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Ceriantharia (Anthozoa, Cnidaria) in the Atlantic Ocean: A Study Through Ecological Niche Modelling

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1 **Research Article**

2 Ceriantharia (Anthozoa, Cnidaria) in the Atlantic Ocean: A Study Through Ecological Niche
3 Modelling

4
5 **Running title:** Ceriantharia in Atlantic: An Ecological Niche Modelling Study

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35 **Abstract**

36 Tube-dwelling anemones, animals belonging to the subclass Ceriantharia, are characterized as
37 essential organisms for reef structures, playing complex ecological relationships with other
38 living beings. However, the difficulty in collecting specimens leads to a lack of detailed
39 environmental and biogeographical studies for the subclass, given the challenges in
40 implementing laboratory cultures. Ecological Niche Modelling (ENM) is an important tool for
41 biodiversity distribution studies as it allows for mapping the environmental aspects related to
42 this distribution. It is useful in studies of species with gaps in ecological and biogeographical
43 knowledge, helping to understand the potential and realized niche aspects. Thus, the present
44 study aimed to analyze the realized niche of nine species of Ceriantharia in the Atlantic Ocean
45 through Ecological Niche Modelling (ENM), implemented with the MaxEnt algorithm, to
46 enrich knowledge about new zones of environmental suitability for ceriantharians and,
47 consequently, identify potential new occurrence sites. All models were statistically significant
48 ($AUC \geq 0.7$; $TSS \geq 0.4$) and aligned with the known biology of the animals, with only a few
49 extrapolations in areas inaccessible to tube anemones. This study aimed to consolidate current
50 knowledge on the ecological niche of ceriantharians in the Atlantic Ocean, assisting in
51 identifying priority areas for marine biodiversity conservation. Based on the results, a
52 highlighted need exists to intensify data collection efforts on these organisms and review
53 database records to minimize potential identification errors.

54

55 **Highlights**

56 1. Benthic organisms play a fundamental role in marine ecosystems, serving as indicators of
57 environmental health, contributing to nutrient cycling, and providing habitat and food for
58 various species.

59

60 2. Ceriantharians are present in all oceans and perform multiple ecological functions through
61 the tubes they build around their bodies. However, although the first studies on tube anemones
62 date back to the 18th century, there are still gaps in most species' ecological and
63 biogeographical knowledge.

64

65 3. The increased availability of environmental information, combined with computational
66 techniques, enables the study of biological phenomena. Ecological Niche Modelling (ENM) is
67 widely used as a correlational method to address ecological and biogeographical questions

68 about species. By estimating the realized niche of ceriantharians in the Atlantic Ocean through
69 ENM, we contribute to the knowledge of environmentally suitable areas for these species.

70

71 4. All models presented optimal performance ($AUC \geq 0.7$; $TSS \geq 0.4$) and were considered
72 statistically valid, revealing potentially suitable areas for ceriantharians in the Atlantic. For
73 some species, the projections extended to zones that lack biological plausibility for certain tube
74 anemones, which can be attributed to sampling bias and the Wallacean shortfall evident in the
75 subclass.

76

77 5. We emphasize the need for increased sampling efforts for this group, and in this context, our
78 models can serve as a valuable tool for identifying new collection sites.

79

80 **Keywords**

81 Anthozoa; Benthic animals; Conservation; Environmental suitability modelling; Marine
82 ecology; Tube-dwelling anemones.

83

84 **Introduction**

85 The subclass Ceriantharia consists of fifty-four benthic species widely distributed.
86 These are generally large anthozoans that reside in tubes and occupy the benthic environment
87 in all oceans (Picton and Manuel, 1985, Mejia et al. 2020; Stampar et al. 2020). Ceriantharians
88 are considered essential in structuring marine megabenthic communities (Molodtsova, 2009)
89 through the tubes they construct around their bodies (Kristensen, 1991; Santos, 2019). By
90 providing shelter for other species, they enable the formation of interspecific ecological
91 relationships with other marine organisms (Ceriello et al. 2019; Stampar et al. 2010).

92 The presence of the tube also protects the ceriantharians themselves. They can retract
93 into the tube at the slightest sign of danger (Molodtsova, 2009) and can remain buried in the
94 substrate (den Hartog, 1977). This behavior of the specimens makes collection more difficult
95 (Stampar et al. 2016), impacting the conduct of laboratory experiments and, consequently,
96 leading to gaps in the biogeographical, ecological, and life cycle knowledge of some
97 ceriantharian species (Stampar et al. 2020).

98 This asymmetry in knowledge about ceriantharians can be seen through the number of
99 occurrences in databases. For example, while *Cerianthus lloydii* (Gosse, 1859) has 33,240
100 occurrences in the Global Biodiversity Facility System (GBIF), *Arachnanthus sarsi* (Calgren,
101 1912) has only 61 records. This indicates a noticeable bias in geographical records and sub-

102 sampling of species, which further limits collection and new research. Thus, it is necessary to
103 employ techniques that can aid in understanding the potentially suitable regions for
104 ceriantharians.

105 Since the late 1980s, with the emergence of techniques that integrate bioinformatics
106 and statistical methods, there has been an expansion in the ability to predict patterns in
107 biodiversity (Guisan et al. 2017). One of the most commonly used techniques for this purpose
108 is Ecological Niche Modelling (ENM), which correlates geographic records with
109 environmental variables (Peterson and Soberón, 2012). Through the implementation of
110 statistical machine learning methods (Zurell et al. 2020), the resulting ENM models can be
111 used to infer regions that may encompass the realized niche of species (Melo-Merino et al.
112 2020). This approach can help expand the understanding of the potentially suitable regions for
113 ceriantharians, given the asymmetry in knowledge about their distribution.

114 Modelling in the marine environment presents greater challenges due to environmental
115 heterogeneity, data scarcity, and limited spatial and temporal resolutions (Guillaumot et al.
116 2021). Given that many ceriantharians are undersampled and there is insufficient knowledge
117 about the geographic occurrence limits of the subclass, along with the lack of classification of
118 these organisms in conservation lists (e.g., International Union for Conservation of Nature -
119 IUCN), this study aimed to analyze the current realized niche of ten species of tube-dwelling
120 anemones in the Atlantic Ocean through Ecological Niche Modelling and the projection of
121 environmental suitability for these organisms.

122

123 **Materials & Methods**

124 We performed all operations in R version 4.4.1 (R Core Team, 2024). We obtained and
125 thinned occurrence data using the packages spocc (Owens, Barve, and Chamberlain 2024) and
126 spThin (Aiello-Lammens et al. 2015). We cropped and masked all the environmental data to
127 the study area via sf (Pebesma 2018; Pebesma and Bivand 2023) and terra (Hijmans, 2024)
128 packages. Variance Factor Analysis (VIF) was checked using the function vifstep,
129 implemented in the package usdm (Naimi et al. 2014). All models were trained and evaluated
130 via the sdm (Naimi, Araújo 2016) package. Other data operations and final map plots were
131 performed via the tidyverse (Wickham et al. 2019) package.

132

133 *Study species and occurrence data*

134 We obtained all the occurrence data from the Global Biodiversity Information Facility
135 (GBIF - www.gbif.org) and the Ocean Biodiversity Information System (OBIS -

136 www.obis.org) databases. We opted not to include unpublished data and information from the
 137 literature in the dataset to standardize and replicate the models. The criteria we used were the
 138 species' presence in the Atlantic Ocean and a minimum of ten records in the final dataset after
 139 data cleaning and spatial thinning. We removed points with incorrect (*e.g.* data on land) or
 140 absent coordinates and also removed duplicate points. To avoid spatial correlation (Aiello-
 141 Lammens et al. 2015), the occurrences were confined inside a 500 km buffer around all points,
 142 and spaced with a distance between points of 10 km. After this process, ten species attended
 143 the minimal threshold, thus being selected for model training (Table 1).

144

145 **Table 1.** Genera, species, and number of occurrences selected for model training.

| Genera | Species | Occurrences | Reference |
|------------------------|----------------------|-------------|--------------------------|
| <i>Arachnanthus</i> | <i>sarsi</i> | 17 | Carlgren, 1912 |
| <i>Ceriantheopsis</i> | <i>americana</i> | 53 | Agassiz in Verrill, 1864 |
| <i>Cerianthus</i> | <i>lloydii</i> | 905 | Gosse, 1859 |
| | <i>membranaceus</i> | 22 | Spallanzani, 1784 |
| <i>Isarachnanthus</i> | <i>maderensis</i> | 18 | Johnson, 1861 |
| | <i>nocturnus</i> | 36 | Hartog, 1977 |
| <i>Pachycerianthus</i> | <i>borealis</i> | 101 | Verrill, 1873 |
| | <i>multiplicatus</i> | 204 | van Beneden, 1924 |
| | <i>solitarius</i> | 13 | Carlgren, 1912 |

146

147 *Environmental data*

148 We defined the initial set of variables based on the general biology of the subclass
 149 Ceriantharia, given the gaps in biological knowledge for several species (Stampar et al. 2020).
 150 We obtained the variables from the Bio-ORACLE database version 3.0 (Assis et al. 2024),
 151 with a resolution of 0.05 arcdegree (approximately 5.5 km at the equator). In total, we
 152 downloaded seven variables for all models: dissolved oxygen, silicate, nitrate, temperature,
 153 salinity, seawater current velocity, and seawater current direction. We obtained variables at
 154 minimum, mean, and maximum depths, totaling 21 layers, and standardized the resolution at
 155 0.05 arcdegree. All variables were cropped and masked to the Atlantic Ocean area. We applied
 156 the Variance Inflation Factor (VIF) technique, using 10 as the cutoff value (Craney and Surles
 157 2002), to test for collinearity among variables, selecting only those below the threshold,
 158 resulting in different numbers of layers per species (Table S2, Supp. Material).

159

160 *Ecological Niche Modelling*

161 We chose the Maximum Entropy (Maxent) algorithm, based on the assumption that it
 162 provides the most unbiased data set for analyzing species distribution information, particularly
 163 given the constraints of non-parametric and non-linear data (Phillips et al. 2006). This
 164 algorithm was implemented due to its documented good performance with small datasets
 165 (Phillips and Dudik 2008; Radosavljevic and Anderson 2014) and it is one of the most widely
 166 used methods in marine environment modelling (Melo-Merino et al. 2020).

