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Research Article

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

Running title: Ceriantharia in Atlantic: An Ecological Niche Modelling Study

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Abstract

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

Highlights

1. This study is crucial for understanding global ecological patterns of ceriantharians (tube-dwelling anemones), a group whose knowledge dates back to the 18th century, yet significant gaps remain in their biological, biogeographical, and ecological data.

2. The use of Ecological Niche Modelling, widely implemented after the advancement of computational techniques, provides information that enables inferences about the realized niche and biogeographical aspects of ceriantharians.

3. As ceriantharians play crucial ecological roles in the structure of megabenthic communities through their tubes, the analysis of potential areas that encompass the realized niche of the species contributes to new strategies for the conservation of marine ecosystems.

Keywords

Anthozoa; Benthic animals; Conservation; Environmental suitability modeling; Marine ecology; Tube-dwelling anemones.

Introduction

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

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

This asymmetry in knowledge about ceriantharians can be seen through the number of occurrences in databases. For example, while *Cerianthus lloydii* (Gosse, 1859) has 33,240 occurrences in the Global Biodiversity Facility System (GBIF), A*rachnanthus sarsi* (Calgren, 1912) has only 61 records. This indicates a noticeable bias in geographical records and sub-sampling of species, which further limits collection and new research. Thus, it is necessary to employ techniques that can aid in understanding the potentially suitable regions for ceriantharians.

Since the late 1980s, with the emergence of techniques that integrate bioinformatics and statistical methods, there has been an expansion in the ability to predict patterns in biodiversity (Guisan et al. 2017). One of the most commonly used techniques for this purpose is Ecological Niche Modelling (ENM), which correlates geographic records with environmental variables (Peterson and Soberón, 2012). Through the implementation of statistical machine learning methods (Zurell et al. 2020), the resulting ENM models can be used to infer regions that may encompass the realized niche of species (Melo-Merino et al.

2020). This approach can help expand the understanding of the potentially suitable regions for ceriantharians, given the asymmetry in knowledge about their distribution.

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

Materials & Methods

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

Study species and occurrence data

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

Figure 1. Ceriantharians in the Atlantic Ocean.

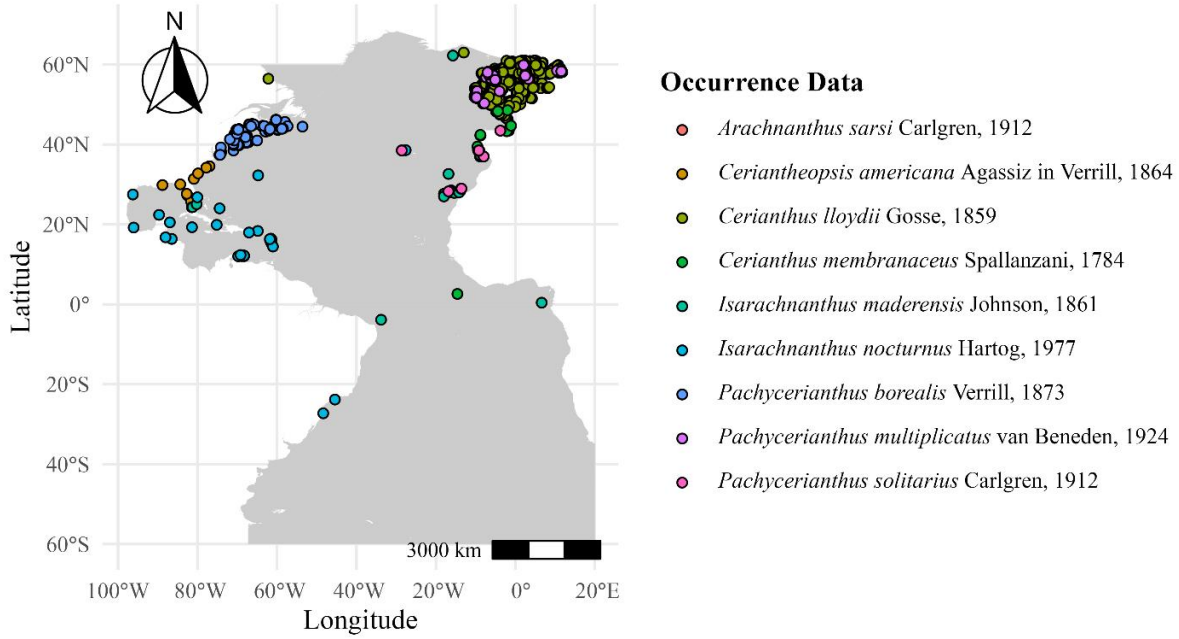


Table 1. Genera, species, and number of occurrences selected for model training.

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

Environmental data

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

below the threshold, resulting in different numbers of layers per species (Table S2, Supp. Material).

Ecological Niche Modelling

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

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

Results

Statistical evaluation and relative variable importance

Model performance (Table 2) was considered excellent, with AUC and TSS values above the minimal threshold (AUC ≥ 0.7; TSS ≥ 0.4), averaging 0.91 ± 0.03 and 0.79 ± 0.1, respectively. The tables with the environmental niche of the species, represented by the mean and standard deviation of the environmental variable values extracted from the occurrence points, are presented in the Supplementary Material (Tables S4, S5 e S6).

Table 2. Average model performance based on AUC and TSS metrics based on a minimal threshold (AUC ≥ 0.7 and TSS ≥ 0.4).

Genera	Species	AUC	TSS
Arachnanthus	*sarsi*	0,91 ± 0.06	0,78 ± 0.14
Ceriantheopsis	*americana*	0,96 ± 0.03	0,86 ± 0.08

Cerianthus	*lloydii*	0,88 ± 0.01	0,62 ± 0.02
	membranaceus	0,94 ± 0.09	0,90 ± 0.10
Isarachnanthus	*maderensis*	0,87 ± 0.09	0,75 ± 0.16
	nocturnus	0,92 ± 0.02	0,76 ± 0.06
Pachycerianthus	*borealis*	0,92 ± 0.02	0,75 ± 0.04
	multiplicatus	0,92 ± 0.02	0,72 ± 0.05
	solitarius	0,98 ± 0.01	0,97 ± 0.02

Of the set of 21 variables, 19 were used for model training (Table 3). Average sea water speed, minimum sea water direction, and minimum sea water speed were selected for 8 of the 9 species (Table 3), averaging 15% ± 20% in relative importance. Average and minimum sea water speed presented relative importance above 20% for *C. americana*, *I. maderensis*, *C. membranaceus*, *I. nocturnus*, and *P. solitarius* (Table 3). Only one variable was common among all 9 species (maximum sea water direction), although with low relative importance (16% ± 21%).

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

Species	Variable	Relative Importance (%)
Arachnanthus sarsi	Average Dissolved Molecular Oxygen	62
	Average Ocean Temperature	58
	Minimum Dissolved Molecular Oxygen	39
Ceriantheopsis americana	Minimum Salinity	41
	Minimum Sea Water Speed	38
	Minimum Silicate	38
	Maximum Nitrate	34
Cerianthus lloydii	Minimum Ocean Temperature	39
	Minimum Silicate	24

Cerianthus membranaceus	Average Nitrate	77
	Average Sea Water Speed	56
	Average Ocean Temperature	43
Isarachnanthus maderensis	Average Sea Water Speed	24
	Minimum Sea Water Speed	20
Isarachnanthus nocturnus	Minimum Sea Water Speed	45
Pachycerianthus borealis	Average Ocean Temperature	76
Pachycerianthus multiplicatus	Maximum Nitrate	60
	Maximum Salinity	29
Pachycerianthus solitarius	Average Ocean Temperature	83
	Average Sea Water Speed	40

Discussion

Relative variable importance and the biological factors of ceriantharians

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

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

However, average and maximum nitrate concentrations, which were also significant for some species (Table 3), play a critical role in habitat development due to their influence

on primary productivity and local trophic networks (Suggett et al. 2012). Ceriantharians inhabit a broad range of depths and utilize available sediment in their environment to construct their tubes (Picton and Manuel, 1985), further emphasizing the importance of nutrient availability.

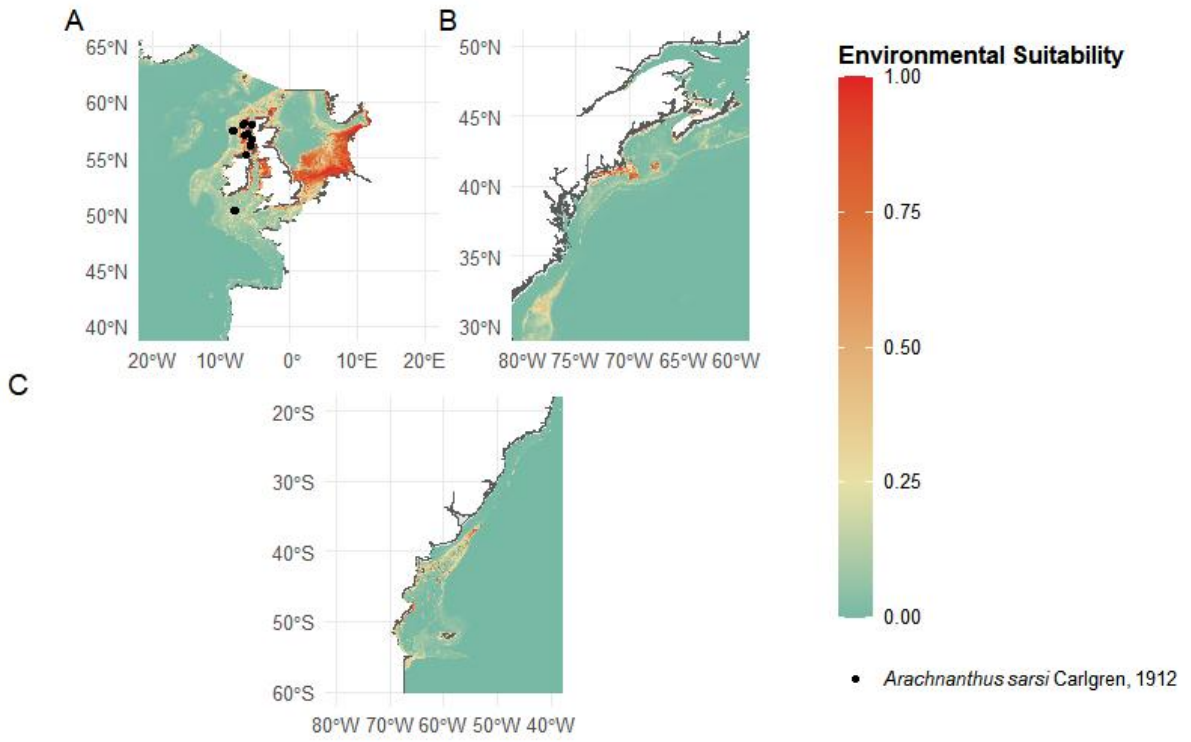
Thus, our findings on the relative contributions of environmental variables are consistent with existing knowledge of ceriantharian ecology and their life cycles, providing valuable insights into how abiotic factors influence their distribution, larval dynamics, and habitat preferences.

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

Arachnanthus sarsi

The model infers potentially suitable areas (≥ 50%) that are consistent with the currently known distribution of the species (Picton and Manuel 1985; Galego et al. 2013; Stampar et al. 2020), in the vicinity of Ireland and the United Kingdom. However, it presents a large area in the North Sea with a zone of environmental suitability (≥ 75%) that extends from the Netherlands, Germany, and Denmark, to the south of Sweden and Norway, regions for which there is still no documented record of the species (Fig. 2A). Additionally, it exhibits a small zone of suitability (≥ 50%) in the northeastern United States and in the southern part of South America, between Uruguay and Argentina, countries also with no record of *Arachnanthus sarsi* (Fig. 2 B-C). Since this is a species commonly found in the colder and deeper waters of the North Atlantic (Stampar et al. 2020), considering the physicochemical and geographical barriers to the dispersal of the species, we disregard the possibility that *A. sarsi* would reach the southern part of South America naturally.

