Spatial distribution of mollusks in the intertidal zone of sheltered beaches in southeastern of Brazil

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ABSTRACT. The spatial distribution of mollusks in the intertidal zone was examined monthly from August 1995 through July 1997, in Enseada, Barra Velha and Araçá beaches in southeastern of Brazil. One study sector was selected in Enseada and Barra Velha, and two sectors in Araçá (Araçá I and Araçá II). The sectors were 10 m wide and equivalent in length to the width of the intertidal zone. Each sector was divided into three horizontal levels: lower, middle and upper, where the samples were taken with a cylinder corer with a base area of 0.16 m^2. In order to characterize the intertidal environment in these areas, some environmental variables were analyzed. In general, the mollusks were distributed in the sectors as follows: Enseada – *Olivella minuta* (Link, 1807) in the lower level and *Tagelus plebeius* (Lightfoot, 1786) in the upper level; Araçá I – *O. minuta* in the lower level, *Tellina lineata* Turton, 1819 and *Anomalocardia brasiliana* (Gmelin, 1791) in the middle levels; Araçá II – *Cerithium atratum* (Born, 1778) in the lower level, *O. minuta* in the lower and middle levels, and *A. brasiliana* and *Corbula caribaea* Orbigny, 1842 in the middle level; Barra Velha – *Tagelus divisus* (Spengler, 1794), *Lucina pectinata* (Gmelin, 1791) and *Tellina versicolor* De Kay, 1843 in the lower level, and *A. brasiliana* and *Macoma constricta* (Brugüière, 1792) in the upper level. The intertidal zone of the study sectors could be divided into two biological zones: the upper zone, where *T. plebeius*, *A. brasiliana* and *M. constricta* were more abundant; and the lower zone, where *O. minuta*, *C. atratum*, *T. lineata*, *T. versicolor*, *C. caribaea*, *T. divisus* and *L. pectinata* were abundant.

KEY WORDS. Caraguatatuba Bay, intertidal zone, mollusk, São Sebastião Channel, sheltered beach, spatial distribution.

Knowledge of the patterns of species distribution is important in understanding how environmental factors influence this distribution. In environments with wide variations in physical characteristics such as beaches or sandflats, community structure is determined by their morphodynamic state. The distribution of the macrofauna is the result of the relationships among environmental factors and species characteristics. The community structure and intertidal distribution of the macro-infauna have been related to abiotic factors such as grain size (Jaramillo & Gonzalez 1991, McLachlan 1996), wave action (Brown & McLachlan 1990), water content (Wendt & McLachlan 1985), and temperature and salinity of the interstitial water (Koh & Shin 1988). Biological factors such as recruitment, predation and competition are also of key importance in the establishment and maintenance of zonation (McLachlan & Jaramillo 1995). Therefore, zonation of the species is maintained by physical factors associated with biological interactions. It is unlikely that a single factor will explain patterns of distribution, since a species can occupy morphologically distinct habitats. The determination of macrofauna distribution in sandy beaches is quite difficult, because of the great instability of environmental conditions and because most organisms live within the sediment (Amaral *et al*. 1990).

Several attempts have been made to construct zonation schemes for sandy beach macro-infauna, either for worldwide application, or at least for littoral areas over wide latitudinal ranges. The most important zonation schemes for macro-invertebrates in sandy beaches were proposed by Dahl (1952) and Salvat (1964), and have been used up to the present for comparative studies of spatial distribution of the macrofauna. However, Jaramillo *et al*. (1993), studying intertidal zonation of macrofauna over a range of exposed sandy beaches in south-central Chile, showed that different beach types may support different intertidal macroinfauna zonation patterns.

In Brazil, most studies of spatial distribution of benthic macrofauna in sandy beaches have been done in the south and southeast. Corbisier (1991), Netto & Lana (1995) and Borzone *et al.* (1996) worked with zonation of macrofauna in beaches of different morphodynamic types. The zonation patterns suggested by Dahl (1952) and Salvat (1964) were compared to patterns in Barranco Beach by Souza & Gianuca (1995), and in São Francisco Beach by Rizzo & Amaral (2001). Lopes & Schaeffer-Novelli (1992), Borzone (1994) and Denadai *et al.* (2001) studied the community structure and spatial distribution of mollusks.

In spite of these investigations, mollusks in tropical and subtropical regions, especially in sheltered beaches, are still considered to be poorly studied. Moreover, data from temperate regions are sometimes conflicting, especially in regard to species diversity. Knowledge of the species distribution of mollusks is very important for managers of economic activities and marine monitoring programs. The aim of the present work was to provide data on the intertidal zonation of mollusks in sheltered beaches in Caraguatatuba Bay and São Sebastião Channel, as well as to evaluate the influence of environmental variables.

MATERIAL AND METHODS

Field samples were taken monthly between August 1995 and July 1997 at low spring tides in Enseada, Araçá and Barra Velha beaches. Enseada Beach is located in Caraguatatuba Bay, and Araçá and Barra Velha beaches in the São Sebastião Channel on the northern coast of São Paulo State (Fig. 1). Because these beaches are located near urban centers and an important oil terminal, they are continuously exposed to low levels of sewage runoff and to the risk of oil spills.

One study sector was selected in Enseada and Barra Velha beaches, and two sectors in Araçá (Araçá I and Araçá II). The sectors were 10 m wide and equivalent in length to the width of the intertidal zone. Each sector was divided into three horizontal levels: lower intertidal, the region nearest the water line during low tide; upper intertidal, adjacent to the dry zone; and middle intertidal, the region between the two former ones. The extension of each level was established by visually estimating the slope, the degree of water saturation, and consequently the air exposure period. One 10 x 10 m sampling area was randomly chosen in each level; each sampling area was also subdivided in 1-m intervals.