167 We randomly generated 10.000 background points (Barbet-Massin et al. 2012) inside
 168 the buffer that constrained the species occurrence data. The models were trained using the
 169 partition method of cross-validation (k = 5), iterating 10 times, resulting in a total of 50 models
 170 per species, splitting the dataset into 70% for training and 30% for testing. We validated the
 171 models based on the Area Under the ROC Curve (AUC) and True Skill Statistics (TSS), with
 172 thresholds of $AUC \geq 0.7$ and $TSS \geq 0.4$ (Buisson et al. 2010). We selected the best models for
 173 ensembling (Marmion et al. 2009) based on the statistical technique of True Skill Statistics
 174 (TSS), selecting models with the best sensibility and specificity ratio.

175

176 **Results and Discussion**

177 *Statistical evaluation and relative variable importance*

178 Model performance (Table 2) was considered excellent, with AUC and TSS values
 179 above the minimal threshold ($AUC \geq 0.7$; $TSS \geq 0.4$), averaging 0.91 ± 0.03 and 0.79 ± 0.1 ,
 180 respectively.

181 **Table 2.** Average model performance based on AUC and TSS metrics based on a minimal threshold
 182 ($AUC \geq 0.7$ and $TSS \geq 0.4$).

| Genera | Species | AUC | TSS |
|-----------------------|---------------------|-----------------|-----------------|
| <i>Arachnanthus</i> | <i>sarsi</i> | $0,91 \pm 0,06$ | $0,78 \pm 0,14$ |
| <i>Ceriantheopsis</i> | <i>americana</i> | $0,96 \pm 0,03$ | $0,86 \pm 0,08$ |
| | <i>lloydii</i> | $0,88 \pm 0,01$ | $0,62 \pm 0,02$ |
| <i>Cerianthus</i> | <i>membranaceus</i> | $0,94 \pm 0,09$ | $0,90 \pm 0,10$ |
| | <i>maderensis</i> | $0,87 \pm 0,09$ | $0,75 \pm 0,16$ |
| <i>Isarachnanthus</i> | <i>nocturnus</i> | $0,92 \pm 0,02$ | $0,76 \pm 0,06$ |

| | | | |
|------------------------|----------------------|-------------|-------------|
| | <i>borealis</i> | 0,92 ± 0.02 | 0,75 ± 0.04 |
| <i>Pachycerianthus</i> | <i>multiplicatus</i> | 0,92 ± 0.02 | 0,72 ± 0.05 |
| | <i>solitarius</i> | 0,98 ± 0.01 | 0,97 ± 0.02 |

183

184 Of the set of 21 variables, 19 were used for model training (Table 3). Average sea water
 185 speed, minimum sea water direction, and minimum sea water speed were selected for 8 of the
 186 9 species (Table 3), averaging $15\% \pm 20\%$ in relative importance. Average and minimum sea
 187 water speed presented relative importance above 20% for *C. americana*, *I. maderensis*, *C.*
 188 *membranaceus*, *I. nocturnus*, and *P. solitarius* (Table 3).

189 These findings align with the life cycle of ceriantharians, which is generally classified
 190 based on the period their larvae remain in the water column, ranging from several weeks to
 191 three months (Stampar et al. 2015). Ocean current velocity and direction are biologically
 192 significant factors (Le Joncour et al. 2023). Variations in depth and dissolved oxygen
 193 concentration further underscore their ecological significance, influencing larval survival and
 194 development.

195 The limitations in the collection of ceriantharians directly impact laboratory cultivation,
 196 making detailed studies on the larval development of these species challenging (Molodtsova,
 197 2009). Consequently, the available information regarding the life cycle of many species
 198 remains restricted (Kraus, 2023). This knowledge gap highlights the importance of
 199 environmental factors such as average ocean temperature, average nitrate, and average
 200 dissolved molecular oxygen, which were found to have a relative importance above 50% in the
 201 models for *P. solitarius*, *I. membranaceus*, *P. borealis*, *A. sarsi*, and *P. multiplicatus* (Table
 202 S3, Supp. Material).

203 Only one variable was common among all 9 species (maximum sea water direction),
 204 although with low relative importance ($16\% \pm 21\%$). However, average and maximum nitrate
 205 concentrations, which were also significant for some species (Table 3), play a critical role in
 206 habitat development due to their influence on primary productivity and local trophic networks
 207 (Suggett et al. 2012). Ceriantharians inhabit a broad range of depths and utilize available
 208 sediment in their environment to construct their tubes (Picton and Manuel, 1985), further
 209 emphasizing the importance of nutrient availability.

210 Thus, our findings on the relative contributions of environmental variables are
 211 consistent with existing knowledge of ceriantharian ecology and their life cycles, providing

212 valuable insights into how abiotic factors influence their distribution, larval dynamics, and
 213 habitat preferences.

214

215 **Table 3.** Variables with 20% or more relative importance. All variables used in model training were
 216 averaged based on a correlative approach (Pearson’s Correlation).

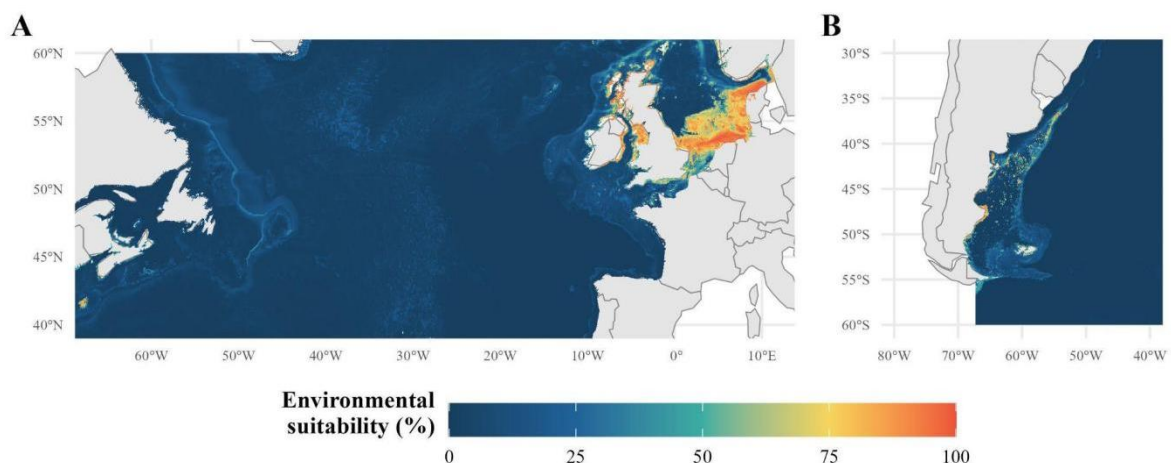
| Species | Variable | Relative Importance (%) |
|--------------------------------------|------------------------------------|-------------------------|
| | Average Dissolved Molecular Oxygen | 62 |
| <i>Arachnanthus sarsi</i> | Average Ocean Temperature | 58 |
| | Minimum Dissolved Molecular Oxygen | 39 |
| <i>Ceriantheopsis americana</i> | Minimum Salinity | 41 |
| | Minimum Sea Water Speed | 38 |
| | Minimum Silicate | 38 |
| | Maximum Nitrate | 34 |
| <i>Cerianthus lloydii</i> | Minimum Ocean Temperature | 39 |
| | Minimum Silicate | 24 |
| <i>Cerianthus membranaceus</i> | Average Nitrate | 77 |
| | Average Sea Water Speed | 56 |
| | Average Ocean Temperature | 43 |
| <i>Isarachnanthus maderensis</i> | Average Sea Water Speed | 24 |
| | Minimum Sea Water Speed | 20 |
| <i>Isarachnanthus nocturnus</i> | Minimum Sea Water Speed | 45 |
| <i>Pachycerianthus borealis</i> | Average Ocean Temperature | 76 |
| | Maximum Nitrate | 60 |
| <i>Pachycerianthus multiplicatus</i> | Maximum Salinity | 29 |
| | Average Ocean Temperature | 83 |
| <i>Pachycerianthus solitarius</i> | Average Sea Water Speed | 40 |

217

218 *Overview of the environmental suitability for Ceriantharia species in the Atlantic Ocean*

219 *Arachnanthus sarsi*

220 The model infers potentially suitable areas ($\geq 50\%$) that are consistent with the currently
 221 known distribution of the species (Picton and Manuel 1985; Galego et al. 2013; Stampar et al.
 222 2020), in the vicinity of Ireland and the United Kingdom. However, it presents a large area in
 223 the North Sea with a zone of environmental suitability ($\geq 75\%$) that extends from the
 224 Netherlands, Germany, and Denmark, to the south of Sweden and Norway, regions for which
 225 there is still no documented record of the species. Additionally, it exhibits a small zone of
 226 suitability ($\geq 50\%$) in the northeastern United States and in the southern part of South America,
 227 between Uruguay and Argentina, countries also with no record of *Arachnanthus sarsi*. Since
 228 this is a species commonly found in the colder and deeper waters of the North Atlantic (Stampar
 229 et al. 2020), considering the physicochemical and geographical barriers to the dispersal of the
 230 species, we disregard the possibility that *A. sarsi* would reach the southern part of South
 231 America naturally.



