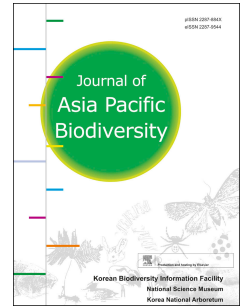# Journal Pre-proof

Distribution and habitat partitioning of cetaceans (Mammalia: Cetartiodactyla) in the Bohol Sea, Philippines.

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1 Original Article

2 **Distribution and habitat partitioning of cetaceans (Mammalia:**

3 **Cetartiodactyla) in the Bohol Sea, Philippines.**

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15

16 **Running title:** Cetaceans of the Bohol Sea, Philippines

17

18 **Abstract**

19

20   Understanding broad-scale species distribution and finer-scale ecological interactions is
21 essential for conservation. We assessed species richness, distribution, habitat use and interspecific
22 associations of cetacean in the Bohol Sea, Philippines. During 72 days of dedicated survey (2010 -
23 2013), we encountered 12 species of cetacean in 291 sightings, 16.8% of which involved mixed
24 species. We used maximum entropy (MaxEnt) models to assess species' habitat suitability and
25 found slope and distance from the coast to be influential contributors to cetacean distribution. To
26 explore habitat use, through foraging ecology and niche segregation of sympatric species, we
27 compared behavioral budgets across species and found significant differences (chi-sq = 21.44; p-
28 value = 0.044). We then used GLMs to determine the foraging likelihood in relation to
29 oceanographic features, group size and presence of associated species. Results from model
30 selection complimented those derived from MaxEnt. However, some inter-specific exclusion
31 behavior might also occur. Overall, our study suggests that the Bohol Sea supports a high cetacean
32 biodiversity while more complex inter-specific dynamics might further shape species' ecological
33 niches. These results highlight the importance of multi-species ecology and can be used to develop
34 management actions.

35

37

Introduction

Marine biodiversity is threatened by anthropogenic activities and climate change (Hazen et al. 2013; Worm and Lotze 2021). Identifying areas of high biodiversity is a key conservation strategy as it allows for the implementation of effective spatial management (e.g., through the identification of marine protected areas) (Jones and Cheung 2015). The conservation of marine megafauna, including cetacean (i.e., whale and dolphin) species is particularly important due to the top-down effect of predators on the broader ecosystem (Castro Tavares et al. 2019). Marine mammal species richness is often higher in areas of human activity, increasing their conservation priority (Pompa et al. 2011). Recently, a new framework has been proposed to identify Important Areas for Marine Mammals (IMMA) to support local and national regulatory and management actions (Important Marine Mammal Areas, www.marinemammalhabitat.org; Tetley et al. 2022).

Tropical areas are characterized by high marine biodiversity, and cetacean occurrence has been studied in many of these places, including the Gulf of Mexico (Maze-Foley and Mullin 2006) the Indian Ocean (Gross et al. 2009), the Bahamas (Macleod 2004) and the Eastern Tropical Pacific Ocean (Ballance et al. 2006). Cetacean communities in these areas feature a wide range of species as *Stenella* spp., common bottlenose (*Tursiops truncatus*) and common dolphins (*Delphinus delphis*), rough-toothed dolphins (*Steno bredanensis*), Risso's dolphin (*Grampus griseus*), melon-headed whales (*Peponocephala electra*), short-finned pilot whales (*Globicephala machrorynchus*), pygmy or dwarf sperm whale (*Kogia* spp.), false killer whale (*Pseudorca crassidens*) and sperm whales (*Physeter macrocephalus*). Moreover, baleen species as humpback whales (*Megaptera novangliae*; Acebes et al. 2007), Bryde's whales (*Balaenoptera brydei*) and blue whales (*Balaenoptera musculus*) are seasonal occupants of the tropical waters (Ballance et al. 2006). The composition of each community and the residency degree of the various species may vary accordingly to the area examined.

Philippine waters are inhabited by 24 species of cetacean, throughout a range of habitat types. Although some areas have been studied extensively, peer-reviewed publications information on current cetacean distribution in these waters are scarce (Dolar et al. 2006; Acebes et al. 2021). The Visayan region, located within the central Philippines, is one of the richest marine biodiversity hotspots in the world and contains Tañon Strait and Bohol Sea Important Marine Mammal Areas (IMMAs), designated by the International Union for the Conservation of Nature (IUCN) (Notarbartolo di Sciara and Hoyt 2020). Although a major area for primary productivity (Cabrera et al. 2011), the Bohol Sea has received relatively low research attention, in contrast to the adjacent Tañon Strait (e.g., Dolar et al. 2006). The Bohol Sea also hosts a profitable marine tourism industry,

72 including whale-watching (Samonte-Tan et al. 2007; Sorongon et al. 2010), has developed after the

73 ban of dolphin hunting in 1992 and further of all cetaceans in 1997 (Acebes 2009; Acebes 2014).

74 While the consumptive use of cetaceans has stopped in the Bohol Sea, wildlife tourism, fishing

75 industry, shipping, ferries, and climate change remain as prominent risks to cetacean populations

76 in the area. Marine biodiversity in South-East Asian waters is generally at risk from human

77 activities (Halpern et al. 2015) but order to protect species from the rapid expansion of marine

78 activities in the Bohol Sea and the global challenge of climate change, is important to provide

79 updated knowledge on the cetacean community. We conducted non-systematic surveys to record

80 presence and relative abundance of cetacean in the northeastern Bohol Sea. We used Maximum

81 Entropy (MaxEnt) software (Breen et al. 2016; Rogan et al. 2017) to model cetacean habitat

82 suitability across the study area and determine response to static environmental features (e.g., Sahri

83 2021; Smith et al. 2021; Hanf et al. 2022). These output scan support effective marine spatial

84 planning and improve species' protective measures (Peterson 2003; Merow et al. 2013; Cañadas et

85 al. 2002). Understanding species' ecological niches, in terms of interactions and habitat use,

86 strengthens conservation efforts (Kiszka et al. 2011; Kiszka et al. 2015) and avoid species

87 displacement to suboptimal areas (Pirotta et al. 2018). Determining the drivers of the fine-scale

88 distribution of cetacean species allows for a better understanding of their resilience in a changing

89 environment (Díaz López and Methion 2018). Foraging ecology is a likely driver of cetacean

90 presence (Hazen et al. 2009) but reproductive needs (i.e., calves' protection from predators) and

91 inter-specific competition can also influence cetacean distribution (Díaz López and Methion 2018).

92 We compared behavioral budgets across species to determine habitat use. For those species with

93 sufficient data, we further explored environmental and biological variables that could affect the

94 likelihood of foraging behavior to test the hypothesis that foraging ecology determine a species

95 spatial distribution. We also reported on group size and composition to explore whether the area

96 could serve as a nursing ground. The exclusion hypothesis states that inter-specific competition for

97 resources can explain fine-scale species distribution for species with overlapping (partially or

98 entirely) home range (Zabala et al. 2009; Pinela et al. 2011; Reisinger et al. 2020). We tested this

99 hypothesis by looking at patterns of mixed-species associations. Our study provides insights on the

100 distribution and behavioral ecology of cetacean species inhabiting the Bohol Sea and provide useful

101 information for management and conservation effort.

102

103 **Material and methods**

104

105 *Study area*

4

106

107   The 2529.3 km^2 study area is located in the northeast Bohol Sea, between Pamilacan Island,

108   in the municipality of Baclayon, (Bohol Province) in the west and San Ricardo, Southern Leyte in

109   the east (Figure 1). The Bohol Sea, also known as the Mindanao Sea, is a semi-enclosed marginal

110   sea extending 29,000 sq km from the Sulu Sea to the Pacific Ocean (Indab and Suarez-Aspilla

111   2004). It is bound by the Visayan Islands of Mindanao (south) and Negros, Bohol and Leyte (north).

112   The Bohol Sea features a complex hydrographic system referred as double-estuarine circulation

113   (Cabrera et al. 2011). The northeastern part of the Bohol Sea is geographically characterized by an

114   inshore deep trench where the Mindanao Current, a bifurcation of the North Equatorial Current

115   coming from the Pacific Ocean, causes an overturning circulation that promotes upwelling of cold,

116   nutrient-rich waters within the Bohol Sea (Cabrera et al. 2011). Due to the Mindanao current and

117   the inshore deep trench most of the biomass is expected to be in the northeastern part of the Bohol

118   Sea. promoting phytoplankton blooms (Cabrera et al. 2011).

119

120   *Data collection*

121

122   Non-systematic, dedicated boat surveys were conducted from March 2010 to July 2013.

123   Boat renting and water access facilities were available only in Jagna (Bohol) and Pamilacan Island

124   (Baclayon, Bohol) (herein referred as Pamilacan). Surveys were undertaken on motorized

125   'Bangkas', traditional Philippine wooden double outrigger boats. Surveys were conducted in good

126   sightings conditions in Beaufort sea state ≤3 and daylight hours (as early as 6:30 am until sunset

127   around 8 pm). Maximum effort was expended during the dry season (from January to April) and

128   limited during the wet season (from May to December) due to restrictive weather conditions. The

129   survey targeted waters off Jagna and Pamilacan (Figure 1), where boats could be rented and

130   launched from. The ability to travel between these areas was hindered by boat engine capability

131   and the amount of fuel that could be carried onboard. Surveys maximized area coverage by

132   encompassing the entire bathymetric range crossing isobaths in a perpendicular fashion. In the

133   survey area, mean depth was 1,129 m, median depth was 1,419 m and greatest depth was 1,869 m.

134   The sampling strategy was constant throughout the survey period. Effort was continuous

135   during the surveys and sightings were recorded by a team of experienced observers ranging from 3

136   to 7 individuals, with multiple years of field experience in cetacean research. Species were

137   identified by experienced marine mammal scientists using morphological characteristics. An

138   encounter started when animals were at less than 500 meters from the research boat or whenever

139   was possible to determine group size and predominant behavior of the group. A group was defined

140 as multiple individuals within 50 meters of each other exhibiting same activity and moving in

141 similar direction. Whenever possible, location coordinates, group size, calf presence and

142 predominant behavioral state (displayed by more than 50% of the group), were recorded for each

143 cetacean encounter. The behavioral state was assigned one of four mutually exclusive categories:

144 foraging, traveling, resting, or socializing.

