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***Research Article***

# Biogeography and biodiversity of gastropod molluscs from the eastern Brazilian continental shelf and slope

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**ABSTRACT.** Biogeographic distributional patterns of gastropods are proposed based on the species' geographic and bathymetric distribution. Samples were collected along the Brazilian continental margin between 18° S and 23° S, at 37 stations with depths from 20 m to 1,330 m. The analysis of the biogeographic distribution patterns confirmed the existence of a transitional zone from tropical to subtropical waters in the area of both the continental shelf and slope, suggesting a relationship with water mass circulation. We observed a high species turnover rate between the shelf and slope. The analysis of gastropod species distribution revealed a similar pattern on the shelf and slope and a large difference between shallow and deep-water faunas.

**Keywords:** macrobenthos, continental margins, geographical distribution, vertical distribution, soft bottoms, Brazil, southwestern Atlantic Ocean.

# Biogeografía y biodiversidad de moluscos gastrópodos de la plataforma y talud continental brasileño

**RESUMEN.** Los patrones de distribución biogeográfica de gastrópodos fueron propuestos basados en la distribución geográfica y batimétrica de las especies. Los muestreos fueron realizados en el margen continental brasileño entre 18°S y 23°S, en 37 estaciones de 20 m a 1.330 m de profundidad. El análisis de los patrones de distribución biogeográfica confirmó la existencia de una zona de transición de aguas tropicales a aguas subtropicales, que se encuentra en la zona de la plataforma continental y también en la zona del talud continental, esto puede sugerir una relación con la circulación de las masas de agua. Se observó una elevada tasa de *turnover* de las especies entre la plataforma y el talud continental. El análisis de las especies de gastrópodos reveló un patrón similar tanto en la plataforma como en el talud y una gran diferencia entre las faunas de las aguas someras y profundas.

**Palabras clave:** macrobentos, margen continental, distribución geográfica, distribución vertical, fondos blandos, Brasil, océano Atlántico sudoccidental.

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## INTRODUCTION

Understanding the patterns of the geographic distribution of life is a very old issue in biology, and one that continues to be debated. In the sea, geographic patterns (e.g., in species assemblages and diversity) have been described for both shallow and deep-sea fauna (Rex, 1993; Rex *et al*., 1993; Clarke & Crame, 1997; Gray, 1998; Willig *et al*., 2003; Hillebrand, 2004).

Longitudinal and latitudinal barriers represented by the arrangement of land masses and oceans, by temperature gradients, and by hydrodynamic patterns and water properties divide the oceans into a series of biogeographic realms with their own characteristic species assemblages (Briggs, 1995; Longhurst, 1998). The sea surface temperature is supposed to be the main force limiting the latitudinal distribution of marine species. Therefore, biogeographic realms are not expected to be the same along a depth gradient. In general, the wider a species' vertical distributional range, the wider its geographical distribution (Harley *et al*., 2003). Eurybathic taxa (those with a broader vertical range) show a wider horizontal distribution than stenobathic taxa (those with a narrow vertical range) (Vinogradova, 1997). Due to the fact that deep-sea species are mainly stenobathic, abyssal and hadal fauna show higher levels of endemism (Vinogradova, 1997; Zezina, 1997). The bulk of shallow-sea fauna is also stenobathic but, according to Menzies *et al.* (1973), the fauna on the continental slope has a wider geographical distribution than that of any other vertical faunal zone.

Several authors have discussed zoogeographic and diversity patterns for Brazilian shallow waters based on benthic invertebrates (e.g., Briggs, 1974; Semenov, 1978; Kempf, 1979; Palacio, 1982; Floeter & Soares-Gomes, 1999), but few have discussed biogeographic patterns of the neighbouring slope or abyssal zones (Allen & Sanders, 1996 is a good example for abyssal basins).

The effect of the latitudinal gradient is so strong on the species diversity of marine molluscs that it is also evident at the genus and family level (Roy *et al.*, 1998; Crame, 2000) and recognized in fossil assemblages (Crame, 2002; Jablonski *et al.*, 2006). However, in spite of the fact that molluscs are one of the earliest taxa used to investigate latitudinal trends in marine biodiversity, some doubts exist as to whether the latitudinal trends observed in the northern hemisphere also occur in the southern hemisphere (Crame, 2000; Valdovinos *et al.*, 2003; Linse *et al.*, 2006). Some results are conflicting. For example, the patterns found for Pacific Ocean molluscs in the southern hemisphere by Valdovinos *et al.* (2003) opposed those found by Fortes & Absalão (2004).

The present study aimed to investigate patterns in both the regional and depth distribution of gastropod molluscs, discussing aspects of slope and shelf diversity and provinciality, contributing to the discussion about the latitudinal diversity gradient in the southern hemisphere.

## MATERIALS AND METHODS

### Study area

The study area comprised the slope and continental shelf between 18°-23°S and 38°-41°W, encompassing an area ranging from the Abrolhos reef bank, situated in the north of Doce River, to the offshore and near-shore region in the vicinity of the Paraíba do Sul River. The study area was divided into two regions: north (18°-19°S), up to 200 km-long, and south (21°-23°S), where the shelf is narrow and shallow, ranging from 10 to 30 km in width (Fig. 1). The continental slope in both regions is narrow and steep (Emery & Uchuoi, 1984). The oceanographic conditions consist of oligotrophic areas that are associated with the tropical waters of the Brazil Current (BC) and mesotrophic areas due to the seasonal upwelling of the cold, nutrient-rich waters of the South Atlantic Central Water (SACW) south of the Doce River (20°S) (Valentin *et al.*, 1987). Primary productivity varies from 0.3 g C m$^{-2}$ d$^{-1}$ to 1.1 g C m$^{-2}$ d$^{-1}$ (Gaeta *et al.*, 1999) and the input of the Doce and Paraíba do Sul rivers is about 900 m$^3$ s$^{-1}$. The grain-size distribution is not uniform in the area, varying with depth; shallower stations have coarse sediments and deeper stations have finer sediments. The clay and silt concentrations revealed a depth gradient as well, with higher concentrations occurring at deeper stations. Concentration of calcium carbonate exhibited a patchy distribution, with higher percentages in the western sector (Soares-Gomes *et al.*, 1999).

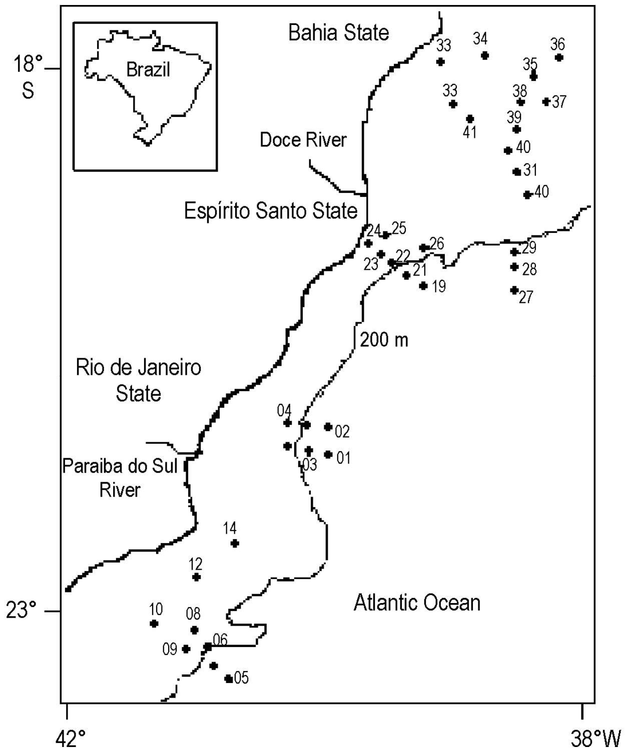

**Figure 1.** Study area with location of sampling stations.

**Figura 1.** Área de estudio y estaciones de muestreo.

### Sampling design and data analysis

Data for this study were obtained in April 1995, during the Joint Oceanographic Project (JOPS-II/ Leg 8), on board the R/V Victor Hansen from Bremen University, Germany. Sampling was carried out at 41 stations, between the depths of 20 m and 1,330 m (Fig. 1 and Table 1). Molluscs were present in 37 of these

**Table 1.** Number of stations per area, location of areas, and depth range per area.

**Tabla 1.** Número de las estaciones por área, ubicación de las áreas y variación de la profundidad por área.

| Area | N° of stations | Latitude (°S) | Longitude (°W) | Depth (m) |
|---|---|---|---|---|
| North shelf | 17 | 18 - 19 | 38 - 39 | 22 - 90 |
| South shelf | 6 | 21 - 23 | 39 - 41 | 25 - 200 |
| North slope | 5 | 18 - 19 | 38 - 39 | 510 - 1330 |
| South slope | 9 | 21 - 23 | 39 - 41 | 300 - 1320 |

41 stations (23 stations in the shelf zone and 14 in the slope zone). The sediment was sampled in triplicate with a 0.1 m² van Veen grab and a 60 x 60 x 30 cm box-corer. Samples were standardized to an area of 0.1 $m^2$ and 10 L of sediment volume. The macrozoobenthos was sieved out with a 0.5 mm mesh size, fixed in 70% ethanol, and sorted under a stereomicroscope for taxonomic identification.

