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ORIGINAL ARTICLE

Biogeography of Brazilian prosobranch gastropods and their Atlantic relationships

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ABSTRACT

Aim The present study uses marine prosobranchs from shallow waters (down to 200 m) as a model to determine biogeographical units along the Brazilian coast and to investigate changes in assemblages along the Western Atlantic.

Location Western Atlantic Ocean.

Methods The composition and species distribution of prosobranchs were determined using secondary data and information gathered from Brazilian scientific collections. The similarities among the areas were calculated using the Sørensen, Simpson and Ochiai Indices, and were illustrated using dendrograms constructed by unweighted pair group method using arithmetic averages. Ordination analysis was performed using non-metric multi-dimensional scaling based on the similarity matrices.

Results As a result of the compilation performed, 700 marine prosobranch species distributed in 81 families from shallow waters were recorded in Brazil. The results show a clear correlation between geographic distance between areas and their faunal similarity. There is a gradual latitudinal variation in marine prosobranch assemblages along the Brazilian coastline. The coastal areas sustain richer gastropod assemblages than the oceanic islands.

Main conclusions Considering the results of cluster and ordination analyses, this study proposes to divide the Brazilian coast into four regions: (1) Guyanese Province (Amapá state), (2) North-eastern Brazil Area (from the mouth of the Amazon to southern Bahia, Brazil), (3) South-eastern Brazil Area (from southern Bahia to Santa Catarina, Brazil, transition zone), and (4) Argentinian Province (Rio Grande do Sul state). The North-eastern and South-eastern Brazil Areas belong to the Brazilian Province. The Brazilian insular areas are biogeographical units distinct from the other regions studied. Each island has its own composition of marine prosobranchs from shallow waters, while they share species with other coastal and island environments.

Keywords

Atlantic Ocean, biodiversity, biogeographical areas, biogeographical barriers, Gastropoda, marine biogeography, regionalization

INTRODUCTION

The classification of geographic regions based on their biota is one of the most frequently discussed topics in biogeography. Historically, the distribution of marine animals was thought to be determined by three primary influences, namely climate, sea composition (chemical and physical properties of seawater) and depth (Forbes, 1844). In the marine realm, biogeographic regions were mainly based on water temperature and isolation – ocean basins separated by land masses (Dana, 1853; Woodward, 1856). Briggs (1974, 1995) offered a synthesis and an update of the classification of marine regions, mainly based on water temperature and isolation of ocean basins (e.g. Eastern Pacific Region and Western Atlantic Region).

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Some marine biogeographers have used endemism rates to subdivide these regions, calling them 'areas of endemism' (Floeter *et al.*, 2008). Briggs (1974), in his classic study of marine biogeography, classified areas with endemism rates > 10% as Provinces. In addition to endemism rates, another approach widely used to determine biogeographical units is the use of cluster analysis, which aims to classify similar objects together (e.g. Kreft & Jetz, 2010; Kulbicki *et al.*, 2013). Several studies attempt to establish marine biogeographical regions based on data collection of multiple taxa (e.g. Ekman, 1953; Balech, 1954; Vannucci, 1964; Briggs, 1974; Palácio, 1982; Spalding *et al.*, 2007; Griffiths *et al.*, 2009; Miloslavich *et al.*, 2010, 2011; Briggs & Bowen, 2013) or specific taxa, such as crustaceans (e.g. Coelho & Ramos, 1972; Boschi, 2000), gastropods (Floeter & Soares-Gomes, 1999), mollusks (Martínez & del Río, 2002; Martínez *et al.*, 2013) and reef fishes (Floeter *et al.*, 2008; Kulbicki *et al.*, 2013).

The present study uses marine prosobranch species (Mollusca: Gastropoda) inhabiting waters down to 200 m deep to determine biogeographical units along the Brazilian coast and to investigate changes in assemblages along the Western Atlantic, since these organisms are easily identified and have a relatively well-studied taxonomy. The term 'prosobranch' will be used in this study to cover all gastropods that do not belong to Heterobranchia (i.e. Patellogastropoda, Neritimorpha, Cocculinoidea, Vetigastropoda and Caenogastropoda).

MATERIALS AND METHODS

Study sites

Brazil is located in the central-eastern part of South America (between 4°25′ N–33°45′ S and 34°47′ W–73°59′ W) and has a coastline of *c.* 9200 km, with the longest typically tropical coastline on the planet, extending mainly in a north-south direction over more than 37 latitudinal degrees (Castro & Miranda, 1998; Dominguez, 2006).

The geographical areas of Brazil considered in this study were the coastal and continental shelf zones, oceanic islands [São Pedro and São Paulo Archipelago – SPSPA (0°56′ N–29°22′ W), Rocas Atoll (3°51′ S–33°49′ W), Fernando de Noronha (3°51′ S–32°25′ W) and Trindade and Martin Vaz Archipelago (20°30′ S–29°20′ W)], and Abrolhos Archipelago (17°20′–18°10′ S, 38°35′–39°20′ W) (Fig. 1).

Trindade and Martin Vaz are the highest outcrops of the Vitória-Trindade mountain chain (20–21° S), which consists of seamounts with the tops reaching shallow depths (10–110 m), aligned along the east–west direction (Gasparini & Floeter, 2001; Gasparini, 2004). In this study, the group consisting of Trindade, Martin Vaz and seamounts (Vitória, Montague, Jaseur, Davis, Dogaressa, and Columbia) was considered as a single geographical unit.

The Abrolhos Archipelago is an enlargement of the Eastern Brazilian continental shelf, covering the largest area of the South Atlantic coral reefs (Leão & Ginsburg, 1997).

Data collection

This study was based on marine prosobranch species inhabiting waters down to 200 m deep along the Brazilian coast and insular areas. Although marine prosobranchs may be considered well-studied in Brazil, there are still knowledge gaps, particularly in the northern region. To minimize potential bias, families belonging to Conoidea (*sensu* Bouchet *et al.*, 2011) were excluded from data analysis, except Conidae and Terebridae, due to their small size and difficult taxonomy. Pelagic species of marine prosobranchs (Janthinidae, Atlantidae, Pterotracheidae and Carinariidae) were also excluded, since the focus of this study is on benthic species.

The composition and species distribution of prosobranchs was determined using secondary data (see Appendix S1 in Supporting Information), as well as through Brazilian scientific collections (Prof. Henry Ramos Matthews Malacological Collection – CMPHRM series A and B, Universidade Federal do Ceará; Paulo Young Invertebrates Collection, Universidade Federal da Paraíba; Malacological Collection from Museu Nacional do Rio de Janeiro – MNRJ; and Malacological Collection from Museu de Zoologia da Universidade de São Paulo – MZUSP). Some sources used in this study are unpublished theses, because they were considered here to be important contributions to the Brazilian coast biodiversity.

Data analysis

For the records in Brazil, the database was built by determining the presence (1) or absence (0) of species in 17 coastal Brazilian states (Amapá, Pará, Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Sergipe, Alagoas, Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul) and insular areas (São Pedro and São Paulo Archipelago, Rocas Atoll, Fernando de Noronha, Trindade and Martin Vaz Archipelago and Abrolhos).

Although the states' borders are political rather than biological, most distribution data in the literature and scientific collections are structured into these political regions. Consequently, this approach allowed us to use the largest possible quantity of data.

The similarities among areas were calculated from a presence/absence matrix of species in the regions, using the Sørensen, Simpson and Ochiai Indices. These three indices do not consider shared absences in their calculations (Legendre & Legendre, 1998). The Simpson and Ochiai indices focus on compositional differences more than differences in species richness, whereas the Sørensen Index implicitly incorporates differences in composition attributable to diversity gradients, but ignores the relative magnitude of species gains and losses (Koleff *et al.*, 2003). The use of different methods improves the insight obtained into compositional change.