232

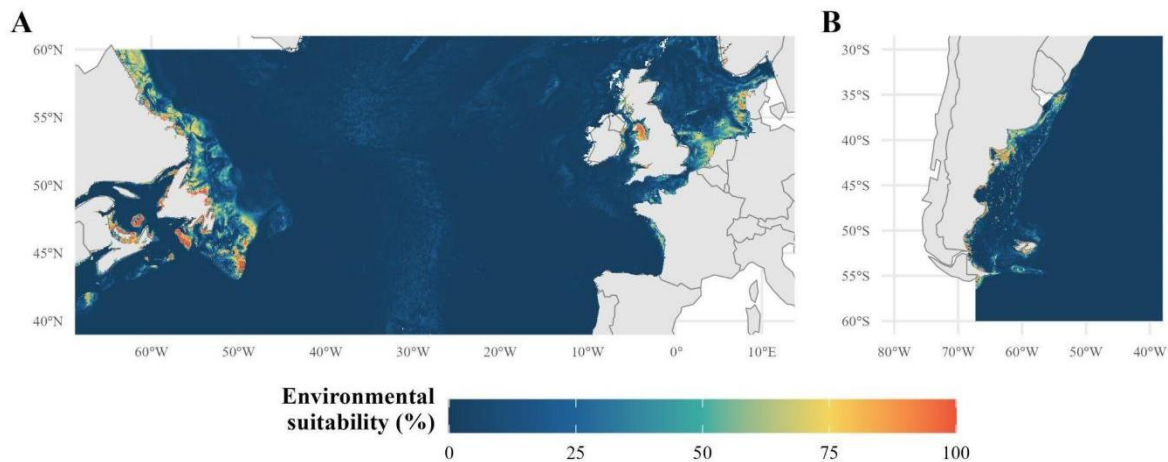
233 **Figure 1.** Ensemble of the environmental suitability of *Arachnanthus sarsi*. A) North Atlantic and B)
 234 Southernmost South America.

235

236 *Ceriantheopsis americana*

237 Considered one of the most studied cerianthids (Stampar et al. 2020), the majority of
 238 the literature on *Ceriantheopsis americana* is dedicated to the ecological, biological, and
 239 sensory processes of the organisms, which are collected in the North Atlantic, mainly in the
 240 United States (Peteya, 1973, Kristensen et al. 1991, Holohan et al. 1998, Sebbens, 1998,
 241 Stampar et al. 2020) and to a lesser extent in Canada (Shepard et al. 1986). However, the model
 242 presented environmental suitability regions for the species consistent with its distribution, but

243 with zones ($\geq 50\%$) along the entire Canadian coast and only a small region near Maine, in the
 244 United States. They also exhibit zones in areas where the species has not yet been recorded: in
 245 the northeastern portion of the North Atlantic Ocean ($\geq 50\%$), with a higher percentage ($\geq 75\%$)
 246 in Ireland, the United Kingdom, northern Germany, Denmark, and southern Norway. In the
 247 locations presented in South America ($\geq 50\%$), between Uruguay and Argentina, including the
 248 Malvinas Islands, there is only an uncertain record made by Hertwig (1882) on the coast of
 249 Uruguay, since the first species described for this biogeographic region, the Warm Temperate
 250 Southwest Atlantic (Spalding et al. 2007) was only made more than a hundred years later, by
 251 Stampar et al. (2015).

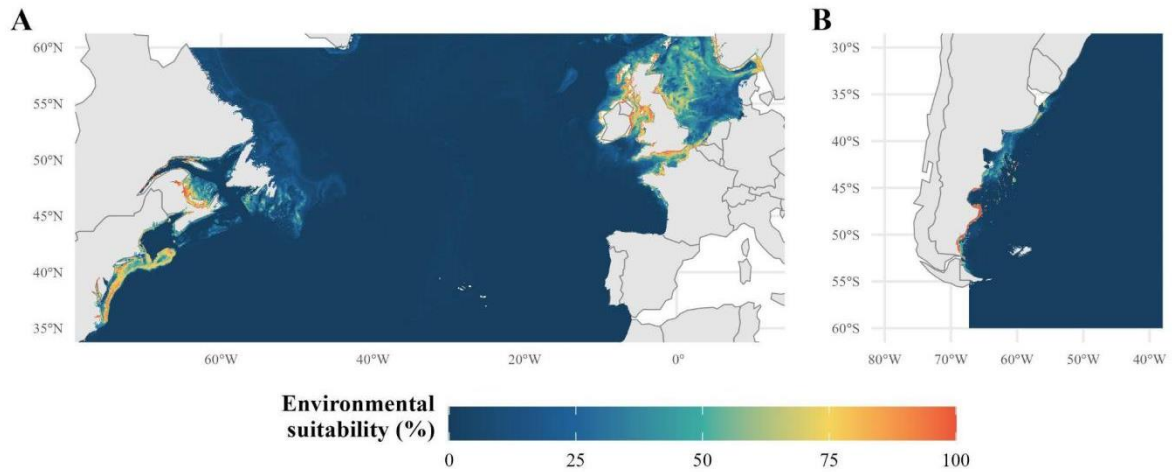


252 **Figure 2.** Ensemble of the environmental suitability of *Ceriantheopsis americana*. A) North Atlantic and B)
 253 Southernmost South America.
 254

255
 256 *Cerianthus lloydii*

257 Grouping the cerianthids recorded in the Arctic and the North Sea (Molodtsova et al.
 258 2023), the model suggested potentially suitable areas ($\geq 75\%$) in the North Sea, near Norway,
 259 Sweden, the Netherlands, Belgium, France, Ireland, and the United Kingdom, consistent with
 260 regions of occurrence and extrapolating to other locations that make biological sense for the
 261 species. We consider that the areas in the far south of South America, since the percentage of
 262 suitability increases latitudinally from Uruguay to Argentina ($50\% \geq 75\%$), are due to
 263 environmental similarity, since *C. lloydii* is documented as a North Atlantic species (Perry,
 264 2016), and would not naturally reach these regions.

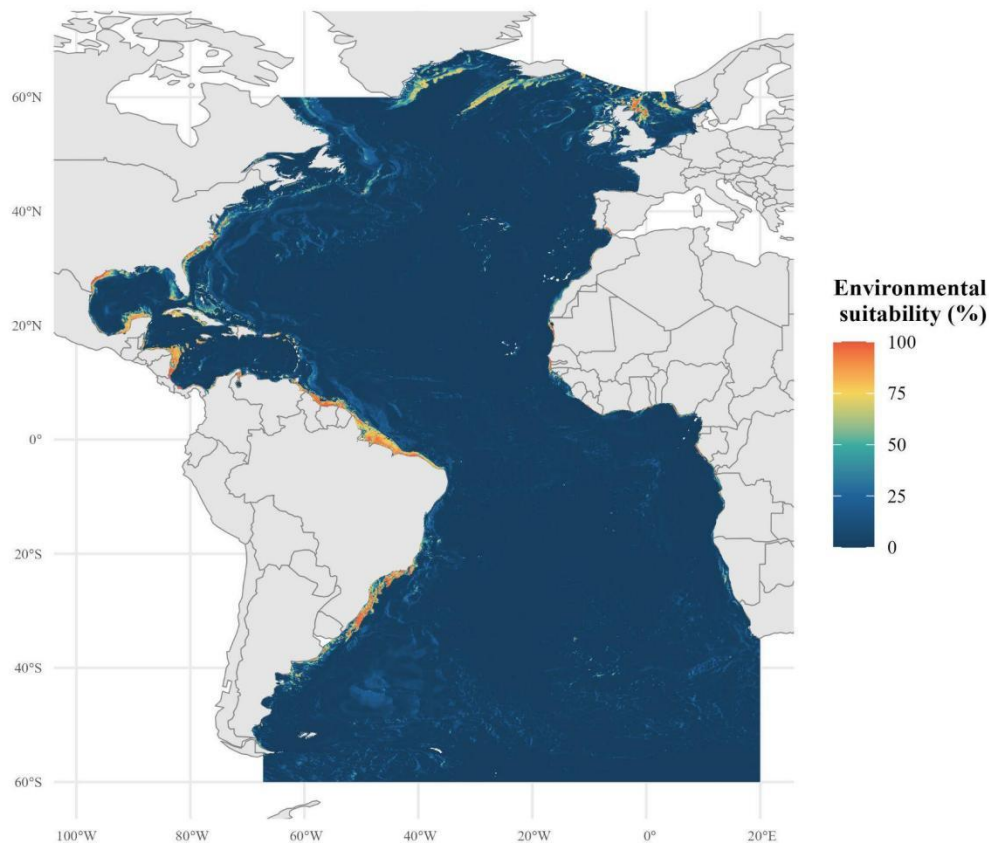
265



266
 267 **Figure 3.** Ensemble of the environmental suitability of *Cerianthus lloydii*. A) North of the North Atlantic and B)
 268 Southernmost South America.

269
 270 *Cerianthus membranaceus*

271 Found extensively in the Mediterranean Sea (Dominguez-Carrió et al. 2021, Riedel et
 272 al. 2008, Stampar et al. 2020), the model suggests suitable areas for *C. membranaceus* ($\geq 50\%$)
 273 in the North Atlantic, in regions near Greenland, Iceland, the United Kingdom, and Norway,
 274 but also on the American continent, from the coast of Canada ($\geq 50\%$), through Central
 275 America, presenting higher percentages in South America ($\geq 75\%$), locations where there are
 276 no records of the species. This species has already been recorded in Madeira Island (Calado,
 277 2006), so access to other areas of the Atlantic Ocean is much more feasible, but no evidence of
 278 occurrence in the Western Atlantic has been verified so far.

