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## Habitat suitability and environmental niche comparison of cold-water coral species along the Brazilian continental margin

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### Abstract :

In face of increasing anthropogenic disturbance in the deep sea, it is a priority to better understand the regional distribution of cold-water corals (CWC). These organisms create some of the most species-rich habitats in the deep sea and, for this reason, they must be properly protected and managed. In this study, we aimed to identify suitable habitat for multiple CWC taxa off the Brazilian continental margin and compare their environmental niches. Habitat suitability models were developed using the Maxent approach, which allowed for the prediction of species distribution and for the identification of potential 'hot spot' areas that may be important for biodiversity conservation. Ecological niches were determined by a PCA-env approach, and niche similarity and equivalence were evaluated based on niche overlap using the Schoener's D metric. Potentially suitable habitat for Octocorallia covered a broad latitudinal range encompassing nearly the entire Brazilian continental margin, whereas Scleractinia had greater potentially suitable habitat in the Central and Southern areas. Scleractinian species were observed to slightly differ in their environmental niche, with non-reef-forming species being more tolerant to a wider range of environmental conditions in comparison with reef-forming species, inhabiting a wider area of the South American continental margin. Due to the high potential suitability for several CWC species, the Central and Southern parts of the Brazilian continental margin should be considered as potential areas high CWC diversity. Considering the current state of the art and strategic assessment tools, these areas are important targets for conservation, management, and environmental impact assessment. Most reef-forming species had similar but not directly equivalent ecological niches, indicating that mapping efforts and management planning should consider CWCs at the species level.

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## Highlights

► Octocorallia demonstrated suitable habitat that encompassed nearly the entire Brazilian continental margin ► Scleractinia suitable habitat covered principally the Central and Southern continental margin. ► The Central and Southern Brazilian continental margin should be considered as areas of high cold-water corals diversity. ► Reef-forming cold-water coral species had similar but not equivalent ecological niches. ► The mapping efforts and management planning should consider cold-water coral at the species level.

**Keywords** : Deep-sea corals, Habitat suitability modelling, *Lophelia pertusa*, Environmental niche, Southwestern Atlantic, Octocorallia, Scleractinia

## 46 INTRODUCTION

47           The deep sea (>200 m depth), the largest biome on Earth that covers 65% of the  
48 surface, has been recognized to be environmentally and biologically diverse, providing  
49 several important ecosystem services for humans (Thurber et al., 2014). Cold-water corals  
50 (CWC) create highly heterogeneous deep-sea habitats that can be used by other organisms  
51 as feeding grounds, refuge and/or substrate (Henry et al., 2009; Buhl-Mortensen et al.,  
52 2010). In the case of some reef-forming stony coral species (Order Scleractinia) these  
53 habitats can be many kilometers long and hundreds of meters high (Roberts et al., 2006).  
54 Non reef-forming scleractinian species and the soft corals from the subclass Octocorallia  
55 also provide habitat due to their occurrence within dense and often diverse aggregations  
56 known as coral gardens (Roberts et al., 2009) in both hard and soft bottoms. CWC are  
57 azooxanthellate corals and present a wide bathymetric distribution generally extending  
58 deeper than 50 m water depth (Cairns, 2007). Ecosystems formed by CWC generally have  
59 a high biodiversity of associated fauna and are considered some of the most species-rich  
60 habitats in the deep sea (Freiwald et al., 2004). However, CWC have a slow growth rate,  
61 high fragility (Hall-Spencer et al., 2002) and low recovery potential (Reed et al., 2007;  
62 Huvenne et al., 2016), consequently, they are considered to form vulnerable marine  
63 ecosystems (VME).

64           There are six main reef-forming Scleractinian cold-water coral species: *Lophelia*  
65 *pertusa* (= *Desmophyllum pertusum*, Linnaeus, 1758); *Madrepora oculata* Linnaeus,  
66 1758; *Solenosmilia variabilis* Duncan, 1873; *Enallopsammia profunda* Pourtalès, 1868;  
67 *Goniocorella dumosa* Alcock, 1902; and *Oculina varicosa* Le Sueur 1820 (Freiwald et  
68 al., 2004). Their importance, distribution and abundance, varies amongst regions  
69 (Freiwald et al., 2004). *L. pertusa* is considered as the primary reef-forming species in the  
70 deep-sea with an almost world-wide distribution (Davies and Guinotte, 2011). *M. oculata*  
71 is widely distributed in the Northeast Atlantic and Mediterranean (Reveillaud et al., 2008;  
72 Orejas et al., 2009; Vertino et al., 2010; Gori et al., 2013), whilst *S. variabilis* is  
73 concentrated within New Zealand waters (Cairns, 1995; Tracey et al., 2011). In the last  
74 decade, habitat suitability models have helped to better understand CWC distribution at  
75 both regional and global scales (e.g. Davies et al., 2008; Tittensor et al., 2009; Davies and  
76 Guinotte, 2011; Howell et al., 2011; Yesson et al., 2012; Vierod et al., 2014; Georgian et  
77 al., 2014; Guinotte and Davies, 2014).

78           The area predicted using habitat suitability models is generally related to the  
79 ecological niche breadth of the species considered (Slatyer et al., 2013). Species that are  
80 geographically widespread normally present broader ecological niches given that they  
81 persist in an area with wider range of environmental conditions, whereas species with  
82 restricted distributions would have a narrower niche breadth (Gaston, 1997). Estimating  
83 the environmental niche of a given species allows for comparison between different  
84 species and may also indicate how sensitive species are to changes in the environment.  
85 Although it is possible to test niche similarity from the outputs of habitat suitability  
86 models, conceptual and statistical challenges exist with this approach (Broenniman et al.,  
87 2012). For example, meaningful niche divergences could be confounded with geographic  
88 distance because the environmental data used in species distribution models are often  
89 spatially correlated (McCormack et al., 2010). To address this, Broennimann et al. (2012)  
90 developed a mathematical approach that can describe species niches in a Principal  
91 Component Analyses delimited by the environmental conditions of the study area (PCA-  
92 env). This promising tool for conservation and management, allows the evaluation of  
93 species niche similarity and serves as a useful complement to habitat suitability models  
94 (e.g. Aguirre-Gutiérrez et al., 2015; Zhu et al., 2016).

95           The exploitation of deep-sea resources is increasing worldwide and there is an  
96 urgent need to have an adequate knowledge of the ecology of CWC to ensure that  
97 appropriate management strategies are applied (e.g. Morato et al., 2006; Davies et al.,  
98 2007). For instance, bottom trawling represents a main threat to CWC (Fosså et al., 2002;  
99 Buhl-Mortensen et al., 2016; Buhl-Mortensen, 2017). Oil and gas offshore activities  
100 could potentially impact CWC (reviewed in Cordes et al., 2016) and, particularly, the  
101 2010 accidental Deepwater Horizon oil spill in the Gulf of Mexico have showed negative  
102 effects on CWC also at 22 km away from the spill site (Fisher et al., 2014) and even 7  
103 years after (Girard and Fisher, 2018). Furthermore, deep-sea mining of massive  
104 polymetallic sulfates deposits and cobalt-rich ferromanganese crusts may potentially  
105 negatively affect some CWC communities in the near future (Miller et al., 2018).

106           Three out of six main scleractinian reef-forming species, i.e. *L. pertusa*, *S.*  
107 *variabilis*, *M. oculata*, together with *E. rostrata*, are known to coexist along the Brazilian  
108 continental slope (Castro et al., 2006; Kitahara, 2007; Pires et al., 2007; Cavalcanti et al.,  
109 2017). With a coastline of 7,491 km, Brazil accounts for a large proportion of the South  
110 American continental margin. This is an extensive area where fisheries, oil and gas

111 exploration are important and ongoing activities. Deep-sea fisheries in the South-eastern  
112 Brazilian EEZ (Exclusive Economic Zone) have been estimated to have swept the  
113 available area more than once from 2003 to 2011 (Port et al., 2016). In addition, fishing  
114 intensity has increased, particularly in the continental slope, from 2000 onwards, due to  
115 government policies that stimulated foreign trawlers to occupy deep areas (Perez et al.,  
116 2009). Furthermore, the oil and gas production has increased during recent years.  
117 Approximately 70% of Brazilian oil production occurs within deep-sea basins  
118 (Bernardino and Sumida, 2017). Despite the magnitude and potential environmental  
119 impacts, there are few studies analysing the impact of these activities on CWC  
120 communities within this region (e.g. Kitahara, 2009; Port et al., 2016).

121         In this study, we evaluated the habitat suitability distribution and niche of several  
122 CWC species along the Brazilian continental margin and slope. We aimed to better  
123 understand differences in CWC potential distribution and corresponding environmental  
124 niches. We compared the Octocorallia Subclass and Scleractinia Order and then focused  
125 on several scleractinian species. Six species of scleractinians were studied in order to  
126 compare their niche and potential distributions representing diverse types of CWC VMEs.  
127 Four reef-forming species *L. pertusa*, *M. oculata*, *S. variabilis* and *E. rostrata* and two  
128 non-reef-forming corals, *Cladocora debilis* Milne Edwards and Haime, 1849 and  
129 *Deltocyathus* Milne Edwards & Haime, 1848. The former type of species represents reef  
130 presence or possible reef-habitat formations and the latter type represents possible coral  
131 fields, being *C. debilis* a colonial species and *Deltocyathus* spp. a solitary cup-coral genus.  
132 The results presented here are a fundamental step in better understanding CWC  
133 distribution and their possible sensitivity to environmental changes both natural and  
134 human-induced within the Brazilian continental margin and slope.

135 METHODS

136 *Study area*

137           The present study focused on the Brazilian continental margin and slope, but also  
138 included international waters to 25° W (Figure 1 a). The Brazilian continental margin was  
139 divided into four areas from north to south based upon their oceanographic and biological  
140 characteristics (after the REVIZEE program - Brazilian project on Living Resources in  
141 the Exclusive Economic Zone, Anon. 2006, [www.mma.gov.br/revizee](http://www.mma.gov.br/revizee)) as follows: (1)  
142 The North Brazil Shelf including the Amazonia, hereafter referred as the "North Area";  
143 (2) the tropical north-eastern Brazil area, including São Pedro and São Paulo and  
144 Fernando de Noronha archipelagos and Rocas Atoll as the "North-eastern Area"; (3) the  
145 Eastern Brazil and Trindade and Martin Vaz Islands as the "Central Area "; and (4) the  
146 warm temperate South-eastern Brazilian area as the "South Area ", including the Rio  
147 Grande Rise (Figure 1 b).

148

149 *Species data*

150           A database was compiled using all available CWC records in the Brazilian  
151 continental margin from three sources: (1) records in available databases, including the  
152 Ocean Biogeographic Information System (OBIS) and the REVIZEE program; (2)  
153 records from specific literature sources, and (3) field observations using remotely  
154 operated vehicles in Campos Basin (Cavalcanti et al., 2017) (Table 1, Supplemental  
155 material). Octocorallia records were mainly from the North and Central Brazilian areas  
156 and principally from 30 to 150 m depth, i.e. mesophotic habitats. In order to exclude  
157 zooxanthellate corals, we used only records deeper than 50 m (Cairns, 2007). To model  
158 habitat suitability of each taxon, all records were filtered to provide only one record per  
159 analysis cell (ca. 1 km<sup>2</sup>) (Table 1, Figure 1 b). We selected mostly published species  
160 records to ensure a good taxonomic classification at species level. Furthermore, records  
161 from other sources were used at taxonomic level higher than genera to avoid possible  
162 identification errors.

163

164 *Environmental data*

165 A total of 34 environmental variables were used to model species habitat  
166 suitability (after Davies and Guinotte, 2011). They were classified in seven broad  
167 categories (after Yesson et al., 2012): carbonate variables (CARB), bathymetric variables  
168 (BATH), hydrodynamic variables (HYDRO), productivity variables (PROD), oxygen  
169 variables (OXY), chemical variables (CHEM), and temperature variable (TEMP) (Table  
170 2). These categories were selected based on biological knowledge or single-factor  
171 analysis (Yesson et al., 2012). After subset the variables into top-level categories, only a  
172 single variable per category was selected by creating species distribution models for each  
173 variable on its own, calculating the validation area under the curve (AUC , see below)  
174 and retaining the most important variable per category for the final analysis (Phillips et  
175 al., 2009).