The quantitative macrofauna samples were taken with a cylinder corer with a base area of 0.16 m² inserted 20 cm deep. Three samples were taken in each level/month (nine samples per sector/month). Sampling units for each month were determined with the aid of a random-number table. The sediment was immediately washed in situ in a 1.0 mm-mesh nylon bag. The remaining sediment was washed in the laboratory with seawater in sieves of 1.0 mm mesh. Mollusks were preserved in 70% alcohol, identified to species level and counted. In Enseada Beach, the samples were taken from August 1995 through July 1996; in Barra Velha, from August 1995 through December 1996; in Araçá I, from August 1995 through February 1997; and in Araçá II, from August 1996 through July 1997.

In order to characterize the intertidal environment in these areas, some environmental variables were sampled: salinity (interstitial water), grain size, silt-clay percentage, organic matter and calcium carbonate content of the sediment. The sediment characterization was done using three replicates,

Figure 1. Locations of the three beaches studied: Enseada, in Caraguatatuba Bay; and Barra Velha and Araçá, on the São Sebastião Channel, in São Paulo State, Brazil.

and the salinity using five replicates taken quarterly in each level. Salinity was analyzed with a Goldberg T/C – Model 1041 portable refractometer, grain size by the Suguio method (Suguio 1973), and organic matter and carbonate contents of the sediment by the methods described by Amoureux (1966). The slope of study sectors was evaluated with a transparent hose filled with water.

Two-way analysis of variance (ANOVA) was performed to compare the environmental variables among the levels according to season (values of $p < 0.05$ were considered significant). This analysis was followed by Tukey's test to access pairwise comparisons between these variables. The diversity and evenness was estimated using the Shannon-Wiener index (index $\log_2$) and the Pielou index (Krebs 1989) for each level by sector using the total number of individuals. A graph of the cumulative number of species by month was made to verify whether the number of samples in each sector was sufficient to establish richness. Canonical Correspondence Analysis [performed by Hill's (1979) method] was used to analyze the influence of environmental variables on the spatial patterns of species distribution. For this multivariate analysis, mean values of the environmental variables were used to characterize each level according to season, and a biological matrix was constructed using levels/seasonally pooled data for the most abundant species, standardized to an area of 0.16 m². Spatial distribution was also investigated by subdividing each 10 x 10 m area sampled into 1 m vertical levels, and noting the densities
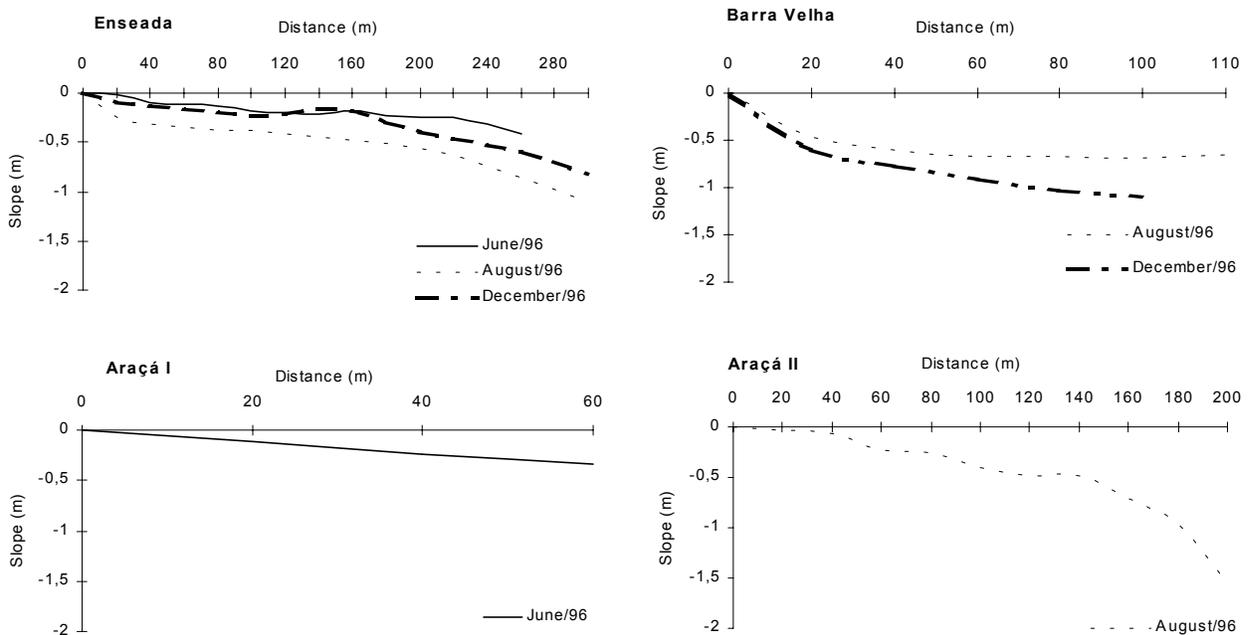
Figure 2. Intertidal slopes of the four study sectors: Enseada, Barra Velha, Araçá I and Araçá II.

of the most abundant species in each levels. Since not all the environmental variables followed a normal distribution, the data were $\log_{10}$-transformed prior to statistical analysis.

