

## BIOGEOGRAPHY AND CONNECTIVITY BETWEEN WESTERN SOUTH AMERICAN AND ANTARCTIC MARINE MOLLUSCS

*Rafael da Rocha Fortes<sup>1</sup> & Ricardo Silva Absalão<sup>2</sup>*

<sup>1</sup> Universidade Federal do Estado do Rio de Janeiro, Inst. Biologia, Departamento de Ecologia e Recursos Marinhos, Laboratório de Ecologia Bêntica, Av Pasteur, 458, CCBS, sala 411, Urca, Rio de Janeiro, RJ, Brasil. CEP: 22290-240.

<sup>2</sup> Universidade Federal do Rio de Janeiro, Instituto de Biologia, Departamento de Zoologia, Laboratório de Malacologia, Av. Carlos Chagas Filho, 73, CCS-BLA, sala A94, Ilha do Fundão, Rio de Janeiro, RJ, Brasil. CEP: 21941-540.  
E-mails: rafaelfortes@hotmail.com, absalao@hotmail.com

### ABSTRACT

The latitudinal diversity gradient is widely recognized, leading researchers to assume that Antarctic fauna is impoverished. However, with increased sampling efforts, some studies have shown a great diversity of certain marine groups surrounding the Antarctic continent, with higher rates of them. Antarctic endemism may be associated with its isolation and climate change over the evolutionary time scale. Despite this relative isolation, recent evidence suggests some degree of connectivity between the Antarctic and South American faunas. Our study used secondary data extracted from Malacolog 4.1.1. The geographical area considered was the entire South American Atlantic coast and the adjacent areas of the Antarctic (Antarctic Peninsula, part of the Weddell Sea and islands of the Scotia Arc). Our survey yielded 6517 species of molluscs. The most diverse province was the North Brazil Shelf, and the least diverse was the Scotia Sea. Endemism rates for low-latitude provinces were close to 15%, in contrast to the highest endemism rate of 40% in the Scotia Sea Province. The highest value for richness was found for the Guianan ecoregion, and the lowest value for the Antarctic Peninsula. Most ecoregions had an endemism rate around 3%, with the highest endemism in South Georgia. The richness gradient increased toward lower latitudes. The cluster analysis for the malacofauna indicated four significant groups. The bathymetric Rapoport's Rule showed the increase of bathymetric range toward higher-latitude ecoregions and whereas Bergmann's Rule showed the opposite relationship. The higher richness at -25°S may be associated with the presence of coral and calcareous algal reefs. At mid-latitudes richness was also high, and this region comprise an ecotone between thermophilic and cryophilic species'. The cluster analysis validated three provinces proposed by Spalding, although it revealed the inadequate knowledge of the North Brazil Shelf province. The higher endemism observed in the Magellanic and Scotia seas demonstrates the influence that Antarctic isolation has on its community structure, although the cluster showed the existence of a connection with South America. The observed converse Bergmann's Rule could be explained by the shorter seasons at higher latitudes, which limit the phenotypic body size that can be attained.

**Keywords:** Atlantic Ocean; diversity gradient; Rapoport's rule; Antarctica; marine mollusca.

### RESUMO

**BIOGEOGRAFIA E CONECTIVIDADE ENTRE A MALACOFAUNA DA COSTA OESTE SUL AMERICANA E ANTÁRTICA.** O gradiente de diversidade associado à latitude é bastante reconhecido, levando muitos pesquisadores a acreditarem no empobrecimento da fauna Antártica. Entretanto, o aumento do esforço amostral, mostrou uma grande diversidade de organismos marinhos na Antártica, com um elevado endemismo para alguns grupos. Este endemismo pode estar associado ao isolamento e as mudanças climáticas ocorridas ao longo do tempo evolutivo. Entretanto, evidências recentes mostraram a conectividade da fauna antártica e sul americana. Este trabalho utilizou dados provenientes do Malacolog 4.1.1. A área geográfica foi a costa atlântica da América do Sul e áreas adjacentes da Antártica (Península Antártica, parte do mar de Weddell e o arco de ilhas Scotia). Nossa amostragem levantou 6517 espécies de moluscos. A província com maior

riqueza foi a Plataforma Continental do Norte do Brasil e a menor foi a do mar de Scotia. A taxa de endemismo para as menores latitudes foi cerca de 15%, contrário ao elevado endemismo na província do mar de Scotia (40%). A maior riqueza foi encontrada na ecoregião da Guiana, e a menor na da Península Antártica. A maioria das ecoregiões possui endemismo em torno de 3%, sendo o maior na Georgia do Sul. O gradiente de riqueza foi corroborado. A análise de grupamento para a malacofauna mostrou quatro grupos significantes. A Regra de Rapoport batimétrica mostrou um aumento da amplitude batimétrica nas ecoregiões das maiores latitudes e a Regra de Bergmann mostrou a sua relação oposta. A elevada riqueza em 25° S pode estar relacionada aos recifes de corais e algas calcáreas. Nas latitudes medianas, observou-se uma elevada riqueza, além de corresponder a um ecótono entre espécies com afinidade termófilas e criófilas. A análise de grupamento validou três províncias propostas por Spalding, todavia invalidou a província da Plataforma Continental do Norte do Brasil. O elevado endemismo observado nas províncias Magelânica e do Mar de Scotia comprovam o isolamento da Antártica, embora a análise de grupamento tenha mostrado uma conexão com a América do Sul. A Regra de Bergmann invertida pode ser explicada pelo curto período favorável ao crescimento que limitaria o tamanho corporal fenotípico nestas regiões.