The frequency of occurrence ($F_o$ = number of occurrences of a species at the shelf or slope stations / total number of shelf or slope stations) was calculated, and species were classified according to their value as constant ($F_o > 50\%$), common ($10\% \leq F_o \leq 50\%$), or rare ($F_o < 10\%$). Species distribution over the shelf and slope was examined by plotting a histogram of the number of species against the number of stations occupied.

We used Estimates 6.0b1 software (Colwell, 1997) to determine whether the species were classified as "unique" (restricted to a single site), "duplicates" (occurring at exactly two sites), "singletons" (represented by a single individual), or "doubletons” (represented by only two individuals), following the terminology of Colwell & Coddington (1994).

To perform a species richness scale analysis, the total data set was divided into four regions according to their location in geographic areas (north and south) and bathymetric zones (shelf and slope): north shelf, south shelf, north slope, and south slope. Due to different sampling efforts, randomized species cumulatives curves were plotted using Primer 6.1.6 software. Thus, we were able to compare species richness among regions, where the y-axis is the cumulative number of species and the x-axis the station numbers (north shelf: 17, south shelf; 6, north slope: 5, south slope: 9). An area of 0.1 $m^2$ was considered for each sampling station. According to Gray (2002), when sample sizes are different, this method is preferable to rarefaction curves as proposed by Sanders (1968). Species diversity was also estimated on a progressive spatial scale, according to Gray’s terminology (2000): sample species richness ($SR_S$) and species richness in large areas (north shelf, south shelf, north slope, south slope) ($SR_L$). Together, the four regions comprised the total area species richness ($SR_T$). In order to calculate the proportion by which a given region is richer than the average of samples within the total area, Whittaker’s (1972) original beta diversity measure ($\beta_W = (\gamma/\alpha) - 1$) was used, where $\gamma$ is the total number of species resulting from merging a number of individual samples and $\alpha$ is the average number of species per individual sample. Beta diversity was measured over sectors [$\beta_W = (SR_L/_{mean}SR_S)$] and total area [$\beta_W = (SR_T/_{mean}SR_S)$] scales, where $_{mean}SR_S$ was the mean sample diversity.

The species’ geographic and bathymetric distribution ranges were determined based on information available in the literature (Abbott, 1974; Merlano & Hegedus, 1994; Rios, 1994, among others) and in the Malacolog 3.1 electronic database (Rosenberg, 1993 - www.erato.acnatsci.org/wasp/findsnail.php). Geographic boundaries were established based on the southwestern Atlantic biogeographic provinces (Tropical, Paulista, Patagonic, Malvinas) defined by Palacio (1982) using the endemism rate. For a better representation of the geographic distribution in the area, the species were grouped according to their occurrence in the north and south regions. The shelf samples provided 211 species: 91 from the south region, 179 from the north region, and 59 from both regions. From the slope samples, 96 species were used: 72 from the south region, 55 from the north, and 31 from both regions. Depending on the bathymetric distribution, species were designated according to the zonation proposed by Zezina (1997) and Vinogradova (1997) as: shallow species (0-200 m depth), bathyal species (200-3,000 m), and abyssal species (3,000-6,000 m). Species found in both the shelf and bathyal zones were designated eurybathic.

We excluded pelagic species and juveniles (12.25% of the total number of species) from the analyses due, not only to the difficulties in identifying juveniles, but also to the aim of the present study, which is to analyze only benthic species. Only individuals identified to the species level or ones that could unequivocally be labelled as species were used in the analysis.

## RESULTS

### Spatial distribution of species

A total of 9,845 specimens, 404 species and morphotypes (including empty shells), 189 genera, and 73 families were collected over the entire study area. A set of 243 species, 93 genera, and 28 families was found exclusively in the shelf zone, whereas 137 species, 43 genera, and 14 families were exclusive to the slope zone. Only 24 species (6%), 20 genera (10.6%), and 16 families (22%) occurred in both zones (Appendix 1 and 2).

Species distribution over the shelf shows that about half the species (130) were restricted to one station and none occurred at all stations. The same pattern was found for the slope, with 110 species restricted to one single site. Considering the shelf and slope, about 3% of the species occurred at more than 50% of all sites (Fig. 2). On the shelf, 2% were constant, 32% common, and 66% rare species. On the slope, the corresponding figures were 1%, 42%, and 57%.

In the whole area, 48% of the species were unique and 18% were duplicates. Singletons and doubletons represented 34% and 13%, correspondingly. The north shelf featured 26% unique species and 17% singletons, and the north slope had 12% unique species and 5% singletons (Table 2).

### Diversity gradients

The cumulative dominance on the shelf was similar for both north and south regions. On the slope, there was a great difference in cumulative dominance between the two regions, with the north presenting the highest evenness (Fig. 3). Comparing the cumulative dominance along a vertical gradient, the evenness of the north slope was almost 10% higher than that of the north shelf, whereas the evenness of the south shelf was 40% higher than that of the south slope (Fig. 3).

The estimated species richness on the north shelf was higher than on the south shelf. However, when the sampling area was standardized to 0.6 m² (considering the area of a station as 0.1 $m^2$), the richness was similar on both shelves (Fig. 4). The south slope displayed a higher total cumulative number of species per area than did the north slope. Conversely, when standardizing the sampling area to 0.5 m², richness was higher on the north slope. In the north, species richness was 0.5 m² higher in the slope zone than in the shelf zone, whereas the opposite pattern was observed in the south (Fig. 4).

In terms of diversity scales, the Alpha diversity ($SR_S$) values found in the study area ranged from 2 to 84 species. The mean alpha diversity was highest on the north shelf, where 84 species were found at one station, followed by the south shelf, where richness ranged from 15 to 43 species within stations. The highest value of beta diversity ($SR_L/_{mean}SR_S$) was found on the north shelf (6.66) and the lowest on the north slope (3.22). $\beta_W$ values almost doubled on the largest scale ($SR_T/_{mean}SR_S$) compared to the highest value found on the large area scale (Table 2).

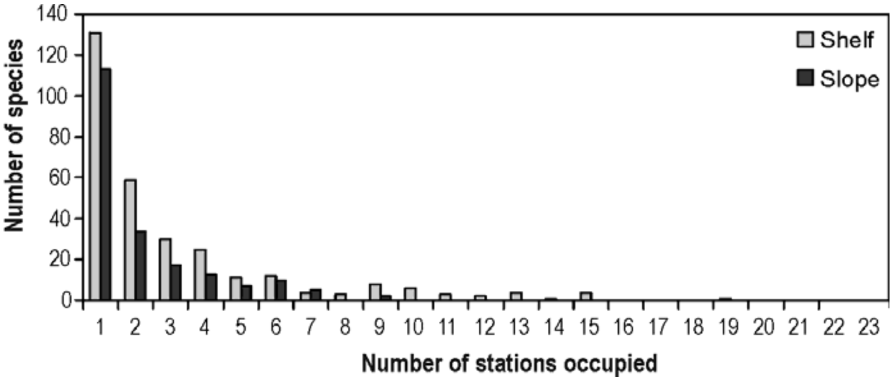

**Figure 2.** Number of stations occupied by a species out of 23 shelf stations and 14 slope stations (distribution of species range sizes).

**Figura 2.** Número de las estaciones que eran ocupadas por las especies de 23 estaciones en la plataforma y 14 estaciones en el talud (distribución de los tamaños de las especies).

**Appendix 1.** Taxonomic list of species from the continental shelf (25-200 m depth).

**Apéndice 1.** Lista taxonómica de especies de la plataforma continental (25-200 m de profundidad).

Family Scissurellidae Gray, 1847
*Scissurella* sp.
*Anatoma aedonia* Watson, 1886
*Sinezona brasiliensis* Mattar, 1987

Family Fissurellidae Fleming, 1822
*Diodora jaumei* Aguayo & Rehder, 1936)
*Diodora meta* (Ihering, 1927)
*Diodora mirifica* Métivier, 1972
*Diodora sayi* (Dall, 1899)
*Diodora* sp.
*Emarginula "aff." phrixodes* Dall, 1927
*Emarginula pumila* (A. Adams, 1851)
*Emarginula tuberculosa* Libassi,1859
*Lucapinella limatula* (Reeve, 1850)
*Puncturella antillana* Farfante, 1947
*Puncturella granulata* Seguenza, 1863

Family Acmaeidae Carpenter, 1857
*Colisella* sp.

Family Trochidae Rafinesque, 1815
*Calliostoma echinatum* Dall, 1881
*Calliostoma gemmosum* (Reeve, 1842)
*Calliostoma* sp.
*Calliostoma vinosum* Quinn, 1992
*Lamellitrochus carinatus* Quinn, 1991
*Lamellitrochus lamellosus* Verrill & Smith,1880
*Lamellitrochus* sp.
*Mirachelus clinocnemus* Quinn, 1979
*Solariella staminea* Quinn, 1992

Family Skeneidae Thiele, 1929
*Cyclostremiscus caraboboensis* Weisbord, 1962
*Cyclostremiscus ornatus* (Olsson & McGinty, 1958)
*Cyclostremiscus pentagonus* (Gabb, 1863)
*Haplocochlias "aff." swifti* Vanatta, 1913
*Parviturbo rehderi* Pilsbry & McGinty, 1945
*Parviturbo weberi* Pilsbry & McGinty, 1945

Family Turbinidae Rafinesque, 1815
*Arene bairdii* (Dall, 1889)
*Arene brasiliana* (Dall, 1927)
*Arene microforis* (Dall, 1889)
*Arene variabilis* (Dall, 1889)
*Arene venusta* (Woodring, 1928)
*Astraea latispina* (Philippi, 1844)
*Turbo* sp.