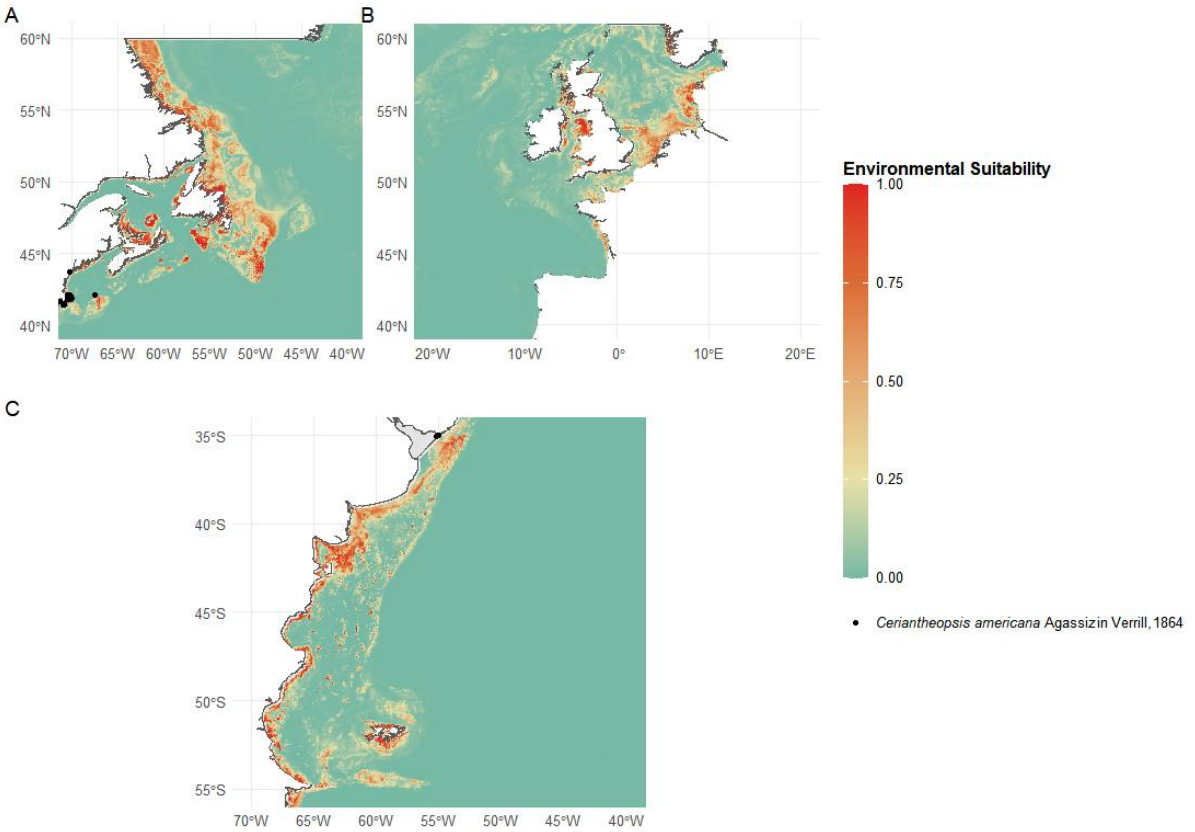
Figure 2. Ensemble of the environmental suitability of *Arachnanthus sarsi*. Areas of high suitability are highlighted in maps A, B, and C. **A**: Northeastern North Atlantic. **B**: North American coast. **C**: Southern South America, including regions near Uruguay and Argentina.



Ceriantheopsis americana

Considered one of the most studied cerianthids (Stampar et al. 2020), the majority of the literature on *Ceriantheopsis americana* is dedicated to the ecological, biological, and sensory processes of the organisms, which are collected in the North Atlantic, mainly in the United States (Peteya, 1973, Kristensen et al. 1991, Holohan et al. 1998, Sebbens, 1998, Stampar et al. 2020) and to a lesser extent in Canada (Shepard et al. 1986). However, the model presented environmental suitability regions for the species consistent with its distribution, but with zones (≥ 50%) along the entire Canadian coast and only a small region near Maine, in the United States (Fig. 3A). They also exhibit zones in areas where the species has not yet been recorded: in the northeastern portion of the North Atlantic Ocean (≥ 50%), with a higher percentage (≥ 75%) in Ireland, the United Kingdom, northern Germany, Denmark, and southern Norway (Fig. 3B). In the locations presented in South America (≥ 50%), between Uruguay and Argentina (Fig. 3C), including the Malvinas Islands, there is only an uncertain record made by Hertwig (1882) on the coast of Uruguay, since the first species described for this biogeographic region, the Warm Temperate Southwest Atlantic (Spalding et al. 2007) was only made more than a hundred years later, by Stampar et al. (2015).

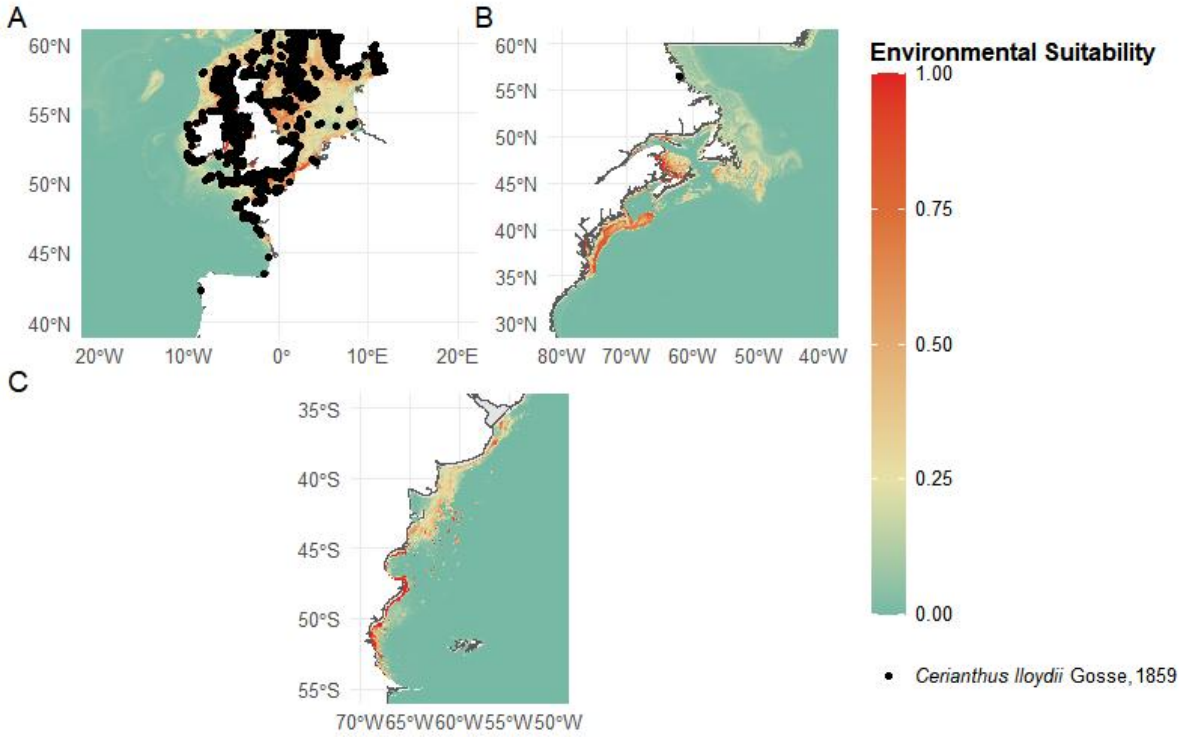
Figure 3. Ensemble of the environmental suitability of *Ceriantheopsis americana*. Areas of high suitability are highlighted in maps A, B, and C. **A**: North American coast. **B**: Northeastern North Atlantic. **C**: Southern South America, including regions near Uruguay and Argentina.



Cerianthus lloydii

Grouping the cerianthids recorded in the Arctic and the North Sea (Molodtsova et al. 2023), the model suggested potentially suitable areas (≥ 75%) in the North Sea, near Norway, Sweden, the Netherlands, Belgium, France, Ireland, and the United Kingdom, consistent with regions of occurrence and extrapolating to other locations that make biological sense for the species (Fig. 4A). We consider that the areas in the far south of South America (Fig. 4C), since the percentage of suitability increases latitudinally from Uruguay to Argentina (50% ≥ 75%), are due to environmental similarity, since *C. lloydii* is documented as a North Atlantic species (Perry, 2016), and would not naturally reach these regions (Fig. 4B).

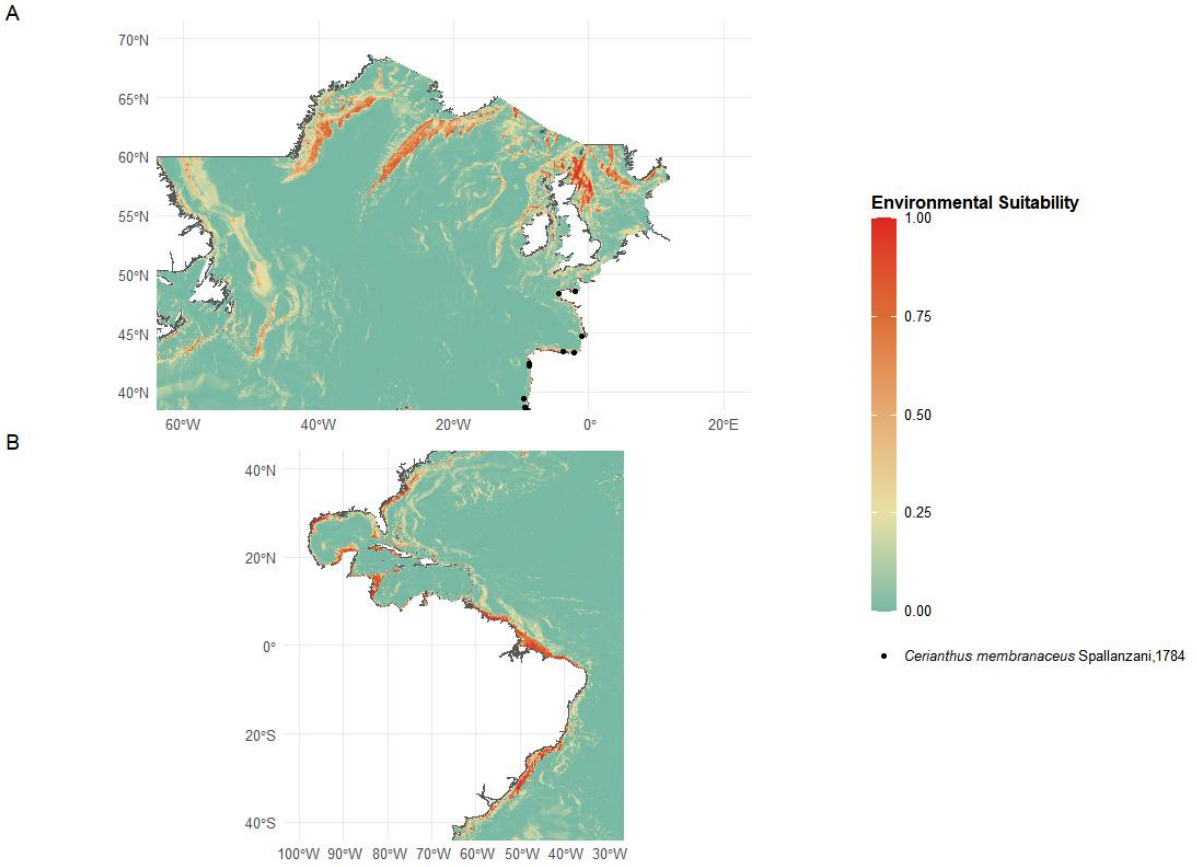
Figure 4. Ensemble of the environmental suitability of *Cerianthus lloydii*. Areas of high suitability are highlighted in maps A, B, and C. **A**: Northeastern North Atlantic. **B**: North American coast. **C**: Southern South America, including regions near Uruguay and Argentina.



Cerianthus membranaceus

Found extensively in the Mediterranean Sea (Dominguez-Carrió et al. 2021, Riedel et al. 2008, Stampar et al. 2020), the model suggests suitable areas for *C. membranaceus* (≥ 50%) in the North Atlantic, in regions near Greenland, Iceland, the United Kingdom, and Norway, but also on the American continent, from the coast of Canada (≥ 50%), through Central America, presenting higher percentages in South America (≥ 75%), locations where there are no records of the species (Fig. 5 A-B). This species has already been recorded in Madeira Island (Calado, 2006), so access to other areas of the Atlantic Ocean is much more feasible, but no evidence of occurrence in the Western Atlantic has been verified so far.

Figure 5. Ensemble of the environmental suitability of *Cerianthus membranaceus*. Areas of high suitability are highlighted in maps A and B. **A**: North Atlantic. **B**: Central and South America.

