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ORIGINAL PAPER

Distribution of sea anemones in the Southwest Atlantic: biogeographical patterns and environmental drivers

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Abstract

In this paper, we explore spatial patterns of shallow-water sea anemones in the Southwest Atlantic (SWA). The following hypotheses were tested: (1) the distribution of sea anemones (Actiniaria and Corallimorpharia) corroborates SWA biogeographic provinces, (2) their distribution presents a richness peak at mid-latitudes, and (3) temperature is the main abiotic driver that structures their species composition. Occurrences/registries were obtained mainly from published sources. We adopted Sørensen dissimilarity and cluster analyses to compare fauna compositions. To verify latitudinal richness patterns, we used a Hill's numbers approach through rarefaction and extrapolation techniques. Partial redundancy analysis was performed to identify which drivers contribute more to the distribution. The sea anemone faunas are congruent with the following SWA provinces: Brazilian province (BP, 0 to 33° S), Argentinian province (36 to 43° S), and Patagonian province (43 to 56° S), and all differ from the Caribbean province (CP). Although there is a high similarity among the BP and the CP, they form significant clusters with well-supported endemism levels (> 19%). An elevated richness was found at 19–23° S, in the BP southeast (34 spp. and 13% of endemism), supporting an SWA biodiversity center. Temperature explained 64% of the distribution, and the Amazonas-Orinoco and La Plata estuaries act as soft barriers. The sea anemone distribution can be explained by features of the local current systems, combined with isolation through barriers and different ecological tolerances. Furthermore, the patterns reported herein (unprecedented for the group) are similar to those of other marine taxa. A transition zone between tropical and subtropical waters indicates diversity and species accumulation in the SWA.

Keywords Biogeography · Endemism · Brazil · Caribbean · Actiniaria · Corallimorpharia

Introduction

The central focus of biogeography is to understand distribution patterns observed in nature, examining organisms in space and time, which is mostly done by establishing endemic areas, biogeographic sectors, and centers of origin (Procheş 2005; Posadas et al. 2006; Juárez-Barrera et al. 2018). Such knowledge is fundamental for biodiversity conservation (Dittus 2017), at both local and global scales. The marine environment challenges biogeographic studies on account of its size, three-dimensionality (depth fashions an important gradient), and gaps in ecological and taxonomic data for several taxa and geographic regions (Miloslavich et al. 2011; Appeltans et al. 2012; Bentlage et al. 2013; Costello et al. 2017). In recent decades, information has advanced, allowing identifying and assessing areas of endemism, centers of origin, and hotspots for many marine taxa (Briggs 2003; Costello et al. 2012, 2017). Examples are the identification of a marine invertebrate hotspot in southern Chile (Fernández et al. 2000), a biodiversity center based on reef fish in Brazil (Pinheiro et al. 2018), patterns of endemism for reef fauna (DiBattista et al. 2016), and more (see Hoeksema 2007; Cowman and Bellwood 2013; Cowman

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et al. 2017). All this information contributes to the understanding of marine biota and their conservation.

The Southwest Atlantic (SWA) has historically been divided into three provinces, i.e., the Brazilian province, the Argentinian province (including Uruguay), and the Patagonian province (Miloslavich et al. 2011; Briggs and Bowen 2012, 2013). Among these provinces, two main barriers were identified: (1) the Amazonas-Orinoco estuary on the northernmost limit of the Brazilian province and (2) the La Plata River further south on the continent and west from the Mid-Atlantic Ridge. Both are categorized as soft barriers for some taxa, such as coral and reef fishes (Fortes and Absalão 2004; Cordeiro et al. 2015; Toonen et al. 2016; Moura et al. 2016). Currents and water bodies contribute to the division between those provinces, whereas isolated oceanic islands also have a major role in this separation concerning endemism and species composition (Fortes and Absalão 2004; Pinheiro et al. 2018).

However, contrary to what is found in terrestrial environments, the latitudinal pattern of diversity (with a reduction of diversity towards the poles) was not confirmed for several marine taxa, such as sea anemones, foraminifera, and oceanic sharks (Tittensor et al. 2010; Miloslavich et al. 2011; Fautin et al. 2013; Chaudhary et al. 2016). This was also observed in the SWA for reef fishes and benthic organisms for which a higher diversity at intermediate latitudes was found (Gappa 2000; De Léo and Pires-Vanin 2006; Pinheiro et al. 2018). As for the Brazilian coast, Aued et al. (2018) found a lower diversity in the tropics for the shallow-water benthic community (ranging from cyanobacteria, turf algae to coral, and other invertebrates) with a peak at mid-latitudes (between 20 and 23° S). On the other hand, sub-province delimitation, fauna composition, and relationships in SWA and neighboring regions are still the focus of several debates and studies (see Andrades et al. 2018).

It is still unclear how the SWA biota has been influenced by the Caribbean province, which is recognized as the main marine biodiversity center of the Atlantic Ocean (Joyeux et al. 2001; Briggs and Bowen 2013). Nonetheless, the endemism found in SWA shows that oceanic island isolation, locally limited patterns, alterations in landmasses (e.g., the rise of Panama isthmus), ocean currents, and water masses had a key role in the diversification of biota (Pinheiro et al. 2018). Despite various studies, there is still a gap in our knowledge regarding the distribution patterns of several taxa in the SWA, as well as in identifying which drivers shape the distributions and historical relations with other provinces.

Sea anemones sensu lato (orders Actiniaria and Corallimorpharia) (Acuña et al. 2013) and other members of the anthozoan subclass Hexacorallia are important to the benthic community, being dominant or abundant in many habitats (Daly et al. 2007; Selander et al. 2010; Gomes et al. 2016). Besides, populations of sea anemones endure little variation in the face of short climate changes (Häussermann and Försterra 2005); have a wide latitudinal, longitudinal, and bathymetric distribution; and occur in all oceans and marine habitats (Daly et al. 2008; Fautin et al. 2013; Rodríguez et al. 2014). This makes sea anemones a suitable model group to study zoogeographic patterns and trend analyses (Riemann-Zürneck 1986). Chaudhary et al. (2017) suggest that temperature has a strong influence on the latitudinal gradient in species richness, as a predictor of biogeographic distributions, particularly because it has a fundamental role in several aspects of animal biology. Aspects of sea anemone biology and ecology, such as physiology, reproduction, and dispersal, are strongly linked to temperature tolerance and gradients, while other factors, such as substrate and salinity, also could play a role in the occurrence of sea anemones (Whalan et al. 2015; Ryan 2017; Gambill et al. 2018; Watson et al. 2018; Glon et al. 2019).

Although sea anemones have been studied in the SWA since the nineteenth century, with an intensification of taxonomic studies in the 1960s/1970s, this group still lacks a broad biogeographic analysis. Considering only taxonomic composition, the SWA sea anemone faunas seem more similar to those of the Caribbean region (Zamponi et al. 1998a), but comprehensive approaches, including environmental drivers that condition their species ranges, were never evaluated.

Here, we present a biogeographic analysis of the distribution of shallow-water sea anemones in the SWA and also access abiotic drivers that shape this pattern. The following hypotheses were tested: (1) the distribution of sea anemones corroborates SWA biogeographic provinces; (2) their distribution is not homogeneous, presenting a richness peak at mid-latitudes (as in other taxa); and (3) temperature is the main abiotic driver that structures their species composition.