176

#### 177 *Maxent model predictions*

178 Maxent version 3.3.3k (Phillips et al., 2006) was used to model habitat suitability.  
179 Presence records were randomly divided in two subsets, one with 70% of records to train  
180 the model and one with the remaining 30% to testing the models. Models were run with  
181 the default parameters of Maxent i.e., convergence threshold of  $10^{-5}$ , a maximum of 500  
182 iterations, and a regularization multiplier of 1. The importance of each variable on each  
183 final model was assessed using a Jackknifing procedure (Phillips et al., 2009). This  
184 procedure compares the contribution of each variable between two models, one without  
185 the variable and a second including it, thereby determining how much new information  
186 the variable contributes to a model and how much is lost when that variable is omitted.  
187 Final model predictions were presented as maps showing a predicted continuous habitat  
188 suitability value. In order to contrast predictions from different taxonomic groups, these  
189 outputs were converted into binary values (0 = unsuitable, 1 = suitable) based on the  
190 maximum sum of sensitivity plus specificity test threshold (Jiménez-Valverde and Lobo,  
191 2007; Liu et al., 2013). This representation allowed to identify potentially suitable areas  
192 for multiple taxon as potential areas of hotspot of cold-water coral diversity.

193

#### 194 *Species niche comparisons*

195           In order to describe and compare the environmental niches, we have represented  
196 the species niche in a multivariate space, measured the niche overlap and tested their  
197 similarity and equivalence. The spatial niche occupied by each species was represented  
198 by an environmental principal component analysis (PCA-env) approach (after  
199 Broennimann et al., 2012) using the seven most important environmental variables for  
200 each taxon (see environmental data session for the variables selection). Despite  
201 differences between Octocorallia and Scleractinia carbonate structures (calcite vs  
202 aragonite, respectively), a unique environmental space is needed to compare their species  
203 niche. Then, whilst not biologically relevant for Octocorallia, aragonite saturation state  
204 (AST), which was highly correlated with the Calcite saturation state (CST) ( $r > 0.9$ ), was  
205 used to construct the PCA-env.

206           Species occurrences were disaggregated with a minimum distance equal to the  
207 grid resolution (ca. 1 km) to reduce sampling bias. The environmental space, delimited  
208 by the axes, was set to  $100 \times 100$  cells. These cells were used to generate a ‘smoothed’  
209 Kernel density of the filtered occurrences, as well as of the available environmental  
210 conditions (in the focal areas, Figure 1). The occupancy of the environment by the entity  
211 was calculated in each cell (Broennimann et al., 2012). Niche overlap was estimated using  
212 Schoener’s  $D$  metric, which ranges from 0 (no overlap) to 1 (complete overlap)  
213 (Schoener, 1970). This metric is used to test niche similarity and equivalence, comparing  
214 the observed  $D$  value and the probability distribution of overlap values resulted from  
215 simulated species occurrence distributions (Warren et al., 2008). The application of a  
216 smoother kernel to standardize species densities allowed moving from the geographical  
217 space to the multivariate environmental space, making the analysis independent of  
218 sampling effort and environmental space resolution (Broennimann et al., 2012).

219           Similarity and equivalence tests are used to evaluate if the environmental niches  
220 of two species are more similar than expected by chance and if both species have the same  
221 use of the niche space, respectively (Warren et al., 2008). The similarity test for each  
222 species pair (a and b) consisted of two reciprocal comparisons. The observed  $D$  value is  
223 compared with the probability distribution of overlap values created from simulations of  
224 random points in the background area. Then, the real overlap is compared with the overlap  
225 between randomly distributed species in the area (same  $n$  of species presence points and  
226 with “background” being the studied area). Whereas equivalence test consisted in the  
227 comparison of the observed  $D$  value and the probability distribution of overlap values



228 from simulated species distribution randomly created from the real presence points of  
229 both species (Warren et al., 2008). Since the species have broad regional and global  
230 distributions, high dispersal capacity is expected, thus, the background area represented  
231 a variety of ecological space that they could colonize as suggested by Barve et al. (2011).  
232 The tests were based on 100 iterations. All the analyses were done in R (R Development  
233 Core Team, 2010) with the “ecospat” package (Broennimann et al., 2016).

234 Niche density center and niche breadth were calculated to determine how the  
235 niches differed, considering the two main principal components. The former indicates the  
236 optimal environmental conditions for the species, while the latter described the capacity  
237 of a species to tolerate deviations from the optima. Smaller values indicated that the  
238 species occupies a more restricted or specialized niche, and larger values that the species  
239 has a wider environmental niche. Niche density center was calculated as the mean of the  
240 Kernel's density value calculated from 10000 random points inside of the environmental  
241 niche space of each taxon. Niche breadth was estimated as the proportion of the available  
242 environmental conditions delimited by the axes (100 × 100 cells) that were estimated as  
243 occupied in the PCA-env, i.e., the percentage of available conditions inhabited by the  
244 species (represented as percentage). To better represent niche center position differences,  
245 the change from Scleractinia niche center to the specific species was represented with an  
246 arrow in the representation of its environmental niche plot.

247

## 248 RESULTS

### 249 *Occupied environmental conditions*

250 The environmental conditions occupied by Octocorallia and Scleractinia were  
251 mostly in waters saturated with calcite and aragonite respectively (i.e.,  $\Omega \geq 1$ ), although  
252 there were some Scleractinia occurrences found in aragonite-depleted waters (Fig 2a).  
253 Octocorallia and Scleractinia were mainly present in depth shallower than 1250 m (Fig  
254 2b). Octocorallia occurrences were found across a broad range of current velocities from  
255 0 to 0.20 m s<sup>-1</sup>, whereas Scleractinia were found at sites with velocities lower than 0.1 m  
256 s<sup>-1</sup> (Fig 2c). Both, Octocorallia and Scleractinia were found in sites with POC that ranged  
257 from 0 to 50 gC C<sub>org</sub> m<sup>-2</sup> y<sup>-1</sup> and in a range of dissolved oxygen conditions ranging  
258 between 4 and 5.5 ml l<sup>-1</sup>, and silicate < 50 μmol l<sup>-1</sup> (Fig 2d, e and f, respectively).  
259 Octocorallia occupied a wider temperature range (ca. 0-30 °C), while Scleractinia  
260 occupied waters less than 25 °C (Fig 2g).

261 The individual scleractinian species had slight differences between them: *E.*  
262 *rostrata*, *M. oculata*, *L. pertusa* and *S. variabilis* were restricted to current velocities  
263 lower than 0.5 m s<sup>-1</sup> (Fig 2j) and, together with *C. debilis* were limited to sites with POC  
264 lower than 20 g C<sub>org</sub> m<sup>-2</sup> y<sup>-1</sup> (Fig 2k); *C. debilis* and *Deltocyathus* spp. were found in a  
265 smaller range of dissolved oxygen conditions, between 4.5- and 5.5 ml l<sup>-1</sup> (Fig 2l), and  
266 were found in waters with silicate concentrations < 50 μmol l<sup>-1</sup> (Figure 2m and n,  
267 respectively): *L. pertusa* and *S. variabilis*, that were mainly restricted to < 20 μmol l<sup>-1</sup>  
268 (Fig 2m): *S. variabilis* had the narrowest temperature range, with most occurrences in a  
269 maximum of 10 °C (Fig 2n).

270

### 271 *Variable selection and contribution*

272 Variables with the highest AUC from each category were selected for model  
273 construction, with the exception of aragonite saturation state (AST), which was selected  
274 for Scleractinia and each scleractinian species as they have aragonitic skeletons. Variables  
275 selected for final models of Octocorallia and Scleractinia were the same, with the  
276 exception of the carbonate variable (Table 3). The variables that most contributed to the  
277 final model for Octocorallia were calcite saturation state (CST), dissolved oxygen and  
278 temperature, whereas for Scleractinia were AST, depth and temperature (Table 4).  
279 Variables selected for specific models of *Deltocyathus* spp., *E. rostrata*, *M. oculata* and

280 *L. pertusa* were AST, depth, current velocity, POC, dissolved oxygen, silicate and  
281 temperature (Table 3). Whereas for *C. debilis* oxygen utilization was selected instead of  
282 dissolved oxygen and for *S. variabilis* salinity in place of silicate (Table 3). The final  
283 models demonstrated differences in the three variables that contributed most. *C. debilis*,  
284 *Deltocyathus* spp., *E. rostrata*, *L. pertusa* and *M. oculata* all showed that AST, depth and  
285 temperature were the best contributors for these species, whilst depth, POC and salinity  
286 were best for *S. variabilis* (Table 4).

287

### 288 *Model performance and habitat suitable area*

289 Octocorallia and Scleractinia models performed well, with AUC of 0.9681 and  
290 0.9551 from test data, respectively. The distribution of suitable habitat for Octocorallia  
291 encompassed along the entire Brazilian continental margin, including the Vitória-  
292 Trindade seamount chain and Rio Grande Rise (30°S, 35°W) (Fig 3). Whereas the habitat  
293 suitability distribution of Scleractinia was more restricted to the Central and South area  
294 of Brazil, between 20°S 37°W and 30°S 50°W, including the Rio Grande Rise (Fig 3,  
295 ESM Fig 1 and 2, respectively). Both, Scleractinia and Octocorallia demonstrated an  
296 overlap in suitable habitat within the Central and South region, as well as in the Rio  
297 Grande Rise (Fig 3).

298 The scleractinian species-level models also exhibited acceptable model  
299 performance (Test-AUC: *C. debilis*, 0.9857; *Deltocyathus* spp., 0.9412; *E. rostrata*,  
300 0.997; *L. pertusa*, 0.9902; *M. oculata*, 0.975; *S. variabilis*, 0.9935). Both, *C. debilis* and  
301 *Deltocyathus* spp., demonstrated suitable habitat around the South and Central areas,  
302 between 20°S 40°W and 42°S 23°W, covering a greater area of continental slope, in terms  
303 of bathymetric extent, than reef-forming species (Fig 3, ESM Fig 3 and 4). The reef-  
304 forming species *L. pertusa* and *M. oculata* were concentrated around the Northeast,  
305 Central and South area (ESM Fig 5 and 6), whilst *E. rostrata* and *S. variabilis* were  
306 restricted to the Central and South area, especially the Vitória-Trindade seamount chain  
307 and Campos and Santos Basins (i.e., between 20°S 40°W and 42°S 23°W) (Fig 3 B and  
308 ESM Fig 7 and 8). Most scleractinian species overlapped in predicted suitable habitat in  
309 some regions of the Northeast area (Fig 3 b, i and ii); the Central area (in Vitoria-Trindade  
310 chain) (Fig 3 b, iii); the South area (Fig 3 b, iv); and the Rio Grande rise (Fig 3 b, v).

311

312 *Ecological species niche comparison*

313 Environmental niches of Scleractinia and Octocorallia were determined mainly by  
314 temperature, depth, CST, POC and regional flux (water current velocity) on the principal  
315 component 1 (PC1) and by dissolved oxygen and silicate on the second principal  
316 component (PC2). These two components explained ca. 65.5% and 18.5%, respectively,  
317 of the environmental conditions occupied (Fig 4 c). Octocorals had a wider environmental  
318 niche than Scleractinia, mainly along the PC1, covering 30% and 16% of the  
319 environmental conditions of the region, respectively (Fig 4 a and 4 b). The center of  
320 density of niches were highly differentiated between both groups reflecting the low niche  
321 overlap between Octocorallia and Scleractinia ( $D=0.28$ ) (Table 5).

322 The environmental niche of Scleractinia presented two subcenters; corresponding  
323 to reef-forming and non-reef-forming species (Fig 4 b). The non-reef-forming species,  
324 i.e. *C. debilis* and *Deltocyathus* spp., had their density center displaced to the down-left  
325 indicating that their niches were determined by higher temperature, POC, current  
326 velocity, AST and dissolved oxygen, as well as shallower depths and lower silicate  
327 concentration (Fig 4 d and e). Both species had an environmental niche that covered the  
328 8% of the environmental conditions available in the region. Reef-forming species had the  
329 niche density center displaced to the top-right showing opposite patterns to non-reef-  
330 forming species (Fig 4 f to i). The environmental niche of *E. rostrata*, *L. pertusa*, *M.*  
331 *oculata* and *S. variabilis* covered 4%, 8%, 7% and 5% of the environmental conditions  
332 available in the region, respectively. The similarity niche hypothesis was accepted for  
333 most pairs of scleractinian species in both directions, except for *E. rostrata* compared to  
334 *C. debilis*, *Deltocyathus* spp. to *L. pertusa*, and for *M. oculata* to *S. variabilis*, in both  
335 directions (Table 5). The niche equivalence hypothesis was rejected for all Scleractinia  
336 species.

