Temporal and spatial variation of rocky shores intertidal benthic communities in Southeast Brazil

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ABSTRACT. The relationships between environmental factors and temporal and spatial variations of benthic communities of three rocky shores of the state of Espírito Santo, Southeast Brazil, were studied. Sampling was conducted every three months, from August 2006 to May 2007, using intersection points. *Chthamalus bisinuatus* (Pilsbry, 1916) (Crustacea) and *Brachidontes* spp. (Mollusca) were the most abundant taxa, occupying the upper level of the intertidal zone of the rocky shore. The species richness was higher at the lower levels. The invasive species *Isognomon bicolor* (C. B. Adams, 1845) (Mollusca) occurred at low densities in the studied areas. The clustering analysis dendrogram indicated a separation of communities based on exposed and sheltered areas. According to the variance analyses, the communities were significantly different among the studied areas and seasons. The extent of wave exposure and shore slope influenced the species variability. The Setibão site showed the highest diversity and richness, most likely due to greater wave exposure. The communities showed greater variation in the lower levels where environmental conditions were less severe, relative to the other levels.

KEYWORDS. Midlittoral, wave exposure, benthos, Espírito Santo

RESUMO. Variação espaço-temporal das comunidades bentônicas do entremarés de costões rochosos no Sudeste do Brasil. Foram realizadas amostragens das comunidades bentônicas de médiolitoral em três costões rochosos do estado do Espírito Santo com o objetivo de estudar a variação espaço-temporal, relacionando com os fatores abióticos. Efetuaram-se coletas trimestrais entre agosto de 2006 e maio de 2007, utilizando o método de pontos de interseção. *Chthamalus bisinuatus* Pilsbry, 1916 (Crustacea) e *Brachidontes* spp. (Mollusca) foram os táxons mais abundantes, ocupando os níveis superiores da zona entremarés dos costões. Nas zonas inferiores ocorreu um maior número de espécies. A espécie invasora *Isognomon bicolor* (C.B. Adams, 1845) (Mollusca) ocorreu em baixa cobertura nas áreas estudadas. O dendrograma indicou a separação das amostras das áreas expostas e abrigadas. Segundo os resultados das análises de variância, as comunidades foram significativamente diferentes entre as áreas e as estações do ano. O grau de exposição às ondas e a inclinação do costão influenciaram a variabilidade de espécies. Setibão apresentou os maiores índices de diversidade e de riqueza, provavelmente devido à maior exposição às ondas. As comunidades apresentaram maiores variações nos níveis inferiores, onde as condições ambientais são menos estressantes em relação aos outros níveis.

PALAVRAS-CHAVE. Médio litoral, exposição às ondas, bentos, Espírito Santo.

Intertidal rocky shores are heterogeneous environments that support a wide variety of organisms (Araújo *et al.*, 2005). These organisms are distributed in horizontal zones in which species are more abundant when environmental conditions favor their survival (Coutinho, 2002). The observation of these patterns has led to the development of various models of vertical zonation (Araújo *et al.*, 2005). Although zonation is the main theme in many discussions of community structure, zonation alone does not explain the entire variability in distribution patterns of rocky shore populations (Menconi *et al.*, 1999).

Several physical variables (e.g., variations in the tidal levels, extent of wave exposure, slope of the shore and substrate heterogeneity) and biological parameters (e.g., predation, herbivory and competition) can influence the distribution of organisms in the intertidal zone (Little & Kitching, 1996; Raffaelli & Hawkins, 1999; Benedetti-Cecchi *et al.*, 2000b; Dethier & Schoch, 2005; Murray *et al.*, 2006). These factors determine the non-homogeneous spatial distribution of intertidal communities. The relative importance of these factors is difficult to define due to the high number of potential factors and the interactions among them (Little & Kitching, 1996). Thus, all of these factors may create locally variable communities, representing differences on scales of centimeters to kilometers (Schoch & Dethier, 1996).

Rocky shores in Brazil are present almost exclusively in the south and southeast regions (Coutinho, 2002), and many studies have described the vertical distribution of benthic fauna and flora of these environments (Oliveira-Filho & Mayal, 1976; Széchy & Paula, 2000; Coutinho, 2002; Oigman-Pszczol *et al.*, 2004; Masi *et al.*, 2009). Although there are many studies on the benthic communities in Espírito Santo (Sá & Nalesso, 2000; Nassar *et al.*, 2001; Nalesso *et al.*, 2005; Costa & Nalesso, 2006; Floeter *et al.*, 2007), few reports have focused on the vertical distribution of the intertidal faunal and floral communities of the region.

Rocky shore organisms are subject to a variety of stresses, such as increasing air exposure, differences in the wave action and topography of the shore (Crowe *et al.*, 2000), and anthropogenic impacts originating both from the land and sea, such as global changes in temperature, sea-level rise, an increased frequency of storms, changes in sediment loading (Thompson *et al.*, 2002), and the introduction of exotic species (Crowe *et al.*, 2000). Increases in temperature can negatively impact the performance and survival of marine organisms and drive important changes at the community level (Harley *et al.*, 2006). The varied impacts on rocky shore environments further increase the importance of obtaining knowledge and monitoring native communities. The invasive bivalve *Isognomon bicolor* (C.B. Adams, 1845) is widely distributed on the Brazilian coast (DOMANESCHI & MARTINS, 2002; FERNANDES *et al.*, 2004; BREVES-RAMOS *et al.*, 2010; ZAMPROGNO *et al.*, 2010). This study aimed to describe and compare the seasonal variations in the midlittoral benthic communities of three rocky shores with different degrees of shore slope and wave exposure. The hypothesis of this study was that benthic communities will vary due to differences in wave action between exposed and sheltered shores.