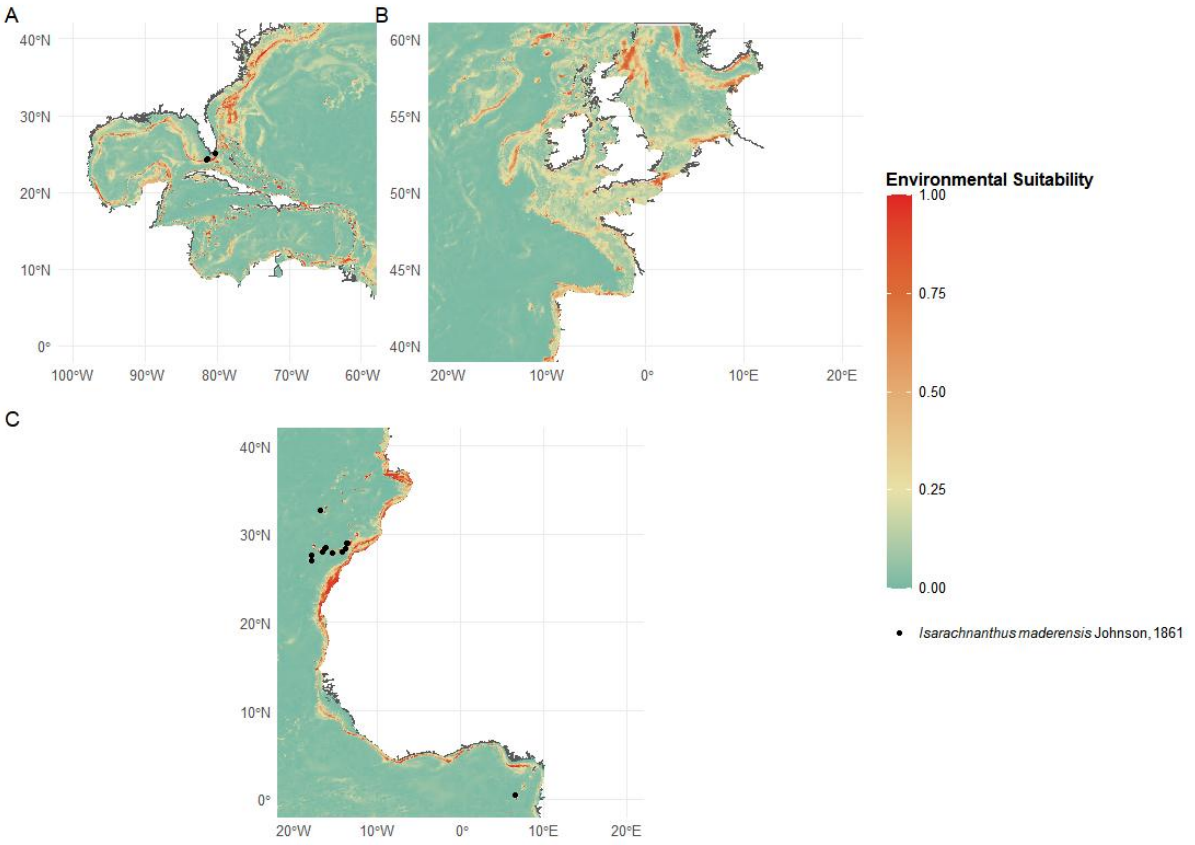


Isarachnanthus maderensis

The *I. maderensis* model extrapolated the areas of environmental suitability and presented a wide area of moderate suitability (≤ 50%) for the species in the entire Atlantic Ocean, with locations both near and distant from the coastal region, including where the absence of *I. maderensis* is theorized (Stampar and Morandini 2017; Stampar et al. 2019; Stampar et al. 2020). However, the species also exhibits greater suitability (≥ 75%) in zones close to areas with records of the species, such as in Central America and Europe, with areas near Portugal (Stampar et al. 2020) and Southern Spain (Fig. 6A-B). On the Northwest coast of Africa, the model inferred zones in regions near Morocco and Western Sahara, however, the species has only been documented a little further south, in São Tomé and Príncipe (GBIF, human observation) (Fig. 6C). In the large region (≥ 75%) that appears in South America, covering the southeastern and southern parts of Brazil, reaching Uruguay, there have been no records of the species yet (Map S5, Supp. Material). Considering that *Isarachnanthus maderensis* is a widely distributed species in the Atlantic Ocean, the geographical distance between the records can bias the analysis of environmental suitability and its distribution,

making it difficult to delineate the potential niche of the species by the algorithms used (Sillero et al. 2021). However, although some regions do not make biological sense, the model extrapolation was more conservative than in other tests performed, adding new points to the existing description of the distribution pattern for the species (Stampar and Morandini, 2017).

Figure 6. Ensemble of the environmental suitability of *Isarachnanthus maderensis*. Areas of high suitability are highlighted in maps A, B and C. **A**: Central America. **B**: North Atlantic. **C**: Northwest coast of Africa.

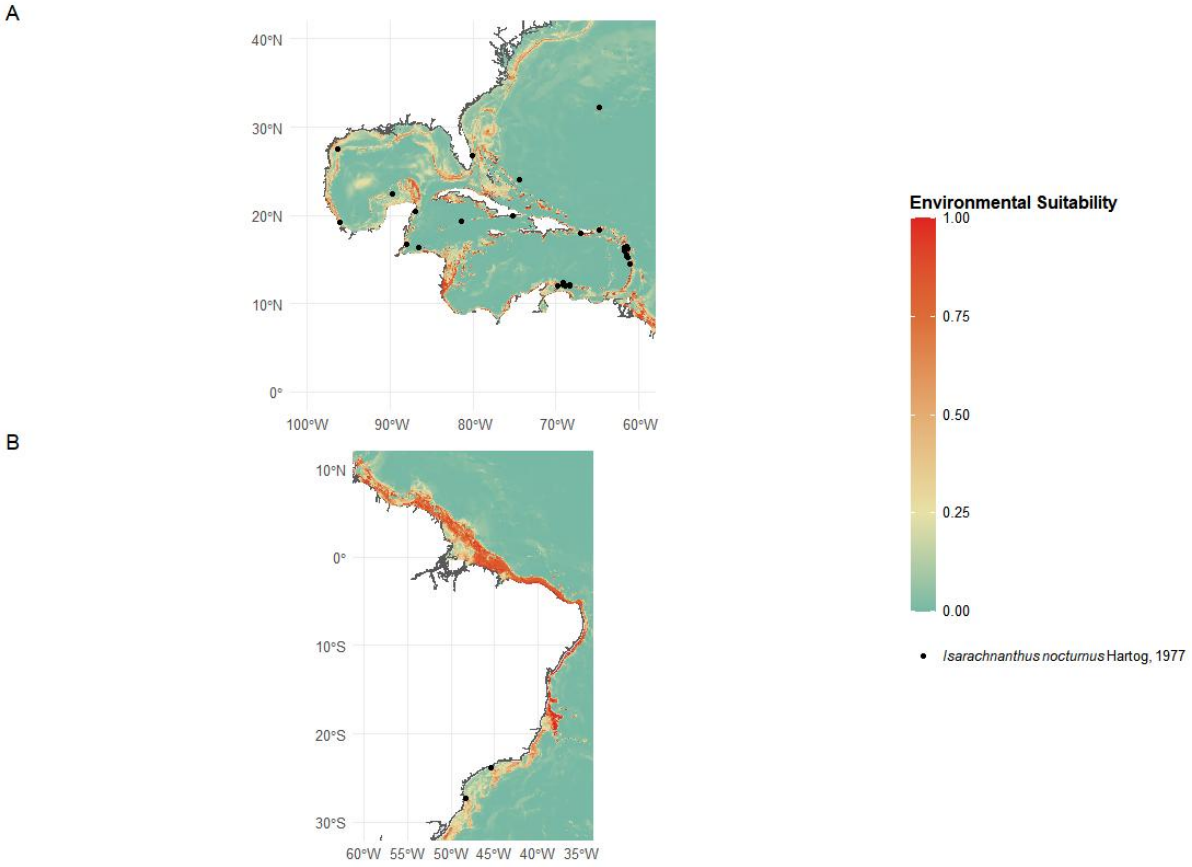


Isarachnanthus nocturnus

The model inferred an extensive latitudinal range of environmental suitability (≥ 50%) on the coast of the American continent, with a higher percentage (≥ 75%) in small locations in Central America and larger areas in South America, with emphasis on northeastern Venezuela, passing through Guyana, Suriname, French Guiana, and reaching northern Brazil, and reaching almost maximum suitability on the coast of Bahia and in the southeast, near Espírito Santo (Map S6, Supp. Material). The suitability regions are consistent with the known distribution of the species, which ranges from the Caribbean to Argentina (Stampar et al. 2020) (Fig. 7A-B). Thus, the extrapolation of the projections of *I. nocturnus* presents a biological sense, since in the most accepted scenario, proposed by Stampar et al. (2012), *I.*

nocturnus presents a more extensive environmental latitudinal gradient than *I. maderensis*, due to larval characteristics in the life cycle and the influence of ocean currents (Lopes et al. 2023).

Figure 7. Ensemble of the environmental suitability of *Isarachnanthus nocturnus*. Areas of high suitability are highlighted in maps A and B. **A**: Central America. **B**: South America.

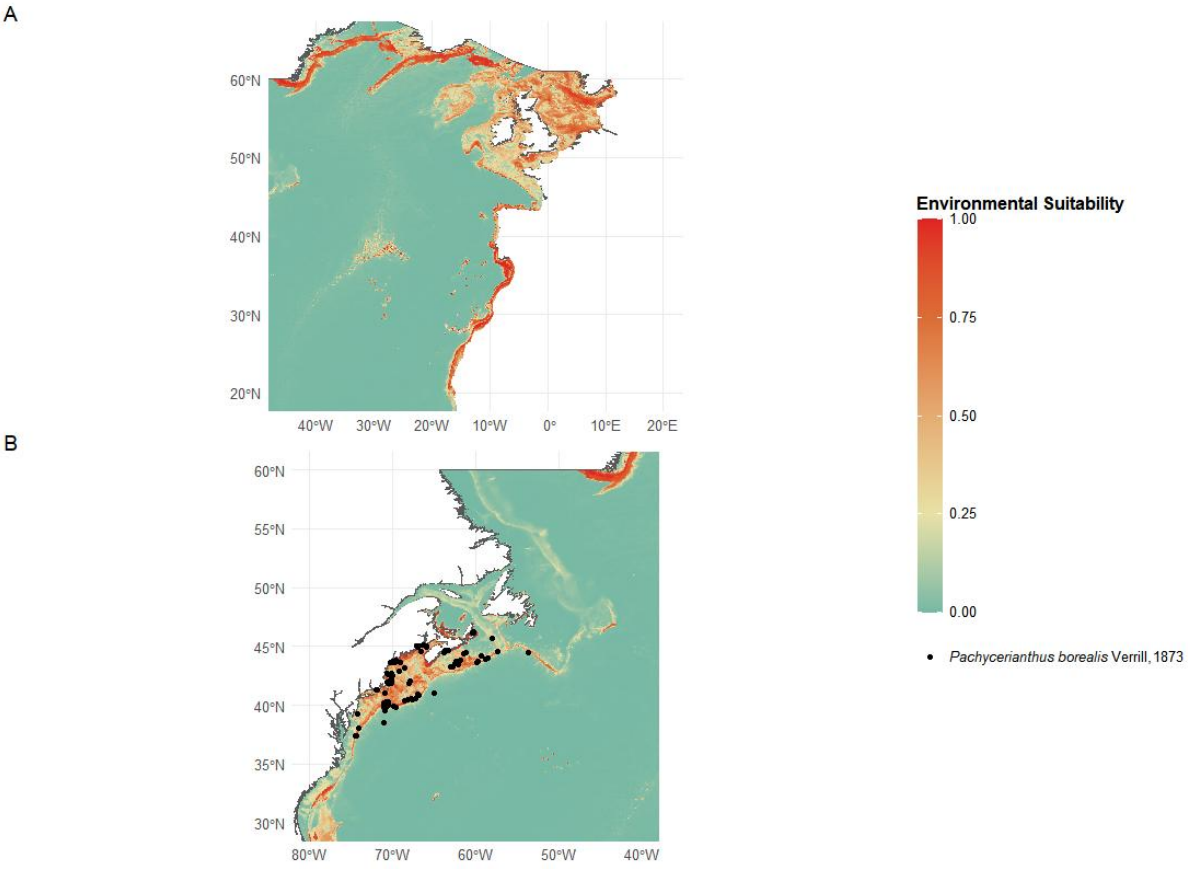


Pachycerianthus borealis

The model inferred suitable regions for the species in the Northwest Atlantic (≥ 75%), near Greenland, Iceland, Norway, Denmark, Germany, Portugal, Morocco, and the Western Sahara (Fig. 8A). Some make sense with the areas consistent with most of the known distribution of the species, which is in the Northwest Atlantic (Stampar et al. 2020), but presented more restricted areas of suitability when compared to other areas in locations that exhibit the highest concentration of records, such as in northern North America (Fig. 8B). However, it extrapolated large zones along the South American coast and the African continent where there have been no records of the species (Map S7, Supp. Material). In addition, most of the records of *P. borealis* are concentrated on the northern coast of North America. The species is documented in some reports associated with the Government of Canada for the characterization of species in some regions of the country, as is the case of

Beazley et al. (2019), in which states that the cerianthids found were in the depth range of 200 to 300 meters, at a temperature ranging between 4.5 to 10.2°C. In the work of Watling and Lapointe (2022), the authors consider *P. borealis* one of the most representative cerianthids in the Northern Atlantic Boreal province (bioregion classified by the study). In this sense, considering the accessibility and the possible environmental preferences of the species, we do not consider that the cerianthid will naturally reach the highlighted regions of the South Atlantic Ocean in the model.