RESULTS

The Enseada, Barra Velha, Araçá I and Araça II sectors are very sheltered environments with a gentle slope (Fig. 2) and substrate composed of fine and very fine sand (Tab. I). The mean values of environmental variables, and the results of the analysis of variance and Tukey's test are shown in table I. Environmental variables did not clearly discriminate the levels in the sectors. In the Enseada sector, salinity was significantly different among levels in winter, spring and summer, being lowest in the upper level; and calcium carbonate content was significantly different in spring, summer and autumn, being highest in the low level. In Barra Velha, silt-clay, organic matter content and sorting coefficient were higher than in other sectors. The sediment grain size and sorting coefficient were significantly different among levels in spring and summer. The sediment in Barra Velha varied from fine to very fine sand, and the high sorting coefficient indicated that the sediment was poorly sorted. Calcium carbonate and organic matter content were significantly different among the levels of the Araçá I sector. Calcium carbonate was higher in the middle level, and organic matter content was higher in the lower level of the Araçá I sector. In Araçá II, the environmental variables were similar among levels. Nevertheless, the sorting coefficient ranged from moderately sorted in the lower and middle levels to poorly sorted in the upper level in winter, spring and summer. Organic matter content differed significantly between summer and autumn.

In general, richness, diversity and evenness tended to be higher in the lower levels in all sectors (Tab. II). The highest values of diversity and evenness were found in the lower level of Barra Velha, and the lowest in the upper level of Enseada. Cumulative species number eventually stabilized in the Enseada, Barra Velha and Araçá II sectors, but tended to increase in Araçá I (Fig. 3).
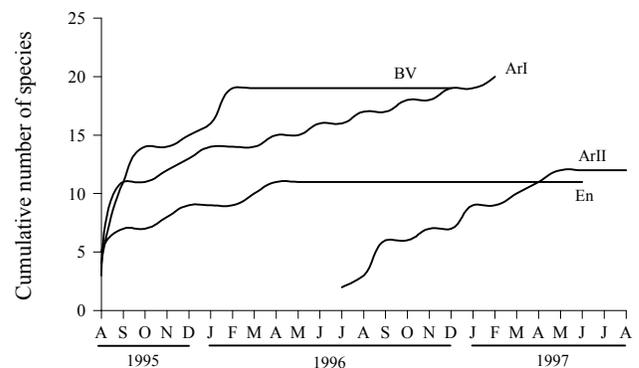
Figure 3. Cumulative number of species by month and sector. (En) Enseada, (BV) Barra Velha, (ArI) Araçá I, (ArII) Araçá II.

The distribution of the most abundant species of mollusks along the sectors is shown in figures 4, 5, 6 and 7. Faunal zonation was more evident in the Enseada, Araçá I and Araçá II sectors than in the Barra Velha sector. In general, the

Table I. Mean of environmental variables and results of analysis of variance (Two-way ANOVA) among levels by seasons. Superscript letters indicate the results of the Tukey's test for pair-wise mean comparisons. Similar labels indicate non-significant differences for pair-wise comparisons. (Degrees of freedom = 2, data transformation by $\log_{10}$).

