-validation (CV) was applied to assess model performance, whereby the  
257 model is fitted to training data and then is tested against a withheld portion (hold-out sample)  
258 of the dataset (Elith *et al.*, 2008). The model's ability to fit the withheld data was then  
259 measured by comparing the area under the receiver operating characteristic curve (AUC) test  
260 statistic (Froeschke *et al.*, 2010; Dedman *et al.*, 2017) for both the training data ( $\tau$ AUC) and  
261 hold-out sample (cross-validation AUC,  $c_v$ AUC) (Dedman *et al.*, 2017; Elith and Leathwick,  
262 2017). The AUC classification ranges from 0 - 1, whereby:  $< 0.5$  (fail),  $0.6 - 0.7$  (poor),  $0.7 -$   
263  $0.8$  (acceptable),  $0.8 - 0.9$  (excellent),  $> 0.9$  (outstanding) (Hosmer and Lemeshow, 2000). The  
264 difference between the  $\tau$ AUC and the  $c_v$ AUC ( $\Delta$ AUC) indicates the level of overfitting of the  
265 primary sample (Dedman *et al.*, 2017). Therefore, better model performance is categorised  
266 by higher AUC values for both  $\tau$ AUC and  $c_v$ AUC, but a lower  $\Delta$ AUC (Dedman *et al.*, 2017).

267 The percentage of deviance explained by the model was determined using the pseudo  
268 determination coefficient ( $D^2$ ), calculated using the following form (Nieto and Mélin, 2017):

$$269 \quad D^2 = 1 - (\text{residual deviance} / \text{total deviance})$$

270 The final model was fitted with  $tc = 6$ ,  $lr = 0.005$ ,  $bf = 0.7$ , and  $ss = 50$  (Table S2). The  
271 relative contribution of predictor variables to the BRT model is measured by averaging the

272 number of times a variable is chosen for splitting and the squared improvement resulting  
273 from these splits (scaled to 100 across all the variables) (Elith *et al.*, 2008). To ensure non-  
274 informative predictors were not hindering model performance, pairwise correlation  
275 coefficients and variance inflation factor (VIF) estimates (Jouffray *et al.*, 2019) were  
276 calculated, all were in an acceptable range; coefficients < 0.6 and/or VIF estimates < 3.5  
277 (Jouffray *et al.*, 2019) (Table S1 and Figure S1).

278         Due to the complex nature of BRTs, model results cannot be easily visualised.  
279 Therefore, partial dependency and interaction plots were generated for interpretation. The  
280 plots display the results of the predicted effect on tag detection probability for a given  
281 predictor, or pair of predictors, after accounting for the mean effects of all other predictors  
282 (Elith *et al.*, 2008; Hastie *et al.*, 2009). Confidence intervals (95%) for the partial dependency  
283 plots were obtained from 1000 bootstrap replicates (Jouffray *et al.*, 2019). For interaction  
284 plots, 100 bootstrap resampling was used to test the significance of the strongest interactions  
285 (Pinsky and Byler, 2015; Jouffray *et al.*, 2019) (interaction strength > 100) by randomly  
286 sampling the occurrence of *M. alfredi* at each location before re-fitting the BRT models  
287 (Jouffray *et al.*, 2019). The size of the interaction was then used to generate a distribution  
288 under the null hypothesis of no interaction among predictors (Jouffray *et al.*, 2019).

## 289 **Results**

### 290 *Detection and resident event summary*

291         Acoustic transmitter tags were deployed on eleven female (adults = 5, sub-adults = 4,  
292 juvenile = 2) and nine male (adults = 3, juvenile = 6) *M. alfredi* (Table 2). Nineteen of the 20  
293 tags returned useable tracks (Table 2). No detections have been recorded for three of the 19  
294 tags since 21<sup>st</sup> November 2019 (CG-MA-0120), 27<sup>th</sup> December 2019 (CG-MA-0161), and 20<sup>th</sup>

295 January 2020 (CG-MA-0141). However, it is not possible to distinguish between acoustic tag  
296 loss and emigration from the study area, and relatively long temporal gaps between  
297 detections of *M. alfredi* in the Chagos Archipelago have previously been reported  
298 (Andrzejczek *et al.*, 2020). Therefore, the current status of these tags has been recorded as  
299 'unknown' rather than 'inactive', pending further data collection.

300 There were a total of 15965 detections during the study period (Table 2). The highest  
301 percentage of detections occurred at the acoustic receiver deployed on the oceanographic  
302 mooring in Manta Alley (51.4%), followed by North IdR Cleaning Station (22.3%) (Figure 4).

303 The overall distribution of detections by hour of the day shows 70.9% of detections  
304 occurred at Egmont Atoll during the day (06:00-18:00) (Figure 5). For adults, only 18.3% of  
305 detections occurred at night (19:00-05:00), while 35% of detections occurred at night for  
306 juveniles.

307 The mean total time between tag deployment when the tags first began transmitting  
308 until the end of the study, when the detection data was downloaded was  $113 \pm 5$  day (range  
309 106-119 days). During this time, tagged *M. alfredi* were tracked (first to last tag detection) for  
310 a mean of  $97 \pm 32$  days (range 3 – 116 days), with a mean of  $50 \pm 23$  detection days (range 2-  
311 92 days). Residency indices show that tagged *M. alfredi* were detected at Egmont Atoll for a  
312 mean of 52% of the days they were tracked (RI =  $52 \pm 15.7\%$ ), with a minimum and maximum  
313 RI of 24% and 80.3%, respectively (Table 2). Mean residency indices were similar for both  
314 adults and juveniles (including sub-adults), which were  $53 \pm 16\%$  and  $51 \pm 16\%$ , respectively.

315 Overall, 2074 resident events were recorded for 19 *M. alfredi* (Figure 6). The highest  
316 number of resident events occurred at Manta Alley (837), totalling 22188 mins (369.8 hrs).  
317 Manta Alley also had the longest individual mean resident event time ( $27 \pm 51$ , Table 3), with

318 the longest resident event of 489 min (8.2 hrs) by a juvenile male (manta-ID CG-MA-0125). Of  
319 the 837 resident events, a total of 35 lasted >120 mins, of which 11 were female (adult = 5,  
320 juvenile = 6) and 24 were males (adult = 3, juvenile = 21).

321 The lowest number of residency events occurred at Ile Sudest (41), totalling 191 mins  
322 (3.1 hrs). Mean resident event time was  $5 \pm 10$  mins, with a maximum resident event time of  
323 56 mins by an adult male (manta-ID CG-MA-0161).

#### 324 *Environmental Influences: Boosted regression trees*

325 Model performance evaluation for the BRT, including all nine predictors, had  
326 outstanding and excellent predictive performance for the training ( $\tau$ AUC = 1) and cross-  
327 validated ( $c_v$ AUC = 0.89) data, respectively, with minimal evidence of overfitting ( $\Delta$ AUC =  
328 0.11). The estimated  $D^2$  suggests that 72 % of the deviance was explained (Table S2).