Figure 8. Ensemble of the environmental suitability of *Pachycerianthus borealis*. Areas of high suitability are highlighted in maps A and B. **A**: Northwest Atlantic. **B**: NorthAmerica.

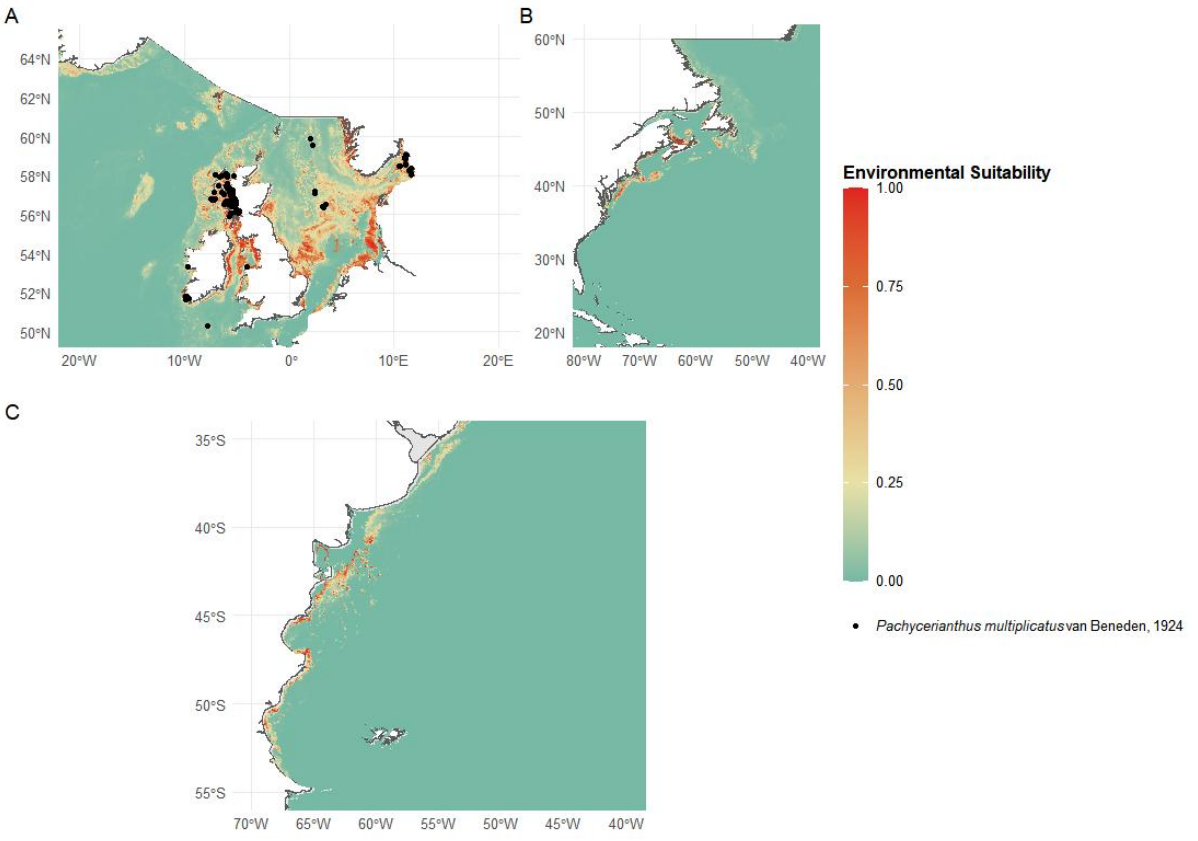


Pachycerianthus multiplicatus

The model suggests potentially suitable areas (> 50%) in Ireland, the United Kingdom, Norway, Sweden, Denmark, Germany, and France, with regions consistent with the distribution of the species, in the northeastern North Atlantic (Jonsson 2001; Stampar et al. 2020) (Fig. 9A). In addition, the projections extrapolate potentially suitable zones (> 50%) on the coast of North and South America coast (Fig. 9B-C). Furthermore, the study by Stampar et al. (2020) indicates that the actual distribution of the species is still uncertain, as the records of individuals on the coast of France and Spain have not yet been detailed, which is

worrying, since the work of Wilding and Wilson (2008) brings several descriptions regarding the tolerance or not of the species to environmental changes, and the authors reported that due to the fragmentation of the populations and the apparent limitation in larval dispersion, it is unlikely that the species will recover if its entire population is eliminated. If there are viable mature individuals nearby that can provide larvae, recovery may be possible, although it will likely take many years. The lack of data on larval dispersion and recruitment, along with the lack of knowledge about the longevity of the species, contributes to a very low recovery assessment and high sensitivity, since *Pachycerianthus multiplicatus* lives in subtidal environments with minimal thermal variations, which may indicate a intolerance to abrupt temperature changes, in which the moderate recovery capacity of the species suggests that it is highly vulnerable to local extinctions. Therefore, if the entire population is extinguished, recovery would be unlikely, as it would depend on recolonization from other existing populations.

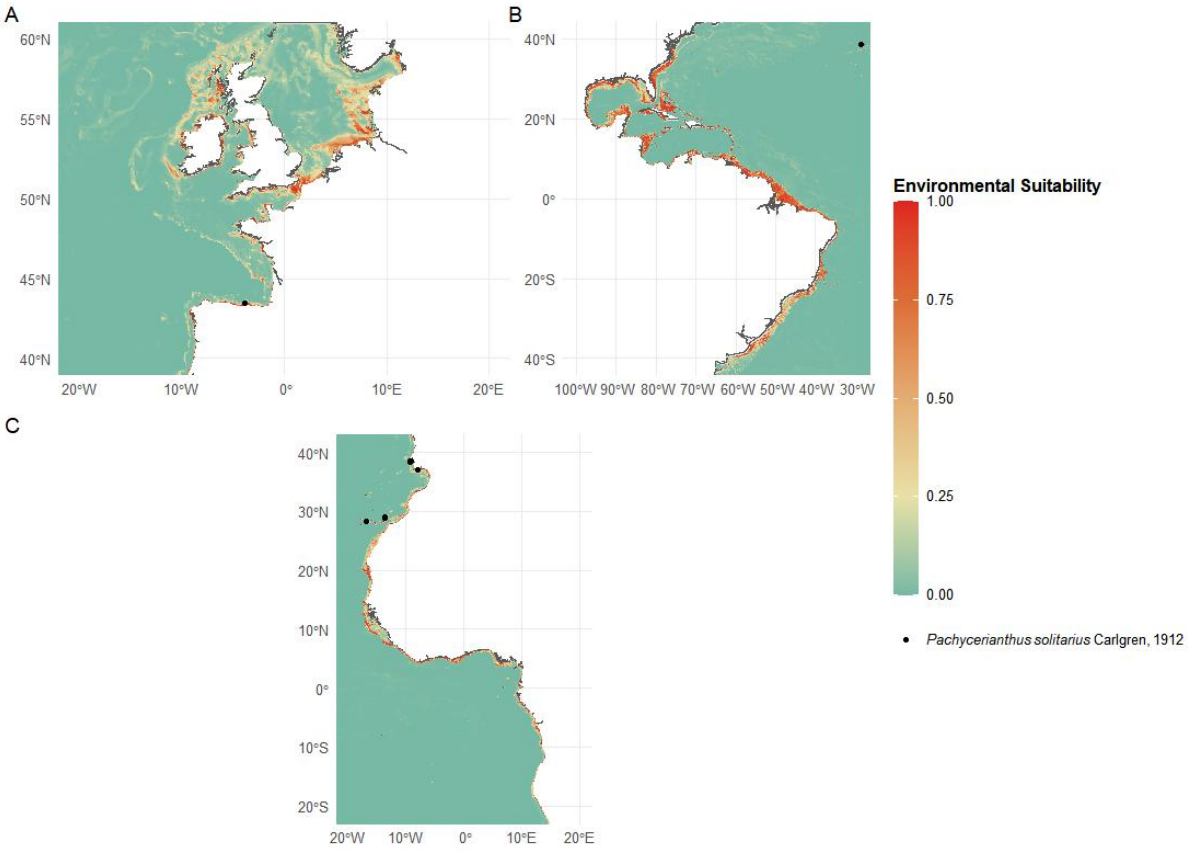
Figure 9. Ensemble of the environmental suitability of *Pachycerianthus multiplicatus*. Areas of high suitability are highlighted in maps A, B, and C. **A**: Northwest North Atlantic. **B**: North American coast. **C**: Southern South America, including regions near Uruguay and Argentina.



Pachycerianthus solitarius

The species has a known distribution in the Mediterranean Sea and the Azores (Stampar et al. 2020), in addition to being representative in the Black Sea (Boltachova et al. 2021). Interestingly, in the model, in addition to the inferred areas of suitability (> 50%) in regions of the North Atlantic (Fig. 10A), they are concentrated on the American coast, from the southern United States to South America (Fig. 10B), and on the Northwest coast of Africa (Fig. 10C).This is the only case in the study where the model, even with statistical validation, showed low performance due to a lack of biological sense since the distribution of *P. solitarius* is well established and presents a large set of occurrence points compared to other cerianthids (e.g. n = 368 in GBIF).

Figure 10. Ensemble of the environmental suitability of *Pachycerianthus solitarius.* Areas of high suitability are highlighted in maps A, B, and C. **A**: Northwest North Atlantic. **B**: Central and South America. **C**: Coast of Africa.



Final considerations

The scarcity of data on the ecology and geographic distribution of many species, including the tube anemone *Pachycerianthus solitarius*, has made it difficult to precisely

understand their habitats and predict how they will respond to environmental changes. Subsampling, that is, the collection of insufficient data in certain areas, and sampling bias, which occurs when the collected data is not representative of the total population, contribute to this knowledge gap. Distribution projections of these species, based on incomplete data, can be inaccurate and lead to erroneous conclusions. Ecological Niche Modelling emerges as a powerful tool to overcome these limitations. This technique allows for analyzing the current distribution of a species and identifying the environmental conditions key to species survival, such as temperature, salinity, and substrate type. By modeling the realized and potential ecological niche of tube anemones, we were able to map the areas of the Atlantic Ocean that offer the most suitable conditions for the survival and potential occurrence of these organisms, helping to identify priority areas for conservation and scientific exploration.

It is important to note that most studies on ceriantharians have focused on issues related to the classification and evolution of these species. Few studies have been dedicated to investigating the ecology and geographic distribution of these organisms. The present study represents an attempt to fill this gap, systematizing the available knowledge on the ecological niche of ceriantharians in the Atlantic Ocean. By generating more accurate information on the ecological needs of these species, this research contributes to the development of more effective strategies for their conservation, ensuring the preservation of marine biodiversity.

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Data Accessibility Statement

All relevant data are available in the Supplemental Material Section or can be publicly accessed through the databases described in the Materials & Methods. The RStudio scripts for the entire process of modeling, occurrence data processing, and environmental variables are provided in a GitHub repository, available for download at https://github.com/marcelapdebarros/ENM_Modelling_Scripts. The ensembles showing the potentially suitable areas for each species across the entire Atlantic Ocean are included in

Appendix A of the Supplemental Material (Maps S1–S9), and the order of species is consistent with that in the Discussion section. For further inquiries, please contact the corresponding author.

Supplemental Material

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

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

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

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

Table S4. Environmental niche of the species represented by the values extracted from environmental variables at minimum depth.