Enseada	Winter					Spring					Summer					Autumn				
	Low	Mid	Upp	F	P	Low	Mid	Upp	F	P	Low	Mid	Upp	F	P	Low	Mid	Upp	F	P
Sediment grain size (φ)	3.24	3.32	3.133	1.078	0.397	3.32	3.23	3.29	1.141	0.38	3.23	3.27	3.20	0.213	0.813	3.26	3.34	3.25	1.169	0.372
Sorting coefficient	0.38	0.32	0.56	1.122	0.385	0.44^{AB}	0.42^A	0.55^B	6.303	0.033	0.52	0.49	0.58	0.146	0.867	0.44	0.37	0.49	1.620	0.279
Silt+Clay (%)	0.15^A	0.20^B	0.19^B	18.93	0.002	11.21	7.25	9.62	0.741	0.515	0.35	0.30	0.24	0.223	0.805	0.18^A	0.28^B	0.26^B	7.301	0.024
Calcium carbonate (%)	3.56	3.58	4.08	1.358	0.326	3.41^A	2.79^{AB}	2.4^B	6.098	0.035	3.25^A	2.25^B	2.89^{AB}	5.375	0.045	2.29^A	2.09^{AB}	1.71^B	5.357	0.046
Organic matter (%)	1.48	1.31	1.73	2.147	0.198	1.38	1.54	1.35	1.056	0.404	2.20	1.39	1.58	3.710	0.089	1.23	1.16	1.32	2.945	0.128
Salinity (‰)	32^A	25.3^A	15.3^B	43.839	<0.001	28.3^A	27.3^{AB}	24.33^B	6.033	0.036	21.5^A	21.33^A	12.0^B	140.21	<0.001	25.66	27	21.66	2.498	0.162
Barra Velha																				
Sediment grain size (φ)	2.34	2.0	2.35	0.547	0.589	2.78^{AB}	3.06^A	2.01^B	5.641	0.014	3.05^A	3.22^B	2.34^B	10.912	0.01	3.06	2.84	2.98	0.187	0.834
Sorting coefficient	1.40	1.49	1.68	2.382	0.126	1.27^A	1.21^A	1.80^B	16.278	<0.001	1.21^A	1.06^A	1.66^B	12.027	0.007	1.47	1.32	1.22	1.838	0.238
Silt+Clay (%)	17.98	14.23	21.39	1.219	0.323	23.9	30.01	20.77	2.189	0.146	21.56	26.07	22.28	0.502	0.628	34.75	18.99	17.99	5.075	0.051
Calcium carbonate (%)	4.48	4.30	3.95	0.138	0.871	5.34	5.41	4.70	0.352	0.708	4.47	5.77	4.57	2.333	0.178	4.95^{AB}	5.69^A	3.84^B	6.188	0.034
Organic matter (%)	7.16	8.10	8.67	0.831	0.454	8.39	8.97	8.93	0.156	0.856	5.93	7.48	6.94	4.731	0.058	14.33	11.68	11.81	2.461	0.165
Salinity (‰)	30.33	26.33	28.33	3.201	0.069	30.2	25.83	30	2.607	0.109	22.33	24	23.66	0.419	0.678	29.66	25.33	29	4.274	0.070
Araçá I																				
Sediment grain size (φ)	3.03	2.74	3.1	0.798	0.468	3.18	2.47	2.93	1.351	0.288	3.23	1.91	3.07	2.166	0.195	2.69	2.76	2.81	0.087	0.917
Sorting coefficient	0.83	1.04	0.82	0.636	0.542	0.73	1.0	0.99	0.557	0.583	0.753	1.30	0.94	3.247	0.110	1.28	1.03	1.03	1.339	0.330
Silt+Clay (%)	6.85	6.53	8.31	0.701	0.511	19.99	11.18	20.05	0.294	0.749	6.7	3.21	3.41	2.595	0.154	4.67	2.43	3.46	2.921	0.130
Calcium carbonate (%)	3.77^A	8.79^B	3.51^A	11.777	<0.001	4.76^{AB}	10.2^A	3.59^B	3.836	0.045	4.91^{AB}	12.8^A	3.03^B	8.181	0.019	7.75	4.74	3.53	3.025	0.123
Organic matter (%)	1.83	1.26	1.57	0.386	0.685	1.40^A	0.95^B	1.46^A	4.133	0.037	2.91^A	1.16^B	1.97^{AB}	5.738	0.040	1.47^{AB}	1.06^A	2.5^B	11.750	0.008
Salinity (‰)	31.33	29.4	30.66	0.588	0.571	32	29.16	31.83	1.740	0.209	15.5	17.66	12.66	0.528	0.619	29	19.33	9.66	2.932	0.129
Araçá II																				
Sediment grain size (φ)	2.0	2.8	1.9	0.621	0.568	3.04	3.14	2.35	3.196	0.113	4.14	6.52	5.28	2.137	0.195	2.99	3.22	3.63	0.517	0.620
Sorting coefficient	0.83	1.0	1.36	3.144	0.116	0.64^A	0.73^A	1.14^B	14.291	0.005	0.873	1.0	1.22	1.694	0.260	0.643	0.61	0.79	1.005	0.419
Silt+Clay (%)	1.84	7.0	4.2	2.406	0.170	3.6	7.61	5.32	3.39	0.103	4.14	6.52	5.28	2.137	0.199	3.84	6.54	5.41	2.436	0.168
Calcium carbonate (%)	7.36	3.62	7.0	0.525	0.615	3.65	4.89	8.89	1.795	0.244	8.34	4.23	10.28	2.959	0.127	3.66^A	4.63^A	7.22^B	20.223	0.002
Organic matter (%)	1.01	2.46	3.18	1.423	0.311	1.07	1.91	1.32	4.193	0.072	1.06^A	1.59^B	1.81^B	31.465	<0.001	1.26^A	1.68^A	3.16^B	14.401	0.005
Salinity (‰)	32	33	32	0.286	0.765	32.66	32.66	33	0.191	0.830	32.66	31.66	32.66	0.364	0.708	34.33	35.33	35	1.411	0.314

Table II. Occurrence, density (ind./0.16 m^2), richness, diversity and evenness of mollusks in the three levels of study sectors: Enseada, Barra Velha, Araçá I and Araçá II. (Low) Lower level, (Mid) middle level, (Upp) upper level.