The similarity matrices obtained from these indices were clustered using the unweighted pair group method using arithmetic averages (UPGMA), and visualized as

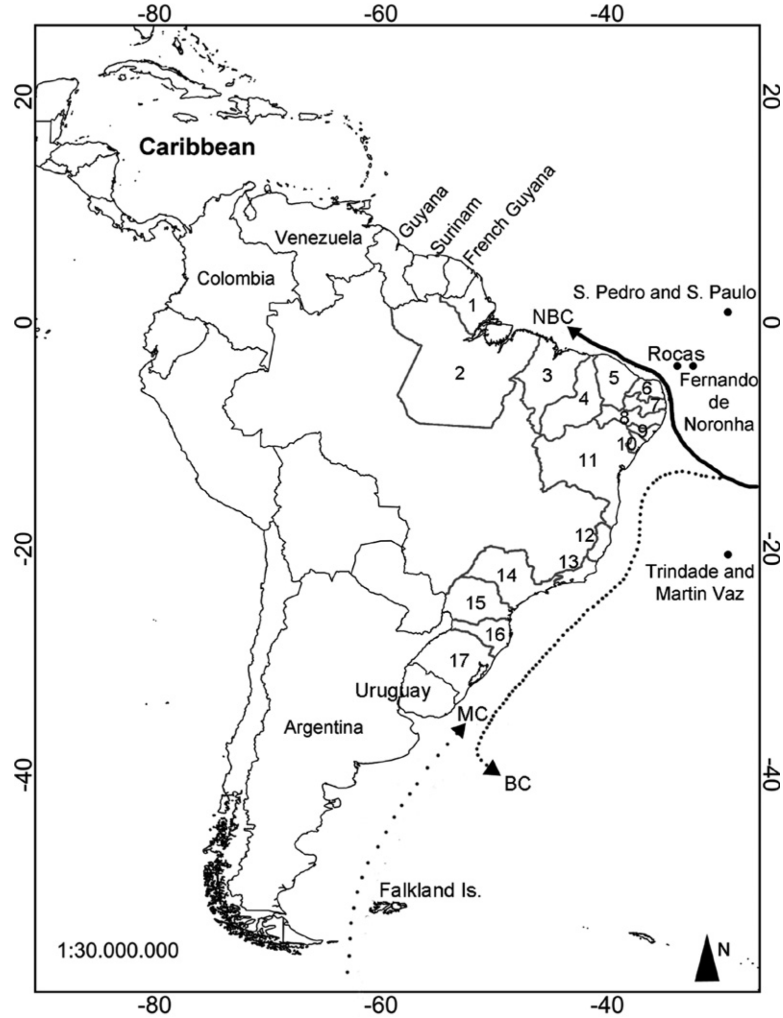

Figure 1 Location of the studied areas in Western Atlantic Ocean and the three major surface water currents that influence the Brazilian coast (North Brazil Current – NBC, Brazil Current – BC and Malvinas Current – MC). The numbers correspond to regions along Brazilian coast: 1 – Amapá, 2 – Pará, 3 – Maranhão, 4 – Piauí, 5 – Ceará, 6 – Rio Grande do Norte, 7 – Paraíba, 8 – Pernambuco, 9 – Alagoas, 10 – Sergipe, 11 – Bahia, 12 – Espírito Santo, 13 – Rio de Janeiro, 14 – São Paulo, 15 – Paraná, 16 – Santa Catarina and 17 – Rio Grande do Sul.

dendrograms. The robustness of the clusters was tested using a multiscale bootstrap resampling technique (Suzuki & Shimodaira, 2006; Dapporto *et al.*, 2013). The robustness estimates, ranging from 1% (low) to 100% (high), were calculated at each node of the dendrogram. The analyses were conducted using 10,000 bootstrap replicates of dendrograms.

Ordination analysis was performed using non-metric multi-dimensional scaling (NMDS) based on all three similarity matrices. All analyses were performed with the software R (R Development Core Team, 2014), using the packages 'pvclust' (Suzuki & Shimodaira, 2006) and 'reclust' (Dapporto *et al.*, 2013), and Primer 6.1.6 (Clarke & Warwick, 2001).

Clustering and ordination analyses were also performed between the Caribbean and South America (Guyana, Surinam, French Guyana, Brazil, Uruguay, Argentina and Falkland Islands) to investigate changes in prosobranch gastropod assemblages along the western Atlantic.

The list of Caribbean species was based on the study of Miloslavich *et al.* (2010), World Register of Marine Species (WoRMS) (Worms Editorial Board, 2015) and Malacolog 4.1.1 (A Database of Western Atlantic Marine Mollusca) (Rosenberg, 2009). The regions of the Caribbean considered in this study were similar to those previously established by Miloslavich *et al.* (2010). A total of 1303 Caribbean species were considered in the present study. The species of Guyana, Surinam and French Guyana were determined based on WoRMS and Malacolog 4.1.1 databases. The number of species considered in each area were 36 (Guyana), 35 (French Guyana) and 105 (Surinam).

The species of Uruguay, Argentina and Falkland Islands were determined based on WoRMS and Malacolog 4.1.1 databases, in addition to studies conducted in this region (Pastorino, 1993, 1994, 2002, 2003, 2005, 2009; Forcelli, 2000; Pastorino & Penchaszadeh, 2009; Teso & Pastorino, 2011; Teso *et al.*, 2011; Rechimont *et al.*, 2013). The number of species considered in each area were 90 (Uruguay), 188 (Argentina) and 102 (Falkland Islands).

RESULTS

Species composition and latitudinal gradient

We recorded 700 marine prosobranch species distributed in 81 families in Brazilian shallow waters (see Appendix S2). Fifteen species still not formally described were considered in this study. The most species-rich families among those included in this study were Muricidae (69 spp.), Epitoniidae (36), Columbellidae (35), Olividae (31), Conidae (31), Marginellidae (30) and Fissurellidae (29).

The coastal areas sustain richer gastropod assemblages in comparison to the oceanic islands. The coastal areas between Bahia and Rio de Janeiro (12–23° S) were the richest. The coastal zone between Bahia and Santa Catarina (12–30° S) showed a great number of northernmost and southernmost limits of species (turnover of species) (Fig. 2, Table 1).

Cluster analysis of Brazil

Sørensen, Simpson and Ochiai Indices showed similar clustering patterns, but with some variations. Only the Sørensen and Simpson Indices are presented here (Fig. 3).

With the Sørensen index, there was a clear separation between coastal and insular areas (bootstrap = 100%, distance *c.* 0.8), and São Pedro and São Paulo appears isolated from other regions (distance > 0.9) (Fig. 3). In the cluster with the Simpson index, the islands are closer to the coastal areas of northern/north-eastern Brazil (bootstrap = 55%, distance *c.* 0.6), and the coastal areas of south-eastern/southern Brazil appear separated from the remaining areas (bootstrap = 78%, distance > 0.6) (Fig. 3). With the Ochiai index, as with the Simpson index, the islands (except São Pedro and São Paulo and Abrolhos) are closer to the coastal areas of N-NE Brazil (bootstrap = 34%, distance *c.* 0.6), and the coastal areas of SE-S Brazil appear separated from the remaining areas (bootstrap = 99%, distance *c.* 0.7). Abrolhos is closer to the group formed by coastal areas of N-NE Brazil and insular areas (Rocas, Fernando de Noronha, and Trindade and Martin Vaz) (bootstrap = 53%, distance *c.* 0.6), even in the Simpson index. As well as in the Sørensen index, São Pedro and São Paulo appears isolated from other regions (distance > 0.9).

Another difference among the three dendrograms is in the groups that included the coastal zones of Bahia and Espírito Santo. With the Sørensen and Ochiai indices, Bahia and Espírito Santo formed a group with a similarity of *c.* 0.7 and 0.8, respectively (bootstrap = 66% and 58%, respectively). However, with the Simpson index, Bahia is closer to the other NE Brazilian coastal zones (Rio Grande do Norte to Sergipe) (bootstrap = 73%, similarity next from 0.9), and Espírito Santo appears isolated from the other NE regions (bootstrap = 65%, similarity next from 0.7).