Table S5. Environmental niche of the species represented by the values extracted from environmental variables at average depth.

Table S6. Environmental niche of the species represented by the values extracted from environmental variables at maximum depth.

Appendix A. Maps S1-S9. Ensembles of the environmental suitability for all ceriantharians.

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Supplementary Material

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

Genera	Species	Number of occurrences	Reference
Arachnanthus	*oligopodus*	46	Cerfontaine, 1891

	sarsi	**112**	**Carlgren, 1912**
Brotruanthus	*mexicanus*	18	Torrey & Kleeberger, 1909
Brotrucnidifer	*novergicus*	53	Carlgren, 1912
	shtokmani	6	Molodtsova, 2006
Ceriantheomorphe	*adelita*	1	Lopes, Morandini & Stampar, 2019
	brasiliensis	19	Mello-Leitão, 1919
Ceriantheopsis	***americana***	**482**	**Agassiz in Verrill, 1864**
	austroafricanus	29	Molodtsova, Griffiths & Acuña, 2011
	lineata	0	Stampar, Scarabino, Pastorino & Morandini, 2015
	nikitai	5	Molodtsova, 2001
Cerianthus	*bathymetricus*	0	Moseley,1877
	incertus	0	Carlgren, 1932
	lloydii	**33.052**	**Gosse, 1859**
	malakhovi	3	Molodtsova, 2001
	membranaceus	**1.265**	**Gmelin, 1791**
	vogti	23	Danielssen, 1890
Isarachnanthus	***maderensis***	**21**	**Johnson, 1861**
	nocturnus	**47**	**Hartog, 1977**
Pachycerianthus	***borealis***	**1922**	**Verrill, 1873**
	curacaoensis	20	den Hartog, 1977
	dohrni	39	van Beneden, 1924
	multiplicatus	**1089**	**Carlgren, 1912**
	schlenzae	10	Stampar, Morandini & Silveira, 2014
	solitarius	**705**	**Rapp, 1829**

682

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

Species	Variable Name

Arachnanthus sarsi	Average Dissolved Molecular Oxygen
	Average Ocean Temperature
	Average Sea Water Speed
	Average Sea Water Direction
	Maximum Sea Water Direction
	Minimum Sea Water Direction
	Average Silicate
	Minimum Sea Water Speed
Ceriantheopsis americana	Minimum Salinity
	Minimum Dissolved Molecular Oxygen
	Minimum Silicate
	Minimum Sea Water Speed
	Maximum Ocean Temperature
	Maximum Sea Water Direction
	Average Sea Water Direction
	Minimum Sea Water Direction
Cerianthus lloydii	Minimum Ocean Temperature
	Maximum Nitrate
	Minimum Silicate
	Minimum Dissolved Molecular Oxygen
	Maximum Sea Water Speed
	Maximum Salinity
	Maximum Silicate
	Minimum Sea Water Speed
	Average Sea Water Speed
	Maximum Sea Water Direction
	Minimum Sea Water Direction
	Average Sea Water Direction
Cerianthus membranaceus	Average Nitrate
	Average Sea Water Speed
	Average Dissolved Molecular Oxygen
	Average Salinity

	Maximum Sea Water Direction
	Maximum Sea Water Speed
	Average Sea Water Direction
	Minimum Sea Water Speed
	Minimum Sea Water Direction
	Minimum Salinity
	Minimum Dissolved Molecular Oxygen
	Average Ocean Temperature
	Average Sea Water Speed
	Minimum Sea Water Speed
	Maximum Sea Water Speed
Isarachnanthus maderensis	Minimum Sea Water Direction
	Average Sea Water Direction
	Average Dissolved Molecular Oxygen
	Maximum Sea Water Direction
	Average Nitrate
Isarachnanthus nocturnus	Minimum Sea Water Speed
	Minimum Ocean Temperature
	Average Sea Water Speed
	Minimum Dissolved Molecular Oxygen
	Maximum Sea Water Direction
	Maximum Silicate
	Minimum Salinity
	Minimum Sea Water Direction
	Average Sea Water Direction
	Average Ocean Temperature
	Minimum Silicate
	Maximum Salinity
	Maximum Sea Water Speed
Pachycerianthus borealis	Minimum Sea Water Direction
	Average Sea Water Speed
	Average Sea Water Direction

	Minimum Dissolved Molecular Oxygen
	Maximum Sea Water Direction
	Maximum Nitrate
	Maximum Salinity
	Minimum Silicate
	Average Ocean Temperature
Pachycerianthus multiplicatus	Maximum Sea Water Direction
	Maximum Silicate
	Average Sea Water Speed
	Minimum Sea Water Direction
	Minimum Sea Water Speed
Pachycerianthus solitarius	Average Ocean Temperature
	Average Sea Water Speed
	Average Dissolved Molecular Oxygen
	Maximum Sea Water Direction
	Minimum Sea Water Speed
	Maximum Sea Water Speed
	Average Salinity

686

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

Species	Variable Name	Average Relative Importance (%)
Arachnanthus sarsi	Average Dissolved Molecular Oxygen	62
	Average Ocean Temperature	58
	Average Sea Water Speed	12
	Average Sea Water Direction	3
	Maximum Sea Water Direction	2
	Minimum Sea Water Direction	2
	Average Silicate	1
	Minimum Sea Water Speed	1
Ceriantheopsis americana	Minimum Salinity	41

	Minimum Dissolved Molecular Oxygen	39
	Minimum Silicate	38
	Minimum Sea Water Speed	38
	Maximum Ocean Temperature	12
	Maximum Sea Water Direction	6
	Average Sea Water Direction	6
	Minimum Sea Water Direction	3
Cerianthus lloydii	Minimum Ocean Temperature	39
	Maximum Nitrate	34
	Minimum Silicate	24
	Minimum Dissolved Molecular Oxygen	5
	Maximum Sea Water Speed	3
	Maximum Salinity	3
	Maximum Silicate	2
	Minimum Sea Water Speed	1
	Average Sea Water Speed	1
	Maximum Sea Water Direction	1
	Minimum Sea Water Direction	1
	Average Sea Water Direction	0
Cerianthus membranaceus	Average Nitrate	77
	Average Sea Water Speed	56
	Average Dissolved Molecular Oxygen	12
	Average Salinity	12
	Maximum Sea Water Direction	10
	Maximum Sea Water Speed	5
	Average Sea Water Direction	4
	Minimum Sea Water Speed	3
	Minimum Sea Water Direction	1
	Minimum Salinity	0
	Minimum Dissolved Molecular Oxygen	0

Isarachnanthus maderensis	Average Ocean Temperature	43
	Average Sea Water Speed	24
	Minimum Sea Water Speed	20
	Maximum Sea Water Speed	10
	Minimum Sea Water Direction	9
	Average Sea Water Direction	8
	Average Dissolved Molecular Oxygen	5
	Maximum Sea Water Direction	4
	Average Nitrate	0
Isarachnanthus nocturnus	Minimum Sea Water Speed	45
	Minimum Ocean Temperature	19
	Average Sea Water Speed	10
	Minimum Dissolved Molecular Oxygen	7
	Maximum Sea Water Direction	6
	Maximum Silicate	4
	Minimum Salinity	3
	Minimum Sea Water Direction	3
	Average Sea Water Direction	2
Pachycerianthus borealis	Average Ocean Temperature	76
	Minimum Silicate	13
	Maximum Salinity	6
	Maximum Sea Water Speed	6
	Minimum Sea Water Direction	5
	Average Sea Water Speed	4
	Average Sea Water Direction	2
	Minimum Dissolved Molecular Oxygen	2
	Maximum Sea Water Direction	1
Pachycerianthus multiplicatus	Maximum Nitrate	60
	Maximum Salinity	29
	Minimum Silicate	13

	Average Ocean Temperature	10
	Maximum Sea Water Direction	9
	Maximum Silicate	9
	Average Sea Water Speed	6
	Minimum Sea Water Direction	5
	Minimum Sea Water Speed	4
Pachycerianthus solitarius	Average Ocean Temperature	83
	Average Sea Water Speed	40
	Average Dissolved Molecular Oxygen	11
	Maximum Sea Water Direction	7
	Minimum Sea Water Speed	6
	Maximum Sea Water Speed	5
	Average Salinity	0

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690 **Table S4.** Environmental niche of the species represented by the values extracted from
691 environmental variables at minimum depth.

	Variable Name						
Species	DMO	NO3	OT	Sal	SWD	SWS	Sil
Arachnanthus sarsi	249,56 ± 31,20	1,62 ± 0,05	6,89 ± 0,79	34,07 ± 0,56	49,67 ± 24,90	0,06 ± 0,02	2,63 ± 0,90
Ceriantheopsis americana	232,56 ± 33,34	1,15 ± 0,01	4,60 ± 2,15	31,28 ± 2,45	43, 90 ±19,36	0,06 ± 0,05	2,73 ± 1,94
Cerianthus lloydii	238,58 ± 24,26	2,60 ± 0,59	6,12 ± 1,43	34,34 ± 1,93	41,65 ± 34,96	0,084 ± 0,06	3,41 ± 1,21
Cerianthus membranaceus	226,60 ± 20,94	0,03 ± 6,50	13,48 ± 3,22	35,04 ± 0,63	72,38 ± 26,43	0,146 ± 0,10	0,89 ± 14,57
Isarachnanthus maderensis	177,70 ± 53,51	14,02 ± 9,20	10,80 ± 6,53	35,37 ± 0,46	65,75 ± 92,76	0,20 ± 0,14	6,07 ± 11,13
Isarachnanthus nocturnus	195,72 ± 25,33	0,03 ± 10,66	21,31 ± 7,59	35,16 ± 1,60	26,06 ± 88,17	0,28 ± 0,13	3,50 ± 7,28
Pachycerianthus borealis	164,79 ± 70,20	4,31 ± 6,82	3,58 ± 2,68	32,83 ± 1,77	55,86 ± 31,66	0,10± 0,089	4,55 ± 8,09
Pachycerianthus multiplicatus	246,80 ± 20,24	1,23 ± 2,40	5,97 ± 1,70	33,66 ± 3,10	30,85 ± 41,92	0,07 ± 0,05	3,25 ± 1,33
Pachycerianthus solitarius	225,50 ± 20,51	0,23 ± 3,74	13,12± 1,83	35,51 ± 0,82	65,44 ± 28,10	0,17 ± 0,05	1,50 ± 1,15

692 **DMO**: Dissolved Molecular Oxygen; **NO3**: Nitrate; **OT**: Ocean Temperature; **Sal**: Salinity; **SWD**: Sea Water
693 Direction; **SWS**: Sea Water Speed; **Sil**: Silicate

694

695 **Table S5.** Environmental niche of the species represented by the values extracted from
696 environmental variables at average depth.

Species	Variable Name						
	DMO	NO3	OT	Sal	SWD	SWS	Sil
Arachnanthus sarsi	279,02 ± 24,87	1,73 ± 3,18	10,52 ± 0,43	34,78± 0,33	94,63 ± 90,50	0,049 ± 0,03	5,23 ± 2,35
Ceriantheopsis americana	288 ± 33,47	0,95 ± 3,11	8,35 ± 5,90	32,13 ± 1,65	198,27 ± 66,63	0,01 ± 0,11	5,36 ± 4,30
Cerianthus lloydii	271,13 ± 16,25	3,48 ± 3,49	9,71 ± 1,92	34,86 ± 1,09	118,30 ± 82,97	0,027 ± 0,03	6,82 ± 2,89
Cerianthus membranaceus	250,97 ± 13,98	1,31 ± 6,52	15,35 ± 3,93	35,54 ± 0,32	141,94 ± 48,50	0,042 ± 0,041	1,80 ± 14,55
Isarachnanthus maderensis	191,04 ± 46,94	14,93 ± 9,64	13,37 ± 7,27	35,70 ± 0,57	203,20 ± 92,80	0,14 ± 0,15	7,02 ± 11,28
Isarachnanthus nocturnus	204,25 ± 25,01	0,44 ± 11	24,19 ± 8,00	35,93 ± 0,81	215,72 ± 0,177	0,08 ± 7,46	5,45 ± 7,46
Pachycerianthus borealis	195,25 ± 70,36	10,62 ± 7,05	8,05 ± 2,56	33,78 ± 1,53	200,81 ± 76,40	0,01 ± 0,03	11,84 ± 11,57
Pachycerianthus multiplicatus	273,47 ± 14,68	3,52 ± 2,94	9,70 ± 1,36	34,57 ± 2	220,94 ± 90,10	0,02 ± 0,02	6,60 ± 2,567
Pachycerianthus solitarius	238,14 ± 25,47	1,95 ± 4,50	16,04 ± 2,07	35,96 ± 0,38	135,75 ± 67,78	0,04 ± 0,02	2,42 ± 1,58

697 **DMO**: Dissolved Molecular Oxygen; **NO3**: Nitrate; **OT**: Ocean Temperature; **Sal**: Salinity; **SWD**: Sea Water
698 Direction; **SWS**: Sea Water Speed; **Sil**: Silicate

699

700 **Table S6.** Environmental niche of the species represented by the values extracted from
701 environmental variables at maximum depth.