329 Partial dependency plots (Figure 7) indicate that the probability of detections  
330 decreased with increased near-bed temperature (temp 2 m, 16.2%), and increased with  
331 increased backscatter strength (13.3%) and near-surface temperature (temp 50 m, 13.3%).  
332 Detection probability was higher with greater downward vertical velocity (12.8%), and during  
333 the early stages of a flood tide (12.1%), approximately two hours following low tide when  
334 near-surface longshore current velocity (longshore (v) 48.5 m, 11.7%) was approximately 0.2  
335  $\text{ms}^{-1}$  near the surface and 0.3  $\text{ms}^{-1}$  near the seabed (longshore (v) 8.5 m, 9.1%). For cross-  
336 shore currents, detection probability increased when near-surface currents were flowing  
337 offshore (cross-shore (u) 48.5 m, 6.1%) at approximately  $-0.05 \text{ m s}^{-1}$ , and when near-bed  
338 currents (cross-shore (u) 8.5 m, 5.4%) were flowing inshore at approximately  $0.15 \text{ ms}^{-1}$ .



339           Eight significant pairwise interactions occurred between eight predictors (Table 4 and  
340 Figure S2). These interactions should not be considered in isolation, as they may arise  
341 separately or simultaneously, and may be affected by other variables. However, they provide  
342 insight into the estimated influence of several paired-environmental processes which can  
343 increase the probability of tag detections. For example, tag detections probability was highest  
344 when upward currents speed (vertical velocity) was increased, and the near-surface  
345 temperature (Figure S2a) was warmer (temp 50 >29.5°C). Tag detection probability also  
346 increased with cooler near-bed temperature (temp 2 m <24°C), and increased near-surface  
347 temperatures (temp 50 m >29.5°C) (Figure S2b). It also increased when near-bed cross-shore  
348 currents (cross-shore (u) 8.5 m) were of a high +ve velocity (>0.15ms<sup>-1</sup>) (flowing into the  
349 lagoon) and backscatter was > 55 (Figure S2c), and with high temp 2 m (> 29°C) and  
350 backscatter > 55 (Figure S2d).

## 351 **Discussion**

352           Overall, *M. alfredi* residency at Egmont Atoll, measured by the residency index (RI),  
353 was high (mean RI =52%), which supports previous reports that Egmont Atoll provides key  
354 habitats for this species (Harris, 2019; Andrzejaczek *et al.*, 2020). Similar high levels of  
355 residency have been observed in the Red Sea (mean RI = 65%) (Braun *et al.*, 2015) and at the  
356 Amirante Islands of Seychelles (mean RI = 62%) (Peel *et al.*, 2019b). Adult and juvenile *M.*  
357 *alfredi* displayed similar residency at Egmont Atoll, which is in contrast to patterns observed  
358 in Seychelles, where the RI was lower for adults (Peel *et al.*, 2019b), indicating that the *M.*  
359 *alfredi* habitat at Egmont Atoll is perhaps consistently important for all life stages.  
360 Alternatively, the similar residency of adults and juveniles could be attributed to the acoustic  
361 array design (Peel *et al.*, 2019b). To establish a more robust RI, future research would benefit

362 from increased spatial coverage, including the deployment of acoustic receivers in locations  
363 which may be frequented by juveniles such as inside the lagoon.

364 Overall, detection data displays diel behaviour patterns, with the highest percentage  
365 of detections at Egmont Atoll occurring during the day. Similar diel patterns have been  
366 recorded during studies of various *M. alfredi* subpopulations, where individuals frequented  
367 shallow coastal and island reef systems more often during daylight hours (Dewar *et al.*, 2008;  
368 Jaine *et al.*, 2012; Couturier *et al.*, 2018; Setyawan *et al.*, 2018; Peel *et al.*, 2019b). These  
369 patterns may be associated with the species use of cleaning stations, where cleaner fish are  
370 only active during the day (Côté, 2000). Diel movement patterns may also be associated with  
371 efficient foraging strategies. For example, *M. alfredi* may predominately frequent shallow reef  
372 habitats during the day to feed on reef-associated zooplankton which can accumulate in  
373 surface waters over shallow reefs when avoiding predation from reef-dwelling diurnal  
374 consumers (Alldredge and King, 2009; Leichter *et al.*, 2013). At night, *M. alfredi* may then  
375 travel offshore to forage (Dewar *et al.*, 2008; Jaine *et al.*, 2012; Couturier *et al.*, 2018) when  
376 diel vertically migrating zooplankton ascends into warmer water (Dewar *et al.*, 2008; Braun  
377 *et al.*, 2014; Couturier *et al.*, 2018). This hypothesis is supported by stable isotope analysis,  
378 which indicates that a large proportion of *M. alfredi* diet is made up of both near-surface and  
379 demersal zooplankton (Couturier *et al.*, 2013b; Peel *et al.*, 2019a). The diel *M. alfredi*  
380 movement pattern was less pronounced for juveniles, which were more frequently detected  
381 at night than adults, suggesting that juvenile *M. alfredi* remain in shallower reef habitats  
382 longer. This pattern has also been observed in other subpopulations and is likely a predator  
383 avoidance strategy by the more vulnerable juveniles (Cerutti-Pereyra *et al.*, 2014; Stewart *et*  
384 *al.*, 2018; Peel *et al.*, 2019b). Their smaller body size may also make it less energetically

385 efficient for juveniles to travel offshore (Nøttestad *et al.*, 1999; Peel *et al.*, 2019b), and/or  
386 their foraging experience may be limited (Peel *et al.*, 2019b).

387 Manta Alley had the highest number of detections, and there were repeated resident  
388 events for 18 of the 19 tagged individuals, indicating a high level of site fidelity. Site fidelity is  
389 a well-reported characteristic of *M. alfredi*, having been observed in photographic  
390 identification, acoustic telemetry and satellite tagging studies (Dewar *et al.*, 2008; Deakos,  
391 2011; Jaine *et al.*, 2014; McCauley *et al.*, 2014; Stevens, 2016; Kessel *et al.*, 2017; Couturier *et*  
392 *al.*, 2018). Site fidelity has been attributed in part to the species' reliance on specific  
393 habitats, which provide a sufficient food resource, protection from predation, and  
394 opportunities to clean, socialise and reproduce (Jaine *et al.*, 2014; McCauley *et al.*, 2014;  
395 Stevens, 2016; Perryman *et al.*, 2019). Resident events were longer at Manta Alley than at  
396 any other location. The depth of the majority of the area within the range of the acoustic  
397 receiver is greater than 40 m. As 40 m is the maximum depth of occurrence for cleaner fish in  
398 the Chagos Archipelago (Kuitert, 2014), it is unlikely that these extended resident events at  
399 Manta Alley are associated with cleaning activities. Furthermore, in-water observations at this  
400 site by the authors during this study observed large *M. alfredi* aggregations feeding (~40  
401 individuals) on the surface down to 20 m on several occasions, while no cleaning stations were  
402 identified. Therefore, the most likely driver of the visitation patterns recorded for *M. alfredi*  
403 at this site during this study is foraging opportunities. For *M. alfredi* foraging activities to be  
404 energetically efficient, high densities of prey are required (Armstrong *et al.*, 2016). The BRT  
405 model suggests that *M. alfredi* presence at Manta Alley is associated with various fine-scale  
406 oceanographic processes, which could be combining to enhance localised zooplankton  
407 abundance.