145

146 *Analyses*

147

148 A combination of MaxEnt, summary statistics and regression analysis   were used to

149 understand cetacean broad-scale distribution and finer-scale habitat use, based on possible

150 ecological interactions. MaxEnt models were used to assess relative habitat suitability across the

151 study area, and the influence of static environmental variables. Drivers of habitat use were explored

152 using two different approaches to determine whether the Bohol Sea could be used as a i) nursing

153 ground and/or ii) foraging ground. We also explored whether inter-specific competition influences

154 species distribution testing the exclusion hypothesis. Summary statistics were used on presence-

155 only data to quantify the relative abundance of cetacean species and group size and composition to

156 determine whether the study area could be used as a nursing ground. We then used estimated species

157 behavioral budgets and utilized generalized linear models (GLMs) to explore foraging likelihood

158 (limited to those species for whom enough data were available). Finally, the number and patterns

159 of mixed species encounters were summarized and compared across species to explore inter-

160 specific competition and to test an exclusion hypothesis.

161

162 *Satellite-derived environmental data*

163

164 Environmental data for use in MaxEnt modelling and GLMs were derived *ex-situ*, using

165 ArcGIS (v 10.4). Static variables (i.e., water depth, slope and distance from the coast) were used to

166 inform both model techniques. Depth was extracted for the survey area from global bathymetry

167 (GEBCO Compilation Group 2008), and slope was derived from this using the "slope tool".

168 Distances from the coast (GADM 2018) were calculated using the ArcGIS Euclidean Distance tool.

169 In addition to the static variables, we also obtained dynamic satellite-derived environmental data

170 (i.e., sea surface temperature (SST) and chlorophyll-a (chl-a)) using Marine Geospatial Ecology

171 Tools (MGET; Roberts et al. 2010). Daily SST were extracted for the immediate study area from

172 Multiscale Ultrahigh Resolution (MUR) blended SST data produced by the NASA Jet Propulsion

173 Laboratory Physical Oceanography Distributed Active Archive Center (PO.DAAC). SST was

174 assessed for study area coverage and explored to determine whether values varied across the spatial

175 and temporal extent of the survey. We used chl-a concentration is also used as a proxy for prey

176 abundance which, in turn, can influence habitat use (Huot et al. 2007; Druon et al. 2019), however

177 dense cloud cover over the Bohol Sea was frequent during our study periods, which resulted in

178 large areas of missing data (Arango et al. 2011). As such, we omitted this variable from further

179 analysis.

180

181 *Habitat suitability*

182

183   We modelled broad-scale habitat suitability by amalgamating cetacean sightings across

184 years, as a presence-only dataset because of the variability in which effort was recorded. We

185 modelled these data using MaxEnt as it is a proven robust approach to modelling when absence

186 data is unavailable or not dependable (Philips et al. 2004; Elith 2011) MaxEnt models were run for

187 melon-headed whales, Fraser's dolphins and spinner dolphins, species for which substantial

188 sightings data were available. Models were not run for the remaining species observed due to the

189 low number of encounters. Depth, slope, and distance from land were modelled as continuous

190 variables. We decided to use the MaxEnt default settings for regularization, features and

191 prevalence. In machine learning, regularization runs a series of model iterations from which the

192 model gains information. MaxEnt uses an automatic regularization setting that has been fine-tuned

193 to suit the number of feature types and sample locations and avoid models from being over-fit

194 (Phillips et al. 2006). Machine learning techniques rely on base functions and transform explanatory

195 data as features. In MaxEnt, the auto features setting applies linear, product, quadratic, hinge,

196 threshold and categorical transformations to the data in order to detect patterns in species response

197 to environmental stimuli, which are often of a complex nature (Elith et al. 2010). We decided not

198 to constrain this setting as we deemed the sample sizes for each species to be large enough to allow

199 MaxEnt to determine which features algorithms were based on, which incorporates a rule regarding

200 the sample size of the species data. We selected the default prevalence of 0.5, which represents a

201 50% change of species occurrence in any cell (Phillips et al. 2004; Elith et al. 2006). Cross-

202 validation was used to test the models. Samples were divided into 25 replicate folds, with each fold

203 in turn used for test data. Cross-validation is preferable to using a single training/test split in the

204 dataset as it uses all the data for validation, thus making better use of available data. Model

205 performance was expressed with the Area Under the Curve (AUC) metric and interpreted following

206 Hosmer and Lemeshow (1989): <0.5 = none; 0.5 to 0.7 = poor; 0.7 to 0.8 = acceptable; 0.8 to 0.9

207 = excellent; >0.9 = outstanding. Mean relative habitat suitability, as a probability distribution from

208   zero to one based on favourable environmental conditions across the study area, was generated in

209   logistic output and generated as maps. We assessed the relationship of species occurrence to each

210   environmental parameter using marginal response curves. Marginal response curve output

211   represents the influence of the variable on species occurrence, without interactions with other

212   variables. The importance of each variable, relative to the other variables, was interpreted from

213   permutations expressed as a percentage contribution to the model algorithm.

214

215   *Habitat use*

216

217   We estimated group size and composition to record the prevalence of groups containing

218   calves as determined by size relative to adults. We compared behavioral budgets across species

219   using Chi-squared parametric test. The observed behavioral frequencies were compared to the

220   expected frequencies and p-values were computed by Monte Carlo simulations based on 10,000

221   replicates. To test the hypothesis that habitat use is driven by foraging ecology, we used GLM to

222   estimate influential parameters on cetacean foraging likelihood. Behavioural data were only

223   available for 2012 and 2013 and for only three species (melon-headed whale, spinner dolphins, and

224   Fraser's dolphin, *Lagenodelphis hosei*) there were sufficient sightings (N > 30) to allow a

225   meaningful estimate of foraging likelihood. We used a binomial response variable (foraging vs

226   non-foraging) and SST, slope, distance from the coast, water depth, presence of associated species

227   and group size as explanatory variables. We chose this set of environmental variables as they have

228   been reported to influence the distribution of cetacean (Gross et al. 2009). In Hawaii, spinner

229   dolphins have predictable daily behavior, resting in shallow waters during the daytime and foraging

230   at night further from the coast (Heennehan et al. 2017). To account for the possibility that spinner

231   dolphins displayed similar behavioral patterns in the Bohol Sea, we also included time as an

232   explanatory variable of foraging likelihood. AIC values were utilized to conduct model selection.

233   Collinearity between explanatory variables and spatial auto-correlation are commonly encountered

234   when modelling species' distributions (Carl and Kühn 2007; Zuur et al. 2009). thus, we first log-

235   transformed the variables slope, distance from the coast and SST, then we tested for collinearity

236   between all pairs of response variables by calculating Spearman's rho. Any two covariates with r_2

237   ≥ 0.5 were considered significantly correlated and hence just one was included in the model.

238   Variance due to spatial correlation in the data is addressed by the explanatory variables used in the

239   models. Residual spatial variation was determined by visual evaluation of the variogram of the

240   models' residuals. Latitude and longitude were initially added to the models as explanatory

241   variables to account for potential spatial autocorrelation (Viddi et al. 2016) but didn't improve the

242   model's fit.

243

244   *Exclusion hypothesis*

245

246   The percentage of mixed-species associations were calculated and predominant behavior

247   during such encounters were reported.

248

249   **Results**

250

251   From March 2010 to June 2013, we surveyed an area of 2529.3 km^2 in the Bohol Sea

252   (Figure 1). A total of 12 cetacean species were encountered (n= 291 sightings, Table 1, Figure 2).

253   Melon-headed whales were the most regularly encountered species, accounting for 41.6% of the

254   sightings (n= 121). Fraser's dolphin (n= 63), were the second mot sighted species, followed by

255   spinner dolphins (*Stenella longirostris*, n= 41). In fewer numbers, other species recorded were

256   short-finned pilot whales (*Globicephala macrorynchus*, n= 9), Risso's dolphin (*Grampus griseus*,

257   n= 8), dwarf sperm whale (*Kogia sima*, n= 5), Bryde's whale (*Balaenoptera edeni*[a], n= 4),

258   Blainville beaked whales (*Mesoplodon densirostris* , n= 3), pantropical spotted dolphins (*Stenella

259   attenuata*, n= 2), Indo-pacific bottlenose dolphins (*Tursiops aduncus*, n= 1), rough-toothed dolphin

260   (*Steno bredanensis*, n= 1), and blue whale (*Balaenoptera musculus*[b], n= 2). Melon-headed whales

261   group size ranged between 1 and 300 (median= 15; μ= 22.1). In one occasion, several groups

262   converged forming a mega pod of over a thousand individuals. Spinner dolphins are also known to

263   form pod of hundreds of individuals, and we report a group size range between 2 and 500 (median=

264   20; μ= 40) while Fraser's dolphin group's size ranged between 1 and 100 (median= 20; μ= 25).

265

266   *Distribution and habitat suitability*

267

268   Melon-headed whales were most commonly found along the steep slopes of the deep trench

269   (max depth= 2011m) that characterize the northeast side of the Bohol Sea, along the municipality

270   of Garcia Hernandez, Jagna and Anda and extending until Sogod Bay in Southern Leyte (Figure

271   3A). Fraser's dolphin distribution resembles the one of melon-headed whales while spinner

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[a] It should be noted that we have limited confidence in the identification of *B. edeni* due to its similarity to *B. Omura*.
[b] According to Acebes et al. (2021), pigmy blue whales (*Balaenoptera musculus brevicauda*) inhabit the Bohol Sea as opposed to *B. musculus*. With limited sightings and no genetic samples, we have no ability to distinguish between the two species.

9

272   dolphins were more frequently encountered in the western part of the study area near Pamilacan
273   Island (Figure 3B and C, respectively). MaxEnt models also predict melon-headed whales and
274   Fraser's although the former prefer a steeper gradient than the latter. Pilot whales occurred at
275   greatest slope while spinner dolphins seem to distribute mainly according to distance from the
276   coast.
277
278   *Habitat use*
279
280   Melon-headed whales were frequently seen accompanied by small calves (μ per sighting=
281   1.3) and in some case newborns. Spinner and Fraser's dolphins were also seen with calves but we
282   weren't able to confidently quantify their numbers due to the large group sizes and the brief duration
283   of the encounters. The most common behavior recorded for every species pooled together was
284   resting but behavioral budgets varied significantly across species (Chi-square = 21.44, p-value =
285   0.0337). The two mysticetes species, blue whale and Bryde's whale, were only sighted travelling
286   and foraging, respectively (Figure 5). Melon-headed whales, Fraser's dolphins, spinner dolphins,
287   Risso's dolphins and pilot whales were mainly encountered while resting with foraging being the
288   second most common activity (Figure 5). Results from GLMs show that melon-headed whales tend
289   to forage in bigger groups and further from the coast, the interaction term between these two
290   variables is negatively correlated with foraging likelihood as groups of melon-headed whales were
291   observed congregate further offshore to rest (Figures 3 and 6; Tables 2 and 4). On the contrary,
292   Fraser's dolphins' foraging likelihood decrease with group size and increase during mixed-species
293   encounters (Figure 7), albeit not significantly (group size: z-val= -0.06, pval= 0.09; mixed-species:
294   z-val=1.80, pval=0.14). Spinner dolphins were found more likely to forage at colder sea surface
295   temperatures and smaller slope gradients (Tables 3 and 4). However, the interaction term between
296   slope and sea surface temperature was also found significant and positively influenced foraging
297   likelihood in spinner dolphins (Tables 3 and 4). Our results do not show any significant influence
298   of time of day on spinner dolphins foraging likelihood.
299
300   *Exclusion hypothesis*
301
302   Mixed species associations represented the 16.8% of the sightings (n= 49) and the most
303   common associated species were melon-headed whales and Fraser's dolphins (Table 5). Pilot
304   whales and melon-headed whales, both belonging to the globicephalinae family, were never
305   encountered together (Table 5). The most common activity recorded during mixed-species

10

306 encountered for all species was socializing (n= 9) although resting was also commonly displayed

307 (n= 8). Mixed species associations have been rarely seen while travelling (n= 4).