Material and methods

Data matrices

Our data covers the entire SWA: Brazilian province (BP, 0 to 33° S) (Miloslavich et al. 2011), Argentinian province (AP, including Uruguay, 36 to 43° S), and Patagonian province (PP, 43 to 56° S) (Miloslavich et al. 2011; Briggs and Bowen 2012, 2013). To compare fauna composition and similarity, we included the Caribbean province (CP), delimited according to Petuch (2013), which includes Antilles, South America, Central America country coasts and South Florida.

The presence points of all valid sea anemone species occurring at depths down to 50 m were considered in this study. This bathymetric limit was chosen because detailed and precise marine invertebrate data is mostly available for this range (Scarabino 2006). Records and occurrences were obtained from open access and georeferenced database such as Ocean Biogeographic Information System (OBIS; https://obis.org/)

and mainly from Hexacorallians of the world (Fautin 2013) available at http://hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm. The latter is maintained and revised by sea anemone taxonomists, and its data is derived from published research. We also used online catalogs of museum collections: National Museum of Natural History-Smithsonian Institution (USA), Museo de La Plata (Argentina), and Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Argentina). Literature records that include species records in SWA and the Caribbean province (checklists, inventories, research papers) were included. We analyzed material from museum collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP; Brazil) and the Museu Nacional from Universidade Federal do Rio de Janeiro (MNRJ) (Latin America's largest Cnidarian collection), and unidentified records with reference material were assessed and compared. The collection from the Anthozoarian Research Group (GPA-UFRPE) was also revised. In all cases, to ensure data reliability, only material recorded, confirmed, or identified by taxonomists was used. In addition, the current classification of sea anemones, synonymy, and the taxonomic status were cross-checked with their names in the electronic databases HoW (Fautin 2013) and World Register of Marine Species (WoRMS Editorial Board 2020). All identifications followed Carlgren (1949) and published articles about genera and species cited in this work. We considered data published and available in databases until June 2018. These references are found in Tables S1, S2, and S3, as well as the cited online databases.

All georeferenced records were plotted in maps made in QGIS 3.6 (Fig. 1). Onward, a 5° longitude-by-5° latitude cell grid was placed on the study area and a binary (presence-only) matrix was generated to be used in statistical analyses. In this way, 16 grid cells were obtained for the Brazilian province, 17 for the Caribbean province, five for the Argentinian province, and five for the Patagonian province (Fig. 1), which were treated as sample units. As the provinces had a different number of grid cells, we calculated the weighted richness (species divided by the number of grid cells) for comparisons across provinces.

To assess the main drivers that influence sea anemone distribution, we gathered abiotic data: temperature, salinity, and substrate type. Data were obtained from the National Oceanic and Atmospheric Administration (NOAA) database (at https://www.nodc.noaa.gov/access/index.html), sampling cruises recorded temperature, and salinity in the water column in 5-m isobath intervals, date, and precise coordinates were also available with each abiotic record. This was crossed with each species occurrence; so, the same date, depth, and location sampling were used to complete the matrix. For the substrate, we only considered two categories: unconsolidated and consolidate. This data is widely available in sampling records. We only used abiotic records where all data were complete. In this regard, due to data reliability and access, only Brazilian province records were used for this aspect.

Brazilian province matrix data resulted in 262 records (Table S1). Of these records, 134 (50.5%) are from research papers and HoW. Additionally, data from museums corresponds to 128 records (48.3%). In the Caribbean province, 453 records (Table S2) were obtained, 88% (401 records) from research papers and HoW. In the Argentinian and Patagonian provinces, 100 records were obtained (Table S3), mostly from HoW, OBIS, and research papers, and only five records were from museums.

Statistical analysis

We used species grid cells to create a binary matrix and evaluate SWA province fauna composition differences (comparing also with the Caribbean) (Fig. 1). From the province matrices, another matrix was generated using the Sørensen dissimilarity coefficient (distance), based on working with incidence (presence-only) data. Unweighted pair group method using arithmetic mean (UPGMA) analyses were performed, and subsequently, a non-metric multidimensional scaling (nMDS) was performed. Similarity profile (SIMPROF) analysis (Clarke et al. 2008) was employed to test if the groups found in the cluster were significantly different. These analyses were performed in PRIMER v7 software (Clarke et al. 2014). To estimate sea anemone fauna richness in the SWA and the Caribbean, we used Chao2 using the software EstimateS 9.

We applied sample-based rarefaction and extrapolation using Hill's diversity to assess if there is a peak in SWA richness in mid-latitudes. We created a matrix of species incidence using the SWA grid cells that contained occurrence records for each species and associated each grid cell with the number of research work (only published data, excluding museum records), thus representing the sampling effort. To get more reliable occurrence data, grids with less than three species and less than four research works were excluded (B1 and B14). As our data had presence-only occurrences, we used $q = 0$ as Hill's order. Then, we performed an extrapolation, doubling the sample sizes ($n = 64$), to estimate richness in the SWA related to the latitudinal gradient. The same method was applied when interpolating, estimating richness in the SWA, using the lowest sampling effort ($n = 4$). This method allows us to standardize and bootstrap the sampling efforts for all SWA, thus reducing the bias, with a 95% confidence interval. These analyses were executed through the "iNext" package (Hsieh et al. 2016) in R 3.4 software (R Core Team 2016).

To understand which drivers contribute more to the spatial distribution of sea anemones, the partial redundancy analysis (RDA) was used. Grid cells B1 and B6 in the Brazilian coast had few or none abiotic data available and, thus, were removed from the analysis as well as some species with incomplete records (Table 1). The test identifies relations between response variables (species presence/absence) which are explained by a set of explanatory variables (temperature, salinity, and