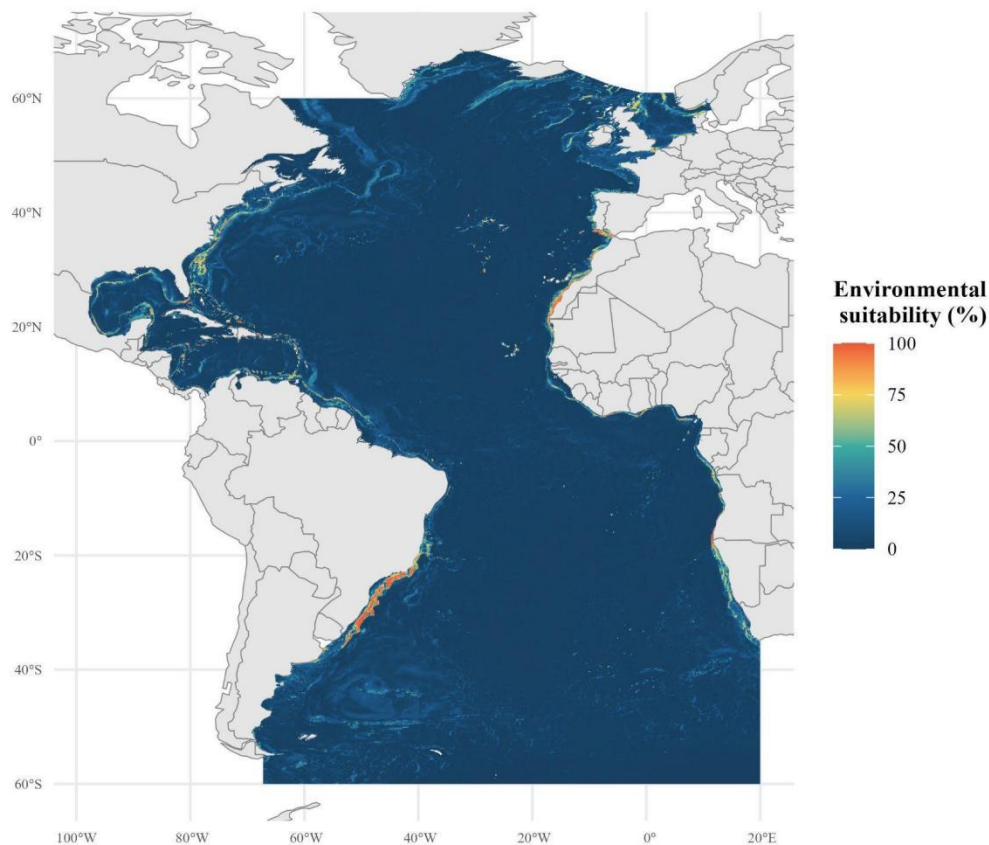


279
 280 **Figure 4.** Ensemble of the environmental suitability of *Cerianthus membranaceus*.

281
 282 *Isarachnanthus maderensis*

283 The *I. maderensis* model extrapolated the areas of environmental suitability and
 284 presented a wide area of moderate suitability ($\leq 50\%$) for the species in the entire Atlantic
 285 Ocean, with locations both near and distant from the coastal region, including where the
 286 absence of *I. maderensis* is theorized (Stampar and Morandini 2017; Stampar et al. 2019;
 287 Stampar et al. 2020). However, the species also exhibits greater suitability ($\geq 75\%$) in zones
 288 close to areas with records of the species, such as in Central America and Europe, with areas
 289 near Portugal (Stampar et al. 2020) and Southern Spain. On the African continent, the model
 290 inferred zones in regions near Morocco and Western Sahara, however, the species has only
 291 been documented a little further south, in São Tomé and Príncipe (GBIF, human observation).
 292 In the large region ($\geq 75\%$) that appears in South America, covering the southeastern and
 293 southern parts of Brazil, reaching Uruguay, there have been no records of the species yet.
 294 Considering that *Isarachnanthus maderensis* is a widely distributed species in the Atlantic
 295 Ocean, the geographical distance between the records can bias the analysis of environmental
 296 suitability and its distribution, making it difficult to delineate the potential niche of the species
 297 by the algorithms used (Sillero et al. 2021). However, although some regions do not make

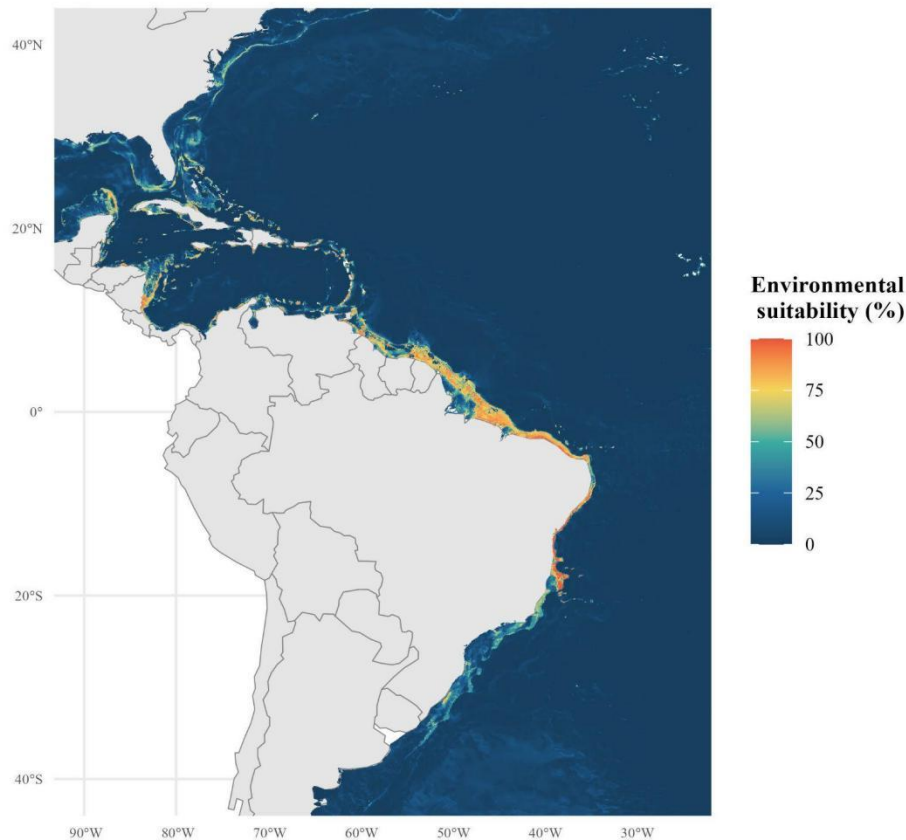
298 biological sense, the model extrapolation was more conservative than in other tests performed,
 299 adding new points to the existing description of the distribution pattern for the species (Stampar
 300 and Morandini, 2017).



301
 302 **Figure 5.** Ensemble of the environmental suitability of *Isarachnanthus maderensis*.

303
 304
 305 *Isarachnanthus nocturnus*

306 The model inferred an extensive latitudinal range of environmental suitability ($\geq 50\%$)
 307 on the coast of the American continent, with a higher percentage ($\geq 75\%$) in small locations in
 308 Central America and larger areas in South America, with emphasis on northeastern Venezuela,
 309 passing through Guyana, Suriname, French Guiana, and reaching northern Brazil, and reaching
 310 almost maximum suitability on the coast of Bahia and in the southeast, near Espírito Santo.
 311 The suitability regions are consistent with the known distribution of the species, which ranges
 312 from the Caribbean to Argentina (Stampar et al. 2020). Thus, the extrapolation of the
 313 projections of *I. nocturnus* presents a biological sense, since in the most accepted scenario,
 314 proposed by Stampar et al. (2012), *I. nocturnus* presents a more extensive environmental
 315 latitudinal gradient than *I. maderensis*, due to larval characteristics in the life cycle and the
 316 influence of ocean currents (Lopes et al. 2023).

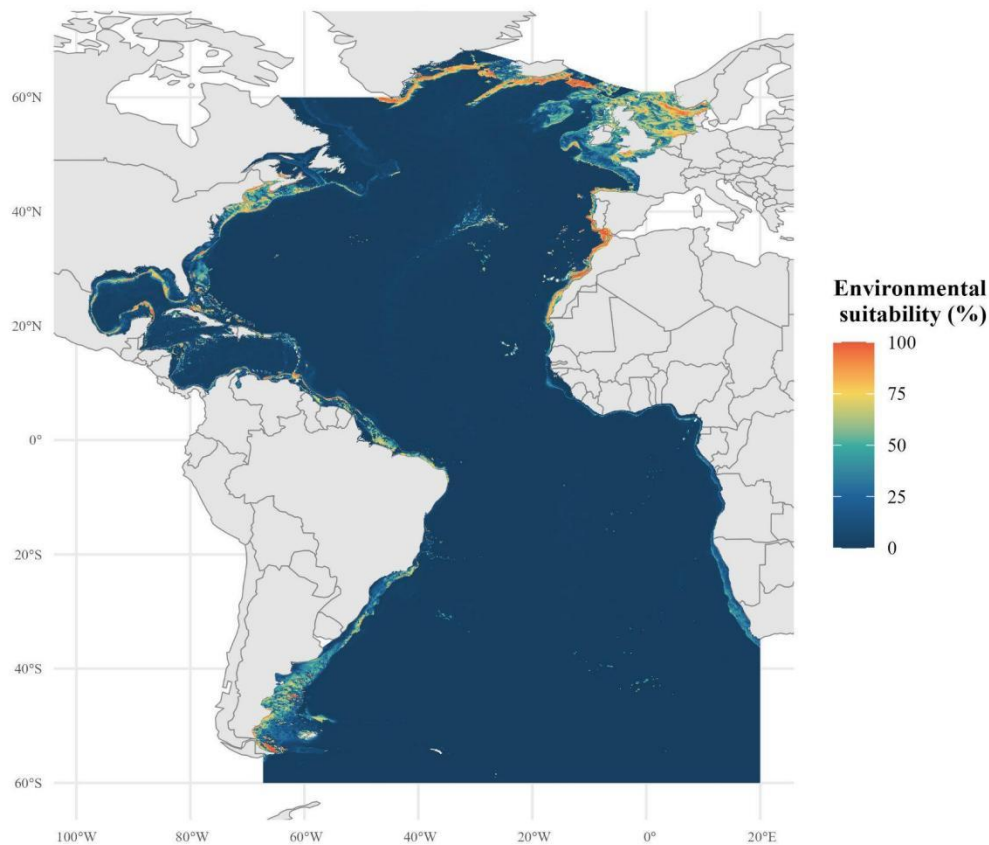


317
 318 **Figure 6.** Ensemble of the environmental suitability of *Isarachnanthus nocturnus*.

319
 320 *Pachycerianthus borealis*

321 The model inferred suitable regions for the species in the northwestern Atlantic (\geq
 322 75%), near Greenland, Iceland, Norway, Denmark, Germany, Portugal, Morocco, and Western
 323 Sahara. Some make sense with the areas consistent with most of the known distribution of the
 324 species, which is in the Northwestern Atlantic (Stampar et al. 2020), but presented more
 325 restricted areas of suitability when compared to other areas in locations that exhibit the highest
 326 concentration of records, such as in northern North America. However, it extrapolated large
 327 zones along the South American coast and the African continent where there have been no
 328 records of the species. In addition, most of the records of *P. borealis* are concentrated on the
 329 northern coast of North America. The species is documented in some reports associated with
 330 the Government of Canada for the characterization of species in some regions of the country,
 331 as is the case of Beazley et al. (2019), in which states that the cerianthids found were in the
 332 depth range of 200 to 300 meters, at a temperature ranging between 4.5 to 10.2°C. In the work
 333 of Watling and Lapointe (2022), the authors consider *P. borealis* one of the most representative
 334 cerianthids in the Northern Atlantic Boreal province (bioregion classified by the study). In this
 335 sense, considering the accessibility and the possible environmental preferences of the species,

336 we do not consider that the cerianthid will naturally reach the highlighted regions of the South
 337 Atlantic Ocean in the model.