MATERIALS AND METHODS

Study sites. This study was conducted in the coastal zone of the state of Espírito Santo, southeast Brazil. This area is characterized by crystalline Precambrian rocks in contact with Quaternary deposits (MARTIN *et al.*, 1996).

The winds are predominantly from the northeast and southeast. The northeast winds occur with greater frequency and are associated with the winds that blow during most of the year. In contrast, the southeast winds are more intense and associated with cold fronts that occur regularly at the littoral zone (ALBINO *et al.*, 2001).

Samples were collected within a horizontal of 18 meters from each of three rocky shores at the three different beaches (Fig. 1): Costa beach, located near Vitória Bay and the Vitória port complex area (20°19'44"S, 40°16'20"N), has a greater population density than the other areas; Setibão beach, which is located 37 km from Costa beach (20°38'06"S, 40°25'28"N); and Ubu beach, located approximately 62 km from Costa beach near the port of Ubu (20°48'20"S, 40°35'15"N).

Sampling design. Sampling was performed quarterly at low tide at each shore between August 2006 and May 2007.

The topographic profile was obtained using the method of MUEHE (2002) employing a topographic level, graduated sight and a metric tape. Distances and differences between the ranges of two points in the profile were measured. Profiles were plotted using a compass. The profiling process consisted of adding the level shifts from the beginning of the profile to the maximum retreat of the wave during the survey. Using these data, it was possible to obtain the degree of shore inclination.

The characterization of the extent of exposure to waves was obtained indirectly according to LITTLE & KITCHING (1996) based on the observation of the direction of the prevailing winds and incident waves on the exposed face of the shore. Sites located in bays were sheltered against winds and currents and were considered protected sites, whereas sites that were directly facing the wind and incident waves were considered exposed, as suggested by SZÉCHY & PAULA (2000).

The non-destructive method of determining percentage cover described by SUTHERLAND (1974) was used to estimate the relative abundance of organisms. Within a horizontal extension of 18 meters

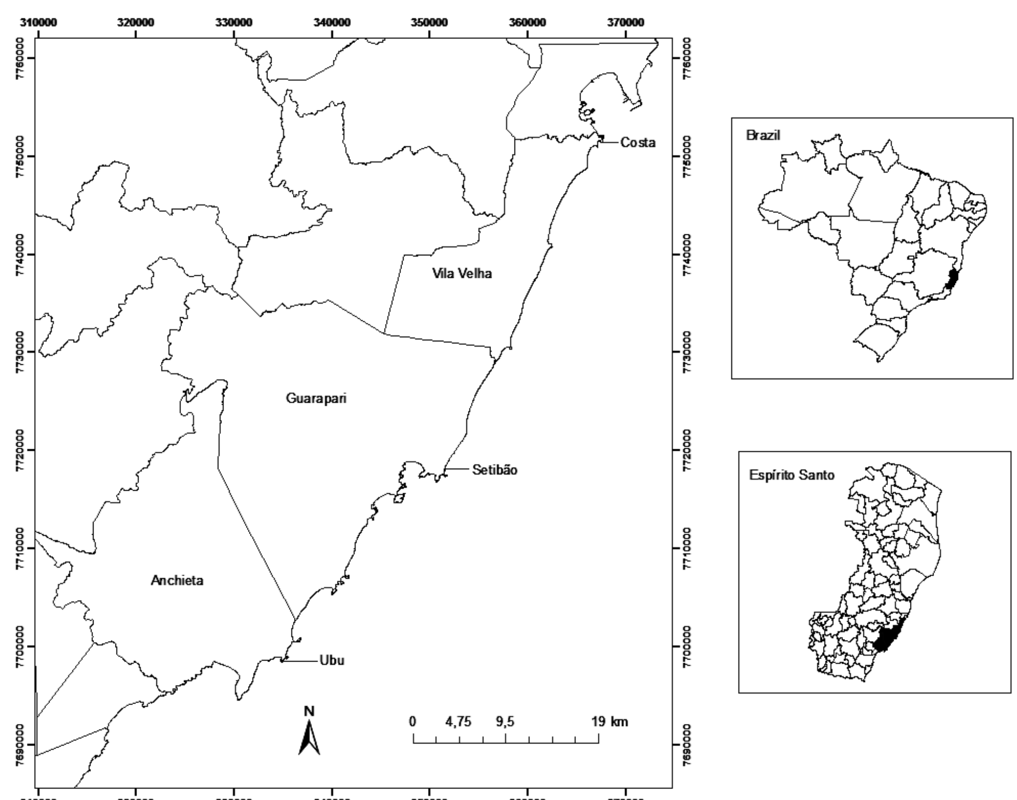

Fig. 1. The location of the study areas in the coastal zone, state of Espírito Santo, Southeast Brazil.

on each shore, five vertical transects were randomly placed from the zone of *Chthamalus bisinuatus* to the beginning of the *Sargassum* spp. range (i.e., the beginning of the infralittoral zone), according to the limits of the midlittoral zone described by Coutinho (2002). Contiguous samples were recorded taken in each 900 cm^2 transect quadrat that was divided into 100 intersections, of which 30 intersections were randomly selected and marked. Individuals present below these intersections were identified to the lowest taxonomic level possible, with the 30 points corresponding to 100%. Only the outer layer of the community was examined. The number of quadrats in each transect varied according to the inclination of the shore. At Costa beach, the midlittoral zone showed the smallest length (ranging from 2.4 m to 3.3 m). In other areas, the length of the midlittoral zone ranged from 3.0 m to 4.2 m. The air temperature was obtained *in situ*.