Family Tricollidae Robertson, 1958
*Gabrielona sulcífera* Robertson, 1973
*Tricolia "aff."* (C.B. Adams, 1850)
*Tricolia bella* (M. Smith, 1937)

Family Seguenziidae Verrill, 1884
*Ancistrobasis costulata* (Wattson, 1879)

Family Neritopsidae Gray, 1847
*Smaragdia viridis* (Linnaeus, 1785)

Family Phenacolepadidae Thiele, 1929
*Phenacolepas hamillei* (Fisher, 1857)

*Family Rissoidea Gray, 1847*
*Alvania valeriae* Absalão, 1993
*Alvania aberrans* (C.B. Adams, 1850)
*Alvania auberiana* (Orbigny, 1842)
*Alvania* sp.
*Benthonella tenella* (Jeffreys, 1883)
*Ceratia rustica* (Watson, 1885)
*Folinia bermudezi* (Aguayo & Rehder, 1936)
*Rissoina cancellata* (Philippi, 1847)
*Rissoina decussata* Montago, 1803
*Rissoina fenestrata* Schwartz, 1860
*Rissoina princeps* (C. B. Adams, 1850)
*Rissoina* sp.

Family Barleeidae Gray, 1857
*Amphithalamus vallei* Aguayo & Jaume, 1947
*Barleeia rubrooperculata* (Castellanus, 1972)
*Caelatura barcellosi* Absalão & Rios, 1995
*Caelatura* sp.

Family Assimineidae H. & A. Adams, 1856
*Assiminea succinea* (Pfeiffer, 1840)
Assiminea sp.

Family Caecidae Gray, 1850
*Caecum brasilicum* Folin, 1874
*Caecum butoti* DeYong & Coomans, 1988
*Caecum cornucopiae* (Carpenter, 1858)
*Caecum floridanum* Stimpson, 1851
*Caecum irregulare* Stimpson, 1851
*Caecum meioceras* Carpenter, 1858
*Caecum* sp.

Family Vitrinellidae Bush, 1897
*Circulus orbignyi* (Fischer, 1857)
*Solariorbis "aff." shumoi* (Vanatta, 1913)
*Solariorbis infracarinatus* Gabb, 1881
*Solariorbis mooreana* (Vanatta, 1904)

*Teinostoma cocolitoris* Pilsbry & McGinty, 1945
*Vitrinella cupidinensis* Altena, 1966

Family Modulidae Fisher, 1884
*Modulus carchedeonius* (Lamarck, 1822)

Family Cerithiidae Fleming, 1822
*Bittium* sp.
*Bittium varium* (Pfeiffer, 1840)
*Cerithium litteratum* (Born, 1778)

Family Litiopidae Gray, 1847
*Alaba incerta* (Orbigny, 1842)

Family Diastomatidae Cossmann, 1893
*Finella dubia* (Orbigny, 1842)

Family Fossaridae Troschel, 1861
*Megalomphalus troubei* (Bavay, 1908)

Family Turritellidae Clarke-Woodward, 1851
*Turritella exoleta* (Linnaeus, 1758)
*Turritella hookeri* Reeve,1849
*Turritella* sp.

Family Calyptraeidae Lamarck, 1809
*Calyptraea centralis* (Conrad, 1841)
*Calyptraea* sp.
*Crucibulum auricula* (Guimelin, 1791)
*Crucibulum striatum* (Say, 1824)

Family Xenophoridae Troschell, 1852
*Xenophora conchyliophora* (Born, 1780)

Family Cypraeidae Rafinesque, 1815
*Cypraea* sp.

Family Triviidae Troschei, 1863
*Trivia candidula* (Gaskoin, 1836)
*Trivia nix* Schilder, 1922
*Trivia occidentalis* Schilder, 1922
*Trivia pediculus* (Linnaeus, 1758)
*Trivia* sp.
*Trivia suffusa* (Gray, 1832)

Family Naticidae Forbes, 1838
*Natica pusilla* Say, 1822
*Natica sulcata* (Born, 1778)
*Sigatica semisulcata* (Gray, 1839)

Family Cerithiopsidae H. & A. Adams, 1853
*Cerithiopsis greenii* (C.B. Adams, 1839)
*Cerithiopsis latum* (C.B. Adams, 1850)
*Cerithiopsis* sp.
*Seila adamsi* (H. Lea, 1845)

Family Triphoridae Gray, 1847
*Metaxia exilis* (C.B. Adams, 1850)
*Triphora decorata* (C.B. Adams, 1850)
*Triphora melanura* (C.B. Adams, 1850)
*Triphora ornata* (Deshayes, 1823)
*Triphora turristhomae* (Holten, 1802)

Family Epitoniidae S.S. Berry, 1910
*Amaea retifera* Dall, 1889
*Epitonium "aff." multistriatum* (Say, 1826)
*Epitonium* sp.

Family Aclididae G.O. Sars, 1878
*Graphis* sp. (Synonym: *Aclis* Lovén, 1846)

Family Eulimidae Risso, 1826
*Eulima auricincta* Abbott, 1959
*Eulima bifasciata* (Orbigny, 1842)
*Eulima hypsela* (Verril & Bush, 1900)
*Melanella arcuata* (C.B. Adams, 1850)
*Scalenostoma* sp.

Family Muricidae Rafinesque, 1815
*Aspella castor* Radwin & D'Attilio, 1976
*Attiliosa* sp.
*Attiliosa striatoides* (E. Vokes, 1980)
*Chicoreus tenuivaricosus* (Dautzenberg, 1927)
*Dermomurex leali* Houart, 1991
*Dermomurex* sp.
*Favartia varimutabilis* Houart, 1991
*Murexiella glypta* (M. Smith, 1938)
*Murexiella* sp.
*Muricopsis* sp.
*Typhis riosi* Bertsch & D'Attilio, 1980

Family Buccinidae Rafinesque, 1815
*Engina* sp.
*Engina turbinella* (Kiener, 1835)
*Pisania bernardoi* P. M. Costa & Gomes, 1998

Family Columbellidae Swainson, 1840
*Aesopus metcalfei* (Reeve, 1858)
*Aesopus* sp.
*Aesopus stearnsi* (Tryon, 1883)
*Amphissa cancellata* (Castellanos, 1982)
*Amphissa* sp.
*Anachis carloslirai* P.M. Costa, 1997
*Anachis fenneli* Radwin, 1968
*Anachis isabellei* (Orbigny, 1841)

*Anachis obesa* (C.B. Adams, 1845)
*Mitrella "aff." lunata* (Say, 1826)
*Mitrella albovittata* Lopes, Coelho & Cardoso, 1965
*Mitrella* sp. 2
*Nassarina minor* (C.B. Adams, 1845)

Family Nassariidae Iredale, 1916

*Nassarius albus* (Say, 1826)

Family Fasciolariidae Gray, 1853

*Fusinus brasiliensis* (Grabau, 1904)
*Fusinus* sp.
*Latirus devyanae* Rios, P.M. Costa & Calvo, 1994
*Latirus* sp.

Family Olividae Latreille, 1825

*Ancilla dimidiata* (Sowerby, 1850)
*Oliva circinata* Marrat, 1870
*Olivancillaria urceus* (Roding, 1798)
*Olivella defiorei* Klappenbach, 1964
*Olivella minuta* (Link, 1807)
*Olivella puelcha* (Duclos, 1840)
*Olivella* sp.1
*Olivella watermani* (McGinty, 1940)

Family Marginellidae Fleming, 1828

*Dentimargo lasallei* Talawera & Princz, 1985
*Eratoidea scalaris* (Jousseaume, 1875)
*Eratoidea* sp.
*Persicula "aff." sagittata* (Hinds, 1844)

Family Mitridae Swainson, 1831

*Mitra staminea* A. Adams, 1853
*Granulina clandestinella* Bavay, 1908/1913
*Granula lavalleana* Orbigny, 1842

Family Mitrinae Swainson, 1831

*Subcancilla candida* (Reeve, 1845)

Family Costellariidae MacDonald, 1860

*Vexilum exiguum* (C.B. Adams, 1845)
*Vexilum hendersoni* (Dall, 1927)
*Vexilum lixa* Petuchi, 1979
*Vexilum* sp.