338
 339 **Figure 7.** Ensemble of the environmental suitability of *Pachycerianthus borealis*.

340
 341 *Pachycerianthus multiplicatus*

342 The model suggests potentially suitable areas (> 50%) in Ireland, the United Kingdom,
 343 Norway, Sweden, Denmark, Germany, and France, with regions consistent with the
 344 distribution of the species, in the northeastern North Atlantic (Jonsson 2001; Stampar et al.
 345 2020). In addition, the projections extrapolate potentially suitable zones (> 50%) on the coast
 346 of Canada and the United States. Furthermore, the study by Stampar et al. (2020) indicates that
 347 the actual distribution of the species is still uncertain, as the records of individuals on the coast
 348 of France and Spain have not yet been detailed, which is worrying, since the work of Wilding
 349 and Wilson (2008) brings several descriptions regarding the tolerance or not of the species to
 350 environmental changes, and the authors reported that due to the fragmentation of the
 351 populations and the apparent limitation in larval dispersion, it is unlikely that the species will
 352 recover if its entire population is eliminated. If there are viable mature individuals nearby that
 353 can provide larvae, recovery may be possible, although it will likely take many years. The lack
 354 of data on larval dispersion and recruitment, along with the lack of knowledge about the

355 longevity of the species, contributes to a very low recovery assessment and high sensitivity,
 356 since *Pachycerianthus multiplicatus* lives in subtidal environments with minimal thermal
 357 variations, which may indicate a intolerance to abrupt temperature changes, in which the
 358 moderate recovery capacity of the species suggests that it is highly vulnerable to local
 359 extinctions. Therefore, if the entire population is extinguished, recovery would be unlikely, as
 360 it would depend on recolonization from other existing populations.

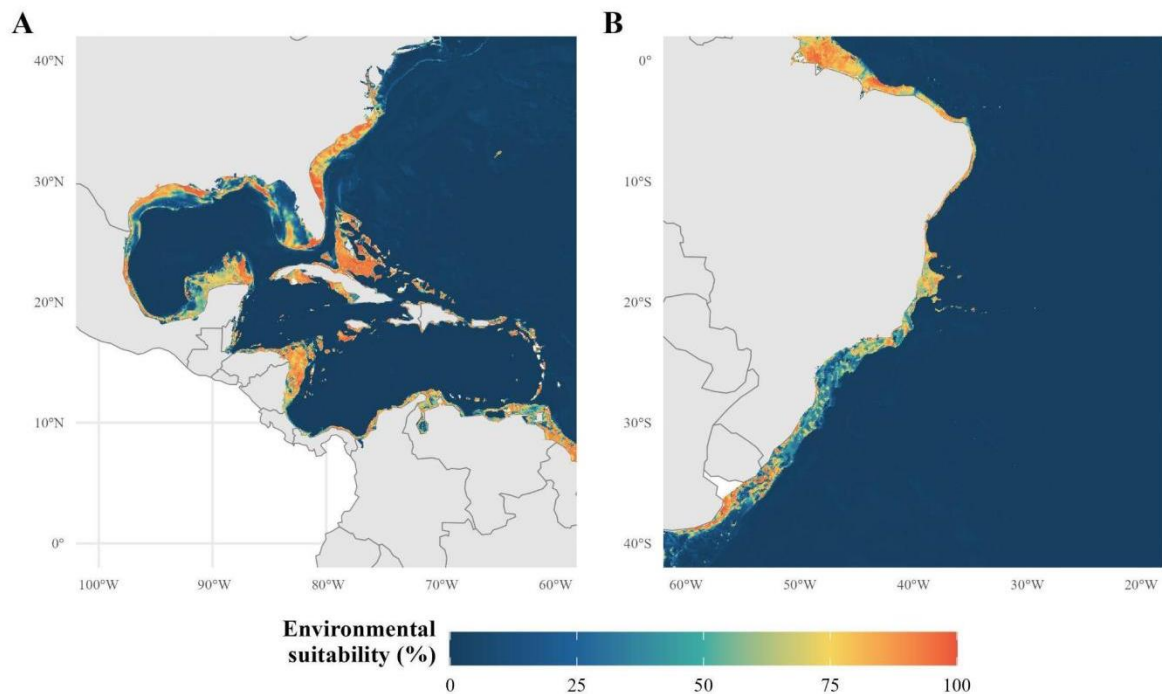
361



362
 363 **Figure 8.** Ensemble of the environmental suitability of *Pachycerianthus multiplicatus*.
 364

365 *Pachycerianthus solitarius*

366 The species has a known distribution in the Mediterranean Sea and the Azores (Stampar
 367 et al. 2020), in addition to being representative in the Black Sea (Boltachova et al. 2021).
 368 Interestingly, in the model, the inferred areas of suitability (> 50%) are concentrated on the
 369 American continent, from the southern United States to South America. This is the only case
 370 in the study where the model, even with statistical validation, showed low performance due to
 371 a lack of biological sense since the distribution of *P. solitarius* is well established and presents
 372 a large set of occurrence points compared to other cerianthids (e.g. n = 368 in GBIF).



373
 374 **Figure 9.** Ensemble of the environmental suitability of *Pachycerianthus solitarius*.
 375

376 **Final considerations**

377 The scarcity of data on the ecology and geographic distribution of many species,
 378 including the tube anemone *Pachycerianthus solitarius*, has made it difficult to precisely
 379 understand their habitats and predict how they will respond to environmental changes.
 380 Subsampling, that is, the collection of insufficient data in certain areas, and sampling bias,
 381 which occurs when the collected data is not representative of the total population, contribute to
 382 this knowledge gap. Distribution projections of these species, based on incomplete data, can
 383 be inaccurate and lead to erroneous conclusions. Ecological Niche Modelling emerges as a
 384 powerful tool to overcome these limitations. This technique allows for analyzing the current
 385 distribution of a species and identifying the environmental conditions key to species survival,
 386 such as temperature, salinity, and substrate type. By modelling the realized and potential
 387 ecological niche of tube anemones, we were able to map the areas of the Atlantic Ocean that
 388 offer the most suitable conditions for the survival and potential occurrence of these organisms,
 389 helping to identify priority areas for conservation and scientific exploration.

390 It is important to note that most studies on ceriantharians have focused on issues related
 391 to the classification and evolution of these species. Few studies have been dedicated to
 392 investigating the ecology and geographic distribution of these organisms. The present study
 393 represents an attempt to fill this gap, systematizing the available knowledge on the ecological

394 niche of ceriantharians in the Atlantic Ocean. By generating more accurate information on the
395 ecological needs of these species, this research contributes to the development of more effective
396 strategies for their conservation, ensuring the preservation of marine biodiversity.

397

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401 Fernanda Azevedo for their valuable insights and suggestions on the initial draft of this work.

402

403 **Data Accessibility Statement**

404 All relevant data are available in the Supplemental Material Section or can be accessed publicly
405 through the databases described in the Materials & Methods. The RStudio scripts for the entire
406 process of modelling, occurrence data processing and environmental variables are provided in
407 a GitHub repository, available for download
408 (https://github.com/marcelapdebarros/ENM_Modelling_Scripts). For further inquiries, please
409 contact the corresponding author.

410

411 **Supplemental Material**

412 This material is available as part of the online article from <https://escholarship.org/uc/fb>.

413 **Table S1.** Ceriantharia spp. in the Atlantic Ocean. Species in bold were selected for modelling.

414 **Table S2.** Environmental variables selected via Variance Inflation Factor analysis for all
415 modeled species of Ceriantharia spp. in the Atlantic Ocean

416 **Table S3.** Average relative variable importance for all modeled species of Ceriantharia spp.
417 in the Atlantic Ocean.

418

419 **References**

420 Aiello-Lammens, M. E., Boria R. A., Radosavljevic A., Vivela B., Anderson R. P. (2015)
421 spThin: an R package for spatial thinning of species occurrence records for use in ecological
422 niche models. *Ecography*, 38, pp. 437 - 545. <https://doi.org/10.1111/ecog.01132>

423

424 Assis J., Fernández Bejarano S. J., Salazar V. W., Schepers L., Gouvêa L., Fragkopoulou E.,
425 Leclercq F., Vanhoorne B., Tyberghein L., Serrão E. A. (2024) Bio-ORACLE v3.0. Pushing
426 marine data layers to the CMIP6 Earth system models of climate change research. *Global
427 Ecology and Biogeography*, 33(4), e13813. <https://doi.org/10.1111/geb.13813>

