1   **Methodological Applications**

2   # The importance of temporal resolution for niche

3   # modelling in dynamic marine environments

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18

19 **ABSTRACT**

20 Aim

21 Highly dynamic ocean environments can experience dramatic changes over

22 relatively short timeframes, affecting the spatial distribution of resources and

23 therefore the presence or absence of highly mobile species. We use simulation

24 studies to investigate how different temporal resolutions might affect the results of

25 species distribution models for highly mobile species (e.g. cetaceans) in marine

26 environments.

27 Location

28 Azores archipelago, Portugal

29 Methods

30 We developed 3 virtual species with different habitat preferences influenced by

31 (i) only static (topographic), (ii) only dynamic (oceanographic), and (iii) both

32 dynamic and static variables. Assuming that species would reposition themselves

33 daily according to these preferences (as has been observed for large marine

34 foragers such as cetaceans), we used two different approaches (generalized linear

35 model and generalized boosted model) to test the effect of using daily, weekly and

36 monthly environmental datasets to model distributions.

37 Results

38   The results showed that the selection of different temporal scales has a very

39   important effect on model predictions. When dynamic variables are important

40   components of habitat preference, models based on daily or weekly timeframes

41   performed best at reconstructing the known niche.

42   Main conclusion

43   It is important that we consider temporal resolution when applying species

44   distribution models. Several factors (e.g. species ecology and oceanographic

45   characteristics of the ecosystem) should be taken into consideration when

46   selecting an adequate temporal scale for niche modelling. For fine scale

47   applications (e.g. dynamic ocean management), highly dynamic ecosystems, and

48   highly mobile species, our results suggest exploring temporal resolution of 7-8

49   days rather than coarser temporal scales. For some applications annual, seasonal

50   or even monthly averages may produce inferior or inaccurate models.

51   Author contributions: M.F. conceived the ideas; M.F., P.M. and C.Y. provided and

52   analysed data; all authors contributed to the writing and revision processes.

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57 **1. INTRODUCTION**

58   It is important to understand the factors that influence species distributions

59 within the application of environmental niche models (Fryxel et al., 2014). Species

60 distribution models (SDMs) are useful tools and can have many applications

61 including informing management and conservation decisions (Hirzel et al., 2001;

62 Peterson et al., 2011). Their widespread use has led to useful discussions regarding

63 their utility and accuracy (Brotons et al., 2004; Lawson et al., 2014). One important

64 factor in the construction of SDMs is the resolution of environmental variables.

65 Typically, the temporal and spatial resolutions of analyses are determined by the

66 availability of environmental data, rather than by a considered assessment of

67 species' characteristics (Barry & Elith, 2006; Jetz et al., 2012). Some studies have

68 investigated how different spatial resolutions affect modelling results (Guisan et

69 al., 2007; Svensson et al., 2013). However, the temporal resolution of

70 environmental variables has received far less attention (e.g. Araújo et al., 2005)

71 and in some cases those studies have focused on scales of centuries to millennia.

72 Many variables used for SDM show significant variation over a variety of

73 timescales. In the natural world, we see potentially significant temperature

74 variations over years, seasons, months, weeks and even days, and these may be

75 important for determining or limiting species distribution. It is common practice

76 for SDM studies to incorporate seasonal variations (e.g. bioclimatical

77 Bioclim/WorldClim variables), but less common to examine variability over larger

78 (multi-year) or shorter (monthly/weekly) periods.

79   When working with very dynamic environments (e.g. small-scale oceanic frontal

80   areas) and/or with species with high mobility (e.g. cetaceans or sharks), short

81   term temporal variation could be an important issue, as ephemeral environmental

82   conditions may determine distribution over short time- frames. When working

83   with top predators, the oceanographic dynamic variables will not affect the species

84   distributions directly, but could be used as distal variables (Austin 2002), e.g. a

85   proxy of prey density. For example biophysical coupling at frontal areas can lead to

86   the formation of pelagic foraging hotspots (Scales et al. 2014), creating

87   aggregations zones for zooplankton advected from surrounding water masses

88   driving bottom-up processes across multiple trophic levels up to apex predators

89   (Bakun 2006).

90   Typically, incorporating temporal dynamics of the environment does not extend

91   beyond the inclusion of seasonal or monthly climatological variables, e.g. data from

92   Bioclim (Busby 1991) for terrestrial studies or from MARSPEC (Sbrocco & Barber

93   2013) for marine studies. Some SDM studies based in the marine environment

94   have used annual or seasonal averages (Cañadas & Hammond 2008; Praca &

95   Gannier 2007), while others have employed monthly averages (MacLeod et al.,

96   2007, Moura et al., 2012, Panigada et al., 2008), and a notable few have considered

97   weekly means (Becker et al., 2010; Becker et al., 2016; Howell et al., 2008;

98   Mannocci et al., 2014; Roberts et al., 2016). Few studies have investigated the

99   adequacy of temporal resolution of environmental data, such as Forney et al.

100   (2012) and Scales et al. (2017).

101   Mannocci et al. (2014), grouping species at broad scales, found improved

102   model results when using seasonal oceanographic data, leading the authors to

103   suggest that there was no apparent short-term reaction of top predators towards

104   oceanographic variability. Conversely, Scales et al. (2017) found that models fitted

105   using seasonal or climatological data fields can introduce bias in presence-

106   availability models. Biologically relevant time scales can vary from thousands of

107   years to minutes, depending on oceanographic processes (Mann & Lazier, 2013).

108   Therefore, it is important we gain a better understanding of how different

109   temporal scales might affect SDMs in the marine realm.

110   The aim of this study is to investigate the effect of using different temporal

111   resolutions in developing SDMs for highly mobile species in dynamic

112   environments.

113   **2. MATERIALS AND METHODS**

114   *2.1. Study area*

115   The study area is located in the Azores archipelago, a group of North Atlantic

116   oceanic islands located approximately 1,800 km west of Lisbon. The region is

117   strongly influenced by the Gulf Stream and all the branches of this current. Its

118   large-scale oceanic circulation is dominated by the Azores Current, which

119   generates considerable mesoscale variability (Santos et al. 1995).

120   *2.2. Environmental data*

121   A set of real marine environmental variables was selected to represent the

122   variability and dynamism of an oceanic system. Variables were chosen based on

123   their reported influence on cetacean distributions (see Appendix S1). These were

124   divided into two thematic groups: static (little or no short term variation – i.e.

125   topographic variables) and dynamic (rapidly changing variable, such as

126   temperature) (Table 1).

127   Four static variables were derived from the digital elevation model (DEM) of the

128   EMODnet Bathymetry portal: depth (the DEM); slope and curvature, calculated

129   using DEM Surface Tools for ArcGIS 10.2; distance to the nearest 200 m

130   bathymetric line, calculated using QGis 2.12. Curvature was used as a proxy of sea

131   bottom roughness, providing an estimate of sea floor relief, which can influence

132   some cetacean species (Lindsay et al., 2016). All static variables were calculated at

133   a spatial resolution of 0.5 x 0.5 km.

134   Daily dynamic variables were derived from NASA's Multi-scale Ultra-high

135   Resolution (MUR) Sea Surface Temperature (SST) dataset, which merges many

136   infrared and passive microwave datasets, gathered from satellites, into global daily

137   maps at 1 km resolution. Thermal ocean fronts were detected from each MUR SST

138   daily map (Miller, 2009) and used to generate daily ocean front metrics. Front

139   distance (Fdist) quantifies the distance to the closest major front (Miller et al.,

140   2015).

141   We calculated weekly and (approximately) monthly layers using the mean

142   values of daily layers. All pairs of variables were tested for pairwise correlation;

143   the final set of selected variables all showed Pearson correlation under 0.75. All

144   layers were rescaled to a 2x2 km grid using bilinear interpolation (Fig. 1).