337

338

339 **DISCUSSION**

340 In this study, we developed habitat suitability distribution models built  
341 specifically for the main CWC taxa found along the Brazilian continental margin. These  
342 results represent significant improvement over previous model predictions for this region,  
343 which were derived from global scale predictions (i.e. Davies et al., 2008; 2011; Yesson  
344 et al., 2012). This improvement is largely determined by the new region-specific  
345 compilation of occurrence records and also the construction of a regional scale model,  
346 which has a higher capability to identify specific niche features as result of the use of a  
347 more focused range of background environmental conditions (Vierod et al., 2014). In  
348 addition, widely distributed species could exhibit regional or local niche differences for  
349 a variety of evolutionary and non-evolutionary reasons (Pianka, 1988; Lesica and  
350 Allendorf, 1995; Leibold et al., 2019) that are not captured in larger scale models.  
351 Representing regional ecological and environmental features allows for a stronger local  
352 predictive power (Osborne and Suarez-Seoane, 2002; Murphy and Lovett-Doust, 2007).  
353 This approach can thus greatly enhance the understanding of CWC habitat suitability  
354 within the Brazilian continental margin and also allowed for an evaluation of the overlap  
355 between the CWCs found within the region.

356 We observed geographical overlap in the predicted suitable habitat for  
357 Octocorallia and Scleractinia, as well as between individual scleractinian species in the  
358 Campos Basin, Santos Basin, Vitória-Trindade chain, Rio Grande rise and Pelotas Basin  
359 (South area). As CWCs constitute high biodiversity habitats in the deep (Henry and  
360 Roberts, 2017), we suggest that these areas may be of special interest, particularly for  
361 biodiversity conservation. This reinforces previous studies that highlight the regional  
362 importance of the Vitória-Trindade chain as a priority area for conservation (Meirelles et  
363 al., 2015; Pinheiro et al., 2015) and addresses the lack of information about the deep-sea  
364 biodiversity in the region. In the Southern area and Rio Grande Rise, however, the  
365 substantial overlap in Octocorallia and Scleractinia habitat suitability needs to be  
366 validated given there are no published presence records of octocorals from the Southern  
367 area, and there are no CWC records from the Rio Grande Rise. This highlights the need  
368 of surveys in these regions, particularly in Rio Grande rise, which could be a site for  
369 future mineral extraction of cobalt crusts, which could impact coral communities and their  
370 associated biodiversity if they are found there.

371           Suitable habitat for *Octocorallia* covered a broad latitudinal range that  
372 encompassed nearly the entire Brazilian continental margin, with large areas of highly  
373 suitable habitat in the Central, North and Northeast areas. In the North area (Amazon  
374 Basin), there was high predicted suitability for *Octocorallia* in the mesophotic region,  
375 which agrees with the many occurrence records (approximately 75%) that were between  
376 50-150 m depth. Their distribution around this region has been recently corroborated by  
377 the observation of several important communities (Cordeiro et al., 2015; Moura et al.,  
378 2016). Even though there are no published records of octocorals in the South area and the  
379 Rio Grande Rise, where our models have shown potentially suitable conditions (Fig 2),  
380 several unpublished records from these areas validate our results (M.V. Kitahara and  
381 P.Y.G. Sumida pers. obs.). The wide distribution of *Octocorallia* was related with a wide  
382 environmental niche breadth, which covered 30% of the available environmental  
383 conditions of the Brazilian continental margin, suggesting that they may be more common  
384 than previously thought.

385           In contrast, *Scleractinia* had a far narrower habitat suitability distribution, mainly  
386 along the Central and South areas of the Brazilian continental margin, and a lower habitat  
387 suitability around the North-east. The deep sea in these three areas is dominated by the  
388 presence of Antarctic Intermediate Water (AIW) (Wilson et al., 2007), which has been  
389 found to be associated with several scleractinian species in this region between 550-1200  
390 m depth (Viana et al., 1998; Sumida et al., 2004; Arantes et al., 2009). The broader habitat  
391 suitability distribution of *Octocorallia* compared to *Scleractinia* can be translated into a  
392 potentially higher tolerance to physical-chemical conditions in the environment by  
393 *Octocorallia* (e.g. mesophotic corals at shallower depths), which generally allows for a  
394 wider geographic distribution (Slatyer et al., 2013).

395           Substrate is a fundamental factor for the settlement of CWC and its availability  
396 strongly control their colonization. Nevertheless, the availability of this information is  
397 generally limited, particularly for big areas as the entire Brazilian continental margin.  
398 Therefore, the realized distribution of corals could be far smaller in area than the potential  
399 one we are presenting here (Guinotte and Davies, 2014; Anderson et al., 2016). CWC that  
400 settle in hard-bottom substrate are likely more restricted than soft-bottom substrate  
401 colonizing species. Then, the larger morphological variety of octocorals, which can  
402 present a peduncle for anchoring in mud and sand (order Pennatulacea), a basal disk for  
403 fixation in hard substrates, or a basal rootlike processes to anchor in sediment substrates

404 (Bayer, 1961), may allow them to inhabit both substrate types. Contrary to Octocorallia,  
405 most scleractinians are restricted to hard-substrate, but some species, such as the cup coral  
406 *Deltocyathus* genus inhabit soft substrates. For instance, octocorals have been observed  
407 colonizing shells and rock fragments due to the scarcity of common hard substrates in the  
408 Amazon Basin (Cordeiro et al., 2015). Whereas in the southeastern area (in Campos  
409 basin), the occurrence of diverse Octocorallia species indicated the presence of both hard  
410 and soft habitats along the continental slope (Arantes et al., 2009). Arantes et al. (2009)  
411 observed co-occurrence of octocorals of both type of substrates and scleractinians in the  
412 middle slope, which corroborates the observed overlap in their suitable distribution (Fig  
413 3 a-i).

414 CST, depth, and temperature accounted for the highest contributions to corals  
415 suitability predictions and agree with findings from previous studies about CWC  
416 distributions (Davies et al., 2008; Dullo et al., 2008; Tittensor et al., 2009; Davies and  
417 Guinotte, 2011). CST and AST have been found to be strong predictors in many CWC  
418 species distribution models, mainly at global scales (Davies et al., 2008; Tittensor et al.,  
419 2009; Davies and Guinotte, 2011; Yesson et al., 2012) and in some specific regions, such  
420 as the Pacific Ocean (Anderson et al., 2016). POC is the main food source for many cold-  
421 water coral species (Kiriakoulakis et al., 2004; 2007), but in this study it was an important  
422 predictor only for *S. variabilis*. POC concentration was relatively low in many areas  
423 where corals were found, as has been observed in other regions, such as in the  
424 Northwestern Pacific (Guinotte and Davies, 2014). Nevertheless, these low values  
425 observed here could be due to the fact that POC was calculated as an annual mean and  
426 would underrepresent important seasonal pulses. For instance, increases in POC resulting  
427 from down-welling events or water movements due to internal waves are important for  
428 some coral species, such as *L. pertusa* (Davies et al., 2009; Purser et al., 2010; van  
429 Oevelen et al., 2016). Silicate environmental conditions have been indicated to have a  
430 negative relationship with *L. pertusa* global distribution (Davies et al., 2008), and a strong  
431 negative correlation with coral species richness (especially within the north-east Pacific)  
432 (Reyes Bonilla and Cruz Piñón, 2002). Low silicate concentration is associated with low  
433 primary productivity waters (Longhurst and Pauly, 1987). Here, silicate was an important  
434 factor to predict species suitability distribution. Silicate was related with depth and could  
435 be an indicator of productivity along the Brazilian continental margin that particularly

436 differentiated the more productive conditions inhabited by Octocorallia compared with  
437 Scleractinia.

438         There were clear differences in environmental niche of the scleractinian species  
439 investigated in this study. Reef-forming species were found in conditions with higher  
440 silicate and depth but in a lower dissolved oxygen concentration range (a minimum of 4.5  
441 ml l<sup>-1</sup>), AST, POC, temperature and regional flow conditions compared with non-reef-  
442 forming species. Non-reef-forming species niches were associated to a larger range of  
443 silicate conditions, regional flow and POC conditions (Fig. 2 and 4). These results suggest  
444 that non-reef-forming species are not limited by environmental conditions as the studied  
445 reef-forming species within the Brazilian continental margin. This is corroborated by their  
446 wide distribution in the neighbor Colombian Caribbean region between 10-153m and 70-  
447 520m, respectively (Santodomingo et al., 2013).

448         Based on the niche conservation theory ecological niches are thought to be more  
449 similar between close-related taxa (reviewed in Wiens and Grahan, 2005). Within both  
450 groups, reef forming and non-reef-forming species, there were significant niche  
451 similarities and differences that were not related with their phylogenetic proximity. For  
452 instance, *E. rostrata* and *M. oculata* are two reef-forming species that present similar  
453 environmental niches and belong to different clades of Scleractinia, i.e., the “Complex”  
454 and “Robust” clades, respectively (Stolarski et al., 2011). On the other hand, *E. rostrata*  
455 and *Deltocyathus* spp., a reef-forming and non-reef-forming species, respectively, are  
456 from the “Complex” clade but presented a non-similar environmental niche. This suggests  
457 that the differentiation between reef-forming and non-reef-forming species could imply a  
458 divergence in the environmental niche, which is likely independent from the evolutionary  
459 divergence of “Complex” and “Robust” clades. The diversity of niche relationships  
460 observed between the studied scleractinian species, with no pattern related with  
461 evolutionary relationships, reflects the complex and poorly understood evolution of  
462 Scleractinia.

463         *L. pertusa*, *M. oculata* and *S. variabilis* and *E. rostrata* are widely considered the  
464 main reef-forming species in the central and south Brazilian areas (Kitahara et al., 2009,  
465 Cavalcanti et al., 2017). In this study, we observed that *E. rostrata* had a predicted  
466 distribution that overlapped with *M. oculata* and *S. variabilis* in the South and Central  
467 area of Brazil, with all having significantly similar niche. This corroborates their role of  
468 reef-forming species in Brazilian waters. It is important to highlight that *E. rostrata*, as



469 well as *S. variabilis*, had a restricted environmental niche (due to inhabit a more restricted  
470 range of temperature, depth, POC, AST and regional flux). Thus, *E. rostrata* and *S.*  
471 *variabilis* niches were quite different to the other species niches, showing a non-similar  
472 niche with *L. pertusa* and *C. debilis*, and with *M. oculata*, respectively. Despite their  
473 restricted niche at regional scale, both species are known to be particularly abundant in  
474 Campos basin (Cavalcanti et al., 2017). *E. rostrata* and *S. variabilis* are more abundant  
475 in the South-west Pacific Ocean, and are infrequently observed in the North Atlantic  
476 (Davies and Guinotte, 2011; Roberts et al., 2006).

477 As discussed for Scleractinia and Octocoralia, substrate habitat type may  
478 determine the real distribution, inside the predicted potential distribution areas of the  
479 scleractinian species. All reef-forming species together with the non-reef-forming *C.*  
480 *debilis* inhabit hard-bottom substrate, whereas *Deltocyathus* spp. inhabit soft-bottom  
481 substrate. For instance, *D. italicus* and *Deltocyathus* sp., solitary species with unattached  
482 bases, were registered in both mid and lower slope in Campos basin (Arantes et al., 2009).  
483 These cup corals can also create large dense fields, as observed in La Foneca canyon by  
484 *Desmophyllum diantus* (Ayma et al., 2019; Lastras et al., 2019), providing hard substrata  
485 and increasing local biodiversity. This indicates that diverse kind of VME are likely  
486 distributed along the Brazilian continental margin. Particularly in the central and south  
487 areas, were a high number of species share habitat suitability (Fig 2 b - ii and iv).

488 Species niche properties as niche breadth are indicators of species sensitivity  
489 (Kotiaho et al., 2005; Thuiller et al., 2005) and generally, species with a restricted or  
490 smaller niche, have been shown to be more sensitive to the loss of habitat caused by  
491 disturbances such as those produced by climate change (e.g., fish: Munday, 2004; birds:  
492 Seane and Carrascal, 2008). Given that *E. rostrata* and *S. variabilis* had smaller niches  
493 than other species in this study, they may be the most sensitive species to variations in  
494 environmental conditions. Conversely, those species with a wider environmental niche,  
495 such as *C. debilis*, *Deltocyathus* spp., *L. pertusa* and *M. oculata* may be less sensitive to  
496 environmental changes. Despite this assumption, some species could be overly  
497 susceptible to changes in one particular environmental factor. For instance, *C. debilis* is  
498 likely to be more sensitive to changes in the dissolved oxygen and silicate concentration  
499 than to other factors studied (Fig 4d). Specific biological traits, such as acclimatization or  
500 adaptive capacity will also influence the species response to environmental changes. For  
501 example, *L. pertusa* has a higher acclimatization capacity to lower temperature than *M.*

502 *oculata* (Naumann et al., 2014). However, *M. oculata* fossils indicate a wider tolerance  
503 to changes in environmental conditions than *L. pertusa* in the Gulf of Cádiz (Wienberg et  
504 al., 2009). Specific experimental research of organisms inhabiting different regions are  
505 fundamental to understanding their ecological niche, physiology and additional sources  
506 of uncertainty that might influence their survival under future environmental  
507 disturbances.