Species	Variable Name						
	DMO	NO3	OT	Sal	SWD	SWS	Sil
Arachnanthus sarsi	309,23 ± 12,49	5,70 ± 3,17	14,72 ± 1,37	35,28 ± 0,133	235,60 ± 50,30	0,157 ± 0,10	9,95 ± 4,27
Ceriantheopsis americana	342,31 ± 35,70	3,84 ± 5	15,9 ± 5,9	32,81 ± 1,31	227,14 ± 53,7	0,08 ± 0,17	10,62 ± 7,31
Cerianthus lloydii	307,36 ± 13,44	7,11 ± 3,62	14,06 ± 3,62	35,24 ± 0,49	235 ± 57	0,12 ± 0,10	11,16 ± 6,31

Cerianthus membranaceus	274,06 ± 13,30	4,54 ± 5,967	18,85 ± 5,17	36,12 ± 0,38	204,09 ± 26,85	0,15 ± 0,05	3,77 ± 14,24
Isarachnanthus maderensis	199,85 ± 39,76	17,03 ± 10,12	16,30 ± 8,24	35,83 ± 0,65	274,60 ± 89,07	0,115 ± 0,26	9,54 ± 11,58
Isarachnanthus nocturnus	211,25 ± 26,53	2,30 ± 11,11	26,33825 ± 8,447516	36,60 ± 0,69	287,13 ± 81,26	0,30 ± 0,23	7,75 ± 7,48
Pachycerianthus borealis	255,54 ± 68,58	15,21 ± 6,40	13,03 ± 4,15	34,65 ± 4,15	243,10 ± 38,10	0,08 ± 0,09	164,80 ± 15,74
Pachycerianthus multiplicatus	309,24 ± 20,29	7,23 ± 2,74	13,80 ± 3,10	35,17 ± 0,70	263,60 ± 55,50	0,09 ± 0,07	10,61 ± 5,75
Pachycerianthus solitarius	257,61 ± 31,28	4,76 ± 4,57	19,17 ± 3,13	36,36 ± 0,30	247,52 ± 54,50	0,18 ± 0,05	4,39 ± 1,97

DMO: Dissolved Molecular Oxygen; **NO3**: Nitrate; **OT**: Ocean Temperature; **Sal**: Salinity; **SWD**: Sea Water Direction; **SWS**: Sea Water Speed; **Sil**: Silicate

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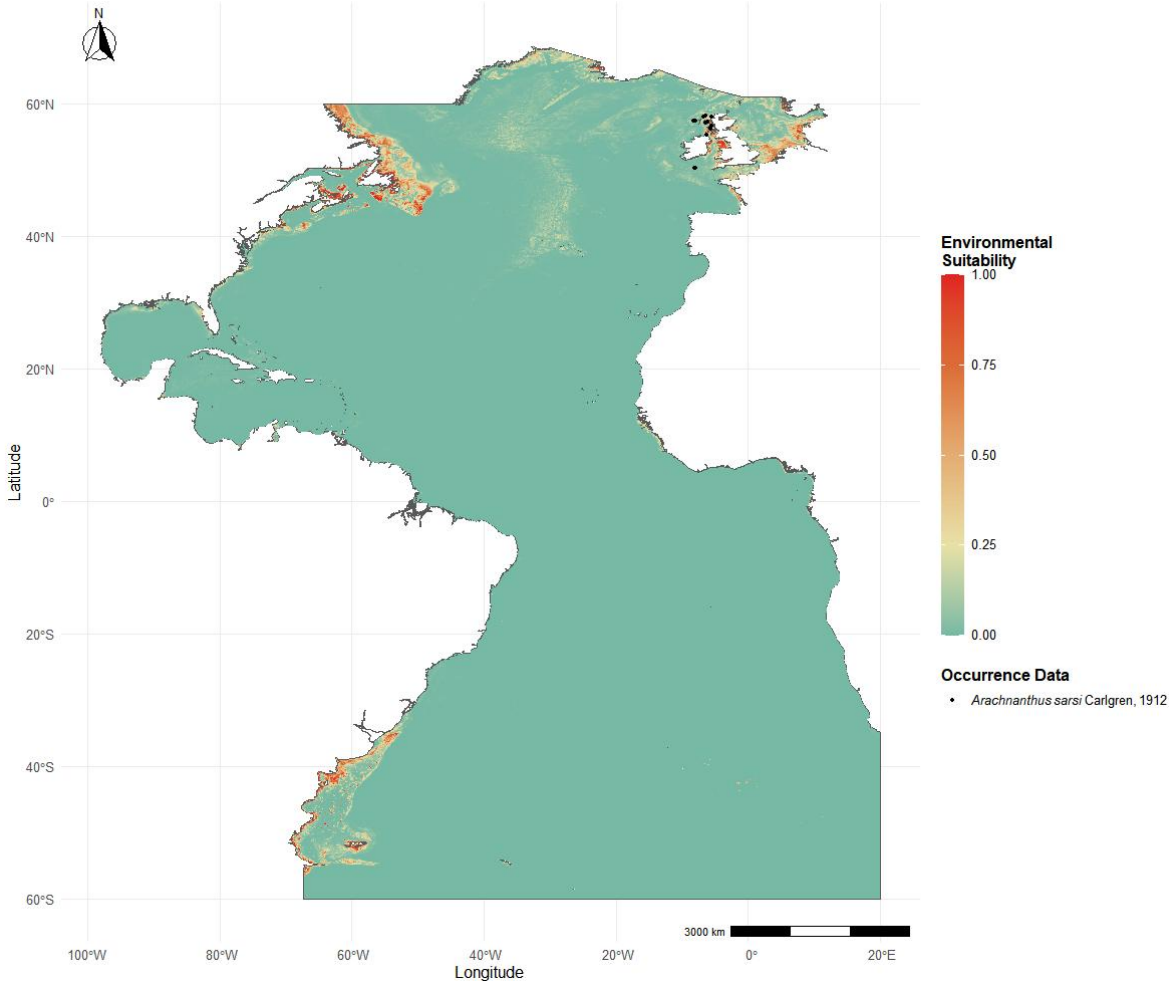
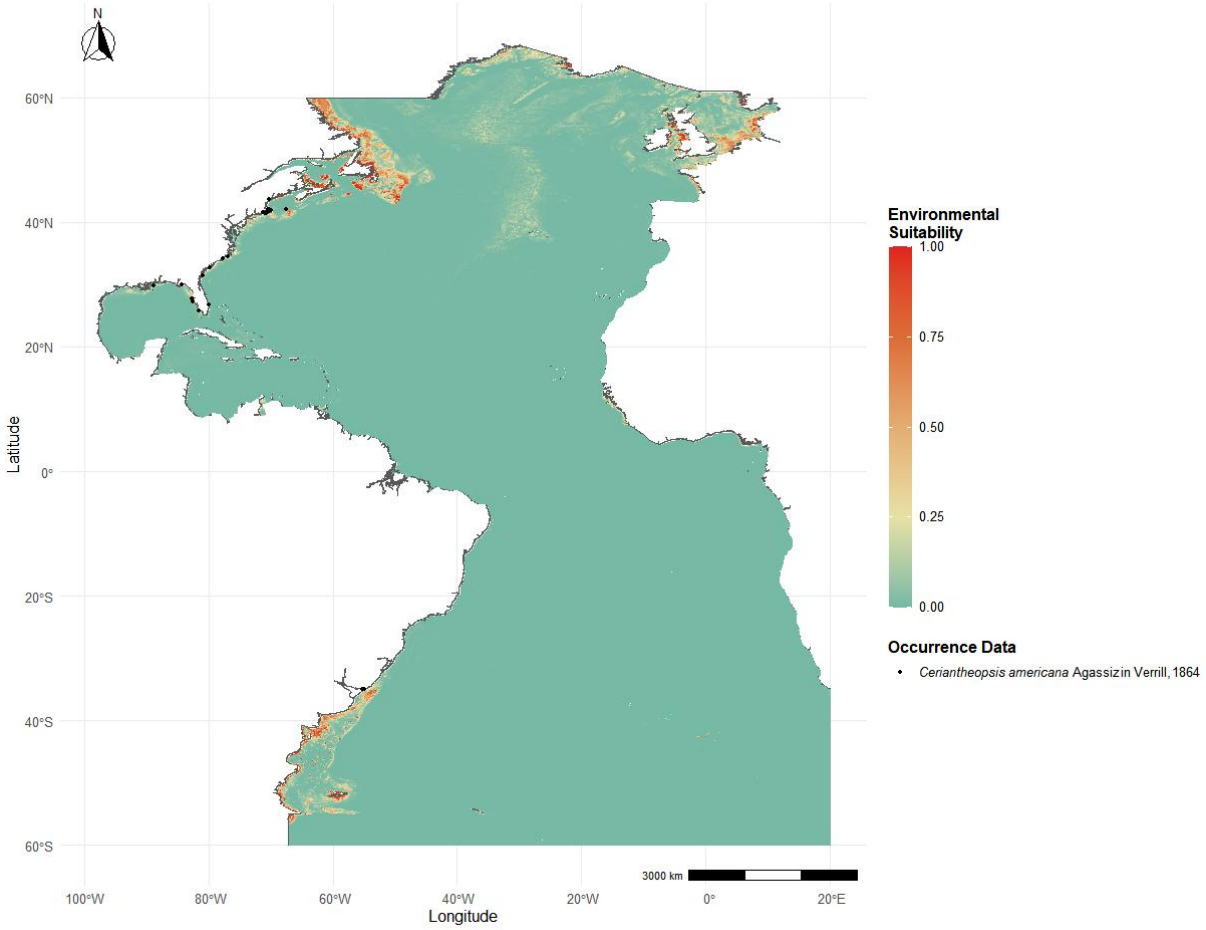
Appendix S1. Ensembles of the environmental suitability for all ceriantharians.

Map S1. Ensemble of the environmental suitability of *Arachnanthus sarsi*.



742 **Map 2.** Ensemble of the environmental suitability of *Ceriantheopsis americana*.



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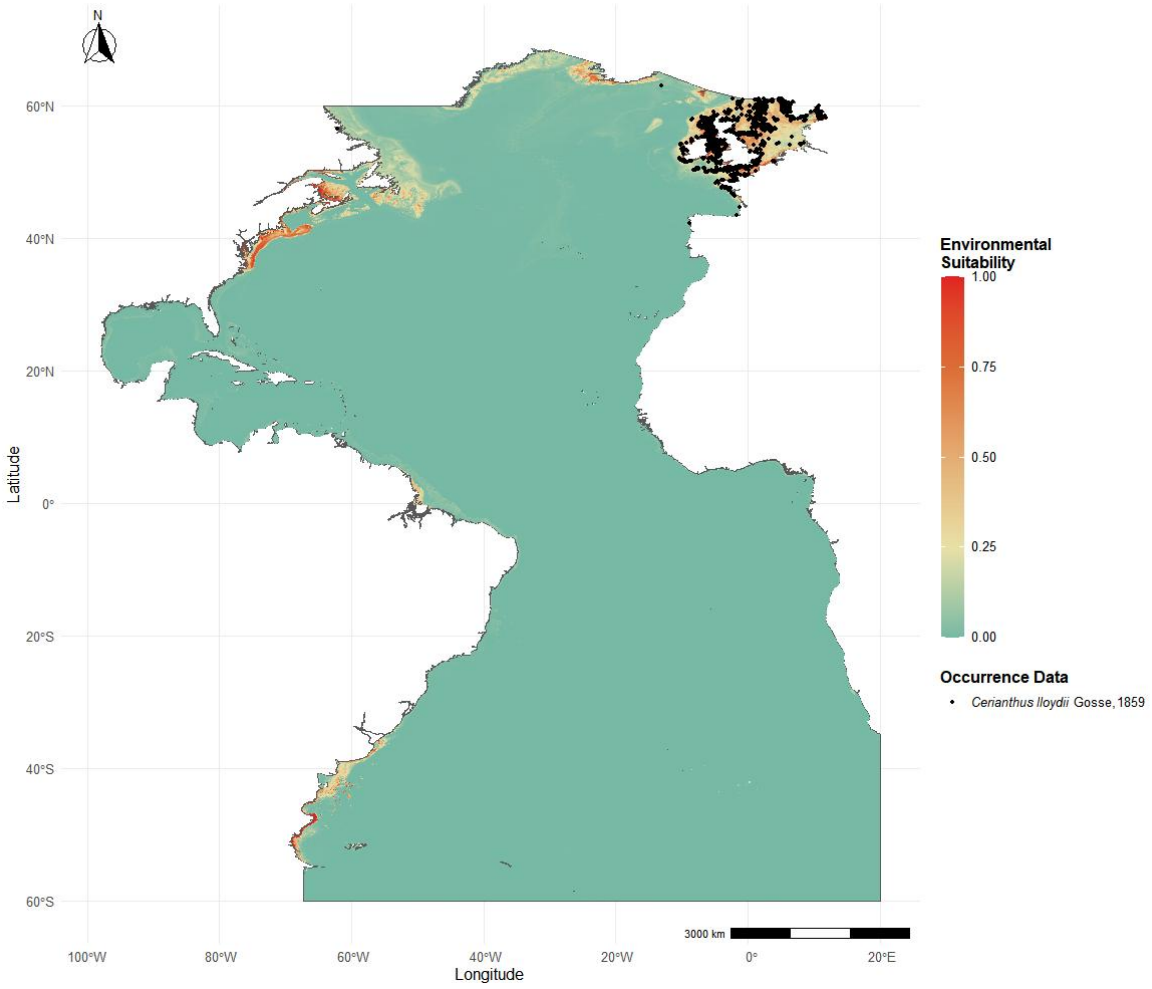
763 **Map 3.** Ensemble of the environmental suitability of *Cerianthus lloydii*.