Analysis of the data. The relative abundance of species recorded in each transect was determined by the ratio between the summation of the percent cover of the quadrats and number of quadrats of the transect.

The Kruskal-Wallis nonparametric test was used to detect differences in the relative abundance of each species among sites and differences in the air temperature among sites and periods. Significance was estimated using Monte Carlo resampling (10,000 runs).

The comparative analysis of areas for benthic associations included an analysis of clustering (dendrogram) using the Bray-Curtis coefficient based on the average relative abundance of species in each area and season calculated as the arc sen.

The permutation test analysis of similarity (ANOSIM) (one factor) was used to assess differences between groups defined by the cluster analysis. The transects (five) of each site and season were treated as replicates to increase the possibility of permutations and the power of the test (Clarke & Warwick, 2001). The percentage of similarity procedure (SIMPER) was used to indicate those species that are mainly responsible for the differences identified in the results of the ANOSIM test (Clarke & Warwick, 2001). A cumulative contribution of 80% was applied as in Boaventura *et al.* (2002).

The Shannon-Wiener diversity index ($\log_{10}$), Pielou evenness index and richness (number of taxa) were calculated for each transect. Significant differences among sites and seasons were tested using a two-factor analysis of variance (ANOVA). The Tukey's test was used *a posteriori* to assess the differences between pairs of means (Zar, 1996). Assumptions of normality and variance in homogeneity were tested prior to all analyses using Kolmogorov-Smirnof and Levene's tests, respectively. For the number of *taxa*, it was necessary to transform the data with ln (x +1). For all tests, α was equal to 0.05.

RESULTS

Site characterization. The air temperature of each area is shown in Figure 2. Temperatures were higher during summer and lower in winter, as expected; however, significant differences between seasonal were not found. The Costa and Setibão beaches were considered exposed to wave action because they receive direct prevailing winds. Ubu beach was considered sheltered because it does not receive direct winds and waves from the northeast or southeast and is located in a bay. The shore of Costa beach had an inclination of 30°, whereas the other sites had inclinations of 27°.

Community characterization. Among the 34 *taxa* that were detected, 20 were recorded at Costa beach, and 27 at Setibão and Ubu beaches (Tab. I).

Arthrocardia flabellata (Kützing) Manza was identified as the dominant species of Corallinaceae articulated algae. However, other algae such as *Corallina* spp. and *Amphiroa* spp. were also observed.

Ubu and Setibão beaches showed the highest percentage of algae cover, occupying an average of 24% and 23% of the community, respectively, whereas algae occupied only 10% of the area at Costa beach.

The species *Centroceras clavulatum*, *Dasya* sp., *Cladophoropsis* sp., *Padina gymnospora*, *Amphiroa* sp. and *Megabalanus* sp. were restricted to Setibão beach, and *Cladophora* sp., *Stramonita haemastoma*, *Zoanthus* sp., and *Palythoa* sp. were recorded only at Ubu beach. The algae of the family Corallinaceae and the bivalve *Brachidontes* spp. and *Isognomon bicolor* occurred in greater abundance at Ubu beach relative to the other sites.

The average percentage of empty space in the rocky shores was higher at Costa beach (6.4 ± 0.41%), followed by Ubu beach (5.09 ± 1.5%) and Setibão beach (3.5 ± 1.3%) ($p = 0.01$).

Figure 3 shows the vertical distribution of benthic organisms from a transect in each area. A transect was selected by the occurrence of the largest number of species with an average abundance of greater than 2%

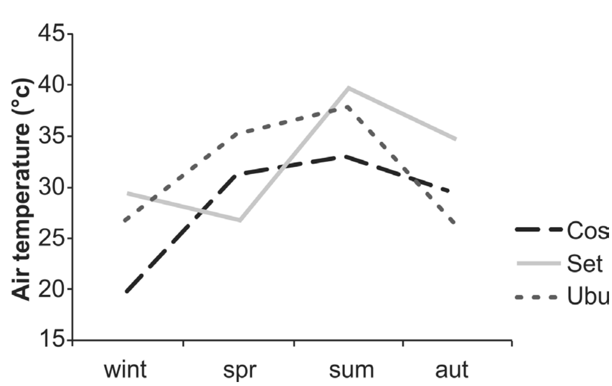

Fig. 2. The air temperature in each area and during each study period. Setibão (Set), Ubu and Costa (Cos) beach, state of Espírito Santo, Brazil, during the winter (win) and spring (spr) of 2006 and summer (sum) and autumn (aut) of 2007.