According to these results, the Brazilian coastal zone can be divided into four subregions (with distances near or lower than 0.3): (A) the coastal zone of Amapá; (B) the coastal zones of Pará to Espírito Santo; (C) the coastal zones of Rio de Janeiro to Santa Catarina; and (D) the coastal zone of Rio Grande do Sul. Each island was considered a separate unit.

Ordination analysis of Brazil

The ordination analyses performed using NMDS demonstrated a clear positive correlation between geographic distance and faunal similarity. In fact, the two dimensional ordination pattern corresponds very well to the real geographic positions, almost reproducing the Brazilian coastline. The insular areas showed up well-separated from each other, with the exception of Fernando de Noronha and Rocas Atoll. Due to the similarity between the NMDS results, only the results based on the Sørensen Index are shown (Fig. 4). The ordination analyses based on the Simpson and Ochiai matrices showed two-dimensional stress equal to 0.13 and 0.07, respectively.

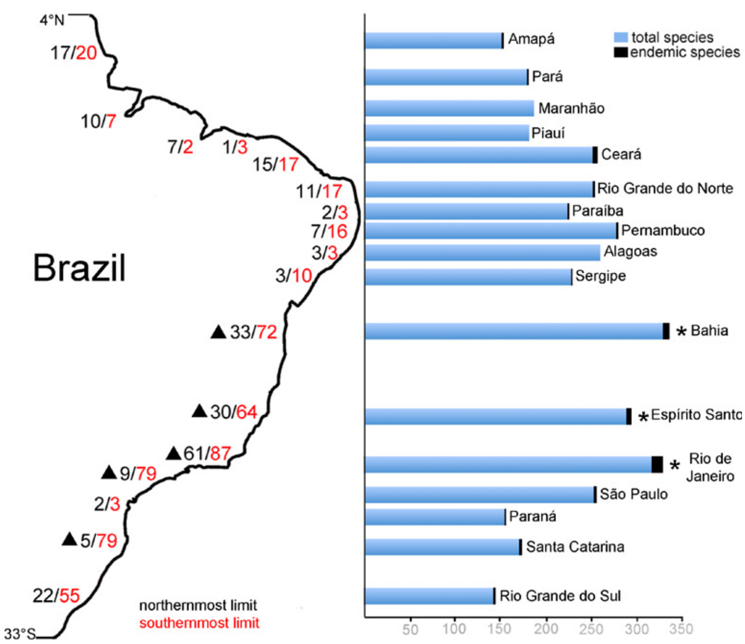

Figure 2 Latitudinal gradient of richness and turnover of prosobranch species along Brazilian coast. Legends: Blue bars: total number of species; black bars: total number of endemic species; black numbers: number of species with northernmost limit in that area; red numbers: number of species with southernmost limit in that area; asterisks: areas with higher species richness; and black triangles: areas with high species turnover.

Table 1 Number of prosobranch species (total and endemics) in each studied insular areas.

	Insular areas				
	São Pedro and São Paulo	Fernando de Noronha	Rocas Atoll	Trindade and Martin Vaz	Abrolhos
Number of species (total)	17	127	81	156	124
Number of endemic species	5	2	0	6	9
% of species which are endemic	29.4	1.6	0	3.8	7.3

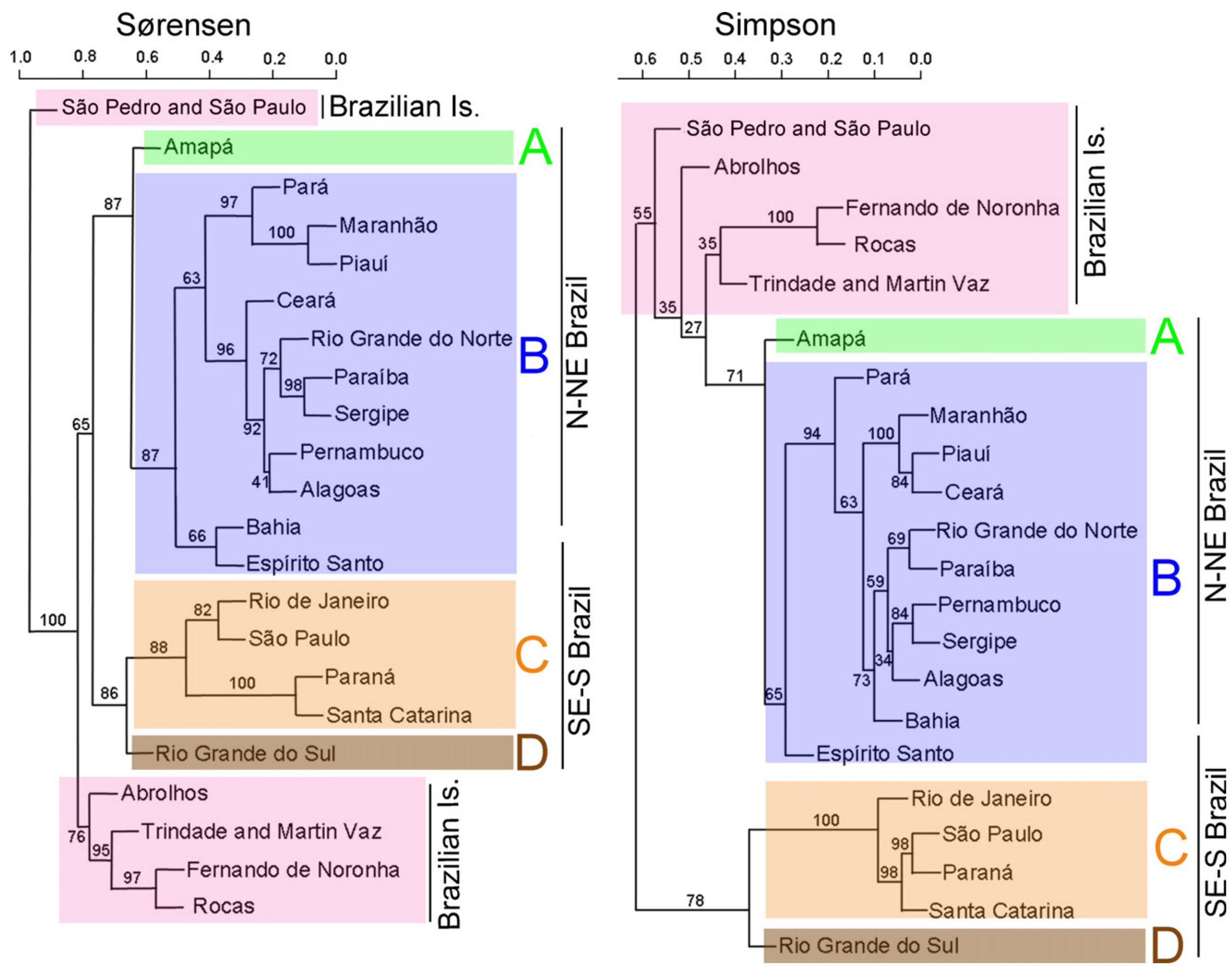

Figure 3 Dendrograms constructed by unweighted pair group method using arithmetic averages, based on Sørensen and Simpson matrices of presence/absence of 700 marine prosobranch species from shallow waters at different coastal and insular areas of Brazil. The values at the base of the branches indicate the % bootstrap support (n = 10,000). The rectangles correspond to sub-regions along the Brazilian coast: **A** – Amapá, **B** – Pará to Espírito Santo, **C** – Rio de Janeiro to Santa Catarina, and **D** – Rio Grande do Sul.

Cluster analysis of the Caribbean and South America areas

Similar to the previous results, Sørensen, Simpson and Ochiai Indices showed similar clusters but with some differences. Only the Sørensen and Simpson Indices are presented (Fig. 5).

With the Sørensen index, there was a clear separation between tropical and temperate zones (bootstrap = 50%, distance > 0.9) (Fig. 5). The tropical region is represented by the Caribbean, Brazilian areas, Guyana, French Guyana and Surinam. The temperate zone comprises Rio Grande do Sul (southern Brazil), Uruguay, Argentina and Falkland Islands. São Pedro and São Paulo appears isolated from the other regions (bootstrap = 59%, distance > 0.9). In this cluster, there is also a clear separation between the Caribbean and Brazilian regions (bootstrap = 50%, distance > 0.85) (Fig. 5).