Family Cancellariidae Forbes & Hanley, 1853

*Cancellaria petuchi* Harasewych, Petit & Verhecken, 1992
*Tritonoharpa lanceolata* (Menke, 1828)
*Tritonoharpa leali* Harasewych, Petit & Verhecken, 1992

Family Conidae Rafinesque, 1815

*Conus jaspideus* Guimelin, 1791
*Conus mindanus* Hwass, 1792

Family Turridae Swainson, 1840

*Acmaturris brisis* Woodring, 1928
*Bellaspira* sp.
*Benthomangelia macra* (Watson, 1881)
*Crassispira cubana* Melvill, 1923
*Crassispira fuscescens* (Reeve, 1843)
*Crassispira* sp.
*Driliola* sp.
*Drilliola comatotropis* (Dall, 1881)
*Eucyclotoma stegeri* (McGuinty, 1955)
*Fenimorea* sp.
*Glyphostoma* sp.
*Ithycythara pentagonalis* (Reeve, 1845)
*Ithycythara* sp.
*Kurtziella dorvillae* (Reeve, 1845)
*Leptadrillia cookei* (E.A. Smith, 1888)
*Lioglyphostoma jousseaumei* (Dautzenberg, 1900)
*Mangelia barbarae* (Lyons, 1972)
*Mangelia biconica* (Dall, 1850)
*Mangelia rugurima* (Dall, 1889)
*Mangelia* sp.
*Mitrolumna biplicata* (Dall, 1889)
*Nannodiella vespuciana* (Orbigny, 1842)
*Neodrillia* sp.
*Pilsbryspira* sp.
*Polystira formosissima* (E.A. Smith, 1915)
*Polystira* sp.
*Pyrgocythara candidissima* (C.B. Adams, 1845)
*Pyrgocythara guarani* (Orbigny)
*Pyrgospira* sp.
*Splendrillia carolinae* (Bartsch, 1934)
*Splendrillia lissotropis* (Dall, 1881)
*Splendrillia* sp.
*Tenaturris fulgens* (E.A. Smith, 1888)
*Tenaturris gemma* (E.A. Smith, 1884)
*Tenaturris* sp.
*Veprecula morra* (Dall, 1881)
*Veprecula* sp.

Family Terebridae Morch, 1852

*Terebra "aff." duellojuradoi* Carcelles, 1953

Family Architectonicidae Gray, 1840

*Architectonica nobilis* Roding, 1798
*Heliacus bissulcatus* (Orbigny, 1845)

Family Mathildidae Dall, 1889

*Mathilda barbadensis* Dall, 1881
*Mathilda* sp.

Family Pyramidellidae Gray, 1840
- *Chrysallida jadisi* Olsson & McGuinty, 1958
- *Chrysallida* sp. 1
- *Chrysallida toroensis* (Olsson & McGuinty, 1958)
- *Eulimastoma canaliculatum* (C.B. Adams, 1850)
- *Eulimastoma didyma* (Verrill & Bush, 1900)
- *Eulimastoma* sp.
- *Eulimastoma weberi* (Morrison, 1965)
- *Fargoa bushiana* Bartsch,1909
- *Miralda havanensis* (Pilsbry & Aguayo, 1933)
- *Odostomia canaliculata* C.B. Adams, 1850
- *Odostomia laevigata* (Orbigny, 1842)
- *Odostomia ovuloide* C.B. Adams, 1850
- *Odostomia seminuda* (C.B. Adams, 1837)
- *Peristichia agria* Dall, 1889
- *Pyramidella crenulata* (Holmes, 1859)
- *Pyramidella* sp.
- *Sayella crosseana* (Dall, 1885)
- *Turbonilla "aff." coomansi* van Aartsen, 1994
- *Turbonilla arnoldoi* Jong & Coomans, 1988
- *Turbonilla iheringi* Clessin, 1900

Family Amathinidae Ponder, 1988
- *Iselica anomala* (C.B. Adams, 1850)

Family Acteonidae Orbigny, 1842
- *Acteon pelecais* Marcus, 1981
- *"Acteon" vagabundus* (Mabille & Rochebrune, 1885)
- Family Cylichnidae H. & A. Adams, 1854
- *Acteocina bidentata* (Orbigny, 1841)
- *Acteocina bullata* (Kiener, 1834)
- *Acteocina candei* (Orbigny, 1842)
- *Acteocina inconspicua* Olsson & McGinty, 1958
- *Acteocina lepta* Woodring, 1928
- *Acteocina* sp.
- *Cylichna discus* Watson, 1883
- *Cylichna verrillii* Dall, 1889
- *Cylichna* sp.
- *Scaphander darius* Marcus, 1967

Family Hamineidae Pilsbry, 1895
- *Atys guildingi* (Sowerby, 1869)
- *Atys mandrewii* E.A. Smith, 1872
- *Atys riiseana* (Morch, 1875)
- *Atys sandersoni* Dall, 1881
- *Haminoea elegans* (Gray, 1825)

Family Retusidae Thiele, 1926
- *Pyrunculus caelatus* (Bush, 1885)
- *Volvulella paupercula* (Watson, 1883)
- *Volvulella persimilis* (Morch, 1875)
- *Volvulella recta* (Morch, 1875)
- *Volvulella* sp.
- V*olvulella texasiana* Harry, 1967

Family Siphonariidae Gray, 1840
- *Williamia krebsi* (Morch, 1877)

**Appendix 2.** Taxonomic List of species from the Continental Slope (300-1330 m depth).

**Apéndice 2.** Lista taxonómica de especies de la plataforma continental (300-1330 m de profundidad).

Family Scissurellidae Gray, 1847
- *Anatoma aedonia* (Watson, 1886)

Family Fissurellidae Fleming, 1822
- *Puncturella antillana* Farfante, 1947
- *Puncturella granulata* Seguenza, 1863
- *Puncturella* sp.

Family Cocculinidae Dall, 1882
- *Cocculina beanii* Dall, 1882

Family Trochidae Rafinesque, 1815
- Calliostoma *"aff." coronatum* Quinn, 1992
- Euchelus sp.
- *Basilissa alta* Watson, 1879
- *Basilissa* sp.
- *Calliotropis actinophora* (Dall, 1890)
- *Calliotropis "aff." calatha* (Dall, 1927)
- *Calliotropis* sp.
- *Echinogurges "aff." clavatus* (Watson, 1879)
- *Echinogurges clavatus* (Watson, 1879)
- *Echinogurges* sp.
- *Echinogurges* sp. 1
- *Echinogurges* sp. 2
- *Echinogurges* sp. 3
- *Microgaza* sp.
- *Mirachelus clinocnemus* Quinn, 1979
- *Solariella lubrica* Dall, 1881
- *Solariella* sp. 1
- *Solariella* sp. 2
- *Tegula* sp.

Family Cyclostrematidae Fisher, 1885
- *Brookula conica* (Watson, 1885)
- *Brookula pfefferi* A.W.B. Powell, 1951
- *Brookula* sp.
- *Brookula spinulata* Absalão, Miyaji & Pimenta, 2001
- *Granigyra* n. sp.

Family Turbinidae Rafinesque, 1815

*Homalopoma boffi* Marini, 1975

Family Tricoliidae Robertson, 1958

*Tricolia aff.inis* (C.B. Adams, 1850)

Family Seguenziidae Verrill, 1884

*Ancistrobasis costulata* (Watson, 1879)
*Hadroconus altus* (Watson, 1879)
*Seguenzia hapala* Woodring, 1928
*Seguenzia* sp. 1
*Seguenzia* sp. 2

Family Rissoidae Gray, 1847

*Alvania auberiana faberi* Jong & Coomans, 1988
*Alvania xantias* (Watson, 1885)
*Benthonella* sp.
*Benthonella tenella* (Jeffreys, 1883)

Family Barleeidae Gray, 1857

*Barleeia* sp.

Family Vitrinellidae Bush, 1897

*Teinostoma "aff." obtectum* Pils. & Mcg., 1945
*Teinostoma "aff." reclusa* Dall, 1889

Family Diastomatidae Cossmann, 1893

*"Finella" mamillatum* (Watson, 1880)

Family Vanikoridae Gray, 1840

*Vanikoro oxychone* Morch, 1877

Family Trichotropididae Gray, 1850

*Lyocyclus pernambucensis* (Watson, 1885)

Family Cypraeidae Rafinesque, 1815

*Cypraea cinerea* Gmelin, 1791

Family Naticidae Forbes, 1838

*Polinices "aff." fringillus* (Dall, 1881)

Family Bursidae Thiele, 1925

*Bursa* sp.

Family Epitoniidae S.S. Berry, 1910

*Amaea retifera* Dall, 1889
*Cylindriscala watsoni* (de Boury, 1911)
*Epitonium "aff." angulatum* (Say, 1830)
*Epitonium* sp.1
*Epitonium* sp.2
*Opaliopsis aff. nitida* (Verrill & Smith, 1885)
*Solutiscala formosissima* de Boury, 1909

Family Janthinidae Leach, 1823

*Recluzia rollandiana* Petit, 1853

Family Eulimidae Philippi, 1853

*Eulima* sp. 1
*Eulima* sp. 2
*Eulima* sp. 3
*Eulima* sp. 4
*Melanella "aff." arcuata* (C.B. Adams, 1850)
*Melanella "aff." sarissa* (Watson, 1883)
*Niso* sp.

Family Velutininae Gray, 1840

*Velutina* sp. (?)

Family Muricidae Rafinesque, 1815

*Chicoreus tenuivaricosus* (Dautzenberg, 1927)
*Trophon* sp.

