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To cite this article: Paulo Alberto Silva da Costa, Michael Maia Mincarone, Adriana da Costa Braga, Agnaldo Silva Martins, Helena Passeri Lavrado, Manuel Haimovici & Ana Paula da Costa Falcão (2015): Megafaunal communities along a depth gradient on the tropical Brazilian continental margin, *Marine Biology Research*, DOI: [10.1080/17451000.2015.1062521](https://doi.org/10.1080/17451000.2015.1062521)

To link to this article: <http://dx.doi.org/10.1080/17451000.2015.1062521>



Published online: 01 Oct 2015.



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ORIGINAL ARTICLE

Megafaunal communities along a depth gradient on the tropical Brazilian continental margin

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Abstract

The species composition, abundance and diversity patterns of the epibenthic megafauna and fish community from the tropical Brazilian continental margin were analysed based on 42 bottom trawls from the Campos Basin continental shelf and slope. Trawls were collected aboard R/V *Gyre* during autumn 2008 from depths of 13 to 2030 m. Overall, 452 species belonging to five main taxa were identified: teleosts (Actinopterygii) were represented by 196 species, crustaceans by 113 species and echinoderms by 108 species. These three groups contributed 92% to the 452 taxa. Several species (289) were recorded only once or twice, and the species accumulation curves showed no signs of being close to reaching asymptotic values. A tendency of increasing diversity and richness with depth was observed. Analysis of the trawls showed the existence of megafaunal assemblages significantly associated with depth and water mass. The shelf group (13–100 m) had subgroups associated with Coastal Water (CW) and South Atlantic Central Water (SACW). The upper-slope group (376–501 m) was found exclusively under the influence of SACW. The mid- and lower-slope group (978–2030 m) had two subgroups associated with the presence of Antarctic Intermediate Water and North Atlantic Deep Water. The 39 typifying species contributed 90% to the global similarity. Teleosts and squids greatly contributed to the within-group similarity over the shelf, while decapods, echinoderms and galatheids contributed to the upper-slope assemblage. Deep-sea isopods and decapods mostly contributed to the mid- and lower-slope assemblages.

Key words: *Abundance, assemblages, diversity, megafaunal*

Introduction

The community structure and the role of habitat heterogeneity in modulating megafaunal communities are issues poorly addressed in the southwestern Atlantic, particularly on the Brazilian continental margin, where a few studies have investigated invertebrates and fishes independently (Costa et al. 2007; De Léo & Pires-Vanin 2006; Haimovici et al. 1994; Pires 1992; Rossi-Wongtschowski & Paes 1993; Sumida & Pires-Vanin 1997; Vazzoler et al. 1999).

The distribution of megafaunal assemblages along continental margins has mostly been studied from temperate and boreal marine environments. These studies focused primarily on the structure of the assemblages (Cartes & Carrasón 2004; Fanelli et al. 2013; Hecker 1990; Wei & Rowe 2009) or distribution and abundance of a particular major group, such as fishes (Powell et al. 2003), decapod crustaceans (Cartes & Sardà 1993; Wicksten & Packard

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2005), echinoderms (Howell et al. 2002) or holothurians (Billet 1991). In general, these studies have demonstrated that changes in faunal composition with depth reflect an underlying continuum of species replacements with distinct boundaries (Wei et al. 2010). Besides depth, the zonal patterns also correlate with hydrographic gradients (water mass, temperature, oxygen), surface productivity, seafloor characteristics, type and quantity of organic matter and biological interactions (Cartes et al. 2009; Gooday et al. 2010; Sellanes et al. 2009).

The role of habitat heterogeneity in generating and maintaining species diversity on margins is increasingly recognized (Levin et al. 2010). However, results from different studies to identify biodiversity trends with water depth, latitude and ocean productivity are controversial (MacDonald et al. 2010). With fish, and depending on the sampling scale, the highest biomass can be found at the middle slope over ~1000–1300 m (D'Onghia et al. 2004; Haedrich et al. 1980; Hecker 1990; Moranta et al. 1998; Pequegnat 1983; Stefanescu et al. 1993).

Despite being included in one of the least productive ocean margins of the world (Jennerjahn et al. 2010), the tropical Brazilian coast is subjected to the episodic intrusion of the cold and nutrient-rich South Atlantic Central Water (SACW) onto the continental shelf (Franchito et al. 2008; Palóczy et al. 2014), which represents a major enrichment factor for benthic fauna (De Léo & Pires-Vanin 2006; Pires-Vanin et al. 1993; Oliveira-Silva et al. 2005; Quintana et al. 2010). In addition, important autochthonous organic matter that can accumulate in the upper and mid slope sediments highlights the significance of phytodetritus decomposition as an important source of energy for secondary benthic producers at slope depths, as already recognized in other oligotrophic areas (Cartes et al. 2013; Fanelli et al. 2013).

The studied area is located at Campos Basin (115 km²), off southeastern Brazil, between 20 and 23°S. Its most important river is the Paraíba do Sul, with an estimated discharge of 98 m³ s⁻¹. According to the Brazilian Petroleum Agency, approximately 71% (~1.655.436 barrels d⁻¹) of national oil is pumped from this area, mostly by the Brazilian oil and gas company PETROBRAS (ANP 2013). For this reason, there is a continuous demand for environmental data to support engineering projects and evaluate the subsequent environmental risk to the coastal and oceanic ecosystems.

Campos Basin contains both neritic and oceanic communities that are associated with multiple under-sea topographical features, such as submarine canyons (Kowsmann & Costa 1979), deep corals (Arantes et al. 2009), rhodolith beds (Amado-Filho

et al. 2007) and dense beds of the endemic kelp *Laminaria abyssalis* (Yoneshigue-Valentin et al. 2006). These features serve to increase the habitat and resource heterogeneity of this region. The continental shelf (< 200 m) has a mostly sandy bottom, with patches of rubble and terrigenous mud (Figueiredo & Madureira 2004). On its slope, hemipelagic carbonatic mud is the predominant cover between the 200 and 2000 m isobaths. In general, the water column productivity of the area is low (Ekau & Knoppers 1999) due to the oligotrophic surface waters of the Brazil Current, except in areas of upwelling where the primary productivity is instead enhanced (Gaeta et al. 1999). Two semi-permanent frontal eddies have been observed in the Campos Basin, SE of Cabo de São Tomé and S of Cabo Frio (Lorenzetti et al. 2009). The prevailing northeast winds induce a coastal upwelling in the region between Cabo Frio and Cabo de São Tomé, which is more intense during the austral spring and summer, uplifting SACW to surface layers (Ikeda et al. 1974). Antarctic Intermediate Water (AAIW) and North Atlantic Deep Water (NADW) occur in the subthermocline region, between 450 and 1500 m and below 1500 m, respectively (Hogg & Owens 1999).