308

309 **Discussion**

310

311   In an ecosystem, the assemblage of species at each site is a result of the diversity of habitats

312 and the competition among the various species, the bigger and more diverse the habitat, the highest

313 number of species it can sustain. Tropical habitats are heterogeneous environments that present

314 multiple habitats features corresponding to many potential ecological niches (Sanciangco et al.

315 2013). Presence of cetacean within a limited range can suggest fine-scale mechanism of habitat and

316 resources partitioning allowing for niche segregation (Kiszka et al. 2007). Niche segregation can

317 occur by differences in spatial distribution, behavioral budgets (indicating how and when the area

318 is utilized by each species) and diet specialization.

319   Cetacean populations in Southeast Asia are subject to several threats including habitat

320 degradation, bycatch, direct killing and whale watching pressure (Perrin et al. 2005) but their

321 distribution and habitat preference is still poorly described. Determining cetacean biodiversity and

322 distribution patterns is of fundamental importance to inform species' protection from anthropogenic

323 impact in the area. Our study provides a comprehensive, albeit preliminary, description of cetacean

324 distribution and niche partitioning in the northern Bohol Sea, Philippines. With further targeted

325 surveys for a consistent dataset with reliable presence-absence and behavioral data, our models can

326 be built upon to gain a deeper and more accurate understanding. Moreover, the limited seasonal

327 coverage of our study needs to be acknowledged. Data were only collected during the dry season

328 with most of the surveys conducted between January and March. Thus, the spatial

329 occurrence,species richness and habitat use recorded in this study, only reflect a seasonal

330 distribution and the yearly home range of the observed species remains unverified. Finally, cetacean

331 species differ in their detectability, affected by their behavior, group size and sea state (Barlow

332 2015). During 291 surveys conducted in the Bohol Sea, we recorded 12 of the 19 cetacean species

333 anecdotally reported in the Bohol Sea (Dolar et al. 2006) confirming this region as a hotspot for

334 cetacean biodiversity. The species assemblage found in this study, resembles the one previously

335 reported for the adjacent waters of the Sulu Sea and the Tañon Strait by Dolar et al. (Dolar et al.

336 2006). Similar high cetacean biodiversity is also found in other tropical archipelagos with complex

337 waters inflows, like Bahamas, Hawaii, Mayotte and French Polynesia. Cetacean survey studies

338 conducted in Hawaii report 14 species of odontocetes (Baird et al. 2013) and 9 species in the

339 Bahamas (Macleod 2004). However, the most encountered species reported by Dolar et al. (2006)

340   was the spinner dolphins while melon-headed whales made up for the vast majority of the sightings

341   in the Bohol Sea. Encounter rate of melon-headed whales in the Bohol Sea (mean= 1.5 sighting/day

342   with a minimum of 0.6 in 2011 and a maximum of 2.28 in 2013, likely due to a larger area covered

343   in each survey day in the latter) is higher than in any other site where the species is commonly

344   sighted, including Hawaii (Aschettino et al. 2012); Mayotte Islands (Kiszka et al. 2007); the

345   northern Gulf of Mexico (Maze-Foley and Mullin 2006); South Carolina (Powell and Wells 2011);

346   and around several Pacific oceanic islands (Brownell et al. 2009). The recorded group sizes are in

347   line with findings of the same species in other areas.

348

349   *Distribution and habitat suitability*

350

351   The different oceanographic characteristic of the Bohol Sea and the presence of the

352   Mindanao current, create a unique and highly productive environment in which steep depth decline

353   and deep isobaths supply an aptly habitat for many deep diving odontocetes. Cetacean species in

354   the Bohol Sea seems to spatially overlap with most species distributing along steep slope gradients.

355   Depth seems to be influential only for spinner dolphins that prefer shallower habitats (median =

356   393m), closer to the coast (median = 3.6km). Interestingly, Dolar et al. (2006) found that

357   bathymetry and sea surface temperature, and not slope, were the most important variables

358   determining the distribution of Fraser's, bottlenose and Risso's dolphins and the short-finned pilot

359   whale in the adjacent Sulu Sea. Melon-headed preferences for offshore waters (median = 6.8 km)

360   is in line with findings from Hawaii where this species is encountered between 3 and 41.2 km

361   (median = 9.8 km) from coastline (Aschettino et al. 2012). However, in Hawaii, melon-headed

362   whales are encountered at greater depth, ranging between 148 and 4779 m (median = 1,610 m).

363   Deep diving species as melon-headed whales, pilot whales and Risso's dolphins feed primarily on

364   cephalopods and thus their distribution along steep slope gradients likely resembles the one of their

365   preys (Aschettino et al. 2012). Beaked whales also share similar habitat preferences and diet

366   characteristics (Moors-Murphy 2014). Data on blue and Bryde's whales, spotted dolphins and

367   bottlenose dolphins were too sparse to comment on their habitat preferences.

368

369   *Habitat use*

370

371   The presence of calves suggests that the Bohol Sea might be an important breeding area,

372   especially for melon-headed whales. Significant differences in activity budgets among species

373   suggest that the different species might use the area in different ways or that the temporal

374 component of niche segregation is more important than the spatial one. Despite behavioral data

375 were scarce for many of the species encountered in the study area preventing us from drawing

376 absolute conclusions, some trends are apparent. For instance, it is not surprising that melon-headed

377 whales, Fraser's dolphins, spinner dolphins, Risso's dolphins and pilot whales were mainly

378 encountered while resting since all these species are known to be deep divers and/or night foragers.

379 However, there is little information on the diet of these species in the study area. Pilot whales,

380 Risso's dolphins, beaked whales and dwarf sperm whales are known to be mainly squid eaters and

381 deep divers (De Stephanis et al. 2008; Moors-Murphy 2014), thus, the distribution of these species

382 is likely to be indicative of the distribution of larger squid species encountered in the Bohol Sea.

383 Melon-headed whales are also known to feed on cephalopods, but their diet might consist of pelagic

384 fish as well making them share a similar ecological niche to spinner dolphins (Brownell et al. 2009).

385 Niche segregation may occur determined by cephalopods sizes, with bigger and deeper diving

386 dolphins as pilot whales and Risso's dolphins targeting bigger preys. A study from Kiszka et al.

387 (2011) found strong diet difference between melon-headed and short finned pilot whales. The larger

388 size of pilot whales and their ability to dive deeper compared to melon headed whales may partially

389 explain their different diet. The same study also reports that spinner dolphins and melon-headed

390 whales both inhabit tropical offshore waters and share similar diets and habitats. GLM results on

391 foraging likelihood confirms that melon-headed whales and spinner dolphins tend to forage in

392 relation to slope gradients, although the former prefers steeper gradients than the latter. This result

393 is in contrast with what reported by Gross et al. (2009) that found melon-headed whales feed at

394 similar slope and distance from the coast of spinner dolphins. Our results, also show that spinner

395 dolphins feed in cooler waters but time of the day doesn't affect spinner dolphins foraging

396 likelihood in contrast to other areas where this species show a clear cycle of resting during the day

397 and feeding at night. In our study, no surveys were conducted after 16:00, possibly too early to

398 detect a change in behavior of spinner dolphins that tend to congregate in the evening to forage

399 offshore (Dolar et al. 2004). Instead, we most likely recorded opportunistic feeding events close to

400 the coast where spinner dolphins tend to rest. However, it is clear that in the Bohol Sea, spinner

401 dolphins exhibit a less clear temporal segregation of behavior. Fraser's dolphins were mainly

402 encountered in mixed species groups which might explain their tendency to forage mainly in

403 association with other cetacean species. The preference for small groups, while foraging, while still

404 associated with bigger groups of a different species, could reflect a trade-off between minimizing

405 intra-specific competition while ensuring protection for predators, assuming that the two cetacean

406 species feed on different preys. Results from our study should be considered preliminary as they

407 would benefit from a larger due to the paucity of behavioral and environmental dataset which would

408   increase the statistical power of our MaxEnt and GLM models. Moreover, we reported on the daily
409   foraging ecology of spinner dolphins and melon-headed whales, species known to predominantly
410   feed at night, thus our results provide only a partial picture of their foraging habits.

411

412   *Exclusion hypothesis*

413

414   Mixed species associations were recorded but not frequently and their ecological advantage
415   still remains unclear. Anti-predator advantages and information sharing between species of the
416   same trophic level are frequently mentioned in literature as possible explanations for mixed-species
417   associations (Goodale et al. 2020; Syme et al. 2021). However, the overlap of home range also
418   underpins some sort of niche segregation, which is a likely scenario in the Bohol Sea. Our results
419   suggest that species associate mostly by size, tolerating the presence of alien species with similar
420   sizes and group dimensions thus possibly posing less of a threat, and by avoiding animals whose
421   diets overlap too much. The lack of observed mixed group encounters of melon-headed and pilot
422   whales might support the competitive exclusion hypothesis among the globicephalinae family
423   whose species, based on literature, have a diet consisting mostly of cephalopods (Lambert et al.
424   2014). However, further research on their feeding ecology, for example through stable isotopes or
425   stomach content analysis, is necessary to confirm the dietary preferences of globicephalinae in the
426   Bohol Sea. In our study, melon-headed whales and Fraser's dolphins were the species most
427   frequently encountered within mixed-species associations. These two species have similar
428   individual and group sizes but forage on different preys (Kiszka et al. 2011). We hypothesize that
429   the two species associate taking advantage of safety in number while not competing for resources.
430   Moreover, while melon-headed whales were found almost exclusively with Fraser's dolphins and
431   rarely with spinner dolphins, Fraser's dolphin were encountered also with pilot whales and Risso's
432   dolphins suggesting that different dietary requirements and diving abilities may play a more
433   important role than similar size in determining mixed-species association in the Bohol Sea. The
434   tendency of melon-headed whales to form mixed-species associations close to shore and single
435   species superpod offshore, could also be an antipredatory strategy.