508

#### 509 *Approach limitations*

510 Whilst habitat suitability modeling has been widely used to determine the  
511 potential distribution of deep-sea species (e.g., Guinotte et al., 2010; Davies and Guinotte,  
512 2011; Tracey et al., 2011; Yesson et al., 2012), there are still limitations that should be  
513 considered during the modeling approach (Vierod et al., 2014, Anderson et al., 2016). For  
514 example, a regularly spaced sampling regime that covers the entirety of the environmental  
515 conditions observed in the region of interest is important (Hirzel and Guisan, 2002).  
516 Independent species presence and/or absence data is also an important aid for model  
517 validation (Anderson et al., 2016). However, deep-sea surveys with this characteristic are  
518 extremely limited due to high cost and significant logistical restrictions such as access to  
519 both ship-time and high-quality sampling equipment. These limitations lead to a  
520 disproportionate effect on sampling quality in some regions, particularly in areas such as  
521 the South Atlantic Ocean, where many countries have restricted access to ocean-going  
522 research vessels. In this study, the focus on the collection of new region-specific  
523 occurrences that were not present within international datasets led to substantial  
524 improvements in the quality and utility of predictions in this region. Nevertheless, future  
525 surveys must be carried out in order to validate the present predictions, principally in the  
526 North and Northeast areas for scleractinian and in the South area to octocorals.

527 It is essential to note that this study only presents suitable areas, which are  
528 statistically likely to contain species presences based upon the environmental data used  
529 in the models. There will be other variables or factors that were not included in the  
530 analysis which could influence these predictions, such as substrate availability and type.  
531 Hard substrate presence is highly variable over small spatial scales and is a strong  
532 constraining variable that limits the distribution of many coral species (Davies and  
533 Guinotte, 2011; Tracey et al., 2011; Guinotte and Davies, 2014; Mackay et al., 2014). For

534 example, suitable predicted areas for reef-forming species in the flat tops of some  
535 seamounts in the South Pacific, were dominated by sand, an unsuitable substrate for most  
536 stony coral species settlement (Anderson et al., 2016). Furthermore, the SRTM30  
537 bathymetry data have shown to overestimate suitable area for some deep-sea corals  
538 (Marshall, 2011; Ross et al., 2015), particularly in regions where local bathymetric data  
539 does not exist (Anderson et al., 2016). Better local surveys and the collection of high-  
540 resolution bathymetric data will improve bathymetric representation. This may provide a  
541 representation of sea-bed physiographical features of importance for the presence of  
542 corals and provide the potential for the elucidation of substrate type, which will  
543 substantially improve regional and local habitat suitability models (e.g., Howell et al.,  
544 2011; Rengstorf et al., 2013; 2014; García-Alegre et al., 2014; Georgian et al., 2014).

545

#### 546 *Conclusions*

547         The information presented in this study represents the first regional scale habitat  
548 suitability modelling effort for CWCs along the Brazilian margin. This study represents  
549 a fundamental step in better understanding the distribution of Brazilian CWCs and  
550 provides essential information to guide future surveys and conservations plans in the  
551 region. For instance, future surveys must be oriented to describe the presence of both,  
552 octocorals and scleractinians corals, to validate the predictions, mainly where suitability  
553 is observed with no presence records. Based upon the areas of predicted suitable habitats  
554 for CWC, we highlight the importance of management plans that combine the oil and gas  
555 exploration areas with conservation and mitigation of potential impacts to these  
556 communities in Campos Basin, Santos Basin, Vitoria-Trindade chain, Rio Grande rise  
557 and Pelotas Basin (South area). Particularly, the Rio Grande Rise area must be  
558 characterized in terms of biodiversity composition, since it contains cobalt crusts and a  
559 possible future extraction of minerals could impact coral communities that may be  
560 currently unknown. The broader habitat suitability distribution of Octocorallia compared  
561 to Scleractinia is related to a broader environmental niche breadth, likely due to the  
562 variety of physiological adaptations of this group. Non-reef-forming scleractinian species  
563 were less restricted by environmental conditions, when compared to reef-forming species,  
564 allowing them to potentially inhabit a broader area of the Brazilian continental margin.  
565 Most reef-forming species presented similar but not equivalent ecological niche,  
566 indicating that management planning, conservation efforts and cruise planning should

567 consider the species individual environmental requirements to be more efficient. For  
568 instance, priority consideration may need to be given to *S. variabilis* and *E. rostrata* since  
569 they had smaller niche breadth and may be more sensitive to changes in the environment.

570

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893

894 FIGURES AND TABLES

895 **Figure 1.** (a) Overview of the study area localization. (b) The Brazilian continental  
896 margin with the CWC presence points of Octocorallia and Scleractinia (light blue and  
897 light grey, respectively), in the focal areas used in the present study. The boundaries of  
898 the Brazilian EEZ along the Brazilian coast are represented by the grey line.

899 **Figure 2.** Kernel density curves of the environmental conditions occupied by corals from  
900 the Brazilian continental margin. Octocorallia (dotted line) and Scleractinia (continuous  
901 line) are shown to the left of the figure, and *Cladocora debilis* (black dotted line),  
902 *Deltocyathus* spp. (yellow dotted line), *Enallopsammia rostrata* (red line), *Lophelia*  
903 *pertusa* (dark green line), *Madrepora oculata* (grey line), and *Solenosmilia variabilis*  
904 (blue line), to the right. Carbonate condition represent aragonite saturation state ( $\Omega$ ) for  
905 Scleractinia and scleractinian species, and calcite saturation state for Octocorallia.

906

907 **Figure 3.** Potential distribution areas and the overlap between the different taxa. A)  
908 Octocorallia (light blue) and Scleractinia group (blue) with their overlapped area (marine  
909 blue). Main overlapping areas: Central area, Rio Grande rise, South area; B) Scleractinian  
910 species (*Cladocora debilis*, *Deltocyathus* spp., *Enallopsammia rostrata*, *Lophelia*  
911 *pertusa*, *Madrepora oculata* and *Solenosmilia variabilis*) overlap, showed as the number  
912 of species potentially distributed in the same area, along the Brazilian continental margin.  
913 Areas with higher number of species potentially distributed there: north of the Northeast  
914 score in front of the Rio Grande do Norte state, ii) east slope of the Northeast area in front  
915 of Bahia state, Central area, including the margins of submersed islands of the Vitoria-  
916 Trindade chain, South area, from Cape of São Tomé to 30° S in Rio Grande do Sul state,  
917 and Rio Grande rise, in Southwestern Atlantic International waters. Potential distribution  
918 areas are represented with the maximum sensitivity plus specificity test threshold.

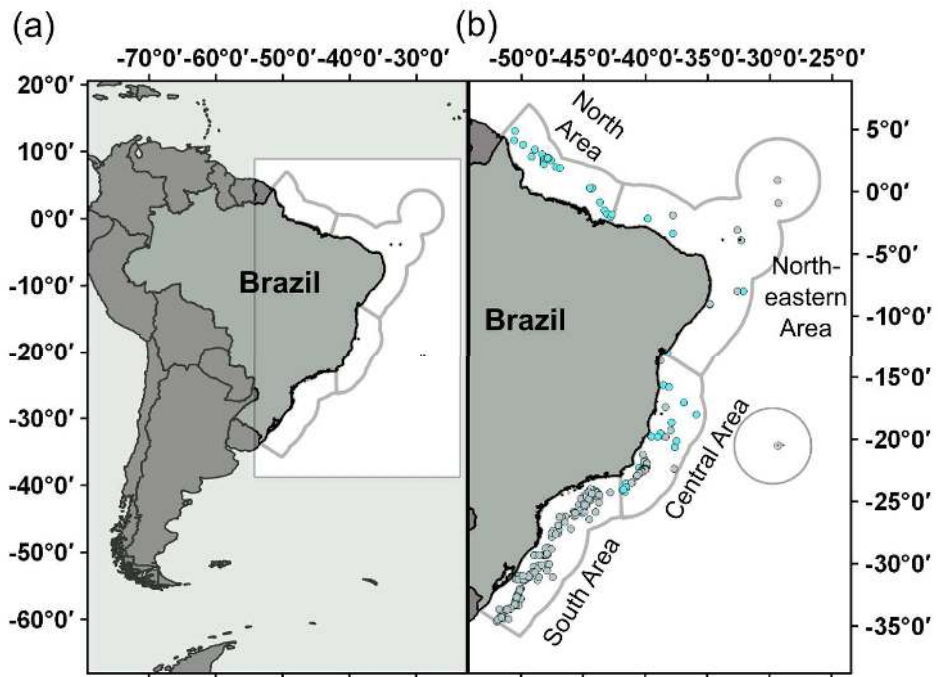
919

920 **Figure 4.** Ecological niche of the cold-water coral species studied in the environmental  
921 space produced by the principal component analysis method and the variables  
922 contribution for loading their two principal components (PC) (c). The results represent  
923 the niche of the species in the two main axes determining different environmental  
924 condition. The grey to black shading represents the grid cell Kernel density of the species  
925 occurrences, black being the highest density. Dashed lines represent the 50% of the  
926 available environmental conditions in the Brazilian continental margin, and the solid line

927 represent the 100%. Red arrows connect density center of the species niche to the density  
928 center of Scleractinia and illustrate their differences. In (c), POC in abbreviation for  
929 particulate organic carbon and AST, aragonite saturation state.