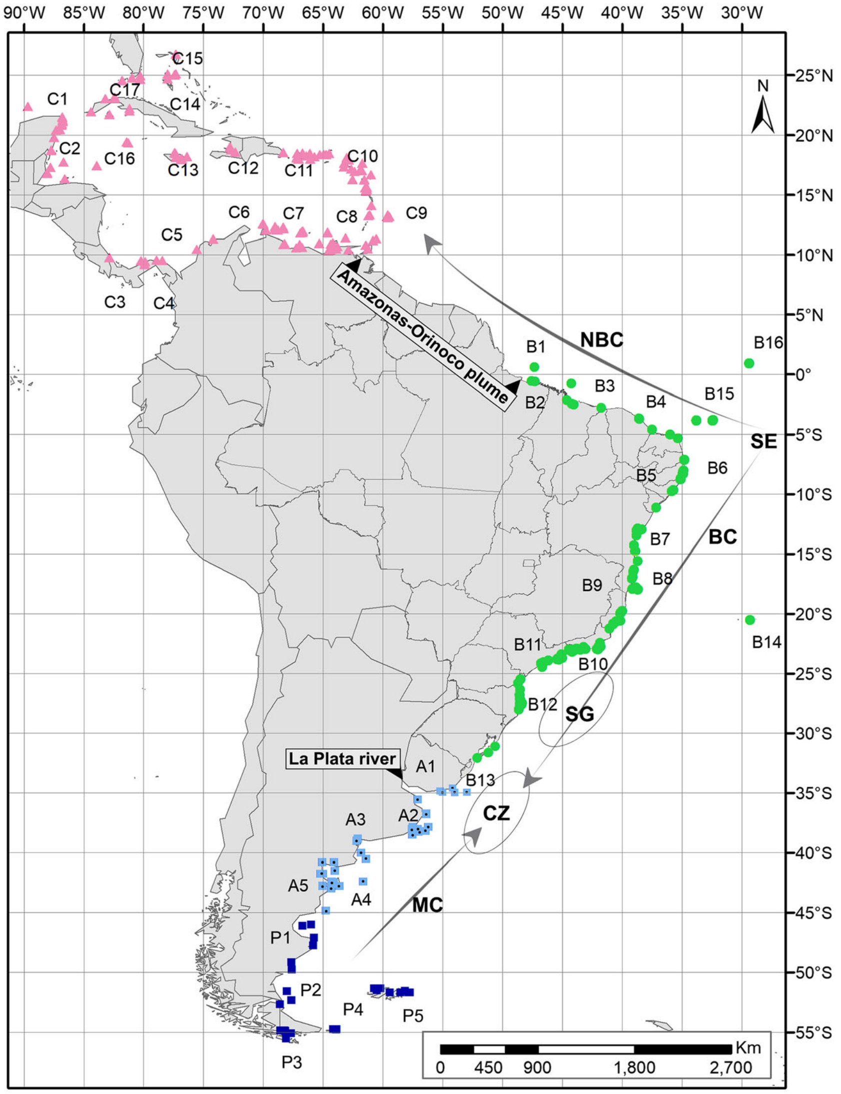


Fig. 1 Map of shallow-water sea anemone occurrences in the SWA (circle, Brazilian province; square with dot, Argentinian province; square, Patagonian province) and Caribbean provinces (triangle), in addition, currents and major biogeographic barriers location. NBC, North Brazilian Current; SE, South Equatorial Current; BC, Brazilian Current; SG, subtropical gyre; CZ, confluence zone; MC, Malvinas Current

substrate). Since natural variation can exist in the latitudinal and longitudinal gradients, the exclusion of spatial variation in the analysis was necessary. Thus, a principal coordinates of neighbor matrices (PCNM) approach was performed to treat the coordinates and then extract the variable "distance" in partial RDA. Later, anova.cca (999 permutations and $p < 0.05$) was used to analyze the significance of environmental axes. These analyses were carried out using the "vegan" package (Oksanen et al. 2013) in R 3.4 software (R Core Team 2016).

Results

SWA composition and relationship with the Caribbean

We recorded 130 valid species occurring in SWA and the Caribbean (Table 1). The SWA sea anemone distribution analysis revealed nine clusters distributed over the three provinces: BP (4 clusters), AP (1 cluster), and PP (1 cluster). All provinces are distinct from each other and are well supported by high endemism levels. The CP was also distinct (3 clusters) (Table 2, Fig. 2). The PP contained the most distinct groups, sharing species only with the AP (Table 1). However, the AP showed a high dissimilarity with the BP and the CP. In contrast, the CP and the BP showed the lowest dissimilarity and most shared species (Table 1). Despite this, all four provinces are distinguishable and different from each other (Fig. 3).

The Brazilian province showed 46 species distributed along 14 families (including *incertae sedis*) (Table 1) with 19% of endemism (9 species). Inside the BP, we found four significant clusters (Fig. 2). The first cluster (1B) contains most grids from northeast and southeast (with one from the Caribbean province, C14), and it is the richest group with 54 species in total (9 from CP) and 10% of endemism. The second cluster (2B) comprises A1 (corresponds to Uruguay), B2, B3, and B6, with 17 species and 4% of endemism. Lastly,

Table 1 List of shallow-water sea anemone species used in this work

Species	BP	AP	PP	CP
Order Actiniaria				
Family Acontiophoridae Carlgren, 1938				
Ramirezia balsae Zamponi, 1980 ◀		■		
Family Actiniidae Rafinesque, 1815				
Actinia bermudensis (McMurrich, 1889)	●	■		▲
Actinia grobbeni Watzl, 1922 ◀				▲
Actinostella correae (Schlenz & Belém, 1992) ◀	●			
Actinostella digitata (McMurrich, 1893) ◀		■		
Actinostella flosculifera (Le Sueur, 1817)	●			▲
Actinostella radiata (Duchassaing & Michelotti, 1860)				▲
Anemonia antillensis Pax, 1924				▲
Anemonia chubutensis Zamponi & Acuña, 1992		■		
Anemonia depressa Duchassaing & Michelotti, 1860 ◀				▲
Anemonia melanaster (Verrill, 1901)				▲
Anemonia sargassensis Hargitt, 1908	●			▲
Anemonia sulcata (Pennant, 1777)	●			
Anthopleura cascaia Corrêa, 1964 in Dube 1981 ◀	●			
Anthopleura krebsi Duchassaing & Michelotti, 1860	●			▲
Anthopleura pallida Duchassaing & Michelotti, 1864				▲
Anthopleura texaensis (Carlgren and Hedgpeth, 1952)				▲
Anthopleura varioarmata Watzl, 1922	●			▲
Aulactinia marplatensis Zamponi, 1977		■		
Bolocera kerguelensis Studer, 1879			□	
Bunodactis curacaoensis Pax, 1924 ◀				▲
Bunodactis octoradiata (Carlgren, 1899)			□	
Bunodactis patagoniensis (Carlgren, 1899) ◀		■		
Bunodactis reynaudi (Milne Edwards, 1857)		■		
Bunodosoma caissarum Corrêa in Belém 1987◀	●			
Bunodosoma cangicum Belém & Preslercravo, 1973	●	■		
Bunodosoma cavernatum (Bosc, 1802)				▲
Bunodosoma granuliferum (Le Sueur, 1817)				▲
Bunodosoma kuekenthali Pax, 1910				▲
Bunodosoma zamponii Gomes, Schama & Solé-Cava, 2011 ◀		■		
Condylactis gigantea (Weinland, 1860)	●			▲
Entacmaea quadricolor (Leuckart in Rüppell and Leuckart 1828)				▲
Epiactis georgiana Carlgren, 1927		■		
Gyrostoma sanctithomae Pax, 1910 ◀				▲
Isoaulactinia stelloides (McMurrich, 1889)				▲
Isotealia antarctica Carlgren, 1899		■		
Neoparacondylactis haraldoi Zamponi, 1974		■		
Oulactis muscosa (Drayton in Dana 1846)		■		▲
Parabunodactis imperfecta Zamponi & Acuña, 1992		■		
Parabunodactis inflexibilis (Carlgren, 1928)		■		
Paracondylactis hertwigi (Wassilieff, 1908)	●			
Parantheopsis cruentata (Couthouy in Dana 1846)			□	
Phlyctenanthus australis Carlgren, 1950		■		
Phlyctenanthus regularis Zamponi & Acuña, 1992 ◀		■		
Phyllactis conquilega (Duchassaing & Michelotti, 1860) ◀				▲
Phyllactis formosa (Duchassaing, 1850) ◀				▲

Table 1 (continued)

