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► **To cite this version:**

R. V. Barbosa, A. J. Davies, P. Y. G. Sumida. Habitat suitability and environmental niche comparison of cold-water coral species along the Brazilian continental margin. *Deep Sea Research Part I: Oceanographic Research Papers*, 2020, 155, pp.103147. 10.1016/j.dsr.2019.103147 . hal-02921156

HAL Id: hal-02921156

<https://hal.science/hal-02921156>

Submitted on 30 Nov 2020

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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.

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) 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 km²) (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 100×100 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⁻¹, whereas Scleractinia were found at sites with velocities lower than 0.1 m
256 s⁻¹ (Fig 2c). Both, Octocorallia and Scleractinia were found in sites with POC that ranged
257 from 0 to 50 g C_{org} m⁻² y⁻¹ and in a range of dissolved oxygen conditions ranging
258 between 4 and 5.5 ml l⁻¹, and silicate < 50 μmol l⁻¹ (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⁻¹ (Fig 2j) and, together with *C. debilis* were limited to sites with POC
264 lower than 20 g C_{org} m⁻² y⁻¹ (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⁻¹ (Fig 2l), and
266 were found in waters with silicate concentrations < 50 μmol l⁻¹ (Figure 2m and n,
267 respectively): *L. pertusa* and *S. variabilis*, that were mainly restricted to < 20 μmol l⁻¹
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⁻¹), 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 Seaone 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

571 **ACKNOWLEDGEMENTS**

572 We acknowledge FUNDESPA (Fundação de estudos e pesquisas aquáticas) for funding
573 a MSc scholarship to R.V.B. PYGS benefitted from a CNPq Research Productivity
574 Grant 301089/2016-7 to whom he is grateful.

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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 (Ω) 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.

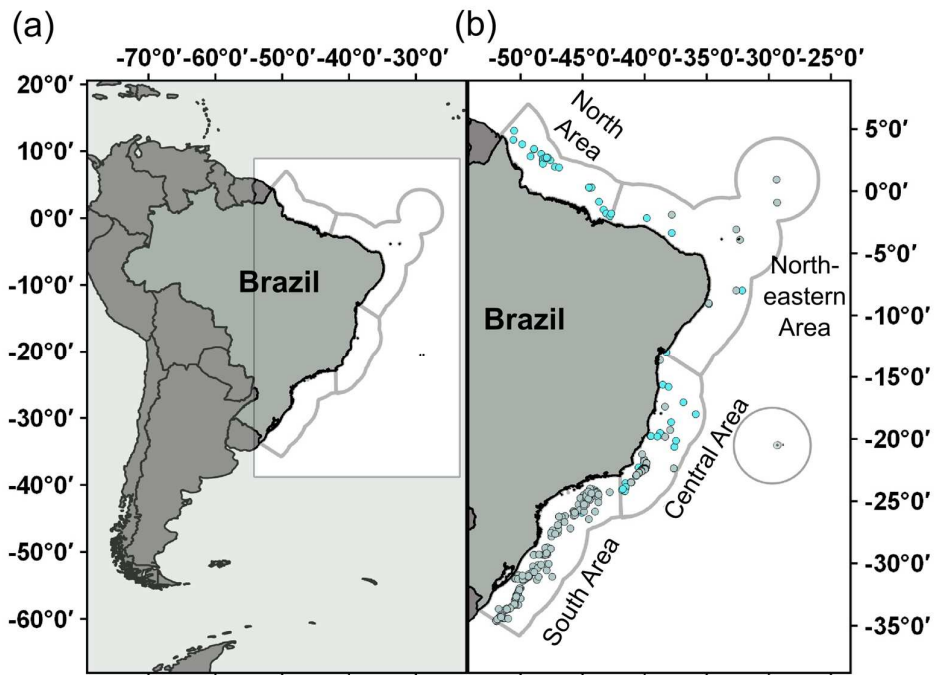
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920 **Figure 4.** Ecological niche of the cold-water coral species studied in the environmental
921 space produced by the principal component analysis method and the variables
922 contribution for loading their two principal components (PC) (c). The 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.

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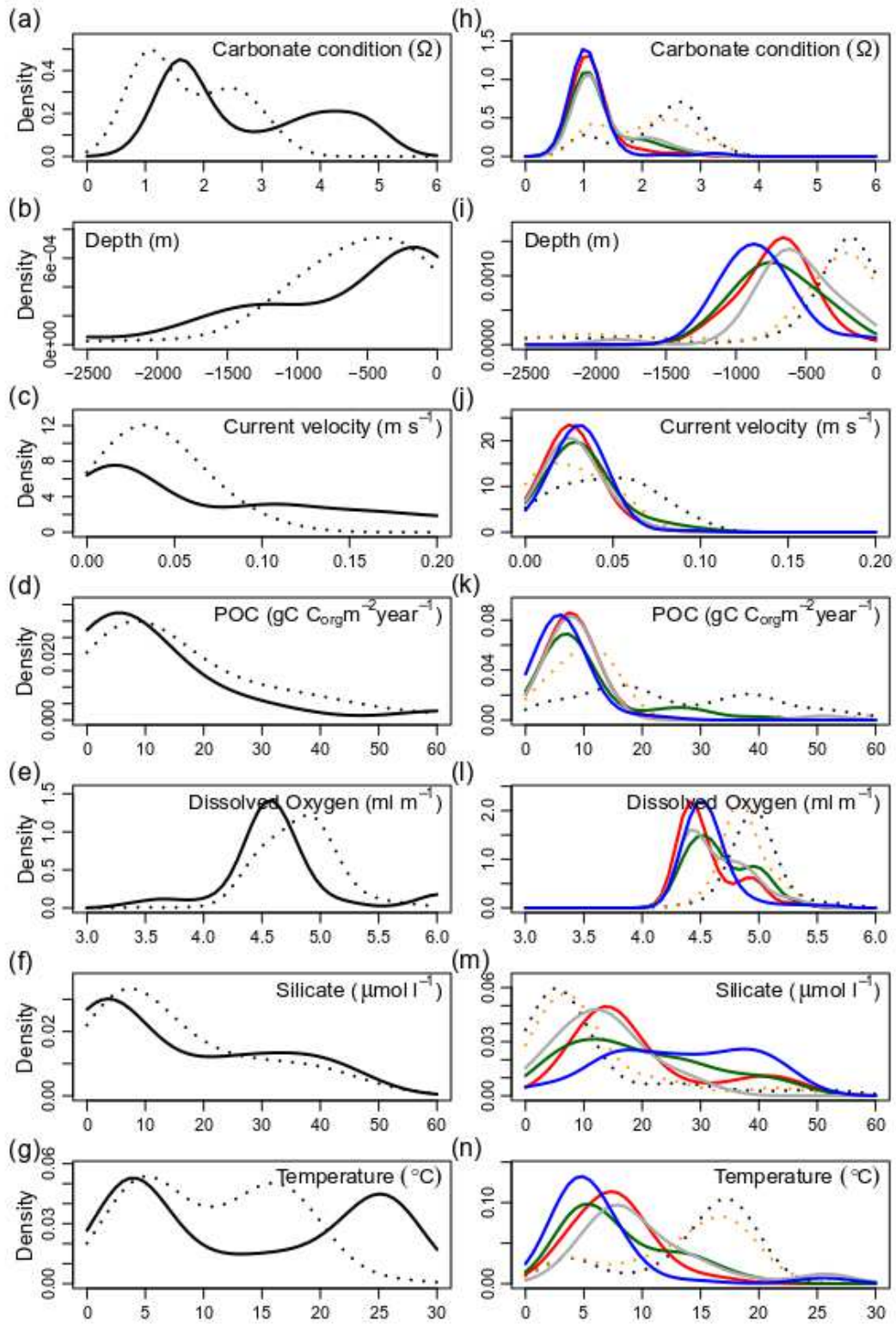