Sectors	Enseada			Barra Velha			Araçá I			Araçá II		
Species/Level	Low	Mid	Upp	Low	Mid	Upp	Low	Mid	Upp	Low	Mid	Upp
Cerithiidae												
Certhium atratum (Born, 1778)										1.27	0.027	
Nassariidae												
Nassarius vibex (Say, 1822)				0.04	0.06		0.01	0.01		0.027		
Olividae												
Olivella minuta (Link, 1807)	0.51						0.64	0.35	0.27	3.22	2.97	0.13
Arcidae												
Anadara ovalis (Bruguìere, 1789)					0.02			0.01				
Lucinidae												
Codakia orbiculata (Montagu, 1808)				0.08								
Codakia costata (Orbigny, 1848)				0.02								
Lucina pectinata (Gmelin, 1791)				0.20	0.22	0.12		0.01				
Diplodonta punctata (Say, 1822)							0.03			0.08		
Mactridae												
Mulinia cleryana (Orbigny, 1846)	0.03											0.05
Tellinidae												
Tellina sp. 1				0.02								
Tellina sp. 2				0.04	0.02							
Tellina lineata Turton, 1819		0.06		0.06	0.02	0.02	0.09	0.18	0.09	0.05	0.05	0.11
Tellina versicolor De Kay, 1843				0.37	0.45	0.02		0.01		0.08		
Strigilla carnaria (Linnaeus, 1758)	0.03	0.03					0.03			0.027		
Macoma urugayensis (E. A. Smith, 1885)				0.04	0.04		0.01					
Macoma constricta (Bruguìere, 1792)			0.09	0.14	0.18	0.5		0.01	0.20		0.11	0.027
Semelidae												
Abra lioica (Dall, 1881)				0.04	0.04	0.02					0.027	
Semele proficua (Pulteney, 1799)										0.16		
Psammobiidae												
Tagelus plebeius (Lighfoot, 1786)		0.03	1.57	0.04	0.02	0.04			0.01			0.08
Tagelus divisus (Spengler, 1794)		0.03		0.33	0.52	0.16	0.03		0.03	0.08		
Donacidae												
Donax gemmula Morrison, 1971							0.01					
Veneridae												
Chione cancellata (Linnaeus, 1767)										0.08	0.027	
Anomalocardia brasiliana (Gmelin, 1791)		0.21	0.06	0.16	0.25	0.68	0.57	0.90	0.55	0.66	2.27	1.69
Tivela mactroides (Born, 1778)	0.12											
Corbulidae												
Corbula caribaea Orbigny, 1842	0.03				0.04		0.11	0.01		0.36	0.80	0.08
Corbula sp.							0.11		0.01	0.05	0.05	
Periplomatidae												
Periploma ovata Orbigny, 1846										0.027		
Density (ind. / 0.16m^2)	0.72	0.36	62	1.87	1.62	1.58	1.92	1.55	1.21	6.14	6.44	2.19
Richness	5	5	3	14	13	8	11	9	7	13	10	7
Diversity	1.356	1.781	0.483	3.209	2.896	2.064	2.374	1.761	2.061	2.126	1.911	1.021
Evenness	0.584	0.767	0.305	0.843	0.782	0.688	0.686	0.555	0.734	0.575	0.552	0.395
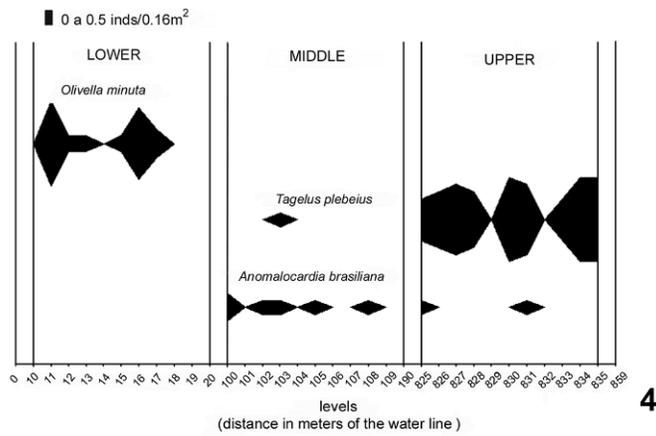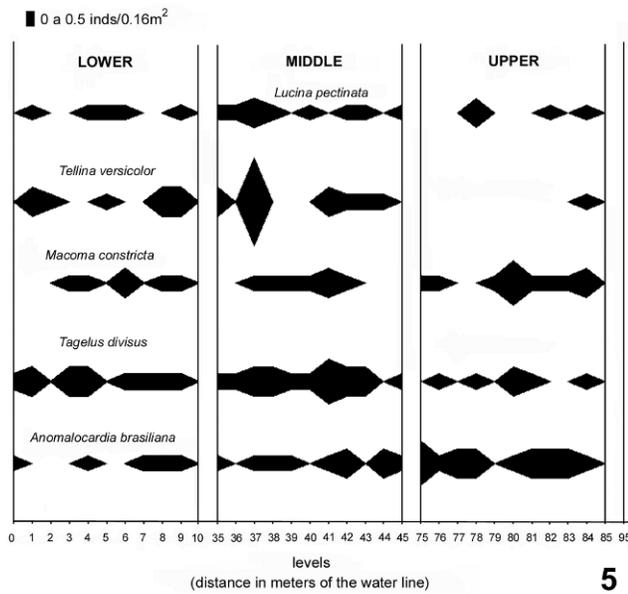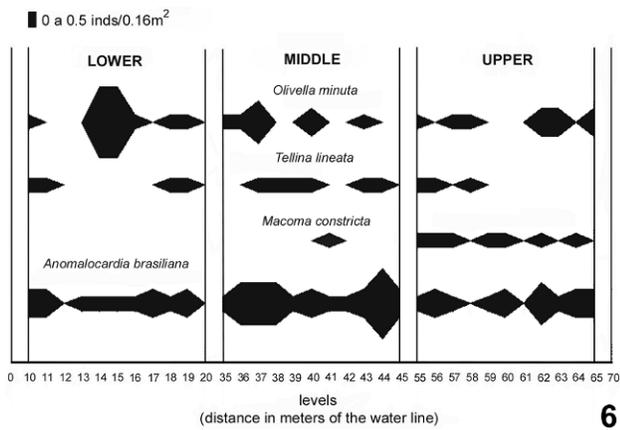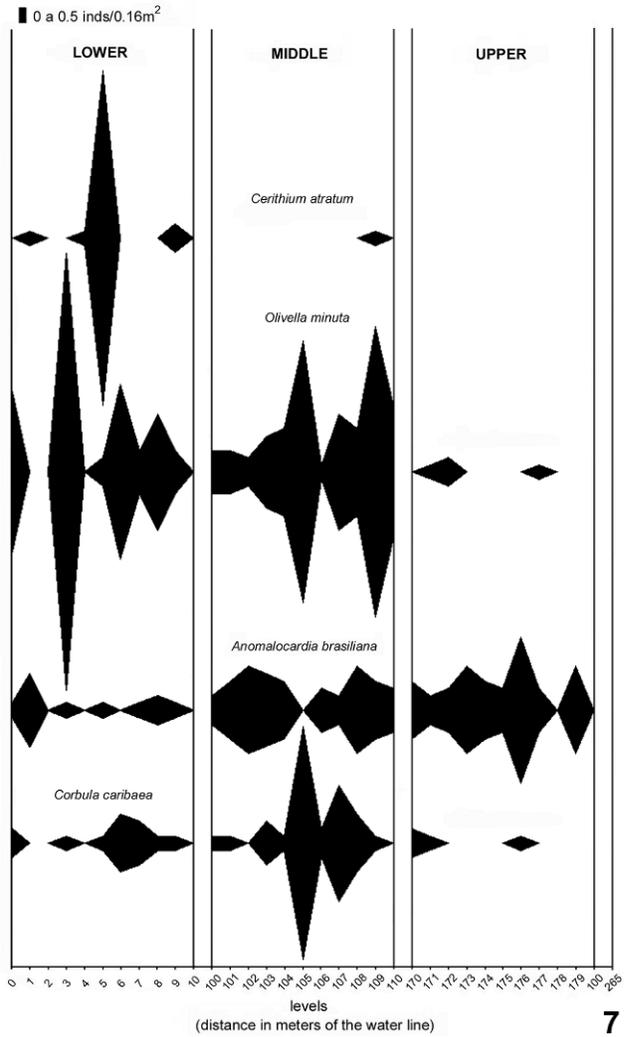
Figures 4-7. Zonation of the most abundant species in all levels (lower, middle and upper) of the: (4) Enseada sector, (5) Barra Velha sector, (6) Araçá I sector, and (7) Araçá II sector.