Few studies have provided information on the Campos Basin fish and invertebrate communities (Costa et al. 2007; Fagundes-Neto & Gaelzer 1991; Pinheiro et al. 2009; Zalmon et al. 2013). In this context, the aim of the current study is to provide a general description of the epibenthic megafauna and fish community found over the shelf and continental slope in an area of significant economic and social importance.

Materials and methods

Sampling

The epibenthic megafauna including fish, cephalopods, crustaceans and echinoderms from the tropical Brazilian continental shelf and slope, at Campos Basin (20–23°S), were sampled with bottom trawls along a depth gradient (13–2030 m). Samples were taken using a 15 m otter trawl with a 3.1 cm stretch mesh aboard the R/V *Gyre* (55 m, 850 HP) in April 2008. The net was towed and opened hydrodynamically by spreading the two 7' × 14' wooden doors, with a single warp cable. The net had a 10.87 m head-rope, a 12.60 m groundrope and 2.08 m of maximum height, resulting in an estimated effective mouth area of 6.3 m².

The resulting data set comprised a total of 42 trawls (Figure 1), 24 over the shelf (13–100 m; 30 minutes on average) and 18 over the slope (376–2030 m; 1:20 h on average). The final distribution

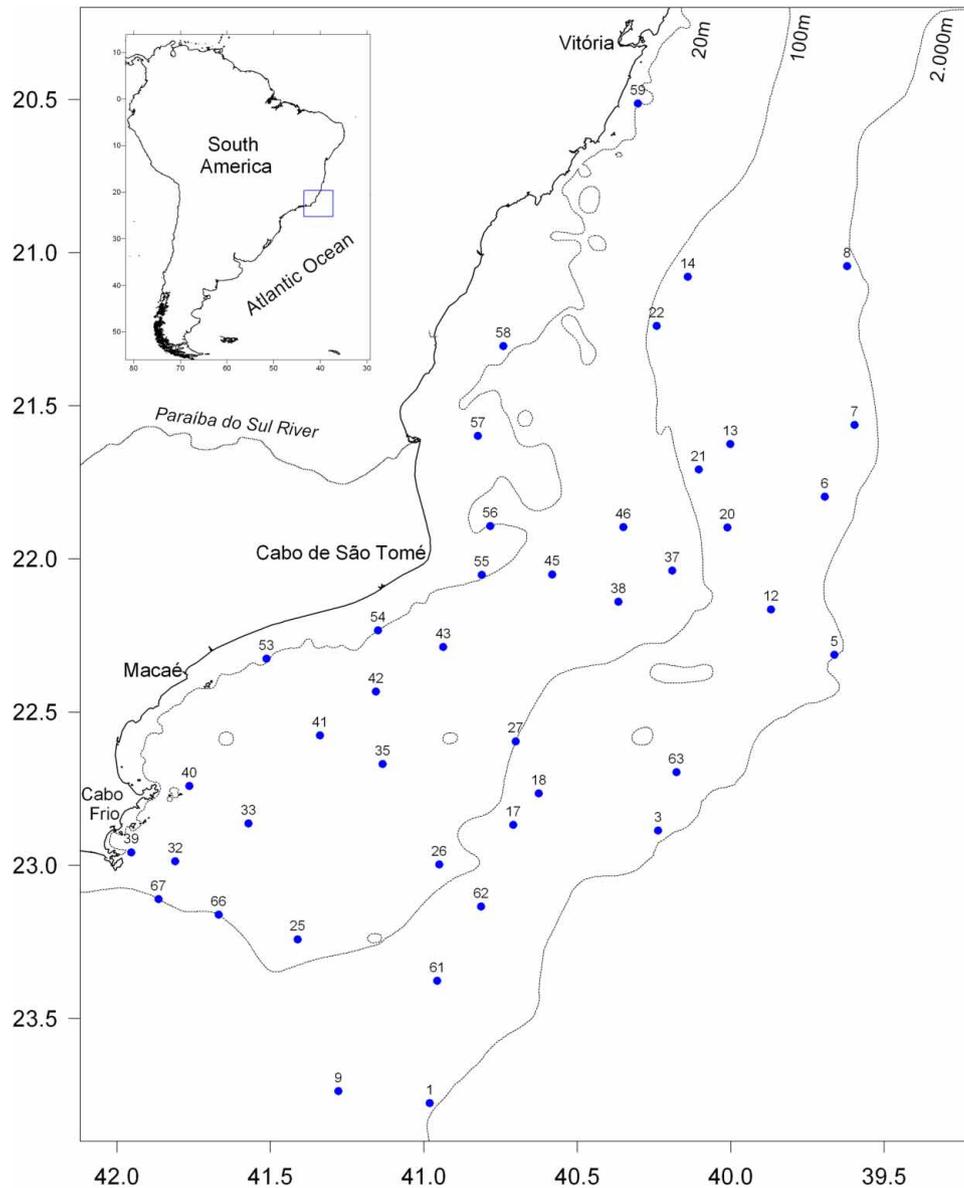


Figure 1. Study area and stations sampled by bottom trawls aboard the R/V *Gyre*.

of trawls was influenced by the presence of kelp beds and hard-bottom and precluded the use of a more randomly or uniformly distributed sampling effort. Differences in duration between shelf and slope trawls was due to logistical constraints and to compensate the natural tendency of rarefaction of numbers in slope populations.