**Palavras-chave:** Oceano Atlântico; gradiente de diversidade; regra de Rapoport; Antártica; moluscos marinhos.

## RESUMEN

**BIOGEOGRAFÍA Y CONECTIVIDAD ENTRE LA MALACOFUNA DE LA COSTA OESTE SUDAMERICANA Y ANTÁRTICA.** El gradiente latitudinal de diversidad es ampliamente reconocido, llevando a los investigadores a asumir que la fauna antártica es pobre. Sin embargo, con el aumento del esfuerzo de muestreo, algunos estudios han mostrado una gran diversidad de organismos marinos en Antártida, con un elevado endemismo para algunos grupos. Este endemismo puede estar asociado con el aislamiento y el cambio climático a lo largo del tiempo evolutivo. A pesar de este aislamiento relativo, la evidencia reciente sugiere cierto grado de conectividad entre la fauna antártica y sudamericana. Nuestro estudio utilizó datos secundarios extraídos de Malacolog 4.1.1. El área geográfica considerada fue la costa atlántica sudamericana y las áreas adyacentes de la Antártida (Península Antártica, parte del Mar de Weddell e islas del Arco de Scotia). En nuestro muestreo se recolectaron 6.517 especies de moluscos. La provincia con mayor diversidad fue la costa del Norte de Brasil y la de menor diversidad fue el Mar de Scotia. La tasa de endemismo para las provincias de menor latitud fue cercana al 15%, en contraste con la mayor tasa de endemismo, de 40 %, registrada en la provincia del Mar de Scotia. El mayor valor de riqueza fue hallado en la ecorregión de Guayana, y el valor más bajo en la Península Antártica. La mayoría de las ecorregiones tienen un endemismo de aproximadamente 3%, con el mayor endemismo en Georgias del Sur. El gradiente de riqueza aumenta hacia las latitudes más bajas. El análisis de cluster para la malacofauna indicó cuatro grupos significativos. La regla batimétrica de Rapoport mostró el aumento del rango batimétrico hacia las ecorregiones de altas latitudes, mientras que la Regla de Bergmann mostró la relación opuesta. La mayor riqueza a 25°S puede estar asociada con la presencia de arrecifes de coral y algas calcáreas. En latitudes medias la riqueza también fue alta, y esta región comprende un ecotono entre especies termofílicas y criofílicas. El análisis de cluster validó tres provincias propuestas por Spalding, aunque reveló el conocimiento inadecuado de la provincia de la Costa del Norte de Brasil. El alto endemismo observado en los mares Magallánico y de Scotia, demuestra la influencia que el aislamiento antártico tiene en la estructura de la comunidad, aunque el cluster mostró la existencia de una conexión con Sudamérica. El valor inverso observado de la Regla de Bergmann puede ser explicado por las estaciones más cortas en altas latitudes, lo cual limita el tamaño corporal fenotípico que puede ser alcanzado.

**Palabras-clave:** Océano Atlántico; gradiente de diversidad; regla de Rapoport; Antártida; moluscos marinos.

## INTRODUCTION

The existence of latitudinal diversity gradients in the distribution of species is widely recognized (Platnick 1991, Rohde 1992, Rosenzweig 1992,

1995, Gaston *et al.* 1995, Kaufman 1995, Colinviaux 1993, Floeter & Gomes 1999, Gaston 2000, Valentine & Jablonski, 2010, among others). Most plant and animal groups show higher biodiversity in the tropics, contrasting with the lower diversity in polar areas.

Several hypotheses have attributed this pattern, in general, to factors such as history, environmental heterogeneity, competition, predation; climate and climatic variability, productivity, disturbance, area extent (Pianka 1966, Rosenzweig 1992, Colinvaux 1993, Krebs 1994, Gaston & Blackburn 2000, Erwin, 2009, among others), mid-domain effect (Colwell & Hurlt 1994) and Rapoport's Rule (Stevens 1989).

For several decades, this biogeographical pattern led researchers to assume that the Antarctic fauna is impoverished. However, as sampling efforts have increased in this region during the first decade of this century (Ausubel *et al.* 2010), this feature has begun to be questioned (Clarke *et al.* 2004, Linse *et al.* 2006, Schiaparelli *et al.* 2006, Schwabe *et al.* 2007, Brandt *et al.* 2009). Some studies show a great diversity of some marine groups around the Antarctic continent, with higher endemism for some taxa, as molluscs (Schiaparelli *et al.* 2006, Schwabe *et al.* 2007, Ausubel *et al.* 2010), pycnogonids (Clarke *et al.* 2004) and echinoderms (Barboza *et al.* in this volume). The higher endemism found in the Antarctic may be associated with its isolation and climate change over evolutionary time periods. Antarctica was completely separated from South America during the Oligocene, resulting in the formation of the Southern Ocean and the Antarctic Circumpolar Current (ACC) (Barker & Thomas 2004).

Although the rise of the ACC promotes the isolation of these waters, known as the Polar Front, some studies suggest the existence of a connectivity of Antarctic marine fauna and flora with the surrounding southern areas of other oceans (Crame 1999, Clarke *et al.* 2004, Clarke *et al.* 2005, Linse *et al.* 2006, Quaglio *et al.* 2007). This Polar Front is characterized by large temperature and salinity differences with the surrounding water masses. The effectiveness of this abrupt oceanographic barrier may be softened by the action of some oceanographic features, including the great depths of the Antarctic continental shelf (Clarke *et al.* 2004, Smith *et al.* 2006) and ocean current dynamics (Clarke *et al.* 2005).