Figure 3

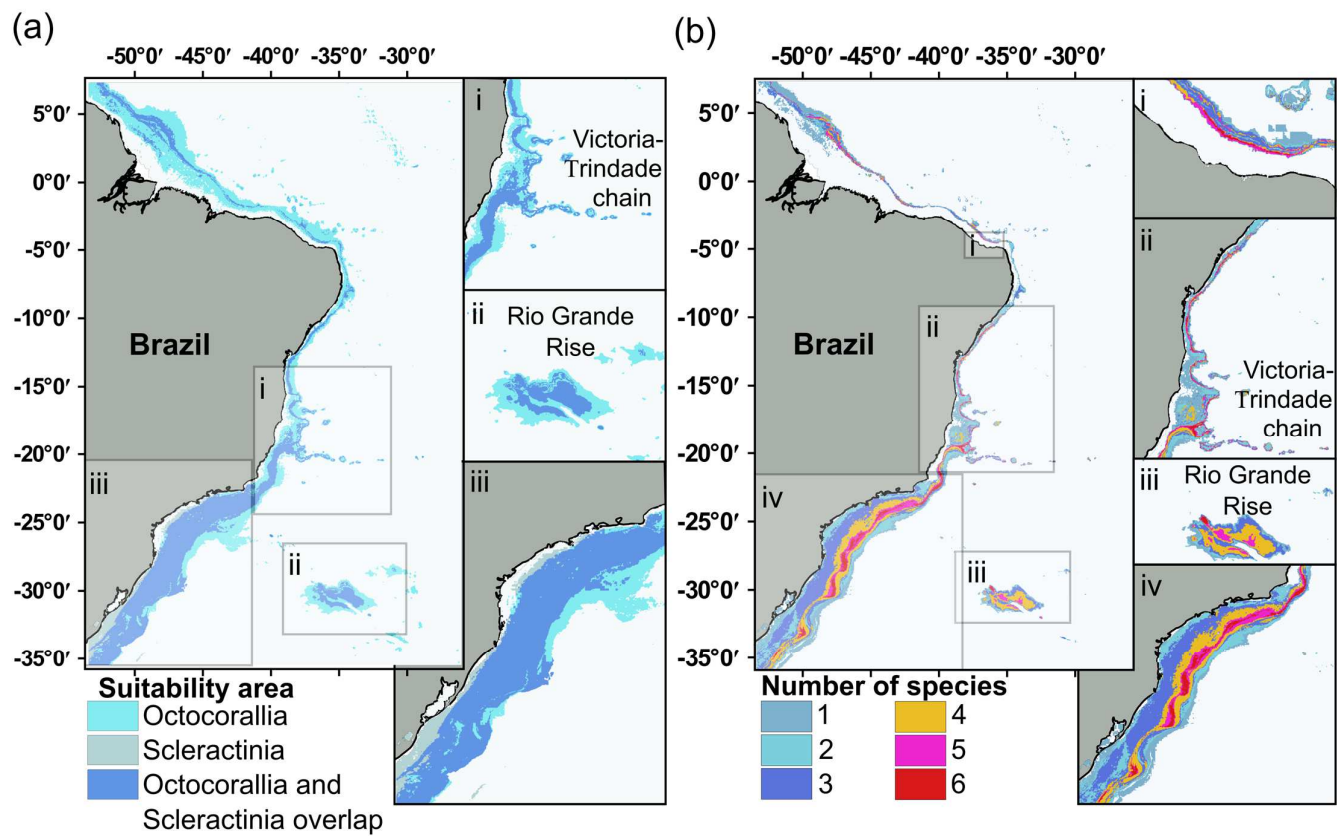


Figure 4

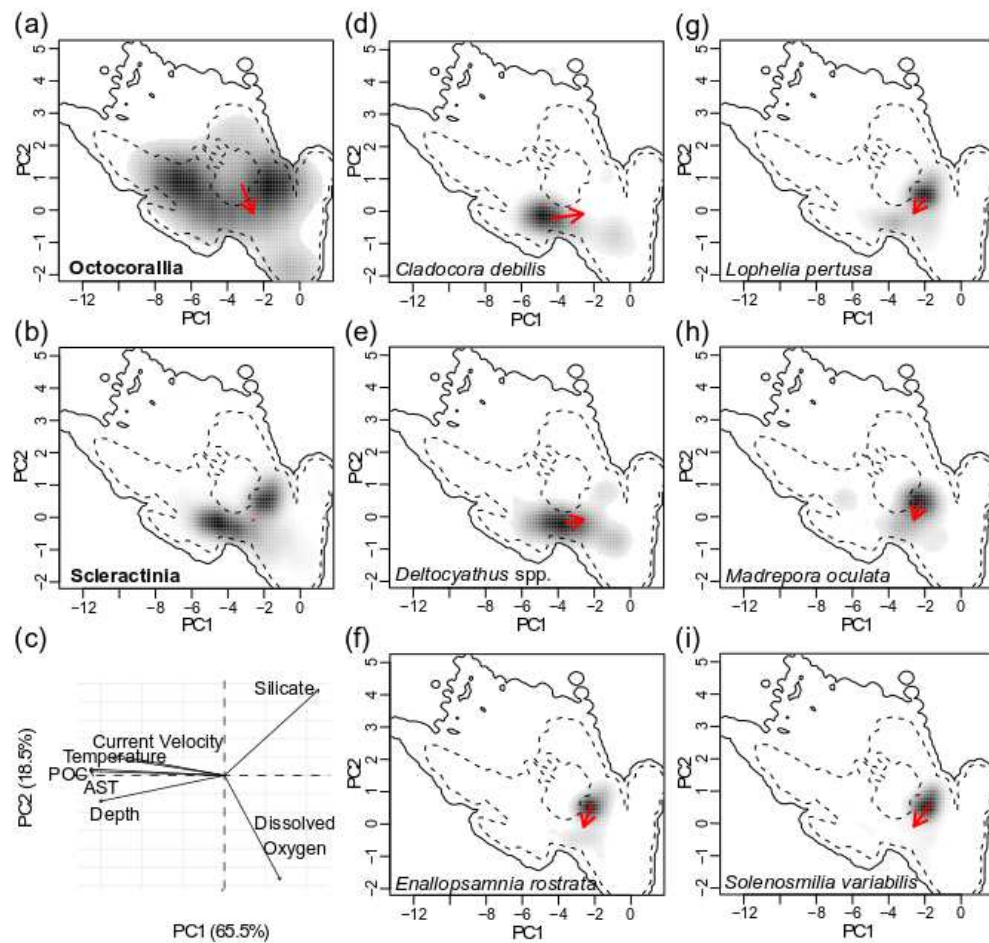


Table 1. Number of occurrence records of azooxanthellate corals from the Brazilian continental margin and slope, including historical records from published sources (see references in supplementary Table 1) and new scleractinian records from Cavalcanti et al. (2017), and the filtered total number of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

Taxonomic group	Historical records	New records	Total records used in models
Order Scleractinia	396	1147	259
Subclass Octocorallia	151		60
Species			
<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
CARB	Aragonite saturation state	arag_orr	Orr et al. (2005)	Ω_{ARAG}
	Aragonite saturation state	arag_stein	Steinacher et al. (2009)	Ω_{ARAG}
	Calcite saturation state	cal_orr	Orr et al. (2005)	Ω_{CALC}
	Calcite saturation state	cal_stein	Steinacher et al. (2009)	Ω_{CALC}
BATH	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)	-	
HYDRO	Current velocity	regfl	Carton et al. (2005)	$m s^{-1}$
	Vertical current velocity	verfl	Carton et al. (2005)	$m s^{-1}$
PROD	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)	$g C m^{-2} y^{-1}$
OXY	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)	$ml l^{-1}$
CHEM	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)	$\mu mol l^{-1}$
TEMP	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>
CARB	arag_orr	0.9525	0.9248	0.9671	0.953	0.9612	0.9624	0.9586	0.9604
	arag_stein	0.9562	0.9233	0.9691	0.9234	0.9588	0.9427	0.9757	0.9135
	cal_orr	0.9579	0.9269	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
BATH	srtm30	0.9664	0.9311	0.9737	0.9659	0.9913	0.9877	0.9951	0.9885
	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	
HY	regfl	0.8705	0.9231	0.9187	0.7648	0.9422	0.8762	0.9566	0.8705
	verfl	0.7004	0.6403	0.33	0.2592	0.743	0.2374	0.7354	0.5
PROD	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	0.9369	0.8621	0.9662	0.9555	0.9878	0.9727	0.9931	0.978
	vgpmean	0.8439	0.809	0.9544	0.8389	0.9449	0.8847	0.9706	0.8819
OXY	aoux	0.8195	0.8954	0.9126	0.677	0.6107	0.7846	0.6575	0.6625
	disso2	0.8913	0.939	0.8654	0.8969	0.9083	0.9375	0.9671	0.9477
	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

CHEM	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	0.9445
	sil	0.9145	0.9273	0.9422	0.8868	0.9312	0.9158	0.9782	0.8753
TEMP	temp	0.9618	0.9309	0.9678	0.953	0.9855	0.9825	0.9951	0.9776

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>
AUC								
calc-orr		0.9403						
arag-orr	0.9457		0.9694	0.9565	0.9543	0.9671	0.9403	0.9683
srtm30	0.9518	0.9492	0.9784	0.9882	0.9812	0.9877	0.9493	0.9595
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	0.9748	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						0.9905		
temp	0.9424	0.9281	0.9698	0.98	0.9761	0.969	0.9281	0.9635

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 and b - a</i>	
<i>C. debilis</i>	<i>Deltocyathus</i> spp.	0.89	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
Octocorallia	Scleractinia	0.28	ns	Different