After each trawl fish, cephalopods, crustaceans and echinoderms were sorted, classified, counted and weighed. For large catches, random samples of 20 kg of fish and invertebrates were classified, and the number and weight of each species was recorded. Densities were calculated as the catch per unit area (CPUA), in numbers ($N\ km^{-2}$) and in weight ($kg\ km^{-2}$), and the number of species in each trawl was calculated (species/trawl). The swept area was

estimated by multiplying the distances between the beginning and the end of the hauls, as recorded by the satellite positioning system and the width of the swept area (calculated as $6.3\ m^2$). Conductivity, temperature and density (CTD) casts made immediately before and after each trawl allowed the identification of the bottom water mass. Raw data were post-processed to remove outliers. Most fish and cephalopods were identified at sea by specialists during the trip, while most invertebrates were sorted at sea and later distributed to specialists for identification.

Data analysis

Species richness, Hill's diversity index and Pielou's evenness index were calculated for each trawl

(Magurran 2004). For exploratory analysis of biomass, richness and diversity the data were depth-stratified, using the same slope depth zones as those chosen by Haedrich & Merrett (1988): 'upper slope': 200–750 m, 'middle slope': 751–1500 m, 'lower slope': 1501–2250 m. In multiple comparisons of abundance, richness and diversity by depth gradients and groups of stations we used the non-parametric Kruskal–Wallis one-way analysis of variance.

Rarefaction curves (Hurlbert 1971) were used to assess the expected number of species as a function of sample size. Cluster analysis and non-metric multidimensional scaling (NMDS) were used to visualize the similarity of community structure among samples after the abundances were log-transformed. The similarities between samples in both methods were determined using the Bray–Curtis similarity index.

Diversity indices, ordination and multivariate analysis were performed in PRIMER (version 6) routines (Clarke & Gorley 2006). Since the multi-factor analysis assumptions (i.e. balanced designs, no missing cells) were not met, a one-way permutation test (PERMANOVA+) for multivariate data was used to test the effect of the factors 'depth-range' and 'water mass' on the similarity matrix (Anderson et al. 2008). The taxa typifying the groups were identified by the SIMPER routine (Clarke 1993).

Results

Water mass distribution in the study area

Five main hydrological domains roughly corresponding to depth intervals were observed in the study area along the cruise line (Figure 2). Up to the 50 m isobath, mixing processes of river discharge, upwelled SACW and residual shelf waters form the Coastal Water (CW, 35.5–36.0 ups, >20–23°C), present at 10 stations. The upwelled SACW had a

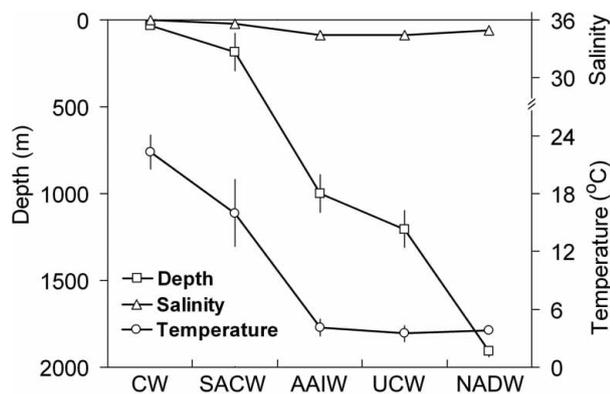


Figure 2. Mean (\pm SE) bottom-water temperature and salinity according to depth for the water masses identified at the study area.

wide range of temperature and salinity (34.6–36.0 ups, 6–20°C) and corresponded to nine stations between 50 and 100 m, and all five upper slope stations between 300 and 500 m. AAIW (34.37–34.4 ups, 3.5–4.2°C) was found at six stations between 1000 and 1200 m. Upper Circumpolar Waters (UCW), devoid of a well-defined thermohaline signature and characterized by a minimum in dissolved oxygen concentration and relative maxima in phosphate and nitrate, extended within 1200–1300 m. NADW (34.93–34.97 ups, 3.6–3.8°C) occurred below the UCW at six stations.

Rarefaction and diversity

The total catch in numbers was 31,873, consisting of bony fishes (14,827), crustaceans (9348), echinoderms (6258), cephalopods (992) and elasmobranchs (448). The biomass of fish and cephalopods was 758 kg, while that of echinoderms and crustaceans was 131 kg. Teleosts (Actinopterygii) were represented by 196 species, crustaceans by 113 species and echinoderms by 108 species. These three groups contributed 92% to the 452 taxa. Elasmobranchs (Chondrichthyes) and cephalopods were represented by only 24 and 11 species, respectively. These figures underestimate the total invertebrate richness, because several other major taxa were excluded from this study (e.g. molluscs other than cephalopods, corals, Bryozoa, Hydrozoa). Echinoderms had a high proportion of unnamed taxa (43%). The fauna was characterized by a high apparent rarity: of the 452 species, 200 (44%) were recorded in a single sample. Species caught in two samples made up another 17% (79 species), while only 12 species were found in 10 or more samples. The high rarity and expected high faunal richness was emphasized in species rarefaction curves that did not appear to approach their asymptotes (Figure 3). The highest megafaunal richness occurred between 50 and 100 m (142 species). The expected richness between 13 and 50 m (113 species) was similar to that found between 1000 and 1200 m (108) and in the deeper areas between 1900 and 2000 m (106). The lowest expected richness found in the 300–500 m range (90) was probably affected by the low number of samples (only five).