145   ***2.3. Virtual species***

146   Three virtual species were created, with different habitat preferences, based on

147   varying responses to static and dynamic variables (Table 2; for full details of

148   construction see Appendix S1). The 'Dynamic' species reacted only to dynamic

149   variables. The 'Static' species was influenced solely by topographic parameters.

150   The 'Pseudoreal' virtual species was influenced by both dynamic and static

151   variables, with dynamic variables having twice the weight of static ones, so that

152   only when dynamic characteristics were suitable (e.g. temperature) would the

153   species prefer a specific static environment (e.g. depth).

154   Ecological niches were simulated in a multidimensional space following Hirzel

155   et al. (2001). We defined the ecological niche of each virtual species as the

156   weighted sum of its hypothetical response curves to three different sets of

157   environmental variables. The ecological niche suitability can be expressed as

158    $H_i \times W_i$, where H_i represented the virtual species' niche suitability index for an ith

159   space and the W_i the weight of this suitability (Duan et al., 2014). Therefore the

160   final suitability, H, was calculated as:

161   Eq. 1

$$H = \frac{1}{\sum_{i=1}^{n} W_i} \sum_{i=1}^{n} W_i H_i + e$$

162

163   For each virtual species a suitability index (H) was calculated for all the areas

164   sampled each day, using a threshold approach (H$\geq$0.6) to select the suitable area

165   for presences (for more details see Appendix S2).

166   The virtual species' responses to environmental variables were either linear or

167   unimodal. The final species distribution was based on a weighted combination of

168   responses to each variable (Figs. S1.1 to S1.3, see Appendix S1 for full details).

169   Suitable areas for each species were projected onto a 2x2 km map of the study area

170   (Figs. S2.1 to S2.3).

171   ***2.4. Sampling survey design***

172   Environmental and effort data for the virtual species mirrored the timeframe of

173   a simulated cetacean detection survey for the Azores archipelago. Surveys were

174   restricted to the Central and Eastern island groups, covering 20,415 km². We

175   modified Faustino et al (2010) tracks (Fig. 2; for more details of construction see

176   Appendix S3) to last two months (8 weeks) per year, with 4 days of sampling per

177   week over two years (July-August 2013 and 2014). Survey transects were mapped

178   onto the 2 km grid that matched the environmental data.

179   As a complementary analysis a second survey was used to test for potential

180   effects of survey design on the results. A non-linear survey design was used; see

181   Appendix S3 for more details.

182   We simulated detections of the target species to infer presence (and absence) data

183   in our models. We randomly selected 300 detection points (150 for training and

184   150 for testing) from the sampled suitable area over the entire sampling period.

185 This generated two datasets, each with 150 presences (or detections) with the

186 other grids cells, noted as absences (details in Appendix S2). This mimics a real

187 world encounter rate of c. 1.22 groups/100 km (Silva et al. 2014). We allowed the

188 encounter rate to change through time; therefore it was related to the amount of

189 suitable habitat per kilometre. With this design, for the species influenced by

190 dynamic variables (Dynamic and Pseudoreal), the daily encounter rate will start

191 low and steadily increase over the course of the season (as suitability areas are

192 more available), with some days with rates much higher than 1.22 groups/100km.

193 Consequently we assumed that these species were some sort of large-ranging

194 seasonal migrant, not present at the beginning of the season and then disperses to

195 the area. To simplify the analysis we assumed a perfect presence/absence

196 detection scenario (all the groups encountered during the sampling were

197 detected), although this is unusual for marine species (Katsanevakis et al., 2012).

198 This random selection was repeated 1,000 times for each species. Data were

199 grouped according to three temporal aggregations. Niche estimates were

200 calculated using two modelling approaches.

201 **2.5. Temporal aggregations**

202 Three temporal aggregations were created: daily, weekly (7-days) and monthly

203 (4 weeks). For daily data, we constructed a data frame containing the

204 environmental data, the sampling effort and the presence or absence of species for

205 all the grid squares sampled each day. Using this approach a given location can be

206 regarded as a presence one sampling day and an absence the next. For the weekly

207   aggregation, data were grouped by 7-day periods, calculating mean values for each

208   environmental variable and aggregating the sightings, recording a single presence

209   on each grid square with a species observation, regardless of the number of times a

210   species was recorded over the 7-day period. The monthly dataset involved the

211   calculation of the average values of the environmental variables corresponding to

212   the four months virtually sampled (with 16 days sampled per month). Presence

213   grids were computed for each period, as in the weekly data.

214   There was almost no reduction of the number of presences with the coarsening

215   of temporal resolution, due to the virtual sampling design. No reduction was found

216   between the daily and the weekly approach, and a very small amount (less than 5

217   over 150 sightings) was found, for the monthly approach.

218   *2.6. Modelling approaches*

219   There are many SDM methods with variable accuracy and applicability, and

220   notably performance may depend upon the characteristics of the target species

221   (Quiao et al., 2015). Therefore, two modelling approaches with different

222   theoretical bases were used: generalized linear models and boosted regression

223   trees. The analyses were performed using the 'MASS', dismo, SDMTools, ecodist

224   and gbm (Ridgeway et al., 2015) packages for R 3.2.2 (R Core Team ,2015).

225   Binomial generalized linear models (GLM) are used widely for predicting

226   species distributions, and perform well when applied to the detection of the most

227   influential environmental variables (Peterson et al., 2011). Models used both linear

228   and quadratic terms for all explanatory variables to allow greater flexibility in

229 fitting. Model selection utilised a stepwise (forward and backward) Akaike

230 information criterion (AIC) procedure, obtaining the best explanatory variables for

231 each case (James et al., 2013).

232 Boosted regression trees (BRT) or generalized boosted regression models

233 (GBM) are a combination of classical statistics approach (regression trees) and a

234 machine learning (ML) technique (boosting). The inclusion of ML adds

235 considerable advantages compared to conventional methods, including the

236 improvement of model selection (Elith et al., 2008). This approach examines a

237 large number of trees and uses a boosting approach to select a linear combination

238 of many trees (usually from hundreds to thousands). Fitted values in the final

239 model are computed as the sum of all trees weighted by an estimate of the

240 contribution of each tree to the growing model. A relatively slow learning rate

241 (0.001) with a higher tree complexity (5), was selected to aim for more than 1,000

242 trees in the final model, avoiding a potential overfitting (Elith et al. 2008).

243 ***2.7. Model evaluation***

244 SDM performance was evaluated using two metrics: (i) a variable contribution

245 index; (ii) the area under the curve (AUC) of the receiver operator curve (ROC) for

246 the training and test dataset. The analyses were performed using the SDMTools,

247 ecodist, pROC and PMCMR packages for R.

248 GLM variable contributions were based on a tally of their inclusion in each

249 stepwise selection procedure. Variable contribution for GBMs was estimated using

250 the relative importance selection tool in the gbm R package.

251   Test AUCs were evaluated using daily environmental data. For each model the

252   training AUC and test AUC were calculated (test dataset = 150 randomly selected

253   presences from the sampled suitable area different from the training data).

254   To support the results, explanation suitability maps were produced for an

255   extended area for randomly chosen dates for the three virtual species (Dynamic,

256   Static and Pseudoreal) using the GLM approach. All analysis and figures were

257   produced using R.

258   **3. RESULTS**

259   We built 6,000 ecological niche models (three temporal aggregations and two

260   modelling algorithms) for each of the three virtual species, making a total of

261   18,000 models. For the two species influenced by dynamic variables, there were

262   important differences in the evaluation metrics between the three temporal

263   aggregations. In general, results improved when using the daily or weekly

264   environmental layers. For species influenced solely by static variables, differences

265   in accuracy between temporal aggregations were smaller.

266   ***3.1. Variable contributions***

267   There were some differences among variable contributions by modelling

268   method (Fig. 3), detailed below.

269   *3.1.1. GLM*

270   Temporal scale affected the models for the dynamic species; models based on

271   daily and weekly aggregations successfully detected the two most important

272   variables (SST and Fdist), but the monthly-based models were unable to detect the

273   influence of Fdist.