- 428 Barbet-Massin M., Jiguet F., Albert C. H., Thuiller W. (2012) Selecting pseudo-absences for
429 species distribution models: how, where and how many?. *Methods in Ecology and Evolution*,
430 3(2), pp. 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>
- 431 Beazley, L., Lirette, C., Guijarro, J. (2019) Characterization of the Corals and Sponges of the
432 Eastern Scotian Slope from a Benthic Imagery Survey. *Characterization of the Corals and*
433 *Sponges of the Eastern Scotian Slope from a Benthic Imagery Survey*, 3302, pp. 83.
- 434 Boltachova, N. A., Lisitskaya, E. V., Podzorova, D. V. (2021) Distribution of Alien
435 Polychaetes in Biotopes of the Northern Part of the Black Sea. *Russian Journal of Biological*
436 *Invasions*, 12(1), pp.11–26. <https://doi.org/10.1134/S2075111721010033>
- 437 Buisson, L., Thuiller W., Casajus N., Lek S., Grenouillet G. (2010) Uncertainty in Ensemble
438 Forecasting of Species Distribution. *Global Change Biology* 16(4), pp. 1145–1157.
439 <https://doi.org/10.1111/j.1365-2486.2009.02000.x>
- 440 Calado, R. (2006) Marine ornamental species from European waters: a valuable overlooked
441 resource or a future threat for the conservation of marine ecosystems?. *Scientia Marina*, 70,
442 pp. 389-398. <https://doi.org/10.3989/scimar.2006.70n3389>
- 443 Carlgren, O. (1912) Ceriantharia. *Danish Ingolf-Expedition*. 5(3), pp. 1-79.
- 444 Ceriello, H., Lopes, C. S. S., Dias, G. M., Stampar, S. N. (2019) A different manner to share
445 a house: Is a colonial species possible in Ceriantharia (Cnidaria; Anthozoa)? *Marine*
446 *Biodiversity*, 49(4), pp. 2017–2020. <https://doi.org/10.1007/s12526-019-00942-2>
- 447 Craney, T.A. and Surlles, J.G. (2002) Model-Dependent Variance Inflation Factor Cutoff
448 Values Model-Dependent Variance Inflation Factor Cutoff Values. *Quality Engineering*, 14,
449 pp. 391-403. <http://dx.doi.org/10.1081/QEN-120001878>
- 450 den Hartog, J. C. (1977) Descriptions of two new Ceriantharia from the Caribbean Region,
451 *Pachycerianthus curacaoensis n. sp.* and *Arachnanthus nocturnus n.sp.*, with a discussion of
452 the cnidome and of the classification of the Ceriantharia. *Zoologische Mededelingen*, 51, pp.
453 211–248.
- 454 Dominguez-Carrió C., Riera J. L., Robert K., Zabala M., Requena S., Gori A., Orejas C., Lo
455 Iacono C., Estournel C., Corbera G. et al. (2021) Diversity, structure and spatial distribution
456 of megabenthic communities in Cap de Creus continental shelf and submarine canyon (NW
457 Mediterranean). *Progress in Oceanography*, 208, 102877.
458 <https://doi.org/10.1016/j.pocean.2022.102877>
- 459 Forero Mejia, A. C., Molodtsova, T., Östman, C., Bavestrello, G., & Rouse, G. W. (2020)
460 Molecular phylogeny of Ceriantharia (Cnidaria: Anthozoa) reveals non-monophyly of
461 traditionally accepted families. *Zoological Journal of the Linnean Society*, 190(2), pp. 397–
462 416. <https://doi.org/10.1093/zoolinnean/zlz158>
- 463 Gallego A., Gibb F M., Tulett D., Wright P. J. (2013) Connectivity of Benthic Priority
464 Marine Species within the Scottish MPA Network. *Scottish Marine and Freshwater Science*,
465 4(2), pp. 18-20. <https://doi.org/10.7489/1512-1>
- 466 Gosse, P. H. (1859) Characters and descriptions of some new British sea-anemones. *Annals*
467 *and Magazine of Natural History*, 3(3), pp. 46–50.
468 <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=288782>

- 469 Guillaumot, C., Danis B., Saucède T. (2021) Species distribution modelling of the Southern
470 Ocean benthos: a review on methods, cautions and solutions. *Antarctic Science*, 33(4), pp.
471 349- 372. <https://doi.org/10.1017/S0954102021000183>
- 472 Guisan, A., Thuiller W., Zimmermann E. (2010) 2 - Overview of the Habitat Suitability
473 Modeling Procedure. In: *Habitat suitability and distribution models: With applications in R*
474 (series ed. by Usher, M.; Saunders, D.; Peet, R.; Dobson, A.), pp. 11-17. Cambridge
475 University Press, United Kingdom.
- 476 Hertwig R. (1882) Report on the Actinaria dredged by H.M.S. Challenger during the years
477 1873–1876. Report on the Scientific Results of the Voyage of the H.M.S. Challenger during
478 the years 1873–76 (Zoology) 6, pp. 1 –136.
- 479 Hijmans R. J. (2024) terra: Spatial Data Analysis Package. R package version 1.7-29.
480 <https://cran.r-project.org/web/packages/terra/terra.pdf>
- 481 Holohan, B. A., Klos, E. G., Oviatt, C. A. (1998) Population Density, Prey Selection, and
482 Predator Avoidance of the Burrowing Anemone (*Ceriantheopsis americanus*) in Narragansett
483 Bay, Rhode Island. *Estuaries*, 21(3), pp. 466–469. <https://doi.org/10.2307/1352844>
- 484 Jonsson, L. G., Lundälv, T., & Johannesson, K. (2001) Symbiotic associations between
485 anthozoans and crustaceans in a temperate coastal area. *Marine Ecology Progress Series*, 209,
486 pp. 189–195. <https://doi.org/10.3354/meps209189>
- 487 Kraus, Y. A. (2023) Cnidarian Larvae: True Planulae, Other-Than-Planulae, and Planulae
488 That Don't Look Like Planulae. *Russian Journal of Developmental Biology* 54(1), S23–61.
489 <https://doi.org/10.1134/S1062360423070044>
- 490 Kristensen, E., Aller, R. C., Aller, J. Y. (1991) Oxic and anoxic decomposition of tubes from
491 the burrowing sea anemone *Ceriantheopsis americanus*: Implications for bulk sediment
492 carbon and nitrogen balance. *Journal of Marine Research*, 49, pp. 589-617.
493 <https://doi.org/10.1357/002224091784995774>
- 494 Le Joncour, A., Maud M., Boris L., Jennifer D., Mathieu L., Marianne R., e Dorothée K.
495 (2023) When bioregionalisation emphasises the presence of vulnerable marine ecosystem
496 indicator species in *Nephrops* fishing grounds: Evidence in the Bay of Biscay/Irish Sea
497 continuum. *Progress in Oceanography* 214:103032.
498 <https://doi.org/10.1016/j.pocean.2023.103032>
- 499 Lopes, C. S. S., Maronna, M. M., Martinelli Filho, J. E., Morandini, A. C., Stampar, S. N.
500 (2023) New evidence to demystify the supposed holoplanktonic life cycle in Ceriantharia
501 (Cnidaria). *Marine Biodiversity*, 53(1), pp. 20. <https://doi.org/10.1007/s12526-022-01327-8>
- 502 Marmion M., Parviainen M., Luoto M., Heikkinen R. K., Thuiller W. (2009) Evaluation of
503 consensus methods in predictive species distribution modelling. *Diversity and Distributions*,
504 15(1), pp. 59–69. <https://doi.org/10.1111/j.1472-4642.2008.00491.x>
- 505 Mejia, A. C. F., Molodotsova, T., Östman C., Bavestrello G., Rouse G. W. (2020) Molecular
506 Phylogeny of Ceriantharia (Cnidaria: Anthozoa) Reveals Non-Monophyly of Traditionally
507 Accepted Families. *Zoological Journal of the Linnean Society*, 190, 397–416.
508 <https://doi.org/10.1093/zoolinnean/zl158>

- 509 Melo-Merino, S. M., Reyes-Bonilla, H., Lira-Noriega, A. (2020) Ecological niche models
510 and species distribution models in marine environments: A literature review and spatial
511 analysis of evidence. *Ecological Modelling*, 415, 108837.
512 <https://doi.org/10.1016/j.ecolmodel.2019.108837>
- 513 Molodtsova, T. (2004) On the taxonomy and presumable evolutionary pathways of
514 planktonic larvae of Ceriantharia (Anthozoa, Cnidaria). *Hydrobiologia* 530/531, pp. 261–266.
515 <https://doi.org/10.1007/s10750-004-2671-7>
- 516 Molodtsova, T. N. (2009) Ceriantharia (Cnidaria) of the Gulf of Mexico, In: *Gulf of Mexico–*
517 *Origins, Waters, and Biota. Biodiversity* (ed. by Felder, D.L. and D.K. Camp), pp. 365–367.
518 Texas A&M University Press, College Station, Texas.
- 519 Molodtsova, T. N., V. N. Moskalenko, E. V. Lipukhin, T. I. Antokhina, M. S. Ananeva, e U.
520 V. Simakova (2023) *Cerianthus Lloydii* (Ceriantharia: Anthozoa: Cnidaria): New Status and
521 New Perspectives. *Biology* 12(9), 1167. <https://doi.org/10.3390/biology12091167>
- 522 Naimi B., Araújo, M. B. (2016) Sdm: a reproducible and extensible R platform for species
523 distribution modelling. *Ecography*, 39, pp. 368–375. <https://doi.org/10.1111/ecog.0188>
- 524 Naimi, B., Hamm N. A. S., Groen T. A., Skidmore A. K., Toxopeus A. G. (2014) Where Is
525 Positional Uncertainty a Problem for Species Distribution Modelling?. *Ecography*, 37(2), pp.
526 191–203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x>
- 527 Owens H., Barve V., Chamberlain S. (2024) spocc: Interface to Species Occurrence Data
528 Sources. R package version 1.2.3.4. <https://github.com/ropensci/spocc>
- 529 Pebesma, E. (2018) Simple Features for R: Standardized Support for Spatial Vector Data.
530 *The R Journal*, 10, pp. 439-446. <https://doi.org/10.32614/RJ-2018-009>
- 531 Pebesma, E., Bivand, R. (2023) *Spacial Data Science With Applications in R*. Available at:
532 <https://r-spatial.org/book/>. Accessed on: November 15, 2024.
- 533 Perry, F. (2016) *Cerianthus lloydii* and other burrowing anemones in circalittoral muddy
534 mixed sediment. Marine Life Information Network: Biology and Sensitivity Key Information
535 Reviews. Retrieved from
536 [https://www.marlin.ac.uk/habitats/detail/1091/cerianthus_lloydii_and_other_burrowing_ane](https://www.marlin.ac.uk/habitats/detail/1091/cerianthus_lloydii_and_other_burrowing_anemones_in_circalittoral_muddy_mixed_sediment)
537 [mones_in_circalittoral_muddy_mixed_sediment](https://www.marlin.ac.uk/habitats/detail/1091/cerianthus_lloydii_and_other_burrowing_anemones_in_circalittoral_muddy_mixed_sediment). Accessed on: November 15, 2024.
- 538 Peterson, A. T., Soberón, J. (2012) Species Distribution Modeling and Ecological Niche
539 Modeling: Getting the Concepts Right. *Natureza & Conservação*, 10 (2), pp. 102–107.
540 <https://doi.org/10.4322/natcon.2012.019>
- 541 Peteya D. J. (1973) A Possible Proprioceptor in *Ceriantheopsis americanus* (Cnidaria,
542 Ceriantharia). *Z. Zellforsch*, 144, pp. 1-10. <https://doi.org/10.1007/BF00306682>
- 543 Phillips, S. J., Anderson R. P., Schapire R. E. (2006) Maximum Entropy Modeling of Species
544 Geographic Distributions”. *Ecological Modelling* 190 (3–4), pp. 231–59.
545 <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- 546 Phillips, S. J., Dudík, M. (2008) Modeling of species distributions with Maxent: new
547 extensions and a comprehensive evaluation. *Ecography*, 31 (2), pp. 161-175.
548 <https://doi.org/10.1111/j.0906-7590.2008.5203.x>