Family Buccinidae Rafinesque, 1815

*Belomitra pourtalesii* (Dall, 1881)
*Belomitra* sp.
*Kryptos tholoides* (Watson, 1881)

Family Columbellidae Swainson, 1840

*Amphissa cancellata* (Castellanos, 1982)
*Anachis* n. sp. 1
*Anachis* n. sp. 2

Family Olividae Latreille, 1825

*Ancilla dimidiata* (Sowerby, 1850)
*Olivella amblia* Watson, 1882
*Olivella (divina)* n.sp.1

Family Mitrinae Swainson, 1831

*Mitra* sp.

Family Cancellariidae Forbes & Hanley, 1853

*Brocchinia "aff." pustulosa* Verhecken, 1991

Family Turridae Swainson, 1840

*Gymnobela* sp.
*Bathytoma "aff." mitrella* Dall, 1881
*Benthomangelia macra* (Watson, 1881)
*Compsodrillia* sp.
*Leptadrillia* sp.
*Drillia "aff." premorra* Dall, 1881
*Drilliola comatotropis* (Dall, 1881)
*Eubela limacina* (Dall, 1881)
*Eucyclotoma* sp.
*Fenimorea "aff." pagodula* (Dall, 1889)
*Kurtziella "aff." serga* (Dall, 1881)
*Kurtziella* sp.
*Leucosyrinx verrillii* (Dall, 1881)

*Leucosyrinx* sp.
*Drilliola comatotropis* (Dall, 1881)
*Nannodiella vespuciana* (Orbigny, 1842)
*Pleurotomella "aff." benedicti* Verrill & Smith, 1884
*Pleurotomella "aff." blakeana* (Dall, 1881)
*Pleurotomella "aff." cala* (Watson, 1886)
*Pleurotomella "aff." ipara* (Dall, 1881)
*Pleurotomella "aff." porcellana* (Watson, 1886)
*Pleurotomella circumvoluta* (Watson, 1881)
*Pleurotomella extensa* (Dall, 1881)
*Pleurotomella perparva* (Synonym: *Philbertia perparva* (Watson, 1881))
*Pleurotomella* sp. 1
*Pleurotomella* sp. 2
*Pleurotomella* sp. 3
*Pleurotomella* sp. 4
*Pleurotomella* sp. 5
*Pleurotomella* sp. 6
*Pleurotomella* sp. 7
*Pleurotomella* sp. 8
*Spirotropis "aff." phaeacra* (Watson, 1881)
*Spirotropis* sp.

Family Mangeliinae Fischer, 1887
*Mangelia comatotropis* Dall, 1881

Family Pyramidellidae Gray, 1840
*Cingulina babylonia* (C.B. Adams, 1845)
*Eulimastoma* sp. 1
*Eulimastoma* sp. 2
*Eulimella smithii* Verrill, 1882
*Eulimella* sp. 1
*Eulimella* sp. 2
*Odostomia "aff." canaliculata* C.B. Adams, 1850
*Sayella crosseana* (Dall, 1885)
Turbonilla *"aff." unilirata* Bush, 1899
*Turbonilla* sp. 1
*Turbonilla* sp. 2
*Turbonilla* sp. 32
*Turbonilla* sp. 35

Family Acteonidae Orbigny, 1842
*"Acteon" vagabundus* (Mabille & Rochebrune, 1885)
*Acteon pelecais* Marcus, 1981
*Acteon perforatus* Dall, 1881
*Rictaxis sp.*

Family Ringiculidae Philippi, 1853
*Ringiculina nitida* Verrill, 1874

Family Cylichnidae H. & A. Adams, 1854
*Cylichna "aff." crispula* Watson, 1883
*Cylichna discus* Watson, 1883
*Cylichna verrillii* Dall, 1889
*Cylichna vortex* Dall, 1881
*Scaphander darius* Marcus, 1967

Family Diaphanidae Odhner, 1914
*Diaphana seguenzae* (Watson, 1886)

Family Bullidae Rafinesque, 1815
*Bulla "aff." abyssicola* Dall, 1881
*Bulla "aff." eburnea* (Dall, 1881)

Family Hamineidae Pilsbry, 1895
*Haminoea elegans* (Gray, 1825)
*Haminoea petitii* (Orbigny, 1842)
*Haminoea* sp.
*Atys guildingi* (Sowerby, 1869)
*Atys mandrewii* E.A. Smith, 1872

Family Retusidae Thiele, 1926
*Pyrunculus ovatus* (Jeffreys, 1870)
*Volvulella persimilis* (Morch, 1875)

## Biogeographic distribution

For the continental shelf samples, 211 species and 89 genera were characterized according to their occurrence in the southwestern Atlantic zoogeographic provinces: 91 species from the south, 179 from the north, and 59 species from both regions. For the continental slope samples, 96 species and 52 genera were characterized: 72 species from the south, 55 from the north, and 31 from both regions.

In terms of the geographical distribution of taxa, the number of genera with a wide distributional range (occurring in more than three provinces) was lower than the genera with narrower distributions for both shelf and slope stations. However, considering the genera that occurred in both zones, the number of wide-range distributions was higher than the narrow-range ones (Table 3).

At the shelf stations, the number of species co-occurring in both Tropical and Paulista (Tropical-Paulista species) provinces was greater than the number of Tropical species occurring in both regions. In addition, the number of Tropical, Paulista, and Tropical-Paulista species decreased and the number of wide-distribution eurythermic species increased in the southwestern Atlantic provinces (Tropical-Paulista-Patagonic species) towards the south (Fig. 5). At the slope stations, Tropical species were the majority in

**Table 2.** Species richness (sample species richness (SRs) = alpha diversity; mean alpha diversity (${}_{\mathrm{Mean}}SR_S$); large area species richness ($SR_L$); total area species richness ($SR_T$), number of individuals (*n*), and beta diversity for the large area and the total area ($\beta_W$). Unique species are those restricted to a single station; duplicates are species occurring at exactly two stations; singletons are species represented by a single individual; doubletons are species represented by only two individuals. CI 95% confidence intervals.

**Tabla 2.** Riqueza de especies (*sample species richness* (SRs) = *diversidad alpha;* diversidad *alpha* media (${}_{\mathrm{Mean}}SRs$); riqueza de especies para áreas grandes ($SR_L$); riqueza de especies por área total ($SR_T$), número de individuos (*n*) y diversidad beta para áreas grandes y área total ($\beta_W$). Especies únicas son las especies limitadas a una sola región; especies duplicadas son las que se enconntraron en dos estaciones; *singletons* son especies representadas para un solo individuo; *doubletons* son especies representadas para solo dos individuos. CI 95% intervalos de confianza.

| | $SR_S$ | | | | $\beta_W$= | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Large Areas | Range | ${}_{\mathrm{Mean}}SR_S$±CI | $SR_L$ | *n* | ($SR_L/{}_{\mathrm{Mean}}SR_S$) | Unique (%) | Duplicates (%) | Singletons (%) | Doubletons (%) |
| North Shelf | 2 – 84 | 33.94±11.7 | 226 | 5082 | 6.66 | 26.35 | 10.83 | 17.48 | 7.63 |
| South Shelf | 15 – 42 | 26.40±11.7 | 113 | 1003 | 4.28 | 20.68 | 3.69 | 12.31 | 3.20 |
| North Slope | 8 – 40 | 28.16±8.9 | 85 | 1014 | 3.02 | 12.31 | 6.15 | 5.66 | 4.43 |
| South Slope | 4 – 46 | 22.77±10.8 | 127 | 2746 | 5.58 | 21.18 | 5.41 | 16.25 | 3.94 |
| Total | 2 – 84 | 29.27±6.3 | $SR_T$ 404 | 9845 | $\beta_W = (SR_T/{}_{\mathrm{Mean}}SR_S)$ 13.80 | 48.52 | 17.98 | 33.74 | 13.30 |

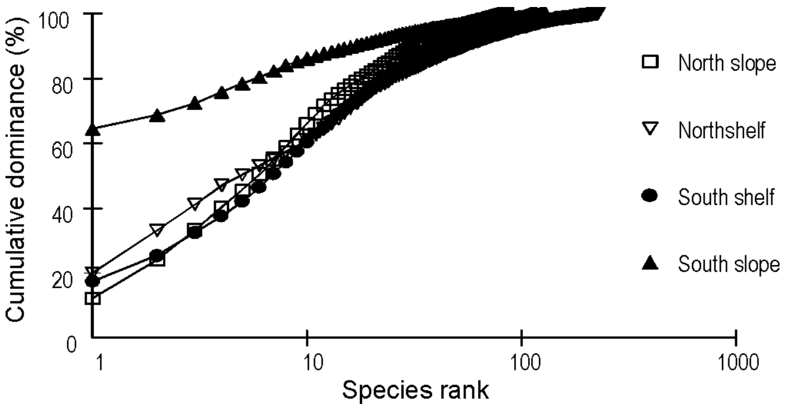

**Figure 3.** Cumulative dominance curve for the large areas.

**Figura 3.** Curva de dominancia acumulativa para las áreas grandes.

both regions. The number of Tropical, Paulista, Tropical-Paulista, Tropical-Paulista-Patagonic, and subtropical Paulista-Patagonic species increased towards the south. The number of endemic species was higher in the north for both shelf and slope stations. In addition, a greater number of Tropical endemic species was present at the slope stations in both the south and north, and the shelf stations displayed the highest occurrence of Paulista endemic species. The number of species occurring in all Western Atlantic Provinces was greater on the south shelf (Table 4). Furthermore, shelf stations showed a higher number of eurybathic species (with a wide bathymetrical range) than did slope stations (Table 5).