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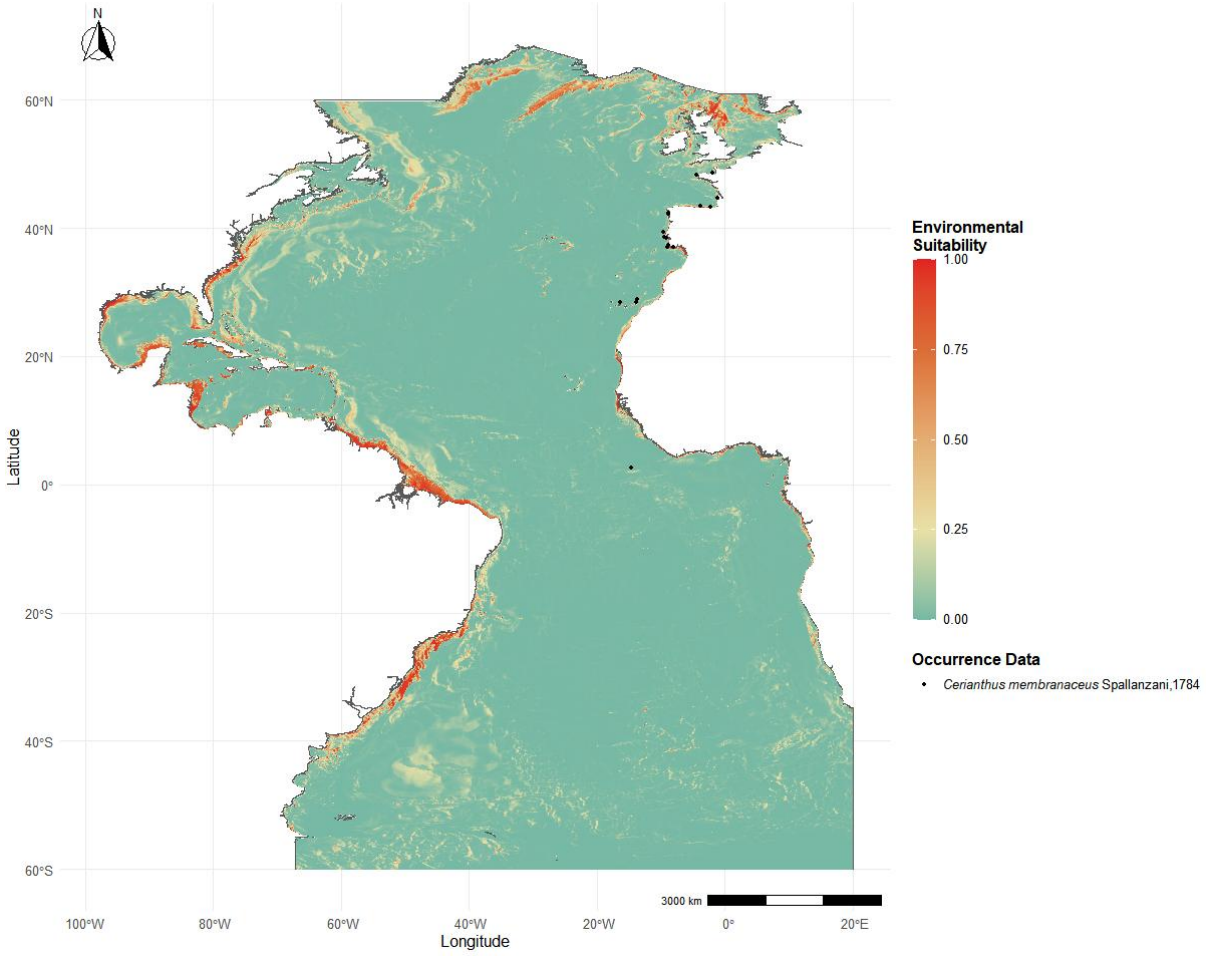
780 **Map 4.** Ensemble of the environmental suitability of *Cerianthus membranaceus*.



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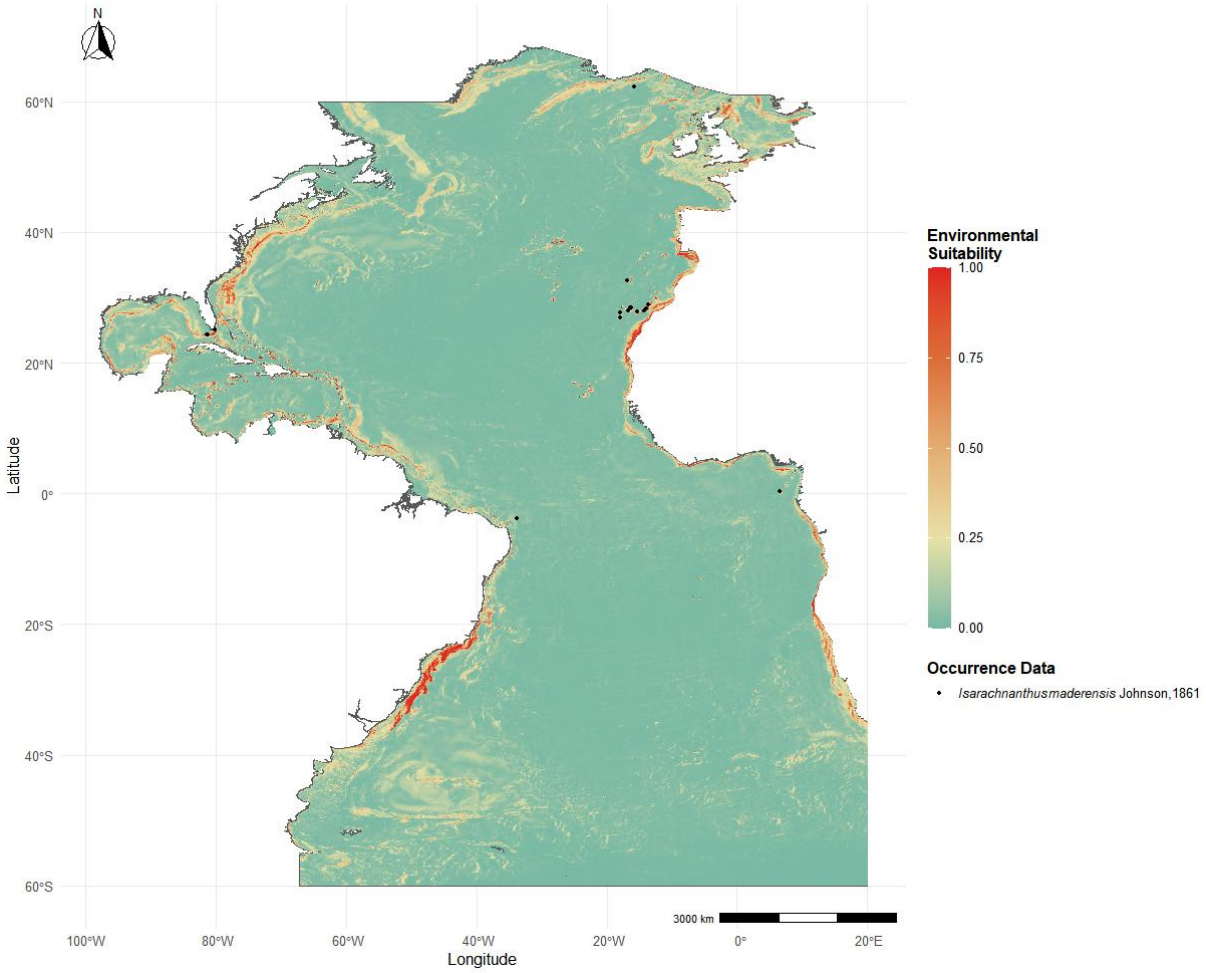
799 **Map 5.** Ensemble of the environmental suitability of *Isarachnanthus maderensis.*