408           A high tag detection probability of *M. alfredi* occurred with cold near-bed and warm  
409 near-surface temperature, and probability increased with increasing difference between  
410 these temperatures. Extreme short-term fluctuations in near-bed temperatures may be  
411 associated with the intrusion of cold-water created by internal waves which disrupt the  
412 thermocline (Shanks *et al.*, 2014). Enhanced concentrations of zooplankton often occur at the  
413 thermocline, the thickness of which can be increased by internal waves (McManus *et al.*,  
414 2005). These internal waves break as they interact with the steep slope of an atoll leading to  
415 the formation of cold-water bores which propagate up the slope (Woodson, 2018; Hosegood  
416 *et al.*, 2019). Bores enhance the upward transport of organisms, and thus the concentration  
417 in surface waters (Stevick *et al.*, 2008), which may provide efficient foraging opportunities for  
418 the zooplanktivorous *M. alfredi*. The upward propagation of cold-water bores has been  
419 observed to vary tidally (Leichter *et al.*, 1996; Hosegood *et al.*, 2019), and can become more  
420 frequent during a flood tide leading to a pulsed delivery of organisms (Leichter *et al.*, 1996;  
421 Woodson, 2018). Here, tag detection probability was high during the early stages of a flood  
422 tide, and was also increased by the interaction effect between a flood tide and cooler near-  
423 surface temperature, which may indicate that cold-water bores propagate up the slope  
424 (Leichter *et al.*, 1996). Plankton sampling and oceanographic measurements obtained inside  
425 the lagoon also indicate that increased zooplankton abundance is associated with the transfer  
426 of plankton into the lagoon from the intrusion of cold water-bores created by breaking  
427 internal waves (Sheehan *et al.*, 2019). The intrusion of cold water may also provide  
428 metabolically advantageous feeding conditions for *M. alfredi* by reducing the energetic cost  
429 of feeding activities (Lawson *et al.*, 2019)

430           In the current study, tag detection probability also increased with the interaction  
431 between high-velocity near-bed cross-shore currents flowing inshore and high levels of

432 backscatter. This interaction may indicate that zooplankton is being carried from the  
433 thermocline into the lagoon during a flood tide and is likely pumped back out during ebb. Due  
434 to the partially enclosed morphology of the lagoon, water entering is likely to be restricted by  
435 the narrow subtidal passages. Even with a low tidal amplitude, strong jet-like currents can be  
436 generated (Dumas *et al.*, 2012), which may increase the density of inflowing (outflowing)  
437 zooplankton approaching low tide (in the early stages of flood), as suggested by the in-water  
438 observations of the current study. During these events, mobile zooplankton may actively seek  
439 refuge zones to avoid predation or import into (export from) the lagoon (Pagano *et al.*, 2017).  
440 Refuge zones include the thermocline and behind shallow back reefs (Leichter *et al.*, 2013),  
441 where zooplankton become concentrated further, providing dense assemblages of prey for  
442 *M. alfredi*. Similar theories of zooplankton retention, which are also related to tide phase,  
443 have been suggested in other regions (Armstrong *et al.*, 2016; Stevens, 2016).

444         The BRT also provided some evidence of the presence of Langmuir Circulation (LC),  
445 which can trap and concentrate particles in the water column (Smith, 2001). The process is  
446 driven by wind and waves which produce helical vortices that appear as rotating cells that  
447 rotate perpendicular to the wind direction (Smith, 2001). The interaction effect between high  
448 velocity near-bed longshore currents flowing when near-surface currents were flowing in the  
449 opposite direction, and high backscatter intensity could be evidence of LC cells. Alternating  
450 cells rotate in opposite directions leading to areas of convergence and divergence (Talley *et*  
451 *al.*, 2011). Downwelling, which increased the probability of tag detections, occurs in areas of  
452 convergence where plankton, other organisms, and particles become trapped in highly  
453 concentrated bands (Kingsford *et al.*, 1991; Thorpe, 2004). These bands may provide ideal  
454 foraging opportunities for *M. alfredi*. As LC can persist for hours or even days (Gargett *et al.*,  
455 2004), it could potentially be associated with resident events which last longer than the

456 influence of the tide (>2 hours). The characteristic surface 'slicks' which often accompany LC  
457 have also been regularly observed by authors in Manta Alley, further supporting this  
458 suggestion.

459 Under well-mixed conditions, LC can develop 'super-cells' which extend the full depth  
460 of the water column (Gargett *et al.*, 2004). These super-cells can transport organisms and  
461 particles from depths up into the water column where they become concentrated in the  
462 narrow bands of the convergence zones (Gargett *et al.*, 2004; Kukulka *et al.*, 2012). Potential  
463 evidence of the presence of super-cells and their positive influence on *M. alfredi* detection  
464 probability is apparent with the interaction effects between high near-bed temperature near-  
465 bed temperature (>28.5°C) and lower near-surface temperature (28-28.5°C), indicating a well-  
466 mixed water column, warmer near-bed temperature (>28.5°C), and high backscatter, and  
467 increased downward vertical velocity (downwelling) and low near-surface temperatures  
468 (<28.5°C). However, high backscatter could also be caused by sediment resuspension events  
469 which can be induced by LC super-cells (Gargett *et al.*, 2004). There may be evidence of the  
470 effect of LC on *M. alfredi* visitation and behaviour patterns in other regions. For example, in  
471 Komodo Marine Park in Indonesia, *M. alfredi* were observed feeding where there were  
472 surface slicks and a high density of particles in the water column (Dewar *et al.*, 2008), which  
473 is characteristic of LC convergence zones (Kingsford *et al.*, 1991). Around Lady Elliot Island  
474 (LEI) in Australia, sightings of foraging individuals and increased acoustic tag detection were  
475 correlated with wind speed (Jaine *et al.*, 2012; Couturier *et al.*, 2018). At LEI, *M. alfredi*  
476 sightings and tag detections peaked at wind speeds around 18 km.h<sup>-1</sup> (approximately 5ms<sup>-1</sup>),  
477 an optimal speed for the development of LC (Langmuir, 1938; Plueddemann *et al.*, 1996). At  
478 LEI, sightings were also associated with cooler sea surface temperatures, with a decrease in  
479 sightings and detections with increased temperature (Jaine *et al.*, 2012; Couturier *et al.*,

480 2018). Strong surface warming can lead to a breakdown of LC by disrupting the balance  
481 between wave-forcing and thermal convection (density-driven circulation) (Li and Garrett,  
482 1994; Min and Noh, 2004), which may reduce the density of prey, leading to a lower number  
483 of sightings and tag detections of *M. alfredi*.