436

437   **Conclusions**

438

439   Our study confirmed the Bohol Sea as a high biodiversity area, likely due to its bathymetric
440   features that promote upwelling and offer wide foraging opportunities for a range of cetacean and
441   other marine megafauna species. Our results don't show a clear spatial segregation among species

442 but suggest different behavioral budgets. While the amount of data available greatly differed across

443 species, most of the species inhabiting the Bohol Sea appears to have similar foraging ecology and

444 habitat requirements. Niche partitioning might occur at finer temporal or behavioral scale than the

445 one explored in this study, or the abundance of preys might be sufficient to allow these species to

446 coexist with limited niche partitioning. The Bohol Sea appears to be a hotspot for biodiversity that

447 sustains a large and diversified cetacean community. The unique oceanographic features of the area

448 make it suitable for deep diving species and the upwelling processes ensure its nutrient richness,

449 highlighting the importance of these waters as a foraging site for tropical cetacean communities.

450 The presence of calves in the area also suggests that the Bohol Sea could be a breeding ground at

451 least for melon-headed whales. More information is needed to better describe environmental and

452 ecological factors that may influence cetacean presence and distribution and stable isotopes

453 analyses between others, would help to shed some light on fine-scale niche partitioning. Despite

454 the necessary caveats, our results provide a baseline to initiate species-specific and taxa-specific

455 management intervention, supporting the designation and implementation of the Bohol Sea as an

456 IMMA.

457   Further research is urgently needed to identify and quantify threats, in particular bycatch

458 and noise pollution, and the current status of the remaining populations of cetaceans in the area, to

459 guide spatial planning and other management interventions to ensure the conservation of these

460 species.

461

462 **Declaration of competing interest**

463

464   The authors declare that they have no known competing financial interests or personal

465 relationships that could have appeared to influence the work reported in this paper.

466

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468

References

Acebes J. 2009. Historical whaling in the Philippines: Origins of 'Indigenous subsistence whaling', mapping whaling grounds and comparison with current known distribution: A HMAP Asia Project Paper. *Murdoch University Asia Research Centre Working Paper* 0:1-37.

Acebes J, Darling J, Yamaguch M. 2007. Status and distribution of humpback whales (*Megaptera novaeangliae*) in northern Luzon, Philippines. *Journal of Cetacean Research and Management* 9:37-439.

Acebes JMV, Silberg JN, Gardner TJ, et al. 2021. First confirmed sightings of Blue Whales Balaenoptera musculus Linnaeus, 1758 (Mammalia: Cetartiodactyla: Balaenopteridae) in the Philippines since the 19th century. *Journal of Threatened Taxa* 13: 17875–17888.

Acebes J. 2014. A History of Whaling in the Philippines: A Glimpse of the Past and Current Distribution of Whales. In: Christensen J, Tull M, editors. *Historical Perspectives of Fisheries Exploitation in the Indo-Pacific.* MARE Publication Series 12. pp 83-105.

Arango HG, Levin JC, Curchitser E, et al. 2011. Development of a Hindcast/Forecast Model for the Philippine Archipelago. *Oceanography* 24: 58-69.

Aschettino JM, Baird RW, Mcsweeney DJ, et al. 2012. Population structure of melon-headed whales (*Peponocephala electra*) in the Hawaiian Archipelago: Evidence of multiple populations based on photo identification. *Marine Mammal Science* 28:666-689.

Baird RW, Webster DL, Aschettino JM, et al. 2013. Odontocete cetaceans around the main Hawaiian islands: habitat use and relative abundance from small-boat sighting surveys. *Aquatic Mammals* 39:253-269.

Ballance LT, Pitman RL, Fiedler PC. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress in Oceanography* 69:360-390.

Barlow J. 2015. Inferring trackline detection probabilities, g(0), for cetaceans from apparent densities in different survey conditions. *Marine Mammal Science* 31:923-943. https://doi.org/10.1111/mms.12205

Breen P, Brown S, Reid D, et al. 2016. Modelling cetacean distribution and mapping overlap with fisheries in the northeast Atlantic. *Ocean and Coastal Management* 134:140-149.

Brownell RL, Ralls K, Baumann-Pickering S, et al. 2009. Behavior of melon-headed whales, *Peponocephala electra*, near oceanic islands. *Marine Mammal Science* 25: 639-658.

Cabrera OC, Villanoy CL, David LT, et al. 2011. Barrier layer control of entrainment and upwelling. *Oceanography* 24:130-141.

Cañadas A, Sagarminaga R, Garcia-Tiscar S, 2002. Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep-Sea Research I* 49:2053-2073.

Carl G, Kühn I. 2007. Analyzing spatial autocorrelation in species distributions using Gaussian and logit models. *Ecological Modelling* 207:159-170.

De Stephanis R, Cornulier T, Verborgh P, et al. 2008. Summer spatial distribution of cetaceans in the Strait of Gibraltar in relation to the oceanographic context. *Marine Ecology Progress Series* 353:275-288.

Díaz López B, Methion S. 2018. Does interspecific competition drive patterns of habitat use and relative density in harbour porpoises? *Marine Biology* 165:1-11.

Dolar MLL, Walker WA, Kooyman GL, et al. 2004. Comparative feeding ecology of spinner dolphins (*Stenella longirostris*) and Fraser's dolphins (*Lagenodelphis hosei*) in the Sulu Sea. *Marine Mammal Science* 19:1-19.

Dolar MLL, Perrin WF, Taylor BL, et al. 2006. Distributional ecology of small cetaceans in the Philippines. *Journal of Cetacean Research and Management* 8:93-111.

Druon JN, Hélaouët P, Beaugrand G et al. 2019. Satellite-based indicator of zooplankton distribution for global monitoring. *Scientific Reports* 9:4732.

Goodale E, Sridhar H, Sieving KE, et al. 2020. Mixed company: A framework for understanding the composition and organization of mixed-species animal groups. *Biological Reviews* 95:889-910.

Gross A, Kiszka J, Van Canneyt O, et al. 2009. A preliminary study of habitat and resource partitioning among co-occurring tropical dolphins around Mayotte, southwest Indian Ocean. *Estuarine, Coastal and Shelf Science* 84:367-374.

Halpern BS, Frazier M, Potapenko J, et al. 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications* 6:1-7.

Hanf, D, Hodgson AJ, Kobryn H, et al. 2022. Dolphin Distribution and Habitat Suitability in North Western Australia: Applications and Implications of a Broad-Scale, Non-targeted Dataset. *Frontiers in Marine Science* 8.

Hazen EL, Jorgensen S, Rykaczewski RR, et al. 2013. Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change* 3:234-238.

Heenehan HL, Van Parijs SM, Bejder L, et al. 2017. Differential effects of human activity on Hawaiian spinner dolphins in their resting bays. *Global Ecology and Conservation* 10:60-69.

Hosmer, D. W. and Lemeshow, S. (1989) *Applied Logistic Regression.* New York: John Wiley & Sons, Inc.

Huot Y, Babin M, Bruyant F, et al. 2007. Does chlorophyll a provide the best index of phytoplankton biomass for primary productivity studies? *Biogeosciences Discussions, European Geosciences Union* 4:707-745.

Indab JD, Suarez-Aspilla PB. 2004. Community-based marine protected areas in the Bohol (Mindanao) Sea, Philippines. *NAGA, WorldFish Center Quarterly* 27:4-8.

Kiszka J, Ersts P, Ridoux V. 2007. Cetacean diversity around the Mozambique Channel island of Mayotte (Comoros archipelago). *Journal of Cetacean Research and Management* 9:105.

Kiszka JJ, Heithaus MR, Wirsing AJ. 2015. Behavioural drivers of the ecological roles and importance of marine mammals. *Marine Ecology Progress Series* 523:267-281.

Kiszka J, Simon-Bouhet B, Martinez L, et al. 2011. Ecological niche segregation within a community of sympatric dolphins around a tropical island. *Marine Ecology Progress Series* 433:273-288.

Lambert C, Mannocci L, Lehodey P, et al. 2014. Predicting cetacean habitats from their energetic needs and the distribution of their prey in two contrasted tropical regions. PLoS ONE 9:e105958.

Macleod K, 2004. Atlas of cetacean distribution in North-West European waters. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14:435-436.

Maze-Foley K, Mullin KD. 2006. Cetaceans of the oceanic Northern Gulf of Mexico: Distributions, group sizes and interspecific associations. *Journal of Cetacean Research and Management* 8:203-2013.

Merow C, Smith MJ, Silander JA. 2013. A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography* 36: 1058-1069.

Moors-Murphy HB. 2014. Submarine canyons as important habitat for cetaceans, with special reference to the Gully: A review. *Deep-Sea Research Part II: Topical Studies in Oceanography* 104:6-19.

Peterson AT 2003. Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology* 78:419–433.

Pinela AM, Borrell A, Aguilar A. 2011. Common dolphin morphotypes: niche segregation or taxonomy? *Journal of Zoology* 284:239-247.

Pirotta, E, Booth, C. G, Costa, D. P, et al. 2018. Understanding the population consequences of *disturbance. Ecology and Evolution.* 0:9934–9946.

Pompa S, Ehrlich PR, Ceballos G. 2011. Global distribution and conservation of marine mammals. *Proceedings of the National Academy of Sciences* 108:13600-13605.

Powell JR, Wells RS. 2011. Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Mammal Science* 27:111–129.

Reisinger RR, Carpenter-Kling T, Connan M, et al. 2020. Foraging behaviour and habitat-use drives niche segregation in sibling seabird species. *Royal Society Open Science* 7:200649.

Report on the second workshop on the biology and conservation of small Cetaceans and Dugongs of Southeast Asia. Convention on Migratory Species (CMS) Technical Series publication no. 9. 2005. Available at: https://iucn-csg.org/wp-content/uploads/2010/03/Perrinetal.0589.pdf [Date accessed: 07 July 2022]

Rogan E, Cañadas A, Macleod K, et al. 2017. Distribution, abundance and habitat use of deep diving cetaceans in the North-East Atlantic. *Deep-Sea Research Part II: Topical Studies in Oceanography* 141:8–19.

Sahri A, Putra MIH, Mustika PLK, et al. 2021. Cetacean habitat modelling to inform conservation management, marine spatial planning, and as a basis for anthropogenic threat mitigation in Indonesia. *Ocean and Coastal Management* 205:105555.

