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Annual variation of the malacofauna on two intertidal sandy substrates with rock fragments in southeastern Brazil

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- ***Abstract:*** The temporal variation in molluscan communities was studied in two intertidal substrates composed of sand and rock fragments (<300 mm) in São Sebastião Channel, Brazil. Samples were taken between August 1995 and July 1996 in São Francisco (mainland) and Engenho d'Água (São Sebastião Island) beaches. A pronounced decrease in abundance and diversity of molluscs was associated with changes in the structure of the environment, caused by sea storms in the beginning of the summer (December), and by the increase of waste water discharge in this same period. Areas not subjected to such events showed no evident modifications in mollusc fauna structure during the sampling period, and the small oscillations observed were attributed to population recruitment. Both natural and human factors may be acting together in determining the community organization in these environments, as is also in typical sandy beaches.

- ***Resumo:*** Estudou-se a variação anual da comunidade de moluscos em dois ambientes entremarés constituídos por areia e fragmentos rochosos (<300 mm) no Canal de São Sebastião, Brasil. As amostras foram obtidas mensalmente entre agosto de 1995 e julho de 1996 nas praias São Francisco (continente) e Engenho d'Água (Ilha de São Sebastião). Uma marcante redução na abundância e diversidade foi associada às mudanças estruturais do ambiente, causada por ressacas do mar no início do verão (dezembro), e ao aumento no fluxo de esgotos domésticos neste período. Em áreas onde estes eventos não foram evidentes, não houve grande alteração na composição faunística, e as pequenas oscilações foram atribuídas ao recrutamento de populações numericamente importantes. Ambos os fatores naturais e antrópicos podem estar atuando em conjunto para determinar a organização da comunidade nestes ambientes, tal como ocorre em praias arenosas típicas.

- ***Descriptors:*** Molluscs, Annual variation, Environmental disturbances, Sandy substrates with rock fragments, São Sebastião Channel, Brazil.

- ***Descritores:*** Moluscos, Variação anual, Distúrbios ambientais, Praias arenosas com fragmentos rochosos, Canal de São Sebastião, Brasil.

Introduction

Seasonal variation in marine communities is an actual topic of research. The importance of such studies lies in the fact that some temporal oscillations in diversity and community composition in coastal regions can be associated to human activities. Most of these activities can be easily detected and monitored, but some, such as oil spills, are unpredictable.

Many studies in sandy beach communities assign to natural oscillations in the abundance of numerically dominant populations as the cause of temporal variation of macrofauna (Holland & Polgar, 1976; Dexter, 1984; Souza & Gianuca, 1995; Veloso *et al.*, 1997). In temperate regions, the community composition is strongly influenced by temperature (Whitlatch, 1977; Leber, 1982), which is directly related to food limitation. Seasonality in tropical areas is generally related to rain periods (Dexter, 1979) and to disturb instead of temperature changes. Macrofauna is directly influenced by changes in the sediment constitution (McLachlan, 1996) and in salinity (Ansell *et al.*, 1972; Ansari *et al.*, 1986, Defeo & de Alava, 1995), beach erosion (Ansell *et al.*, 1972, Ong & Krishnan, 1995), organic enrichment (Beukema, 1991; Tsutsumi *et al.*, 1991), and fisher activity (Defeo & de Alava, 1995).

Studies on sandy substrates constituted by rock fragments as well as knowledge of the factors that organize their communities are lacking. The presence of rock fragments enhances environmental heterogeneity and creates moist and shady microhabitats (pers. obs.). According to Woodin (1981), the patterns of distribution and abundance of macrofauna are frequently correlated with environmental heterogeneity, i. e., presence and abundance of physical and/or biogenic structure. These rock fragments can also protect the organisms against desiccation, predation, and water movements, and, in association with sand, enable the settlement and recruitment of both sandy beach and rocky shore organisms (Denadai & Amaral, 1999).

Furthermore, in some intertidal rocky shores inundated by sand, the structural change in the substrate may cause an increase in the faunal diversity because of the higher environmental heterogeneity (McQuaid & Dower, 1990). On the other hand, the exclusion of psammophobic species (not tolerant to sand) may cause a reduction in the richness and abundance (Brown *et al.*,1991).

In this study we describe the annual variation in the molluscan communities, and the factors which influence it, of two structurally similar intertidal environments constituted by sand and rock fragments (São Francisco and Engenho d'Água Beaches).

Materials and methods

This study was conducted in two intertidal environments constituted by sand and rock fragments, São Francisco and Engenho d'Água, located in the São Sebastião Channel, northern coast of São Paulo State, Brazil. Random samples were taken monthly between August 1995 and July 1996, during low spring tides, totaling 19.08 m^2. The temperature (air and sediment), salinity of interstitial water, sediment grain size and calcium carbonate and organic matter contents were also evaluated. Refer to Denadai & Amaral (1999) for detailed description of the study area and sampling procedure. The molluscan individuals were identified to the lowest taxonomic level possible using the current literature that includes Brazilian species (Warmke & Abbott, 1975; Abbott & Dance, 1991; Rios, 1994).