484         There were some limitations to the current study. For example, the position of tagged  
485 *M. alfredi* in the water column and the distance the individual was from the acoustic receiver  
486 and oceanographic equipment could not be established. The acoustic doppler current  
487 profiler (ADCP) was also deployed on the edge of the range of the acoustic receiver.  
488 Therefore, it is possible that some of the changes in the oceanographic conditions which  
489 influence *M. alfredi* visitation patterns were not fully resolved here. These limitations may be  
490 mitigated in future by using acoustic transmitters which also deliver distance and depth  
491 information when the individual is detected. A reconfiguration of the mooring to include an  
492 ADCP in line with all other sensors would also be beneficial. Future research would also  
493 benefit from oceanographic monitoring within the lagoon passage and the Manta Alley  
494 feeding location concurrently to help further resolve the fine-scale processes occurring at the  
495 lagoon-ocean interface. Further investigation into the potential presence of LC and its  
496 influence on *M. alfredi* visitation patterns at Manta Alley is also required. Research should  
497 incorporate *in situ* wind directions measurements of the same spatial and temporal resolution  
498 as the longshore and cross-shore current directions. These measurements should be  
499 accompanied by ADCP backscatter data to detect zones of high echo intensity and periods of  
500 downwelling in relation to *M. alfredi* visitation patterns, and plankton sampling to assess the  
501 content of the water column during LC events.

502           Studying *M. alfredi* at Egmont Atoll provides valuable insight into how the species  
503 respond to fine-scale changes in their oceanographic environment, thus improving our  
504 current knowledge of *M. alfredi* foraging ecology. Evidence provided in this study suggests  
505 that the species regularly take advantage of feeding opportunities which are influenced by  
506 fine-scale oceanographic processes that occur close to the lagoon-ocean interface. These  
507 feeding opportunities appear to occur with tidal periodicity. During a flood tide, cold-water  
508 bores frequently propagate up the slope, transporting zooplankton from the thermocline into  
509 the lagoon through the narrow inlet. During an ebb tide, the zooplankton then flows back out  
510 of the lagoon with the highest concentrations occurring close to low tide. Mobile zooplankton  
511 may become trapped and concentrated around reef structures as they attempt to avoid  
512 predation by moving back into deeper water. High concentrations of zooplankton which  
513 occur during these tidal phases are likely to be short-lived, occurring in pulses, providing  
514 temporally limited feeding opportunities for *M. alfredi*. However, under suitable conditions,  
515 for example, in the presence of LC, highly concentrated bands of zooplankton may persist for  
516 hours, potentially providing extended feeding opportunities which result in *M. alfredi*  
517 spending long periods of time at the location.

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832 **Table 1:** Description of the predictor variables used in boosted regression trees analysis of tagged *Mobula alfredi*  
 833 occurrence at Manta Alley. All predictors are in 5-min means unless otherwise specified. All distances are metres  
 834 above the seabed. Mean values show the value at which the predictor is held for partial dependency and  
 835 interaction plots.

Predictor No.	Predictor	Unit	Mean	Description
1	Temp 2 m	°C	27.7	Temperature 2 m above the bed (depth 64.1 m)
2	Temp 50 m	°C	29.1	Temperature 50 m above the bed (depth 13.4 m)
3	Backscatter	dB	46.1	Depth-mean linearly interpolated into 5-min bins
4	Cross-shore (v) 48.5 m	ms <sup>-1</sup>	-0.007	Surface current 48.5 m above the bed (depth 17.6 m) flowing 27° (-ve) and 207° (+ve) relative to N
5	Cross-shore (v) 8.5 m	ms <sup>-1</sup>	-0.016	Near bed current 8.5 m above the bed (depth 57.6 m) flowing 27° (-ve) and 207° (+ve) relative to N
6	Longshore (u) 48.5 m	ms <sup>-1</sup>	-0.095	Near surface current 48.5 m above the bed (depth 17.6 m) flowing 117° (-ve) and 297° (+ve) relative to N
7	Longshore (u) 8.5 m	ms <sup>-1</sup>	-0.078	Near bed current 8.5 m above the bed (depth 57.6

				m) flowing 117° (-ve) and 297° (+ve) relative to N
				Upward (+ve) and downward (-ve) current flow.
8	Vertical velocity	ms <sup>-1</sup>	0.002	
9	Time to high tide	0.083 h	0.014	Time relative to high tide in steps of 5-min (0.083h) with high tide zero, negative values before (flood) and positive values after (ebb).

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838 **Table 2:** Summary of *Mobula alfredi* acoustic tag deployments (n=19), tracking, detections and Residency Index (RI) for Egmont Atoll. Status refers to the known status of  
 839 tags at the time of last detection data download (17<sup>th</sup> March 2020).

Manta ID	Sex	Maturity status	Tag ID	Deployment Date	Deployment Location	Lat	Long	Last Detection	Total No. of Detection	Tracking Days	Detection Days	Residency Index (RI%)	Status
CG-MA-0035	F	Sub-adult	18890	20/11/2019	Ile Sipaille	-6.67	71.32	13/03/2020	1159	115	92	80	ACTIVE
CG-MA-0046	F	Adult	18892	25/11/2019	Ile Tattamucca	-6.69	71.38	10/03/2020	846	107	61	57	ACTIVE
CG-MA-0070	F	Adult	18891	01/12/2019	Ile Lubine	-6.67	71.32	17/03/2020	1059	108	46	43	ACTIVE
CG-MA-0088	M	Juvenile	18897	28/11/2019	Ile Lubine	-6.67	71.32	15/03/2020	907	109	43	40	ACTIVE
CG-MA-0094	F	Sub-adult	18894	30/11/2019	Ile Sipaille	-6.66	71.31	13/03/2020	1116	105	67	64	ACTIVE
CG-MA-0112	M	Juvenile	18893	01/12/2019	Ile Lubine/Sipaille	-6.66	71.31	13/03/2020	1129	104	49	47	ACTIVE
CG-MA-0117	F	Sub-adult	18887	20/11/2019	Ile Lubine	-6.67	71.32	13/03/2020	718	115	50	44	ACTIVE
CG-MA-0118	M	Juvenile	18900	19/11/2019	Ile Sipalle	-6.66	71.31	11/03/2020	678	114	41	36	ACTIVE
CG-MA-0119	F	Juvenile	18901	19/11/2019	Ile Sipalle	-6.67	71.32	13/03/2020	801	116	54	47	ACTIVE
CG-MA-0120	F	Adult	18902	19/11/2019	Ile Sipalle	-6.67	71.32	21/11/2019	15	3	2	76	UNKNOWN
CG-MA-0121	M	Juvenile	18903	19/11/2019	Ile Sipalle	-6.67	71.32	13/03/2020	1770	116	84	73	ACTIVE
CG-MA-0124	M	Adult	18885	20/11/2019	Ile Lubine	-6.67	71.32	12/03/2020	559	114	44	39	ACTIVE
CG-MA-0125	M	Juvenile	18895	20/11/2019	North IDR Cleaning St	-6.64	71.32	14/03/2020	1272	116	60	52	ACTIVE
CG-MA-0139	F	Adult	18899	25/11/2019	Ile Tattamucca	-6.69	71.38	15/03/2020	763	112	73	66	ACTIVE
CG-MA-0140	M	Juvenile	18898	30/11/2019	North IDR Cleaning St	-6.64	71.32	13/03/2020	711	105	25	24	ACTIVE