Abundance and biomass

Sampling effort between 300 and 500 m was greatly reduced due to the presence of rodolith beds and hard-bottoms. Nevertheless, the mean biomass ($804 \pm 184 \text{ kg km}^{-2}$) and density ($20,191 \pm 4583 \text{ kg km}^{-2}$) recorded at these depths were significantly ($P < 0.05$) higher (Table I). The second highest

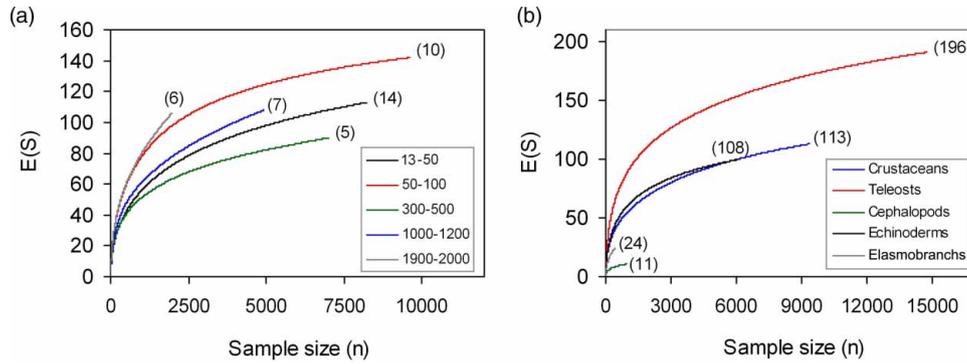


Figure 3. Rarefaction curves of the expected number of species $E(S)$ as a function of the sample size according to depth interval (a) and major taxonomic grouping (b). Numbers in parentheses indicate the number of samples by depth interval (a) and the total number of species by major taxonomic grouping (b).

Table I. Distribution of sampling effort, mean (\pm SE) biomass, density, richness and diversity by depth intervals.

Depth (m)	13–50	50–100	300–500	1000–1200	1900–2000
Samples	14	10	5	7	6
Hour trawling (h)	6.50	5.80	2.16	8.61	10.0
Swept area (km ²)	0.22	0.18	0.06	0.23	0.28
Biomass (kg km ⁻²)	734 \pm 191	417 \pm 201	804 \pm 184	267 \pm 90	53 \pm 13
Density (N km ⁻²)	12500 \pm 3323	7951 \pm 2421	20191 \pm 4583	10219 \pm 3519	4733 \pm 976
Species richness (S)	113	142	90	108	106
Diversity (H')	5.7 \pm 3	9.0 \pm 3	7.8 \pm 2	9.2 \pm 5	14.2 \pm 6
Evenness (J) ^c	0.50 \pm 0.2	0.65 \pm 0.1	0.58 \pm 0.1	0.62 \pm 0.2	0.69 \pm 0.1
Species hour ⁻¹	54 \pm 21	52 \pm 16	78 \pm 12	31 \pm 15	25 \pm 8

megafaunal biomass, between 25 and 50 m (734 \pm 191 kg km⁻²), was mostly attributable to elasmobranchs and teleosts (Figure 4), particularly the guitarfish *Zapteryx brevirostris* (Müller & Henle, 1841) (638 \pm 868 kg km⁻²), the flying gurnard *Dactylopterus volitans* (Linnaeus, 1758) (361 \pm 553 kg km⁻²) and the banded croaker *Paralonchurus brasiliensis* (Steindachner, 1875) (247 \pm 445 kg km⁻²). The abundance of cephalopods was very low and significantly different with depth ($P = 0.003$). Two species of coastal myopsid squids *Doryteuthis sanpaulensis* (Brakoniecki, 1984) and *Doryteuthis plei* (Blainville, 1823) mostly accounted for greater catches at 13–50 m (42 \pm 10 kg km⁻²).

Invertebrate biomass changed parabolically with depth (Figure 4), and species that most contributed to the 300–500 m maxima included the echinoid *Stylocidaris lineata* Morentsen, 1910 (576 \pm 357 kg km⁻²), decapod crustaceans (*Penaeopsis serrata* Bate, 1881: 154 \pm 212 kg km⁻²; *Acanthocarpus alexandri* Stimpson, 1871: 132 \pm 118 kg km⁻²) and teleosts (the longnose greeneye fish *Parasudis truculenta* (Goode & Bean, 1896): 266 \pm 198 kg km⁻²; the argentine hake *Merluccius hubbsi* Marini, 1933: 203 \pm 185 kg km⁻²).

Assemblage structure

Cluster analysis identified three main groups of trawl stations that were associated with the depth ranges (Figure 5). The shelf group included 23 trawls between 13 and 100 m, the upper-slope group included five trawls between 376 and 501 m and the mid- and lower slope group included two subgroups (both with six stations), one between 978 and 1200 m and another in deeper waters (1975–2030 m).

Although 72 species were used to define the overall assemblages (Figure 6), 39 contributed 90% to the global similarity. Among these, a set of 10 species occurred in more than one assemblage. Considering these three assemblages, teleosts greatly contributed to the within group similarity on the shelf (63%) and upper-slope (38%) assemblages. Non-galatheid decapods (36%), followed by echinoids (8%) and galatheids (6%) contributed mostly to the upper-slope internal similarity. In the mid- and lower-slope groups, isopods contributed mostly (39%) to the similarity while fish and decapods contributed with comparable levels (19%).

Using the same similarity matrix, the ordination of the samples in the NMDS scaling revealed four subgroups that can also be interpreted with respect to the

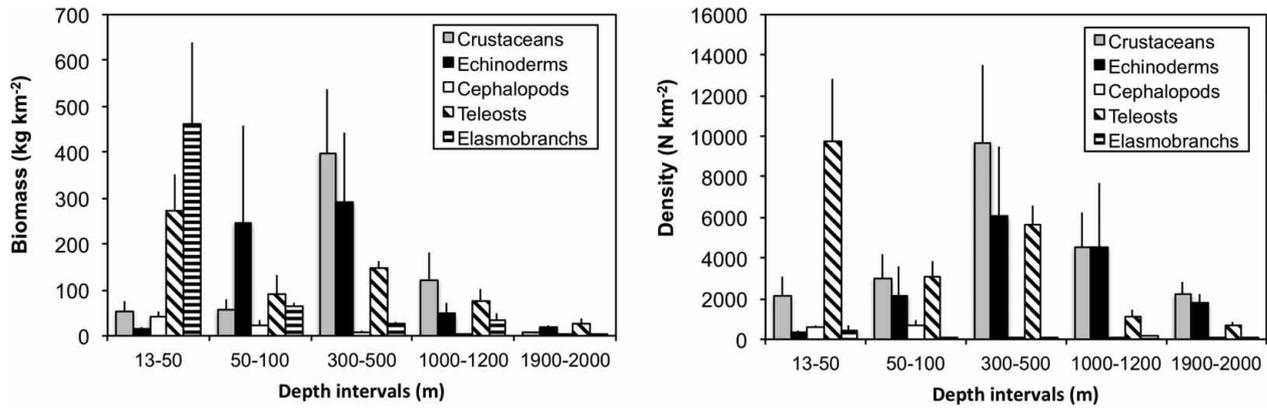


Figure 4. Mean biomass and density (\pm SE) in major taxonomic groupings according to depth intervals.