## DISCUSSION

The shelf-slope transition zone is known to have a high species turnover rate (Rex *et al.*, 1977). Moreover, species typically found on continental shelves and species from continental slope zones can coexist there, leading to higher species richness. However, evidence from studies done on the Brazilian continen-

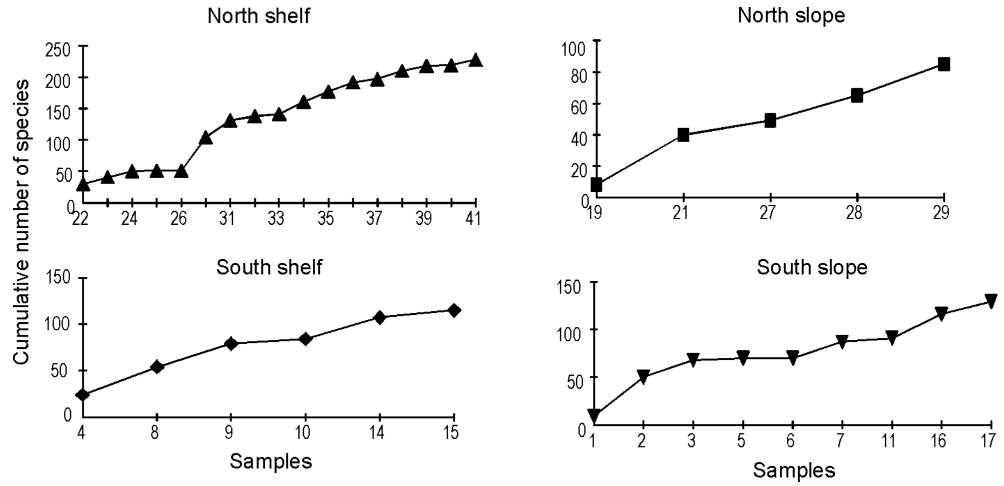

**Figure 4.** Species accumulation curve for the large areas.

**Figura 4.** Curva de acumulación de las especies para las áreas grandes.

**Table 3.** Biogeographical distribution of genera found only on the shelf, only on the slope, and in both (shelf and slope) zones.

**Tabla 3.** Distribución biogeográfica de los generos encontrados solo en la plataforma, solo en el talud y encontrados en ambas áreas (plataforma y talud).

| Biogeographic distribution | Shelf | Slope | Shelf and Slope |
|---|---|---|---|
| Tropical | 20 | 18 | 4 |
| Tropical-Paulista | 45 | 6 | 14 |
| Tropical-Paulista-Patagonic | 6 | 7 | 15 |
| Tropical-Paulista-Patagonic-Malvina | 13 | 11 | 17 |
| Paulista-Patagonic | 1 | 0 | 0 |
| Paulista-Patagonic-Malvina | 0 | 0 | 1 |
| Others | 4 | 10 | 14 |

Others = Occurrence in the S.W. Atlantic and in other regions such as E. Pacific, W. Africa, the Mediterranean, the Arctic.

tal slope showed that the depth where this species turnover begins is variable. In this study, we found high species turnover at station 16 (300 m depth), where some deep-sea species, such as *Alvania xantias* (Watson, 1885), *Brookula spinulata* (Absalão, Miyaji & Pimenta, 2001), and *Solariella lubrica* (Dall, 1881) showed a high dominance. Miyaji (2001) found a rough change, with 8% of sampled species occurring exclusively at depths greater than 400 m, whereas Sumida & Pires-Vanin (1997) found a different community from shallow areas occurring between 320 m and 500 m depth.

Analyzing the vertical distribution of species found in this study (Table 2), we observed the occurrence of shallow-water and eurybathic species (shallow-bathyal, shallow-bathyal-abyssal, bathyal-abyssal distributions) at the slope stations. This pattern might constitute evidence of the slope's capacity to allow the co-existence of shallow and deep-water species.

The depth gradient differed between the north and south regions: the north shelf showed the highest local, regional, and between-habitat species richness, whereas the south slope had the highest species richness, with values close to the shelf ones. Along local gradients, the general pattern observed is that species richness changes with depth, increasing from ca. 200 m to 1500-2500 m or more, and then decreasing towards the abyssal plain (Rex *et al.*, 1993, 2000; Gray, 2002). Nevertheless, those unimodal patterns do not

**Table 4.** Biogeographical distribution of species in the shelf and slope zones and in the north and south sectors.

**Tabla 4.** Distribución biogeográfica de las especies en las áreas de plataforma y talud, y en los sectores norte y sur.

| North Section | | |
|---|---|---|
| Biogeographical distribution | Shelf | Slope |
| Southwestern Atlantic | 10 | 1 |
| Endemic to Brazil | 3 | 0 |
| Endemic to Tropical Province | 4 | 7 |
| Endemic to Paulista Province | 5 | 1 |
| Others | 8 | 2 |
| South Section | | |
| Biogeographical distribution | Shelf | Slope |
| Southwestern Atlantic | 14 | 3 |
| Endemic to Brazil | 1 | 1 |
| Endemic to Tropical Province | 1 | 4 |
| Endemic to Paulista Province | 4 | 1 |
| Others | 0 | 8 |

appear to be universal (Rex *et al.*, 1997; Stuart *et al.*, 2001), showing that the change in species richness is not related to depth itself (Gray, 2002).

The highest species richness values observed on the north shelf could be a result of the fact that the highest number of samples were taken in this area, but also of the greater environmental heterogeneity in the area. Larger areas potentially support more species richness on a variety of scales and harbor higher overall richness, whereas the number of habitats also increases, as well as the number of biomes, or of biogeographic provinces within them (Rosenzweig, 1995; Willig *et al.*, 2003). On the north shelf, species can find a wide continental shelf (200 km) featuring a high variety of bottom types, as well as the presence of corals and calcareous algae bank habitats. On the other hand, the south region is characterized by a narrow shelf area (10-30 km) and a less heterogeneous bottom (Soares-Gomes *et al.*, 1999). Additionally, because of the constant presence of the Brazil Current, the north region is oligotrophic, which may limit the abundance of species. Conversely, the south region is considered to be mesotrophic due to the seasonal upwelling of cold, nutrient-rich, SACW waters (Gaeta *et al.*, 1999), leading to higher richness.

In addition to the above-mentioned patterns, environmental features also changed with depth. Both north and south slopes are narrow and steep, with more homogeneous bottoms that are dominated by silt fractions and a higher concentration of organic carbon.

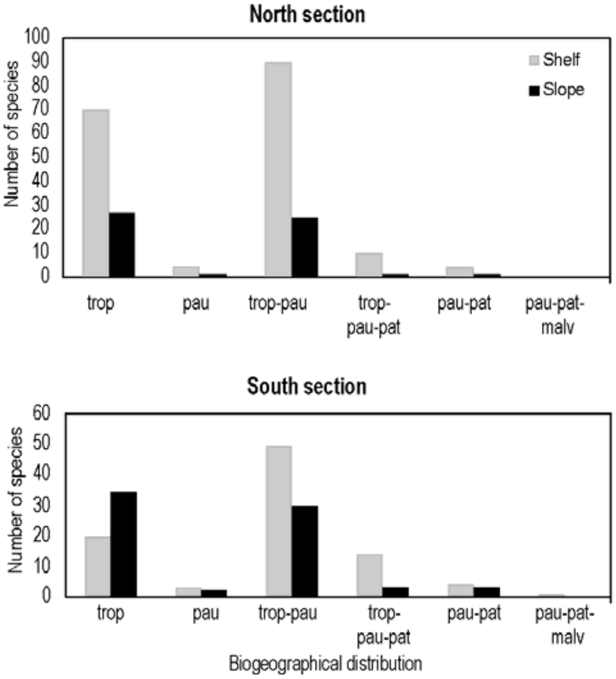

**Figure 5.** Occurrence of species in the southwestern Atlantic zoogeographical provinces, comparing their geographical (north and south regions and bathymetric (shelf and slope stations) distribution in the area studied.

**Figura 5.** Incidencia de las especies en las provincias zoogeográficas del Atlántico sudoriental, comparando sus distribución geográficas (las regiones del norte y del sur y las estaciones batimétricas de la plataforma y talud) en el área de estudio.

**Table 5.** Vertical distribution of species sampled at shelf and slope stations based on the literature (Abbott, 1974; Rosenberg, 1993; Rios, 1994; Merlano & Hegedus, 1994).