mollusks were distributed within the sectors as follows: a) Enseada: *Olivella minuta* (Link, 1807) abundant in the lower level and *Tagelus plebeius* (Lightfoot, 1786) in the upper level; b) Barra Velha: *Tagelus divisus* (Spengler, 1794), *Tellina versicolor* De Kay, 1843 and *Lucina pectinata* (Gmelin, 1791) abundant in the lower and middle levels, *Anomalocardia brasiliana* (Gmelin, 1791) and *Macoma constricta* (Brugüière, 1792) abundant in the upper level; c) Araçá I: *Olivella minuta* abundant in the lower level; *Tellina lineata* Turton, 1819 occurring in the middle level and *A. brasiliana* abundant in all three levels, principally in the middle level; d) Araçá II: *Cerithium atratum* (Born, 1778) abundant in the lower level, *O. minuta* in the lower and middle levels, *Corbula caribaea* Orbigny, 1842 in the middle level and *A. brasiliana* abundant in the middle and upper level; d) *Anomalocardia brasiliana* occurred in all four sectors and in all levels, except in the lower level in the Enseada sector.

Canonical Correspondence Analysis was used to determine the relationship among species distribution and the environmental variables (Fig. 8). In Enseada, 51.5% of the total was explained by axis 1, and 16.5% by axis 2. The species *T. plebeius* occurred at sites with low salinity and well sorted sediment. In Barra Velha, axis 1 explained 36.7% of the total variance and axis 2 explained 11.8%. Salinity, silt-clay and sorting coefficient seem to play an important role in the species distribution, contrasting with a lesser influence of organic matter, grain size and calcium carbonate. The occurrence of *Lucina pectinata*, *T. divisus* and *T. versicolor* was associated with high silt-clay and calcium carbonate contents. The species *M. constricta* and *A. brasiliana* occurred in environments with high sorting coefficient and salinity. In Araçá I, 44.3% of the total was explained by axis 1, and 11.3% by axis 2, while in Araçá II axis 1 explained 37.3% and axis 2 explained 24.6%. In Araçá I, calcium carbonate content and salinity showed a better correlation with the distribution of mollusks and in Araçá II, calcium carbonate, salinity, silt-clay and organic matter seem to play an important role in species distribution. In these two sectors *O. minuta* occurred at sites with high salinity and with moderately sorted sediment, and *T. lineata* and *A. brasiliana* occupied environments with high calcium carbonate and poorly sorted sediment. *Tellina lineata* and *M. constricta* were also associated with high organic matter content in the Araçá II sector. In Araçá I, the occurrence of *M. constricta* was also associated with high values of sorting coefficient, and in Araçá II *C. caribaea* occurred at a site with high salinity and silt-clay.

DISCUSSION

The study sectors are protected from wave action and have fine and very fine sand predominating. Canonical Correspondence Analysis showed that silt-clay, sorting coefficient, organic matter content, calcium carbonate and salinity played an important role in the distribution of species, contrasting with the lesser influence of mean grain size. According to RHOADS (1974), grain size is one of the main factors influencing the distribution of macrofauna. Although numerous studies have supported the animal-sediment hypothesis, there is little evidence that sedimentary grain size alone is the primary determinant of infaunal species distributions (SNELGROVE & BUTMAN 1994).

In the Barra Velha, Araçá I and Araçá II sectors, diversity increased from the upper toward the lower levels, confirming the results found by many investigators (MCLACHLAN 1990, RIZZO & AMARAL 2001). *Olivella minuta* showed clear zonation patterns, being more abundant in the lower levels, especially in the Araçá I and Araçá II sectors. This pattern may be related to more sediment moisture at the lower level and less desiccation. According to SMITH (1977), the moisture content in sand at low tide and the grain size influence animals to burrow. EDWARDS (1969) observed that larger individuals of *O. biplicata* (Sowerby, 1825) can tolerate longer exposure to dry air than can small ones. *Olivella minuta* probably cannot tolerate longer exposure to dry air. The high salinity in the lower levels may also have influenced the distribution of *O. minuta*. Physical and chemical factors such as salinity and temperature may influence zonation patterns in sandy beaches and mudflats (KOH & SHIN 1988). The time of exposure to dry air tends to be longer in sandflats, creating well-defined gradients of temperature and salinity. The Enseada sector, located in a tide flat, showed a clear salinity gradient. The upper level of this sector was characterized by high densities of *Tagelus plebeius* and low salinity. This species tolerates wide variations of salinity and is commonly found in estuaries (HOLLAND & DEAN 1977).