930

931





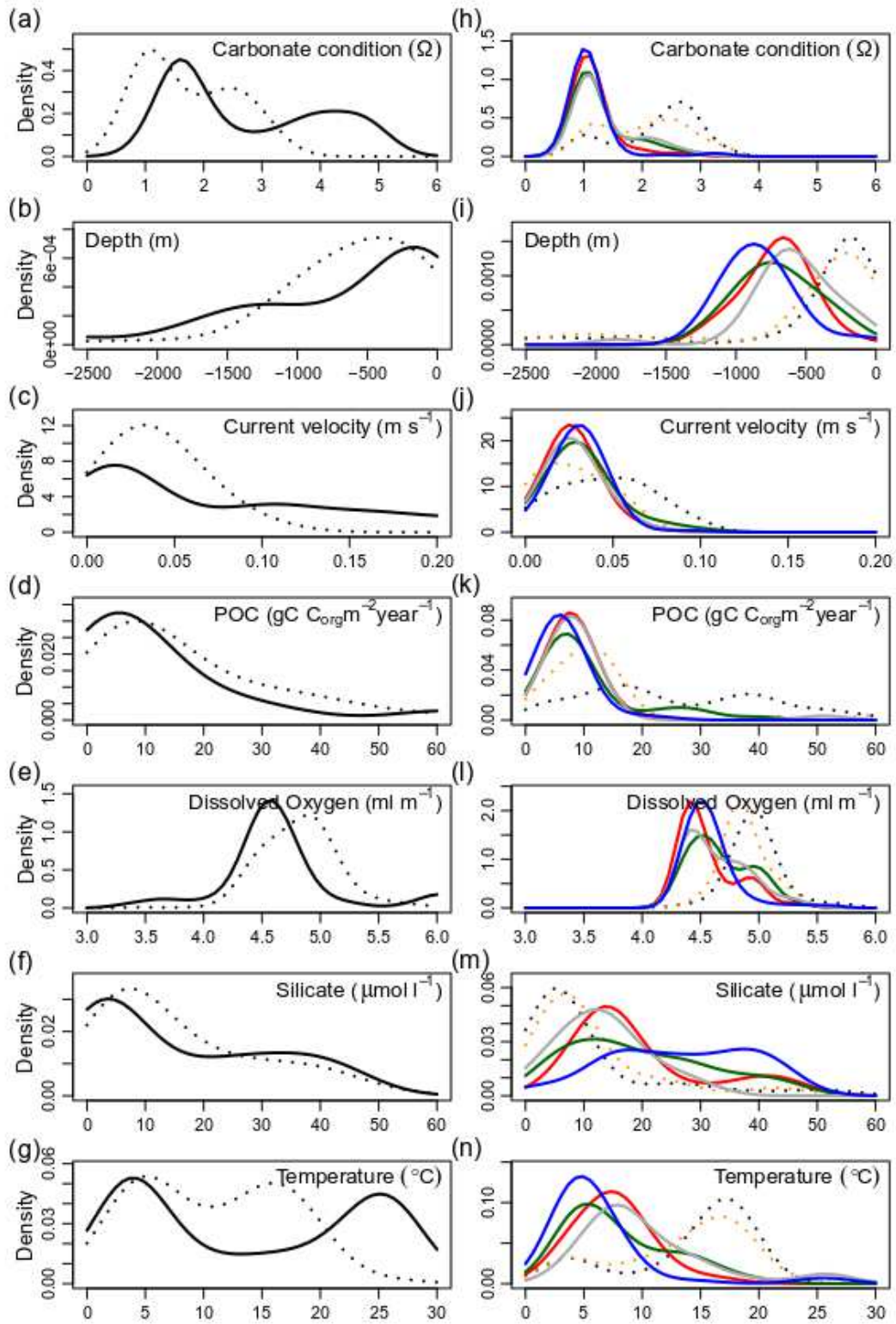


Figure 3

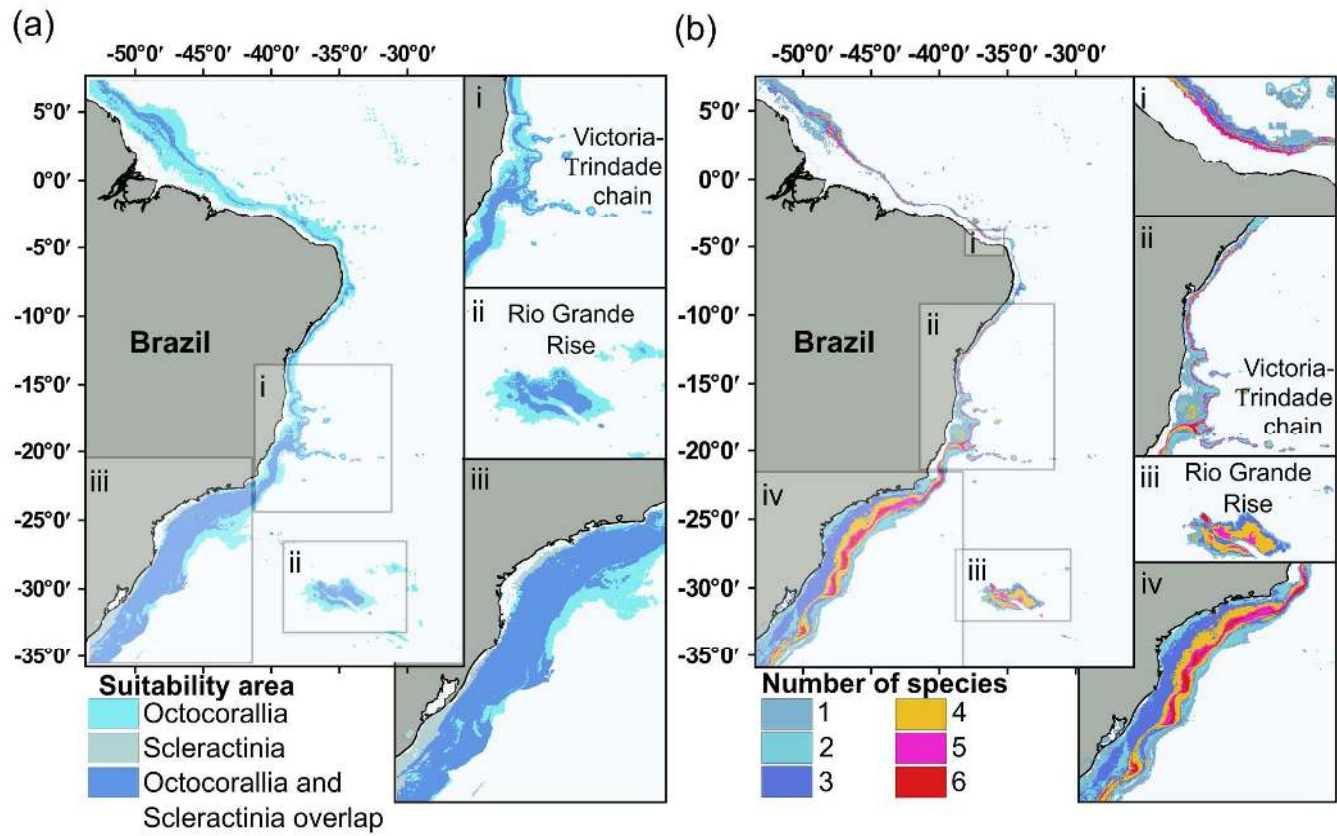
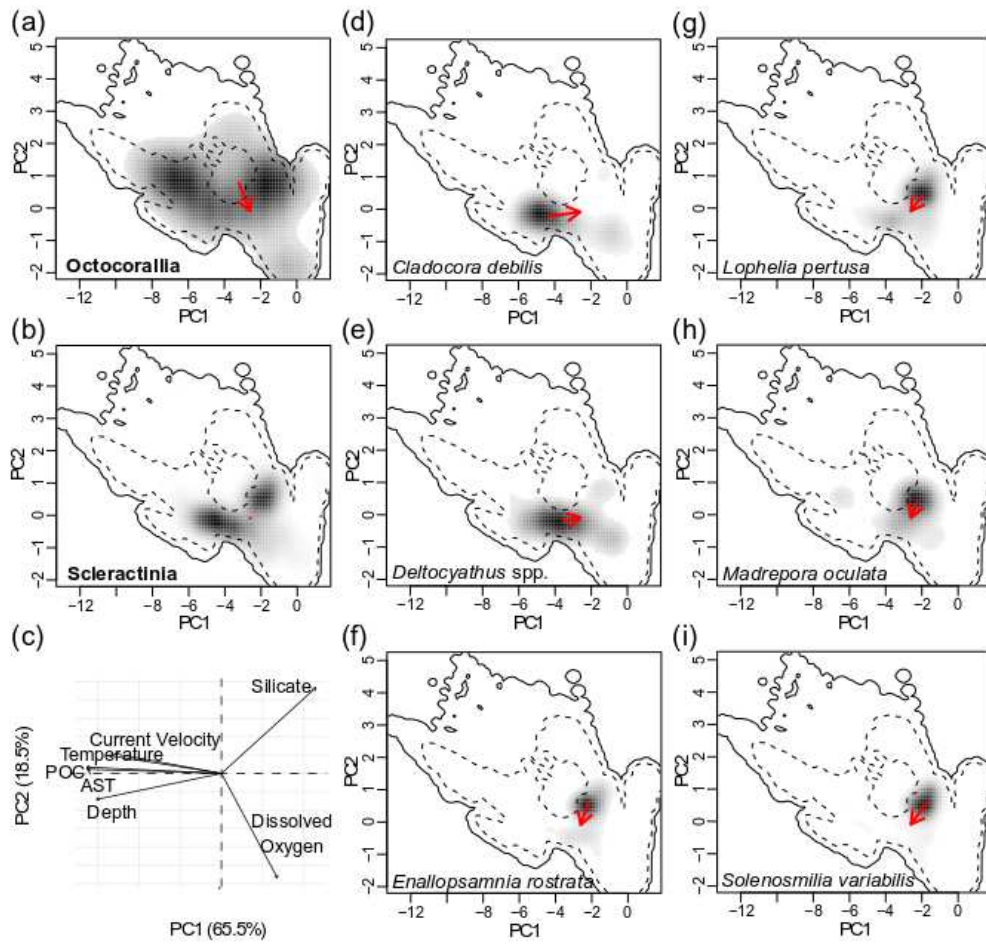


Figure 4



**Table 1.** Number of occurrence records of azooxanthellate corals from the Brazilian continental margin and slope, including historical records from published sources (see references in supplementary Table 1) and new scleractinian records from Cavalcanti et al. (2017), and the filtered total number of records (with one record for analysis cell) that were used to model habitat suitability.

<b>Taxonomic group</b>	<b>Historical records</b>	<b>New records</b>	<b>Total records used in models</b>
<b>Order Scleractinia</b>	396	1147	259
<b>Subclass Octocorallia</b>	151		60
<b>Species</b>			
<i>Cladocora debilis</i>	57		54
<i>Deltocyathus</i> spp.	36		33
<i>Enallopsammia rostrata</i>	8	222	33
<i>Lophelia pertusa</i>	77	342	75
<i>Madrepora oculata</i>	21	97	29
<i>Solenosmilia variabilis</i>	26	486	72

**Table 2.** Environmental variables used to the variables selection divided in seven categories: carbonate variables (CARB), bathymetric variables (BATH), hydrodynamic variables (HYDRO), productivity variables (PROD), oxygen variables (OXY), chemical variables (CHEM), and temperature (TEMP).

	VARIABLE	NAME	REFERENCE	UNIT
<b>CARB</b>	Aragonite saturation state	arag_orr	Orr et al. (2005)	$\Omega_{ARAG}$
	Aragonite saturation state	arag_stein	Steinacher et al. (2009)	$\Omega_{ARAG}$
	Calcite saturation state	cal_orr	Orr et al. (2005)	$\Omega_{CALC}$
	Calcite saturation state	cal_stein	Steinacher et al. (2009)	$\Omega_{CALC}$
<b>BATH</b>	Aspect	aspect	Jenness (2013)	degrees
	Aspect- Eastness	eastness	Wilson et al. (2007)	-
	Aspect- Northness	northness	Wilson et al. (2007)	-
	Curvature - Plan	plancurve	Jenness (2013)	-
	Curvature - Profile	profilecurve	Jenness (2013)	-
	Curvature - Tangential	tangcurv	Jenness (2013)	-
	Roughness	roughness	Wilson et al. (2007)	-
	Rugosity	rugosity	Jenness (2013)	-
	Slope	slope	Jenness (2013)	degrees
	Bathymetry	srtm30	Becker et al. (2009)	m
	Terrain Ruggedness Index	tpi	Wilson et al. (2007)	-
Topographic Position Index	tri	Wilson et al. (2007)	-	
<b>HYDRO</b>	Current velocity	regfl	Carton et al. (2005)	$m s^{-1}$
	Vertical current velocity	verfl	Carton et al. (2005)	$m s^{-1}$
<b>PROD</b>	Seasonal index variation	lutzs	Lutzs et al. (2007)	-
	Primary productivity (maximum)	modismax	NASA Ocean Color	$g C m^{-2} y^{-1}$
	Primary productivity (mean)	modismean	NASA Ocean Color	$g C m^{-2} y^{-1}$
	Primary productivity (minimum)	modismin	NASA Ocean Color	$g C m^{-2} y^{-1}$
	Particulate carbon	Organic poc	Lutz et al. (2007)	$g C_{org} m^{-2} y^{-1}$
	Primary Productivity (Vertically generalised productivity model)	vpgmean	Behrenfeld & Falkowski (1997)	$g C m^{-2} y^{-1}$
<b>OXY</b>	Apparent utilisation	oxygen oaxu	Garcia et al. (2006)	$mol O_2$
	Percent saturation	oxygen poxs	Garcia et al. (2006)	$\% O_2$
	Dissolved oxygen	disso2	Garcia et al. (2006)	$ml l^{-1}$
<b>CHEM</b>	Nitrate	nit	Garcia et al. (2006)	$\mu mol l^{-1}$
	Phosphate	phos	Garcia et al. (2006)	$\mu mol l^{-1}$
	Salinity	sal	Boyer et al. (2005)	PSS
	Silicate	sil	Garcia et al. (2006)	$\mu mol l^{-1}$
<b>TEMP</b>	Temperature	temp	Boyer et al. (2005)	$^{\circ}C$

**Table 3.** Test AUC values for Maxent model of Octocorallia and Scleractinia taxa and for six scleractinian species in the Brazilian continental margin, based in a single variable. A value close to 0.5 indicates a model no better than a random prediction, values greater than this and closer to 1 indicate models with better predictive power. A value of 1 indicates a theoretically perfect model. Values in bold indicate the main variable of each categorical group and which were selected to run the final models with the exception of arag\_orr which was used to Scleractinia and the scleractinian species due their ecological importance (See section 2.2. Variables selection and contribution). Category and variable name abbreviations are presented in Table 2.