Electronic supplementary materials

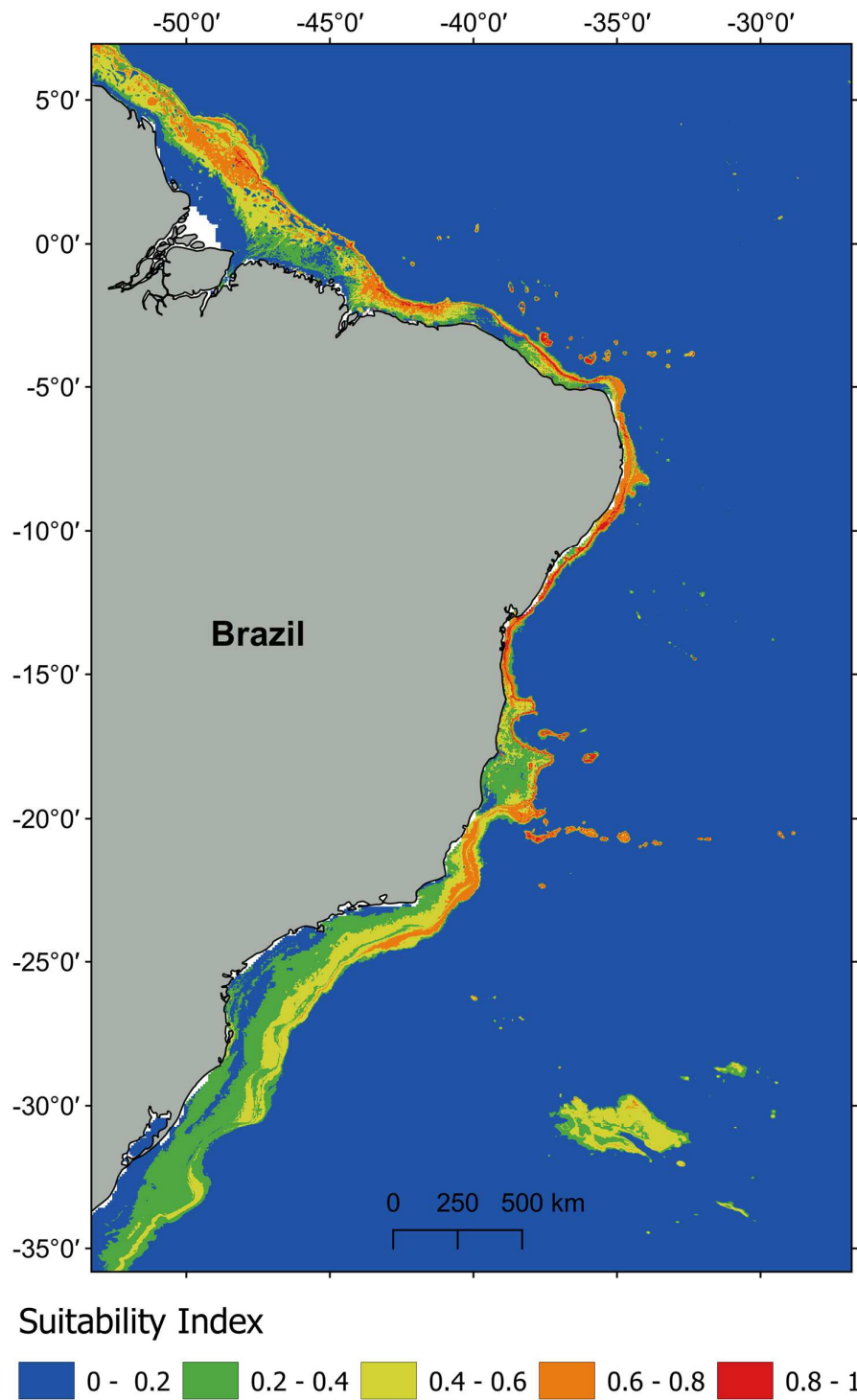
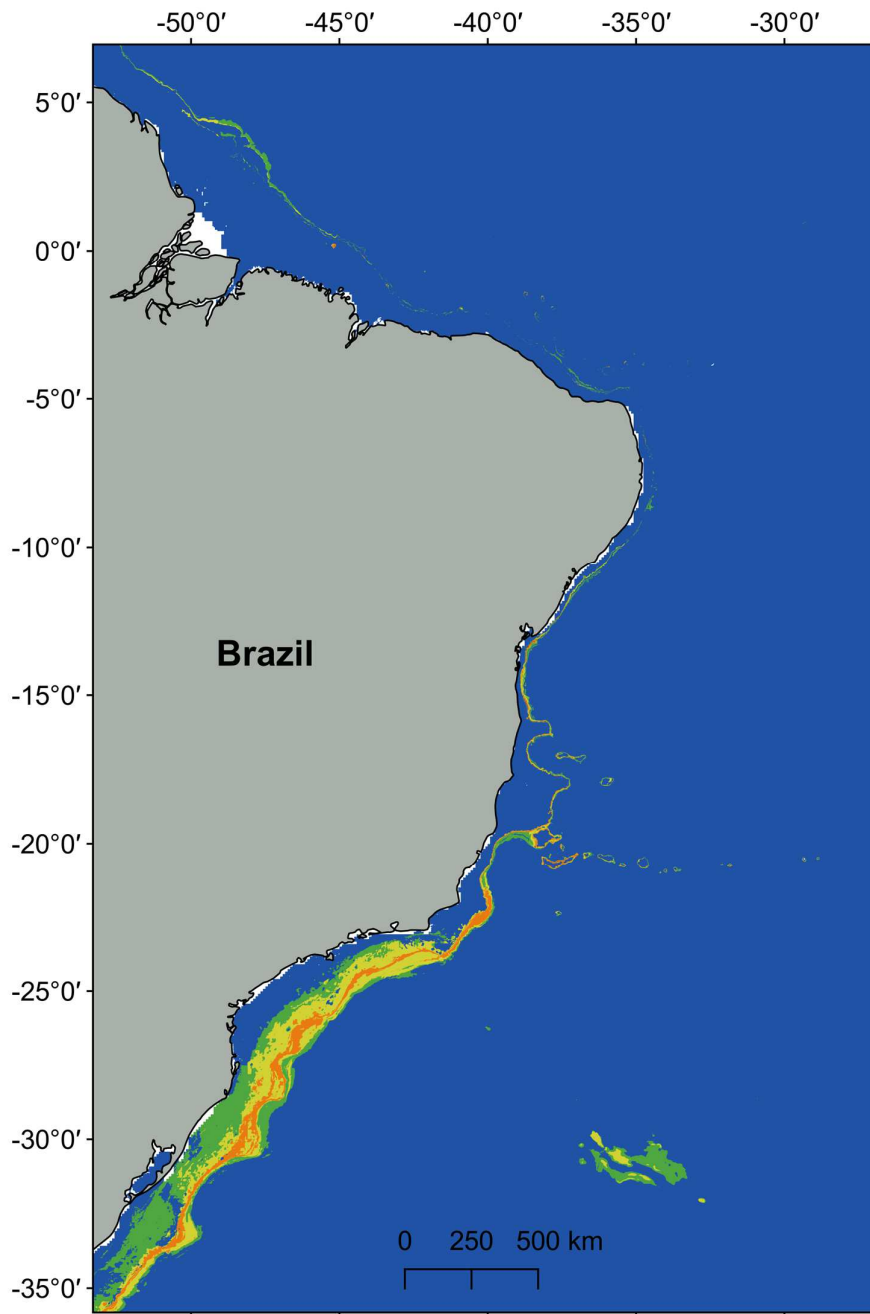