Anomalocardia brasiliana occurred widely, but reached its highest population densities in sites with poorly sorted sediments rich in calcium carbonate and organic matter, as in the upper levels of Araçá II and Barra Velha. In the Enseada sector this species occurred predominantly in the middle level, and in the Araçá I sector it was abundant in all levels. DENADAI & AMARAL (1999) also observed that *A. brasiliana* tended to occur in environments rich in calcium carbonate and organic matter. NETTO & LANA (1995) found *A. brasiliana* in the highest level in Paranaguá Bay, while the highest organic matter contents were recorded in the lower level. Nevertheless, the organic matter contents recorded by NETTO & LANA (1995) were higher than those recorded by DENADAI & AMARAL (1999) and in the present study. LOPES & SCHAEFFER-NOVELLI (1992) observed that *A. brasiliana* only occurred in the intertidal zone in Saco da Ribeira Beach. This species can tolerate wide environmental variations. It is euryhaline (LEONEL *et al.* 1982), can survive in anoxic environments, and occurs in different types of sediment (SCHAEFFER-NOVELLI 1980).

Macoma constricta reached its highest population densities in sites with poorly sorted sediments rich in organic matter, as in the upper level of Barra Velha. According to SNELGROVE & BUTMAN (1994), organic matter may be an important causal factor because organic matter is a primary source of food for deposit-feeders and indirectly for suspension-feeders. Although organic matter may not be the only variable determining the distribution of *M. constricta*, it does play an important role.

Although the availability of food was not analyzed, this factor may influence the distribution of the mollusks. The herbivorous gastropod *Cerithium atratum* occurred only in the Araçá II sector, where there was seaweed on the sediment. LOPES & SCHAEFFER-NOVELLI (1992) found this species near rocky shores where seaweed was growing. *Cerithium atratum* showed no tendencies related to sediment type or tide level. There are reports of *C. atratum* occurring on both rocky and soft-bottom shores, in the intertidal and sublittoral zones (LOPES & SCHAEFFER-NOVELLI 1992).

Biological factors such as recruitment, predation and competition are important in the establishment and mainte-
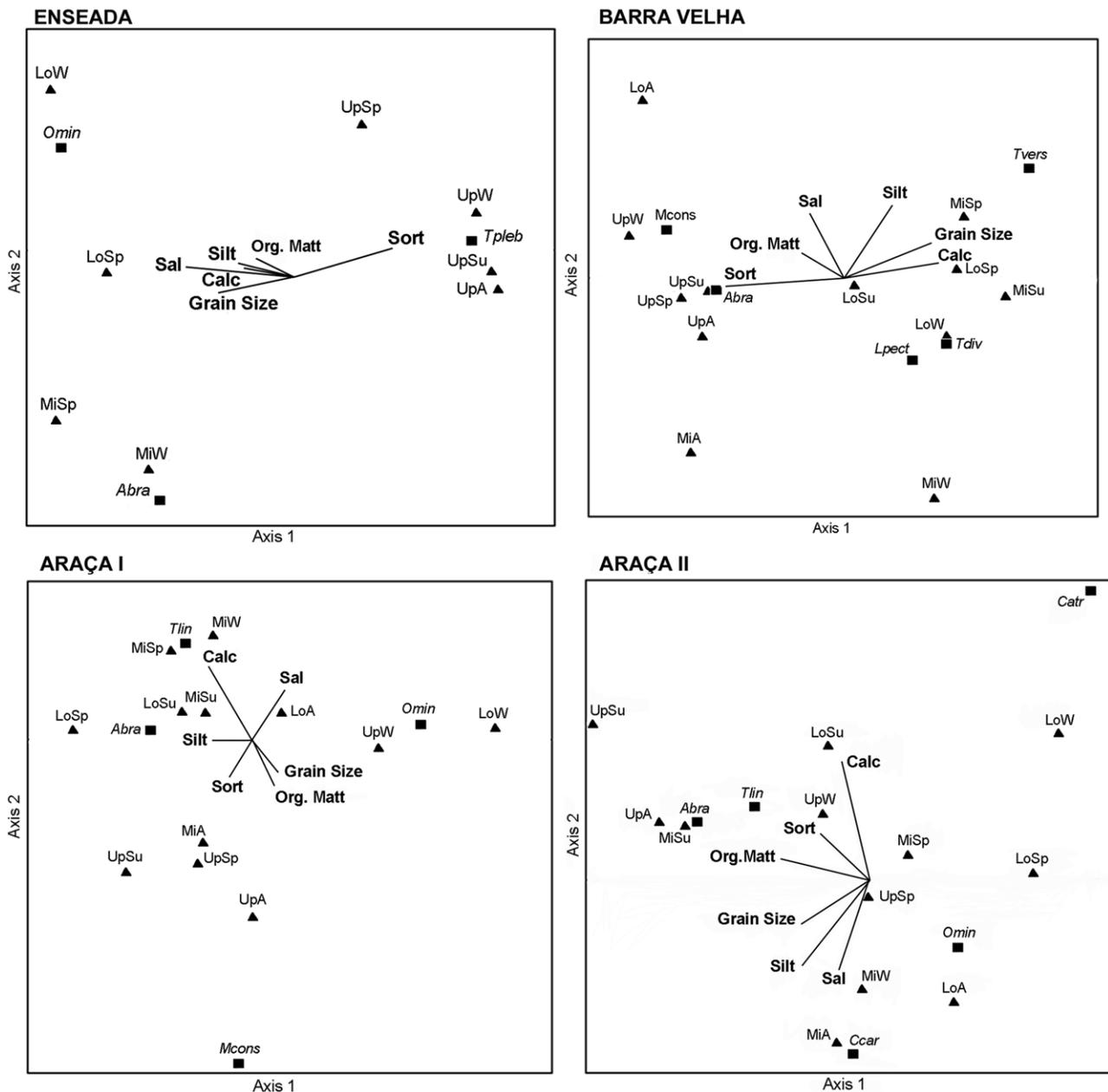
Figure 8. Canonical Correspondence Analysis (CCA) of the most abundant species and levels/seasons in relation to certain environmental variables in the Enseada (A), Barra Velha (B), Araçá I (C) and Araçá II (D) sectors, (Org. Mat) organic matter content, (Silt) silt-clay, (Sort) sorting coefficient, (Cal) calcium carbonate content, (Grain Size) mean grain size, (LoW) low/winter, (MiW) middle/winter, (UpW) upper/winter, (LoSp) low/spring, (MiSp) middle/spring, (UpSp) upper/spring, (LoSu) low/summer, (MiSu) middle/summer, (UpSu) upper/summer, (LoA) low/autumn, (MiA) middle/autumn, (UpA) upper/autumn, (Tpleb) *Tagelus plebeius*, (Tdiv) *Tagelus divisus*, (Tlin) *Tellina lineata*, (Tvers) *Tellina versicolor*, (Abra) *Anomalocardia brasiliana*, (Omin) *Olivella minuta*, (Mcons) *Macoma constricta*, (Ccar) *Corbula caribaea*, (Lpect) *Lucina pectinata*, (Catr) *Cerithium atratum.* The low and middle levels of summer and autumn in the Enseada sector were not included in the analysis because in these levels not any species were collected.