Samonte-Tan GPB, White AT, Tercero MA, et al. 2007. Economic Valuation of Coastal and Marine Resources: Bohol Marine Triangle, Philippines. *Coastal Management* 35:319-338.

Sanciangco JC, Carpenter KE, Etnoyer PJ, et al. 2013. Habitat Availability and Heterogeneity and the Indo-Pacific Warm Pool as Predictors of Marine Species Richness in the Tropical Indo-Pacific. *PLoS ONE* 8:e56245.

Smith JN, Kelly N, Renner IW. 2021. Validation of presence-only models for conservation planning and the application to whales in a multiple-use marine park. *Ecological Applications* 31:14.

Sorongon, PME, Acebes, JM, Dolar, L, et al. 2010. The effect of tourism on cetacean populations in southern Philippines. In: Palomares, M.L.D., Pauly, D. editors, Marine Biodiversity of Southeast Asian and Adjacent Seas. *Fisheries Centre Research Reports* 18:78-96.

Syme J, Kiszka JJ, Parra GJ. 2021. Dynamics of cetacean mixed-species groups: a review and conceptual framework for assessing their functional significance. *Frontiers in Marine Science* 8:678173.

Tetley MJ, Braulik GT, Lanfredi C, et al. 2022. The Important Marine Mammal Area Network: A Tool for Systematic Spatial Planning in Response to the Marine Mammal Habitat Conservation Crisis. *Frontier in Marine Science* 9:841789.

Viddi FA, Harcourt RG, Hucke-Gaete R. 2016. Identifying key habitats for the conservation of Chilean dolphins in the fjords of southern Chile. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26:506-516.

Zabala J, Zuberogoitia I, Martínez-Climent JA. 2009. Testing for niche segregation between two abundant carnivores using presence-only data. *Folia Zoologica* 58: 385-395.

Zuur A, Ieno E, Walker N, Saveliev A, et al. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science+Business Media
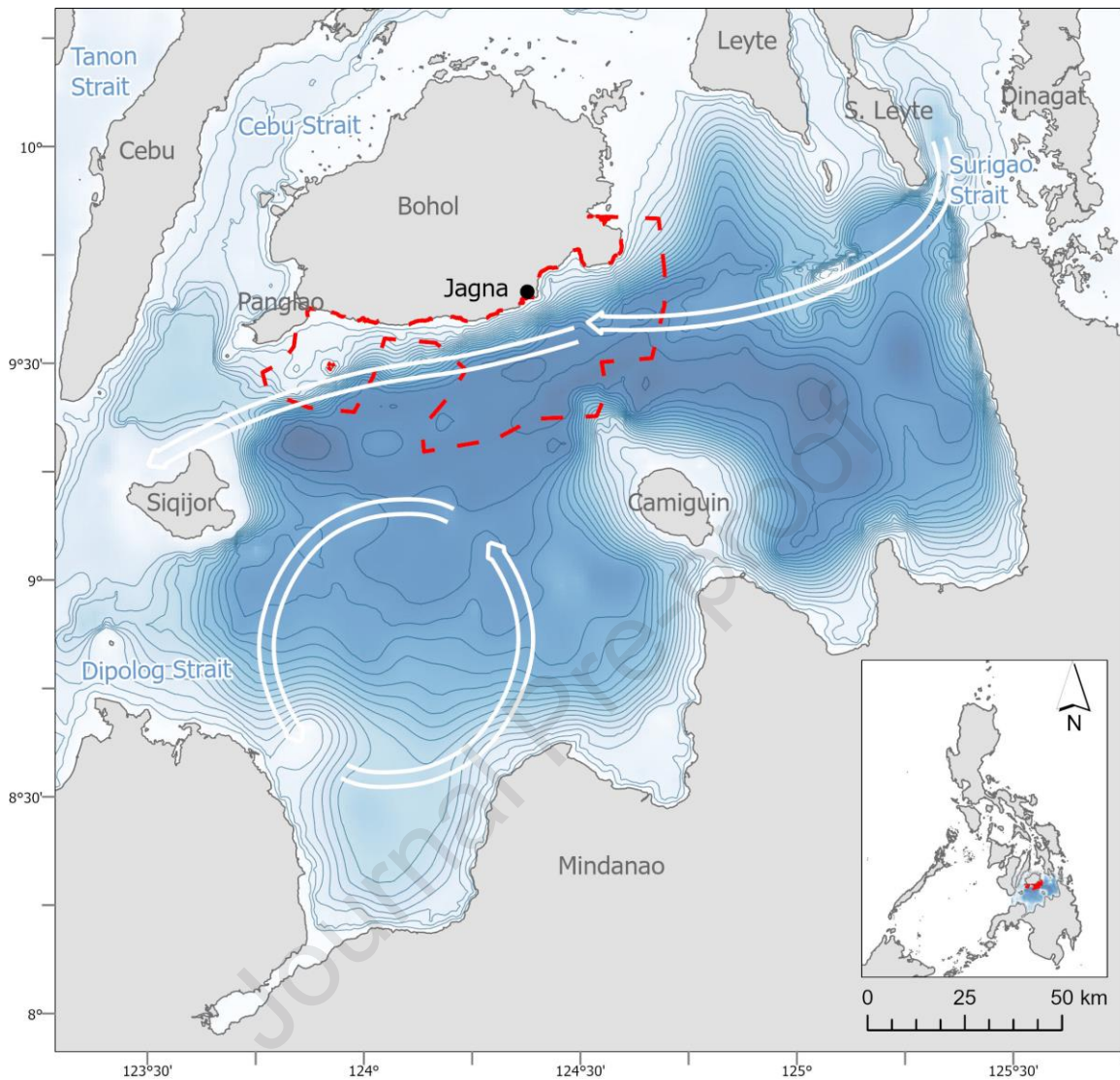
Figure legends

Figure 1. Study area (red dashed lines) location within the Bohol Sea. Modified from Cabrera et al. (2011), the white arrows represent the westward flow of the Bohol Jet and circular flow of the Illigan Bay Eddy, responsible for promoting upwelling and phytoplankton entrainment. Insert: Location within the Philippines.
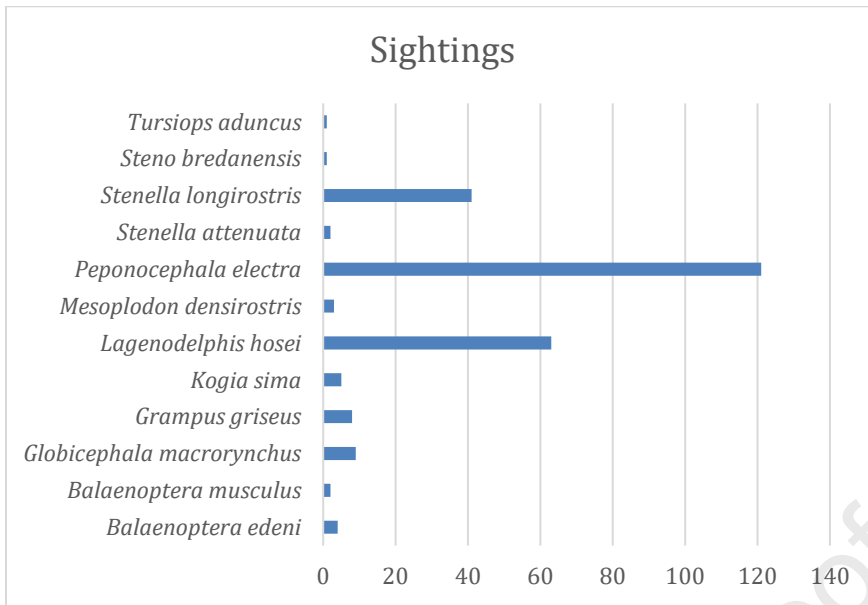
Figure 2. Total number of sightings per species from 2010-2013.
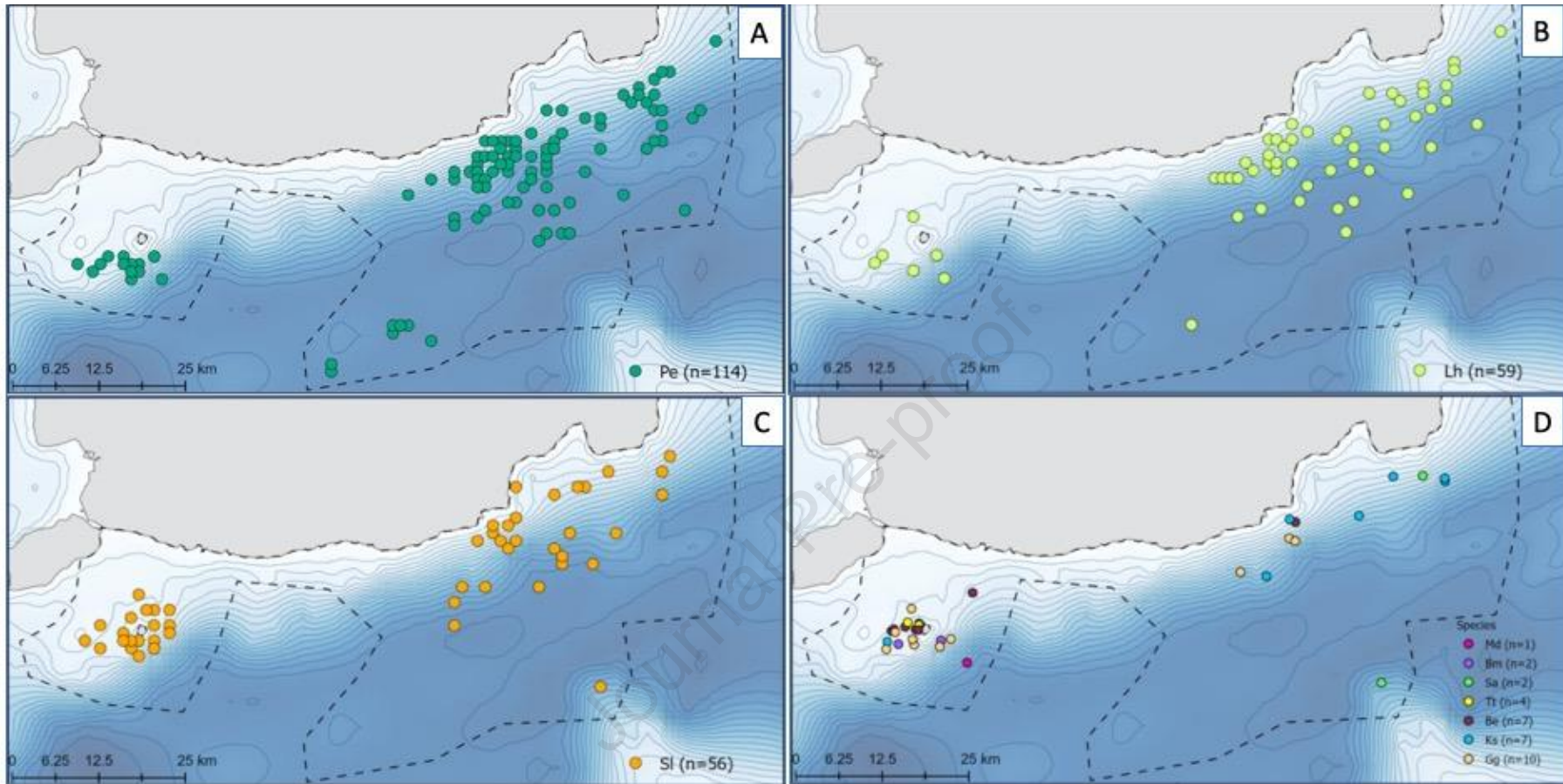
Figure 3. Point distribution of: A, melon-headed whales (*Peponocephala electra*; 'Pe'; upper left corner); B, Fraser's dolphins (*Lagenodelphis hosei*; 'Lh'; upper right corner); C, spinner dolphins (*Stenella longirostris*, 'Sl'; lower left corner); D, less commonly encountered species (lower right corner), namely Blainville's beaked whale (*Mesoplodon densirostris*, 'Md'); blue whales (*Balaenoptera musculus*, 'Bm'), pantropical spotted dolphins (*Stenella attenuata*, 'Sa'); common bottlenose dolphins (*Tursiops truncatus*, 'Tt'); Bryde's whales (*Balaenoptera edeni*, 'Be'); dwarf sperm whales (*Kogia sima*, 'Ks') and Risso's dolphins (*Grampus griseus*, 'Gg').