	VARIABLE	SCLERACTINIA	OCTOCORALLIA	<i>C. DEBILIS</i>	<i>DELTOCYA THUS SPP.</i>	<i>E. ROSTRATA</i>	<i>L. PERTUSA</i>	<i>M. OCULATA</i>	<i>S. VARIABILIS</i>
<b>CARB</b>	arag_orr	<b>0.9525</b>	0.9248	<b>0.9671</b>	<b>0.953</b>	<b>0.9612</b>	<b>0.9624</b>	<b>0.9586</b>	<b>0.9604</b>
	arag_stein	0.9562	0.9233	0.9691	0.9234	0.9588	0.9427	0.9757	0.9135
	cal_orr	0.9579	<b>0.9269</b>	0.9663	0.9524	0.9648	0.9634	0.9637	0.9736
	cal_stein	0.9567	0.9206	0.9697	0.9255	0.9642	0.9487	0.9763	0.9256
<b>BATH</b>	srtm30	<b>0.9664</b>	<b>0.9311</b>	<b>0.9737</b>	<b>0.9659</b>	<b>0.9913</b>	<b>0.9877</b>	<b>0.9951</b>	<b>0.9885</b>
	roughness	0.5204	0.5195	0.475	0.6183	0.6258	0.5883	0.5	0.6505
	rugosity	0.5518	0.6296	0.5243	0.6131	0.3548	0.5759	0.3915	0.6288
	slope	0.599	0.7215	0.4622	0.5222	0.7734	0.7702	0.8024	0.756
	TPI	0.7852	0.5012	0.7461	0.782	0.8196	0.7119	0.9248	0.8564
	TRI	0.7088	0.483	0.6351	0.5874	0.7472	0.6516	0.8489	0.7573
	aspect	0.7332	0.4834	0.6824	0.7362	0.7748	0.6292	0.8729	0.744
	eastness	0.4767	0.5079	0.4937	0.5686	0.431	0.6141	0.5	0.6238
	northeness	0.5467	0.6074	0.5552	0.6484	0.4031	0.5142	0.5	0.5696
	plancurve	0.602	0.7327	0.4447	0.5135	0.763	0.7649	0.8147	0.7787
	longcurve	0.7057	0.7277	0.4079	0.5455	0.7977	0.7677	0.8069	0.7629
tangcurve	0.5981	0.7435	0.4055	0.5352	0.7673	0.7676	0.8106	0.7608	
<b>HY</b>	regfl	<b>0.8705</b>	<b>0.9231</b>	<b>0.9187</b>	<b>0.7648</b>	<b>0.9422</b>	<b>0.8762</b>	<b>0.9566</b>	<b>0.8705</b>
	verfl	0.7004	0.6403	0.33	0.2592	0.743	0.2374	0.7354	0.5
<b>PROD</b>	lutzs	0.8487	0.7848	0.947	0.9316	0.9044	0.8349	0.9645	0.7948
	modismax	0.8086	0.8456	0.9491	0.7766	0.9128	0.8689	0.9669	0.8357
	modismean	0.8351	0.8334	0.9498	0.8157	0.9265	0.9004	0.9779	0.8681
	modismin	0.8086	0.8456	0.9491	0.7766	0.9128	0.8689	0.9669	0.8357
	POC	<b>0.9369</b>	<b>0.8621</b>	<b>0.9662</b>	<b>0.9555</b>	<b>0.9878</b>	<b>0.9727</b>	<b>0.9931</b>	<b>0.978</b>
	vgpmean	0.8439	0.809	0.9544	0.8389	0.9449	0.8847	0.9706	0.8819
<b>OXY</b>	aoux	0.8195	0.8954	<b>0.9126</b>	0.677	0.6107	0.7846	0.6575	0.6625
	disso2	<b>0.8913</b>	<b>0.939</b>	0.8654	<b>0.8969</b>	<b>0.9083</b>	<b>0.9375</b>	<b>0.9671</b>	<b>0.9477</b>
	poxs	0.7796	0.8992	0.894	0.6299	0.5998	0.7486	0.4196	0.7295
	dic_stein	0.8889	0.9214	0.9345	0.7986	0.8179	0.7632	0.9426	0.6993
	nit	0.8281	0.8829	0.8761	0.7474	0.5964	0.8172	0.6385	0.6625

<b>CHEM</b>	phos	0.8442	0.9249	0.8669	0.8148	0.6673	0.868	0.6667	0.7377
	sal	0.8962	0.9082	0.8425	0.6082	0.784	0.8779	0.5401	<b>0.9445</b>
	sil	<b>0.9145</b>	<b>0.9273</b>	<b>0.9422</b>	<b>0.8868</b>	<b>0.9312</b>	<b>0.9158</b>	<b>0.9782</b>	0.8753
<b>TEMP</b>	temp	<b>0.9618</b>	<b>0.9309</b>	<b>0.9678</b>	<b>0.953</b>	<b>0.9855</b>	<b>0.9825</b>	<b>0.9951</b>	<b>0.9776</b>

**Table 4.** Test AUC values for Scleractinia, Octocorallia and six different scleractinian species models, based in a single variable model. Values corresponding to the three most significant variables for each taxon are in bold. Variable name abbreviations are presented in Table 2.

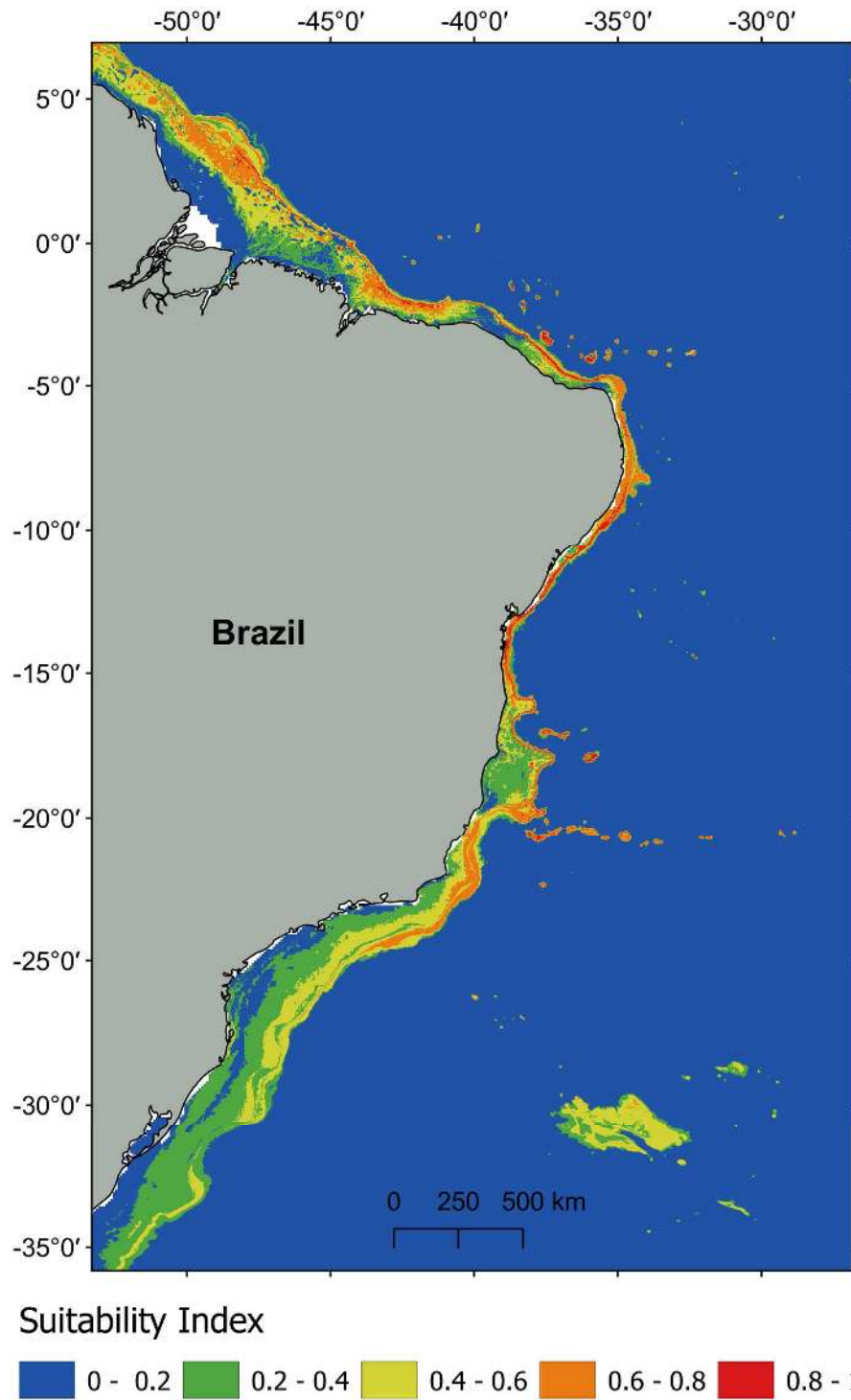
	<i>Scleractinia</i>	<i>Octocorallia</i>	<i>C. debilis</i>	<i>L. pertusa</i>	<i>M. oculata</i>	<i>S. variabilis</i>	<i>E. rostrata</i>	<i>Deltocyathus spp.</i>
<b>AUC</b>								
calc-orr		<b>0.9403</b>						
arag-orr	<b>0.9457</b>		<b>0.9694</b>	<b>0.9565</b>	<b>0.9543</b>	0.9671	<b>0.9403</b>	<b>0.9683</b>
srtm30	<b>0.9518</b>	<b>0.9492</b>	<b>0.9784</b>	<b>0.9882</b>	<b>0.9812</b>	<b>0.9877</b>	<b>0.9493</b>	<b>0.9595</b>
regfl	0.8812	0.8234	0.9223	0.8743	0.916	0.8874	0.8234	0.6203
POC	0.9214	0.8326	0.9685	0.9335	0.8644	<b>0.9748</b>	0.8326	0.9434
diso2	0.8941	0.9206		0.934	0.8869	0.9431	0.9206	0.8913
aoxu			0.8877					
sil	0.8864	0.8639	0.9358	0.9088	0.9527		0.8639	0.9484
sal						<b>0.9905</b>		
temp	<b>0.9424</b>	<b>0.9281</b>	<b>0.9698</b>	<b>0.98</b>	<b>0.9761</b>	0.969	<b>0.9281</b>	<b>0.9635</b>



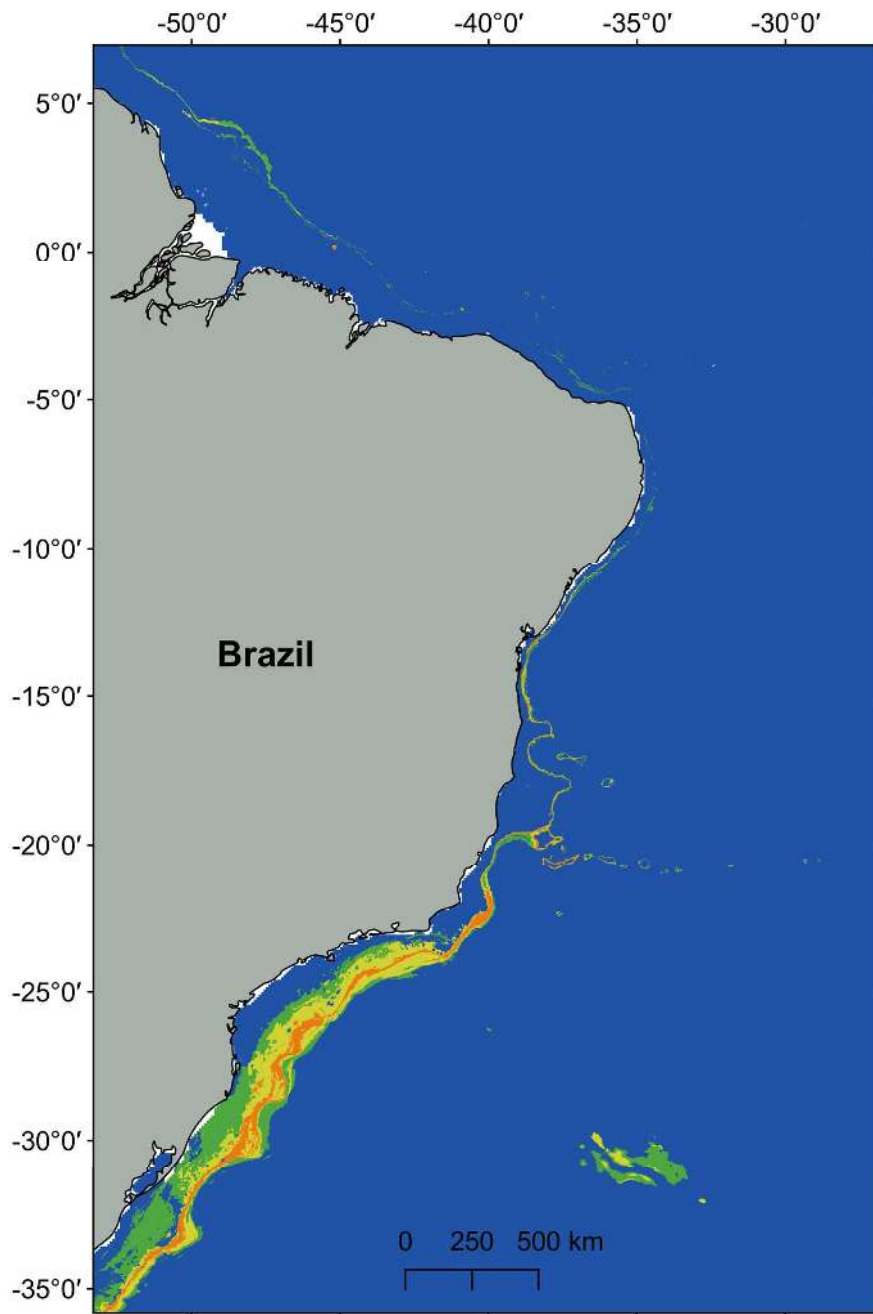
**Table 5.** Niche comparison for cold water corals in the Brazilian continental margin. Niche overlap values Schoener's *D* (Schoener, 1970; Broennimann et al., 2012) and the significance of similarity and equivalence tests are giving for each pair-wise comparison (ns: not significant). The higher overlap value is presented in bold and the lowest in italics.