CG-MA-0141	F	Adult	18889	28/11/2019	Ile Lubine	-6.67	71.32	20/01/2020	411	54	31	58	UNKNOWN
CG-MA-0142	F	Sub-adult	18884	02/12/2019	Ile Tattamucca	-6.70	71.40	15/03/2020	1216	105	59	56	ACTIVE
CG-MA-0151	M	Adult	18896	01/12/2019	Ile Lubine	-6.68	71.33	12/03/2020	794	103	62	60	ACTIVE
CG-MA-0161	M	Adult	18888	02/12/2019	Ile Carre Pate	-6.68	71.35	27/12/2019	41	26	7	27	UNKNOWN

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851 **Table 3:** Summary of acoustic receiver deployment locations, recording times and resident event durations.

Location	Deployed	Lat	Long	Depth (m)	Height above seabed (m)	No. days recording	No. <i>M.</i> <i>alfredi</i>	Mean resident event (min±SD)	Max resident event (mins)
Ile Sipaille	19/11/2019	71.32	-6.67	14.6	1.5	116	19	15±26	200
Ile Sudest	01/12/2019	71.40	-6.70	15	1.8	104	11	5±10	56
Manta Alley	30/11/2019	71.35	-6.64	70	48	109	18	27±51	489
North IdR Cleaning Station	19/11/2019	71.32	-6.64	13.6	1.6	116	17	19±36	294
South Manta Alley	30/11/2019	71.39	-6.67	14.2	1.8	105	18	16±26	133

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857 **Table 4:** Pairwise interactions between predictor variables with all other variables held to their respective mean (Table 1). Higher interaction size values indicate a more  
 858 substantial interaction effect; near zero indicates negligible interactions. All interactions were significant ( $p < 0.01$ ). The suggested influence of the interaction on the  
 859 probability of detections is described along with the maximum detection probability estimated for each interaction.

Plot	Predictor 1	Predictor 2	Interaction size	Nature of interaction increasing tag detection probability	Max detection probability (%)
S2a	Temp 50 m	Vertical velocity	768.77	Warmer near-surface temperature and increased upward vertical velocity.	90
S2b	Temp 50 m	Temp 2 m	741.86	Cooler near-bed temperature and increased near-surface temperature indicating the water column is stratified. Warmer near-bed temperature (>28.5°C) with similar near-surface temperature (28-28.5°C)	92
S2c	Cross-shore (v) 8.5 m	Backscatter	427.88	Near-bed longshore currents flowing at velocity of >0.15ms <sup>-1</sup> (+ve, flowing into the lagoon) and high backscatter intensity (>55).	85

S2d	Temp 2 m	Backscatter	405.69	Warmer near-bed temperature (>29.5°C) and high backscatter intensity (>55).	98
S2e	Longshore (u) 8.5 m	Time to high tide	165.86	During the early stages of flood with increasing near-bed longshore current velocity (+ve, flowing from North IdR Cleaning Station towards South Manta Alley) flowing from the	86
S2f	Longshore (u) 48.5 m	Time to high tide	124.66	During the early stages of flood with moderate velocity (approximately 0.3-0.4 ms <sup>-1</sup> ) longshore near-surface current (+ve, flowing from North IdR Cleaning Station towards South Manta Alley)	66
S2g	Temp 50 m (53%)	Time to high tide	182.1	During the early stages of flood with cooler near-surface temperature (<29°C) and during ebb close to low tide with warmer near-surface temperature (>29.5°C).	59
S2h	Longshore (v) 8.5 m	Backscatter	100.63	Longshore near-bed currents flowing at moderate to the maximum speed observed (-0.66 ms <sup>-1</sup> ) from South Manta Alley towards North IdR Cleaning Station, and high backscatter intensity (>55).	73

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861 **Figure 1:** The Central Indian Ocean with Chagos Archipelago; British Indian Ocean Territory  
862 indicated within the red box (left inset). The Chagos Archipelago with Egmont Atoll indicated  
863 within the red box (left). Egmont Atoll and the location of the oceanographic and acoustic  
864 receiver mooring in Manta Alley (red and yellow dots) and four acoustic receivers (green dots)  
865 (top right). Bathymetric view of Manta Alley obtained via multibeam survey (Robinson and  
866 Hosegood *et al.*, unpublished data) showing the location of the moorings (bottom right).  
867 Bottom right legend showing instrument configurations of the long thermistor string (red  
868 dot/pin) and subsurface ADCP moorings (yellow dot/pin) deployed 182 m apart anchored at  
869 a depth of 66 m. Z is the height above the seabed.

870 **Figure 2:** Reef manta rays (*Mobula alfredi*) engaged in feeding activities at the Manta Alley  
871 feeding aggregation site in north Egmont Atoll. Photo by Simon Hilbourne, Manta Trust.

872 **Figure 3:** Original current u and v components (yellow dashed lines) and after clockwise  
873 rotation 117° relative to north (white lines). Arrows on the white lines show the direction of  
874 longshore u (LS U-ve and LS U+ve) and cross-shore v (CS V-ve and CS V+ve). Showing mooring  
875 locations: long thermistor string (red dot) and subsurface ADCP moorings (yellow dot).

876 **Figure 4:** Percentage of detections at each site.

877 **Figure 5:** Percentage distribution of detections by hour of the day at Egmont Atoll for all  
878 tagged *M. alfredi* (left), adults only (middle) and juveniles only (right).

879 **Figure 6:** Resident events at each site showing location (by colour) and time at the location  
880 (by size).

881 **Figure 7:** Partial dependency plots showing the effect of each predictor variable: temperature  
882 2 m above the bed (Temp 2 m), depth-mean backscatter intensity linearly (Backscatter),

883 temperature 50 m above the bed (Temp 50 m), upward (+ve) and downward (-ve) current  
884 flow (Vertical velocity), time relative to high tide in steps of 5-min (0.083h) with high tide zero,  
885 negative values before (flood) and positive values after (ebb) (Time to high tide), near-surface  
886 current 48.5 m above the bed (depth 17.6 m) flowing 117° (-ve) and 297° (+ve) relative to N  
887 (Longshore (u) 48.5 m), near bed current 8.5 m above the bed (depth 57.6 m) flowing 117° (-  
888 ve) and 297° (+ve) relative to N (Longshore (u) 8.5 m), near-surface current 48.5 m above the  
889 bed (depth 17.6 m) flowing 27° (-ve) and 207° (+ve) relative to N (Cross-shore (v) 48.5 m),  
890 near bed current 8.5 m above the bed (depth 57.6 m) flowing 27° (-ve) and 207° (+ve) relative  
891 to N (Cross-shore (v) 8.5 m), on the occurrence of tagged *M. alfredi* at Manta Alley while  
892 keeping all other variables at their mean. The green line shows smoothed partial decency.  
893 Rugs display the distribution of the data for presence (top, blue), and absence (red, bottom).