Tab. I. A taxonomic list and average relative abundances (± standard deviation) (n = 60) of the species recorded in the rocky shore of the Costa, Setibão and Ubu areas, state of Espírito Santo, Brazil. The result of the Kruskal-Wallis test is included (α = 0.05) (*P*, probability value associated with the test; NS, not significant).

Taxa	Costa	Setibão	Ubu	*P*
CHLOROPHYCEAE				
Anadyomene stellata (Wulfen in Jacq.) C. Agardh	0.17±0.41	0.01±0.05	0.12±0.26	NS
Centroceras clavulatum (C. Agardh in Kunth) Mont. in Durieu de Maisonneuve	0	3.83±9.27	0	0.02
Chaetomorpha antennina (Bory) Kützing	1.31±1.57	0.93±0.88	0.38±0.86	0.003
Cladophora sp.	0	0	1.78±2.82	<0.001
Cladophoropsis sp.	0	2.48±6.54	0.04±0.17	0.007
Codium sp.	0	0	0.01±0.04	NS
Ulva spp.	0.92±2.00	4.95±6.00	0.56±0.48	<0.001
PHAEOPHYCEAE				
Colpomenia sinuosa (Roth) Derbès & Solier	0.12±0.36	0.28±0.49	0.26±0.69	NS
Padina gymnospora (Kützing) Sond.	0	0.06±0.26	0	NS
Sargassum spp.	1.10±1.54	1.13±1.45	1.59±2.27	NS
RHODOPHYCEAE				
Acrosorium sp.	0.23±0.79	2.49±3.18	0.14±0.35	<0.001
Amphiroa sp.	0	0.11±0.28	0	NS
Corallinaceae articulated	5.68±4.84	5.22±4.62	13.01±5.06	<0.001
Corallinaceae fouling	0.36±0.71	0.59±1.37	3.18±2.72	<0.001
Dasya sp.	0	0.05±0.12	0	NS
Hypnea spinella (C. Agardh) Kützing	0.02±0.08	0.21±0.62	2.13±5.20	NS
Ochtodes secundiramea (Mont.) M. Howe	0	2.10±5.22	0.17±0.51	0.001
CNIDARIA				
Palytoa sp.	0	0	0.56±1.55	0.008
Zoanthus sp.	0	0	0.29±0.52	0.001
MOLLUSCA				
Brachidontes spp.	25.75±5.47	31.22±8.05	35.55±7.08	<0.001
Crassostrea rhizophorae (Guilding, 1828)	0.04±0.16	0	0.03±0.08	NS
Collisella subrugosa (Orbigny, 1846)	2.21±1.40	0.91±0.84	0.84±0.75	<0.001
Fissurella spp.	0.36±0.72	0.33±0.34	0.12±0.25	0.045
Isognomon bicolor (C. B. Adams, 1845)	1.68±1.01	2.17±1.30	3.40±1.00	<0.001
Leucozonia nassa (Gmelin, 1791)	0	0.04±0.09	0.01±0.05	NS
Littorina ziczac Gmelim, 1791	1.07±0.84	1.01±0.73	0.86±0.52	NS
Perna perna (Linnaeus, 1758)	12.74±6.15	1.35±1.78	0	<0.001
Siphonaria hispida E. A. Smith, 1890	0	0.03±0.10	0.30±0.30	<0.001
Stramonita haemastoma (Linnaeus, 1767)	0	0	0.01±0.05	NS
ANNELIDA				
Phragmatopoma sp.	1.80±2.56	3.26 ± 3.03	0	<0.001
CRUSTACEA				
Chthamalus bisinuatus Pilsbry, 1916	34.27±5.56	30.95±11.81	30.21±8.82	NS
Megabalanus sp.	0	0.05±0.10	0	0.03
Tetraclita stalactifera (Lamarck, 1818)	3.73±2.02	1.27±1.68	0.14±0.20	<0.001
ECHINODERMATA				
Echinometra lucunter Linnaeus, 1758	0.14±0.23	0	0.06±0.11	0.018

in each area. The species with a lower average cover that occurred in the analyzed transects were grouped as "other invertebrates" or "other algae".

In general, the higher levels of the shore were dominated by *Brachidontes* spp. and *Chthamalus bisinuatus*. A larger number of *taxa* occurred in the lower levels relative to the upper levels. Among the algae, the articulated Corallinaceae was more abundant in all areas. Algae occurred in the lower levels, except for *Ulva* spp. and *Ochtodes secundiramea*, which at Setibão beach also occurred at the higher levels (Fig. 3).

At Costa beach, *Collisella subrugosa*, *Isognomon bicolor* and *Littorina ziczac*, classified as other invertebrates in Fig. 2, occurred mainly at the higher levels. The articulated Corallinacea algae and the *Tetraclita stalactifera* and *Perna perna* invertebrates were very abundant in the lower levels.

At Setibão beach, a greater number of species occurred with an average abundance greater than 2%. Although *Cladophoropsis* sp. and *Centroceras clavulatum* algae had an average abundance of greater than 2%, they were not represented in Fig. 3 to permit a better graphic representation of the transect. *Isognomon bicolor* occurred at the higher levels. For the *taxa* classified as "other invertebrates" in Fig. 3, i.e., *Collisella subrugosa*, *Fissurella* sp. and *Littorina ziczac*, also occurred at the higher levels, while *Perna perna* and *Tetraclita stalactifera* were recorded in the lower levels. Articulated Corallinacea algae, *Acrosorium* sp. and the polychaete *Phragmatopoma* sp. were more abundant at the lower levels.