274   For the Pseudoreal species, influenced by two dynamic (SST, Fdist) and one

275   static variable (slope), models based on daily and weekly environmental data

276   recovered all influencing variables. The greater relative importance of the dynamic

277   variables was reflected by the contribution measures. Models based on monthly

278   data performed poorly in selecting the influence of the Fdist variable for the niche

279   of the Pseudoreal species.

280   The GLM analysis for the Static species showed smaller differences in variable

281   selection between temporal aggregations. The two most important variables (SST

282   and slope) were selected in more than 80% of iterations for all temporal

283   groupings.

284   *3.1.2. GBM*

285   The GBM models performed well for the dynamic and the Pseudoreal species.

286   For the Dynamic species, the 'daily' model was able to successfully detect all

287   influencing variables, although the contribution of the main variable (SST) was

288   smaller than its theoretical weight. The 'weekly' models detected the two main

289   variables (SST and Fdist). However, for the 'monthly' models, only the influence of

290   SST was detected.

291   For the Pseudoreal species, the daily approach identified the effects of SST and

292   slope. However a relative upweighting of Fdist was found. The weekly analysis

293   showed an almost perfect correlation between the variable contributions and their

294   theoretical weight. Models using monthly data had Fdist contributions lower than

295   expected, while the curvature contribution was overestimated. In general, models

296   from this scenario showed the poorest accuracy regarding variable selection.

297   For the Static species, the three temporal aggregations produced similar

298   results, with depth as the main contributing variable, as expected. However, some

299   noise can be observed in the model for the monthly scenario, which exhibited a

300   larger variation of contribution values.

301   ***3.2. Train and test AUC results***

302   Ignoring the influence of mobility, we would expect that coarsening temporal

303   resolution would decrease model performance for the Dynamic species, but would

304   have little impact on the Static species, with the Pseudoreal species (influenced by

305   both static and dynamic variables) showing an intermediate position. The AUC

306   train and test results from the GBM and GLM approach confirm this hypothesis

307   (Fig. 4). However when looking at the Static species, the monthly models

308   performed slightly worse for the GLM modelling approach in the AUC test and for

309   the GBM approach in the AUC train.

310   Results of the AUC test for the non-linear survey design (transects not

311   following a pre-designed line and with unequal effort distribution) showed the

312   same patterns (Fig. S3.2): finer temporal resolutions produced better AUC values

313   for the Dynamic and the Pseudoreal species.

314   ***3.3. Suitability map projections***

315   The visualized predictions (Fig. 5), showed the same pattern as previous

316   evaluations. For the Dynamic and Pseudoreal differences are visible as temporal

317   resolution coarsens. The Static species were less influenced by the temporal

318   resolution of environmental variables, with no difference between temporal grain

319   selections.

320   **4. DISCUSSION**

321   Selection of temporal resolution can be important for SDMs. When working in

322   highly dynamic areas like the marine environment, and with species responding to

323   daily environmental changes, the selection of temporal resolution can play an

324   important role for environmental niche modelling procedures. In particular, the

325   use of models based on an environmental dataset with finer temporal resolution

326   can improve predictions of distribution.

327   The results obtained suggest these findings are not related to survey design,

328   although further analysis with other designs and applying detectability indexes

329   would be useful to discard any potential undetected effects.

330   ***4.1. Dynamic cetacean movements***

331   The virtual species used in the present study were designed based on a review of

332   previous distributional cetacean studies. A daily response to rapidly changing

333   oceanographic patterns, as assumed for the present study, has been described or

334   suggested for some cetacean species, such as baleen whales (Doniol-Valcroze et al.

335   2007, Druon et al. 2012). Similarly, small delphinids seem to be strongly influenced

by dynamic oceanographic structures (Balance et al., 2006; Becker et al., 2010). Furthermore, daily environmental variation at small to medium spatial scales (approx. 5 km) can be important for other marine mobile pelagic species such as tuna (Hobday & Hartman, 2006). These responses are probably related with prey movements associated with local/regional oceanographic features. However other cetacean species appear to respond to broad-scale oceanographic patterns (Becker et al., 2010). Non-dynamic factors, such as bathymetric features (e.g. seamounts) can also play an important role for some cetacean species (e.g. bottlenose dolphins, Risso's dolphins, or pilot whales; Azzellino et al., 2008; Cañadas et al., 2002). Therefore, for species that may be more influenced by topographic features (such as deep-diving cetaceans) or broad/medium scale oceanographic features (such as the year-round presence of blue whales in the Costa Rica Dome; Reilly & Thayer, 1990), the dynamism captured by fine (temporal) scale oceanographic patterns may not be relevant. Even so, some of the results presented here suggest that a species responding to static factors could still be influenced by the temporal scale selected. Although it might be expected that dynamic variables would have no impact on models for these species, implicit relationships between static and dynamic variables can result in some explanatory power for dynamic variables.

4.2. Temporal resolution of dynamic variables

Generally, modelling with weekly environmental data produced the best results. Using monthly aggregations produced inconsistent results, with SST patterns more routinely detected than frontal distance. This might be a consequence of two factors: the variable dynamism and the species relation with the predictors. The

359   level of variable dynamism could have a clear effect: SST is typically slower to

360   change, while the location of thermal fronts can move rapidly. Consequently, a

361   finer temporal resolution might be needed to detect the effects of highly dynamic

362   variables (Fdist in this case). Moreover, the species ecology and their relation with

363   the environment could be also essential. Response curves for SST in the present

364   study were always based on a linear function, while those for distance to fronts

365   were created using a unimodal function, leading to a more restricted range of

366   suitable values for distances to frontal areas than for SST. Therefore the species

367   modelled will be more sensitive to changes on thermal front locations than to SST

368   changes. Likewise, the use of a finer temporal grain might be important when

369   species are strongly related to specific ranges of one or more dynamic variables.

370   However, for species with a more generalist relation with dynamic predictors, a

371   coarser resolution could be suitable.

372   Scales et al. 2017 found that models using broader temporal scales can

373   introduce bias in presence-availability for simulated blue whale movements for the

374   California upwelling system. However, Mannocci et al. (2014) concluded that

375   modelling using a climatological temporal scale (corresponding to seasonal

376   oceanographic conditions averaged over 7 years) performed better than using

377   weekly data. These authors examined a tropical system, which are typically more

378   constant, with stable oceanographic phenomena that can be used by top predators

379   in a predictable fashion. In contrast, the (temperate) Azores region has been

380   described as an area with high mesoscale activity strongly influenced by the Gulf

381   Stream and associated currents (Santos et al., 1995). In order to produce accurate

382   models it is essential to have a good understanding of the oceanographic

383   characteristics of the study area. When producing distribution estimates for areas

384   with higher dynamism (such as temperate oceanic islands or coastal upwelling

385   systems) the use of fine temporal resolution may be important.

386   We found little evidence that modelling with daily (rather than weekly)

387   environmental data could lead to significant improvement in model performance.

388   Weekly environmental aggregations may prove a fairly consistent representation

389   of average daily conditions, as has been suggested for SST products in relatively

390   dynamic environments, such as the California current (Becker et al., 2010).

391   It is important to consider the quality of the environmental data being

392   analysed, particularly the characteristics of gap-free remote sensing products.

393   Remote sensing datasets can have cloud-masked missing data which may reduce

394   the predictive ability of the models (Scales et al. 2017). Some products include

395   large areas of interpolation in order to cover cloud gaps. For example the MUR SST

396   dataset used in this study performs spatio-temporal interpolation to fill gaps, but

397   does this at multiple resolutions in order to preserve small-scale features

398   (Vazquez-Cuervo et al., 2013). There is a trade-off to be made in deciding between

399   daily and weekly aggregates. Our study indicates that weekly means may be the

400   best choice at present.