894

#### 895 **Data Accessibility**

896 The data that supports these findings are available from FigShare (doi:  
897 10.6084/m9.figshare.13139309) following a one-year embargo from the date of publication  
898 to allow for further publication of research findings.

899

#### 900 **Competing Interests**

901 There are no competing financial, professional, or personal interests that might have  
902 influenced the performance or presentation of the work described in this manuscript.

#### 903 **Author contributions**

904 **Joanna L. Harris:** Conceptualisation; data curation; formal analysis; investigation;  
905 methodology; project administration; software; visualisation; writing – original draft  
906 preparation; writing – review & editing. **Phil Hosegood:** Conceptualisation; investigation;  
907 project administration; supervision; writing – review & editing. **Edward Robinson:** Data  
908 curation; software; investigation; writing – review & editing. **Clare B. Embling:** Supervision;  
909 writing – review & editing. **Simon Hilbourne:** Investigation; writing – review & editing. **Guy**  
910 **M. W. Stevens:** Conceptualisation; supervision; writing – review & editing.

911

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921

## 922 **Authors' Contributions**

923 Joanna Harris: Conceptualization-Lead, Data curation (lead); Formal analysis (lead);  
924 Investigation (lead); Methodology (lead); Writing-original draft (lead); Writing-review &  
925 editing (lead). Phil Hosegood: Conceptualization (supporting); Funding acquisition (equal);  
926 Investigation (supporting); Project administration (lead); Supervision (equal); Writing-review

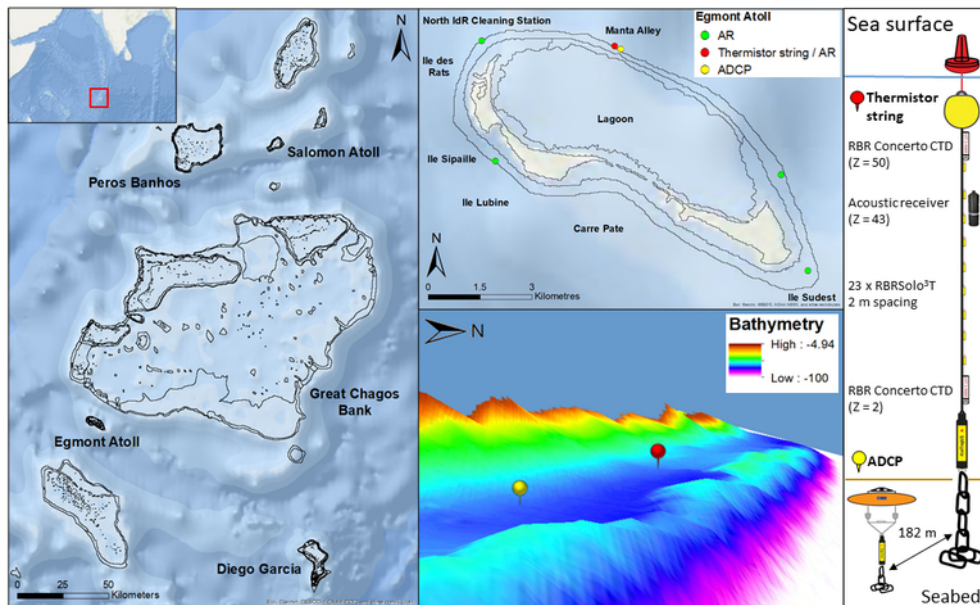


927 & editing (supporting). Edward Robinson: Data curation (supporting); Investigation  
928 (supporting); Software (supporting); Writing-review & editing (supporting). Clare Embling:  
929 Supervision (equal); Writing-review & editing (supporting). Simon Hilbourne: Investigation  
930 (supporting); Writing-review & editing (supporting). Guy Stevens: Conceptualization  
931 (supporting); Funding acquisition (equal); Supervision (equal); Writing-original draft  
932 (supporting); Writing-review & editing (supporting).

933

934 **Conflict of Interest.**

935 None declared.



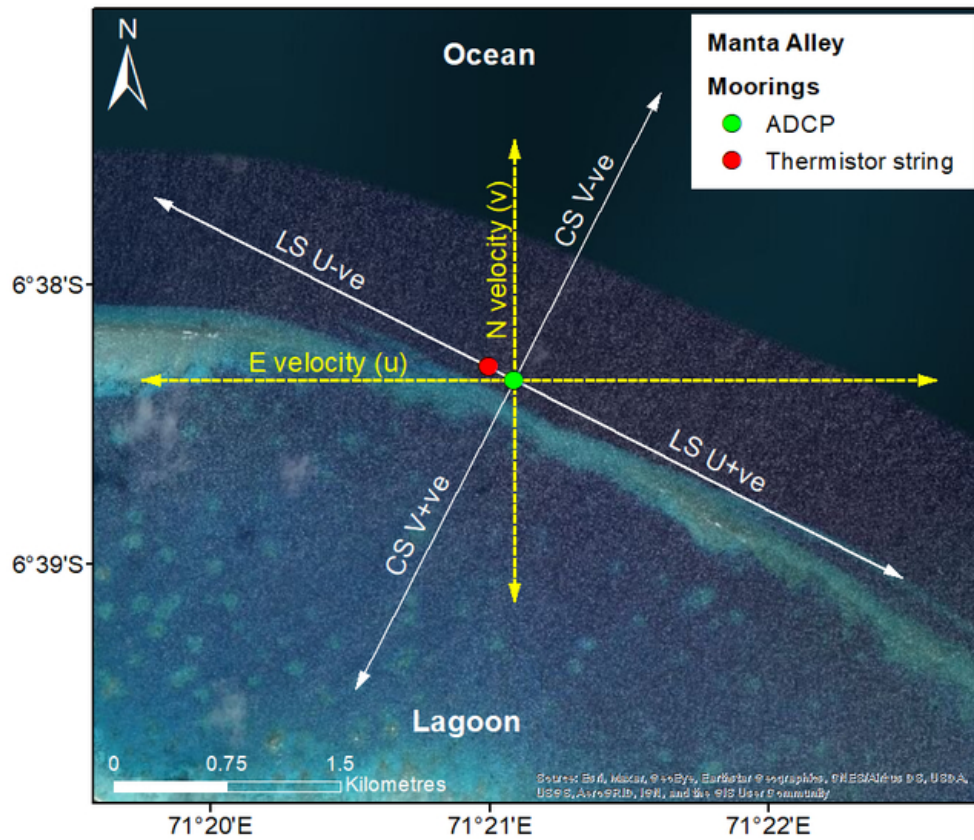
The Central Indian Ocean with Chagos Archipelago indicated within the red box (left inset). The Chagos Archipelago with Egmont Atoll indicated within the red box (left). Egmont Atoll and the location of the oceanographic and acoustic receiver mooring in Manta Alley (red and yellow dots) and four acoustic receivers (green dots) (top right). Bathymetric view of Manta Alley obtained via multibeam survey (Robinson and Hosegood *et al.*, unpublished data) showing the location of the moorings (bottom right). Bottom right legend showing instrument configurations of the long thermistor string (red dot/pin) and subsurface ADCP moorings (yellow dot/pin) deployed 182 m apart anchored at a depth of 66 m. Z is the height above the seabed.