Species	BP	AP	PP	CP
Phyllactis praetexta (Couthouy in Dana 1846)	●			▲
Phymactis pustulata (Couthouy in Dana 1846)	●			
Pseudactinia infecunda (McMurrich, 1893)	●			
Urticina macloviana (Lesson, 1830) ◄			□	
Family Actinostolidae Carlgren, 1932				
Actinostola callosa (Verrill, 1882)			□	
Actinostola crassicornis (Hertwig, 1882)		■	□	
Antholoba achates (Drayton in Dana 1846)		■	□	
Paranthus niveus (Lesson, 1830)				▲
Paranthus rapiformis (Le Sueur, 1817)	●			
Pseudoparactis tenuicollis (McMurrich, 1904)		■		
Family Aiptasiidae Carlgren, 1924				
Aiptasia prima (Stephenson, 1918)	●	■		
Bartholomea annulata (Le Sueur, 1817)				▲
Bartholomea pseudotagetes Pax, 1924 ◄				▲
Bartholomea werneri Watzl, 1922 ◄				▲
Bellactis ilkalyseae Dube, 1983	●			▲
Exaiptasia brasiliensis Grajales & Rodríguez, 2016	●			▲
Exaiptasia pallida (Agassiz in Verrill 1864)	●			▲
Laviactis lucida (Duchassaing & Michelotti, 1860)				▲
Family Aiptasiomorphidae Carlgren, 1949				
Aiptasiomorpha texaensis Carlgren & Hedgpeth, 1952				▲
Family Aliciidae Duerden, 1895				
Alicia mirabilis Johnson, 1861	●			▲
Lebrunia coralligens (Wilson, 1890)	●			▲
Lebrunia neglecta Duchassaing & Michelotti, 1860	●			▲
Family Andvakiidae Danielssen, 1890				
Isophellia madrynensis Zamponi & Acuña, 1992		■		
Telmatactis cricoides (Duchassaing, 1850)	●			▲
Telmatactis roseni (Watzl, 1922)	●			▲
Telmatactis rufa (Verrill, 1900)	●			▲
Telmatactis solidago (Duchassaing & Michelotti, 1864)				▲
Telmatactis vernonia (Duchassaing & Michelotti, 1864)				▲
Family Bathyphelliidae Carlgren, 1932				
Phelliogeton falklandicus Carlgren, 1927 ◄			□	
Family Boloceroididae Carlgren, 1924				
Boloceroides mcmurrichi (Kwietniewski, 1898)		■		
Bunodeopsis antilliensis Duerden, 1897 ◄				▲
Bunodeopsis globulifera (Duchassaing, 1850)				▲
Family Capneidae Gosse, 1860				
Actinoporus elegans Duchassaing, 1850	●			▲
Family Condylanthidae Stephenson, 1922				
Condylanthus magellanicus Carlgren, 1899		■	□	
Family Diadumenidae Stephenson, 1920				
Diadumene leucolena (Verrill, 1866)	●			
Diadumene lineata (Verrill, 1869)	●	■		
Diadumene paranaensis Beneti et al., 2015 ◄	●			
Tricnidactis errans Pires, 1988	●	■		
Family Edwardsiidae Andres, 1881				

Table 1 (continued)

Species	BP	AP	PP	CP
Edwardsia migottoi Gusmão & Brandão, 2016 ◄	●			
Nematostella vectensis (Stephenson, 1935)	●			
Scolanthus curacaoensis (Pax, 1924) ◄				▲
Family Halcampidae Andres, 1883				
Parahalcampa antarctica Carlgren, 1927			□	
Family Haloclavidae Verrill, 1899				
Harenactis argentina Lauretta et al., 2011		■		
Metapeachia schlenzae Gusmão, 2016 ◄	●			
Peachia hastata Gosse, 1855		■	□	
Peachia koreni McMurrich, 1893 ◄		■		
Family Homostichanthidae Carlgren, 1900				
Homostichanthus duerdeni Carlgren, 1900	●			▲
Family Hormathiidae Carlgren, 1932				
Calliactis androgyna Riemann-Zürneck, 1975 ◄ rda	●			
Calliactis polypus (Forskål, 1775)				▲
Calliactis tricolor (Le Sueur, 1817)	●			▲
Hormathia pectinata (Hertwig, 1882)		■		
Family Isanthidae Carlgren, 1938				
Austroneophellia luciae Zamponi, 1978 ◄		■		
Isoparactis fionae Lauretta et al., 2014 ◄			□	
Family Metridiidae Carlgren, 1893				
Metridium senile (Linnaeus, 1761)		■		
Family Phelliidae Verrill, 1868				
Phellia coreopsis (Duchassaing & Michelotti, 1864) ◄				▲
Family Phymanthidae Andres, 1883				
Phymanthus crucifer (Le Sueur, 1817)				▲
Family Sagartiidae Gosse, 1858				
Actinothoe paradoxa (McMurrich, 1893) ◄		■		
Actinothoe patagonica (Carlgren, 1899)		■		
Actinothoe sanmatiensis (McMurrich, 1893) ◄		■		
Anthothoe chilensis (Lesson, 1830)	●	■		
Anthothoe stimpsonii (Verril, 1869)	●			
Botryon lisandroi Laureta & Penchaszadeh, 2016		■		
Carcinactis dolosa Riemann-Zürneck, 1975	●			
Sagartia troglodytes (Price in Johnston, 1847)		■		
Sagartianthus fasciarum Zamponi, 1980 ◄		■		
Family Stichodactylidae Andres, 1883				
Stichodactyla helianthus (Ellis, 1768)				▲
Order Corallimorpharia				
Family Corallimorphidae Hertwig, 1882				
Corynactis caribbeorum (den Hartog, 1980)				▲
Corynactis carnea Studer, 1879		■		
Corynactis denticulosa (Le Sueur, 1817) ◄				▲
Corynactis parvula Duchassaing & Michelotti, 1860	●			▲
Corynactis sanmatiensis (Zamponi, 1976)		■		
Corynactis viridis Allman, 1846 rda	●			
Family Discosomidae Verrill, 1869				
Discosoma carlgreni (Watzl, 1922)	●			▲
Discosoma neglecta (Duchassaing & Michelotti, 1860)				▲

Table 1 (continued)

Species	BP	AP	PP	CP
Rhodactis osculifera (Le Sueur, 1817)	●			▲
Family Ricordeidae Watzl, 1922				
Ricordea florida Duchassaing & Michelotti, 1860				▲
Actiniaria Incertae Sedis				
Actinodactylus boscii Duchassaing, 1850 ◀				▲
Cystiactis eugenia Duchassaing & Michelotti, 1864 ◀				▲
Cystiactis gaudichaudi Milne-Edwards, 1857 ◀ rda	●			
Cystiactis koellikeri Pax, 1910 ◀				▲
Paractis dietzii Duchassaing & Michelotti, 1864 ◀				▲
Paractis laevis (Carlgren, 1899)			□	
Paractis sanctaecatherinae (Lesson, 1830) ◀	●			
Petalactis calendula (Hughes in Ellis and Solander 1786) ◀				▲

Black left-pointing arrows indicate endemic species (exclusive to the respective province); rda means that the species was not used in RDA as data was incomplete/species complex

BP Brazilian province (filled circles), *AP* Argentinian province (filled squares), *PP* Patagonian province (hollow squares), *CP* Caribbean province (filled triangles)

there are two small clusters: the first one (3B) is located in the north of Brazil (B1 and B4), and the second one (4B) corresponds with the extreme south and Trindade and Martim Vaz islands (B13 and B14). Both clusters account for a low richness and endemicity: 0% endemism and three species for the former and 2% endemism and five species. This means that except for the edges in the BP (coinciding with the river's proximity, La Plata River, and Amazon-Orinoco plume, Fig. 1) and one of the oceanic islands (Trindade and Martim Vaz), the remaining area is homogeneous in sea anemone fauna composition. Inside the BP, the most represented families are Actiniidae and Diadumenidae with 15 and 4 species, respectively.