Two-way analysis of variance (ANOVA) was used to compare the environmental variables among the sites and months, followed by Scheffé's test (Zar, 1984). All tests were performed at the 0.05 significance level. Ordination analysis (Reciprocal Averaging) was used to interpret the temporal distribution. This analysis was performed using Hill's method (Hill, 1979), giving equal weight to the species, considering outliers, and standardizing the data by square-root transformation. Diversity (H') was calculated using the Shannon-Wiener index in $\log_2$ (Krebs, 1989). Student's t-test was used to compare the density of molluscs between the present study and that of Salvador (1995), which was performed in the same area and using the same methodology during the period 1992/93.

Results

The environmental variables differed between the studied sites and among periods (Table 1). In São Francisco, coarse sand grains dominated the sediment, while medium-sized particles were more abundant in Engenho d'Água (Fig. 1). The composition of the sediment at SF and EA was similar only in summer, when finer sand grains were observed in SF. In EA, the sediment composition did not vary during the year. Calcium carbonate content was higher in SF than in EA, with exception of the spring period (Fig. 1). The organic matter content was higher in the spring in SF, evidencing an organic enrichment in this period (Fig. 1). Significant differences in salinity were recorded in the study period between SF and EA (Table 1). Salinity variation was higher at SF than at EA because of the presence of a waste-water canal in its supralittoral region (Fig. 1). Air temperature varied from 15°C in June to 31°C in January, and sediment temperature from 15.5°C in September to 32°C in January.

Table 1. Two-way ANOVA for the effects of study area (SF x EA), in São Sebastião Channel, Brazil, and seasons (period August 1995 to July 1996) on sediment grain size, calcium carbonate content, organic matter content, and salinity. (df, degrees of freedom; MS, mean square).

Source of variation	df	MS	F	p
Sediment grain size (*phy*)				
Area	1	21.657	66.152	<0.001
Season	3	1.138	3.477	0.018
Area*Season	3	0.868	2.652	0.051
Calcium carbonate content (%)				
Area	1	1.619	20.634	<0.001
Season	3	1.122	14.301	<0.001
Area*Season	3	1.248	15.905	<0.001
Organic matter content (%)				
Area	1	0.062	0.842	0.360
Season	3	1.301	17.535	<0.001
Area*Season	3	2.176	29.331	<0.001
Salinity (‰)				
Area	1	674.123	44.254	<0.001
Season	3	213.361	14.007	<0.001
Area*Season	3	84.501	5.547	0.001

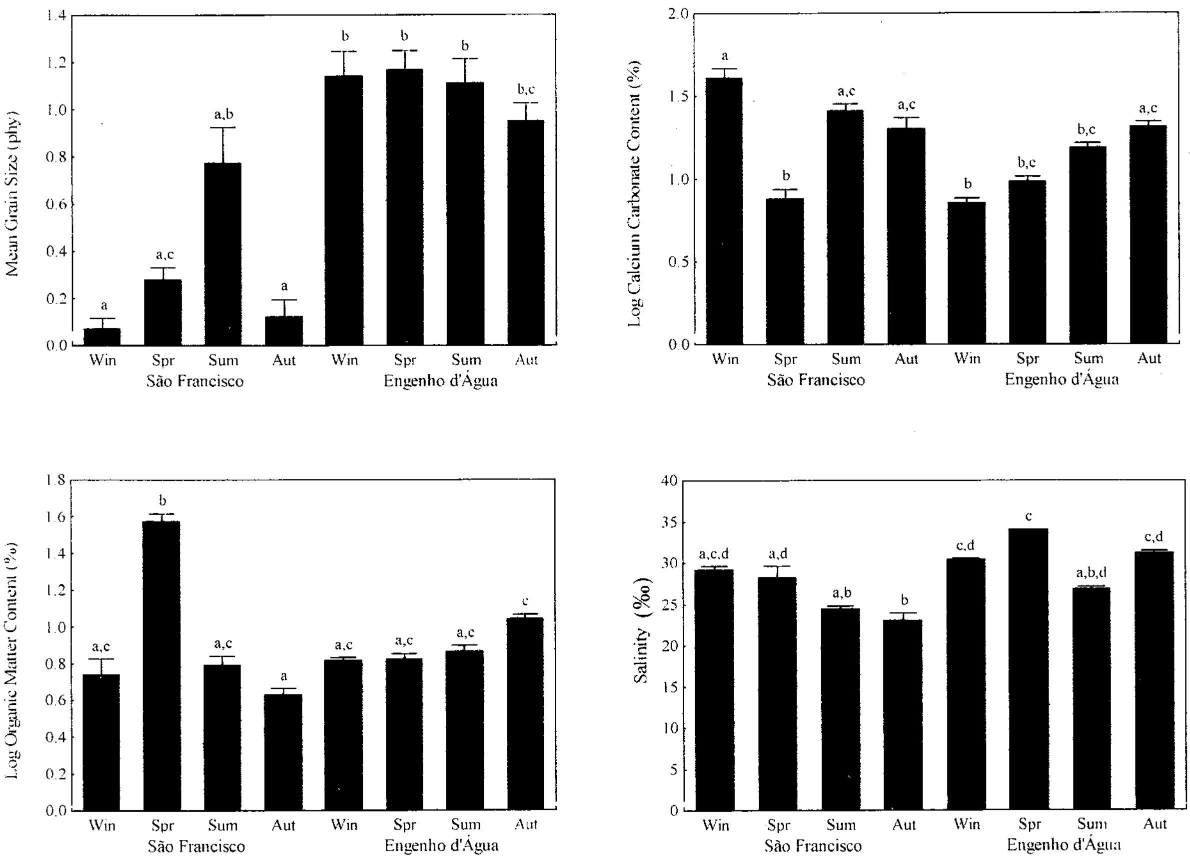

Fig. 1. Comparison of mean values of salinity, sediment grain size, calcium carbonate and organic matter contents between the two studied areas in São Sebastião Channel, Brazil and among the seasons (period August 1995 to July 1996). Superscript labels indicate the results of the Sheffé's test for pairwise multiple comparisons. Similar labels indicate non-significant differences for pair-wise comparisons. (Horizontal bars indicate +1 Standard error).