401   **4.3. Relationship between spatial and temporal scales**

402   In the present study we found differences in model predictions between the

403   different temporal grain sizes, although we did not test the combined effects of

404   spatial and temporal scales. The temporality of oceanographic and biological

405   processes can be dependent on spatial scale, consequently temporal variability

406   tends to be higher at finer spatial scales (Haury et al., 1978; Hunt & Schneider

407   1978). Both Redfern et al. 2006 and Balance et al. 2006 reinforced the importance

408   of using adequate resolutions to the scale of the data collected, matching spatial

409   and temporal grain size to the specific research question. However, Becker et al.

410   (2010) suggested that effects of the use of different spatial grain sizes are

411   relatively small, finding similar functional relationships between SST response

412   variables across different spatial resolution. Additionally, Scales et al. (2017) found

413   that spatial effects at small temporal grain sizes (daily-monthly) are relatively

414   small compared to climatological scales. Other studies of modelling applications

415   suggest similar effects of spatial resolution for different areas and taxonomic

416   groups (Guisan et al., 2007; Redfern et al., 2008, Becker et al., 2010). Therefore, the

417   results obtained in the present study might be useful for different spatial scales

418   when working at relatively small temporal scales.

419   Nonetheless, the detectability of the influence of particular environmental

420   factors can be dependent on the spatial resolution. Guinet et al. (2001) found that

421   different spatial scales resulted in different variable influences on fur seal niche

422   models. The relative importance of oceanic features will change with geographical

423   scale, from oceanic gyres down to random turbulence (Parsons et al., 2013). For

424   example, a weekly dataset might fail to detect an ocean gyre. Thus, coarsening

425   temporal resolution might have a similar effect as coarsening the spatial

426   resolution. The use of a fine temporal grain may negatively impact the detection of

427   some large-scale oceanographic features that can influence cetacean distributions,

428   such as island-generated eddies or domes (e.g. Ballance et al., 2006), adding a

429   temporal dimension to the Redfern et al. (2008) hypothesis of the relationship

430   between signal-to-noise ratio and spatial scale.

431   It is possible that for studies focusing on mesoscale/global distributions, a

432   coarser temporal and spatial resolution may be more appropriate (e.g. Kaschner et

433   al., 2006; Mannocci et al., 2014), while studies focused on species distribution

434   modelling on regional and local scales may be improved by examining finer

435   temporal resolutions (e.g. Becker et al., 2016). Yet, this might limit model

436   applicability. Models built using seasonal environmental data won't be able to

437   predict distributions at finer grain sizes, and models using a weekly resolution

438   might fail when projected into a global scale (Redfern et al. 2006). In contrast,

439   Scales et al. 2017 found that even when working with large spatial scales (111 km)

440   the use of seasonal and climatological fields increased the model error

441   substantially but admit that this observation may not be valid in all biogeographic

442   provinces. Our simulation results support the suggestion that care is needed when

443   matching different scales (Scales et al., 2017). In fact we found that, in some cases,

444   even if working at small spatial scales the use of a monthly resolution can produce

445   unrealistic predictions.

446   Redfern et al. (2006) suggest the simultaneous modelling of cetacean

447   distributions at different scales as a way to overcome this problem. Further

448   research is needed to understand better the relationship between temporal and

449   spatial scales.

450   ***4.4. Further considerations***

451   It could be argued that temporal dynamics are not an issue for mobile species

452   with high residency, or for those species that are mainly dependent on more stable

453   environmental conditions. In these cases, animals would tend not to move from

454   their preference areas, within reasonable environmental boundaries. Migratory

455   species traveling long distances can have strong site fidelity between migrations

456   (Rasmussen et al. 2007). However it is important to keep in mind that species can

457   interact with the environment at multiple scales (e.g. hourly feeding, daily foraging,

458   seasonal migration). This behaviour-dependent habitat utilisation may be

459   detectable at different scales, for instance in baleen whale migrations (Corkeron &

460   Connor, 1999; Rasmussen et al., 2007).

461   Given that a species' niche is not usually well understood prior to modelling, it

462   would be a good practice to include dynamic, static, and climatological variables in

463   the model fitting process to test for influences at multiple spatial and temporal

464   scales. However, high quality environmental data for many oceanographic

465   variables rarely exists at daily temporal resolutions in most parts of the ocean and

466   fine-scale prey distribution is non-existent on most temporal scales. As these data

467   become available it would be worth testing their influence. Meanwhile the

468   inclusion of variability measures (e.g. minimum daily temperature in a given

469   month) when using coarser grains can provide a way of adding some finer

470   temporal resolution data, improving model predictions.

471   Approaches using a finer grain (both on biological, spatial and temporal scales)

472   may be more suitable for effective conservation measures (Stelzenmüller et al.,

473 2013). In fact, recent studies (e.g. Maxwell et al., 2016) highlighted the importance

474 of management that changes in space and time in response to changes in the ocean

475 and its users. Dynamic management techniques are appealing for areas with

476 substantial temporal and spatial variability (e.g. seasonal tourism, Becker et al.,

477 2016). However other approaches might be useful: for species with low or

478 moderate sighting rates the use of models using broader temporal resolutions

479 might be justified (Roberts et al., 2016). For example if the goal of the study is to

480 produce distribution maps of beaked whales, which are rarely sighted, the use of a

481 fine temporal scale might be an unrealistic choice. There are several factors to take

482 into consideration before choosing a specific temporal resolution, such as the

483 ecology of the target species, the dynamism of the environment, the species

484 detectability, the spatial scale to be used, the main objectives of the analysis or

485 even the data availability.

486 ### 4.5. Final remarks

487 The combination of mobility and habitat dynamism is a key issue when

488 selecting the best temporal resolution to model a species' ecological niche. In this

489 study we used theoretical species responding to daily changes of environmental

490 variables to test these effects, and we found important differences between

491 temporal resolutions. Even if theoretical species can differ from real world

492 examples, it is important to emphasize the potential impact of these dynamic

493 factors. Assuming that low-frequency environmental data will sufficiently

494 reproduce high-frequency variation in species distributions might lead to

495 inaccurate distribution models.

496   It is essential to have some knowledge of the species ecology and variable

497   dynamism to select the best predictors and resolutions. For fine scale applications

498   (e.g. dynamic ocean management), when using variables with high temporal

499   dynamism (e.g. distance to frontal areas), and highly mobile species (or for species

500   strongly related to dynamic environmental predictors), our results suggest

501   exploring weekly temporal resolution. Coarser resolutions might be useful when

502   working with variables with low dynamism or for species less dependent on

503   dynamic variables (e.g. some deep diving cetaceans). However one must take into

504   consideration that averaging environmental variables over larger time periods

505   may mask the underlying dynamic patterns and produce a less realistic niche

506   model, which may be misleading and even detrimental for conservation purposes.

523 **REFERENCES**

524 Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–
525   climate impact models under climate change. *Global Change Biology*, **11**,
526   1504-1513.

527 Azzellino, A., Gaspari, S., Airoldi, S., Nani, B. (2008) Habitat use and preferences of
528   cetaceans along the continental slope and the adjacent pelagic waters in the
529   western Ligurian Sea. *Deep-Sea Research I*, **55**, 296-323.

530 Austin, M. (2002) Spatial prediction of species distribution: an interface between
531   ecological theory and statistical modelling. *Ecological modelling*, **157**, 101-
532   118.

533 Bakun, A. (2006) Fronts and eddies as key structures in the habitat of marine fish
534   larvae: opportunity, adaptive response and competitive advantage. *Scientia*
535   *Marina*, **70**, 18.

536 Ballance, L.T., Pitman, R.L., Fiedler, P.C. (2006) Oceanographic influences on
537   seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress in*
538   *Oceanography*, **69**, 360-390.

539 Barry, S. & Elith, J. (2006) Error and uncertainty in habitat models. *Journal of*
540   *Applied Ecology*, **43**, 413-423.