In the cluster with the Simpson and Ochiai indices, the separation between tropical and temperate zones is not clear. The

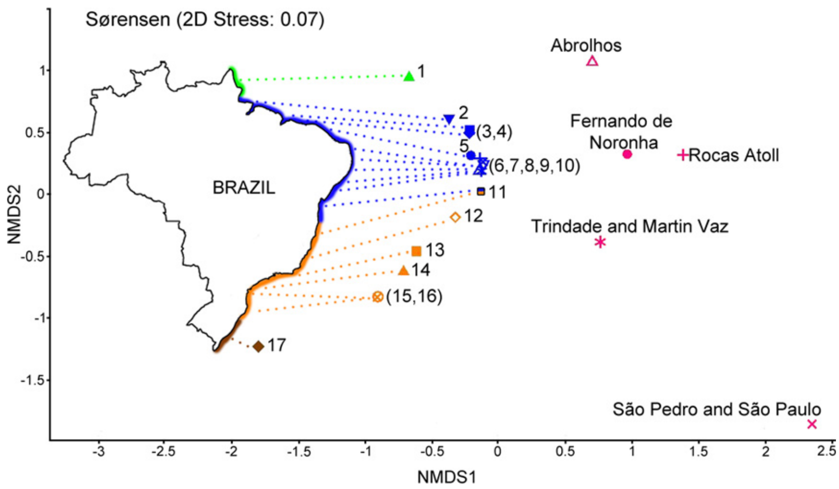

Figure 4 Ordination in two dimensions performed using non-metric multi-dimensional scaling, based on Sørensen similarity index based on a matrix of presence/absence of 700 marine prosobranch species from shallow waters on the Brazilian coast and islands (São Pedro and São Paulo, Fernando de Noronha, Rocas Atoll, Abrolhos, and Trindade and Martin Vaz). The numbers correspond to regions along Brazilian coast: 1 – Amapá, 2 – Pará, 3 – Maranhão, 4 – Piauí, 5 – Ceará, 6 – Rio Grande do Norte, 7 – Paraíba, 8 – Pernambuco, 9 – Alagoas, 10 – Sergipe, 11 – Bahia, 12 – Espírito Santo, 13 – Rio de Janeiro, 14 – São Paulo, 15 – Paraná, 16 – Santa Catarina and 17 – Rio Grande do Sul.

coastal areas of Rio Grande do Sul and Uruguay are more similar to those of south-eastern (Rio de Janeiro to Santa Catarina) than to Argentina and Falkland Islands. The group formed by Argentina and Falkland Islands appears isolated from other regions (distance > 0.9 in both indices). South-east Brazil (Rio de Janeiro to Santa Catarina) comprises a transition zone (tropical/subtropical). In the analyses with the Simpson and Ochiai indices, there is also a clear separation between the Caribbean and Brazilian regions (Amapá to Espírito Santo and insular areas) (bootstrap = 38% and 39%, distance > 0.55 and near 0.7, respectively) (Fig. 5).

In this cluster with the Simpson index, the typically tropical zone is represented by the Caribbean, Guyana, French Guyana, Surinam and Brazilian coastal (Amapá to Espírito Santo) and insular areas. São Pedro and São Paulo is more similar to Trindade and Martin Vaz (bootstrap = 33%, distance *c.* 0.5).

With the Ochiai index, the group formed by Guyana, French Guyana and Surinam appears isolated from the Caribbean and Brazilian coastal (Amapá to Espírito Santo) and insular (Rocas, Fernando de Noronha, and Trindade and Martin Vaz) areas (bootstrap = 44%, distance *c.* 0.9). Abrolhos is closer to the group formed by coastal areas of N-NE Brazil and insular areas (Rocas, Fernando de Noronha, and Trindade and Martin Vaz) (bootstrap = 51%, distance *c.* 0.6). São Pedro and São Paulo appears isolated from Caribbean, Guyana, French Guyana, Surinam, Uruguay, and Brazilian coastal and insular areas (bootstrap = 50%, distance *c.* 0.9).

Ordination analysis of the Caribbean and South America

Ordination analyses performed using NMDS demonstrated a clear separation among northern South America (Guyana, Surinam and French Guyana), Caribbean, Brazil coastal areas, Brazilian islands and Southern South America (Uruguay, Argentina and Falkland Island). The coastal zone of Rio Grande do Sul (South Brazil) appears next to Uruguay. The results were also similar, so only the Sørensen Index is presented (Fig. 6). The ordination analyses based on the Simpson and Ochiai matrices showed two-dimensional stress equal to 0.15 and 0.11, respectively.

DISCUSSION

The Brazilian coastal zone exhibits a wide range of environments that evolved during the Quaternary in response to climate and sea level changes (Dominguez, 2006). Previous studies by Silveira (1968), Coutinho (1996), Castro & Miranda (1998) and Tessler & Mahiques (2009) characterize the geological setting of the Brazilian coastal zone and continental shelf. The SE-S coast is dominated by siliclastic bottoms on the shelf and sandy beaches interrupted by crystalline rocky shores. The central and NE coasts, on the other hand, have a greater carbonatic influence, and the crystalline rocks are replaced by sandstone outcrops. Another major transition occurs in the northern section of the coast, by influence of the Amazon River drainage depositing more muddy sediments over the platform. In terms of water circulation, the Brazilian coast is influenced by three major surface water currents: the warm North Brazil Current (NBC), the warm Brazil Current (BC), and the cold Malvinas Current (MC) [see Peterson & Stramma (1991) and Silveira *et al.* (2000)].

Brazil has one of the largest typically tropical coasts on the planet, including the whole N-NE through the central portion of the coast, with temperatures consistently over 25 °C. The SE coast, on the other hand, is under influence of an