A reduction in community richness and abundance occurred in SF after January (Table 2). A total of 22 species and 367 individuals were recorded in the first half of the studied period (August to December/95) compared to 9 species and 188 individuals collected from January to July/96 (Table 2). Correspondence analysis organized the species in two distinct groups: one with species that occurred only in the first period (*Tegula viridula, Cerithium atratum, Semele proficua* and *Corbula cubaniana*), and another with species that were found over the entire year (*Codakia orbiculata, Lucina pectinata, Tellina lineata* and *Anomalocardia brasiliana*), but in lower abundance after January (Fig. 2).

Table 2. Occurrence and abundance of molluscs along the year in São Francisco Beach, São Sebastião Channel, Brazil.

	1995					1996							
SPECIES	A	S	O	N	D	J	F	M	A	M	J	J	TOT
Tegula viridula (Gmelin, 1791)	2	2	7	8	2	2							23
Cerithium atratum (Born, 1778)	2	6	24	19	3								54
Bittium varium (Pfeiffer, 1840)			1									1	2
Epitonium sp.												1	1
Stramonita haemastoma (Linnaeus, 1767)			1										1
Nassarius sp.	2				3								5
Nassarius vibex (Say, 1822)		1	4		1								6
Leucozonia nassa (Gmelin, 1791)			2										2
Ischnochiton striolatus (Gray, 1822)					1								1
Arcopsis adamsi (Dall, 1886)	1		1	1									3
Brachidontes solisianus (Orbigny, 1846)	1												1
Codakia orbiculata (Montagu, 1808)	1		5	1	4				1	1	1		14
Lucina pectinata (Gmelin, 1791)		1	1	1	1	1	1		2		3	1	12
Diplodonta punctata (Say, 1822)				1						1			2
Mactra fragilis Gmelin, 1791				1									1
Tellina lineata Turton, 1819	2	5	7	1	5		1	1		1	1	1	25
Semele proficua (Pulteney, 1799)		4	6	7	3								20
Tagelus divisus (Lightfoot, 1716)	1	1											2
Chione cancellata (Linnaeus, 1767)	1					1					1		3
Chione subrostrata (Lamarck, 1818)		1	2	1	3								7
Anomalocardia brasiliana (Gmelin, 1791)	13	38	20	22	60	23	15	6	6	6	25	14	248
Corbula caribaea Orbigny, 1842	1	2			2								5
Corbula cubaniana Orbigny, 1853	20	3	7	6	1								37
TOTAL	47	64	88	69	89	27	17	7	9	9	31	18	475