33x22mm (600 x 600 DPI)



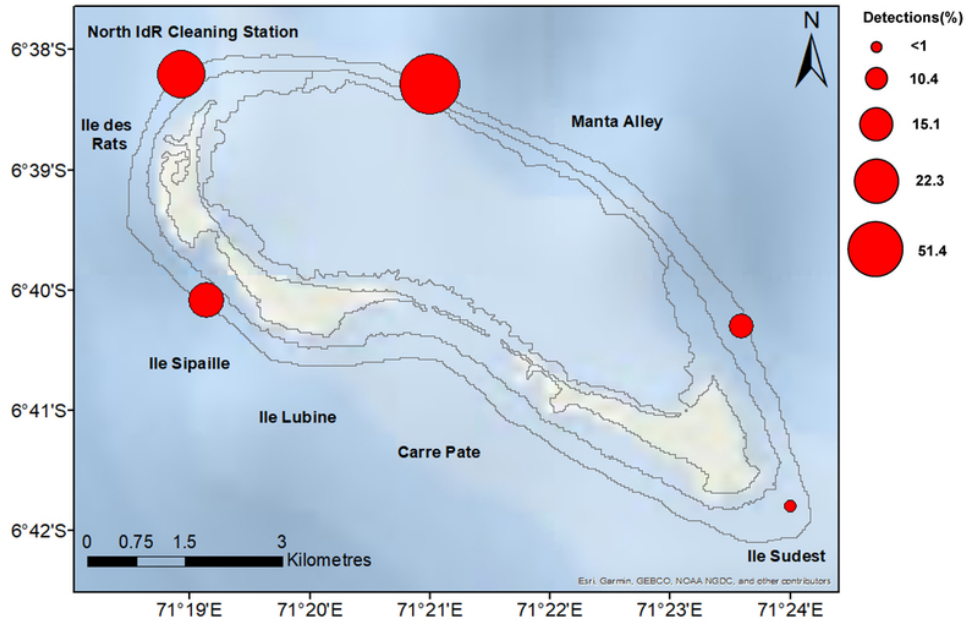
Reef manta rays (*Mobula alfredi*) engaged in feeding activities at the Manta Alley feeding aggregation site in north Egmont Atoll.

169x113mm (600 x 600 DPI)



Original current  $u$  and  $v$  components (yellow dashed lines) and after clockwise rotation  $117^\circ$  relative to north (white lines). Arrows on the white lines show the direction of longshore  $u$  (LS U-ve and LS U+ve) and cross-shore  $v$  (CS V-ve and CS V+ve). Showing mooring locations: long thermistor string (red dot) and subsurface ADCP moorings (yellow dot).

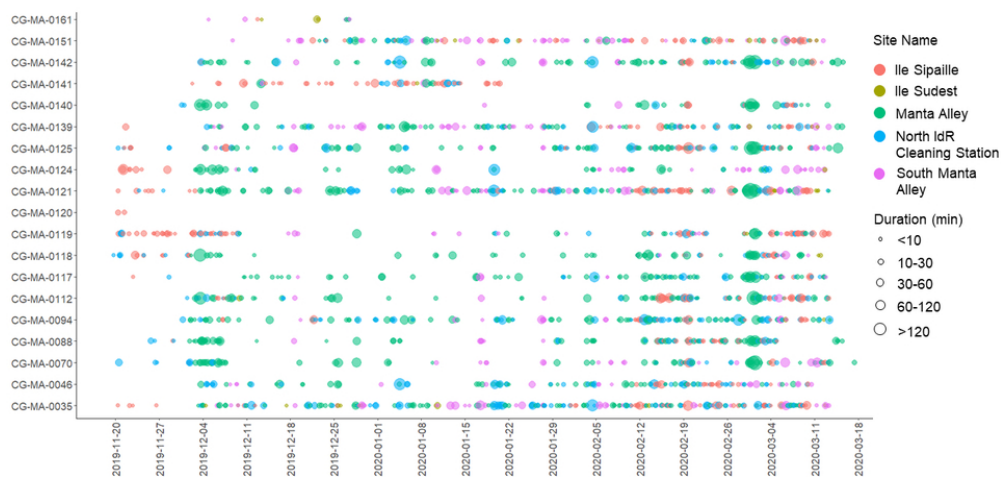
27x25mm (600 x 600 DPI)



Percentage of detections at each site.

34x22mm (600 x 600 DPI)

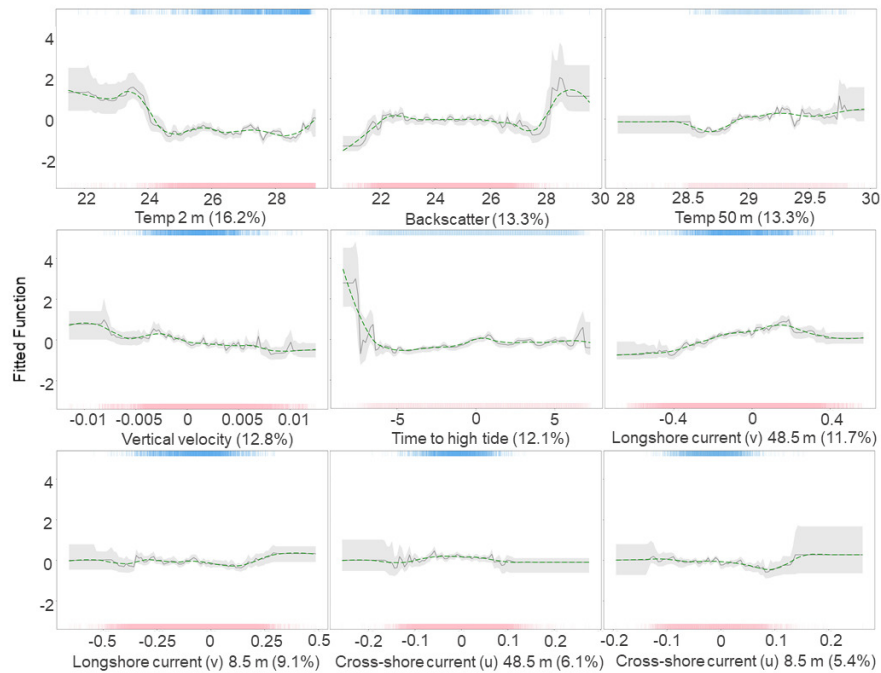




Resident events at each site showing location (by colour) and time at the location (by size).