Rather than the high endemism of Antarctic waters, Stevens (1989) proposed that the greater richness often seen in the tropics is explained by the very narrow ranges of tropical species, as opposed to the higher proportion of species with wider ranges at higher latitudes (lower endemism); he named

this pattern Rapoport's Rule (RR). The connection between this biogeographical pattern and richness lies in the 'rescue effect', where the patchy distribution of the tropical fauna leads to greater richness in this region, resulting from a constant inflow of migrant species from adjacent patches. Stevens (1989) explained the pattern on the basis of differing tolerances of tropical and temperate species to climate variations. Organisms inhabiting lower latitudes are subject to less variation in climate, and therefore their geographical distributions tend to be limited to a narrow latitudinal range. However, higher-latitude species would be adapted to more marked climate variation. Stevens (1996) assessed the application of RR to the depth gradient, in which the bathymetric ranges of organisms increase at greater depths (Stevens 1996, Macpherson 2003, Kendall & Haedrich 2006, Fortes & Absalão 2004, 2010). In addition, the study indicated a positive relationship between latitude and bathymetric range. In this pattern, organisms inhabiting shallow waters in the tropics are subject to less variation in climate, and therefore their bathymetric ranges tend to be narrow. As a result, this wider bathymetric range of the high-latitude species could overcome the oceanographic barrier formed by the Polar Front.

Another biogeographical inconsistency can be characteristic of Antarctic waters. Bergmann's Rule proposes a tendency toward a positive relationship between the body size of species belonging to higher monophyletic taxa and the latitude inhabited by these species, although other studies showed its opposite form (Gaston & Blackburn 2000). This pattern contrasts with the expected gigantism of the organisms that inhabit these waters (Clarke & Johnston 2003). Five hypotheses could be applied to explain Bergmann's rule. Two of them are related to phylogenetic features (Gaston & Blackburn 2000). The third hypothesis relates the relative scarcity of smaller-bodied species at higher latitudes to a lower dispersal capacity of these species (Roy *et al.* 2001). Most often, the major hypothesis relates the pattern to the heat-conservation capacity of the larger species with their higher surface-to-volume ratios (Blackburn & Hawkins 2004). The final hypothesis states that larger animals can better tolerate resource scarcity, by increasing fat reserves rather than increasing their metabolic rates (Blackburn & Hawkins 2004, Rodríguez *et al.* 2006).

Despite the relative isolation of the Antarctic continent by the ACC, evidence indicates some degree of connectivity between the Antarctic and the South American marine faunas. The improvement of our knowledge of the fauna of Antarctic and surrounding areas has inspired us to investigate these features for the molluscan fauna of the western Atlantic and the surrounding Southern Ocean.

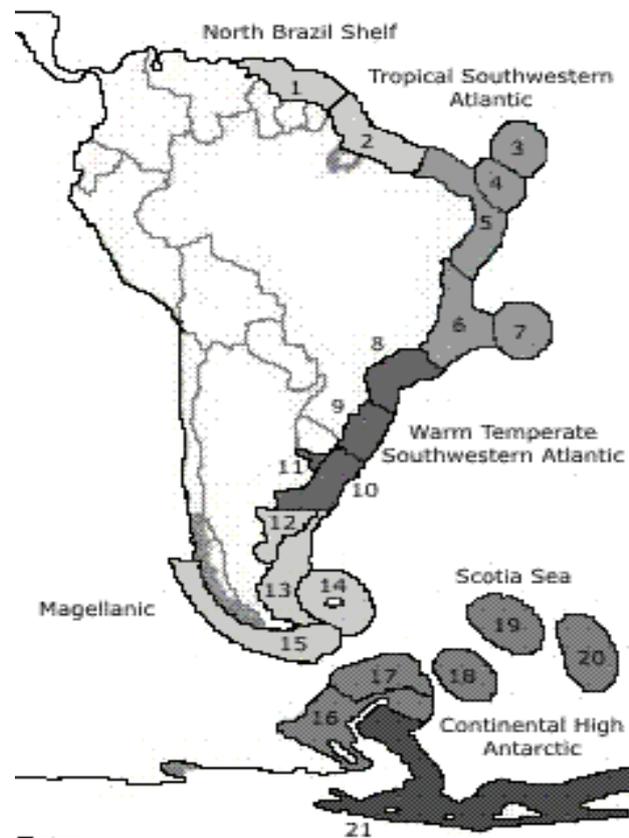
## MATERIALS AND METHODS

This study used secondary data extracted from Malacolog 4.1.1 (Rosenberg 2009), a western Atlantic Mollusca database. Because of the potential pitfalls inherent in using this kind of a data (Blackburn *et al.* 2004, Robertson 2008), we performed a test of the updates of this database. Most of all new mollusc species descriptions in recent manuscripts (Aldea *et al.* 2009, Martynov & Schrödl 2009, Aldea & Troncoso 2010, Signorelli & Scarabino 2010, Zelaya 2010) were included in Malacolog, proving the quality of this resource. In this study, we worked with all molluscan taxa inhabiting the continental shelf (below 200 meters) of geographical areas with available information about their geographical range (latitudinal geographical range), rather than other investigated features (bathymetric range, maximum total length, longitudinal geographical range).

In marine environments, temperature has a role as a promoter of diversity, in addition to its role as the most important factor in the determination of the species geographical range and the limits of biogeographical provinces (Briggs 1974, 1995, Palacio 1982, Absalão 1989, Floeter & Gomes 1999, Spalding 2007). The patterns of geographical distribution of the coastal marine fauna are the main features in the determination of marine biogeographical provinces, because their relationship with to the geographical features of the environment is accepted. Furthermore, these patterns are essential for the determination of certain macroecological patterns, like Rapoport's Rule (Roy *et al.* 1994, Fortes & Absalão 2004, 2010). Because of this feature, our analyses were based on the biogeographical realms, provinces and ecoregions defined by Spalding *et al.* (2007) (Crame 2009, Roy *et al.* 2009, Harnik *et al.* 2010). We considered this biogeographical perspective because is a result from a great manuscript done by several authors

from different parts of the world, considering the knowledge of different taxa.