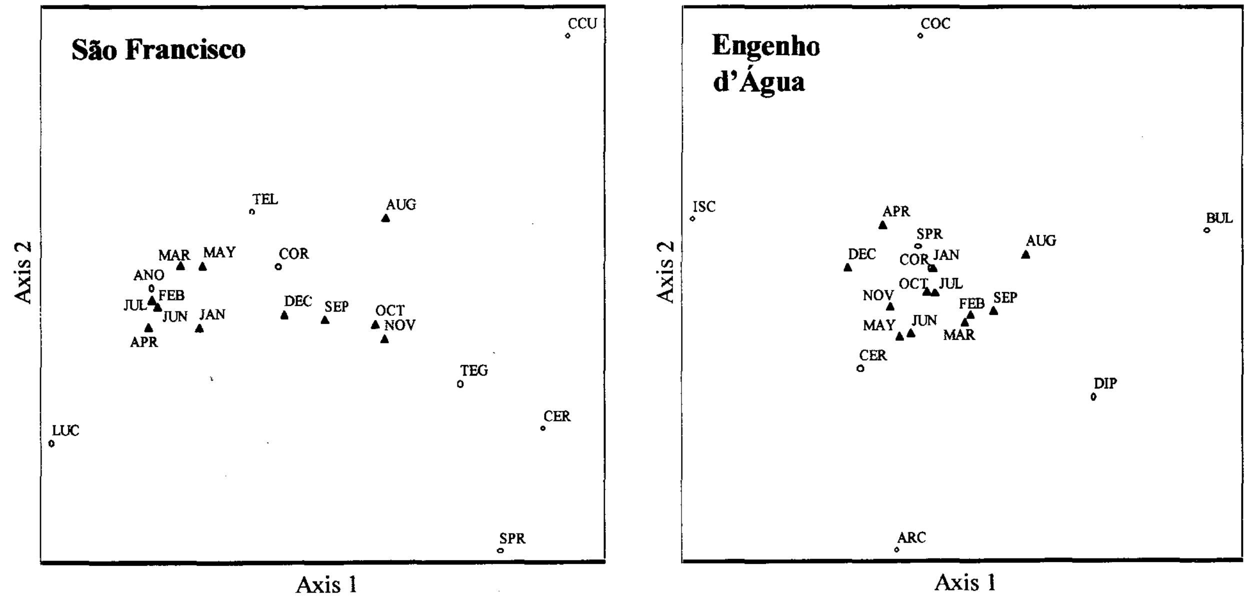

Fig. 2. Correspondence analysis of the most abundant species and of the sample months at São Francisco (total variation explained: axis 1 = 65.4 %, and axis 2 = 5.0 % -ANO= *Anomalocardia brasiliana*, CER= *Cerithium atratum*, COR= *Codakia orbiculata*, CCU= *Corbula cubaniana*, LUC= *Lucina pectinata*, SPR= *Semele proficua*, TEG= *Tegula viridula*, TEL= *Tellina lineata*) and at Engenho d'Água (total of variation explained: axis 1 = 34.3 %, and axis 2 = 2.6% - ARC= *Arcopsis adamsi*, BUL= *Bulla striata*, CER= *Cerithium atratum*, COC= *Codakia costata*, COR= *Codakia orbiculata*, DIP= *Diplodonta punctata*, ISC= *Ischnochiton striolatus*, SPR= *Semele proficua*).

Higher values of richness and abundance were recorded in EA, with only a small reduction from January to May/96 (Table 3). Species were ordered in relation to their presence and abundance in the months (Fig. 2). A major group was formed by species that were frequent during the entire year (*Cerithium atratum, Arcopsis adamsi, Codakia costata, C. orbiculata* and *Semele proficua*). Other species as *Ischnochiton striolatus* (spring – October, November and December), *Bulla striata* (winter/spring – August, September, and October) and *Diplodonta punctata* (earlier spring - September) showed distinct seasonal distributions. In general, the abundance decreased in the autumn (March, April), but most of the species remained present.

Figure 3 shows the Shannon diversity index of the sampled months (abscissa) vs. the number of species (ordinate). The fitted line represents the log of the number of species, i.e., the highest diversity value that the community can attain for a given richness. The distance between points and this line is an indirect measure of evenness. Diversity in SF was higher from August to December than at other periods, but evenness was low for all months. In EA, medium to high diversity values was recorded for all sampling periods, but with low values in April. Evenness in EA was high in all periods.

Table 3. Occurrence and abundance of molluscs along the year in Engenho d'Água Beach, São Sebastião Channel, Brazil.

	1995					1996							
SPECIES	A	S	O	N	D	J	F	M	A	M	J	J	TOT
Fissurella rosea (Gmelin, 1791)	1												1
Tegula viridula (Gmelin, 1791)			1	3	1			1				1	7
Astraea phoebia Röding, 1798			1										1
Neritina virginea (Linnaeus, 1758)		2											2
Phenacolepas hamillei (Fischer, 1857)	1				1		1					1	4
Modulus modulus (Linnaaeus, 1758)							1	1		1			3
Cerithium atratum (Born, 1778)	1	6	6	8	9	3	3	1	1	6	17	26	87
Natica pusilla Say, 1822												1	1
Chicoreus (Siratus) senegalensis Gmelin,1791		1											1
Trachypolia nodulosa (C.B.Adams, 1845)	1		3				1	1		1	1	4	12
Pisania pusio (Linnaeus, 1758)				1								2	3
Nassarius sp.	1												1
Leucozonia nassa (Gmelin, 1791)					2		1	1					4
Olivella minuta (Link, 1807)	1												1
Bulla striata Bruguière, 1792	20	7	10			2	12	1			2	5	59
Ischnochiton striolatus (Gray, 1828)			12	7	15	3	1		1	2	4	2	47
Nucula semiornata Orbigny, 1846				1									1
Arcopsis adamsi (Dall, 1886)		2	10	12	1	1	11	4		3	7	2	53
Lioberus castaneus (Say, 1822)										1			1
Limaria pelucida (C.B.Adams, 1846)			1										1
Codakia costata (Orbigny, 1842)	2	1	3	4	2	4	1	1	2			3	23
Codakia orbiculata (Montagu, 1808)	10	5	11	9	6	9	11	5	5	8	11	15	105
Diplodonta punctata (Say, 1822)	4	9	2	2		3	4	2		2	1	3	32
Laevicardium brasilianum (Lamarck, 1819)						1							1
Mactra fragilis Gmelin, 1791				1									1
Solen tehuelchus Orbigny, 1843			1						1	1			3
Tellina lineata Turton, 1819	1	2	2			1			1	3	1	1	12
Tellina versicolor De Kay, 1843				2									2
Semele proficua (Pulteney, 1799)	9	6	16	20	10	9	11	2	2	4	5	11	105
Semele purpurascens (Gmelin, 1791)				1			1			2	1	1	6
Ervilia nitens (Montagu, 1806)	1							3		1		10	15
Tagelus divisus (Spengler, 1794)	3		1							1	1		6
Ventricolaria rigida (Dillwyn, 1817)		1				1							2
Anomalocardia brasiliana (Gmelin, 1791)								1			1		2
Gouldia cerina (B.B.Adams, 1845)	2	1	1	1	4			1					10
Dosinia concentrica (Born, 1778)	1												1
Corbula caribaea Orbigny, 1843			1	1			1		1	1			5
Corbula cubaniana Orbigny, 1853			1	3	2	1							7
TOTAL	59	43	83	76	53	38	60	25	14	37	52	88	628