541 Becker, E., Forney, K., Ferguson, M., Foley, D., Smith, R., Barlow, J. & Redfern, J.
542   (2010) Comparing California Current cetacean–habitat models developed
543   using in situ and remotely sensed sea surface temperature data. *Marine*
544   *Ecology Progress Series*, **413**, 163-183.

545 Becker, E., Forney, K., Fiedler, P., Barlow, J., Chivers, S., Edwards, C., Moore, A. &
546   Redfern, J. (2016) Moving Towards Dynamic Ocean Management: How Well
547   Do Modeled Ocean Products Predict Species Distributions? *Remote Sensing*,
548   **8**, 149.

549 Brotons, L., Thuiller, W., Araújo, M.B. & Hirzel, A.H. (2004) Presence-absence
550   versus presence-only modelling methods for predicting bird habitat
551   suitability. *Ecography*, **27**, 437-448.

552 Busby, J.R. (1991) BIOCLIM-a bioclimate analysis and prediction system. *Plant*
553   *Protection Quarterly (Australia)*.

554 Cañadas, A. & Hammond, P.S. (2008) Abundance and habitat preferences of the
555   short-beaked common dolphin Delphinus delphis in the southwestern
556   Mediterranean: implications for conservation. *Endangered Species Reserach*,
557   **4**, 309-331.

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

561 Corkeron, P.J. & Connor, R.C. (1999) Why do baleen whales migrate? *Marine*
562   *Mammal Science*, **15**, 1228-1245.

563 Doniol-Valcroze, T., Berteaux, D., Larouche, P., Sears, R. (2007) Influence of thermal
564   fronts on habitat selection by four rorqual whale species in the Gulf of St.
565   Lawrence. *Marine Ecology Progress Series*, **335**, 207 - 216.

566 Doniol-Valcroze, T., Lesage, V., Giard, J. & Michaud, R. (2012) Challenges in marine
567   mammal habitat modelling: evidence of multiple foraging habitats from the
568   identification of feeding events in blue whales. *Endangered Species*
569   *Research*, **17**, 255-268.

570 Druon, J.N., Panigada, S., David, L., Gannier, A., Mayol, P., Arcangeli, A., Cañadas, A.,
571   Laran, S., Di Méglio, N. & Gauffier, P. (2012) Potential feeding habitat of fin
572   whales in the western Mediterranean Sea: an environmental niche model.
573   *Marine Ecology Progress Series*, **464**, 289-306.

574 Duan, R.-Y., Kong, X.-Q., Huang, M.-Y., Wu, G.-L. & Wang, Z.-G. (2014) SDMvspecies:
575   a software for creating virtual species for species distribution modelling.
576   *Ecography*, **38**, 108 - 110.

577 Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression
578   trees. *Journal of Animal Ecology*, **77**, 802-813.

579 Faustino, C.E.S., Silva, M.A., Marques, T.A. & Thomas, L. (2010) Designing a
580   shipboard line transect survey to estimate cetacean abundance off the
581   Azores archipelago *Arquipélago - Life and Marine Sciences*, **27**, 49-58.

582 Forney, K.A., Ferguson, M.C., Becker, E.A., Fiedler, P.C., Redfern, J.V., Barlow, J.,
583   Vilchis, I.L. & Ballance, L.T. (2012) Habitat-based spatial models of cetacean

584 density in the eastern Pacific Ocean. *Endangered Species Research*, **16**, 113-
585 133.

586 Fryxell, J, Sinclair A. & A. Cughley, G. (2014) Wildlife ecology, conservation, and
587 management, 3rd edn. Wiley-Blackwell

588 Guinet, C., Dubroca, L., Lea, M.-A., Goldsworthy, S.D., Cherel, Y., Duhamel, G.,
589 Bonadonna, F. & Donnay, J.-P. (2001) Spatial distribution of foraging in
590 female Antarctic fur seals Arctocephalus gazella in relation to
591 oceanographic variables: a scale-dependent approach using geographic
592 information systems. *Marine Ecology Progress Series*, **219**, 251-264.

593 Guisan, A., Graham, C.H., Elith, J., Huettmann, F. & the, N.S.D.M.G. (2007) Sensitivity
594 of predictive species distribution models to change in grain size. *Diversity*
595 *and Distributions*, **13**, 332-340.

596 Haury, L., McGowan, J. & Wiebe, P. (1978) Patterns and processes in the time-space
597 scales of plankton distributions. *Spatial pattern in plankton communities*, pp.
598 277-327. Springer.

599 Hirzel, A.H., Helfer, V. & Metral, F. (2001) Assessing habitat-suitability models with
600 a virtual species. *Ecological Modelling*, **145**, 111-121.

601 Hobday, A.J. & Hartmann, K. (2006) Near real-time spatial management based on
602 habitat predictions for a longline bycatch species. *Fisheries Management*
603 *and Ecology*, **13**, 365-380.

604 Howell, E.A., Kobayashi, D.R., Parker, D.M., Balazs, G.H. & Polovina, A. (2008)

605 TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles

606 Caretta caretta in the Hawaii-based pelagic longline fishery. *Endangered*

607 *Species Research*, **5**, 267-278.

608 Hunt Jr, G. & Schneider, D. (1987) Scale-dependent processes in the physical and

609 biological environment of marine birds. *Seabirds: feeding ecology and role in*

610 *marine ecosystems*, 7-41.

611 James, G., Witten, D., Hastie, T. & Tibshirani, R. (2013) *An introduction to statistical*

612 *learning*. Springer.

613 Jetz, W., McPherson, J.M. & Guralnick, R.P. (2012) Integrating biodiversity

614 distribution knowledge: toward a global map of life. *Trends in ecology &*

615 *evolution (Personal edition)*, **27**, 151-159.

616 Kaschner, K., Watson, R., Trites, A.W. & Pauly, D. (2006) Mapping world-wide

617 distributions of marine mammal species using a relative environmental

618 suitability (RES) model. *Marine Ecology Progress Series*, **316**, 285-310.

619 Katsanevakis, S., Weber, A., Pipitone, C. et al. (2012) Monitoring marine

620 populations and communities: methods dealing with imperfect

621 detectability. *Aquatic Biology*, **16**, 31-52.

622 Lawson, C.R., Hodgson, J.A., Wilson, R.J. & Richards, S.A. (2014) Prevalence,

623 thresholds and the performance of presence–absence models. *Methods in*

624 *Ecology and Evolution*, **5**, 54-64.

625 Lindsay, R.E., Constantine, R., Robbins, J., Mattila, D.K., Tagarino, A. & Dennis, T.E.
626   (2016) Characterising essential breeding habitat for whales informs the
627   development of large-scale Marine Protected Areas in the South Pacific.
628   *Marince Ecology Progress Series* ,**54** , 263-275.

629 MacLeod, C.D., Weir, C.R., Pierpoint, C. & Harland, E.J. (2007) The habitat
630   preferences of marine mammals west of Scotland (UK). *Journal of the*
631   *Marine Biological Association of the United Kingdom*, **87**, 157 - 164.

632 Mann, K. & Lazier, J. (2013) *Dynamics of marine ecosystems: biological-physical*
633   *interactions in the oceans.* John Wiley & Sons.

634 Mannocci, L., Laran, S., Monestiez, P., Dorémus, G., Van Canneyt, O., Watremez, P. &
635   Ridoux, V. (2014) Predicting top predator habitats in the Southwest Indian
636   Ocean. *Ecography*, **37**, 261-278.

637 Maxwell, S.M., Hazen, E.L., Lewison, R.L., Dunn, D.C., Bailey, H., Bograd, S.J., Briscoe,
638   D.K., Fossette, S., Hobday, A.J., Bennett, M., Benson, S., Caldwell, M.R., Costa,
639   D.P., Dewar, H., Eguchi, T., Hazen, L., Kohin, S., Sippel, T. & Crowder, L.B.
640   (2015) Dynamic ocean management: Defining and conceptualizing real-
641   time management of the ocean. *Marine Policy*, **58**, 42-50.