The Argentinian province had 41 species distributed over 14 families with 24% of endemism (10 species). Families with the majority of species are Actiniidae (16 spp.) and Sagartiidae (7 species) (Table 1). In the Patagonian province, 13 species in eight families were recorded (including *incertae sedis*) with 23% endemism (3 spp.). The most representative families were Actiniidae (4 spp.) and Actinostolidae (3 spp.).

Table 2 Levels of Sørensen dissimilarity (upper part) and the number of shared species (lower part) between the Caribbean province (CP), Brazilian province (BP), Argentinian province (AP), and Patagonian province (PP) and the total number of species in each province (richness)

	CP	BP	AP	PP
CP	–	0.58	0.96	1
BP	22	–	0.90	1
AP	2	6	–	0.8
PP	0	0	4	–
Richness	63	46	41	13

The AP and PP did not present subgroups, and these provinces are more homogeneous in composition.

The Caribbean province had 63 species recorded with 26% endemism (17 spp.) and a weighted richness of 3.7 species per grid cell. Grid cell C14 (Antilles) appears inside the Brazilian cluster (Fig. 2a), implying that the faunal composition of this cell is more similar to that of the Brazilian fauna than of the Caribbean province.

We estimated that 180 species could be found in total and 124 considering only the SWA (Chao2 SWA + Caribbean province mean = 179.8, SD = 18.8; SWA mean = 123.8, SD = 14.7). Our inventory represents almost 72% of the total estimated species for the SWA and Caribbean provinces.

Richness patterns and biodiversity centers

In the SWA, the highest species per grid cell value was found in the AP (8.2) followed by the BP (3) and the PP (2.6). However, the richest grid cell in SWA is located in the southeast region of Brazil, B10 (32 species and 13% of endemism), followed by B11 (18 spp.), showing that the richness pattern in the BP follows a tendency of species accumulation in the southeast region (Fig. 3). The lowest richness in the BP belongs to B1 (1 species) followed by B4 (2 species). In the AP, the richest grid cell was A2 with 25 species.

Estimates of latitudinal diversity using species occurrence data clearly show a tendency of decreasing richness towards the equator (Fig. 4). When doubling our current sampling efforts, the estimated latitudinal diversity shows a peak in richness in mid-latitudes, around 19–23° S (Fig. 4a). However, with a low sampling effort estimation, this pattern became non-distinct (Fig. 4b).

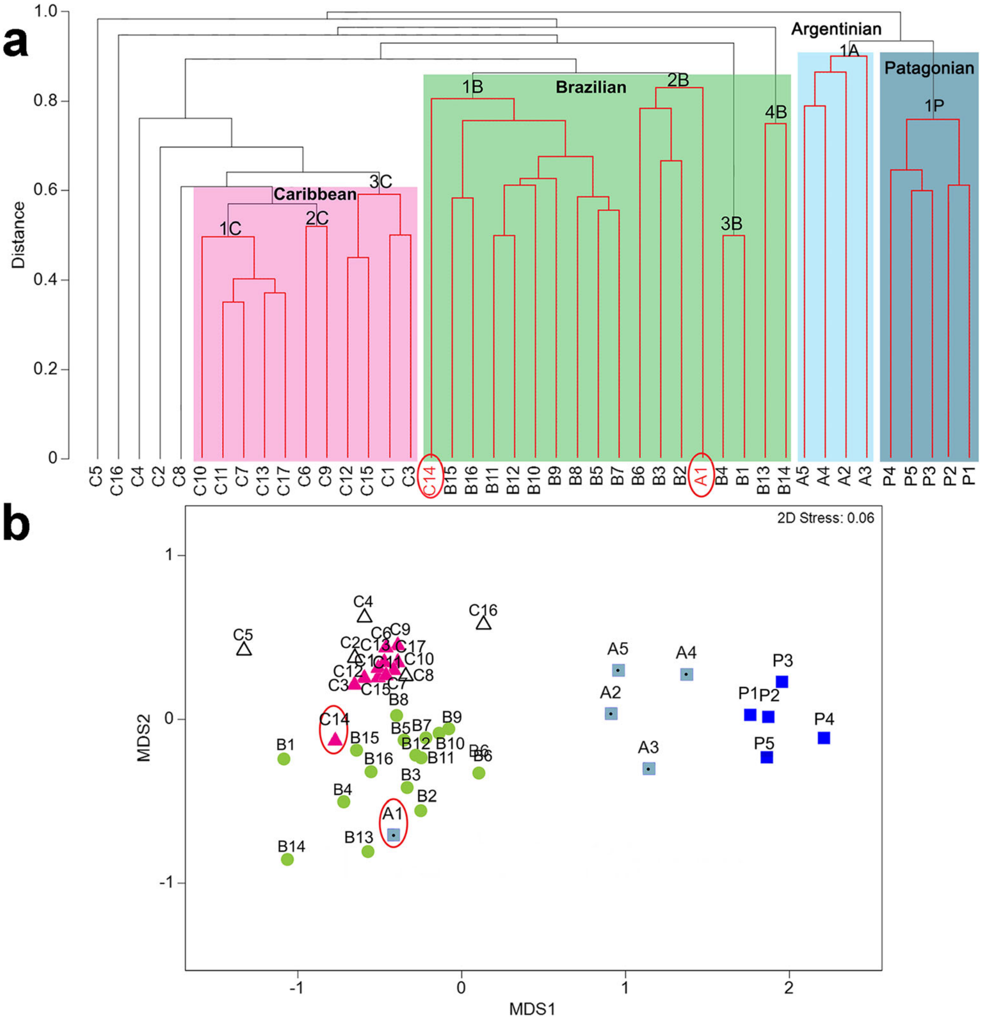


Fig. 2 **a** SWA and Caribbean Sørensen dissimilarity cluster (UPGMA). The nine significantly different clusters are market with a red line (SIMPROF). Colored squares identify the biogeographical provinces corresponding to the location of the groups. Cophenetic correlation = 0.92; **b** nMDS (stress = 0.06). Circles highlight Uruguay and a Caribbean island grid cell. Squares, Brazilian province; triangles, Caribbean province; squares with dots, Argentinian province; squares, Patagonian province. Hollow triangles are not significantly different grid cells

Community drivers

RDA showed which drivers contribute more to sea anemone distribution in the BP. Between temperature, salinity, and substrate type, temperature is most responsible for the sea anemone composition and distribution in the country (64%, $p < 0.001$), followed by salinity (22%, $p < 0.001$) and substrate type (13%, $p = 0.01$) (Fig. 5). The whole model with the three variables together was also significant ($p < 0.001$), showing an explanation for the total variation of 43%.

Discussion

In exploring the biogeographical and ecological patterns of the Southwest Atlantic provinces, we also compared these with those of the Caribbean provinces to better understand the processes that shape shallow-water sea anemone biodiversity and distribution. The sea anemone fauna supports the distinction of three provinces in the SWA, Brazilian, Argentinian, and Patagonian provinces as separate from the Caribbean province. In the SWA, a richness peak was observed in the southeast of Brazil and temperature was the most important abiotic driver to explain species distribution.