At Ubu beach, *Isognomon bicolor*, *Collisella subrugosa* and *Littorina ziczac* occurred at higher levels. Corallinacea and *Hypnea spinella* of the algae family were the *taxa* more abundant at lower levels (Fig. 3).

Multivariate analysis. The cluster analysis with a similarity of 73% resulted in the formation of two main groups. Group 1 included samples from exposed shores (Setibão and Costa beaches), and group 2 included samples from the sheltered shore (Ubu beach) (Fig. 4). The analysis of similarity (ANOSIM) revealed significant differences between groups 1 and 2 ($R = 0.609$, $p = 0.001$).

The SIMPER analysis defined the species that had the greatest contribution to the similarity within groups relative to the sampling sites. The taxa *Chthamalus bisinuatus* and *Brachidontes* spp. contributed most to the similarity within groups in the three areas. The average similarity was highest at Costa beach (82.42) and lowest at Setibão beach (72.95).

The dissimilarity between the samples of Setibão and Ubu beaches was mainly determined by *Phragmatopoma* sp., which did not occur in Ubu, and articulated Corallinaceae, which had a higher abundance in Ubu. *Perna perna*, with a higher abundance at Costa beach, and *Ulva* sp., with a higher abundance in Setibão beach, contributed most to the separation between the samples of these two beaches. The average dissimilarity between each pair of group combinations was higher among the samples of Costa and Ubu beaches (35.82. The species that occurred in the lower levels had the greatest contribution to the site differentiation.

Univariate analysis. Setibão beach presented the highest average diversity value (0.74 ± 0.12) (± standard deviation), followed by Costa beach (0.73 ± 0.06) and Ubu beach (0.68 ± 0.10) (Fig. 5). According to the Tukey test, the diversity of Setibão was significantly different from that of Ubu. For the different seasons, the lowest

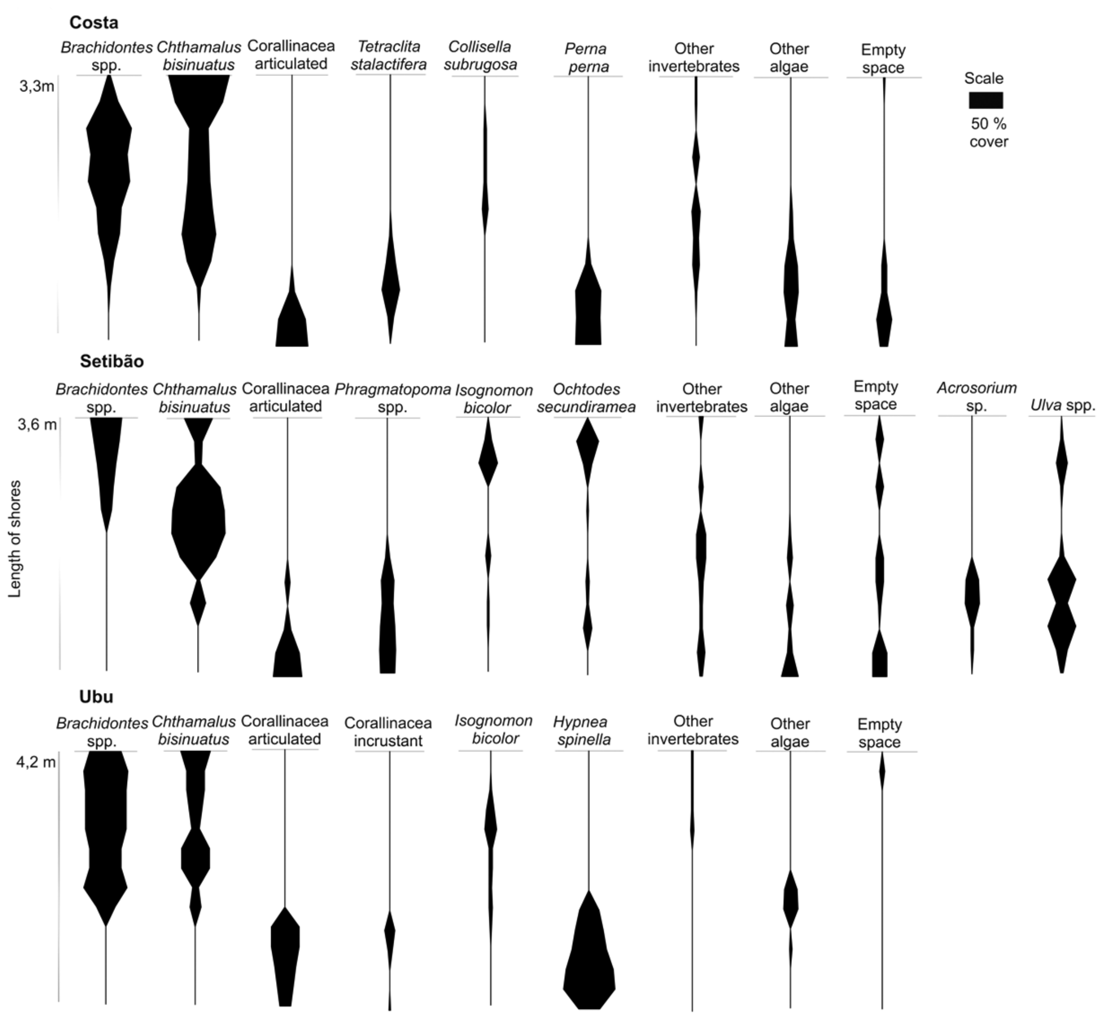

Fig. 3. The vertical distribution of the most representative species detected on the rocky shore of the midlittoral zones of Costa, Setibão and Ubu beaches.