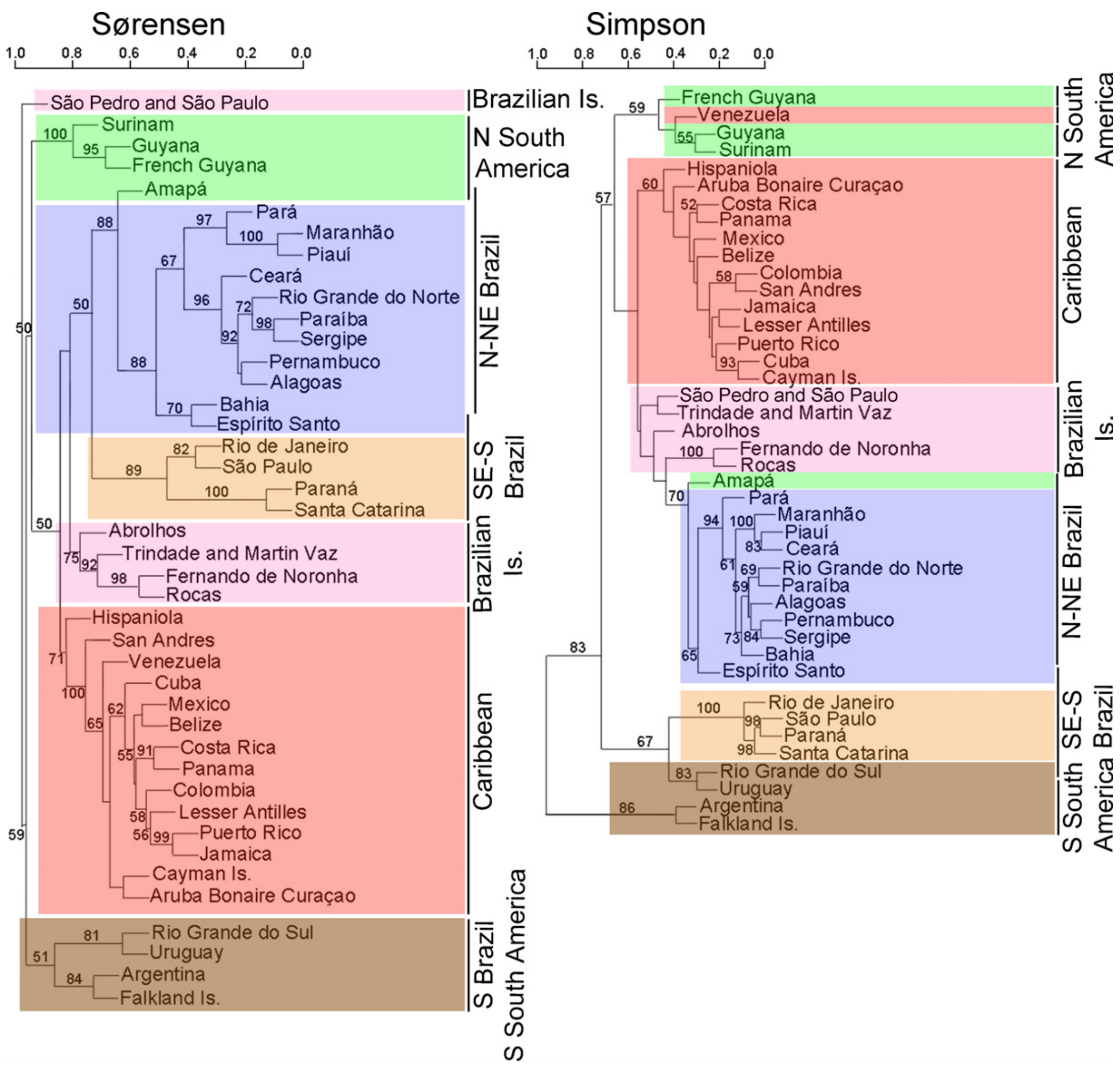

Figure 5 Dendrograms constructed by unweighted pair group method using arithmetic averages, based on Sørensen and Simpson similarity based on presence/absence matrices of marine prosobranch species from shallow waters at different Caribbean and South America regions. The values at the base of the branches indicate the % bootstrap support (n = 10,000; % $\geq$ 50).

upwelling, especially along Rio de Janeiro, bringing colder water from the Southern Atlantic Central Water mass, and also increasing the productivity throughout this region. The combination of these and other elements of the physical setting are certainly major drivers of the distribution of organisms along the coast and explain most of the biogeographical divisions proposed for the Western Atlantic.

Despite this, there is considerable variation in the delimitation between tropical and subtropical/temperate faunas. There is also great variation in the nomenclature used in the definition of regions and their significance, as well as in the methods used to classify biota.

Considering the results of the cluster analyses (groups with distances equal or lesser than 0.3), ordination analyses, and environmental characteristics of each area, we propose the following regionalization of the coastal and shelf areas along the Brazilian coast, mainly based on the classifications proposed by Floeter *et al.* (2008) and Briggs & Bowen (2012): 1. Western Atlantic Region (tropical and temperate warm waters), 1.1. Guyanese Province (Amapá, state), 1.2. Brazilian Province, 1.2.1. North-eastern Brazil Area (from the mouth of the Amazon River to southern Bahia, Brazil), 1.2.2. South-eastern Brazil Area (from southern Bahia to Santa Catarina, Brazil, a transition zone), and 1.3. Argentinian Province (Rio Grande do Sul state) (see Appendix S3).

The cluster and ordination analyses indicate that the Brazilian insular areas are biogeographical units distinct from other studied regions. Each island has its own fauna of marine prosobranchs, despite sharing species with other coastal and insular areas. All the Brazilian oceanic islands (São Pedro and São Paulo, Fernando de Noronha, Rocas Atoll, and Trindade and Martin Vaz Archipelago) are considered

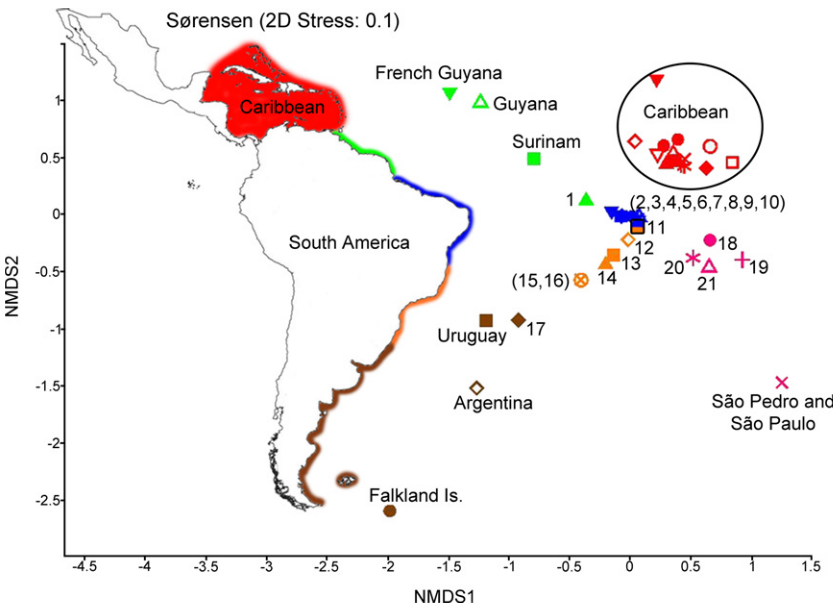

Figure 6 Ordination in two dimensions performed using non-metric multi-dimensional scaling, based on Sørensen similarity index calculated from a presence/absence matrix of marine prosobranch species from shallow waters at different Caribbean and South America regions. The numbers correspond to regions along the Brazilian coast and insular areas: 1 – Amapá, 2 – Pará, 3 – Maranhão, 4 – Piauí, 5 – Ceará, 6 – Rio Grande do Norte, 7 – Paraíba, 8 – Pernambuco, 9 – Alagoas, 10 – Sergipe, 11 – Bahia, 12 – Espírito Santo, 13 – Rio de Janeiro, 14 – São Paulo, 15 – Paraná, 16 – Santa Catarina, 17 – Rio Grande do Sul, 18 – Fernando de Noronha, 19 – Rocas Atoll, 20 – Trindade and Martin Vaz, and 21 – Abrolhos.

here as belonging to the Brazilian Province, in agreement with the proposal by Floeter *et al.* (2008) and Briggs & Bowen (2012). The changes in the affinity of São Pedro and São Paulo with the other studied areas appear to be a direct reflection of low species richness due to its small area and isolation. With the exception of the five endemic species, all species recorded for SPSPA also have records for the Caribbean, 11 are also registered for the Brazilian coast, and nine are also present in Trindade and Martin Vaz Archipelago. São Pedro and São Paulo is influenced by the warm Equatorial Undercurrent (EUC) and the branches of South Equatorial Current (SEC) (Stramma & England, 1999). The greatest similarity between Fernando de Noronha and Rocas Atoll can be explained by the fact that these two areas are part of a seamount chain extending in the east–west orientation and reaching closer to Ceará state, NE Brazil (Morais, 1969), influenced by the warm central branch of SEC (Stramma & England, 1999). The connection with the continent through the seamount chain and the short distance from both areas to the mainland (< 300 km) explains the similarity between the group formed by Fernando de Noronha/Rocas and coastal areas of N-NE Brazil.

Just like the oceanic islands, Abrolhos Archipelago is considered an 'Area' belonging to the Brazilian Province. Despite being an enlargement of the Eastern Brazilian continental shelf, the uniqueness of Abrolhos must not be disregarded. As the Abrolhos Reef Complex represents the most extensive and richest area of coral reefs in the south-western Atlantic, its marine prosobranchs richness is certainly still underestimated (124 species recorded in this study). Its uniqueness is highlighted by the cluster analyses with Simpson and Ochiai Indices, where Abrolhos appears closer to the group formed by coastal areas of N-NE Brazil and some insular areas. This happens because Abrolhos shares many species with continental and insular areas, even though it has a considerable rate of endemism. Coltro (2004) described six new species of the genus *Conus* (Conidae) from Abrolhos. Spotorno *et al.* (2012) also indicate two new species of Vermetidae for this region (not yet formally described). Further studies in the Abrolhos region will certainly provide more records and new descriptions of prosobranch species.