In the Brazilian province, the majority of the species belongs to the family Actiniidae. This family is the largest of the Actiniaria with more than 200 species (Daly et al. 2007; Fautin et al. 2013). It is also a common family in shallow-water habitats (McCommas 1991). In Argentinian and Patagonian provinces, we found a higher frequency and a predominance of families common to colder and deeper waters such as Actinostolidae, Bathyphelliidae, Isanthidae, and Halcampidae, with the latter known for its burrowing species (Daly et al. 2007; Castorani 2008). Of particular interest is that of the 13 species in the PP, only one was described in the last century. All other ones were described in the eighteenth and first half of the nineteenth century, when most data resulted from large oceanographic expeditions. This temporal hiatus could reflect a low sampling in the region and explain, in part, the low richness. The Argentinian province has the highest richness/grid cell and endemism. This region includes the Buenos Aires coast, the most studied region of this province.

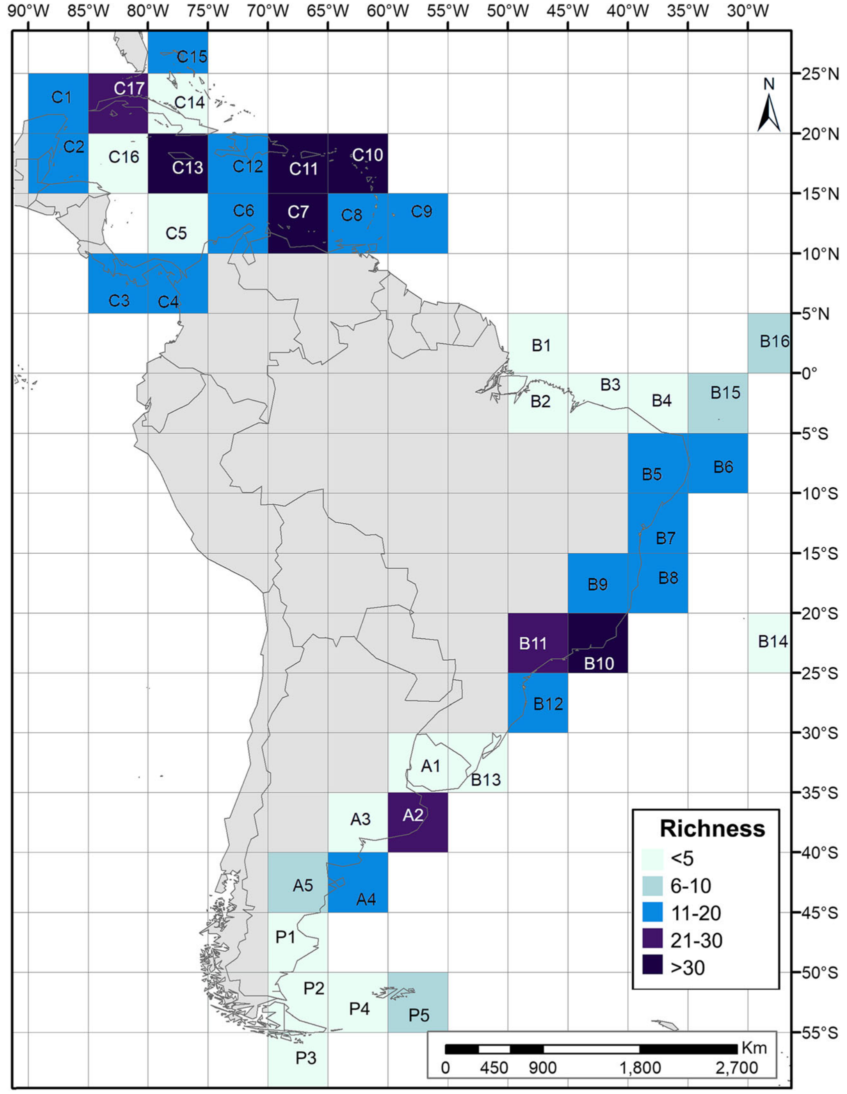


Fig. 3 Richness of shallow-water sea anemones in the SWA and Caribbean provinces

Beyond Actiniidae, this province is also characterized by Sagartiidae, which is the second largest actiniarian family with approximately 85 valid species in 14 genera. Such a heterogeneous family (Daly et al. 2007) is expected to be well represented.

The results show a marked faunal similarity between the BP and the CP, as previously noted by Zamponi et al. (1998a) and observed for other taxa such as fishes and azooxanthellate corals (Rocha 2003; Kitahara 2007; Cordeiro et al. 2015). However, the BP and the CP share less than 50% of shallow-water sea anemones and each province has more than 20% of endemism. This high endemism level supports the designated provinces. Toonen et al. (2016) stated that biogeographic provinces should present at least 10% of species endemism, even when published inventories are used to measure it. In our clustering, the provinces appear as different groups, supporting the hypothesis of distinct fauna composition.

The CP and the BP are separated by the Amazonas-Orinoco estuary (Fig. 1), a biogeographic barrier that is responsible for almost 20% of the global fluvial discharge (da Silva et al. 2005), which could explain the high degree of endemism in Brazil for several marine taxa, like fish and corals (Cox and Moore 2000; Joyeux et al. 2001). However, the possibility of migration routes in deeper waters, below the plume, and the permeability shifting during the seasons may explain the shared species between Brazil and the Caribbean province (Rocha 2003; Cordeiro et al. 2015; de Oliveira Soares et al. 2018). For example, Venezuela, on the other side of the estuary, shares about 30% of shallow-water species with Brazil (based on an extensive survey of sea anemone fauna performed by González-Muñoz et al. (2016)). The presence of freshwater inflow is usually responsible for a lower coral diversity and reef habitats (see Hoeksema 2015). The mesophotic reefs in the Amazonas-Orinoco region could also contribute, serving as a stepping stone to species dispersion