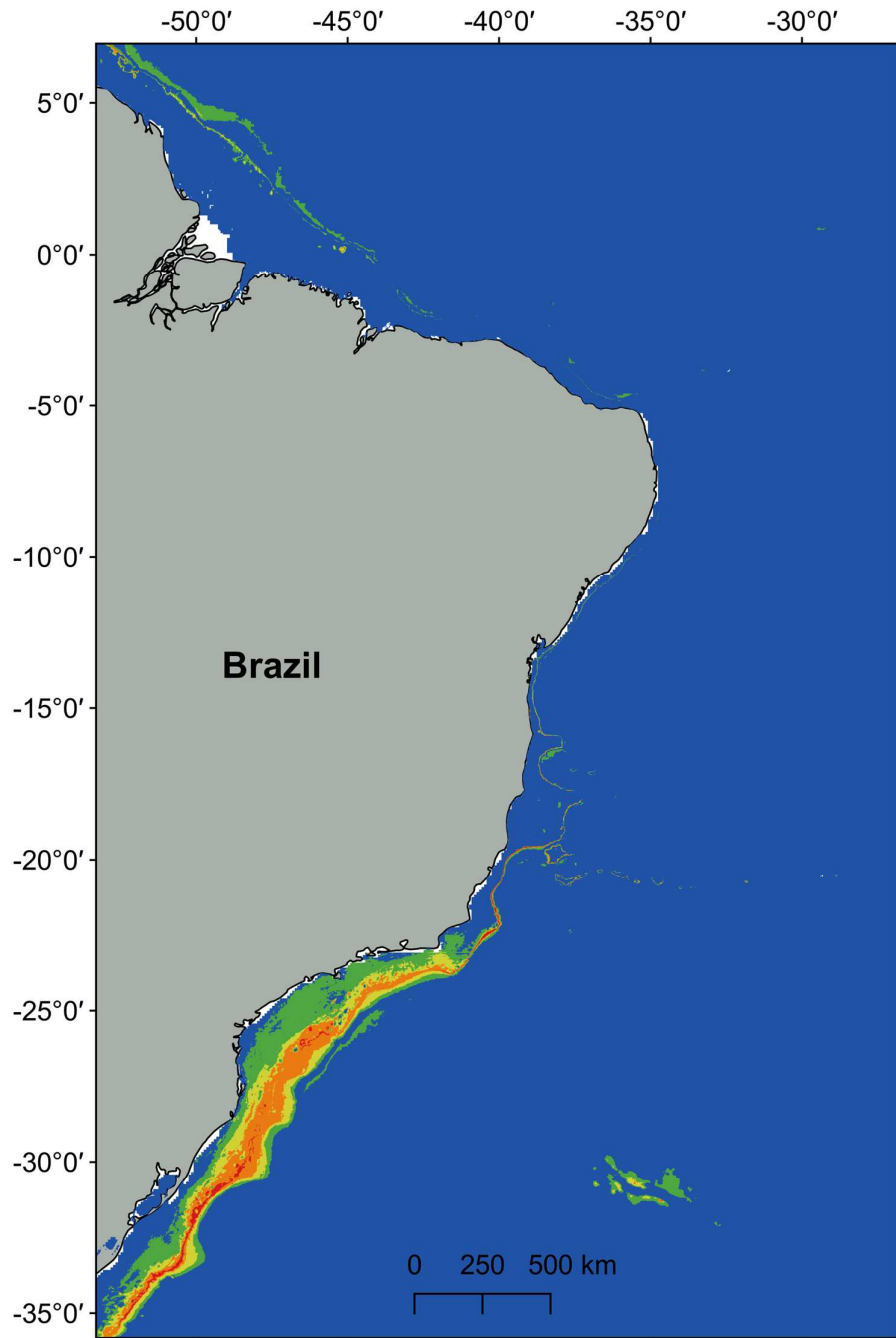
Figure 1. Habitat suitability prediction for Octocorallia in the southwest Atlantic Ocean. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