- 549 Picton, B. E., Manuel R. L. (1985) *Arachnanthus sarsi* Carlgren, 1912: a redescription of a
550 cerianthid anemone new to the British Isles. *Zoological Journal of the Linnean Society*, 83,
551 343–349. <https://doi.org/10.1111/j.1096-3642.1985.tb01180.x>
- 552 R Core Team (2024) A language and environment for statistical computing. R Foundation for
553 Statistical Computing, Vienna. Retrieved from <https://www.R-project.org>. Accessed on:
554 November 15, 2024.
- 555 Radosavljevic, A., Anderson, R. P. (2014) Making better Maxent models of species
556 distributions: complexity, overfitting and evaluation. *Journal of biogeography*, 41(4), pp.
557 629–643. <https://doi.org/10.1111/jbi.12227>
- 558 Riedel, B., M. Zuschin, A. Haselmair, e M. Stachowitsch. (2008) Oxygen depletion under
559 glass: Behavioural responses of benthic macrofauna to induced anoxia in the Northern
560 Adriatic. *Journal of Experimental Marine Biology and Ecology* 367(1), pp. 17–27.
561 <https://doi.org/10.1016/j.jembe.2008.08.007>.
- 562 Santos, C. L. da S., Ceriello, H., Morandini, A. C., Stampar, S. N. (2019). Revision of the
563 genus *Ceriantheomorpha* (Cnidaria, Anthozoa, Ceriantharia) with description of a new
564 species from the Gulf of Mexico and northwestern Atlantic. *ZooKeys*, 874, 127–148.
565 <https://doi.org/10.3897/zookeys.874.35835>
- 566 Sebens, K. P. (1998). Marine flora and fauna of the eastern United States: Anthozoa:
567 Actiniaria, Corallimorpharia, Ceriantharia, and Zoanthidea. In: NOAA Technical Report
568 NMFS 141 (edited by Pearce J. B.) Department of Commerce, National Oceanic and
569 Atmospheric Administration (NOAA), United States.
- 570 Sillero, N., Arenas-Castro S., Enriquez-Urzelai U., Vale C. G., Sousa-Guedes D., Martínez-
571 Freiría F., Real R., e Barbosa A. M. (2021) Want to model a species niche? A step-by-step
572 guideline on correlative ecological niche modelling. *Ecological Modelling* 456 109671. doi:
573 [10.1016/j.ecolmodel.2021.109671](https://doi.org/10.1016/j.ecolmodel.2021.109671).
- 574 Shepard A. N., Theroux R. G., Cooper A., Uzmann J. R. (1986) Ecology of Ceriantharia
575 (Coelenterata, Anthozoa) of the Northwest Atlantic from Cape Hatteras to Nova Scotia.
576 *Fishery Bulletin*, 84 (3), pp. 626–646.
- 577 Sillero, N., Arenas-Castro, S., Enriquez-Urzelai, U., Vale, C. G., Sousa-Guedes, D.,
578 Martínez-Freiría, F., Real, R., & Barbosa, A. M. (2021) Want to model a species niche? A
579 step-by-step guideline on correlative ecological niche modelling. *Ecological Modelling*, 456,
580 109671. <https://doi.org/10.1016/j.ecolmodel.2021.109671>
- 581 Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M.,
582 Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A. et al. (2007) Marine Ecoregions of
583 the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, 57(7), pp. 573–583.
584 <https://doi.org/10.1641/B570707>
- 585 Stampar, S. N., Beneti, J. S., Acuña, F. H., & Morandini, A. C. (2015) Ultrastructure and tube
586 formation in Ceriantharia (Cnidaria, Anthozoa). *Zoologischer Anzeiger - A Journal of*
587 *Comparative Zoology*, 254, pp. 67–71. <https://doi.org/10.1016/j.jcz.2014.11.004>
- 588 Stampar, S. N.; Emig, C. C.; Morandini, A. C.; Kodja, G.; Balboni, A.; Lang de Silveira, F.
589 (2010). Is there any risk in a symbiotic species associating with an endangered one? A case of

- 590 a phoronid worm growing on a Ceriantheomorpha tube. *Cahiers de Biologie Marine*, 51, pp.
591 206-209.
- 592 Stampar, S. N., Lopes, C. S. S., Angelis, S. A., Morandini, A. C. (2019) DNA Barcoding
593 revealing the occurrence of *Isarachnanthus* (Cnidaria; Anthozoa; Ceriantharia) in Cape
594 Verde. *Papéis Avulsos de Zoologia*, 59, e20195940. [https://doi.org/10.11606/1807-
595 0205/2019.59.40](https://doi.org/10.11606/1807-0205/2019.59.40)
- 596 Stampar, S. N., Maronna, M. M., Kitahara, M. V., Reimer, J. D., Beneti, J. S., Morandini, A.
597 C. (2016) Ceriantharia in Current Systematics: Life Cycles, Morphology and Genetics. In: S.
598 Goffredo & Z. Dubinsky (Orgs.), *The Cnidaria, Past, Present and Future* (pp. 61–72).
599 Springer International Publishing. https://doi.org/10.1007/978-3-319-31305-4_5
- 600 Stampar, S. N., Maronna, M. M., Vermeij, M. J. A., Silveira, F. L. d., Morandini, A. C. (2012)
601 Evolutionary Diversification of Banded Tube-Dwelling Anemones (Cnidaria; Ceriantharia;
602 *Isarachnanthus*) in the Atlantic Ocean. *PLOS ONE*, 7(7), e41091.
603 <https://doi.org/10.1371/journal.pone.0041091>
- 604 Stampar, S., Morandini, A. (2017) Occurrence of *Isarachnanthus* (Cnidaria: Anthozoa:
605 Ceriantharia) at Ascension Island: A test of hypothesis. *Journal of the Marine Biological
606 Association of the United Kingdom*, 97(4), pp. 689–693.
607 <https://doi.org/10.1017/S0025315414000423>
- 608 Stampar, S. N., Reimer, J. D., Maronna, M. M., Lopes, C. S. S., Ceriello, H., Santos, T. B.,
609 Acuña, F. H., & Morandini, A. C. (2020) Ceriantharia (Cnidaria) of the World: An annotated
610 catalogue and key to species. *ZooKeys*, 952, pp. 1–63.
611 <https://doi.org/10.3897/zookeys.952.50617>
- 612 Suggett D. J., Hall-Spencer J. M., Rodolfo-Metalpa R., Boatman T. G., Payton R., Pettay D.
613 T., Johnson V. R., Warner M. E., Lawson T. (2012) Sea Anemones May Thrive in a High
614 CO2 World. *Global Change Biology* 18(10), pp. 3015–3025. [https://doi.org/10.1111/j.1365-
615 2486.2012.02767.x](https://doi.org/10.1111/j.1365-2486.2012.02767.x)
- 616 Watling, L., & Lapointe, A. (2022) Global biogeography of the lower bathyal (700–3000 m)
617 as determined from the distributions of cnidarian anthozoans. *Deep Sea Research Part I:
618 Oceanographic Research Papers*, 181, 103703. <https://doi.org/10.1016/j.dsr.2022.10370>
- 619 Wickham H., Averick M., Bryan J., Chang W., D'Agostino McGowan L., François R.,
620 Grolemond G., Hayes A., Henry L., Hester J. (2019) Welcome to the Tidyverse. *Journal of
621 Open Source Software*, 4 (43), 1686. <https://doi.org/10.21105/joss.01686>
- 622 Wilding, C. Wilson, E. (2008) *Pachycerianthus multiplicatus* Fireworks anemone. In (edited
623 by Tyler-Walters H. and Hiscock K.) *Marine Life Information Network: Biology and
624 Sensitivity Key Information Reviews*, [online]. Plymouth: Marine Biological Association of
625 the United Kingdom. Retrieved from <https://www.marlin.ac.uk/species/detail/1272>. Accessed
626 on: November 15, 2024.
- 627 Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng,
628 X., Guillerá-Arroita, G., Guisan, A. et al. (2020) A standard protocol for reporting species
629 distribution models. *Ecography*, 43(9), pp. 1261–1277. <https://doi.org/10.1111/ecog.04960>
- 630

631 **Supplementary Material**

632 **Table S1.** Ceriantharia *spp.* in the Atlantic Ocean. Species in bold were selected for
 633 modelling. **Sources:** Santos et al. 2019, Stampar et al. 2020, Global Biodiversity Information
 634 Facility (GBIF) and Ocean Biodiversity Information System (OBIS) databases.