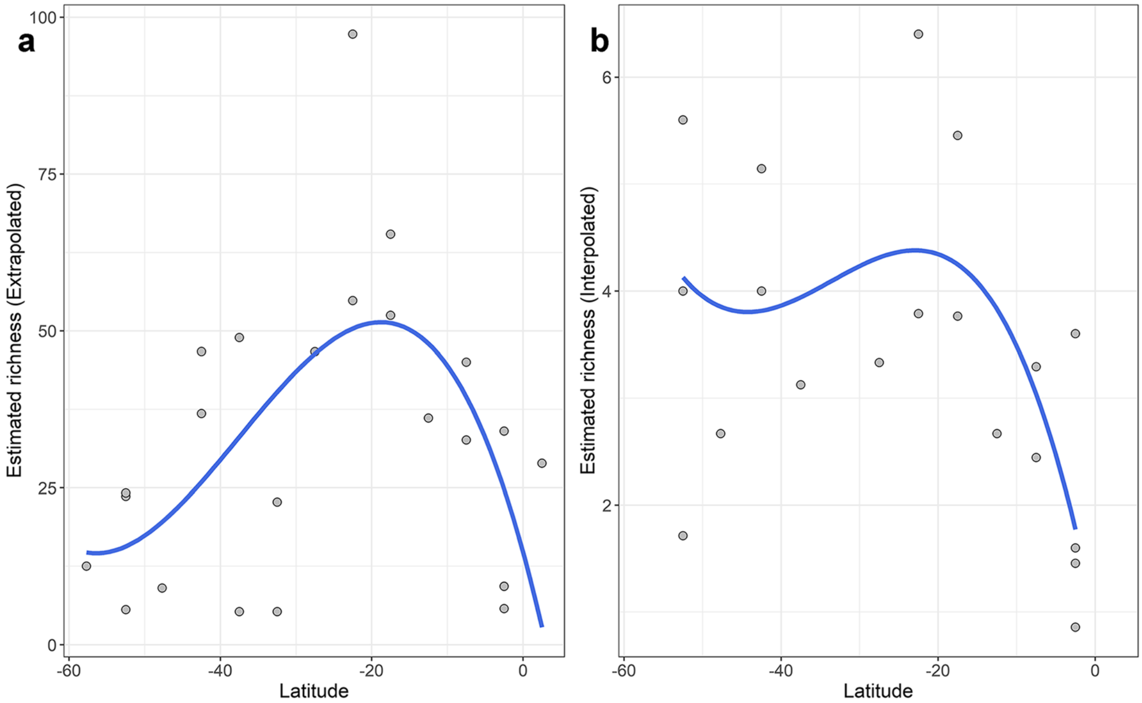
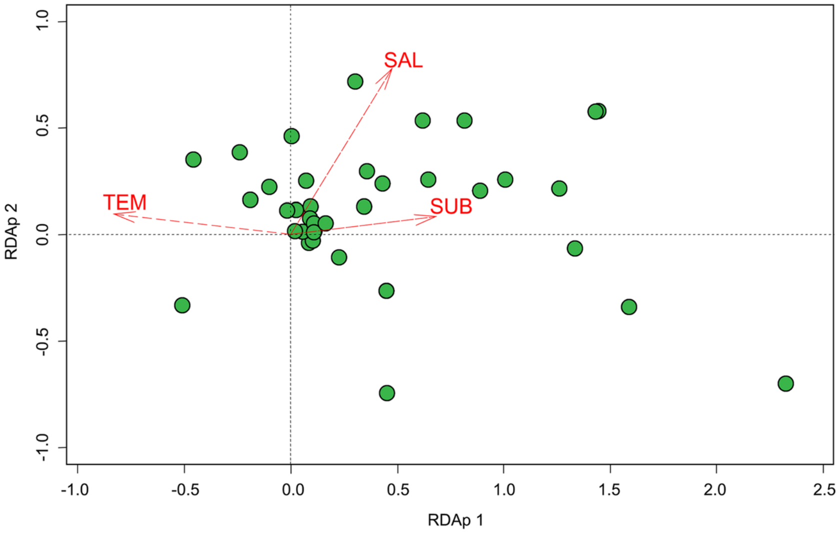


Fig. 4 Estimates of the latitudinal pattern of shallow-water sea anemones in the SWA. **a** Extrapolated richness at Hill's order $q = 0$; **b** Interpolated richness at Hill's order $q = 0$

(Luiz et al. 2012; Cordeiro et al. 2015; Moura et al. 2016). Thus, the estuarine plume seems to act as a soft barrier, allowing passage for some species and preventing others, especially those generally restricted to shallow waters, with reproduction periods when the barrier is more effective, or further, species with a smaller dispersion and/or tolerance range. Therefore, added to local selective aspects, it could explain why despite the Brazil and Caribbean provinces shared species, there is a biota differentiation with a high endemism level, which justifies the provinces' distinction.

The provinces Argentinian and Patagonian were the most differentiated, with higher homogeneity in their composition. The PP was the most singular, with zero species shared with the BP and the CP and only four with the AP. This particular fauna pattern was observed in fish groups (Pinheiro et al. 2018) and related to the temperature and marine currents. Argentina is under the influence of the cold and nutrient-rich Malvinas Current (MC), which reaches the south of Brazil (Miloslavich et al. 2011). The confluence zone (30–46° S) (Fig. 1), where the MC meets the Brazil Current (BC), has particular oceanographic characteristics (Acha et al. 2004). The nearby La Plata River is the largest freshwater flow of the region and an important biogeographic barrier (Zamponi et al. 1998a; Ferretti et al. 2018). The MC, with opposite

Fig. 5 Partial redundancy analysis (RDA) biplot of temperature (TEM), salinity (SAL), and substrate (SUB). Axis 1, 64% explanation; axis 2, 22%. Eigenvalues are 0.4841, 0.1703, and 0.1031. Adjusted $R^2 = 0.148$



characteristics to the BC, together with the freshwater stream, could explain the fauna disparity between Brazil and Argentina. More locally, differences in the habitat strengthen fauna dissimilarity. Along the Argentinian coast, consolidated substrate is less available and its waters are colder and more turbid when compared with most parts of Brazil (Zamponi et al. 1998b; Gallardo and Penchaszadeh 2001; Lutz et al. 2003). Indeed, the distribution of the majority of Argentinian sea anemones is restricted to colder waters.

Uruguay grouped with the BP (grid cell A1, Fig. 2a), a pattern also found by Costello et al. (2017) when studying several benthic and pelagic taxa. However, some authors suggest that Uruguay should be inside the AP (Briggs 1974; Briggs and Bowen 2012), and Lutz et al. (2003) classify the Argentinian province ranging from Peninsula Valdés through the north, including Uruguay and the south of Brazil. Deserti et al. (2012) found six species of sea anemones shared among Uruguay and Argentina and then concluded that the La Plata River does not represent an important barrier to sea anemone dispersion. Our data does not fully support this idea, but this could be the effect of analyzing only shallow-water fauna. Deserti et al. (2012) described mostly deep- and cold-water fauna. Spalding et al. (2007) proposed a warm temperate Southwestern Atlantic province, where southeastern Brazil, Uruguay, and north of Argentina appear to group together. When taking a closer look into smaller biogeographic units, the La Plata River appears as an ecoregion (see Spalding et al. 2007), and Uruguay groups with Brazil, which is consistent with our data. However, even grouping together the dissimilarity from A1 to other BP grid cells is almost 80%, suggesting a transition in the fauna.

For the SWA and the Caribbean, almost 70% of the sea anemone fauna is known, and in the BP, this is 80%. This correlates well with the world sea anemone knowledge prediction (73% according to Fautin et al. (2013)). Efforts have been increased in the last 10 years to incorporate marine species records and data to open source databases. However, even the most studied region in the SWA has much to discover (Miloslavich et al. 2011; Longo and Amado Filho 2014). Despite current efforts, some regions at the edges of the BP (cluster 4B) have remained underexplored, while there are potential locations for new species and records. Naturally, oceanic islands tend to have fewer species than localities along the continental coastline, where more environmental gradients can be found (e.g., Cleary et al. 2008, 2016). The Brazilian northern oceanic islands have 20% endemism, which is very high and can be explained due to their isolation (Costello et al. 2017). The Trindade and Martim Vaz islands (grid cell B13) show a low species richness, which was expected as the marine biodiversity of the archipelago is regarded as one of the lowest in the world (Floeter et al. 2008). This is probably related to its distance from the coast, a small shallow coastline, and harsher oceanographic conditions than those of the other islands (Aued et al. 2018).