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

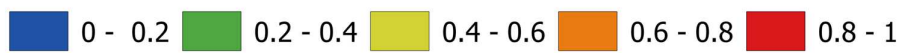
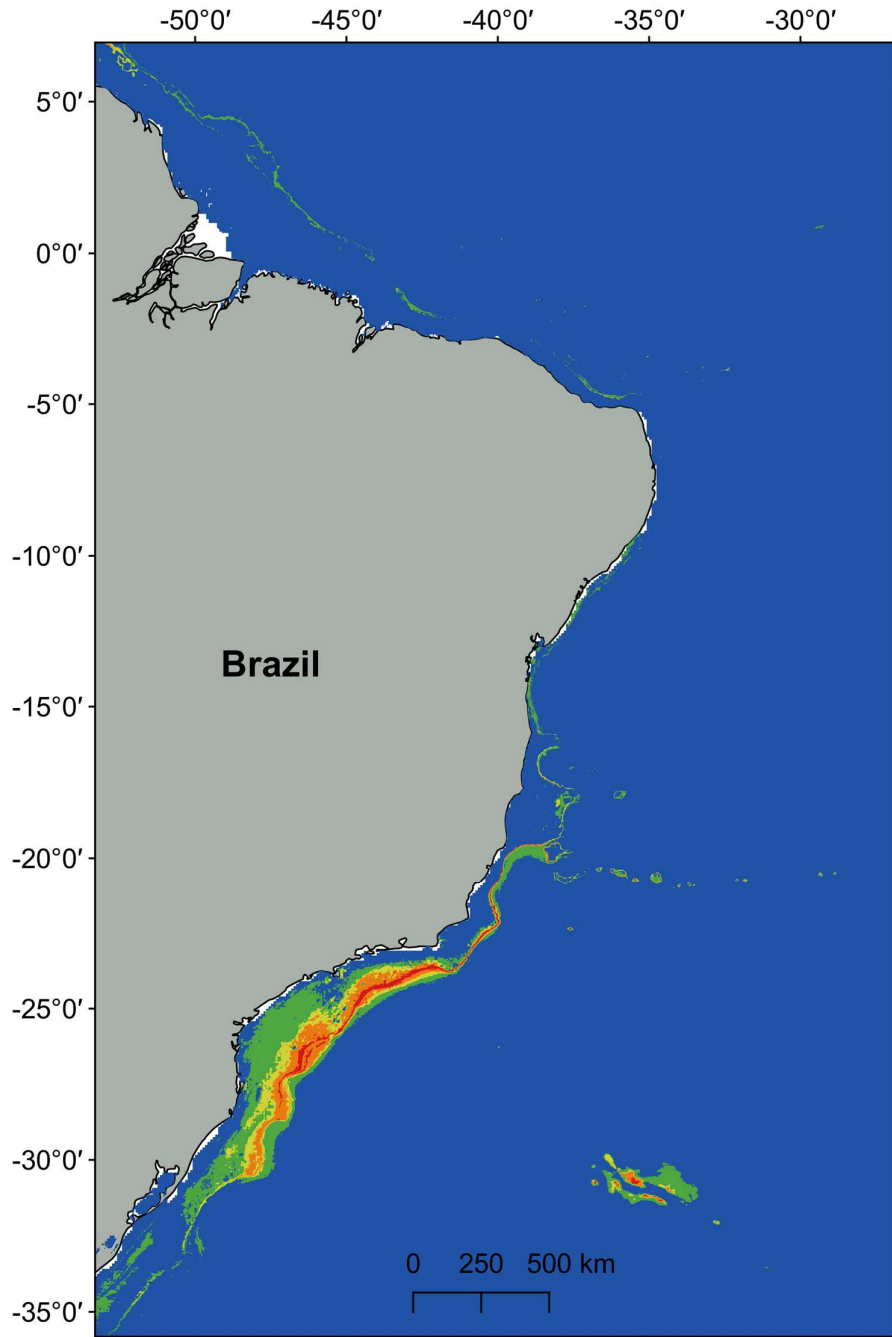


Figure 3. Habitat suitability prediction for *Cladocora debilis* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



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.