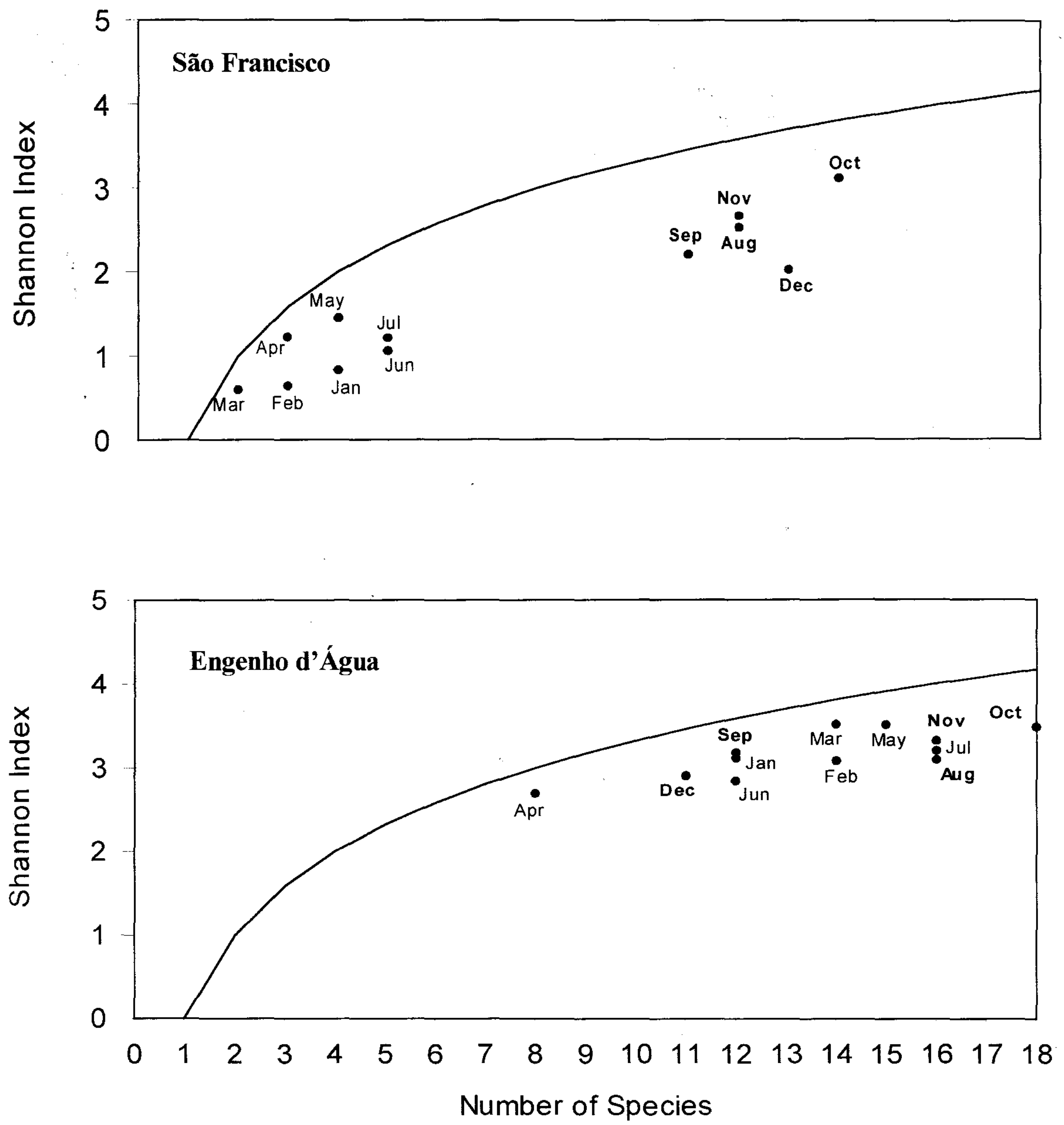

Fig. 3. Relationships between diversity (Shannon Index) and richness at the sample months in São Francisco and Engenho d'Água, evidencing the log $_2$(evenness) curve.

A comparison between the present investigation and a previous study in EA (Salvador, 1995) revealed some differences in environmental variables and community composition (Table 4). The mean diameter of sand particles tended to decrease from the previous to the present study (t=2.442, df=5, p=0.059; ϕ=0.912±0.094 and ϕ=1.091±0.098, respectively). Organic matter content was higher in the first period (%OM=1.659±0.096) than in the second (%OM=1.342±0.078; t=-4.655, df=5, p=0.006). Forty-one species and 238 individuals were collected in the earlier study (1992/93), in comparison to 39 and 628 were recorded in the present study (1995/96). Only 26 species were common to both periods, with evident differences in their abundance. *Tegula viridula, Olivella minuta, Codakia costata, Diplodonta punctata, D. semiaspera, Ervilia nitens,* and *Gouldia cerina* were more abundant in the first period, while *Cerithium atratum* and *Codakia orbiculata* were more abundant in the second. *Bulla striata, Ischnochiton striolatus, Arcopsis adamsi,* and *Semele proficua* showed high densities in both studies.