The present study involving marine shallow-water prosobranch gastropods reinforces the separation between the Caribbean and Brazil areas that had already been established previously (e.g. Balech, 1954; Coelho & Ramos, 1972; Briggs, 1974; Díaz & Puyana, 1994; Spalding *et al.*, 2007; Petuch, 2013). Cluster and ordination analyses performed in this study also showed that closer coastal areas have more similar faunas, as expected. This pattern reflects a gradual latitudinal variation in marine prosobranch assemblages, following the changes along Brazilian coast.

Although the analyses presented here did not indicate the regionalization of the area between the mouths of the Orinoco and the Amazon, as proposed by Díaz & Puyana (1994) and Petuch (2013), this hypothesis is considered (Guyanese Province). The coastal area of Amapá (4° N–0° N) appears separated from other regions of Brazil in all clusters and ordination analysis, suggesting the uniqueness of its fauna. The environmental setting of the part of Venezuela, Guyana, Surinam, French Guyana and Amapá coastal zone reinforces this singularity, with the presence of large mangrove forests and extensive muddy banks, and the absence of shallow coral reefs, beach rocks and rocky shores. The shelf of Amapá is characterized by mud, quartz sand and biodetritic sand (Coutinho, 1996). The absence of hard substrates limits the occurrence of typical species of these environments, which are present in the Caribbean and the rest of the Brazilian coast. This study also proposes that the influence of the Amazon freshwater discharge is greater just north from its mouth, due to the direction of the warm North

Brazil Current. The absence of conclusive results can be a consequence of still insufficient knowledge about marine prosobranchs of this area. The species richness of this group in Brazil is still underestimated, with knowledge gaps particularly in the northern region (Simone, 2003; Amaral & Jablonski, 2005). Future works will confirm or refute Díaz & Puyana's (1994) and Petuch's (2013) hypothesis about the regionalization of the area between the Orinoco and Amazon rivers, also suggested here.

The cluster analyses performed in this study indicate a region characterized by typically tropical prosobranch assemblages, comprising the coastal areas between Pará and Bahia (0°–15° S). This area was denominated North-eastern Brazil, supporting the study of reef fish performed by Floeter *et al.* (2008). This area is influenced by the warm (between 25–29 °C) and oligotrophic South Equatorial Current (SEC) (Peterson & Stramma, 1991), and is characterized by the presence of muddy and sandy banks, mangroves, coral reefs, beach rocks and rocky shores (at Bahia coastal zone). The shelf of the North-eastern Brazil Area is characterized by mud, quartz sand, calcareous algae and biodetritic sand (Coutinho, 1996).

The location of the southern limit for tropical fauna is a point of disagreement in the studies. Here, we corroborate the Lotufo (2002) and Almeida (2009) hypothesis, which establishes the northern boundary of the transition zone on the coast of Bahia (between 13° S and 18° S). Cluster and ordination analyses showed that Bahia's coastal area has affinity with both Espírito Santo and other coastal areas from NE Brazil (Rio Grande do Norte to Sergipe). These results can be explained in part by edaphic, hydrographic and thermal factors, as previously cited by Lotufo (2002) and Almeida (2009). Lotufo (2002) highlighted the role of the colder South Atlantic Central Water (SACW) and the replacement of sandstone reefs by crystalline substrate starting from south of Bahia in establishing this transitional zone. Almeida (2009) also cited the replacement of calcareous algae bottoms (highly developed in NE Brazil) by biodetritic sand starting from a region near Cabo Frio. This author mentioned the possible influence of relatively large drainage basins located between Bahia and Rio de Janeiro. This factor was not considered in previous studies. Several studies have suggested the Cabo Frio region as a transition area between tropical and subtropical biota (Balech, 1954; Vannucci, 1964; Briggs, 1974; Absalão, 1989; Petuch, 2013); others have suggested southern Espírito Santo/northern Rio de Janeiro (23° S) (Coelho & Ramos, 1972; Palácio, 1982; Floeter & Soares-Gomes, 1999). Floeter *et al.* (2001) mentioned the north of Espírito Santo (20° S) as the northern limit of this transition area. The analyses performed in this study did not indicate Cabo Frio as a transition area. A greater refinement of the current data will provide a more accurate location of the northern boundary of the transition area on the coast of Bahia.

South from this tropical distribution limit, there would be a mixing zone of tropical and subtropical faunas. This transition zone would extend to the limit where there is predominance of subtropical/temperate species (Balech, 1954; Vannucci, 1964; Coelho & Ramos, 1972; Palácio, 1982; Floeter *et al.*, 2001; Lotufo, 2002; Almeida, 2009). This study points to a transition zone (South-eastern Brazil Area) along the Brazilian coast beginning in southern Bahia and extending to Santa Catarina. This area is characterized by high species richness, a significant portion of endemic species, and the northernmost and southernmost limits of several species. This great turnover of species reinforces the transitional nature of this area, where there is a mix of tropical and subtropical fauna. The ordination analysis showed affinities between Espírito Santo and other SE Brazilian areas (Rio de Janeiro to Santa Catarina). Espírito Santo also exhibited affinity with NE Brazil (cluster analysis). Santa Catarina was chosen as the southern limit of this transition zone because the Rio Grande do Sul coast has always appeared separated from other areas of Brazil and closer to Uruguay and Argentina shores. Briggs & Bowen (2012) considered the Brazilian Province as comprising the area between the Amazon River mouth and Santa Catarina (SE Brazil). The study of Floeter *et al.* (2001) was the first to extend the Brazilian Province up to Santa Catarina. On the other hand, Floeter & Soares-Gomes (1999), based on marine gastropod data, consider the existence of a wide transition zone between southern Espírito Santo (21° S) and Rio Grande do Sul (32° S), characterizing this region as very heterogeneous with a low rate of endemism. A greater refinement of the current data will provide a more accurate location of the southern boundary of the transition area somewhere on the coasts of Santa Catarina and Rio Grande do Sul.

Petuch (2013) proposed wide transition zones with shared faunal elements (warm-tolerant or cold-tolerant) and endemic species that are not found in other overlapping areas. These broad overlap areas were referred to as a Provinciatone by Petuch (2013), and they are always between two Provinces. Our results agree with the definition of Provinciatone by Petuch (2013), since the region between southern Bahia and Santa Catarina features a mix of tropical and subtropical fauna, with endemic elements. However, unlike Petuch (2013), this broad transition zone is here considered to be an Area (South-eastern Brazil Area). This is just like the region between the coasts of Pará and southern Bahia (North-eastern Brazil Area), with both Areas belonging to the Brazilian Province.

The richest areas in terms of prosobranchs are located between Bahia and Rio de Janeiro (18–23° S), possibly due to the mixture of tropical and subtropical elements. In terms of latitude, this maximum coincides with other animal groups, such as fish (Floeter *et al.*, 2001) and crabs (Levinton & Mackie, 2013). This wide area is characterized by the presence of beach rocks, coral reefs, sandy coastal plains (restingas), rocky shores, as well as sandy, mud and calcareous algae bottoms (Silveira, 1968; Coutinho, 1996; Castro & Miranda, 1998). This region is also under the influence of the warm Brazil Current and also the colder SACW, which brings low-temperature and nutrient-rich waters close to the coastline (Peterson & Stramma, 1991; Ekau & Knoppers, 1999). This mix of tropical and subtropical waters, and the wide variety of ecosystems, can then explain the greater richness of the region. São Paulo, however, shows a gradual transition towards a more impoverished fauna found in the southern region. From Santa Catarina southward, rocky bottoms almost disappear, giving way to extensive and sandy coastal plains (Silveira, 1968). This large transition zone (southern Bahia to Santa Catarina) is characterized by great shifts in prosobranch assemblages, as it is also the northernmost/southernmost limit of several species.