642 Miller, P. (2009) Composite front maps for improved visibility of dynamic sea-
643   surface features on cloudy SeaWiFS and AVHRR data. *Journal of Marine*
644   *Systems*, **78**, 327-336.

645   Miller, P.I., Scales, K.L., Ingram, S.N., Southall, E.J. & Sims, D.W. (2015) Basking

646   sharks and oceanographic fronts: quantifying associations in the north-east

647   Atlantic. *Functional Ecology*, **29**, 1099-1109.

648   Moura, A.E., Sillero, N. & Rodrigues, A. (2012) Common dolphin (Delphinus

649   delphis) habitat preferences using data from two platforms of opportunity.

650   *Acta Oecologica-International Journal of Ecology*, **38**, 24-32.

651   Panigada, S., Zanardelli, M., MacKenzie, M., Donovan, C., Melin, F. & Hammond, P.S.

652   (2008) Modelling habitat preferences for fin whales and striped dolphins in

653   the Pelagos Sanctuary (Western Mediterranean Sea) with physiographic

654   and remote sensing variables. *Remote Sensing of Environment*, **112**, 3400-

655   3412.

656   Parsons, T.R., Takahashi, M. & Hargrave, B. (2013) *Biological oceanographic

657   processes*. Elsevier.

658   Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E.,

659   Nakamura, M. & Araújo, M.B. (2011) *Ecological Niches and Geographic

660   Distributions (MPB-49)*. Princeton University Press.

661   Praca, E. & Gannier, A. (2007) Ecological niche of three teuthophageous

662   odontocetes in the northwestern Mediterranean Sea. *Ocean Science Discuss.*,

663   **4**, 785-815.

664   R Core Team (2015). R: A language and environment for statistical computing. R

665   Foundation for Statistical Computing, Vienna, Austria. Version 3.2.2.

666   Rasmussen, K., Palacios, D.M., Calambokidis, J., Saborío, M.T., Dalla Rosa, L., Secchi,

667   E.R., Steiger, G.H., Allen, J.M. & Stone, G.S. (2007) Southern Hemisphere

668   humpback whales wintering off Central America: insights from water

669   temperature into the longest mammalian migration. *Biology Letters*, **3**, 302-

670   305.

671   Redfern, J.V., Barlow, J., Ballance, L.T., Gerrodette, T. & Becker, E.A. (2008) Absence

672   of scale dependence in dolphin–habitat models for the eastern tropical

673   Pacific Ocean. *Marine Ecology Progress Series*, **363**, 1-14.

674   Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Good, C., Barlow, J.,

675   Kaschner, K., Baumgartner, M.F., Forney, K.A., Ballance, L.T., Fauchald, P.,

676   Halpin, P., Hamazaki, T., Pershing, A.J., Qian, S.S., Read, A., Reilly, S.B., Torres,

677   L. & Werner, F. (2006) Techniques for cetacean habitat modeling. *Marine*

678   *Ecology Progress Series*, **310**, 271-295.

679   Reilly, S.B. & Thayer, V.G. (1990) Blue whale (Balaenoptera musculus) distribution

680   in the eastern tropical Pacific. *Marine Mammal Science*, **6**, 265-277.

681   Ridgeway G. et al. (2015). Gbm: Generalized Boosted Regression Models. R package

682   version 2.1.1.

683   Roberts, J.J., Best, B.D., Mannocci, L., Fujioka, E., Halpin, P.N., Palka, D.L., Garrison,

684   L.P., Mullin, K.D., Cole, T.V.N., Khan, C.B., McLellan, W.A., Pabst, D.A. &

685   Lockhart, G.G. (2016) Habitat-based cetacean density models for the U.S.

686   Atlantic and Gulf of Mexico. *Scientific Reports*, **6**, 22615.

687   Santos, R.S., Hawkins, S., Monteiro, L.R., Alves, M., Isidro, E.J. (1995) Marine

688   research, resources and conservation in the Azores. *Aquatic Conservation:*

689   *Marine and Freshwater Ecosystems*, **5**, 311-354.

690   Sbrocco, E.J., & Barber, P.H. (2013) MARSPEC: ocean climate layers for marine

691   spatial ecology. *Ecology*, **94.4** , 979-979.

692   Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W. & Votier, S.C. (2014)

693   REVIEW: On the Front Line: frontal zones as priority at-sea conservation

694   areas for mobile marine vertebrates. *Journal of Applied Ecology*, **51**, 1575-

695   1583.

696   Scales, K.L., Hazen, E.L., Jacox, M.G., Edwards, C.A., Boustany, A.M., Oliver, M.J. &

697   Bograd, S.J. (2017) Scale of inference: on the sensitivity of habitat models

698   for wide-ranging marine predators to the resolution of environmental data.

699   *Ecography*, **40,** 210-220.

700   Stelzenmüller, V., Breen, P., Stamford, T., et al. (2013) Monitoring and evaluation of

701   spatially managed areas: A generic framework for implementation of

702   ecosystem based marine management and its application. *Marine Policy*, **37**,

703   149-164.

704   Svensson, J.R., Jonsson, L. & Lindegarth, M. (2013) Excessive spatial resolution

705   decreases performance of quantitative models, contrary to expectations

706   from error analyses. *Marine Ecology Progress Series*, **485**, 57-73.

707 Vazquez-Cuervo, J., Dewitte, B., Chin, T.M., Armstrong, E.M., Purca, S. &

708   Alburqueque, E. (2013) An analysis of SST gradients off the Peruvian Coast:

709   The impact of going to higher resolution. *Remote Sensing of Environment*,

710   **131**, 76-84.

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712 **Supporting Information**

713 Additional Supporting Information may be found in the online version of this

714 article:

715 **Appendix S1** Virtual species design

716 **Appendix S2** Virtual species suitability projections and presence/absence

717 generation

718 **Appendix S3** Survey details and results

719 **Bioskecth:** Marc Fernandez is a PhD candidate of the 3CBIO program at the

720 University of Azores and a current member of the Azorean Biodiversity Group of

721 the Centre for Ecology, Evolution and Environmental Changes. His main research

722 interests are marine spatial ecology, particularly niche modelling of cetaceans.

723 Chris Yesson is a research fellow for the Institute of Zoology (ZSL), focussing his

724 research on the impact of trawling on benthic habitats in Greenland, abundance of

725 large brown seaweeds and phyloclimatic modelling. Alexandre Gannier is the

726 president of the GREC. His work has been related with the study of the general

727 ecology of cetaceans, focusing on populations' ecology, acoustic ecology and

728 acoustic impact.

729   Editor: Richard Pearson

730

731

732 **Table 1.** Environmental variables used to construct the virtual species suitability indexes.

Variables	Definition	Source
Oceanographic (dynamic)		
SST	Sea surface temperature (°C)	NASA's Multi-scale Ultra-high Resolution (MUR) Sea Surface Temperature (SST) - http://mur.jpl.nasa.gov/. Downloaded with spatial resolution of 1kmx1km on a daily basis.
Fdist	Distance from major thermal front (km)	Processed from NASA's Multi-scale Ultra-high Resolution (MUR) Sea Surface Temperature (SST) following Miller (2009) methodology.
Physiographic (static)		
depth	Depth (m)	Bathymetric metadata and Digital Terrain Model data products derived from the EMODnet Bathymetry portal - http://www.emodnet-bathymetry.eu. Downloaded with a spatial resolution of: 0.125x0.125 minutes.
slope	Slope (degrees)	Processed from EMODnet Bathymetry using DEM Surface Tools for ArcGIS 10.2
d200	Distance from 200 m bathymetric line (km)	Processed from EMODnet Bathymetry using QGIS 2.1.2
curv	Bottom general curvature	Processed from EMODnet Bathymetry using DEM Surface Tools for ArcGIS 10.2

733   **Table 2.** Formulas used to build the suitability values for each virtual species according to

734   the environmental variables.