Table 4. Absolute abundance (N) and Density/m² of molluscs in Engenho D'Água Beach, São Sebastião Channel, Brazil in the periods 92/93 (Salvador, 1995) and 95/96 (Denadai & Amaral, 1999; Present study).

	1992/93		1995/96			1992/93		1995/96	
SPECIES	N	Dens.	N	Dens.	SPECIES	N	Dens.	N	Dens.
Fissurela rosea			1	0.06	*Diplodonta punctata*	21	13.04	32	5.45
Tegula viridula	5	3.23	7	0.90	*Diplodonta semiaspera*	7	4.79	1	0.55
Astraea phoebia			1	0.55	*Trachycardium muricatum*	1	0.11		
Neritina virginea			2	0.11	*Laevicardium brasilianum*	1	0.11	1	0.06
Phenacolepas hamillei	1	0.11	4	0.73	*Mactra fragilis*	1	0.11	1	0.06
Modulus modulus	1	0.11	3	0.17	*Solen tehuelchus*	2	0.22	3	0.67
Cerithium atratum	5	5.91	86	16.48	*Tellina* sp.	1	0.11		
Polinices lacteus	1	0.11			*Tellina lineata*			12	0.69
Natica pusilla			1	0.55	*Tellina versicolor*	5	0.55	2	0.11
Chicoreus senegalensis			1	0.06	*Macoma cleryana*	1	1.45		
Trachypolia nodulosa	5	1.89	12	1.69	*Semele proficua*	29	19.28	105	15.09
Stramonita haemastoma	1	0.11			*Semele purpurascens*	2	0.22	6	0.84
Pisania pusio			3	0.17	*Ervilia nitens*	8	8.92	15	0.86
Nassarius sp.			1	0.06	*Tagelus divisus*	2	0.22	6	1.40
Nassarius vibex	3	0.33			*Ventricolaria rigida*			2	0.06
Leucozonia nassa	3	1.67	4	0.23	*Chione subrostrata*	5	1.89		
Olivella minuta	5	4.57	1	0.06	*Chione intapurpurea*	1	1.45		
Bulla striata	14	9.58	59	9.88	*Anomalocardia brasiliana*	2	0.22	2	0.61
Ischnochiton striolatus	19	8.80	47	6.76	*Transennella stimpsoni*	1	1.45		
Nucula semiornata			1	0.06	*Gouldia cerina*	35	14.59	10	1.57
Lunarca ovalis	1	0.11			*Pitar fulminatus*	7	2.11		
Arcopsis adamsi	13	5.46	53	8.04	*Pitar palmeri*	1	0.11		
Lioberus castaneus	3	1.67	1	0.55	*Dosinia concentrica*			1	0.06
Limaria pelucida			1	0.06	*Corbula caribaea*	4	1.78	5	0.79
Codakia costata	13	5.46	23	2.33	*Corbula cubaniana*	1	1.45	7	2.39
Codakia orbiculata	5	1.89	105	15.65	*Thracia similis*	1	0.11		
Divaricella quadrisulcata	1	1.45							
					TOTAL	238	126.81	628	96.47

Discussion

The substrate constitution of the studied sites, with sand and rock fragments, create an heterogeneous environment that support both sandy beach and rocky shore species (Denadai & Amaral, 1999), leading to higher diversities in comparison to typical sandy beaches (Bally, 1983; Dexter, 1984; Defeo *et al.* 1992; Veloso *et al.*, 1997). McQuaid & Dower (1990) observed an increase in the fauna richness when rocky substrates were inundated by sand, through increasing the environmental heterogeneity. These authors classified the intertidal organisms in a spectrum of sand tolerance as: (1) psammophobic, restricted to rocky substrates free of sand; (2) sand-tolerant, occurring in both inundated and sand free rocky areas; (3) sand-dependent, found only in association with sand, and (4) psammophilic, restricted to sand column.

In December (summer) a reduction in environmental heterogeneity was evident given the rock fragments of SF were covered by sand due to sea storms common to this period. An accentuated decrease in the mollusc fauna richness and abundance was observed after this disturb, with the exclusion of species associated with rocks (Denadai & Amaral, 1999), mainly gastropods and some bivalves (*A. adamsi, Corbula caribaea* and *C. cubaniana*). In fact, storms and monsoons are known to play an important role in community structure by eroding sandy beaches (Ansell *et al.*, 1972; Ong & Krishnan, 1995). McLachlan (1996) observed changes in the macrofaunal composition (abundance and species exclusion) in a sandy beach after coarse sand addition originating from diamond mines in Namibia, thus reinforcing the importance of sediment constitution to sandy beach macrofaunal structure (Dexter, 1984; McLachlan, 1990).