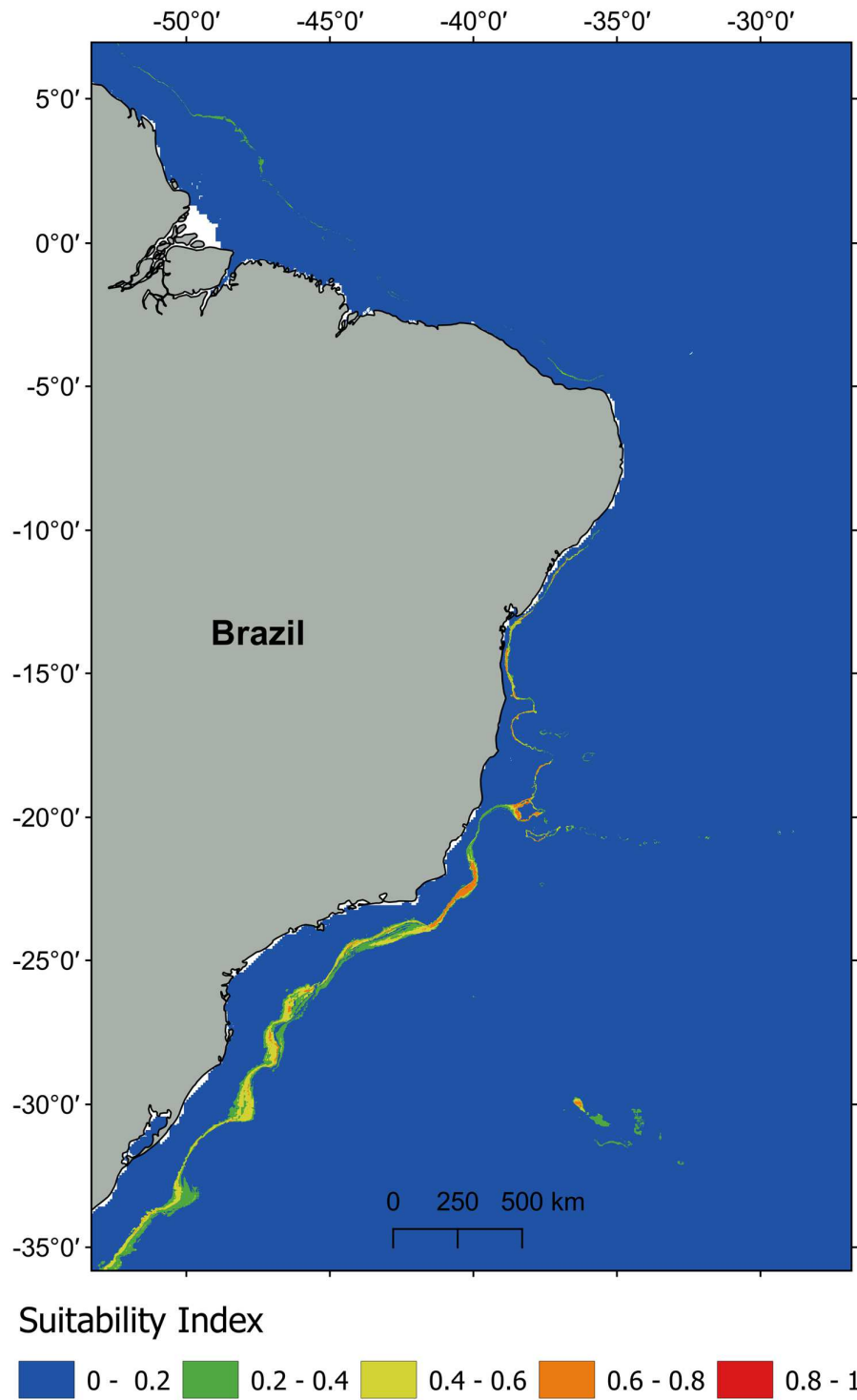
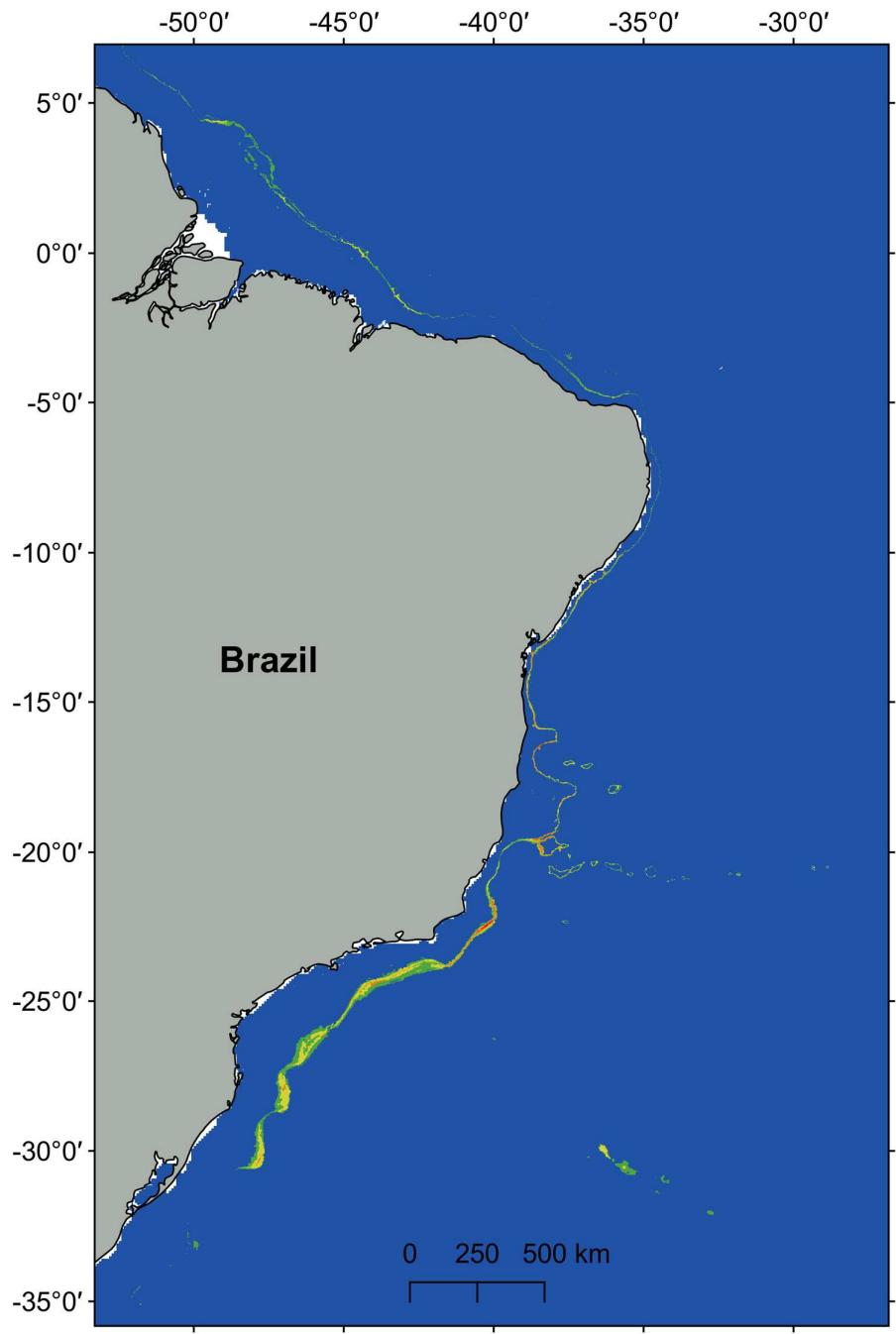


Figure 5. Habitat suitability prediction for *Lophelia