Species	Suitability index
Dynamic	$H_D = \dfrac{1}{(2+1.5)}(2SST + 1.5Fdist)$
Static	$H_S = \dfrac{1}{(2+1.5+1)}(2Depth + 1.5D200 + Slope)$
Pseudoreal	$H_{PR} = \dfrac{1}{(2+1.5+1)}(2SST + 1.5Slope + Fdist)$

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746 **Figure 1:** Example of environmental variables for the 20th of August 2013.

747 Variables are categorized as dynamic/oceanographic (SST (a) and Fdist(b)) or

748 static/geographic (Depth(c), Slope(d), Dcoast(e) and Curvature(f)).

749 **Figure 2:** Study area map (Eastern Group and Central Group, Azores Archipelago)

750 with the virtual transects (with the nine substratum divisions) used for the niche

751 modelling calculations.

752 **Figure 3:** Results of variable selection for the three temporal aggregations (daily,

753 weekly and monthly – in rows), two models algorithms (GLM and GBM), and 3

754 virtual species (Dynamic, Static and Pseudoreal – in columns). Results of the GBM

755 models are expressed as mean variable contribution over the 1000 iterations

756 according to variable relative importance. Results of the GLM are expressed as the

757 number of times a specific variable was selected for the model after the AIC

758 stepwise selection procedure.

759 **Figure 4:** Results for the training and testing AUC using sampling data for the GBM

760 and GLM model algorithms (rows), and the three temporal grain selections (daily,

761 weekly and monthly) and three virtual species (dynamic, static and pseudoreal),

762 (columns). AUC ranges from 0 to 1.

763 **Figure 5:** Suitability maps for randomly chosen dates. Projections were made for

764 the three virtual species (Dynamic, Static and Pseudoreal) using the GLM approach.

765 Columns represent the different temporal resolutions and the theoretical

766 suitability (noted as Theoretical in the figure) for each species. The worm-like

767   pattern observed in the Dynamic species it is related to the preference for a given

768   distance to the thermal front.

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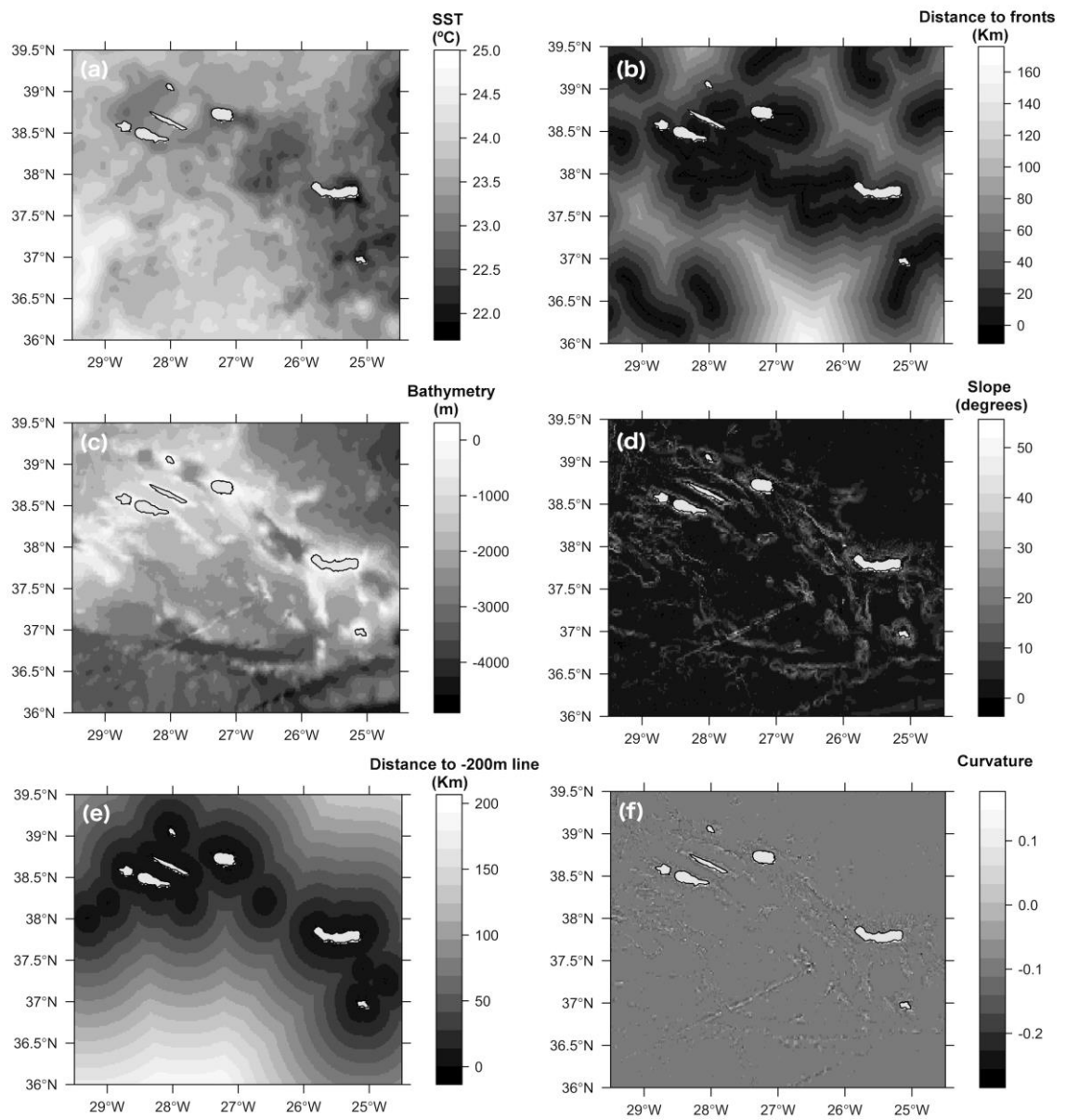
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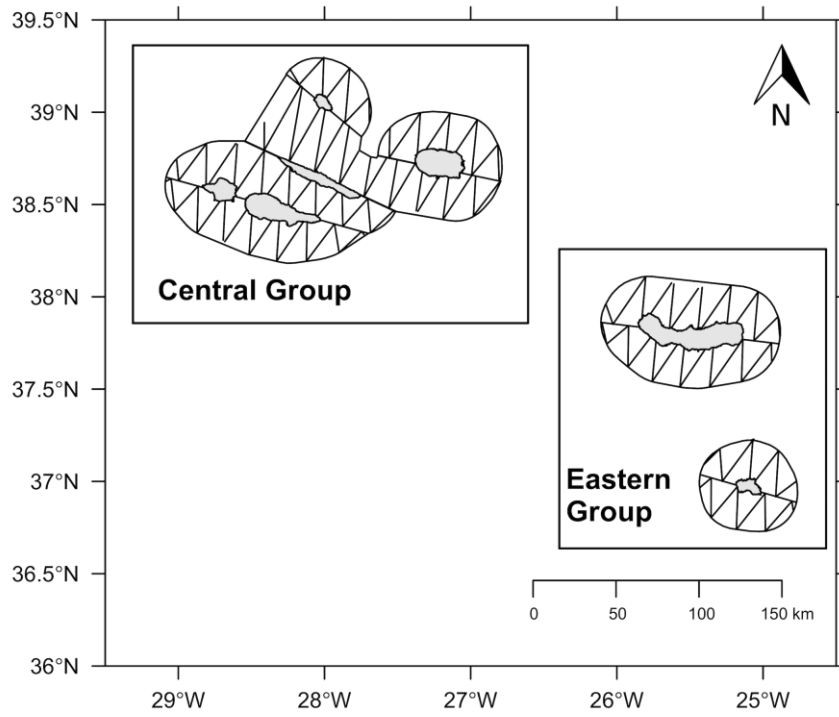
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784   **Figure 1:**