The geographical area covered by our study was the entire South American Atlantic coast (beginning at 12° N) and the Antarctic area adjacent to the Atlantic Ocean – the Antarctic Peninsula, part of the Weddell Sea and the islands of the Scotia Arc (Figure 1).



**Figure 1.** Biogeographical areas of this study (adaptated from Spalding 2007). Provinces: North Brazil Shelf, Tropical Southwestern Atlantic, Warm Temperate Southwestern Atlantic, Magellanic, Scotia Sea, Continental High Antarctic. Ecoregions: 1- Guianan, 2- Amazonia, 3- São Pedro and São Paulo Islands, 4- Fernando de Noronha and Atoll das Rocas, 5- Northeastern Brazil, 6- Eastern Brazil, 7- Trindade and Martin Vaz Islands, 8- Southeastern Brazil, 9- Rio Grande, 10- Uruguay-Buenos Aires Shelf, 11- Rio de la Plata, 12- North Patagonian Gulfs, 13- Patagonian Shelf, 14- Malvinas/Falklands, 15- Channels and Fjords of Southern Chile, 16- Antarctic Peninsula, 17- South Shetland Islands, 18- South Orkney Islands, 19- South Georgia, 20- South Sandwich Islands, 21- Weddell Sea.

The biodiversity gradient was evaluated by plotting the molluscan richness (Y axis) along the latitudinal gradient (X axis), in each 1- degree latitudinal band. The Shapiro-Wilk test determined that richness data were nonparametric ( $W = 0.886$ ,  $p < 0.0001$ ). The Fisher Test determined that the variances are different ( $F = 1.523$ ,  $p < 0.0001$ ). The relationship of this pattern

was tested by Kernel's regression (Gheriballah *et al.* 2010) - robust lowess regression method, with the significance threshold set at 95%.

Because latitude is a bidirectional gradient, we considered the taxa of the Northern and Southern hemispheres separately, dividing each ocean part into a Northern Hemisphere and a Southern Hemisphere region. We considered the geographical/bathymetric distribution of each species as the difference between the maximum and minimum latitudes / depth where the species occurs, considering the total latitudinal range in both hemispheres. In the analyses, we applied the global range of a species to all the regions in which the species occurs. In macroecological studies, this kind of geographical-distribution measurement is no worse than other kinds of measurement (Quinn *et al.* 1996). For the Rapoport's Rule (bathymetric range) analyses we used Stevens' method (Stevens 1989), which compares the size of the mean bathymetric range of all species residing in each ecoregion (Y axis) along the depth gradient (X axis). The Shapiro-Wilk test determined that bathymetric range data were nonparametric ( $W = 0.840$ ,  $p < 0.003$ ). The Fisher Test determined that the variances are different ( $F = 2.526$ ,  $p < 0.0001$ ). The relationship of this pattern was tested by Kernel's regression (robust lowess regression method), with the significance threshold set at 95%.

To evaluate Bergmann's rule, we utilized the maximum total length of the species as the measure for body size. In these analyses, we plotted the mean body size of all species residing in each ecoregion (Y axis) within the latitudinal gradient (X axis). The Shapiro-Wilk test determined that bodysize data were parametric ( $W = 0.978$ ,  $p < 0.893$ ). The Fisher Test determined that the variances are similar ( $F =$

$2.526$ ,  $p < 0.337$ ). The relationship of this pattern was tested by Pearson's linear regression, with the significance threshold set at 95%.

We used the software package PAST (Hammer *et al.* 2001) to analyse biogeographic relationships amongst molluscs in our study areas. Faunal association between areas was measured by Jaccard Index of non-transformed binary (presence-absence) data. Hierarchical clustering with group-averaged linking was then performed using the similarity matrix. Possible differences in faunistic composition between groups of stations were tested using a one-way ANOSIM test. We used the software package XLSTAT (Addinsoft 2011) to analyse biogeographic patterns, as the Kernel's regression analysis used in Rapoport's rule.

## RESULTS

Our bibliographic survey yielded a total of 6517 species of molluscs known from all Atlantic and adjacent Southern oceans, with 3841 species restricted to the study area, of which 2801 species inhabit the continental shelf (our working database). This survey is composed by 2267 Gastropoda, 474 Bivalvia, 31 Scaphopoda, 24 Polyplacophora, 4 Cephalopoda, 1 Aplacophora species.

Of the six biogeographical provinces of this study, the most diverse was the North Brazil Shelf Province, and the least diverse was the Scotia Sea Province (Table 1). The Continental High Antarctic Province was excluded because of the lack of information for most of this region (Rosenberg 2009). The endemism rates for the low-latitude provinces were close to 15%, contrasting with the higher endemism found at higher latitudes, with the maximum value for Scotia Sea Province.

**Table 1:** Geographical limits and biodiversity patterns of molluscs species within biogeographical provinces (adapted from Spalding 2007).