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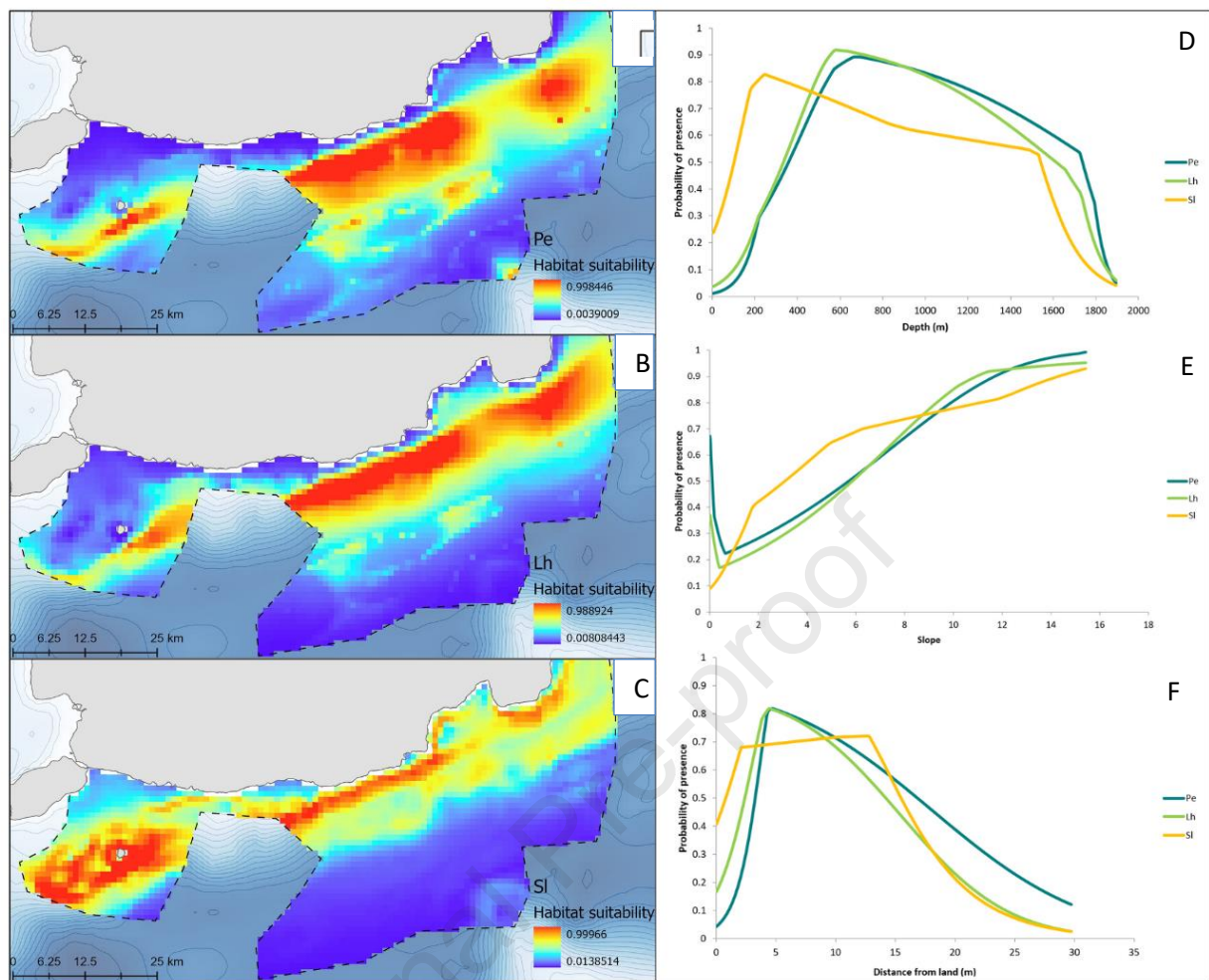
Figure 4. Left panel: Relative habitat suitability for A, melon-headed whales (*Peponocephala electra*; 'Pe'); B, Fraser's dolphins (*Lagenodelphis hosei*; 'Lh'); C, spinner dolphins (*Stenella longirostris*, 'Sl'), at 500 x 500 m grid cell resolution. Right panel: Probability of D, melon-headed whale; E, Fraser's dolphin; F, spinner dolphin presence as a response to Depth; Slope; Distance from land. m=metres.
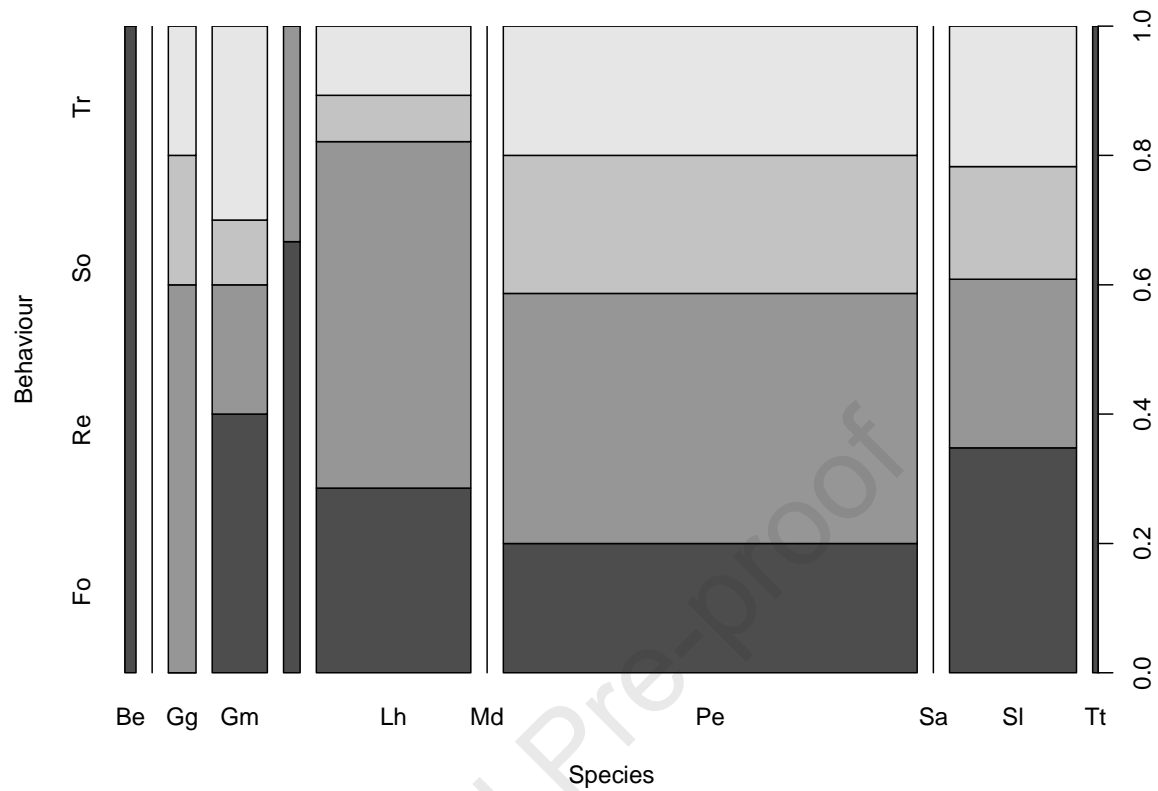
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Figure 5. Behavioural budgets per species. Fo = foraging, Re = resting, So = socializing; Tr= travelling. Pe = melon-headed whales (*Peponocephala electra*); Lh = Fraser's dolphins (*Lagenodelphis hosei*); Sl = spinner dolphins (*Stenella longirostris*); Sa = Pantropical spotted dolphins (*Stenella attenuata*); Tt = common bottlenose dolphins (*Tursiops truncatus*); Gm = short-finned pilot whales (*Globicephala macrorynchus*); Gg = Risso's dolphins (*Grampus griseus*); Be = Brydes whales (*Balaenoptera edeni*); Bm = blue whales (*Balaenoptera musculus*); Ks = dwarf sperm whales (*Kogia sima*); Md = Blainville's beaked whales (*Mesoplodon densirostris*); Sb = rough-toothed dolphins (*Steno bredanensis*).
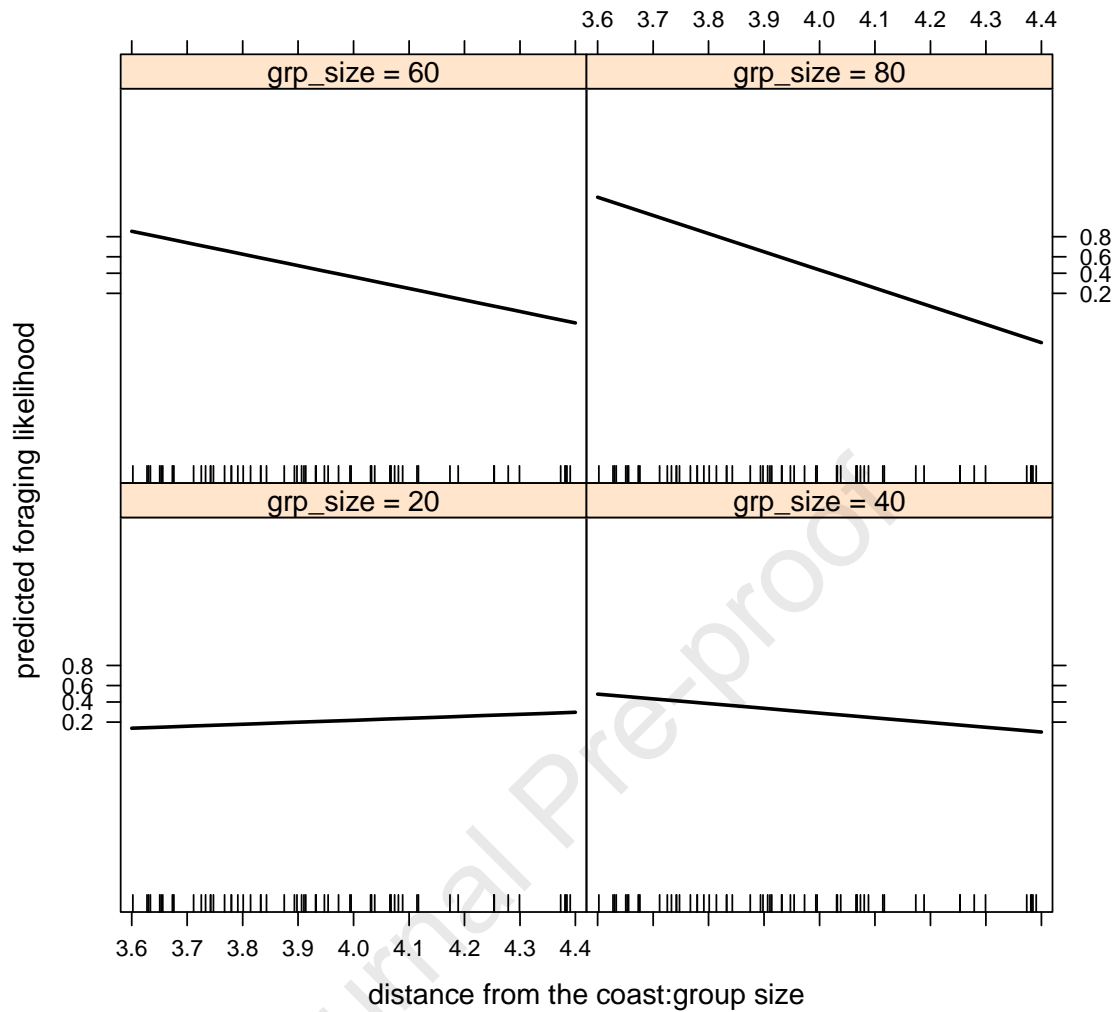
Figure 6. Predicted foraging likelihood (between 0 and 1) of melon-headed whales in relation to the interactive effect of group size and distance from land. Given the big range of group size encountered, we divided group size into bins, each with 20 individuals increment, starting from a minimum of 20 to a maximum of 80 plus.
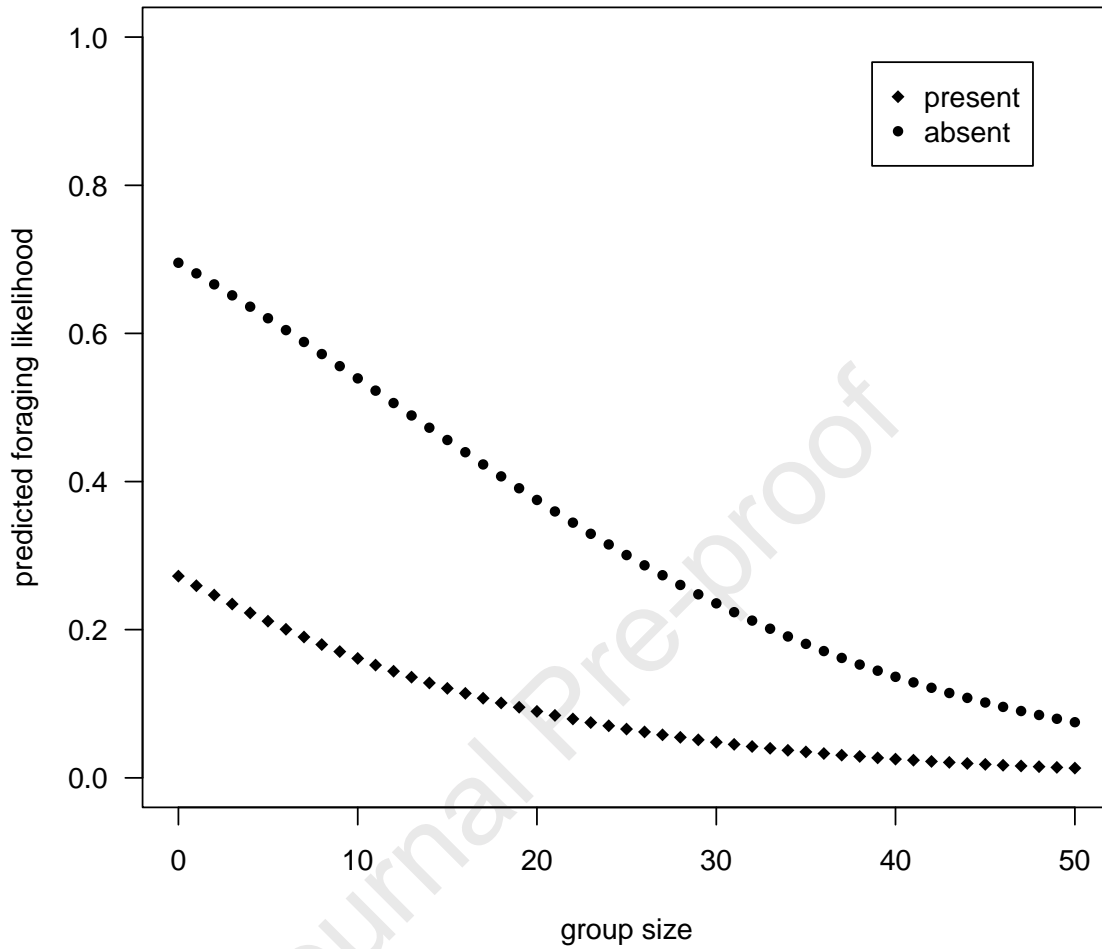
Figure 7. Predicted foraging likelihood of Fraser's dolphins in relation to group size. The two curves refer to encounters when an associated species was present (romboids) and absent (circles) respectively.