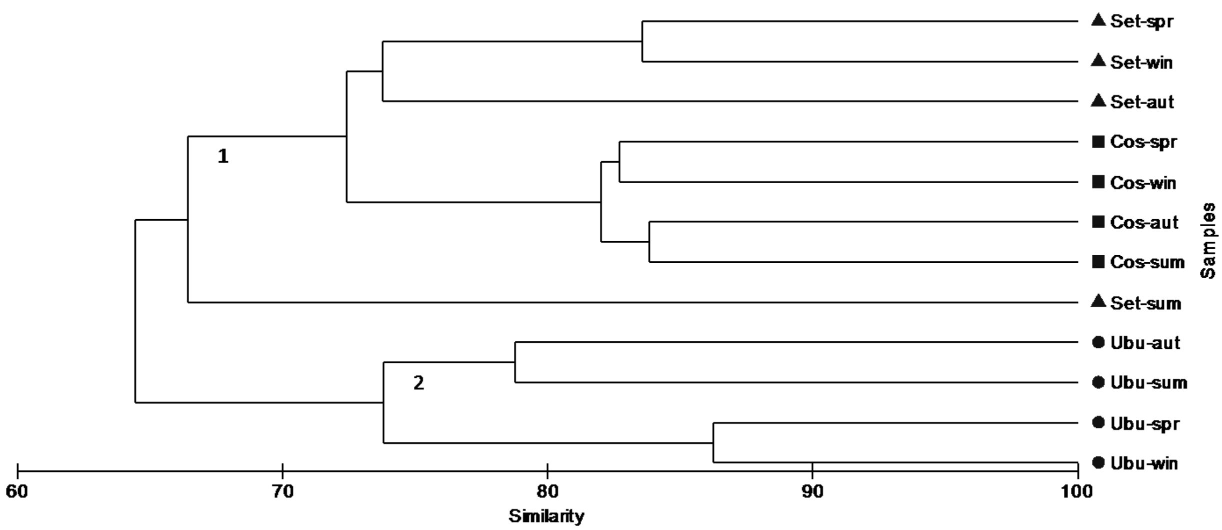

Fig. 4. Analysis of the benthic community groups based on the transformed (fourth root) average relative abundances for species in each area and season (Bray-Curtis coefficient). Setibão (Set), Ubu and Costa (Cos) beaches, state of Espírito Santo, Brazil, in the winter (win) and spring (spr) of 2006 and summer (sum) and autumn (aut) of 2007.

average value (0.64 ± 0.06) was recorded in the spring and was significantly different from those recorded in the summer (0.75 ± 0.07) and autumn (0.76 ± 0.06). There was no significant difference in the interaction between sites and seasons for this index (Tab. II).

The benthic community of Costa beach had the highest average evenness value (0.70 ± 0.05) and was different from the other areas (evenness values of 0.64 ± 0.11 and of 0.63 ± 0.08 for Setibão and Ubu beach, respectively). The lowest mean value (0.59 ± 0.05) was recorded in the spring and was significantly different from the summer (0.69 ± 0.05) and autumn (0.67 ± 0.03) values. The interaction test for this index showed the existence of significant differences (Tab. II).

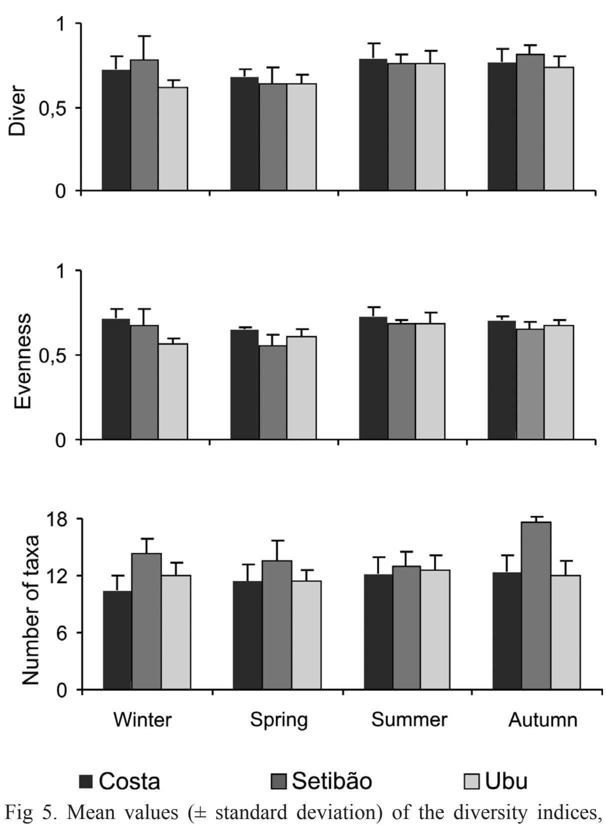

Fig 5. Mean values (± standard deviation) of the diversity indices, evenness and richness (number of *taxa*) of the benthic communities of the midlittoral zones at the Costa, Setibão and Ubu areas, state of Espírito Santo, Brazil, between July 2006 and May 2007.