**Tabla 5.** Distribución vertical de las especies muestreadas en las estaciones de la plataforma y del talud, basada en la literatura (Abbott, 1974; Rosenberg, 1993; Rios, 1994; Merlano & Hegedus, 1994).

| Bathymetric zone | Shelf region | Slope region |
|---|---|---|
| Shallow (0-200 m) | 149 | 22 |
| Bathyal (200-3000 m) | 2 | 42 |
| Shallow-Bathyal | 55 | 28 |
| Shallow-Bathyal-Abyssal | 1 | 1 |
| Bathyal-Abyssal | 0 | 2 |
| Abyssal (> 3000 m) | 0 | 0 |

The study area is included in a wide transition zone known as the Paulista province (Palacio, 1982). The present study found a lower number of tropical species and a higher number of subtropical ones (species that are common to the Paulista and Patagonic provinces) towards the south. Moreover, a great presence of species common to both the Tropical and Paulista provinces was observed over the entire area. Other studies carried out at more southerly latitudes on the Brazilian coast show the same distribution for molluscs (Mello, 1993; Miyaji, 1995) and polychaetes (Lana, 1987; Attolini, 1997). Furthermore, on the Uruguayan coast (Scarabino, 2004), 16 among 182 gastropods were the same as the species reported in this study (carried out in the Tropical and Paulista provinces). The presence of species that are considered to be endemic to the Paulista Province (i.e., *Anachis fenelli* Radwin, 1968; *Favartia varimutabilis* Houart, 1991; *Olivella defiorei* Klappenbach, 1964) and subtropical species from the Patagonic Province in the north region (Tropical Province) corroborate the notion of a broader transition zone between tropical and temperate waters (Van nucci, 1964; Lana, 1987; Miyaji, 1995; Floeter & Soares-Gomes, 1999).

The disappearance of some tropical species towards the south suggests that the southernmost limit of the Tropical Province is located close to 21°S, according to the results found for gastropods (Floeter & Soares-Gomes, 1999); cirripeds (Young, 1995), and polychaetes (Lana, 1987). Nevertheless, the location of that limit remains uncertain (Absalão, 1989; Mello, 1993; Briggs, 1995). Recently, Joyeux *et al.* (2001) and Floeter *et al.* (2008) found that, for tropical reef fishes, the southern limit is 28°S.

Many studies have demonstrated that the boundaries of shallow-water faunal distribution are correlated to water masses boundaries (Stevenson *et al.*, 1998; Culver & Buzas, 2000). The presence of species with tropical affinities over the shelf area could be explained by the predominance of the warm and saline water mass of the Brazil Current (BC) (Absalão, 1989; Miyaji, 1995, 2001) that flows southwards (parallel to the shelf break) to 35°S (Emilsson, 1961). In that region, the BC mixes with the cold and less saline water mass of the Malvina Current and the water characteristics become markedly subtropical, with salinity and temperature ranging between 36-35 and 20°-10°C, respectively (Emilsson, 1961). This fact influences the occurrence of cold-water affinity species (Semenov & Berman, 1977; Palacio, 1982).

However, the most significant factor for the maintenance of cold-water species, as well as of eurybathic species in the shelf zone, particularly in the north region, might be the penetration of the South Atlantic Central Water (SACW) into the continental shelf regions. This water mass acts as a vehicle for larval dispersal from cold, deeper regions to warm, shallower areas (Absalão, 1989; Miyaji, 1995, 2001), and extends northwards to Espírito Santo State (Gaeta *et al.*, 1999).

Important changes occur in the benthic faunal structure within the large vertical interval of the bathyal zone. The most obvious difference between shallow and deep-bottoms is the reduction in the number of latitudinal or climatic belts, both in terms of biomass and of faunal structures (Zezina, 1997). As there is a simplification in the water mass structure of the continental slope floor region, a reduction in the number of faunal provinces is to be expected (Semenov & Berman, 1977; Zezina, 1997; Culver & Buzas, 2000). Culver & Buzas (2000) found that the differences in benthic foraminifera fauna between shallow (< 200 m) and deep water (> 200 m) provinces at the same latitude were greater than between adjacent shallow water provinces.

As expected, species occurring in the shelf zone were very distinct from those in the slope area, with only 24 (out of 315) species shared between the two zones. When the latitudinal distribution of slope species is analyzed, the pattern is similar to the shelf species distribution. However, the number of Tropical and Tropical-Paulista species increased in the south region.

Studies on geographical distributions of deep-sea species have shown a greater number of species with wider horizontal ranges (Vinogradova, 1997; Zezina, 1997). However, the present study found few species with wide range distributions towards the slope stations. Similar results were observed for the geographic distribution of genera. The restricted-range genera (1 to 2 provinces) were represented by six more genera than the wide-range ones (> 2 provinces). It is, however, possible that the lower number of samples for the slope region (14 stations vs. 23 in the shelf zone) might induce such contradictory results. It is expected that enhanced sampling efforts will not only tend to increase the more sparsely distributed species, but also the number of "rare" endemic species (Allen & Sanders, 1996).

Comparing the species found in the present study area (18°-23°S) with their incidence in other geographical regions studied by others authors along the Brazilian continental slope (Merlano & Hegedus, 1994; Sumida & Pires-Vanin, 1997; Miyaji, 2001; Scarabino, 2004) revealed some shared species. Nineteen species were shared between the present study and works done on the northeast region (11.37%), from a total of 167 species found. Among those, the most dominant species were *Brookula conica* (Watson, 1985), *Anatoma aedonia* (Watson, 1886), *Benthonella tenella* (Jeffreys, 1883), and *Alvania xantias* (Watson, 1885). The southeast region shared 10 (7.57%) of a total of 132 species, with the dominant species being *Brookula pfefferi* A.W.B. Powell, 1951; *Seguenzia hapala* Woodring, 1928; *Nannodiella vespuciana* (Orbigny, 1842); and *Solariella lubrica* (Dall, 1881). Finally, the south region shared four (3.15%) of a total of 127 species; the most dominant species were *Ancilla dimidiata* (Sowerby, 1850); *Basilissa alta* (Watson, 1886); *Pyrunculus ovatus* (Jeffreys, 1870); and *Puncturella granulata* (Seguenza, 1863). As Allen & Sanders (1996) found for the zoogeographic distribution of protobranch bivalves through inter-basin comparisons on the percentage of shared species, the species number is higher between adjacent basins. Moreover, the majority of shared species are those from the Tropical Province and from both Tropical and Paulista Provinces. Analyses of the biogeographic distribution of bathyal species indicated a transitional pattern, as suggested for the shelf zone. However, the higher number of eurythermic species with tropical affinities found at the slope stations could be an indication that the limit of tropical bathyal species distribution is wider than that of tropical shelf boundaries.

Zezina (1997) proposed biogeographic schemes for the bathyal zone based on a recent brachiopod distribution, which is very similar to the results found in the present study for gastropods from the continental slope. This scheme proposed, for depths greater than 700 m in the northeast and central Brazilian bathyal zone (similar to the schemes for shallow-water fauna in the southwestern Atlantic), a sub-area named the Atlantic-Central American (divided into Caribbean and Brazilian provinces) and the south Brazilian-Uruguayan subtropical area in the southeast and south bathyal zones. Also, for recent brachiopods living below 700 m, Zezina (1997) defined only one area for the entire southwestern Atlantic Ocean: the Amphi-Atlantic Bathyal area within the central Atlantic Province.

A great species turnover rate was observed between the shelf and slope. An analysis of the gastropod species distribution revealed a similar pattern of regional distribution in shelf and slope zones and a great difference between shallow and deep-water faunas. Although the present analysis of biogeographic distribution patterns confirmed the existence of a transitional zone from tropical to subtropical waters in the case of the slope zone, the sampling effort done on the southeastern Atlantic slope is still too little and those results should be viewed with caution.

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## REFERENCES

Abbott, R.J. 1974. American seashells, Van Nostrand Reinhold, New York, 663 pp.

Absalão, R.S. 1989. Padrões distributivos e zoogeografia dos moluscos da plataforma continental brasileira Parte III. Comissão oceanográfica Espírito Santo I. Mem. Inst. Oswaldo Cruz, Rio de Janeiro, 84(4): 1-6.

Allen, J.A. & H.L. Sanders. 1996. The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic: The epilogue. Progr. Oceanogr., 38: 95-153.

Attolini, F.S. 1997. Composição e distribuição dos anelídeos poliquetas na plataforma continental da região da Bacia de Campos, RJ, Brasil. MSc. Thesis, Universidade de São Paulo, São Paulo, 102 pp.

Briggs, J.C. 1974. Marine zoogeography. McGraw-Hill, New York, 475 pp.

Briggs, J.C. 1995. Global biogeography. Developments in paleontology and stratigraphy. Elsevier, Amsterdam, 472 pp.

Clarke, A. & J.A. Crame. 1997. Diversity, latitude and time: patterns in the shallow sea. In: R.F.G Ormond, J.D. Gage & M.V. Angel (eds.). Marine biodiversity. Patterns and processes, Cambridge University Press, Cambridge, pp. 122-147.

Colwell, R.K. 1997. Estimates: statistical estimation of species richness and shared species from samples, Version 5. User's guide and application. Department of Ecology and Evolutionary Biology, University of Connecticut Storrs, CT, USA. http://viceroy.eeb.unconn.edu/estimates. Revised: 18 Jun 2008.

Colwell, R.K. & J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Phil. Trans. R. Soc. Bull., 345: 101-118.

Crame, J.A. 2000. Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of recent bivalve faunas. Paleobiology, 26: 188-241.

Crame, J.A. 2002. Evolution of taxonomic diversity in the marine realm: a comparison of Late Jurassic and recent bivalve faunas. Paleobiology, 28: 184-207.