Table captions

Table 1. Summary of cetacean encountered during the study period in the Bohol Sea. N represent the total number of sightings per each species; S is the group size for which mean, median and maximum values are provided; E is the percentage of encounter per species.

Species	N	S			E (%)
		mean	median	max	
Melon headed whales	121	22.1	15	300	41.6
Fraser's dolphins	63	25	20	100	21.6
Spinner dolphins	41	40	20	500	14.1
Pantropical spotted dolphins	2	15	15	15	0.7
Bottlenose dolphins	1	20	20	20	0.3
Short-finned pilot whales	9	19.7	18	60	3.1
Risso's dolphins	8	6.3	5.5	12	2.7
Dwarf sperm whale	5	3	3	3	1.7
Blainville beaked whales	3	NA	NA	NA	1
Rough-toothed dolphins	1	1	1	1	0.3
Bryde's whale	4	1	1	1	1.3
Blue whale	2	1	1	1	0.6

Table 2. Models of foraging likelihood developed for Peponocephala electra and Lagenodelphis hosei.

Model	AIC	
	Pe	**Lh**
Foraging ~ 1	75.2	34.8
Foraging ~ distance from coast	74.4	36.4
Foraging ~ time	77.0	36.5
Foraging ~ slope	76.3	34.2
Foraging ~ SST	77.1	36.0
Foraging ~ presence of associated species	75.6	34.3
Foraging ~ group size	75.8	33.6
Foraging ~ distance from coast + SST	76.2	37.8
Foraging ~ group size+ presence of associate	76.7	**32.9**
Foraging ~ slope+ SST	78.3	35.4
Foraging ~ slope+ SST+ time	80.2	36.7
Foraging ~ distance from coast + behaviour+ presence of associate	75.7	34.0
Foraging ~ distance from coast + behaviour+ presence of associate + SST	77.7	34.9
Fo**raging ~ group size* distance from coast**	**72.6**	36.9

Table 3. Models of foraging likelihood developed for Stenella longirostris.

| Model	AIC
Foraging ~ 1	29.5
Foraging ~ distance from coast	31.2
Foraging ~ time	30.3
Foraging ~ slope	29.0
Foraging ~ SST	31.4
Foraging ~ group size	31.1
Foraging ~ distance from coast + SST	33.2
Foraging ~ slope+ SST+ time	32.6
Foraging ~ slope+ time	30.7

31

|	
Foraging ~ slope* SST	**27.8**

Table 4. Matrix of species associations. N represent the percentage of sightings in which the two species were found associated, the sum can exceed 100% since several species can occur in one sightings. N in the diagonal represents the %of time that the species was seen in pure schools. The matrix results asymmetrical because the number of sighting varies by species.

	Pe	Lh	Sl	Sa	Tt	Gm	Gg	Ks	Md	Be	Bm	Sb
Pe (121)	**62**	37	2.5									
Lh (63)	71.4	**12.7**	3.2			6.4	6.4					
Sl (41)	7.3	4.9	**83**	2.4			2.4				2.4	
Sa (2)			50	**50**								
Tt (1)					**100**							
Gm (9)		44.4				**55.5**						
Gg (8)		50	12				**37.5**					
Ks (5)								**100**				
Md (3)									**100**			
Be (4)										**100**		
Bm (2)			50								**50**	
Sb (1)												**100**

Table 5. Summary of MaxEnt performance and environmental variable contribution for each model. AUC = Area Under the Curve; SD = Standard Deviation. The AUC metric ranges from 0.5 to 1, with a score of 0.5 suggesting that a model has 50% chance of being correct (Fielding and Bell 1997). Hosmer and Lemeshow (1989) recommend model performance by interpreted as <0.5 = none; 0.5 to 0.7 = poor; 0.7 to 0.8 = acceptable; 0.8 to 0.9 = excellent; >0.9 = outstanding. Environmental variable contribution is relative to one another within each model, and is expressed as a percentage.