Biogeographical Provinces	Limits		Richness	Endemism (%)
	Latitudinal	Longitudinal		
North Brazil Shelf	12,5 – 2,75N	74.25 – 41,75W	1733	16
Tropical Southwestern Atlantic	4.5N – 23,75S	41.75 – 25W	1047	14
Warm Temperate Southwestern Atlantic	41 – 23S	62 – 42W	872	10
Magellanic	57 – 41S	75 – 54W	444	35
Scotia Sea	71 – 53S	78 – 24.5W	401	40
Continental High Antarctic (Only one ecoregion)	77 – 55S	69 – 17W	66	3

The higher values for richness of our ecoregions were found in the low-latitude ones, with the highest value for the Guianan Ecoregion. In contrast, low values were found for the higher-latitude provinces, with the lowest value for the

Antarctic Peninsula Ecoregion (Table 2). Most of the ecoregions had an endemism rate around 3%, with four ecoregions with a higher endemism of about 10% a high rate of 25% for the South Georgia Ecoregion.

**Table 2.** Geographical limits and biodiversity patterns of molluscs species within ecoregions (adapted from Spalding 2007).

Ecoregions	Limits		Richness	Endemism (%)
	Latitudinal	Longitudinal		
Guianan	12.5 – 9.75N	74.2 – 60W	1647	9
Amazonia	9.75 – 2.75N	61.5 – 41.75W	1187	2
São Pedro and São Paulo Islands	4.5N – 2.75S	29.5 – 25W	1097	0
Fernando de Noronha and Atol das Rocas	8.5 – 2.45S	35.25 – 29.5W	635	3
Northeastern Brazil	2.75N – 13S	41.75 – 34.5W	1047	0
Eastern Brazil	23.75 – 13S	39 – 32W	647	3
Trindade and Martin Vaz Islands	23 – 11.5S	32 – 25W	242	1
Southeastern Brazil	28.5 – 23S	48.5 – 42W	589	7
Rio Grande	32 – 28.5S	53.25 – 48.25W	332	0
Rio de la Plata	37 – 34.25S	58.5 – 55W	313	1
Uruguay–Buenos Aires Shelf	41 – 32S	62 – 55.5W	323	1
North Patagonian Gulfs	47 – 41S	65 – 56.5W	220	2
Patagonian Shelf	55 – 41S	69 – 55.5W	406	14
Malvinas/Falklands	55 – 47S	65.5 – 54W	285	10
Channels and Fjords of Southern Chile	57 – 55S	75 – 55W	156	4
South Sandwich Islands	60.5 – 55.5S	30 – 24.5W	46	0
South Georgia	55.5 – 53S	54.5 – 33.5W	167	25
South Orkney Islands	62.5 – 60.5S	61.5 – 61W	68	0
South Shetland Islands	65 – 60.75S	68 – 50W	97	11
Antarctic Peninsula	71 – 65S	78 – 52W	54	2
Weddell Sea	77 – 65S	69 – 17W	66	3

The diversity gradient (richness) showed an increase of richness toward lower latitudinal bands. Although the general trend agreed with the expected pattern, the highest richness was

observed at the mid-latitudes in the Southern Hemisphere, followed by a slow decrease toward lower latitudes and a steeper decrease toward higher latitudes.

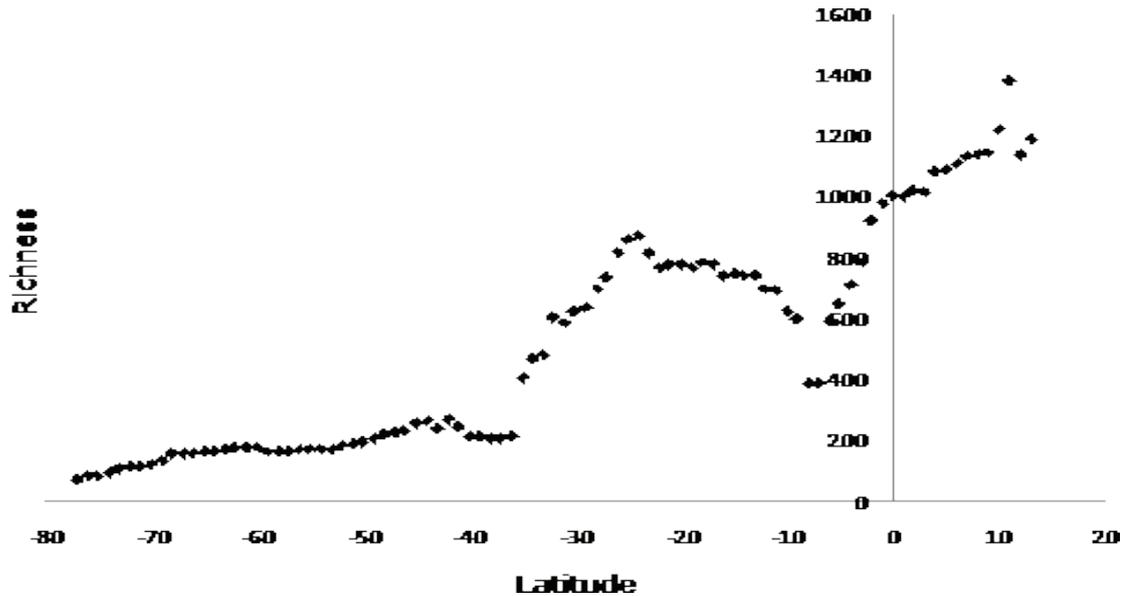


Figure 2. Latitudinal richness (richness) gradient of molluscs at Eastern South America. Latitudinal bands of 1o degree. Statistical parameters:  $\beta = 12.74$ ,  $R^2 = 0.805$ ,  $p < 0.01$

The cluster analysis showed four significant groups (Figure 3), which coincide with three biogeographical provinces defined by Spalding *et al.* (2007), Warm Temperate Southwestern Atlantic (URU, LAPLATA, RGRA, SE BRA), Magellanic (GEO I, S CHI, MALV, PAT, N PAT) and Scotia

Sea (SAN I, SHE I, ORK I, ANT PEN, WED). The fourth group observed in the cluster, was formed by ecoregions from the Tropical Southwestern Atlantic (S PED, NE BRA, L BRA, NOR, TRIN) and the from North Brazil Shelf (AMAZ and GUIANA).