Culver, S.J. & M.A. Buzas. 2000. Global latitudinal species diversity gradient in deep-sea benthic foraminífera. Deep-Sea Res. I, 47: 259-275.

Emery, K.O. & E. Uchuoi. 1984. The geology of the Atlantic Ocean. Springer Verlag, New York, 1050 pp.

Emilsson, I. 1961. The shelf and coastal waters off southern Brazil. Boln. Inst. Oceanogr. São Paulo, 11(2): 101-112.

Floeter, S.R. & A. Soares-Gomes. 1999. Biogeographic and species richness patterns of Gastropoda on the southwestern Atlantic. Rev. Bras. Biol., 59(4): 567-575.

Floeter, S.R., L.A. Rocha, D.R. Robertson, J.C. Joyeux, W.F. Smith-Vaniz, P. Wirtz, A.J. Edwards, J.P. Bareiros, C.E.L. Ferreira, J.L. Gasparini, A. Brito, J.M. Fálcon, B.W. Bowen & G. Bernerdi. 2008. Atlantic reef fish biogeography and evolution. J. Biogeogr., 35: 22-47.

Fortes, R.R. & R.S. Absalão. 2004. The applicability of Rapoport's rule to the marine molluscs of the Americas. J. Biogeogr., 31: 1909-1916.

Gaeta, S.A., J.A. Lorenzzetti, L.B. Miranda, S.M.M., Susini-Ribeiro, M. Popeu & C.E.S. Araújo. 1999. The Vitória eddy and its relation to the phytoplankton biomass and primary productivity during the austral fall of 1995. Arch. Fish. Mar. Res., 47(2/3): 253-270.

Gray, J.S. 1998. Gradients in marine biodiversity. In: R.F.G Ormond, J.D. Gage & M.V. Angel (eds.). Marine biodiversity, Cambridge University Press, Cambridge, pp. 18-34.

Gray, J.S. 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. J. Exp. Mar. Biol. Ecol., 250: 23-49.

Gray, J.S. 2002. Species richness of marine soft sediments. Mar. Ecol. Progr. Ser., 244: 285-297.

Harley, C.D.G., K.F. Smith & V.L Moore. 2003. Environmental variability and biogeography: the relationship between bathymetric distribution and geographical range size in marine algae and gastropods. Global Ecol. Biogeogr., 12: 499-506.

Hillebrand, H. 2004. Strength, slope and variability of marine latitudinal gradients. Mar. Ecol. Prog. Ser., 273: 251-267.

Jablonski, D., K. Roy & J.W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science, 314: 102-106.

Joyeux, J.C., S.R. Floeter, C.E.L. Ferreira & J.L. Gasparini. 2001. Biogeography of tropical reef fish: the South Atlantic puzzle. J. Biogeogr., 28: 1-11.

Kempf, M. 1979. Bionomia bentonica de la costa del Brasil tropical. Memorias del seminario sobre ecología bentónica y sedimentación de la plataforma del Atlántico sur. UNESCO, Montevideo, pp. 171-184.

Lana, P.C. 1987. Padrões de distribuição geográfica dos poliquetas errantes (Annelida: Polychaeta) do Estado do Paraná. Ciência Cul., São Paulo, 39(11): 1060-1063.

Linse, K., H.J. Griffiths, D.K.A. Barnes & A. Clarke. 2006. Bidiversity and biogeography of Antarctic and sub-Antarctic mollusca. Deep-Sea Res. II, 53: 985-1008.

Longhurst, A. 1998. Ecological geography of the sea. Academic Press, San Diego, 398 pp.

Mello, R.L.S. 1993. Moluscos do Brasil. I. Gastropoda, bivalvia e scaphopoda coletados durante as viagens do Navio Oceanográfico "Almirante Saldanha". Comissão Sul I. Considerações biogeográficas. Bolm. Museu Malacol., Recife 1: 31-49.

Menzies, R.J., R.Y. George & G.T. Rowe. 1973. Abyssal environment and ecology of the world ocean. Wiley, New York, 488 pp.

Merlano, J.M.D. & M.P. Hegedus. 1994. Moluscos del Caribe Colombiano. Un catálogo ilustrado. Colciencias, Fundación Natura, Invemar, Bogotá, 291 pp.

Miyaji, C. 1995. Composição e distribuição da fauna de moluscos gastrópodes e bivalves da plataforma continental da região da Bacia de Campos (Rio de Janeiro, Brasil). MSc. Thesis, Universidade de São Paulo, São Paulo, 128 pp.

Miyaji, C. 2001. Gastrópodes prosobrânquios da plataforma continental externa e talude superior da costa sudeste brasileira. PhD Thesis, Universidade de São Paulo, São Paulo, 128 pp.

Palácio, J.F. 1982. Revisión zoogeográfica marina del Sur del Brasil. Boln. Inst. Oceanogr. São Paulo, 31(1): 69-92.

Rex, M.A. 1993. Zonation in deep-sea gastropods: the importance of biological interactions to rates of zonation. Proc. Europ. Symp. Mar. Biol., 11: 521-530.

Rex, M.A., R.J. Etter & C.T. Stuart. 1997. Large-scale patterns of species diversity in the deep-sea benthos. In: R.F.G Ormond, J.D. Gage & M.V. Angel (eds.). Marine biodiversity. Patterns and processes. Cambridge University Press, Cambridge, pp. 94-121.

Rex, M.A., C.T. Stuart. & G. Coyne. 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. Proc. Natn, Acad. Sci. USA, 97: 4082-4085.

Rex, M.A., C.T. Stuart, R.R. Hessler, J.A. Allen, H.L. Sanders. & G.D.F. Wilson. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature, 365: 636-639.

Rios, E.C. 1994. Seashells of Brazil. Museu Oceanográfico da Fundação Universidade de Rio Grande, Rio Grande, 368 pp.

Rosenberg, G. 1993. A database approach to studies of molluscan taxonomy, biogeography and diversity, with examples from western Altantic marine gastropods. Am. Malacol. Bull., 10(2): 257-266.

Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, 436 pp.

Roy, K., D. Jablonski, J.W. Valentine & G. Rosenberg. 1998. Marine latitudinal diversity gradients: tests of casual hypotheses. Proc. Natn. Acad. Sci. USA, 95: 3699-3702.

Sanders, H.L. 1968. Marine benthic diversity: a comparative study. Am. Natur., 102: 243-282.

Scarabino, F. 2004. Lista sistemática de los Gastropoda marinos y estuarinos vivientes de Uruguay. Comum. Soc. Malacol. Uruguay, 8(84-85)/(86-87): 305-346.

Semenov, V.N. 1978. Geographical distribution of benthos on the South American shelf as a function of the distribution of coastal waters. Oceanology, 18(1): 77-87.

Semenov, V.N. & I.S Berman. 1977. Biogeographic aspects of the distribution and dynamics of water masses off the South American coast. Oceanology, 17(6): 710-718.

Soares-Gomes, A., C.M.R.C. Abreu, T.M. Absher & A.G. Figueiredo. 1999. Abiotic features and the abundance of macrozoobenthos of continental margin sediments of east Brazil. Arch. Fish. Mar. Res., 47(2-3): 321-334.

Stevenson, M.R., D. Dias-Brito, J.L. Stech & M. Kampel. 1998. How do cold water biota arrive in a tropical bay near Rio de Janeiro, Brazil? Cont. Shelf Res., 18: 1595-1612.

Stuart, C.T., M.A. Rex & R.J. Etter. 2001. Large scale spatial and temporal patterns of deep-sea benthic species diversity. In: P.A. Tyler (ed.). Ecosystems of the world: ecosystems of deep oceans, Elsevier, Amsterdam, pp. 295-312.

Sumida, P.Y.G. & A.M.S. Pires-Vanin. 1997. Benthic associations of the shelfbreak and upper slope off Ubatuba-SP, south-eastern Brazil. Estuar. Coast. Shelf Sci., 44(6): 779-784.

Valdovinos, C., A.S. Navarrete & P.A. Marquet. 2003. Mollusc species diversity in the southeastern Pacific: why are there more species towards the pole? Ecograph., 26: 139-144.

Valentin, J.L., D.L. André & A.S. Jacob. 1987. Hydrobiology in the Cabo Frio (Brazil) upwelling: two-dimensional structure and variability during a wind cycle. Cont. Shelf Res., 7(1): 77-88.

Vannucci, M. 1964. Zoogeografia marinha do Brasil. Boln. Int. Pesq. Mar. Rio de Janeiro, 7: 113-121.

Vinogradova, N.G. 1997. Zoogeography of the abyssal and hadal zones. Adv. Mar. Biol., 32: 325-387.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon, 21: 213-251.

Willig, M.R., D.M. Kaufman & R.D. Stevens. 2003. Latitudinal gradients of biodiversity: patterns, process, scale, and synthesis. Ann. Rev. Ecol. Evol. Syst., 34: 273-309.

Young, P.S. 1995. New interpretations of South America patterns of barnacle distribution. Crustacean Issues, 10: 229-253.

Zezina, O.N. 1997. Biogeography of the bathyal zone. Adv. Mar. Biol., 32: 389-425.

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