The mean richness was higher at Setibão beach (14.65 ± 2.53) and was significantly different from the other areas. Ubu and Costa beach had average mean richness values of 11.90 ± 1.45 and 11.50 ± 1.97, respectively. Autumn had the highest mean value (13.93 ± 2.96), whereas spring had the lowest richness (12.06 ± 1.90). Significant differences were found between the interactions (site and season) (Tab. II).

DISCUSSION

Rocky shore organisms are subjected to a natural vertical gradient of increasing physical stress with increased exposure to air (i.e., higher on the shore) due to variations in tidal levels (CROWE *et al.*, 2000). Consequently, a greater shore height results in a lower species richness (DAVIDSON, 2005) and greater species dominance (BOAVENTURA *et al.*, 2002). The higher midlittoral levels in this study are dominated by *Brachidontes* spp. and *Chthamalus bisinuatus*. This result was also reported in other studies of the Brazilian coast (OLIVEIRA-FILHO & MAYAL, 1976; COUTINHO, 2002; MASI *et al.*, 2009), demonstrating that these genera are tolerant to stress at the shore. The physical stress due to desiccation is decreased lower on the shore, corresponding to a larger number of recorded species.

According to COUTINHO (2002), higher midlittoral levels are predominantly occupied by *Chthamalus bisinuatus*, whereas *Tetraclita stalactifera* occupies the middle midlittoral zone and *Megabalanus* sp. occupies the upper zone of the infralittoral zone. This distribution

Tab. II. Results of a two-factor ANOVA using diversity indices, evenness and richness data for the Costa, Setibão (Set) and Ubu areas, state of Espírito Santo, Brazil, and the seasons (winter and spring of 2006 and summer and autumn of 2007). The richness values were transformed by ln (x +1). The homogeneous groups determined by the Tukey test were ranked from lowest to highest averages (F, test value; *P*, probability value associated with the test, α = 0.05; NS, not significant).

Variable	Source of variation	Degrees of freedom	F	*P*	Tukey HSD
Diversity	site	2	3.932	0.026	Ubu Cos Set
	season	3	7.798	<0.001	Sp W Su A
	site x season	6	1.447	NS	
Evenness	site	2	7.555	<0.001	Ubu Set Cos
	season	3	8.172	<0.001	Sp W Su A
	site x season	6	2.506	0.034	
Richness	site	2	18.589	<0.001	Cos Ubu Set
	season	3	3.413	0.025	Sp W Su A
	site x season	6	2.331	NS	

was also observed in this study for *C. bisinuatus* and *T. stalactifera* in all areas. However, *Megabalanus* sp. occurred at the lower levels of the midlittoral only at Setibão beach. This occurrence can be attributed to the possibility that species in exposed locations may occupy higher levels due to the high reach of spraying water, thereby reducing the physical stress during periods of low tide (Underwood, 1981).

The invasive bivalve *Isognomon bicolor* occurred only in the intermediate midlittoral level and presented reduced average abundance in comparison with the study of Arraial do Cabo (Fernandes *et al.*, 2004), in which the organisms were distributed in the lower midlittoral and in the infralittoral zone. In this study, this species occurred at all sites and all seasons of the year, showing its stabile establishment in the studied region. In many cases, the introduction of an exotic species has no dramatic influence on marine communities (Crowe *et al.*, 2000). However, the absence of previous studies in the sampled areas impedes the verification of the adverse impact of an invasive species on the native community. According to Fernandes *et al.* (2004), it is possible that *I. bicolor* competes for space and food with the mussel *P. perna*. In Santos Bay, the two species occupy the same area with *I. bicolor* commonly adhering to the byssus of *P. perna* (Casarini & Henriques, 2011). In this present study, the two species occupied different levels of the midlittoral zone with *I. bicolor* occurring at higher levels, demonstrating a lack of competition for space between these species. However, future monitoring is necessary to further examine this phenomenon.

Rocky shore organisms are subject to a horizontal gradient of physical stress due to differences in wave action (Crowe *et al.*, 2000). The difference between the intertidal communities of exposed and sheltered areas, as demonstrated by several authors (Oliveira-Filho & Mayal, 1976; McQuaid & Branch, 1984; McQuaid & Lindsay, 2000; Branch & Steffani, 2004; Araújo *et al.*, 2005), also occurred in this study as demonstrated by the clustering analysis. The impact of waves is also an important factor influencing the intertidal benthic communities (Little & Kitching, 1996; Barreto, 1999; Branch & Steffani, 2004; Araújo *et al.*, 2005). Sibaja-Cordero & Cortés (2008) concluded that the interaction between species (predation and space monopolization) was a possible cause of differences in abundance between wave-exposed and sheltered areas.

Filter-feeding organisms are well-suited for exposed conditions due to increased food supply (Raffaelli & Hawkins, 1999). In the studied areas, *Perna perna* occurred only on exposed shores. Boaventura *et al.* (2002) noted that along the Portuguese coast, mussels also occur in the lower portion of the midlittoral zone of the most exposed sites, which is in agreement with our study. *Phragmatopoma* sp. is also restricted to the exposed coast and most frequently found in these environments (Széchy & Paula, 2000; Masi & Zalmon, 2008).