40x22mm (600 x 600 DPI)

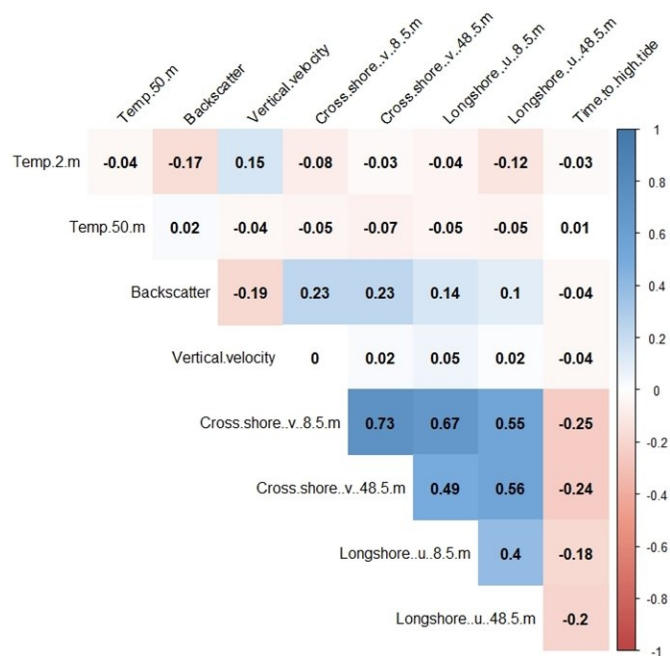




Partial dependency plots showing the effect of each predictor variable: temperature 2 m above the bed (Temp 2 m), depth-mean backscatter intensity linearly (Backscatter), temperature 50 m above the bed (Temp 50 m), upward (+ve) and downward (-ve) current flow (Vertical velocity), time relative to high tide in steps of 5-min (0.083h) with high tide zero, negative values before (flood) and positive values after (ebb) (Time to high tide), near-surface current 48.5 m above the bed (depth 17.6 m) flowing 117° (-ve) and 297° (+ve) relative to N (Longshore (u) 48.5 m), near bed current 8.5 m above the bed (depth 57.6 m) flowing 117° (-ve) and 297° (+ve) relative to N (Longshore (u) 8.5 m), near-surface current 48.5 m above the bed (depth 17.6 m) flowing 27° (-ve) and 207° (+ve) relative to N (Cross-shore (v) 48.5 m), near bed current 8.5 m above the bed (depth 57.6 m) flowing 27° (-ve) and 207° (+ve) relative to N (Cross-shore (v) 8.5 m), on the occurrence of tagged *M. alfredi* at Manta Alley while keeping all other variables at their mean. The green line shows smoothed partial decency. Rugs display the distribution of the data for presence (top, blue), and absence (red, bottom).

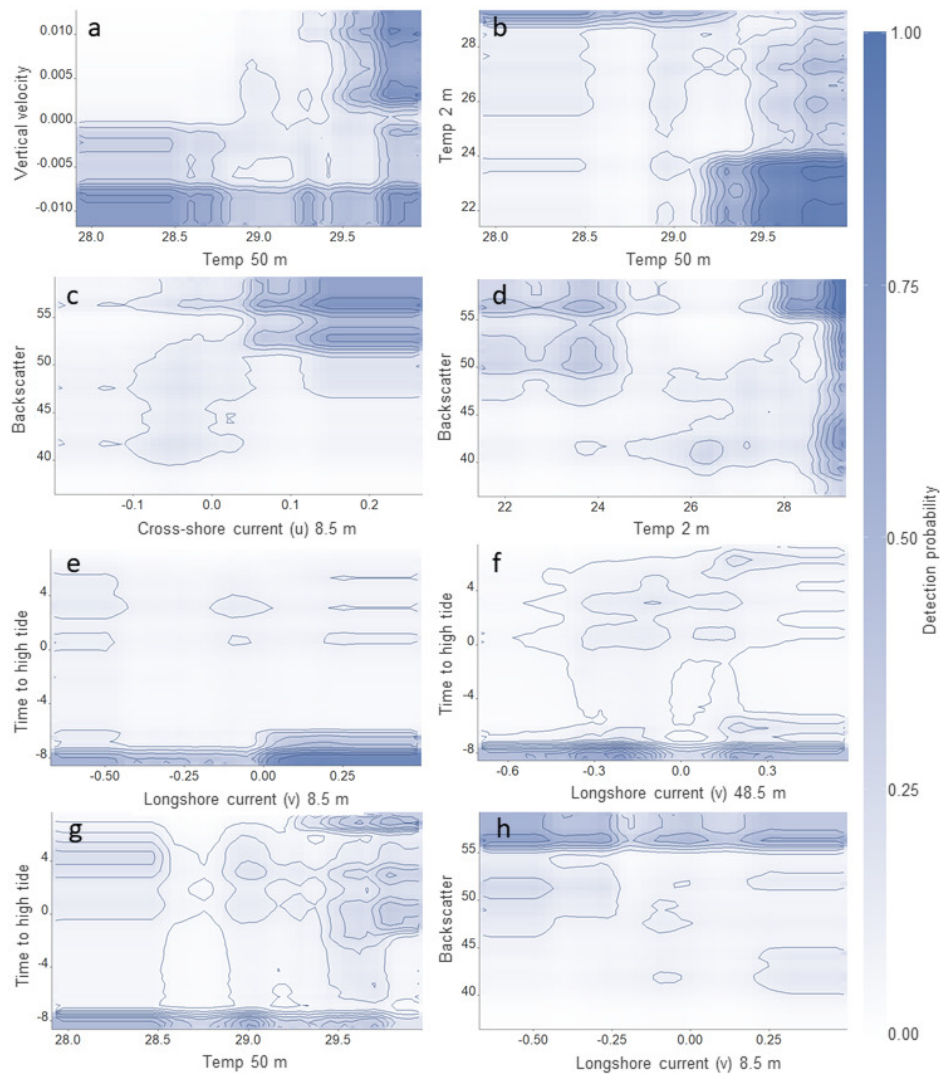
99x67mm (300 x 300 DPI)





Correlation matrix for all predictors used in the boosted regression trees model.

88x60mm (300 x 300 DPI)



Pairwise interactions between predictor variables contour lines highlight the probability of *M. alfredi* tag detection at Manta Alley while keeping all other variables at their mean. All interactions were significant ( $p < 0.01$ ). Plot number related to the interaction effect shown in Table 3. A detailed description of each variable can be found in Table 1.

67x73mm (300 x 300 DPI)