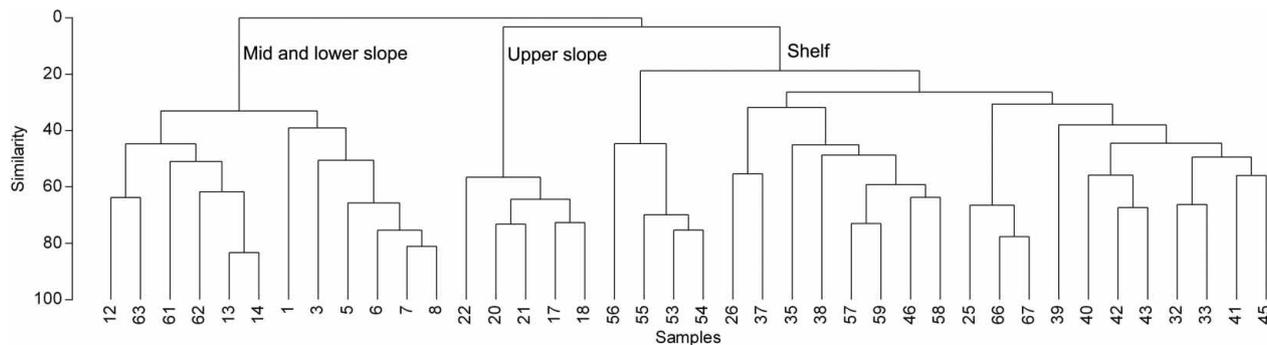


Figure 5. Cluster analysis constructed using the Bray-Curtis similarity matrix with square root transformation of abundance data in the samples. Similarity reported as percentages.

water mass (Figure 7). The shelf group had a subgroup associated with high temperature coastal waters, CW (20.3–25.4°C), and another with the upwelled SACW (16.2–19.7°C). The upper-slope group was exclusively under the influence of the subtropical SACW (9.0–12.8°C). The mid-slope samples were associated with the presence of AAIW (3.8–4.2°C) while the lower-slope trawls were associated with NADW (3.5–3.7°C).

One-way PERMANOVA pairwise comparison indicated highly significant values for the factors ‘depth-range’ and ‘water-mass’, indicating that the assemblages identified were all significantly different from each other (Table II). The episodic intrusion of deeper SACW onto the continental shelf (<100 m) creates an assemblage significantly different ($P = 0.001$) from that observed only under the influence of coastal waters (CW). At mid- and lower-slope depths, the assemblages also differ significantly ($P = 0.004$) according to the presence of water masses (AAIW or NADW).

The similarity percentage procedure (SIMPER) was applied to identify those species that contribute most to the observed differences between shelf and slope samples under the influence of different water

masses (Table III). The flying gurnard fish *Dactylopterus volitans* and the squid *Doryteuthis plei* were the top contributing species to the within-group similarity on the shelf, either under the influence of warm shelf waters (CW) or the upwelled SACW. Despite many species co-occurring in both assemblages showing some degree of a continuous distribution, the highest densities were observed under the influence of a specific hydrological domain (CW or SACW). The upper-slope assemblage was exclusively under the influence of SACW and the structuring species were the echinoid *Stylocidaris lineata*, the pink speckled shrimp *Penaeopsis serrata* and the decapod *Parapenaeus politus* (Smith, 1881).

Under the influence of AAIW, the mid- and lower-slope assemblage was dominated by the deep-sea penaeid *Benthescymus bartletti* Smith, 1882, the endemic deep-sea eel *Synphobranchius calvus* Melo, 2007 and the galatheid *Munida microphthalmia* A. Milne Edwards, 1880, while the serolid isopod *Acutiserolis coineauae* Albuquerque & Costa, 2008, the caridean shrimp *Nematocarcinus exilis* (Spence Bate, 1888) and the ophiuroid *Ophiomusium eburneum* Lyman, 1869 contributed most to the within-group similarity under the influence of NADW.

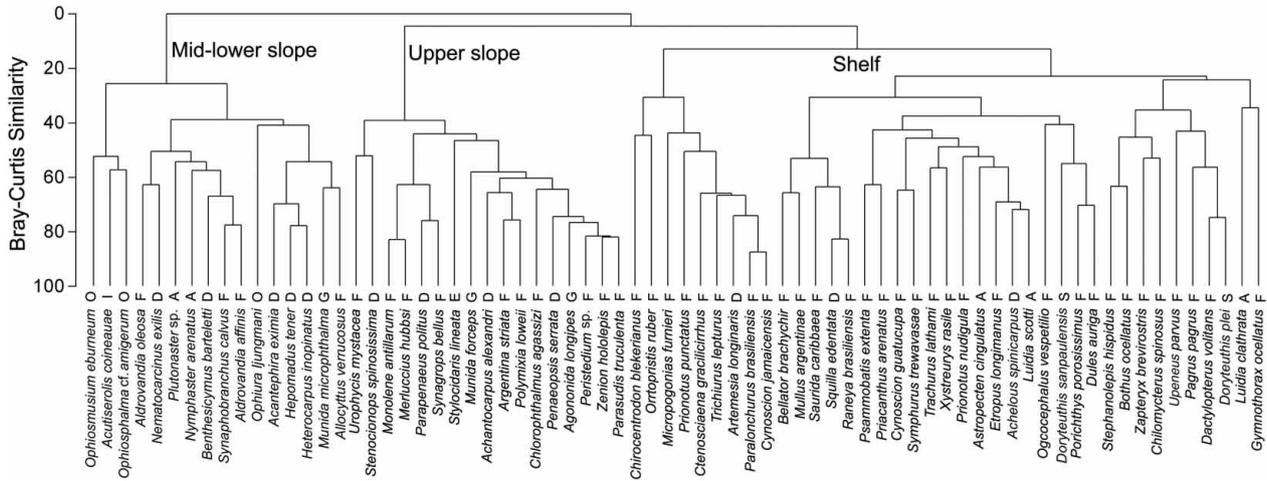


Figure 6. Dendrogram of the 72 most abundant and frequent species used to define megafaunal assemblages in the study area. Codes for the main taxonomic groupings as follows: A – Asteroids; D – Decapod crustaceans (excluding galatheids); E – Echinoids; F – Fish; G – Galatheids; I – Isopods; O – Ophiuroids; S – Squids.