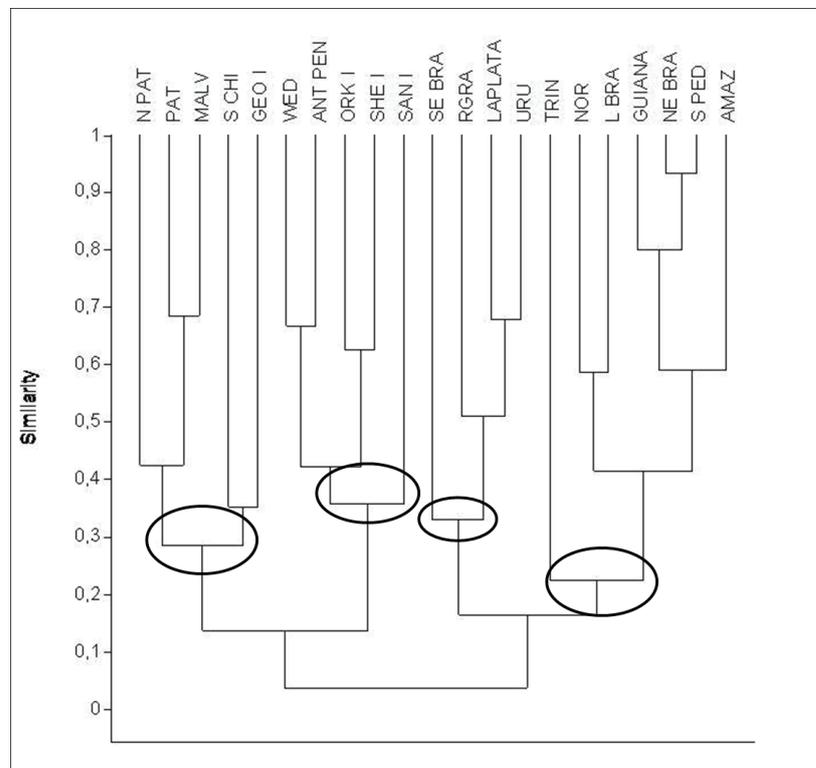
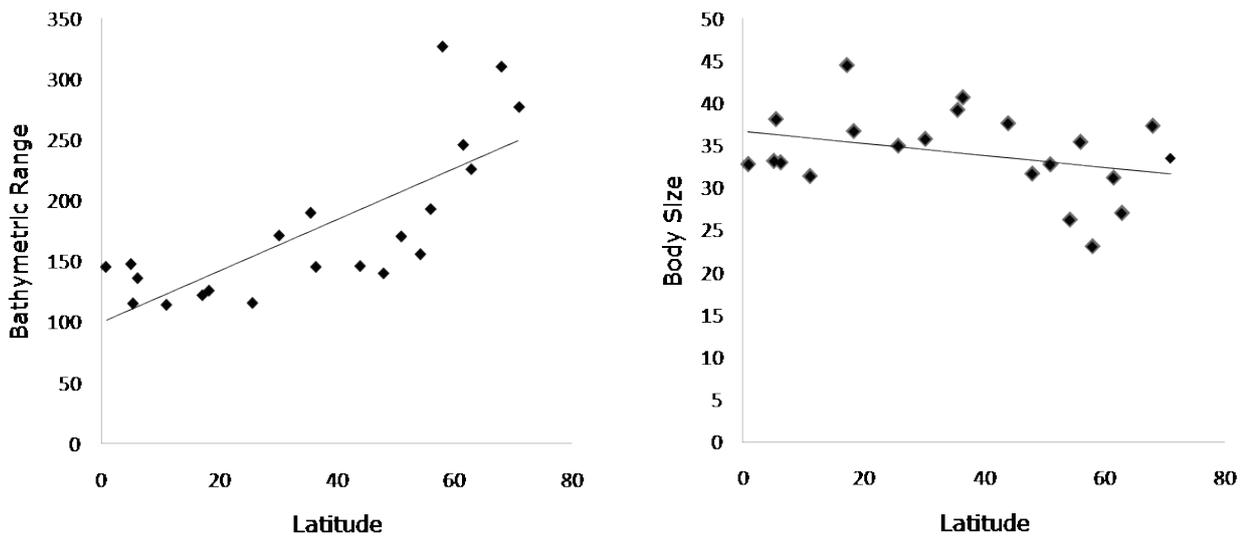


Figure 3. Cluster Analysis of the ecoregions based on molluscs species (adapted from Spalding, 2007). Association Jaccard Index (Cophenetic correlation coefficient = 0,92). Ecoregions: Guianan (GUIANA), Amazonia (AMAZ), São Pedro and São Paulo Islands (S PED), Fernando de Noronha and Atol das Rocas (NOR), Northeastern Brazil (NE BRA), Eastern Brazil (L BRA), Trindade and Martin Vaz Islands (TRIN), Southeastern Brazil (SE BRA), Rio Grande (RGRA), Rio de la Plata (LAPLATA), Uruguay–Buenos Aires Shelf (URU), North Patagonian Gulfs (N PAT), Patagonian Shelf (PAT), Malvinas/Falklands (MALV), Channels and Fjords of Southern Chile (S CHI), South Sandwich Islands (SAN I), South Georgia (GEO I), South Orkney Islands (ORK I), South Shetland Islands (SHE I), Antarctic Peninsula (ANT PEN), Weddell Sea (WED).