pertusa* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



Suitability Index

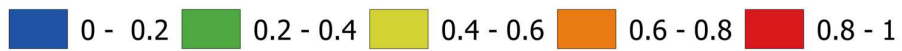
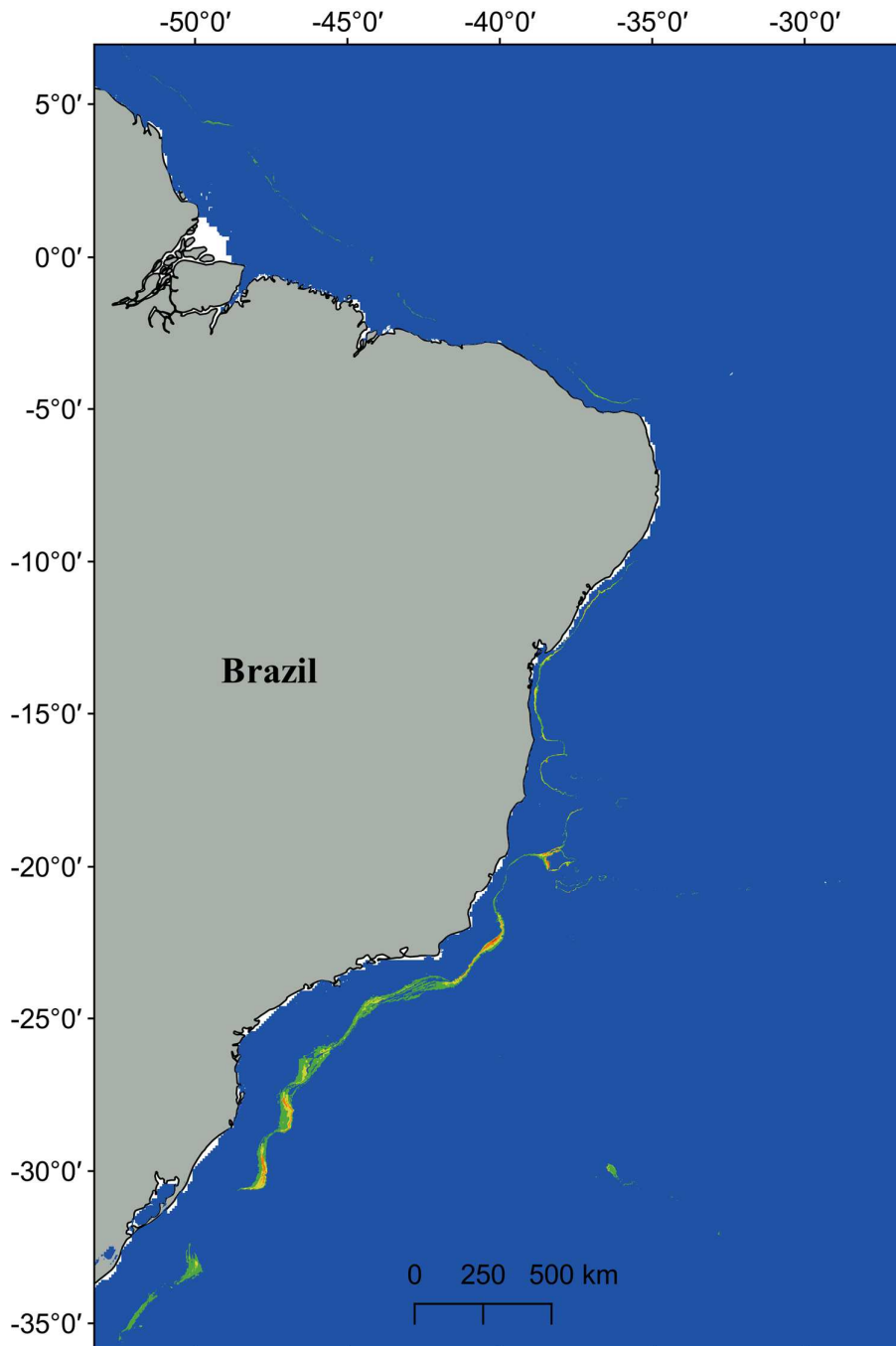