The South-eastern Brazil Area is the most studied region of Brazil, especially the coasts of Rio de Janeiro and São Paulo. However, we do not believe that these well-sampled regions affect the analyses and conclusions of this study, due to the environmental characteristics mentioned above. Additionally, we can mention that São Paulo (the area with the highest number of studies) has fewer species than less studied regions, such as Espírito Santo. We believe that further studies will reinforce the patterns found here (mainly the northern region of Brazil – Guyanese Province), and that more refined analysis will provide a more accurate location of the limits of each proposed area.

Here, we show that the region with typically subtropical/temperate faunas begins on the coast of Rio Grande do Sul and would extend to Valdez Peninsula (Argentina), corroborating previous studies (Balech, 1954; Coelho & Ramos, 1972; Almeida, 2009; Briggs & Bowen, 2012, 2013). This area is historically called the Argentinian Province.

The coastal area of Rio Grande do Sul, just like Amapá, proved to be quite unique. The Brazilian southern coast is strongly influenced by the cold Malvinas Current (a branch off of the Antarctic Circumpolar Current) (Peterson & Stramma, 1991). Rio Grande do Sul is characterized by the presence of extensive muddy and sandy banks, and the absence of mangroves, coral reefs, rocky shores and beach rocks. The temperature seems to be the major factor in delineating this region. The absence of hard substrates limits the occurrence of typical species of these environments, and the cold water hinders the establishment and development of typical tropical species.

The distribution of marine prosobranchs is a result of the interplay of many different biological and abiotic drivers, many of them not considered here. Dispersal, for instance, is one of the main features to be considered and is strongly dependent of the type of development in their life cycle. This aspect and its relation with distribution ranges will be analysed and discussed elsewhere. Also, the change in pace in the climatic conditions observed in the last century may give to the biogeographical limits a more dynamic character, in a way that a continuous reassessment of the fauna distribution is not just desirable, but essential.

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REFERENCES

Absalão, R.S. (1989) Padrões distributivos e zoogeografia dos moluscos da plataforma continental brasileira. Parte III. Comissão Oceanográfica Espírito Santo I. *Memórias do Instituto Oswaldo Cruz*, **84**, 1–6.

Almeida, A.O. (2009) *Composição taxonômica e zoogeografia de crustáceos decápodos marinhos e estuarinos da Bahia, Brasil*. PhD Thesis, Universidade Federal de Pernambuco, Recife.

Amaral, A.C.Z. & Jablonski, S. (2005) Conservation of marine and coastal biodiversity in Brazil. *Conservation Biology*, **19**, 625–631.

Balech, E. (1954) División zoogeográfica del litoral sudamericano. *Revista de Biologia Marina*, **4**, 184–195.

Boschi, E.E. (2000) Species of decapod crustaceans and their distribution in the american marine zoogeographic provinces. *Revista de Investigación y Desarrollo Pesquero*, **13**, 7–136.

Bouchet, P., Kantor, Y.I., Sysoev, A. & Puillandre, N. (2011) A new operational classification of the Conoidea (Gastropoda). *Journal of Molluscan Studies*, **77**, 273–308.

Briggs, J.C. (1974) *Marine zoogeography*. McGraw-Hill Book Company, New York.

Briggs, J.C. (1995) *Global biogeography*. Elsevier, Amsterdam.

Briggs, J.C. & Bowen, B.W. (2012) A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography*, **39**, 12–30.

Briggs, J.C. & Bowen, B.W. (2013) Marine shelf habitat: biogeography and evolution. *Journal of Biogeography*, **40**, 1023–1035.

Castro, B.M. & Miranda, L.B. (1998) Physical oceanography of the western Atlantic continental shelf located between 4°N and 34°S – coastal segment (4°W). *The sea* (ed. by A.R. Robinson and K.H. Brink), pp. 209–251. J Wiley & Sons, New York.

Clarke, K.R. & Warwick, R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. PRIMER-E, Plymouth.

Coelho, P.A. & Ramos, M.A. (1972) A constituição e a distribuição da fauna de decápodos do litoral leste da América do Sul entre as latitudes de 5°N e 39°S. *Trabalhos Oceanográficos da Universidade Federal de Pernambuco*, **13**, 133–236.

Coltro, J. (2004) New species of Conidae from north-eastern Brazil (Mollusca: Gastropoda). *Strombus*, **11**, 1–16.

Coutinho, P.N. (1996) Oceanografia geológica. *Levantamento do Estado da Arte da Pesquisa dos Recursos Vivos Marinhos do Brasil* (ed. by P.N. Coutinho), pp. 1–75. Ministério do

Meio Ambiente dos Recursos Hídricos e da Amazônia Legal - MMA, Secretaria de Coordenação dos Assuntos do Meio Ambiente - SMA, Brasília.

Dana, J.W. (1853) On an isothermal oceanic chart, illustrating the geographical distribution of marine animals. *The American Journal of Science and Arts, 2nd series*, **16**, 153–167; 314–327.

Dapporto, L., Ramazzotti, M., Fattorini, S., Talavera, G., Vila, R. & Dennis, R.L.H. (2013) Recluster: an unbiased clustering procedure for beta-diversity turnover. *Ecography*, **36**, 1070–1075.

Díaz, J.M. & Puyana, M. (1994) *Moluscos del Caribe Colombiano: un catálogo ilustrado*. Colciencias y Fundacion Natura Colombia, Santafe de Bogota.

Dominguez, J.M.L. (2006) The coastal zone of Brazil: an overview. *Journal of Coastal Research*, **39**, 16–20.

Ekau, W. & Knoppers, B. (1999) An introduction to the pelagic system of the North-East and East Brazilian shelf. *Archive of Fishery and Marine Research*, **47**, 113–132.

Ekman, S. (1953) *Zoogeography of the sea*. Sidgwick & Jackson Ltda, London.

Floeter, S.R. & Soares-Gomes, A. (1999) Biogeographic and species richness patterns of Gastropoda on the Southwestern Atlantic. *Revista Brasileira de Biologia*, **59**, 567–575.

Floeter, S.R., Guimarães, R.Z., Rocha, L.A., Ferreira, C.E., Rangel, C.A. & Gasparini, J.L. (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecology & Biogeography*, **10**, 423–431.

Floeter, S.R., Rocha, L.A., Robertson, D.R., Joyeux, J.C., Smith-Vaniz, W.F., Wirtz, P., Edwards, A.J., Barreiros, J.P., Ferreira, C.E.L., Gasparini, J.L., Brito, A., Falcón, J.M., Bowen, B.W. & Bernardi, G. (2008) Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, **35**, 22–47.

Forbes, E. (1844) Report on the Mollusca and Radiata of the Aegean sea, and on their distribution, considered as bearing on geology. *Reports of the British Association for the Advancement of Science*, **1843**, 130–193.

Forcelli, D.O. (2000) *Moluscos magallánicos: guia de los moluscos de la Patagonia y del sur del Chile – Parte I: Classe Gastropoda, Subclasse Prosobranchia*. Vázquez Mazzini, Buenos Aires.

Gasparini, J.L. (2004) *Ilha da Trindade e Arquipélago Martin Vaz: pedaços de Vitória no azul atlântico*. GSA, Vitória.

Gasparini, J.L. & Floeter, S.R. (2001) The shore fishes of Trindade Island, western South Atlantic. *Journal of Natural History*, **35**, 1639–1656.

Griffiths, H.J., Barnes, D.K.A. & Linse, K. (2009) Towards a generalized biogeography of the Southern Ocean benthos. *Journal of Biogeography*, **36**, 162–177.

Koleff, P., Gaston, K.J. & Lennon, J.J. (2003) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, **72**, 367–382.

Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, **37**, 2029–2053.

Kulbicki, M., Parravicini, V., Bellwood, D.R., Arias-Gonzàlez, E., Chabanet, P., Floeter, S.R., Friedlander, A., McPherson, J., Myers, R.E., Vigliola, L. & Mouillot, D. (2013) Global biogeography of reef fishes: a hierarchical quantitative delineation of regions. *PLoS ONE*, **8**, e81847.