The bathymetric Rapoport's Rule showed the expected increase of bathymetric range toward higher-latitude ecoregions ( $\beta = 2.10$ ,  $R^2 = 0.649$ ,  $p < 0.01$ ). Although the general trend agreed with the expected pattern, the lowest bathymetric range was observed for a mid-latitude ecoregion

(Southeastern Brazil). Bergmann's Rule showed the opposite relationship, the Converse Bergmann's Rule ( $\beta = -0.071$ ,  $R^2 = 0.11$ ,  $p < 0.01$ ), a decrease in body size toward higher-latitude ecoregions. The smallest body size was observed for a high-latitude ecoregion, South Georgia.



**Figure 4.** A, Rapoport's Rule (bathymetric range); B, Bergmann's Rule of marine molluscs from South America and adjacent Antarctic region. Latitudinal points were represented by the latitudinal mid-point inside each ecoregion. Statistical parameters: Rapoport's Rule ( $\beta = 2.10$ ,  $R^2 = 0.649$ ,  $p < 0.01$ ) and Bergmann's Rule ( $\beta = -0.071$ ,  $R^2 = 0.17$ ,  $p < 0.01$ ).

## DISCUSSION

The low richness value found below 10° S (Figure 2) does not invalidate the central idea of the latitudinal richness gradient, which agrees with the pattern established by Wallace (1878), which has been repeatedly confirmed by several authors (Spight 1977, Krebs 1994, Rosenzweig 1995, Floeter & Gomes 1999, Fortes & Absalão 2004). This incongruence could be explained by the influence of a feature that appears at the regional scale, such as the mouths of the Amazon and Orinoco rivers (surrounding the equator). It is well known (Barreto 1995, Syms & Jones 2001) that marine environmental heterogeneity is a major factor in determining species richness, and that the principal agents of this are biological (calcareous algae, coral). The northern coast of South America receives a huge amount of sediment from these rivers, which inhibits coral reef development in this region (Nybakken 1988). Therefore, the low richness found in this region can be explained by the absence of the rich coral reef environment.

The higher value for mollusc richness found around the 25° S band may be associated with the presence of coral and calcareous algal reefs in this region. The steep decrease seen in the next band may result from the absence of these biological agents. Both corals and calcareous algae have an important role in the formation of organogenic hard substrates (Barcellos *et al.* 1989) and are influenced by the same ecological factors that affect the establishment of coral reefs, such as the decreasing temperature towards the poles.

Leão *et al.* (1988) showed that there is a positive relationship between the decline in coral abundance, and latitude. The mollusc richness seems to follow this tendency, and although it was not possible to test this, we can postulate that the decrease in environmental heterogeneity (created by the coral structures) is a reasonable explanation for the observed latitudinal gradient of mollusc richness in this region (Floeter & Gomes 1999).

There was a relatively high richness between 23° and 17° S. This region corresponds to an ecotone

between thermophile and cryophile species', benefited by the presence of both types of species. While thermophile species are carried southwards by the warm Brazil Current, the cryophile are carried northwards by the temperate Malvinas/Falkland Current. The southern coast of Brazil is seasonally influenced by one or the other current in a dynamic system known as the Subtropical Convergence (Colling 2004) that flows along the southern Brazilian coast, reflecting the strength of Malvinas Current during the winter months and of the Brazil Current during the summer months. This system creates a mobile thermal barrier that is recognized by biogeographers (Briggs 1974, Palácio 1982, Floeter & Gomes 1999). In addition, the geographical position of Cabo Frio in the state of Rio de Janeiro and wind patterns cause local upwelling (Yoneshigue-Valentin & Valentin 1992). In association with some branches of the Malvinas/Falklands Current (Boltovskoy 1981), creates a thermal discontinuity that is, especially abrupt during the summer when the water is warm (Yoneshigue-Valentin & Valentin 1992, Bravin 2001). The presence of this cold water limits the survival of the stenothermal corals and calcareous algae up to latitude 22° S, leading to the above-mentioned impoverishment and resulting in a simple biogenic physically structured assemblage.

Below this biogeographical ecotone zone (17° to 23°S), we observed a steeper decrease in malacofauna richness, from 816 species at 26°S to 213 species at 36°S. This region marks the beginning of the Temperate South America realm (Spalding *et al.* 2007), at the Warm Temperate Southwestern Atlantic Province (named in past as Paulista and Patagonic provinces by Palácio 1982, or Argentinean Province by Briggs 1974). The main driving factors that can influence the development of this biota and set a lower limit to this richness are the unfavorable climate features of this realm, as the low temperature and high climate variability (Colinvaux 1993, Pianka 2000).

Pianka (2000) emphasized that species richness is not explainable by one factor alone. Several factors may be influencing this pattern at the same time on different spatial and temporal scales. Our study showed (Figure 2) that climate factors such as temperature are important for determining diversity at a global scale; otherwise other factors such as environmental heterogeneity and the deposition of sediments determine diversity at the regional scale.