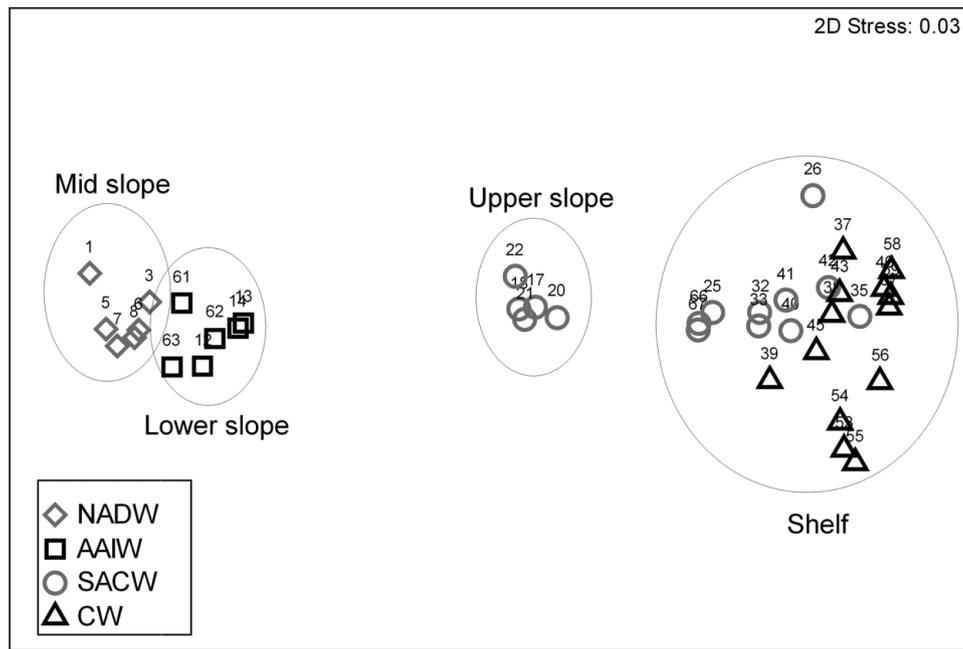


Figure 7. Ordination of megafaunal assemblages according to depth gradient and water masses at the study area.

Overall, each of these two species groups contributed 67% and 59%, respectively. The contribution of ophiuroids to the within-group similarity in the mid- and lower-slope assemblages was strengthened by the presence of NADW.

Discussion

This study has resulted in a description of the local assemblages of epibenthic megafauna (cephalopods, crustaceans, echinoderms) and fish community along a depth gradient of the tropical Brazilian

continental margin (20–23°S, Campos Basin). This issue is poorly addressed in the southwestern Atlantic, and particularly on the Brazilian continental margin; the few studies developed have investigated invertebrates and fishes separately (Costa et al. 2007; De Léo & Pires-Vanin 2006; Haimovici et al. 1994; Pires 1992; Rossi-Wongtschowski & Paes 1993; Sumida & Pires-Vanin 1997; Vazzoler et al. 1999).

Three sample groups were identified in the studied area, but depth boundaries for each assemblage are conditional on the sampling limitations, since there is a ~270 m gap between the shelf (maximum depth

Table II. Results of one-way PERMANOVA pairwise comparisons for factors 'depth-range' and 'water-mass'.

Variable	<i>t</i>	<i>P</i> (perm)
<i>Depth range</i>		
Shelf vs. Upper slope	3.381	0.001
Shelf vs. Mid-lower slope	4.482	0.001
Upper slope vs. Mid-lower slope	4.267	0.001
<i>Water mass</i>		
CW vs. SACW	2.263	0.001
CW vs. AAIW	3.696	0.001
CW vs. NADW	3.747	0.001
SACW vs. AAIW	3.158	0.002
SACW vs. NADW	3.208	0.001
AAIW vs. NADW	2.576	0.004

sampled: 100 m) and the upper slope (minimum depth sampled: 376 m). On the inner shelf, these gaps were caused by the presence of dense kelp beds, while rodoliths and deep corals precluded the sampling of some trawls on the upper slope. Nevertheless, considering that this is the first study of the area to describe marine communities, the boundaries found among assemblages might be better defined in future analyses, filling the depth gaps in our sampling.

Globally, depth has been confirmed to be the main structuring factor of megafaunal assemblages (Gordon et al. 1995; Hecker 1990; Stefanescu et al. 1993). However, it is often argued that the distribution of marine organisms may respond not only to depth but also to a combination of depth-related factors such as the water mass characteristics (temperature, salinity and dissolved oxygen), bottom type and food availability (Cartes et al. 2004, Williams et al. 2010). Our results agree with Fanelli et al. (2013) among many others, since water masses seem to determine the structure of megafaunal assemblages. Two groups with distinct species assemblages and rather different taxon numbers were identified both on the shelf and on the mid and lower slope. The influence of differing water masses at similar depths confirms a typical pattern for deep-sea settings of small-scale variability in hydrographic factors contributing to an uneven distribution of fauna (Jumars & Eckman 1983; Cartes et al. 2014).

The abundance of fish and cephalopods decreased from the shelf towards the mid and lower slope. These results are in agreement with Powell et al. (2003), but differ from those obtained on continental margins elsewhere, where the peak abundance and biomass of fishes were found at 1200 m (Cartes & Sardà 1992; Haedrich et al. 1980; Hecker 1990; Pequegnat 1983) and 1000–1300 m (Cartes et al. 2013; Fanelli et al. 2013). These differences might be explained by sampling limitations, since depth intervals and gear selectivity differ greatly between studies,

making direct numerical comparisons troublesome. When commercial nets with larger vertical openings were used to sample a neighbouring area (11–22°S) to a depth of 2137 m, typical deep-sea large-sized benthopelagic fish (Synphobranchidae, Macrouridae, Moridae, Ophidiidae, Alepocephalidae) were caught in abundance on the mid (922–1293 m) and lower (1545–2137 m) slopes (Costa et al. 2007).