Leão, Z.M.A.N. & Ginsburg, R.N. (1997) Living reefs surrounded by siliciclastics sediments: the Abrolhos coastal reefs, Bahia, Brazil. *Proceedings of 8th International Coral Reef Symposium*, **2**, 1767–1772.

Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier Science B.V, Amsterdam.

Levinton, J. & Mackie, J. (2013) Latitudinal diversity relationships of fiddler crabs: biogeographic differences united by temperature. *Global Ecology and Biogeography*, **22**, 1050–1059.

Lotufo, T.M.C. (2002) *Ascidiacea (Chordata: Tunicata) do litoral tropical brasileiro*. PhD Thesis, Universidade de São Paulo, São Paulo.

Martínez, S. & del Río, C. (2002) Las provincias malacológicas miocenas y recientes del Atlántico sudoccidental. *Anales de Biologia*, **24**, 121–130.

Martínez, S., del Río, C.J. & Rojas, A. (2013) *Biogeography of the Quaternary Molluscs of the Southwestern Atlantic Ocean*. Springer, Dordrecht, the Netherlands.

Miloslavich, P., Díaz, J.M., Klein, E., Alvarado, J.J., Día, C., Gobin, J., Escobar-Briones, E., Cruz-Motta, J.J., Weil, E., Cortés, J., Bastidas, A.C., Robertson, R., Zapata, F., Martín, A., Castillo, J., Kazandjian, A. & Ortiz, M. (2010) Marine biodiversity in the Caribbean: regional estimates and distribution patterns. *PLoS ONE*, **5**, e11916.

Miloslavich, P., Klein, E., Díaz, J.M., Hernandéz, C.E., Bigatti, G., Campos, L., Artigas, F., Castillo, J., Penchaszadeh, P.E., Neill, P.E., Carranza, A., Retana, M.V., Astarloa, J.M.D., Lewis, M., Yorio, P., Piriz, M.L., Rodríguez, D., Yoneshigue-Valentin, Y., Gamboa, L. & Martín, A. (2011) Marine biodiversity in the Atlantic and Pacific coasts of South America: knowlegde and gaps. *PLoS ONE*, **6**, 1–43.

Morais, J.O. (1969) Aspectos correlativos de geologia litoral e submarina no Nordeste do Brasil. *Arquivos de Ciências do Mar*, **9**, 127–131.

Palácio, F.J. (1982) Revisión zoogeográfica marina del sur del Brasil. *Boletim do Instituto Oceanográfico*, **31**, 69–92.

Pastorino, G. (1993) The taxonomic status of *Buccinanops* d'Orbigny, 1841 (Gastropoda: Nassariidae). *The Veliger*, **36**, 160–165.

Pastorino, G. (1994) Moluscos costeros recipientes de Puerto Piramide, Chubut, Argentina. *Acadamia Naciel de Ciencia de Cordoba*, **93**, 1–35.

Pastorino, G. (2002) Systematics and phylogeny of the genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) from Patagonia and Antarctica: morphological patterns. *Bollettino Malacologico*, **4**, 127–134.

Pastorino, G. (2003) A new species of Ancillariinae (Gastropoda: Olividae) from the southwestern Atlantic Ocean. *The Nautilus*, **117**, 15–22.

Pastorino, G. (2005) A revision of the genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) from Southern South America. *The Nautilus*, **119**, 55–82.

Pastorino, G. (2009) The genus *Olivella* Swainson, 1831 (Gastropda: Olividae) in Argentine waters. *The Nautilus*, **123**, 189–201.

Pastorino, G. & Penchaszadeh, P.E. (2009) Egg capsules, eggs and embryos of *Trophon acanthodes* (Gastropoda: Muricidae) and its new generic position. *Journal of Molluscan Studies*, **75**, 337–341.

Peterson, R.G. & Stramma, L. (1991) Upper-level circulation in the South Atlantic Ocean. *Progress in Oceanography*, **26**, 1–71.

Petuch, E.J. (2013) *Biogeography and biodiversity of western Atlantic mollusks*. CRC Press, New York.

R Development Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. Available at: http://www.r-project.org. (accessed 12 February 2014).

Rechimont, M.E., Galván, D.E., Sueiro, M.C., Casas, G., Piriz, M.L., Diez, M.E., Primost, M., Zabala, M.S., Márquez, F., Brogger, M., Alfaya, J.E.F. & Bigatti, G. (2013) Benthic diversity and assemblage structure of a north Patagonian rocky shore: a monitoring legacy of the NaGISA project. *Journal of the Marine Biological Association of the United Kingdom*, **93**, 2049–2058.

Rosenberg, G. (2009) *Malacolog 4.1.1: A database of Western Atlantic marine Mollusca* [WWW database (version 4.1.1)]. Available at: http://www.malacolog.org/ (accessed 2 April 2015).

Silveira, I.C.A., Schmidt, A.C.K., Campos, E.J.D., Godoi, S.S. & Ikeda, Y. (2000) A Corrente do Brasil ao Largo da costa leste brasileira. *Revista Brasileira de Oceanografia*, **48**, 171–183.

Silveira, J.D. (1968) Morfologia do litoral. *Brasil: a Terra e o homem - vol. 1: As bases físicas* (ed. by A. Azevedo), pp. 253–305. Companhia Editora Nacional, São Paulo.

Simone, L.R.L. (2003) Histórico da malacologia no Brasil. *Revista de Biología Tropical*, **51**, 139–147.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, N., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., Mcmanus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine ecoregions of the World: a bioregionalization of coastal and shelf areas. *BioScience*, **57**, 573–583.

Spotorno, P., Tâmega, F.T.S. & Bemvenuti, C.E. (2012) An overview of the recent vermetids (Gastropoda: Vermetidae) from Brazil. *Strombus*, **19**, 1–8.

Stramma, L. & England, M. (1999) On the water masses and mean circulation of the south Atlantic Ocean. *Journal of Geophysical Research*, **104**, 20863–20883.

Suzuki, R. & Shimodaira, H. (2006) Pvclust: an R package for assessing the uncertainty in hierarchical clustering. *Bioinformatics (Oxford, England)*, **22**, 1540–1542.

Teso, V. & Pastorino, G. (2011) A revision of the genus *Olivancillaria* (Mollusca: Olividae) from the southwestern Atlantic. *Zootaxa*, **2889**, 1–34.

Teso, V., Signorelli, J.H. & Pastorino, G. (2011) Shell phenotypic variation in the southwestern Atlantic gastropod *Olivancillaria carcellesi* (Mollusca: Olividae). *Journal of the Marine Biological Association of the United Kingdom*, **91**, 1089–1094.

Tessler, M.G. & Mahiques, M.M. (2009) Processos oceânicos e produtos sedimentares. *Decifrando a Terra* (ed. by W. Teixeira, T.R. Fairchild, M.C.M. Toledo and F. Taioli), pp. 376–399. Companhia Editora Nacional, São Paulo.

Vannucci, M. (1964) Zoogeografia Marinha do Brasil. *Boletim do Instituto de Biologia Marinha*, **7**, 113–121.

Woodward, S.P. (1856) *A manual of the Mollusca: or, rudimentary treatise of fossil and recent shells*. Willian Ostell, London.

Worms Editorial Board (2015) *World Register of Marine Species*. Available at: http://www.marinespecies.org at VLIZ (accessed 2 April 2015).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data sources used in this study.
Appendix S2 Marine prosobranchs from Caribbean and South America.
Appendix S3 Comparative chart of biogeographic divisions.

BIOSKETCHES

Cristiane X. Barroso is a biologist and completed her PhD in Marine Sciences at Universidade Federal do Ceará, Brazil. Her research interests are related to the taxonomy, ecology and biogeography of marine mollusks. In particular, she is most interested in understanding biogeographic patterns in shallow-water marine gastropods.

Tito Lotufo completed his PhD in Zoology at Universidade de São Paulo, Brazil. He was a professor at Universidade Federal do Ceará, from 2002 until 2014. He is currently a professor at Instituto Oceanográfico, Universidade de São Paulo. His main research subjects are reef ecology and biodiversity, with a focus on ascidians and fishes.

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