In the BP, cluster 1B comprises a great portion of the coast (approximately 3.400 km) and two oceanic islands. This “subprovince” (with the most species-rich cells B5, B7, B8, B9, B10, B11, and B12) has well-supported endemism (almost 18% and 39 spp. in total), and it includes a diversity center in the SWA. Southward, we found lower temperatures and a higher influence of the Malvinas Current and the La Plata River, whereas further northward, the proximity of the Amazonas-Orinoco with low levels of salinity could also explain the composition in clusters 2B and 3B. Extreme environmental factors such as sedimentation and salinity from freshwater flows in the extremes of BP (in addition to more wind exposure and narrower and shallower shelf in the north) could affect the fauna composition since benthic taxa are strongly influenced by these coastal conditions (Macpherson 2002; Barros and Rocha-Barreira 2014; Pinheiro et al. 2018). Since these areas and the Trindade and Martim Vaz islands have a research deficiency, with further exploration and assessment, a more extensive panorama of sea anemone distribution in the BP could be pictured and relations among regions in the north and south of Brazil could become clarified.

Marine currents have an important role in regional connectivity and can act as a way of distribution, especially to oceanic islands (Spalding et al. 2007). The South Equatorial Current bifurcates between 10 and 14° S in Brazil, becoming the North Brazilian Current (NBC) and the BC (Fig. 1). The NBC flows between north Brazilian oceanic islands until it reaches the Caribbean (Stampar et al. 2012). Many species shared between Brazil and the Caribbean (e.g., *Telmatactis cricoides*) occur only in the northern oceanic islands of both provinces, as grid cell C14 (with almost 80% dissimilarity) has several species shared with the BP. Sea anemones have complex life histories, and the dispersion through a planktonic larval phase is one of the most common means of reproduction and dispersal in the group. In general, sea anemone larvae can survive 26–35 days after release, while some species can even remain in the water column for 59 days (Scott and Harrison 2007; Larson 2017). This could explain the connectivity between grid cell C14 and oceanic islands and the coast of Brazil. This similarity could also be due to ecological, environmental, and stochastic factors. Caribbean and Brazilian islands have extremely similar conditions with respect to temperature, local water dynamics, and turbidity (Rocha 2003). Therefore, oceanic islands could promote connectivity and population persistence, particularly in species that cannot remain on the continental shelf (Pinheiro et al. 2018).

Traditionally, it was believed that the southeast region of Brazil had a higher concentration of researchers and thus a higher sampling effort than other SWA regions (see Amaral and Jablonski 2005) and this could affect latitudinal richness gradient evaluations. However, we found that shallow-water sea anemones follow a tendency of a higher diversity at 19–23° S, which is independent of sampling effort (Fig. 4a), reinforcing the idea of a biodiversity center in the SWA, previously discussed for reef fishes by Pinheiro et al. (2018). This region has particular features that constitute a transition zone between tropical and subtropical reefs. These reefs harbor the majority of species (mostly consolidated substrate species) and could also support a higher richness as species from both zones coexists. Furthermore, the Brazil Current flows towards south and can restrict movement in the opposite flows (Pinheiro et al. 2018). This richness peak in Brazil's southeast was also observed for azooxanthellate scleractinians (Kitahara 2007), gastropods (Barroso et al. 2016), algae, fish, and invertebrates (Miloslavich et al. 2011), and recently, a study observing benthic communities (several taxa belonging to Anthozoa, Demospongiae, Ascidiacea, and other invertebrates; also Cyanobacteria, Chlorophyta, and other algae) in Brazil also observed this tendency (Aued et al. 2018).

We observed that temperature was the strongest explanatory driver for sea anemone distribution in the BP. However, only three drivers could be selected reliably, which is a limitation of this work. Several physiological and ecological processes of sea anemones are linked to temperature tolerance: reproductive seasonality, asexual reproduction, development, larval survival, growth, and settlement (Chomsky et al. 2004; Scott and Harrison 2007; Koldewey and Martin-Smith 2010; Ryan 2017; Gambill et al. 2018). Furthermore, zooxanthellate sea anemones are sensitive to environmental variations, such as elevated sea water temperature (Hobbs et al. 2013). Several other species are sensitive to salinity and temperature, such as, for example, *Bunodosoma caissarum* (Scremin et al. 2013). Water masses, thermohaline conditions, and habitat availability could, in part, be responsible for the distribution of sea anemones. For some coral groups, a lower availability of reef habitats, deeper sea floor, and soft substrate is linked with a decline in species diversity and, consequently, composition (Hoeksema 2015). Some sea anemones species are restricted to temperate or tropical waters, such as *Carcinactis dolosa* and *Actinoporus elegans*, ranging from southeast to the south of Brazil (19 to 24 °C). Temperature also interacts with other factors, such as salinity and oxygen availability, directly affecting the life history of sea anemones. Overall, temperature appears to be one of the most decisive factors in the delimitation of SWA provinces.

Salinity and substrate have smaller contributions to sea anemone distribution but should not be ignored. Habitat availability to larvae settlement is decisive for cnidarians (Whalan et al. 2015). In general, sea anemones can be divided into two main morphological groups regarding the type of the substrate: burrowing in unconsolidated substrate (sand, mud) and adherent to consolidated substrate (rock) (Rodríguez et al. 2014). The majority of BP sea anemones live in a consolidated substrate. This kind of substrate is available in most parts along the coast, but it becomes scarce in the south region (Ferreira et al. 2004), until reaching Argentinian waters (Zamponi et al. 1998b). Additionally, coral reefs, which represent a consolidated and diverse substrate, have a southernmost distribution in the Atlantic at 24° S and this could also impact sea anemone distribution in SWA (Pereira-Filho et al. 2019). The extreme north of Brazil is characterized by sandy beaches with scattered beachrock of recent formation (see Miloslavich et al. 2016). Furthermore, between north and southeast of BP, there is a variation in reefs and rocky habitats present (Floeter et al. 2001). Salinity is stable along the coast, 36 on average, except in river estuaries as the Amazonas-Orinoco plume in the north of Brazil where salinity fluctuates between < 20 at superficial depths and then return to around 36 near depths of 20 m (Moura et al. 2016), and this may explain, more locally, the low species occurrence in this region. Our three variables, together, explain 43% of sea anemone distribution along and off the Brazilian coastline. This suggests the presence of a complex environmental driver system, while interactions among abiotic and biotic factors are not assessed in this study. Mechanisms that drive biodiversity are not always clear; in the marine environment, physical isolation is not the only (or the strongest) speciation driver, and several species have diverged through ecological barriers (or filters as currents, substrate) that create opportunities for speciation (Bowen et al. 2013).

The new data input will allow a better understanding of the shallow-water sea anemone composition and important drivers. With the current data, we can observe that the distribution of sea anemones corresponds with previously proposed biogeographic provinces. A richness peak in the mid-latitudes of the SWA was found, with a species peak at 19–23° S. Among three selected drivers, temperature is the most responsible for the sea anemone distribution in the SWA. This work reveals unprecedented patterns and answers to important questions about the sea anemone distribution in the SWA.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No animal testing was performed during this study.

Sampling and field studies The study does not contain sampling material or data from field studies.

Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files.

Author contribution AKGT and PBG conceived, designed, and conducted the research; analyzed the data; and wrote the manuscript. All authors read and approved the manuscript.

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