nance of zonation on rocky shores. On soft-bottom shores, however, the factors controlling communities are not necessarily the same as on rocky shores, and there are fewer studies of the influence of biological factors in these communities. Detection of intra- and interspecific competition is very complex for two main reasons: the inherent difficulties in experimentally manipulating the generally small and mobile infauna, and the three-dimensional structure of the habitat, which enables horizontal and vertical space partitioning (WILSON 1991 *apud* DEFEO *et al.* 1997). According to McLACHLAN & JARAMILLO (1995), because of this mobility, larval recruitment is less critical in establishing or maintaining zones than for sessile species on rocky shores, and predation and competition for food are the only biological factors that are likely to be important in affecting zonation in sandy beaches.

Biological zones are valid if they include the center of gravity of at least one characteristic species, and should be percepible without recourse to sophisticated statistical techniques (McLACHLAN & JARAMILLO 1995). Biological zones in sandy beaches, however, are not as clearly defined, as a consequence of the dynamic environment of the beach. Biological zones are clearest in the upper beach, and also tend to be narrowest at the upper shore and to widen downshore, because the concave slope of most beaches results in more gradual horizontal changes, associated with the intertidal gradient toward the lower shores (McLACHLAN & JARAMILLO 1995).

DAHL (1952), studying the crustacean fauna, established three zones: supralittoral, midlittoral and sublittoral. SALVAT (1964) established four zones, defined on the basis of water content, from high to low beach levels: dry sand zone; retention zone, where the sediment retains a small amount of water; resurgence zone, where water circulates among the sand grains, and saturation zone, where the sediment is constantly saturated by water.

In the present study, the beach sectors could be divided into two biological zones. In the upper zone, which corresponds to the highest part of the midlittoral described by DAHL (1952) and to the retention zone of SALVAT (1964), the species *T. plebeius*, *A. brasiliana* and *M. constricta* were more abundant. In the lower zone, which is equivalent to the resurgence zone of SALVAT (1964), *O. minuta*, *T. lineata*, *C. caribaea*, *C. atratum*, *T. divisus*, *T. versicolor* and *L. pectinata* were more abundant. The middle level included the upper part of the lower zone, and the transition zone between lower and upper. DENADAI *et al.* (2001), studying the zonation of the mollusks in the midlittoral of São Franscisco Beach, established two biological zones: upper, in which *A. brasiliana* dominated; and lower, in which *C. atratum*, *C. caribaea*, *Tegula viridula* (Gmelin, 1791), *Codakia orbiculata* (Montagu, 1808), *Semele proficua* (Pulteney, 1799) and *Chione subrostrata* (Lamarck, 1818) were abundant.

The equivalence between the schemes of Dahl and Salvat is evident, but there is some disagreement. BALLY (1983) believed that the resurgence and saturation zones of Salvat correspond to the sublittoral of Dahl. Other researchers conceived of the resurgence zone as part of the midlittoral of Dahl (McLACHLAN 1990, RAFAELLI *et al.* 1991, JARAMILLO & GONZALEZ 1991). According to McLACHLAN (1990), resurgence zone species are intertidal forms that require wet sand during low tide, while retention zone species are also intertidal forms, but are capable of remaining in sand that is only slightly damp during the low tide period. In the sectors studied, the resurgence zone species

(lower zone) occurred nearest to the water line, and their distribution may extend to the sublittoral.

Although beach zones are not clearly defined, there is evidence that the subdivision of the intertidal region into biological zones can be observed in many sandy beaches. Independent of the different opinions and nomenclature, the intertidal region of Enseada, Barra Velha, Araçá I and Araçá II sectors could be differentiated into two zones, in which the lower level showed higher diversity and richness. The results obtained in the present work show that the heterogeneous sediment, the organic matter content, and salinity were important for distribution of the mollusk community. Moreover, the distributions of some species could be related to variations in tide level and the availability of food.

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