Táxon		Niche Overlap ( <i>D</i> )	Niche similarity <i>y</i>	Niche equivalence
<i>a</i>	<i>b</i>		<i>a - b</i> and <i>b - a</i>	
<i>C. debilis</i>	<i>Deltocyathus</i> spp.	<b>0.89</b>	Similar	Different
	<i>E. rostrata</i>	0.01	ns	Different
	<i>L. pertusa</i>	0.72	Similar	Different
	<i>M. oculata</i>	0.32	Similar	Different
	<i>S. variabilis</i>	0.008	Similar	Different
<i>Deltocyathus</i> spp.	<i>E. rostrata</i>	0.04	ns	Different
	<i>L. pertusa</i>	0.80	Similar	Different
	<i>M. oculata</i>	0.40	Similar	Different
	<i>S. variabilis</i>	0.035	Similar	Different
<i>E. rostrata</i>	<i>L. pertusa</i>	0.21	ns	Different
	<i>M. oculata</i>	0.48	Similar	Different
	<i>S. variabilis</i>	0.77	Similar	Different
<i>L. pertusa</i>	<i>M. oculata</i>	0.57	Similar	Different
	<i>S. variabilis</i>	0.20	Similar	Different
<i>M. oculata</i>	<i>S. variabilis</i>	0.41	ns	Different
<b>Octocorallia</b>	Scleractinia	0.28	ns	Different

Electronic supplementary materials



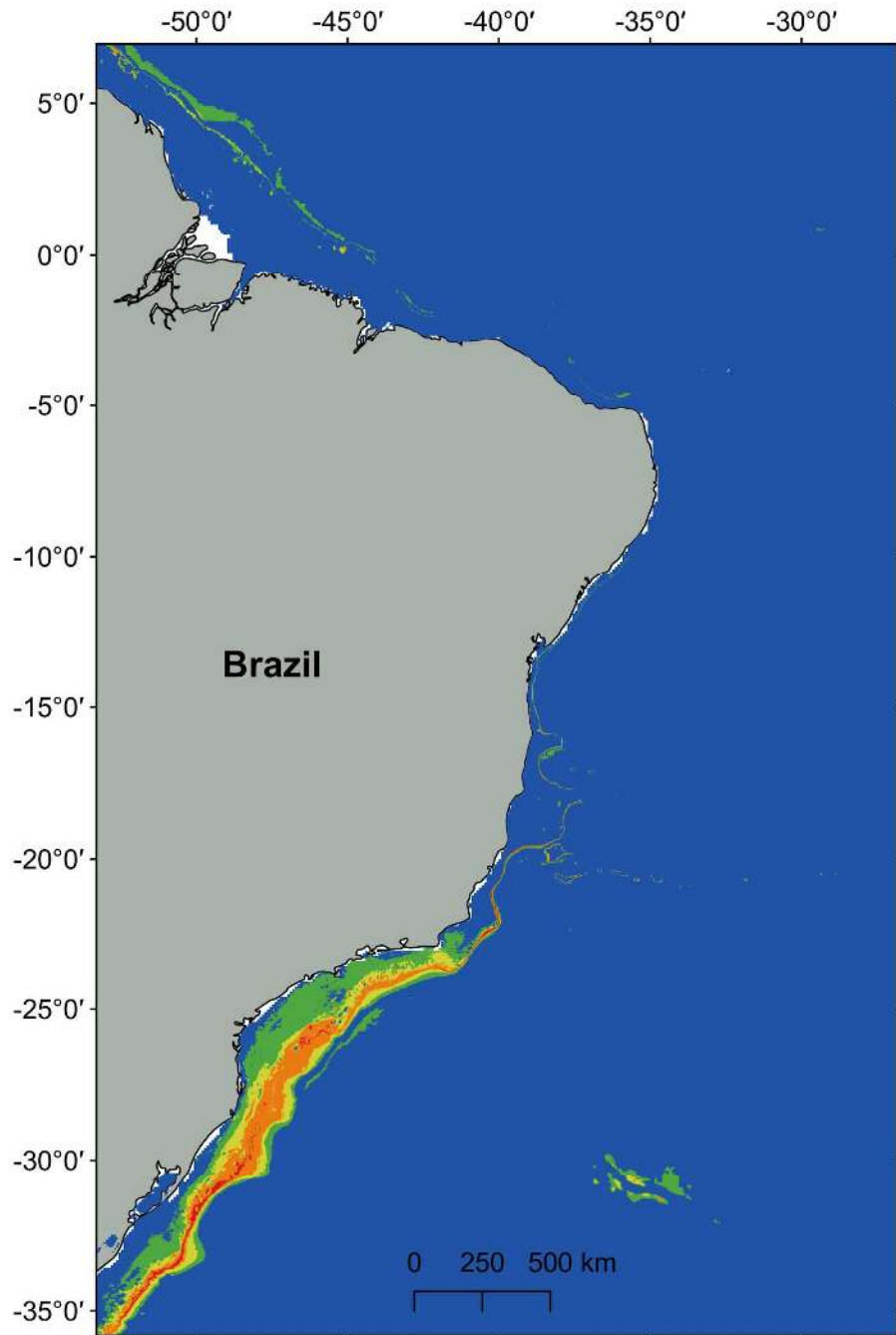
**Figure 1.** Habitat suitability prediction for Octocorallia in the southwest Atlantic Ocean. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



**Suitability Index**



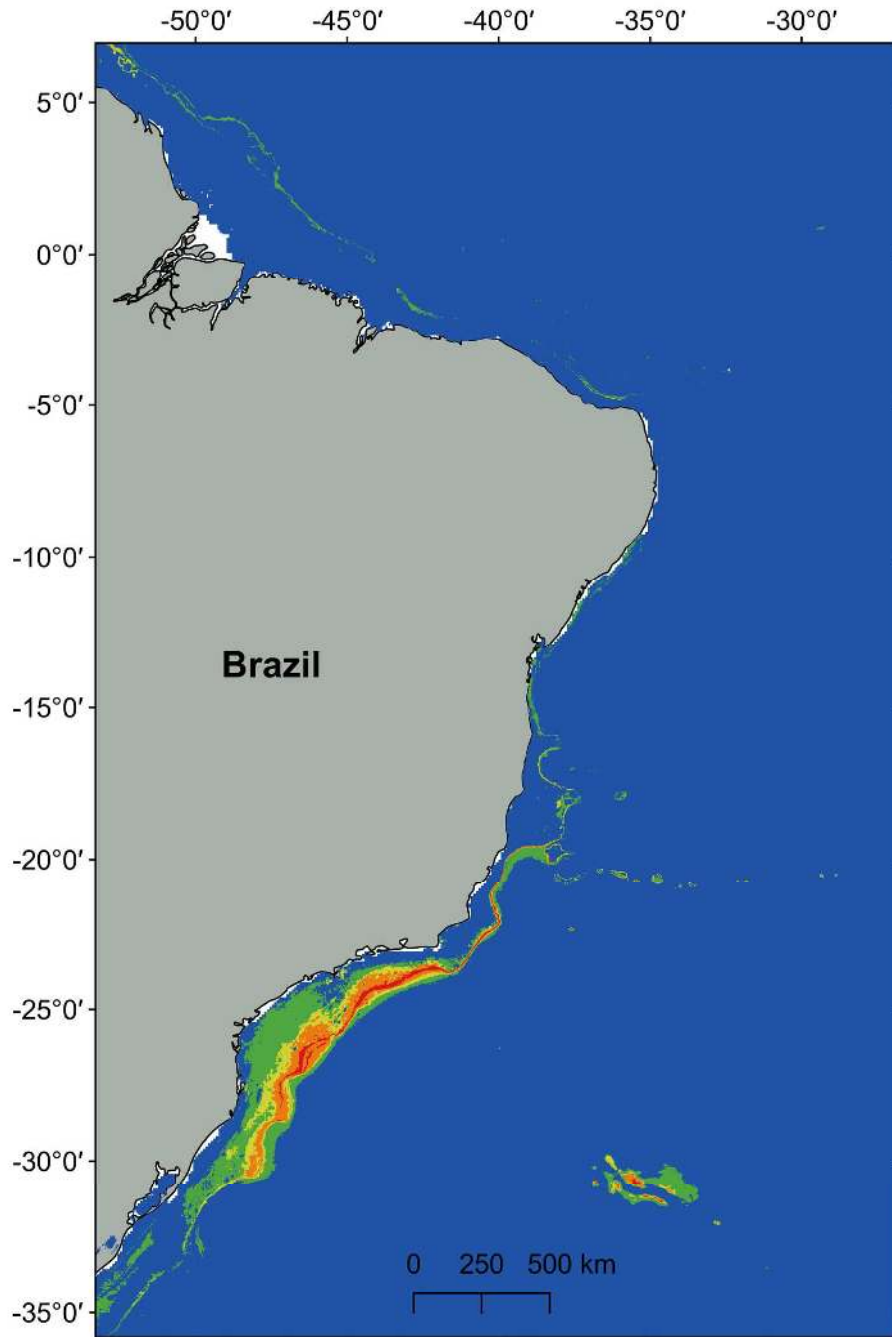
**Figure 2.** Habitat suitability prediction for Scleractinia in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



### Suitability Index



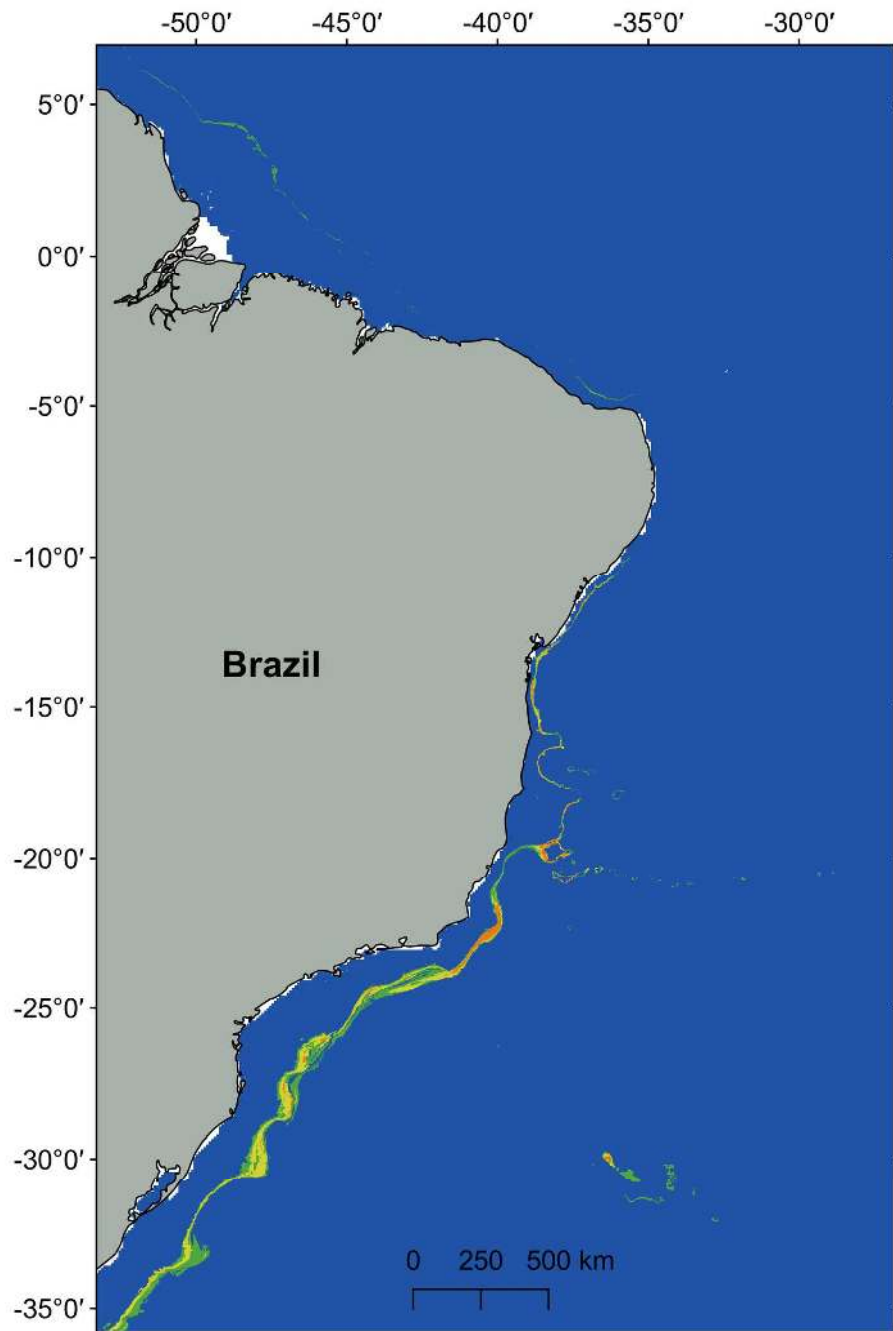
**Figure 3.** Habitat suitability prediction for *Cladocora debilis* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