Figure 6. Habitat suitability prediction for *Madrepora oculata* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



Suitability Index

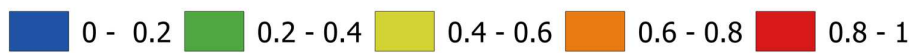
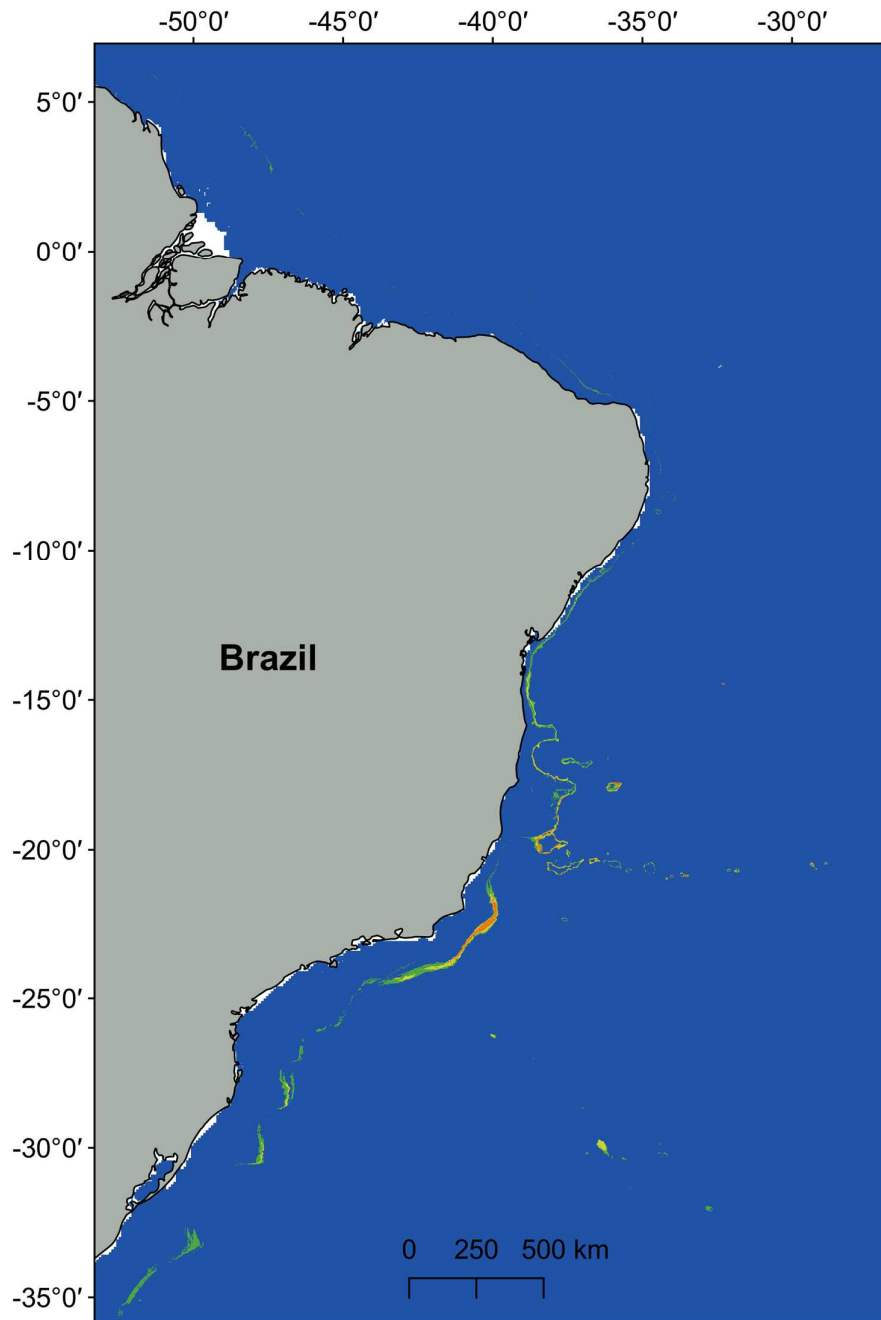


Figure 7. Habitat suitability prediction for *Enallopsammia rostrata* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



Suitability Index



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