The composition of typifying species within assemblages changed with depth. Fishes were particularly important in the structure of the shelf and upper slope assemblages, while crustaceans and echinoderms more than doubled from upper to mid and lower slope. Among the invertebrates, top carnivore epifaunal species such as *Achelous spinicarpus* Stimpson, 1871 were dominant on the shelf. Decapod biomass was highest on the upper slope (400–500 m), which is in accordance with results from the Mid-Atlantic Bight (Wenner & Boesch 1979), off Nova Scotia (Markle et al. 1988), the deep Catalan Sea (Cartes & Sardà 1992) and the Balearic Basin slope (Cartes et al. 2013; Fanelli et al. 2013). The dominance of deposit-feeding species (*Stylocidaris lineata*, *Penaeopsis serrata*, *Agononida longipes* (A. Milne Edwards, 1880), *Parapenaeus politus*) on the upper slope could possibly result from the accumulation of OM at these depths, since the highest concentrations of OM in the area are found between 400 and 1000 m (Oliveira et al. 2013). Fanelli et al. (2013) explained most of the composition of fish and decapod species over slopes of the Balearic Basin by the accumulation and quality of the organic matter in the sediment. On the Campos Basin mid and lower slope an increasing importance of the scavengers *Nematocarcinus exilis*, *Benthesicymus bartletti*, *Ophiosphalma* cf. *armigerum* (Lyman, 1878), *Ophiomusium eburneum* Lyman, 1869, and *Nymphaster arenatus* (Perrier, 1881) was evident. *Nematocarcinus exilis* and *Acantheephyra eximia* Smith, 1884 were among the most abundant crustaceans on the middle-lower slope of the deep Catalan Sea (Cartes & Sardà 1992), while *Benthesicymus* spp. are frequently key components of the deep-sea Gulf of Mexico crustacean assemblage (Escobar-Briones et al. 2008). Our results of ophiuroid prevalence on mid and lower slope depths confirmed previous local results (Frensel et al. 2010) and a pattern already stated in several bathyal regions (Tyler 1980). Nevertheless, our data set might have underestimated the contribution of infaunal or semi-infaunal families, since to efficiently sample an entire ophiuroid assemblage a combination of methods is recommended (Summers & Nybakken 2000). *Ophiosphalma* cf. *armigerum* and *Ophiomusium eburneum*, the dominant ophiuroid species in the studied area, are epifaunal and more motile (Summers & Nybakken 2000), possibly

Table III. Simper analysis showing discriminating species between water-mass station groups as indicated in NMDS ordination. Density ($N\ km^{-2}$); Sim (individual contribution to within-group similarity). Codes for main taxonomic groupings as follows: A, Asterooids; D, Decapod crustaceans (excluding galatheids); E, Echinoids; F, Fish; G, Galatheids; I, Isopods; O, Ophiuroids; S, Squids.

Species	Code	Shelf				Upper slope		Mid and lower slope			
		CW		SACW		SACW		AAIW		NADW	
		Density	Sim	Density	Sim	Density	Sim	Density	Sim	Density	Sim
<i>Dactylopterus volitans</i> (Linnaeus, 1758)	F	800.0	63.0	206.0	13.8	–	–	–	–	–	–
<i>Doryteuthis plei</i> (Blainville, 1823)	S	50.9	19.0	39.9	9.6	–	–	–	–	–	–
<i>Artemesia longinaris</i> Bate, 1888	D	238.3	4.5	0	0	–	–	–	–	–	–
<i>Ctenosciaena gracilicirrus</i> (Metzelaar, 1919)	F	35.7	1.9	0	0	–	–	–	–	–	–
<i>Chilomycterus spinosus</i> (Linnaeus, 1758)	F	18.5	2.0	4.1	1.0	–	–	–	–	–	–
<i>Achelous spinicarpus</i> Stimpson, 1871	D	11.4	1.2	18.2	1.9	–	–	–	–	–	–
<i>Pagrus pagrus</i> (Linnaeus, 1758)	F	23.3	1.4	46.5	5.2	–	–	–	–	–	–
<i>Etropus longimanus</i> Norman, 1933	F	6.9	1.4	23.3	2.2	–	–	–	–	–	–
<i>Prionotus nudigula</i> Ginsburg, 1950	F	2.3	0.9	30.5	1.1	–	–	–	–	–	–
<i>Zapteryx brevirostris</i> (Müller & Henle, 1841)	F	7.8	2.4	35.5	1.2	–	–	–	–	–	–
<i>Trichiurus lepturus</i> Linnaeus, 1758	F	28.1	0.1	0.07	0.9	–	–	–	–	–	–
<i>Doryteuthis sanpaulensis</i> (Brakoniecki, 1984)	S	11.0	0.1	22.7	3.1	–	–	–	–	–	–
<i>Trachurus lathami</i> Nichols, 1920	F	3.9	0.1	22.0	1.7	–	–	–	–	–	–
<i>Parasudis triculenta</i> (Goode & Bean, 1896)	F	–	–	–	–	41.9	2.6	–	–	–	–
<i>Bellator brachyhir</i> (Regan, 1914)	F	–	–	–	–	49.2	2.0	–	–	–	–
<i>Parapenaeus politus</i> (Smith, 1881)	D	–	–	–	–	104.0	7.3	–	–	–	–
<i>Synagrops bellus</i> (Goode & Bean, 1896)	F	–	–	–	–	38.8	4.2	–	–	–	–
<i>Zenion hololepis</i> (Goode & Bean, 1896)	F	–	–	–	–	55.9	4.0	–	–	–	–
<i>Monolene antillarum</i> Norman, 1933	F	–	–	–	–	19.3	2.8	–	–	–	–
<i>Merluccius hubbsi</i> Marini, 1933	F	–	–	–	–	18.1	2.6	–	–	–	–
<i>Stylocidaris lineata</i> Mortensen, 1910	E	–	–	–	–	330.7	11.1	–	–	–	–
<i>Agononida longipes</i> (A. Milne Edwards, 1880)	G	–	–	–	–	112.1	1.6	–	–	–	–
<i>Luïdia ludwigi scotti</i> Bell, 1917	A	–	–	–	–	8.1	1.5	–	–	–	–
<i>Peristedion</i> sp.	F	–	–	–	–	38.1	1.4	–	–	–	–
<i>Stephanolepis hispidus</i> (Linnaeus, 1766)	F	–	–	–	–	10.7	1.3	–	–	–	–
<i>Mullus argentinae</i> Hubbs & Marini, 1933	F	–	–	–	–	23.9	1.3	–	–	–	–
<i>Penaeopsis serrata</i> Spence Bate, 1881	D	–	–	–	–	216.8	9.0	0.5	0.1	–	–
<i>Munida microphthalmala</i> A. Milne Edwards, 1880	G	–	–	–	–	–	–	37.5	12.9	–	–
<i>Allocyttus verrucosus</i> (Gilchrist, 1906)	F	–	–	–	–	–	–	17.5	8.3	–	–
<i>Benthesicymus bartletti</i> Smith, 1882	D	–	–	–	–	–	–	216.4	37.6	5.5	6.8
<i>Synaphobranchus calvus</i> Melo, 2007	F	–	–	–	–	–	–	18.7	16.6	2.3	1.0
<i>Nymphaster arenatus</i> (Perrier, 1881)	A	–	–	–	–	–	–	14.3	4.8	3.0	4.6
<i>Aldrovandia affinis</i> (Günther, 1877)	F	–	–	–	–	–	–	12.7	4.5	4.9	2.1
<i>Acanthephyra eximia</i> Smith, 1884	D	–	–	–	–	–	–	19.5	3.3	0.1	0.1
<i>Acutiserolis coineauae</i> Albuquerque & Costa, 2008	I	–	–	–	–	–	–	19.5	3.4	77.2	51.6
<i>Ophiophalma</i> cf. <i>armigerum</i> (Lyman, 1878)	O	–	–	–	–	–	–	0.2	–	16.7	7.2
<i>Nematocarcinus exilis</i> (Bate, 1888)	D	–	–	–	–	–	–	–	–	6.4	8.6
<i>Ophiomusium eburneum</i> Lyman, 1869	O	–	–	–	–	–	–	–	–	31.9	8.4
<i>Aldrovandia oleosa</i> Sulak, 1977	F	–	–	–	–	–	–	–	–	6.4	6.6