Organic enrichment influences the community composition, reducing the diversity by exclusion of low tolerant especies and increasing the biomass associated with the dominance of a few opportunistic species (Pearson & Rosenberg, 1978; Warwick, 1986, 1988). There are two waste-water canals in the supralittoral region of São Francisco that are responsible by an increase in the coliform bacteria in the summer period (Denadai *et al.*, in press). In fact, the dominance of the polychaetes *Capitella capitata*, *Scolelepis squamata,* and *Laeonereias acuta,* and of the tubificid oligochaetes, species largely known as indicators of organic pollution (Grassle & Grassle, 1974; Pearson & Rosenberg, 1978; Amaral *et al.*, 1998), in the same period in SF (Rizzo & Amaral, 2000) evidence the organic pollution. Despite the clam *Anomalocardia brasiliana*, the dominant species in São Francisco (Denadai & Amaral, 1999), is common in organically-enriched areas (Schaeffer-Novelli, 1980), it also decreased in density after summer as the other ones. This species showed a tendency to increase in abundance after June, the start of its recruitment period (Salvador, 2001), indicating a successional event. Organic pollution showed to be a relevant factor in structuring the studied communities (Denadai *et al.*, in press), as in other marine environments. Despite the significant variation in the contents of calcium carbonate during the year in both sites, this environmental variable did not show any clear relationship with the temporal variation of the molluscs.

Temporal oscillations in communities not subject to disturbances, such as Engenho d'Água, are probably a consequence of the reproductive cycles of the dominant species, as suggested by several authors (Holland & Polgar, 1976; Dexter, 1984; Souza & Giannuca, 1995; Veloso et al., 1997). Studies on the molluscan population dynamics in São Sebastião Channel have been made with the bivalves *Anomalocardia brasiliana* and *Corbula cubaniana* (Salvador, 2001) and the gastropod *Cerithium atratum* (Denadai, 2001). According Salvador (2001), *Anomalocardia brasiliana* presents new recruits from early winter to early summer (June to November) and *Corbula cubaniana* along winter, spring and summer (July to February). *Cerithium atratum* also presents a large recruitment period, between April and October, with the peak in June (earlier winter). The species that were common to both SF and EA sites (*Cerithium atratum, Codakia orbiculata* and *Semele proficua*) did not present the same temporal pattern, occurring only in the earlier period in SF and along all the year in EA. These differences although can be attributed to specific causes in each site, i.e., disturbs in SF and recruitment patterns in EA.

Natural marine communities are continually changing as showed by the comparison of the faunistic composition in Engenho d'Água Beach between the periods of 95/96 (present study) and 92/93 (Salvador, 1995). Such changes are generally explained by environmental modifications (Ansell *et al.*, 1972; Whitlatch, 1977; Dexter, 1979; McLachlan, 1996), but they may be a consequence of the non-stable relationships among the populations that constitute the community (Dexter, 1984; Veloso *et al.*, 1997). Engenho d'Água is a visually dynamic intertidal area given the degree of exposure of the stones as well as the algae coverage, are constantly changing. A significant alteration in the sediment constitution was evidenced by a reduction in the mean grain size and organic matter content. The fauna also showed a marked variation between these two periods. Fifteen species disappeared while thirteen species were recorded for the first time. Twenty-six species were common to both periods but with a great variation in their abundances. Despite the absence of information on how the sediment grain size and organic matter influence such species, a relationship may be stablished between environmental and faunistic variation in EA.

Structural changes, such as the coverage of the rock fragments by sand, play a major role controlling the fauna distribution, contrasting to the marked influence of the hydrodynamics and sediment constitution in typical sandy beaches. The high community diversity in such habitats is associated with the presence of moist and shady microhabitats and by the presence of both rocky shore and sandy beach organisms.

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References

Abbott, R. T. & Dance, S. P. 1991. Compendium of seashells. London, Charles Letts e Co. Ltd. 411p.

Amaral, A. C. Z.; Morgado, E. H. & Salvador, L. B. 1998. Poliquetas bioindicadores de poluição orgânica em praias paulistas. Rev. Bras. Biol., 58(2):307-316.

Ansari, Z. A.; Ingole, B. S.; Banerjee, G. & Parulekar, A. H. 1986. Spatial & temporal changes in benthic macrofauna from Mandovi & Zuari Estuaries of Goa, West Coast of India. Indian J. mar. Sci., 15(4):223-229.

Ansell, A. D.; Sivadas, P.; Narayanan, B.; Sankaranarayanan, V. N. & Trevallion, A. 1972. The ecology of two sandy beaches in South West India. I. Seasonal changes in physical and chemical factors, and in macrofauna. Mar. Biol., 17(1):38-62.

Bally, R. 1983. Intertidal zonation on sandy beaches of the west coast of South Africa. Cah. Biol. mar., 24(1):85-103.

Beukema, J. J. 1991. Changes in composition of bottom fauna of a tidal-flat area during a period of eutrophication. Mar. Biol., 111(2):293-301.

Brown, A. C.; Wynberg, F. R. P. & Harris, S. A. 1991. Ecology of shores of mixed rock and sand in False Bay. Trans. R. Soc. S. Afr., 47(4-5):563-573.

Defeo, O. & de Alava, A. 1995. Effects of human activities on long-term trends in sandy beach populations: the wedge clam *Donax hanleyanus* in Uruguay. Mar. Ecol. Progr. Ser., 123(1-3):73-82.

Defeo, O.; Jaramillo, E. & Lyonnet, A. 1992. Community structure and intertidal zonation of the macroinfauna on the Atlantic coast of Uruguay. J. coast. Res., 8(4):830-839.

Denadai, M. R. 2001. Moluscos de praias do litoral norte do Estado de São Paulo: Comunidades de ambientes entremarés de baixo hidrodinamismo; Biologia populacional e produção secundária de *Cerithium atratum* (Born, 1778). Tese de doutorado. Rio Claro, UNESP, Instituto de Biociências. 89 p.