**Suitability Index**



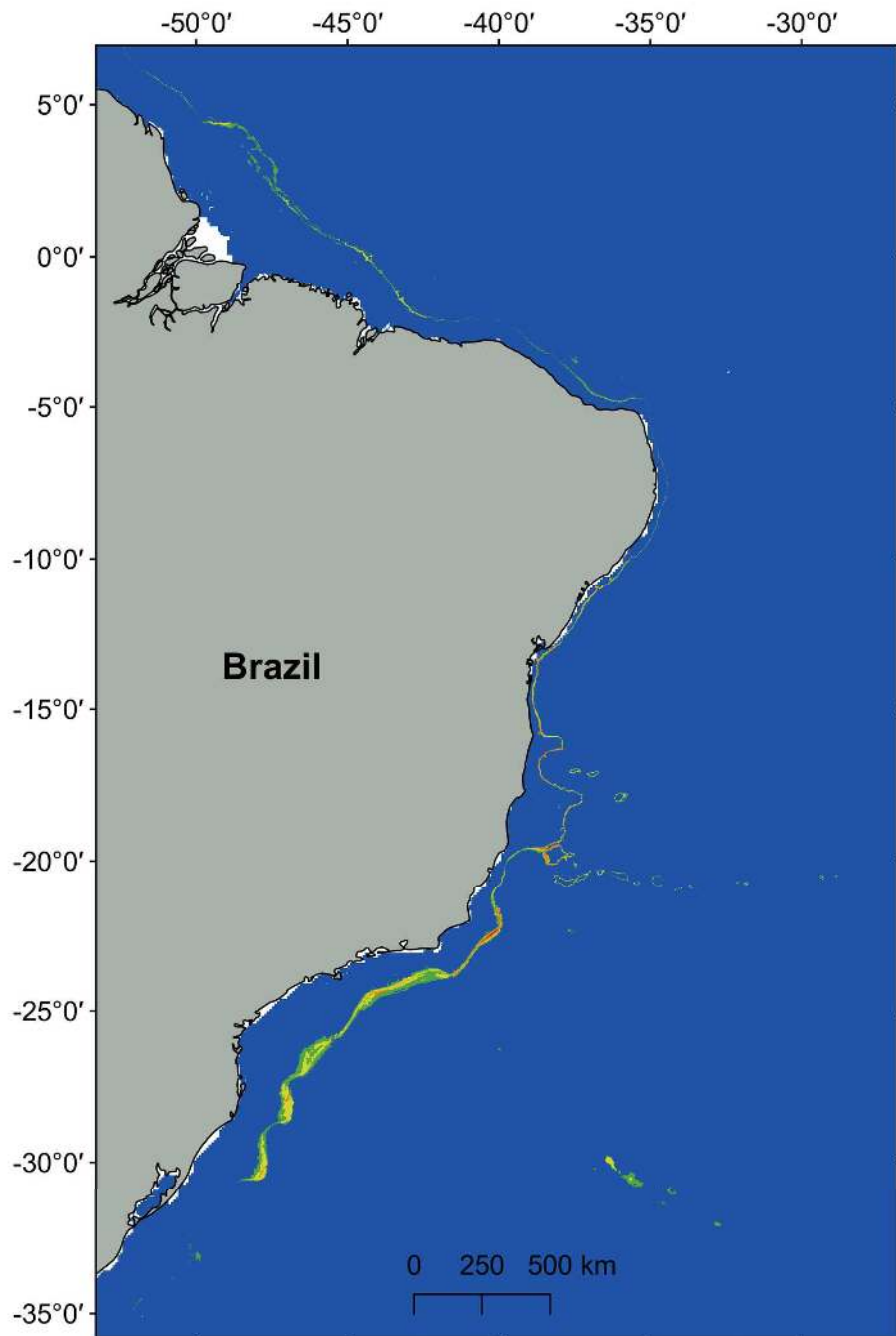
**Figure 4.** Habitat suitability prediction for *Deltocyathus* spp. in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



**Suitability Index**



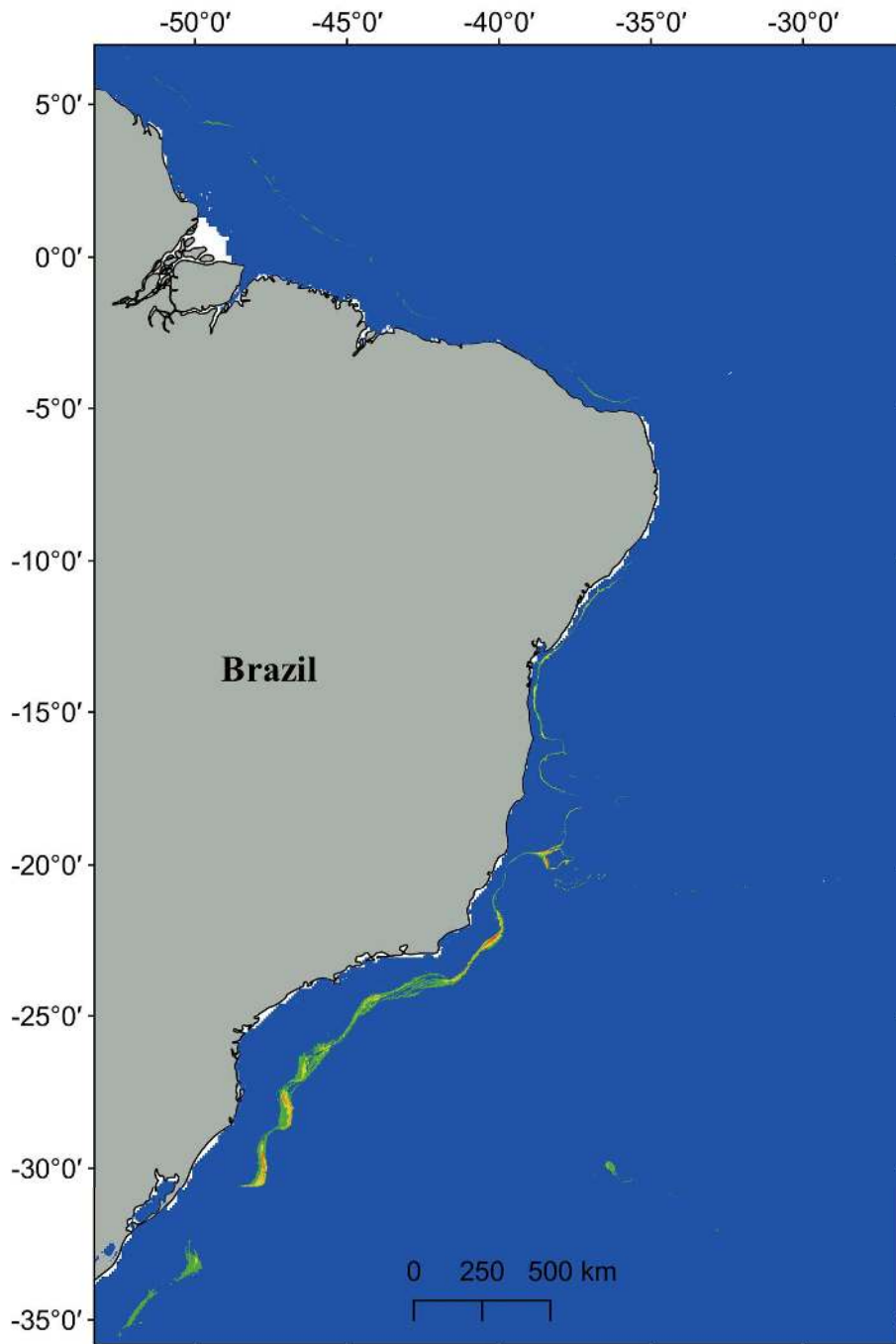
**Figure 5.** Habitat suitability prediction for *Lophelia pertusa* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



Suitability Index



**Figure 6.** Habitat suitability prediction for *Madrepora oculata* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

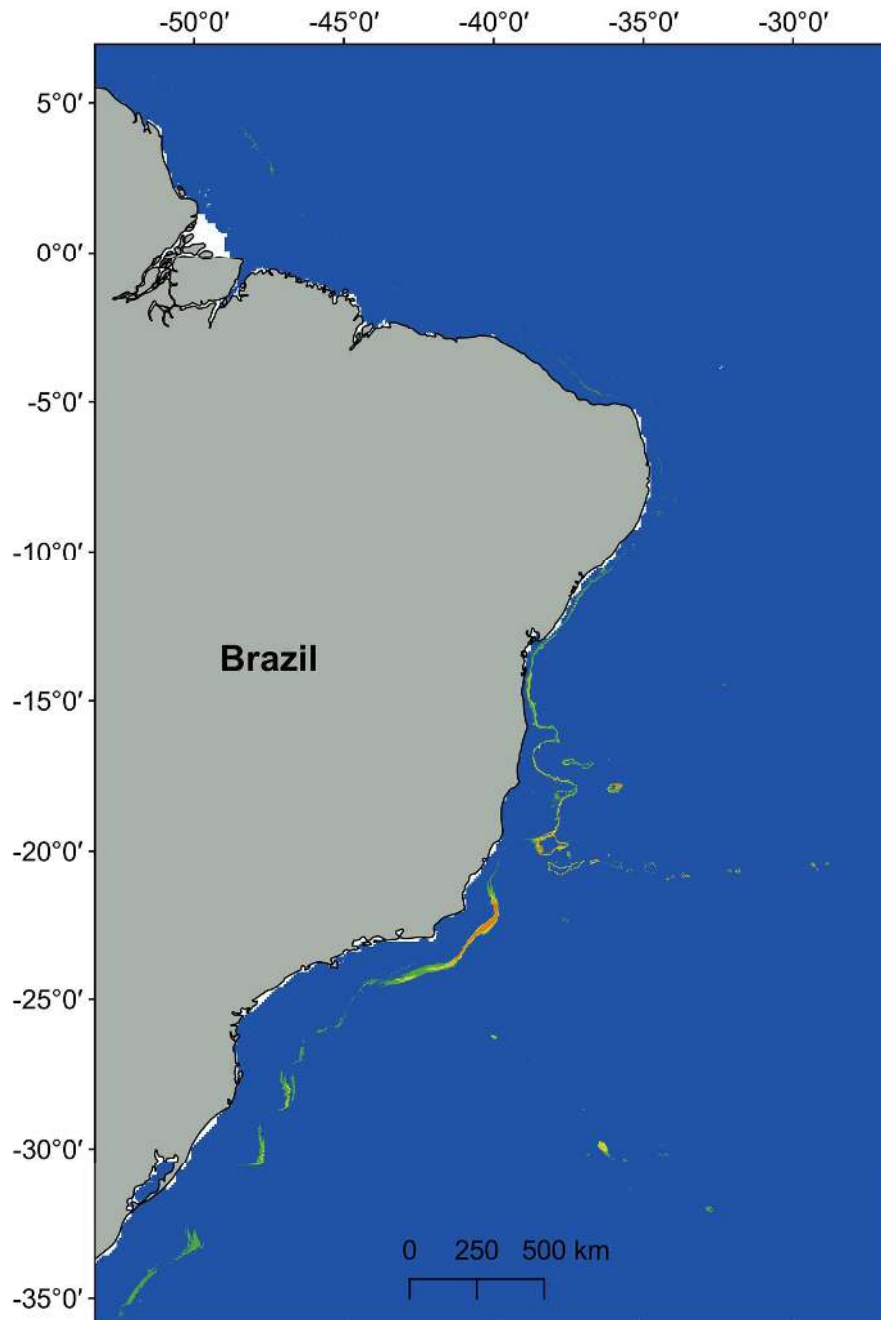


### Suitability Index



**Figure 7.** Habitat suitability prediction for *Enallopsammia rostrata* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.





**Suitability Index**



**Figure 8.** Habitat suitability prediction for *Solenosmilia variabilis* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.