responding quickly to spatially and seasonally patchy food input (Iken et al. 2010). In a contiguous basin, *Ophiomusium anaelsiae* Tommasi & Abreu, 1974 contributed 72% to the fauna collected by dredging the coral rubble and sediments from pockmarks (Sumida et al. 2004).

Depth and habitat are known to explain a large proportion of variability in fish assemblages (Fitzpatrick et al. 2012), and the presence of a hard substratum is known to significantly increase local biodiversity (Wienberg et al. 2008), which is reflected in an inflected species-accumulation curve and elevated

H' diversity and richness values (MacDonald et al. 2010). Despite hard substrates such as rhodoliths and deep corals being well represented on the shelf break (70–150 m) and slope (550–1200 m), respectively (Henriques et al. 2012), these habitats were intentionally avoided during our trawling survey due to the risk of damaging both the biocoenosis and the gear itself. As a consequence, possibly a great bulk of shallow water biodiversity has remained unsampled, since rhodoliths form extensive beds along the shelf. This possibility, which could explain our pattern of increasing diversity with

water depth, is reinforced by the poor representation in our samples of fish families strongly associated with rhodolith beds, such as Carangidae, Balistidae, Tetraodontidae and Serranidae (Fitzpatrick et al. 2012).

Many of the 452 taxa identified in this study were rare (64%) and were found in only one or two of the 42 trawls performed. This pattern resembles that found in Australian waters either for megafauna between 100 and 1100 m (Williams et al. 2010) or demersal fishes from ~200 to 1500 m (Williams et al. 2001). Grassle & Maciolek (1992) suggested that most abundant species in deep-sea communities represent less than 10% of the fauna. This is in contrast to shallow water environments where common species represent more than 30% of the species present. Apparent rarity is a common finding in megafaunal studies, but most studies do not include the replicate sampling that would be necessary to distinguish rarity from sampling efficiency or patchiness (Williams et al. 2010). Despite being concentrated on the Campos Basin, much of the information on the deep Brazilian macrofauna and megafauna (Frensel et al. 2010) and its benthic biodiversity has probably still not been thoroughly sampled, as the species-accumulation curves appear not to approach their asymptotes. For this reason, studies using multiple sampling methods to assess the megafauna would be important, as it is highly probable that further sampling will reveal additional species and more precise zonation patterns.

Acknowledgements

The authors are grateful to the following taxonomists: Marcelo Rodrigues de Carvalho (Elasmobranchii), Dominique Didier (Holocephali), Fabio Di Dario (Clupeiformes), Marcelo Roberto Souto de Melo (Gadiformes), Luciano Gomes Fischer (Perciformes), Rodrigo Leão de Moura (Tetraodontidae), Celso Rodrigues Abreu Junior (Galatheidae), Elaine Albuquerque (Isopoda), Fernando Mantelatto (Paguridae), Ingrid Ávila da Costa (Serolidae), Irene de Azevedo Cardoso (Penaeidae), Joel Braga (Stomatopoda), Lucia de Siqueira Campos (Ophiuroidea and Holothuroidea), Renato Ventura (Crinoidea, Echinoidea and Asteroidea), and Valéria Veloso (Brachyura). We also thank two anonymous reviewers for providing helpful comments and suggestions.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study is part of a larger project entitled 'HABITATS – Campos Basin Environmental Heterogeneity' conducted by 'CENPES/PETROBRAS'. PASC (302.392/2010-6), ASM and MH (309282/2011-0) are supported by CNPq. Financial support to MMM provided by FAPERJ (E-26/110.118/2010).

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Editorial responsibility: Javier Sellanes