The macroalgae *Chaetomorpha antennina* occurred at the three sites but at a greater abundance in the exposed areas, and *Centroceras clavulatum* was recorded only at Setibão beach. Algae are common in areas subjected to strong wave impacts (Oliveira-Filho & Mayal, 1976; Széchy & Paula, 2000; Coutinho, 2002).

For certain species, feeding processes, such as foraging or predation, may be more difficult at exposed sites (Raffaelli & Hawkins, 1999). The predator *Stramonita haemastoma* occurred only on sheltered coasts at a low percentage. According to Menge & Sutherland (1976), predators such as gastropods are rare exposed area and confined to crevices. Thus, the lack of analysis of crevices may explain their observed absence on the exposed coast in this study.

The data from this study were similar to those of Zamprogno *et al.* (2010), showing that *Isognomon bicolor* occurs at a low abundance in the rocky shores of the state of Espírito Santo, contrary to the findings of Breves-Ramos *et al.* (2010) for Rio de Janeiro. However, when comparing the three sampling locations, *I. bicolor* occurred in a greater percentage at Ubu beach, a sheltered area. According to Casarini & Henriques (2011), the lowest densities of this species are found in exposed locations. Branch & Steffani (2004) observed that the larval supply may increase with greater water flux; however, opportunities for recruitment can be reduced in more exposed environments relative to sheltered areas. *I. bicolor* may require conditions that facilitate attachment on the shores of Espírito Santo, which may include rock crevices (ZAMPROGNO *et al.*, 2010) or areas sheltered from wave action.

OIGMAN-PSZCZOL *et al.* (2004), reported that the distribution of cnidarians on infralittoral rocky shores was positively correlated to the depth due to the increased stability of environments with increasing depth. The two species of cnidarians (*Palythoa* sp. and *Zoanthus* sp.) recorded in this study occurred at higher levels (midlittoral) only at Ubu. This occurrence was most likely due to the lower observed wave impact and corresponding increased stability of the midlittoral zone in this area compared to other studies.

The shore slope may have been responsible for the differences recorded between Costa and other sites. The slope dissipates wave energy; a more inclined area sustains greater wave exposure (MURRAY *et al.*, 2006) with the intensity of insulation, whereas the radiation is reduced in more inclined areas (BENEDETTI-CECCHI *et al.*, 2000b).

According to SOMSUEB *et al.* (2001), the variation of algal communities in areas with different inclinations can be attributed to differences in the incident light associated with the variations in water movement. The lowest abundance of algae was observed at Costa beach, which was the steepest site with the narrowest midlittoral zone. This area likely receives less incident light, restricting the development of algae relative to Setibão and Ubu beaches (which have lower angles of inclination).

In this study, *Chthamalus bisinuatus* and *Brachidontes* spp. dominated the communities, resulting in low diversity values compared to the infralittoral communities reported by OIGMAN-PSZCZOL *et al.* (2004). According to these authors, diversity increased with depth, resulting in more complex communities, a trend that can be explained by the reduction in frequency of disturbance caused by physical factors.

The average diversity and richness values were higher on the exposed coast of Setibão, most likely due to greater wave exposure relative to the other study sites. COUTINHO (2002) suggested that with increasing wave action, the limits of the supralittoral and midlittoral zone are expanded, leading to increased biodiversity.

Costa beach had the lowest number of species, most likely due to less available area in comparison to the other two sites. However, the highest value of evenness was found in the same area, indicating less dominance of species in comparison with other areas.

According to the SIMPER analysis, *Brachidontes* spp. and *Chthamalus bisinuatus* were the *taxa* that contributed most to the similarity between group areas, demonstrating that the greater abundance of these *taxa* did not vary in time and space because the most abundant species within the group contribute more to the similarity (CLARKE & WARWICK, 2001). According to the model proposed by UNDERWOOD & CHAPMAN (2000), physical stress at higher levels of coastreduces the temporal variability of communities. These authors also proposed that in the lower levels, environmental conditions are less harsh and the number of animals is generally highly variable over time due to fluctuations in recruitment, predation, and competition. The results of this study support this hypothesis, as the differences between the studied areas in the multivariate analysis were determined according to invertebrates and algae that occurred in the lower levels on the shore.

According to community analyses of BAULCH *et al.* (2005), biotic responses to climate changes are not easily understood or predictable because the responses differ between the types of communities, suggesting that the disturbance history may be an important determinant in the occurrence of changes. It is necessary to have prior knowledge and temporal monitoring of benthic communities to recognize the disturbances and consequent responses to climate change.

This study demonstrated that differences among the areas, the extent of wave exposure and the slope of the shore contributed to the variability between areas. However, other factors not considered in this study, such as reproduction, recruitment and competition, may have influenced the distributions during the different seasons. Community patterns are the result of physical and biological processes that influence the growth, recruitment and mortality of organisms on temporal and spatial scales (BENEDETTI-CECCHI *et al.*, 2000a). Thus, the zonation of benthic organisms along the rocky shore reflects the interaction of various physical and biological factors that establish precise limits of distribution (COUTINHO, 1995).

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