Although the biases in the biodiversity patterns can be explained by some biogeographical features, as discussed above, we cannot ignore the influence of the degree of knowledge in some ecoregions along the South American coast. The unexpected low richness values observed along the Northeast coast of Brazil may result from a bias caused by inadequate taxonomic knowledge of the molluscs of this area (Mora *et al.* 2008, Ausubel *et al.* 2010). On the other hand, the observed highest richness in the Southern Ocean (South Georgia ecoregion), can be attributed to the good knowledge of its malacofauna, resulting from a concentrated sampling effort in this relatively small region. In this ecoregion, 22 (47%) of 47 species are endemic. Most of them were described by Strebel (1905–1908), based on material collected during the Scottish National Antarctic Expedition (1902-1904), and 11 (23%) were described by Powell (1951) from material collected during the B.A.N.Z. Antarctic Research Expedition (1929-1931). This island and the surrounding archipelago are a British overseas territory in the southern Atlantic Ocean. In 1908 the United Kingdom annexed both South Georgia and the South Sandwich Islands, which have two permanent research bases of the British Antarctic Survey – the King Edward Point Research Station and Bird Island Research Station (NERC-BAS 2007). The presence of these bases has increased even more the sampling effort in this area.

An overall view of the cluster analysis (Figure 3) validated three provinces proposed by Spalding *et al.* (2007), the Warm Temperate Southwestern Atlantic, Magellanic, and Scotia Sea provinces. The ecoregions within the limits of these provinces shared around 25-35% of their malacofauna.

The interpretation of the cluster analysis (Figure 3) revealed the inadequacy of present knowledge of the North Brazil Shelf Province. The Guiana ecoregion showed more similarity with two ecoregions of the Tropical Southwestern Atlantic (São Pedro and São Paulo Islands and Northeastern Brazil) than with the other ecoregion of the North Brazil Shelf province (Amazonia). This cluster and the statistically significant group defined by the One-Way Anosim (S PED, NE BRA, L BRA, NOR, TRIN, AMAZ, and GUIANA) showed that all these ecoregions constitute the same biogeographical province (Tropical Province *in* Palácio 1982). Although the region defined as the North Brazil Shelf Province (Spalding *et al.* 2007)

is characterized by distinct oceanographic features, such as the sediment discharge from the Orinoco and Amazon basins, these were not sufficient, at present, to distinguish this region from the Tropical Southwestern Atlantic Province. Considering that this region has, historically, not received the same sampling effort as other Brazilian regions, our results with respect to it should be treated with caution.

Although the Weddell Sea ecoregion is not part of the Scotia Sea Province, it clustered together with the ecoregions of the latter. This may result from its geographical proximity to the Antarctic Peninsula ecoregion and the absence of other ecoregions of the Continental High Antarctic Province.

The unexpected clustering of the South Georgia ecoregion with the Magellanic Province ecoregions, can be explained by its high endemism, which excluded 25% of the species that could be paired, and its proximity to the Malvinas/Falkland Islands. The South Georgia ecoregion, rather, paired with the Channels and Fjords of Southern Chile instead of the Malvinas/Falkland ecoregion, as was expected (see Spalding *et al.* 2007). Unfortunately, due to the smaller size of this group (SCHI and GEO I; N PAT, PAT, and MAL), this clustering did not show statistical significance and will therefore not be discussed further.

The higher endemism rates observed at the Magellanic (35%) and Scotia Sea (40%) were the opposite (Table 2) to that expected from Rapoport's Rule (Stevens 1989). This aspect proves the influence which the isolation of the Antarctic exerted on the community structure of this region (Barker & Thomas 2004, Clarke *et al.* 2004). Although the Polar Front promotes the isolation of the Southern Sea, there is a connection between this area and the surrounding areas of South America (similarity of 13%) (Clarke *et al.* 2004). For the Magellanic Province, the highest endemism rates were observed for the Patagonian Shelf and Malvinas/Falklands ecoregions. These ecoregions are linked to the Scotia Sea Province by the Scotia Arc islands, including South Georgia which had the highest endemism rate (25%) of all ecoregions of the South American Atlantic coast. Therefore, the higher endemism of these high latitudes areas influences their surrounding mid-high-latitude areas, which may dilute the effect Rapoport's Rule (Table 2) at these latitudes (35-55°S). Furthermore, the

increase in the bathymetric range along the latitudinal gradient (Figure 4) may influence the capacity of species inhabiting high latitudes to cross the polar front through great depths, which could enhance the connection of these faunas (Clarke *et al.* 2004, Brandt *et al.* 2009, Barboza *et al.* in this volume). Therefore, despite the relatively high endemism rates shown by the ecoregions of the Magellanic and Scotia Sea provinces, they still shared about 31% of this malacofauna, emphasizing the connectivity between the Antarctic and South America and 12% with the Warm Temperate Southwestern Atlantic Province. Otherwise, this shared fauna may be related with the history of the taxa and / or the area (Martínez & del Rio 2002, Kiel & Nielsen 2010).

The expected gigantism of the Antarctic fauna (Clarke & Johnston 2003) was not observed in our analysis for Bergmann's Rule (Figure 4). Our results showed a weak effect ( $\beta = -0.071$ ,  $R^2 = 0.17$ ) of the Converse Bergmann's Rule. For the taxon Mollusca, Bergmann's Rule may often show a weak relationship because of their lower-mid trophic-level position. If we consider the hypothesis of toleration of resource scarcity, the greater energy supply available at these lower trophic levels, together with the generally small size of molluscs, may bias the determination of Bergmann's rule. Beyond this, the inversion of the pattern could be explained by the shorter seasons at higher latitudes, which limit the time available for foraging, growth, and development and hence the phenotypic body size that can be attained (Blanckenhorn & Demont 2004).

Another possible explanation for the observed Converse Bergmann's Rule is the strong influence of the phylogenetic effect (Gaston & Blackburn 2000). The higher endemism observed in these higher-latitude ecoregions shows the originality of this malacofauna, further indicating the strong influence of the history on the structure of these assemblages. Unfortunately, the lack of a general phylogeny for this group did not allow us to test this biogeographical pattern with a phylogenetically controlled analysis.

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