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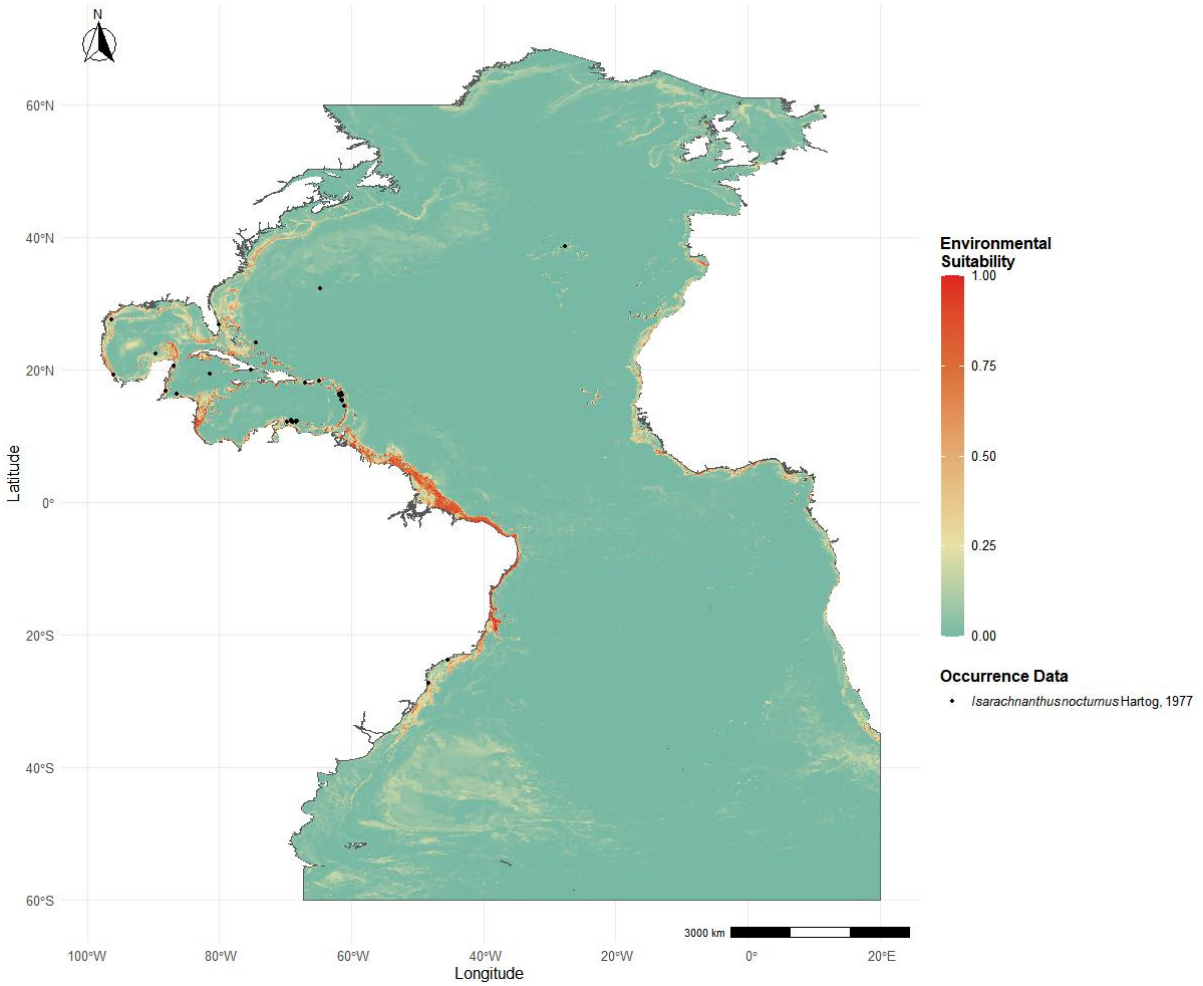
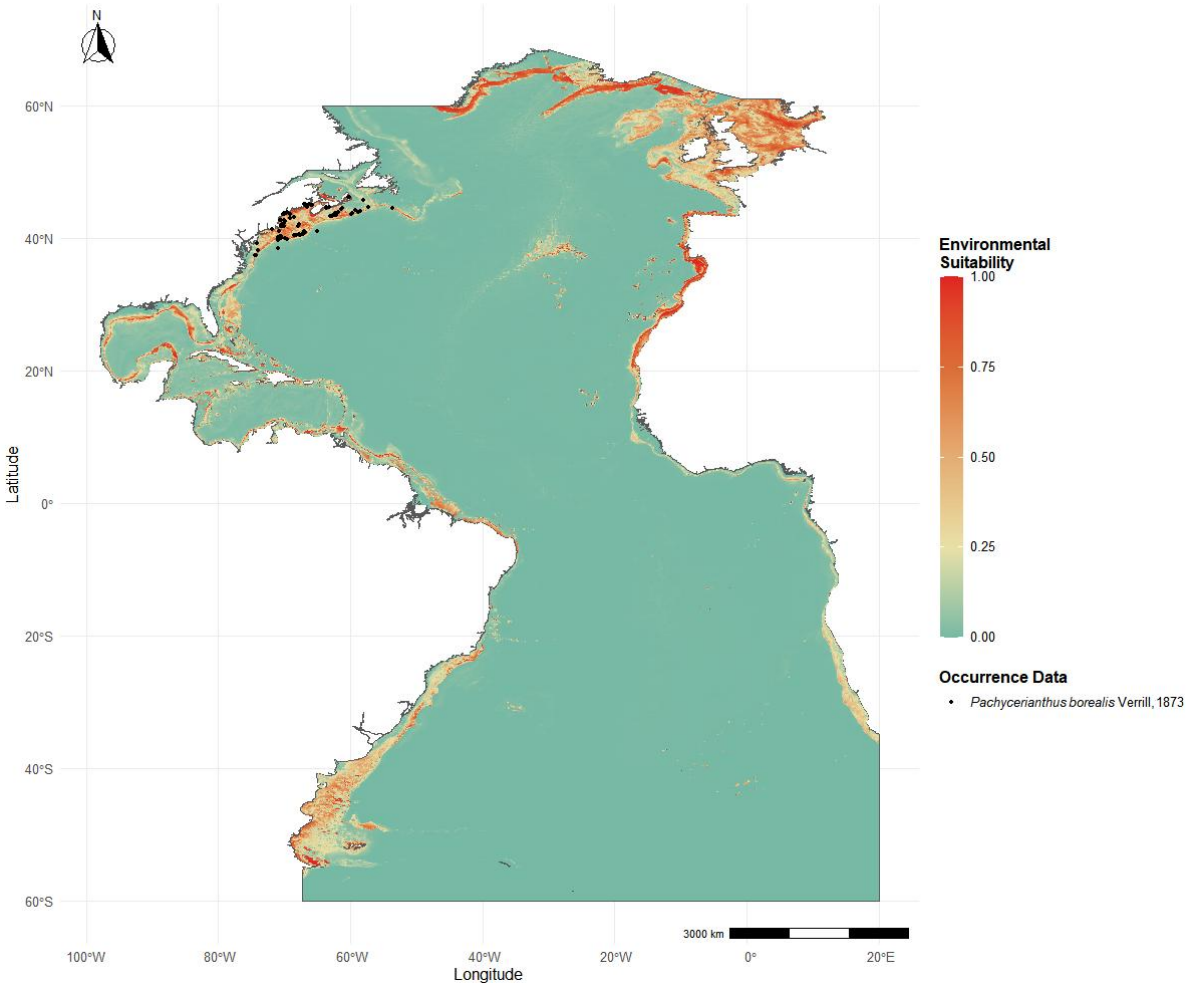
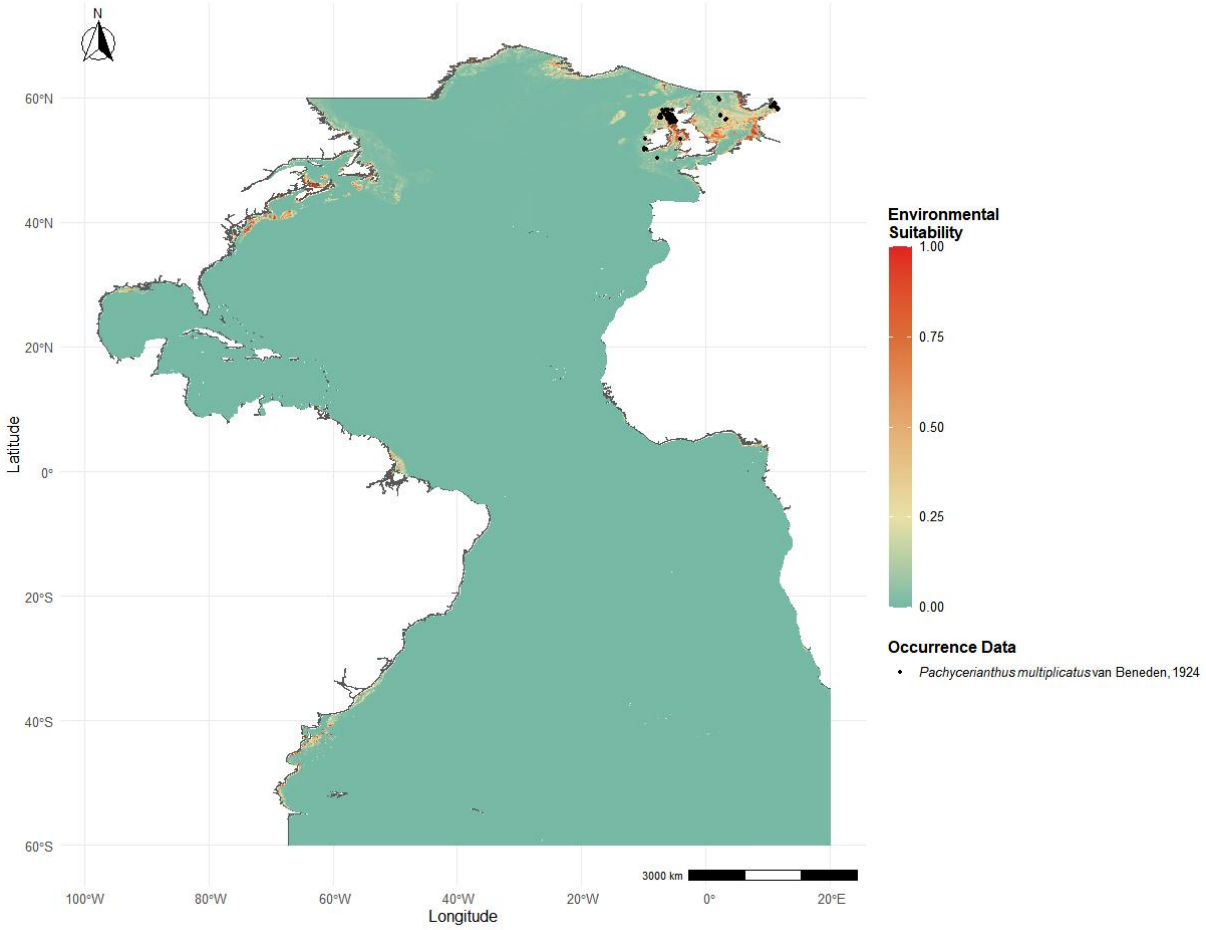
Map 6. Ensemble of the environmental suitability of *Isarachnanthus nocturnus.* Areas of high suitability are highlighted in maps A, and B.



Map 7. Ensemble of the environmental suitability of *Pachycerianthus borealis.*



860 **Map 8.** Ensemble of the environmental suitability of *Pachycerianthus multiplicatus*.



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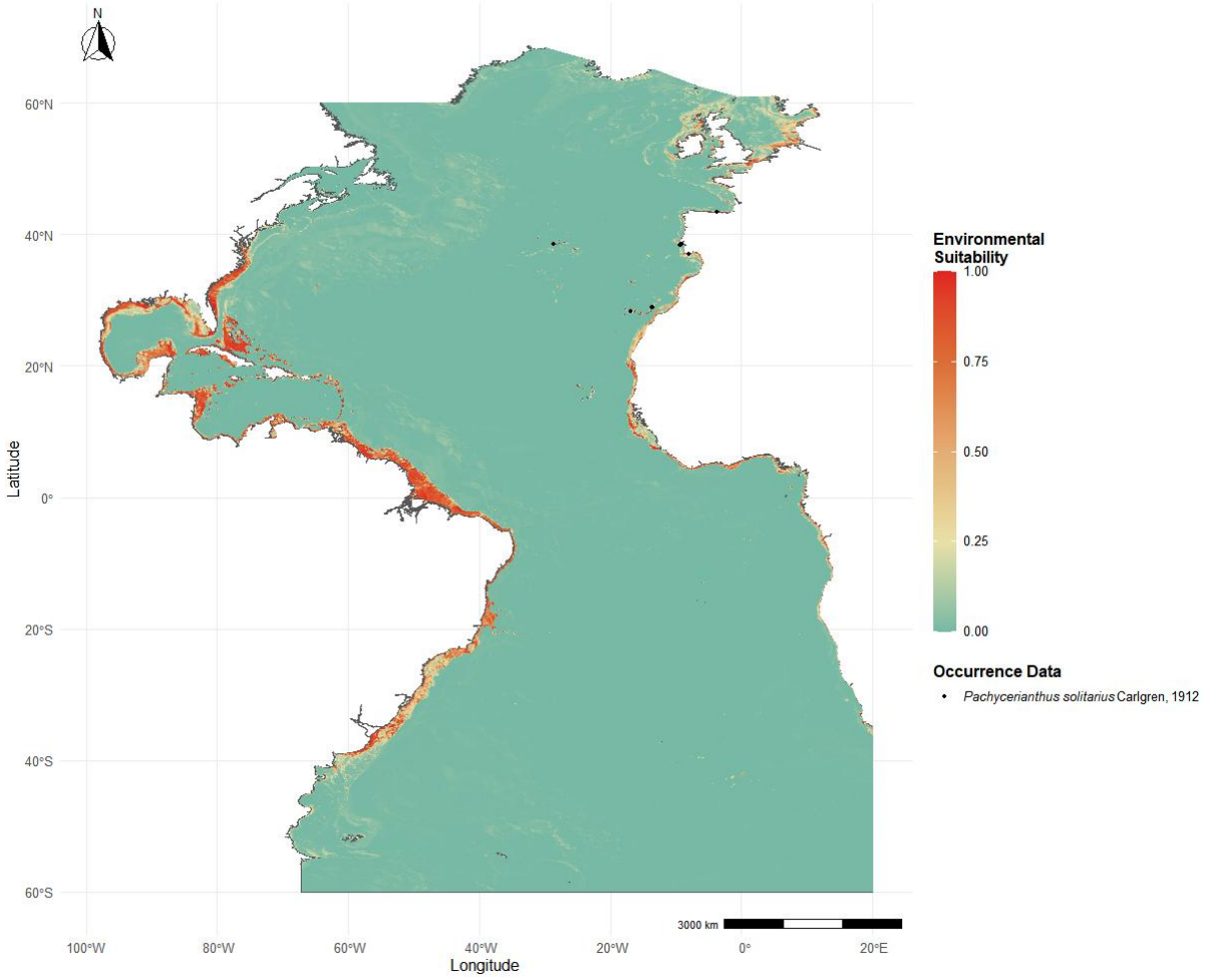
881 **Map 9.** Ensemble of the environmental suitability of *Pachycerianthus solitarius.*



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