Denadai, M. R. & Amaral, A. C. Z. 1999. A comparative study of intertidal molluscan communities in sandy beaches, São Sebastião Channel, São Paulo State, Brazil. Bull. mar. Sci., 65: 91-103.

Denadai, M. R.; Amaral, A. C. Z.; Turra, A. (in press). Spatial distribution of molluscs on sandy intertidal substrates with rock fragments in southeastern Brazil. Estuar. coast. Shelf Sci.

Dexter, D. M. 1979. Community structure and seasonal variation in intertidal Panamaian Sandy Beaches. Estuar. coast. mar. Sci., 9(5):543-558.

Dexter, D. M. 1984. Temporal and spatial variability in the community structure of the fauna of four sandy beaches in south-eastern New South Wales. Austr. J. mar. Freshwat. Res., 35(6):663-672.

Grassle, J. F. & Grassle, J. P. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. J. mar. Res., 32(2):253-284.

Hill, M. O. 1979. Twinspan - A Fortran program for arranging multivariate data in a ordered two-way table by classification of the individual and attributes. New York, Cornell University Press.

Holland, A. F. & Polgar, T. T. 1976. Seasonal changes in the structure of an intertidal community. Mar. Biol., 37(4):341-348.

Krebs, C. J. 1989. Ecological methodology. New York, Harper & Row. 654p.

Leber, K. M. 1982. Seasonality of macroinvertebrates on a temperate, high wave energy sandy beach. Bull. mar. Sci., 32(1):86-98.

McLachlan, A. 1990. Dissipative beaches and macrofauna communities on exposed intertidal sands. J. coast. Res., 6(1):57-71.

McLachlan, A. 1996. Physical factors in benthic ecology: effects of changing sand particle size on beach fauna. Mar. Ecol. Progr. Ser., 131(1-3):205-217.

McQuaid, C. D. & Dower, K. M. 1990. Enhancement of habitat heterogeneity and species richness on rocky shores inundated by sand. Oecologia, 84(1):142-144.

Ong, B. & Krishnan, S. 1995. Changes in the macrobenthos community of a sand flat after erosion. Estuar. coast. Shelf Sci., 40(1):21-33.

Pearson, T. H. & Rosenberg, R. 1978. Macrobenthic succesion in relation to organic enrichment and pollution of the marine environment. Oceanogr. mar. Biol. a. Rev., 16: 229-311.

Rios, E. C. 1994. Seashells of Brazil. 2ª ed. Rio Grande, Editora da FURG. 492 p.

Rizzo, A. E. & Amaral, A. C. Z. 2000. Temporal variation of annelids in the intertidal zone of beaches of the São Sebastião Channel, southern Brazil. J. mar. biol. Ass. U. K., 80(6):1007-1017.

Salvador, L. B. 1995. Distribuição espaço-temporal das populações de moluscos da região entremarés de praias da Ilha de São Sebastião (SP). Dissertação de mestrado. Rio Claro, UNESP, Instituto de Biociências. 139 p.

Salvador, L. B. 2001. Malacofauna da região entremarés de praias de areia com fragmentos de rocha: Distribuição temporal e espacial; Dinâmica populacional e produção secundária de *Anomalocardia brasiliana* (Gmelin, 1791) e *Corbula cubaniana* Orbigny, 1853. Tese de doutorado. Rio Claro, UNESP, Instituto de Biociências. 73 p.

Schaeffer-Novelli, Y. 1980. Análise populacional de *Anomalocardia brasiliana* (Gmelin, 1791) na Praia do Saco da Ribeira, Ubatuba, Estado de São Paulo. Bolm Inst. oceanogr., S Paulo, 29(2):351-355.

Souza, J. R. B. & Gianuca, N. M. 1995. Zonation and seasonal variation of the intertidal macrofauna on a sandy beach of Paraná State, Brazil. Sci. Mar., 59(2):103-111.

Tsutsumi, H.; Kikuchi, T.; Tanaka, M.; Higashi, T.; Imasaka, K. & Miyazaki, M. 1991. Benthic faunal succession in a cove organically polluted by fish farming. Mar. Pollut. Bull., 23:233-238.

Veloso, V. G.; Cardoso, R. S. & Fonseca, D. B. 1997. Spatio-temporal characterization of intertidal macrofauna at Prainha Beach (Rio de Janeiro State). Oecol. Brasil., 3:213-225.

Warmke, G. L. & Abbott, R. T. 1975. Caribbean seashells. New York, Dover publications. 348p.

Warwick, R. M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. Mar. Biol., 92(4):557-562.

Warwick, R. M. 1988. The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. Mar. Pollut. Bull., 19(6):259-268.

Whitlatch, R. B. 1977. Seasonal changes in the community structure of the macrobenthos inhabiting the intertidal sand and mud flats of Barnstable Harbor, Massachusetts. Biol. Bull., 152(2):275-294.

Woodin, S. A. 1981. Disturbance and community structure in a shallow watter sand flat. Ecology, 62(4):1052-1066.

Zar, J. H. 1984. Biostatistical analysis. 2nd ed. Englewood Cliffs, N.J., Prentice-Hall. 718p.

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