| Genera | Species | Number of occurrences | Reference |
|-------------------------|-----------------------------|-----------------------|---|
| <i>Arachnanthus</i> | <i>oligopodus</i> | 46 | Cerfontaine, 1891 |
| | <i>sarsi</i> | 112 | Carlgren, 1912 |
| <i>Brotruanthus</i> | <i>mexicanus</i> | 18 | Torrey & Kleeberger, 1909 |
| <i>Brotrucidifer</i> | <i>novergicus</i> | 53 | Carlgren, 1912 |
| | <i>shtokmani</i> | 6 | Molodtsova, 2006 |
| <i>Ceriantheomorphe</i> | <i>adelita</i> | 1 | Lopes, Morandini & Stampar, 2019 |
| | <i>brasiliensis</i> | 19 | Mello-Leitão, 1919 |
| <i>Ceriantheopsis</i> | <i>americana</i> | 482 | Agassiz in Verrill, 1864 |
| | <i>austroafricanus</i> | 29 | Molodtsova, Griffiths & Acuña, 2011 |
| | <i>lineata</i> | 0 | Stampar, Scarabino, Pastorino & Morandini, 2015 |
| | <i>nikitai</i> | 5 | Molodtsova, 2001 |
| <i>Cerianthus</i> | <i>bathymetricus</i> | 0 | Moseley, 1877 |
| | <i>incertus</i> | 0 | Carlgren, 1932 |
| | <i>lloydii</i> | 33.052 | Gosse, 1859 |
| | <i>malakhovi</i> | 3 | Molodtsova, 2001 |
| | <i>membranaceus</i> | 1.265 | Gmelin, 1791 |
| | <i>vogti</i> | 23 | Danielssen, 1890 |
| <i>Isarachnanthus</i> | <i>maderensis</i> | 21 | Johnson, 1861 |
| | <i>nocturnus</i> | 47 | Hartog, 1977 |
| <i>Pachycerianthus</i> | <i>borealis</i> | 1922 | Verrill, 1873 |
| | <i>curacaoensis</i> | 20 | den Hartog, 1977 |
| | <i>dohrni</i> | 39 | van Beneden, 1924 |
| | <i>multiplicatus</i> | 1089 | Carlgren, 1912 |
| | <i>schlenzae</i> | 10 | Stampar, Morandini & Silveira, 2014 |

solitarius

705

Rapp, 1829

635

636 **Table S2.** Environmental variables selected via Variance Inflation Factor analysis for all
 637 modeled species of *Ceriantharia spp.* in the Atlantic Ocean. **Source:** Bio-ORACLE v3.0
 638 database (Assis et al., 2024).

| Species | Variable Name |
|---------------------------------|------------------------------------|
| <i>Arachnanthus sarsi</i> | Average Dissolved Molecular Oxygen |
| | Average Ocean Temperature |
| | Average Sea Water Speed |
| | Average Sea Water Direction |
| | Maximum Sea Water Direction |
| | Minimum Sea Water Direction |
| | Average Silicate |
| | Minimum Sea Water Speed |
| <i>Ceriantheopsis americana</i> | Minimum Salinity |
| | Minimum Dissolved Molecular Oxygen |
| | Minimum Silicate |
| | Minimum Sea Water Speed |
| | Maximum Ocean Temperature |
| | Maximum Sea Water Direction |
| | Average Sea Water Direction |
| | Minimum Sea Water Direction |
| <i>Cerianthus lloydii</i> | Minimum Ocean Temperature |
| | Maximum Nitrate |
| | Minimum Silicate |
| | Minimum Dissolved Molecular Oxygen |
| | Maximum Sea Water Speed |
| | Maximum Salinity |
| | Maximum Silicate |
| | Minimum Sea Water Speed |
| Average Sea Water Speed | |

| | |
|----------------------------------|------------------------------------|
| | Maximum Sea Water Direction |
| | Minimum Sea Water Direction |
| | Average Sea Water Direction |
| <i>Cerianthus membranaceus</i> | Average Nitrate |
| | Average Sea Water Speed |
| | Average Dissolved Molecular Oxygen |
| | Average Salinity |
| | Maximum Sea Water Direction |
| | Maximum Sea Water Speed |
| | Average Sea Water Direction |
| | Minimum Sea Water Speed |
| | Minimum Sea Water Direction |
| | Minimum Salinity |
| | Minimum Dissolved Molecular Oxygen |
| | Average Ocean Temperature |
| | Average Sea Water Speed |
| | Minimum Sea Water Speed |
| | Maximum Sea Water Speed |
| <i>Isarachnanthus maderensis</i> | Minimum Sea Water Direction |
| | Average Sea Water Direction |
| | Average Dissolved Molecular Oxygen |
| | Maximum Sea Water Direction |
| | Average Nitrate |
| <i>Isarachnanthus nocturnus</i> | Minimum Sea Water Speed |
| | Minimum Ocean Temperature |
| | Average Sea Water Speed |
| | Minimum Dissolved Molecular Oxygen |
| | Maximum Sea Water Direction |
| | Maximum Silicate |
| | Minimum Salinity |
| | Minimum Sea Water Direction |
| | Average Sea Water Direction |

| | |
|--------------------------------------|------------------------------------|
| | Average Ocean Temperature |
| | Minimum Silicate |
| | Maximum Salinity |
| | Maximum Sea Water Speed |
| <i>Pachycerianthus borealis</i> | Minimum Sea Water Direction |
| | Average Sea Water Speed |
| | Average Sea Water Direction |
| | Minimum Dissolved Molecular Oxygen |
| | Maximum Sea Water Direction |
| | Maximum Nitrate |
| | Maximum Salinity |
| | Minimum Silicate |
| | Average Ocean Temperature |
| <i>Pachycerianthus multiplicatus</i> | Maximum Sea Water Direction |
| | Maximum Silicate |
| | Average Sea Water Speed |
| | Minimum Sea Water Direction |
| | Minimum Sea Water Speed |
| <i>Pachycerianthus solitarius</i> | Average Ocean Temperature |
| | Average Sea Water Speed |
| | Average Dissolved Molecular Oxygen |
| | Maximum Sea Water Direction |
| | Minimum Sea Water Speed |
| | Maximum Sea Water Speed |
| | Average Salinity |

639

640 **Table S3.** Average relative variable importance for all modeled species of *Ceriantharia spp.*
 641 in the Atlantic Ocean.

| Species | Variable Name | Average Relative Importance (%) |
|---------------------------|------------------------------------|---------------------------------|
| <i>Arachnanthus sarsi</i> | Average Dissolved Molecular Oxygen | 62 |
| | Average Ocean Temperature | 58 |

| | | |
|---------------------------------|------------------------------------|----|
| | Average Sea Water Speed | 12 |
| | Average Sea Water Direction | 3 |
| | Maximum Sea Water Direction | 2 |
| | Minimum Sea Water Direction | 2 |
| | Average Silicate | 1 |
| | Minimum Sea Water Speed | 1 |
| <i>Ceriantheopsis americana</i> | Minimum Salinity | 41 |
| | Minimum Dissolved Molecular Oxygen | 39 |
| | Minimum Silicate | 38 |
| | Minimum Sea Water Speed | 38 |
| | Maximum Ocean Temperature | 12 |
| | Maximum Sea Water Direction | 6 |
| | Average Sea Water Direction | 6 |
| | Minimum Sea Water Direction | 3 |
| <i>Cerianthus lloydii</i> | Minimum Ocean Temperature | 39 |
| | Maximum Nitrate | 34 |
| | Minimum Silicate | 24 |
| | Minimum Dissolved Molecular Oxygen | 5 |
| | Maximum Sea Water Speed | 3 |
| | Maximum Salinity | 3 |
| | Maximum Silicate | 2 |
| | Minimum Sea Water Speed | 1 |
| | Average Sea Water Speed | 1 |
| | Maximum Sea Water Direction | 1 |
| | Minimum Sea Water Direction | 1 |
| | Average Sea Water Direction | 0 |
| <i>Cerianthus membranaceus</i> | Average Nitrate | 77 |
| | Average Sea Water Speed | 56 |
| | Average Dissolved Molecular Oxygen | 12 |
| | Average Salinity | 12 |
| | Maximum Sea Water Direction | 10 |

| | | |
|----------------------------------|------------------------------------|----|
| | Maximum Sea Water Speed | 5 |
| | Average Sea Water Direction | 4 |
| | Minimum Sea Water Speed | 3 |
| | Minimum Sea Water Direction | 1 |
| | Minimum Salinity | 0 |
| | Minimum Dissolved Molecular Oxygen | 0 |
| <i>Isarachnanthus maderensis</i> | Average Ocean Temperature | 43 |
| | Average Sea Water Speed | 24 |
| | Minimum Sea Water Speed | 20 |
| | Maximum Sea Water Speed | 10 |
| | Minimum Sea Water Direction | 9 |
| | Average Sea Water Direction | 8 |
| | Average Dissolved Molecular Oxygen | 5 |
| | Maximum Sea Water Direction | 4 |
| | Average Nitrate | 0 |
| <i>Isarachnanthus nocturnus</i> | Minimum Sea Water Speed | 45 |
| | Minimum Ocean Temperature | 19 |
| | Average Sea Water Speed | 10 |
| | Minimum Dissolved Molecular Oxygen | 7 |
| | Maximum Sea Water Direction | 6 |
| | Maximum Silicate | 4 |
| | Minimum Salinity | 3 |
| | Minimum Sea Water Direction | 3 |
| | Average Sea Water Direction | 2 |
| <i>Pachycerianthus borealis</i> | Average Ocean Temperature | 76 |
| | Minimum Silicate | 13 |
| | Maximum Salinity | 6 |
| | Maximum Sea Water Speed | 6 |
| | Minimum Sea Water Direction | 5 |
| | Average Sea Water Speed | 4 |
| | Average Sea Water Direction | 2 |

| | | |
|--------------------------------------|------------------------------------|----|
| | Minimum Dissolved Molecular Oxygen | 2 |
| | Maximum Sea Water Direction | 1 |
| <i>Pachycerianthus multiplicatus</i> | Maximum Nitrate | 60 |
| | Maximum Salinity | 29 |
| | Minimum Silicate | 13 |
| | Average Ocean Temperature | 10 |
| | Maximum Sea Water Direction | 9 |
| | Maximum Silicate | 9 |
| | Average Sea Water Speed | 6 |
| | Minimum Sea Water Direction | 5 |
| | Minimum Sea Water Speed | 4 |
| <i>Pachycerianthus solitarius</i> | Average Ocean Temperature | 83 |
| | Average Sea Water Speed | 40 |
| | Average Dissolved Molecular Oxygen | 11 |
| | Maximum Sea Water Direction | 7 |
| | Minimum Sea Water Speed | 6 |
| | Maximum Sea Water Speed | 5 |
| | Average Salinity | 0 |