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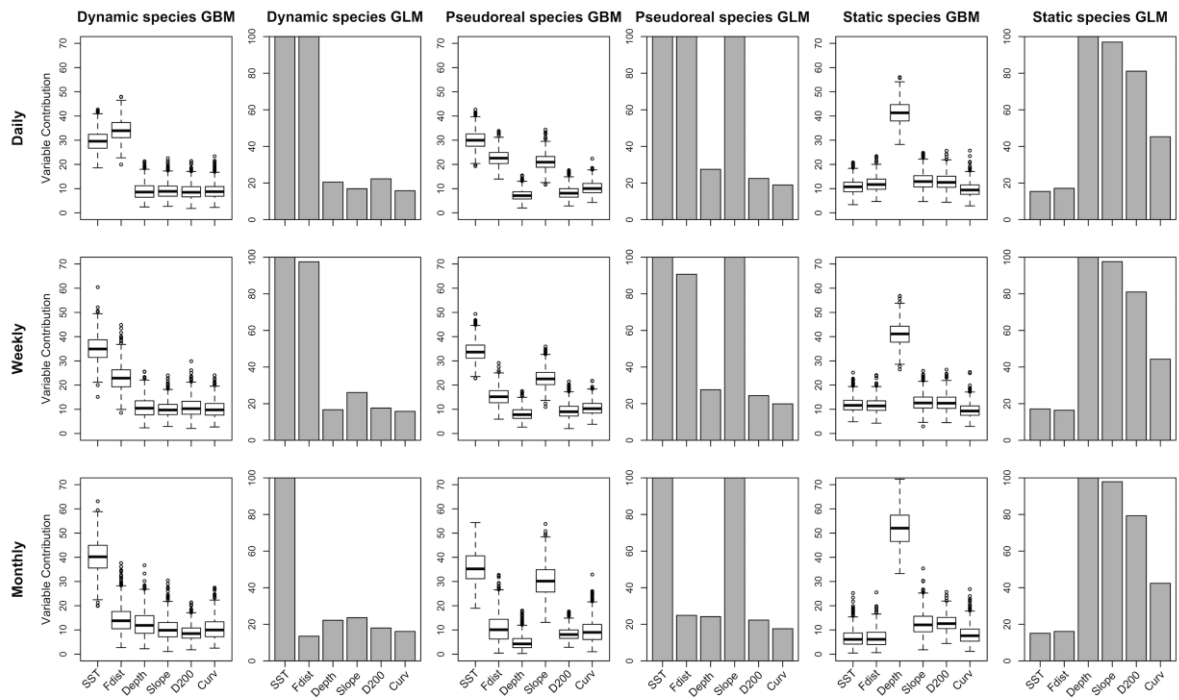
789   **Figure 2:**

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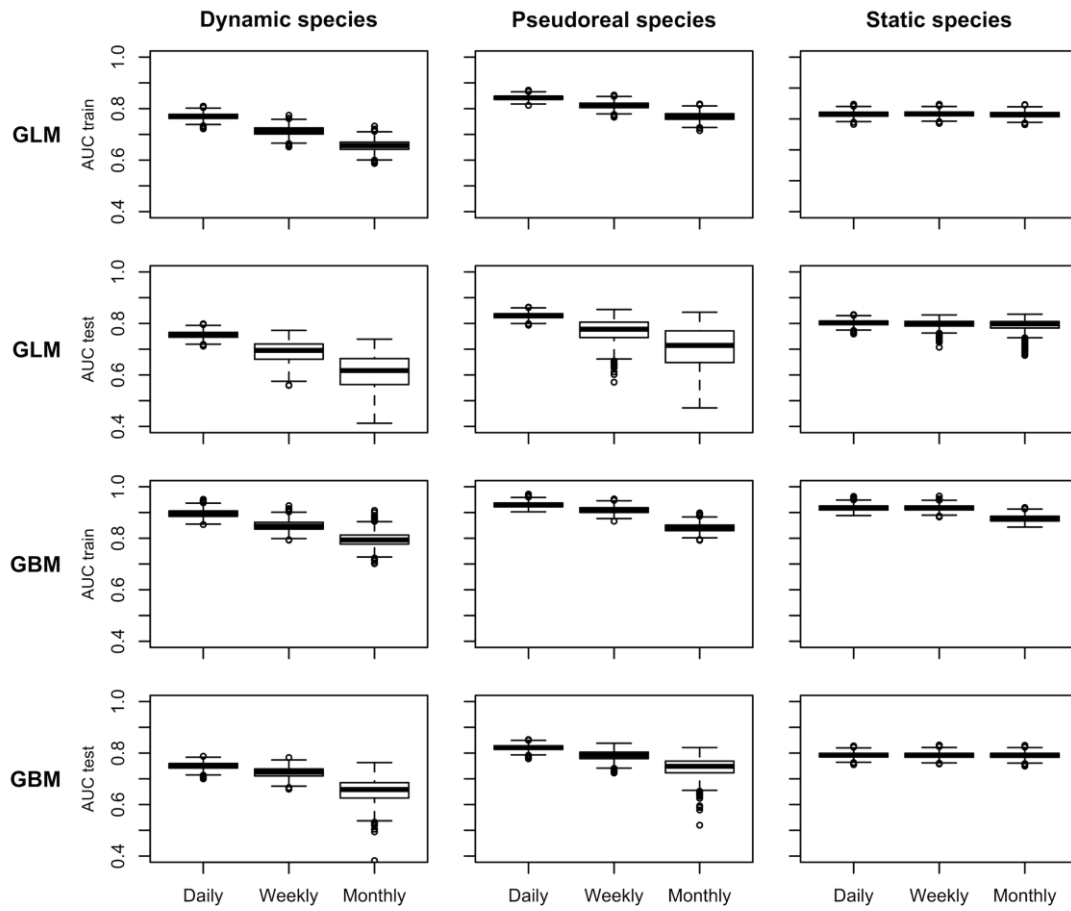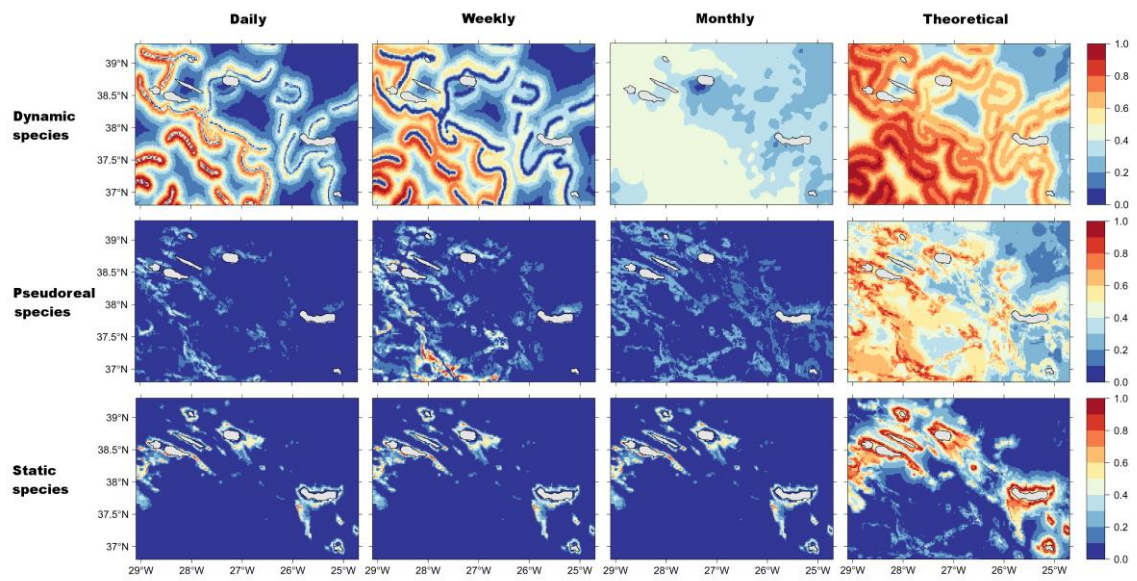
808   **Figure 4:**

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816 **Figure 5:**

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