Model	Training		Test AUC (SD)		Variable contribution (%)		
	Sample no.	AUC (SD)	Sample no.	AUC (SD)	Depth	Slope	Dist. land
Melon headed whale	53	0.814 (±0.862)	2	0.784 (±0.096)	32.2	47.7	20.1
Fraser's dolphin	95	0.817 (±0.784)	4	0784. (±0.153)	18.6	53.6	27.8
Spinner dolphin	48	0.819 (±0.781)	2	0.780 (±0.162)	69.1	16.4	14.5

33
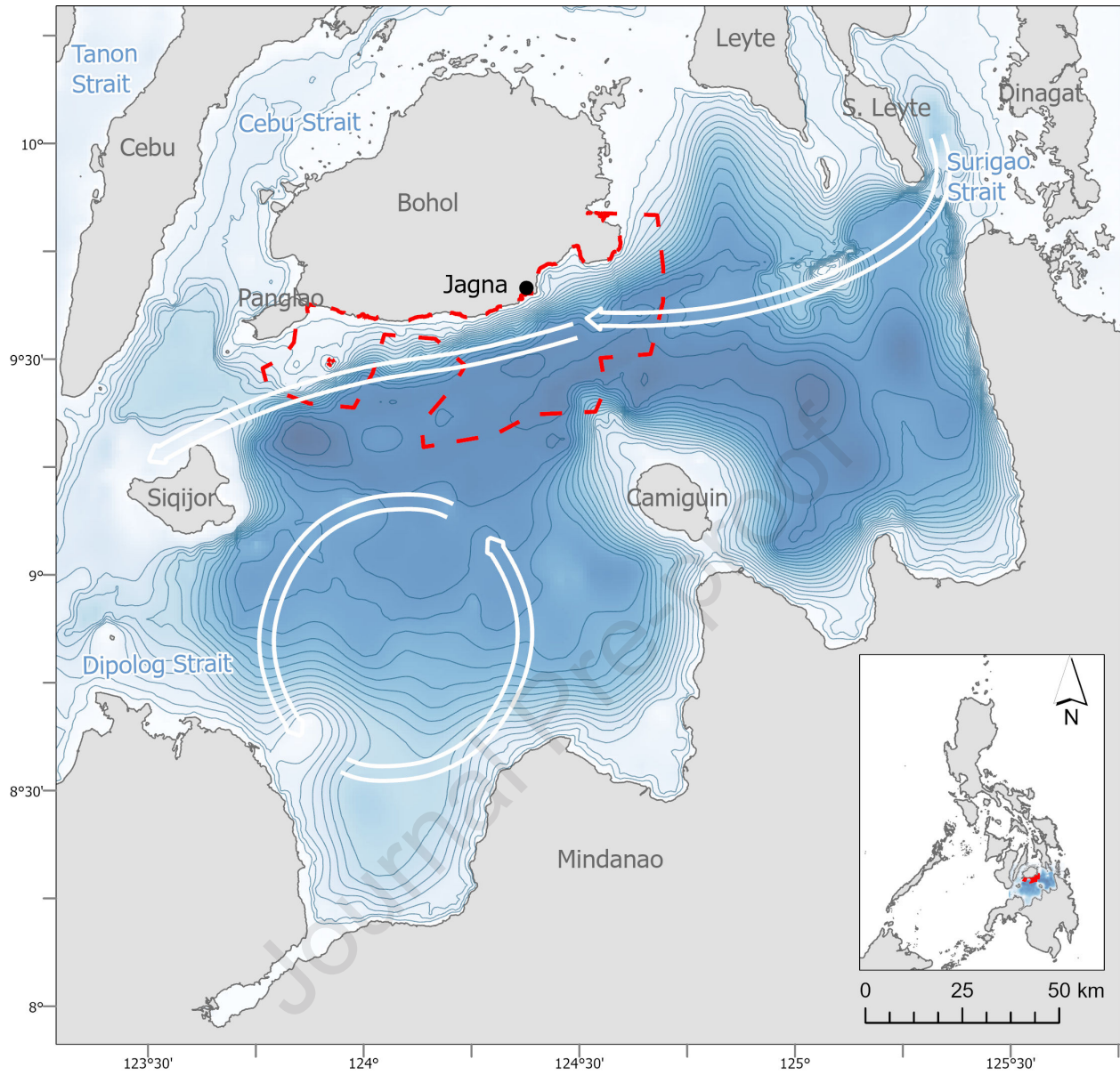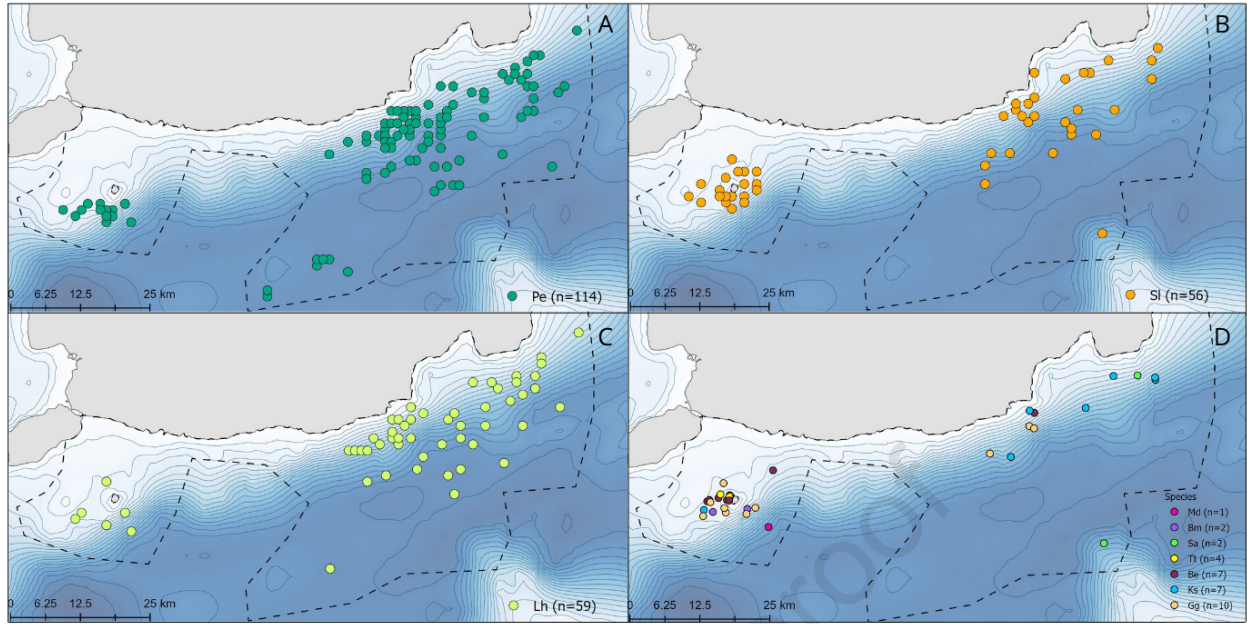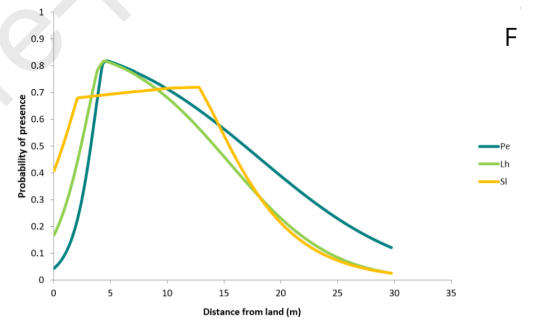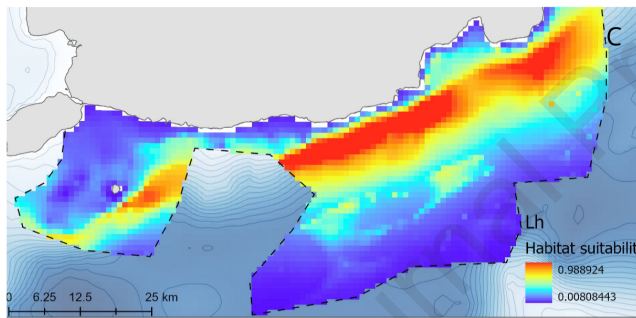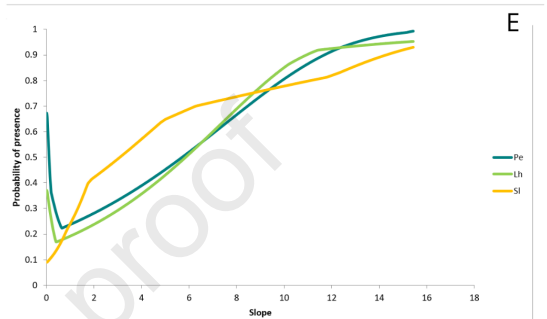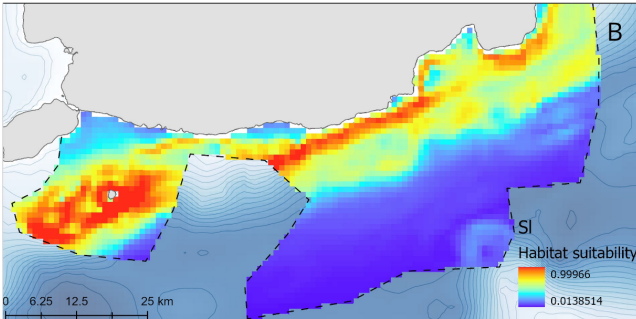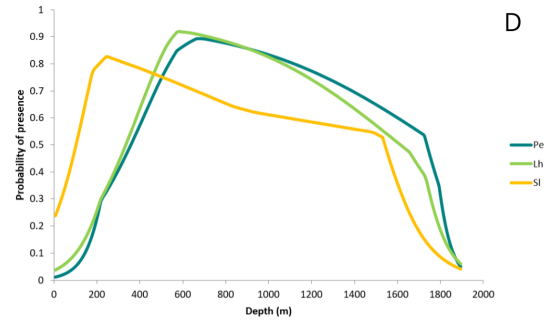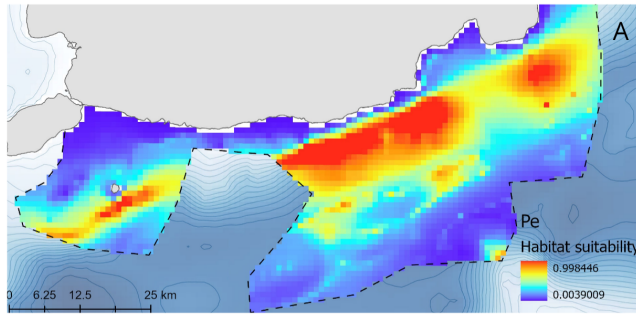
Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: