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Composition and distribution of benthic molluscs on intertidal flats of Paranaguá Bay (Paraná, Brazil)*

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SUMMARY: Mollusc species composition, abundance and spatial distribution were analysed from April 1996 to October 1997 on two tidal flats in Paranaguá Bay (SE Brazil) at the entrance (St. I) (Lat. 25°32'S) and in the intermediate sector (St. II) (Lat. 25°30'S) of the estuary. At St. I, with the highest and least variable salinity, species richness ($R = 40$) and diversity ($H' = 1$; $D_S = 0.85$) were higher than at St. II ($R = 22$ and $H' = 0.54$; $D_S = 0.57$). The tropical clam *Anomalocardia brasiliana* was the most conspicuous mollusc of the two assemblages, followed by *Cerithium atratum*, *Neritina virginea* and *Crassostrea* sp. at St. I and by *Macoma constricta* and *N. virginea* at St. II. On the two flats, the decrease in species richness and abundance towards the upper tidal levels suggests a strong relationship between relative tolerance to physiological stress in the organisms and the degree of immersion/submersion.

Key words: Benthic molluscs, species composition, spatial distribution, tidal flats, *Anomalocardia brasiliana*, Paranaguá Bay, southeastern Brazil.

RESUMEN: COMPOSICIÓN Y DISTRIBUCIÓN DE MOLUSCOS BENTÓNICOS EN LLANOS INTERMAREALES DE LA BAHÍA DE PARAGUANÁ (PARANÁ, BRASIL). – Se ha analizado la composición específica de moluscos, abundancia y distribución espacial en dos llanos intermareales de la bahía de Paraguaná (SE de Brasil), entre abril de 1996 y octubre de 1997, en la boca (estación I) (Lat. 25°32'S) y en el sector intermedio (estación II) (Lat. 25°30' S) del estuario. En la estación I, con la salinidad más elevada y menos variable, la riqueza específica ($R = 40$) y diversidad ($H' = 1$; $D_s = 0.85$) fueron superiores a los valores detectados en la estación II ($R = 22$ y $H' = 0.54$; $D_s = 0.57$). El bivalvo tropical *Anomalocardia brasiliana* fue el molusco más conspícuo de las dos zonas, seguido por *Cerithium atratum*, *Neritina virginea* y *Crassostrea* sp. en la estación I y por *Macoma constricta* y *N. virginea* en la estación II. En los dos llanos, el descenso en riqueza específica y en abundancia hacia los niveles mareales superiores sugiere una fuerte relación entre la tolerancia relativa al estrés fisiológico en los organismos y en el grado de inmersión/emersión.

Palabras clave: moluscos bentónicos, composición específica, distribución espacial, llanos intermareales, *Anomalocardia brasiliana*, Bahía de Paraguaná, Brasil.

INTRODUCTION

Tidal flats generally have a rich benthic community that serves as a food resource for visiting species such as birds, demersal fish and decapods.

According to Reise (1985), the areal extension of the tidal flats (determined by the coastal slope and the tidal range), their sediment stability and composition (resulting from the energy of waves and tidal currents) and the frequency and length of low tide exposure (imposed by the tidal pattern), together with climatic conditions and geomorphology, all

affect the distributional patterns of the organisms in these environments. Peterson (1991) also noted disturbances in the sediment, the settling patterns of larvae, predation and competition for space and food as factors that affect the spatial macrofauna distribution in the intertidal flats.

On the coast of Paraná State (SE Brazil), tidal flats occupy an area of approximately 310 km², and they are formed locally by mangroves (composed of *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia schaueriana* vegetation), monospecific *Spartina alterniflora* marshes, and non-vegetated intertidal banks (Angulo, 1992). In Paranaguá Bay, the non-vegetated intertidal banks occur mainly in the falls of tidal rivers and at the extremities of islands in the interior of the estuary (Bigarella *et al*., 1978). Molluscs, together with polychaete worms and crustaceans, are the dominant organisms of these communities (Netto and Lana, 1997).

The present study sought to analyse two non-vegetated intertidal flats of Paranaguá Bay with respect to the species composition and spatial distribution of benthic molluscs.

MATERIAL AND METHODS

The estuarine complex of Paranaguá Bay, situated in the extreme east of Paraná State (25º30'S 48º30'W), comprises diverse sectors and is largely bordered by mangrove swamps. This complex forms part of an extensive subtropical estuarine system, which includes Iguape-Cananéia Bay on the southern coast of São Paulo State (Lana *et al*., 2000). The estuary tide, with an average range of 1.7 m, is predominantly semidiurnal (Portobrás, 1988; Marone and Camargo, 1994), the salinity forms a decreasing

FIG. 1. – Map of the region, with the sampling points indicated.

horizontal gradient from the entrance to the interior of the system, and the water temperature ranges on average from 20ºC (winter) to 30ºC (summer) (Knoppers *et al*., 1987).

Monthly sampling was carried out from April 1996 to October 1997 at two tidal flats, one (St. I) (Lat. 25º32'S) close to the entrance of Paranaguá Bay and the other (St. II) (Lat. 25º30'S) at the midpoint of the estuary (Fig. 1). A transect of 400 m was established over the non-vegetated intertidal flats between the *Spartina alterniflora* belt line and the emersion line at low spring tide, with 3 equidistant sampling levels (N1-upper, N2-intermediate and N3-lower). Samples with 10 aleatory replicates at each level were collected with a corer 0.049 m² in area, buried to a depth of 10 cm. Sediment samples were sieved through 1 mm mesh size, and all biological material fixed in 4% buffered formaldehyde solution and preserved in 70% ethanol. Molluscs were identified, quantified, and measured with a vernier caliper to 0.01 mm (gastropods spire to the base of the operculum, and bivalves and chitons anterior-posterior axis). The material is held by the authors (CEM-UFPR, Pontal do Sul, PR, Brazil).

Observations made by Boehs (2000) indicated low slope on both of the flats (St. I: 0.28 cm·m⁻¹ and St. II: 0.14 cm·m⁻¹), a predominance of very fine sands at St. I and fine sands at St. II (Wentworth scale), and a decreasing gradient in grain size from the lower to the upper intertidal levels. From April 1996 to October 1997, the seawater temperature at the two locations varied between 16°C in winter and 27°C in summer, and the salinity showed an average of 31 ppt (28-35 ppt) at St. I and 25 ppt (14-30 ppt) at St. II (Boehs, 2000).

The species frequency was obtained from the index $C=P/N(100)$, in which C=Constance, P=number of samples containing the species and N=total number of samples (Bodenheimer, 1955). Diversity was estimated by the following indices, according to Brower *et al*. (1990): (a) Margalef [$D_a=(s-1)/\log N$, in which s=number of species and N=number of individuals; (b) Shannon-Wiener, at base 10 [$H'=-\sum p_i \log_{10} p_i$, in which $p_i=n_i/N$ and p_i=proportion of the total of individuals that occur in species i, equation equivalent to $H'=(N \log N - \sum n_i \log n_i)/N$]; and (c) Simpson [$D_s=1-l$], obtained by applying Simpson's Dominance Index [$l=\sum n_i(n_i-1)/N(N-1)$, where n_i=number of individuals of the species and N=total number of individuals in the sample]. The similarity in the malacofauna between and at the locations was assessed by the following indices (Brower *et al*.,
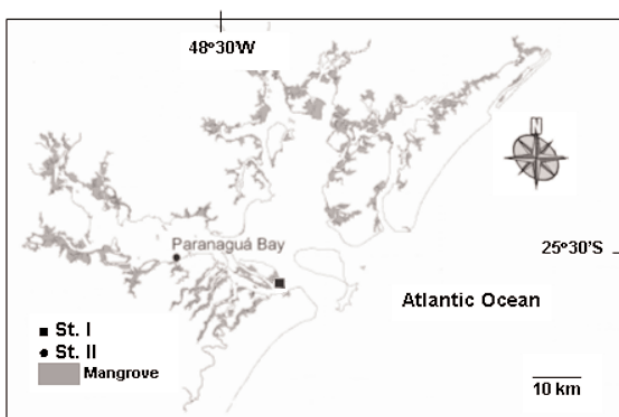
TABLE 1. – Species composition, absolute frequency (*Af*), constancy (*C*), species richness, total abundance, diversity and dominance of the benthic molluscs on intertidal flats of Paranaguá Bay (SE Brazil). Monthly sampling between April1996 and October 1997 (N/location=18).

	Af St. I	*C* (%) St. I	*Af* St. II	*C* (%) St. II
Polyplacophora Blainville, 1816	11	27.7		
Gastropoda Curvier, 1797:				
Neritina virginea (Linnaeus, 1758)	840	100	1,406	100
Littorina angulifera (Lamarck, 1822)	1	5.5		
Solariobis shumoi (Vanatta, 1913)	2	5.5	2	5.5
Bittium varium (Pfeiffer, 1840)	140	61.1		
Cerithium atratum (Born, 1778)	1,061	100		
Finella dubia (Orbigny, 1842)	195	33.3	1	5.5
Natica micra (Haas, 1953)	1	5.5		
Seila adamsi (H. Lea, 1845)	3	16.6		
Epitonium albidum (Orbigny, 1842)	2	11.1		
Thais haemastoma (Linnaeus, 1767)	17	38.8	3	16.6
Thais mariae Morretes, 1954			81	83.3
Anachis catenata (Sowerby, 1844)	56	66.6	3	11.1
Nassarius vibex (Say, 1822)	143	100	281	100
Olivella minuta (Link, 1807)	3	5.5		
Turridae Swaison, 1840			1	5.5
Turbonilla interrupta (Totten, 1835)	3	11.1		
Cylichna sp. Loven, 1846	255	50	69	44.4
Acteocina sp. Gray, 1847	14	16.6		
Bulla striata Bruguìère, 1792	78	77.7		
Haminoea elegans (Gray, 1825)	6	5.5	2	5.5
Pelecypoda Goldfuss, 1820:				
Nucula sp. Lamarck, 1799	2	5.5	1	5.5
Anadara ovalis (Bruguìère, 1789)	1	5.5		
Mytella charruana (Orbigny, 1842)			10	5.5
Mytella guyanensis (Lamarck, 1819)	5	16.6	18	44.4
Crassostrea sp. Sacco, 1897	737	88.8		
Lucina pectinata (Gmelin, 1791)	228	100	198	100
Codakia costata (Orbigny, 1842)	19	61.1		
Ctena pectinella C. B. Adams, 1852	63	94.4		
Divaricella quadrisulcata (Orbigny, 1842)	145	88.8		
Felaniella candeana (Orbigny, 1842)	11	38.8		
Tellina nitens C. B. Adams, 1845	70	66.6	27	61.1
Macoma sp. Leach, 1819	5	16.6		
Macoma constricta (Bruguìère, 1792)	315	100	1,699	100
Tagelus divisus (Spengler, 1794)	32	66.6	243	88.8
Tagelus plebeius (Lightfoot, 1786)			15	27.7
Chione cancellata (Linnaeus, 1767)	2	11.1		
Chione subrostrata (Lamarck, 1818)			12	50
Anomalocardia brasiliana (Gmelin, 1791)	1,950	100	6,724	100
Prothothaca pectorina (Lamarck, 1818)	1	5.5	2	11.1
Pitar fulminatus (Menke, 1828)	2	11.1		
Sphenia antillensis Dall & Simpson, 1901	70	55.5	15	33.3
Corbula caribaea Orbigny, 1842	10	38.8		
Periploma ovata Orbigny, 1846	1	5.5		
Cardiomya cleryana (Orbigny, 1846)	1	5.5		
Total no. of species	40		22	
Total no. of individuals	6,501		10,813	
Diversity - Margalef (*D_a*)	10.23		5.21	
Diversity - Shannon-Wiener, in base 10 (*H'*)	1		0.54	
Diversity - Simpson (*D_s*)	0.85		0.57	
Dominance - Simpson (*l*)	0.15		0.43	

1990): (a) Jaccard [$CC_J = c/(s_1 + s_2 - c)$, equivalent to $CC_J = c/S$, where s_1 and s_2 represent the number of species of communities 1 and 2 respectively, *c* is the number of species common to both communities and *S* is the number of species found in the two communities]; (b) Sşrensen [$CC_S = 2c/s_1 + s_2$]; (c) Percentage of Similarity [$PS = 1 - \sum |p_i - q_i|/2$, where p_i is the proportional composition of the species *i* in the first community and q_i that of the second community, $p_i = x_i/N_1 \times 100$ being the percentage of individuals in the first community (where x_i is the number or density of the species *i*) and $q_i = y_i/N_2 \times 100$ the percentage of individuals in the second community (where y_i is the number or density of the species *i*)]; (d) Bray-Curtis [$I_{BC} = 1 - \sum |x_i - y_i|/\sum (x_i + y_i)$, where x_i is the abundance of the species *i* in the first community and y_i is the abundance of that species in the second community]; and (e) Horn [$H' = (N \log N - $

$\sum x_i \log x_i - \sum y_i \log y_i)/ N]$, calculated from Shannon-Wiener's Diversity Index (H').

RESULTS

A total of 45 mollusc species were sampled. Species richness and diversity were highest at the entrance to the bay (St. I) than in the middle sector (St. II), where the abundance and the dominance were more marked (Table 1).

Approximately 40% of the species occurring in more than 50% of the samples were considered constant species. These species formed 94% of the total of individuals at St. I and 98% at St. II. Among the constant species, the gastropods *Bittium varium*, *Cerithium atratum* and *Bulla striata* and the bivalves *Crassostrea* sp., *Codakia costata*, *Ctena pectinella* and *Divaricella quadrisulcata* were exclusive to St. I. *Thais mariae* and *Chione subrostrata* were exclusive to St. II. Uncommon species (frequency of occurrence less than 25% in

TABLE 2. – Spatial distribution of the benthic molluscs on intertidal flats of Paranaguá Bay (SE Brazil), with average densities (ind.· m^{-2}) represented by: * less than 10 individuals; ** between 10 and 30 individuals; *** between 30 and 50 individuals; **** between 50 and 100 individuals; ***** between 100 and 200 individuals; ****** more than 200 individuals and ******* over 700 individuals. Monthly sampling between April 1996 and October 1997.

Species	(St. I) N1 Upper	(St. I) N2 Intermediate	(St. I) N3 Lower	(St. II) N1 Upper	(St. II) N2 Intermediate	(St. II) N3 Lower
Polyplacophora			*			
Neritina virginea	**	*	*****	*	*****	*****
Littorina angulifera		*				
Solariobis shumoi		*				*
Bittium varium		**	**			
Cerithium atratum		*	*****			
Finella dubia	*	***	*			*
Natica micra			*			
Seila adamsi			*			
Epitonium albidum			*			
Thais haemastoma	*		*		*	*
Thais mariae					*	**
Anachis catenata		*	*		*	*
Nassarius vibex	*	*	**	*	**	**
Olivella minuta			*			
Turridae						*
Turbonilla interrupta		*	*			
Cylichna sp.	*	****		*	*	*
Acteocina sp.	*	*				
Bulla striata	*	**	*			
Haminoea elegans	*				*	*
Nucula sp.			*			*
Anadara ovalis			*			
Mytella charruana						*
Mytella guyanensis		*		*	*	*
Crassostrea sp.		*	****			
Lucina pectinata	**	**	*	***	*	*
Codakia costata			*			
Ctena pectinella			*			
Divaricella quadrisulcata			**			
Felaniella candeana	*	*	*			
Tellina nitens	*	*	*	*	*	*
Macoma sp.			*			
Macoma constricta	***	*	*	****	*****	*****
Tagelus divisus	*	*	*	***	*	*
Tagelus plebeius				*	*	*
Chione cancellata			*			
Chione subrostrata					*	*
Anomalocardia brasiliana	***	******	****	***	*******	*******
Prothotaca pectorina			*			*
Pitar fulminatus		*	*			
Sphenia antillensis		*	*	*	*	*
Corbula caribaea			*			
Periploma ovata			*			
Cardiomya cleryana		*				
Total no. of species	14	23	33	11	16	22
Total no. of individuals	905	1,962	3,634	870	4,967	4,976

the samples) comprised 45% of the species at St. I and 41% at St. II, and formed only 1% of the total of individuals at St. I and 0.2% at St. II. Bivalves were the most abundant molluscs on both of the flats (St. I: 56% and St. II: 83%). *Anomalocardia brasiliana*, numerically, was the most common of the two assemblages (St. I: 30% and St. II: 62%), followed by *C. atratum* (16%), *Neritina virginea* (13%) and *Crassostrea* sp. (11%) at St. I and by *Macoma constricta* (16%) and *N. virginea* (13%) at St. II (Table 1).

At both locations, a decrease in species richness and abundance of the molluscs occurred from the lowest (N3) to the highest level (N1) (Table 2). Chitons were restricted to the N3 level (St. I), gastropods occupied preferentially the intermediate (N2) and lower (N3) levels, and bivalves generally showed the broadest distribution on the flats. *Bittium varium*, *Cerithium atratum*, *Thais mariae*, *Anachis catenata* and the oysters *Crassostrea* sp., all constant species, were observed exclusively in the intermediate (N2) and lower (N3) belts of the flats, and *Codakia costata*, *Ctena pectinella* and *Divaricella quadrisulcata* were only observed at N3 (Table 2). The uncommon species (with frequency of occurrence of less than 25%, Table 1) were also restricted to the lower belt of the shallows, mainly in N3 (Table 2). For the bivalves *Anomalocardia brasiliana*, *Lucina pectinata*, *Tagelus divisus* and *T. plebeius*, the clear presence of recruits and young was noted in the upper belt of the shallows.

The two flats exhibited a similarity of 46% (average between indices: CC_J and CC_S) with regard to the specific composition of molluscs, of 55% (average among indices: PS, I_{BC} and H') with reference to the proportional composition, and of 51% taking the average of all indices (Fig. 2a). St. I exhibited the most marked zonation of molluscs, with an average dissimilarity of 51% among the three sampling levels with regard to the presence-absence of species and of 67% with regard to the relative abundance of species. At this location, with respect to species (CC_J and CC_S) and proportional composition (PS, I_{BC} and H'), the greatest similarity was observed at the intermediate (N2) and upper (N1) levels (Fig. 2b). At St. II, the similarities exhibited a higher average than at St. I (specific composition 70% and proportional composition 65%). This was most marked between the intermediate (N2) and lower (N3) levels of the flat, particularly in the proportional composition (Fig. 2c).
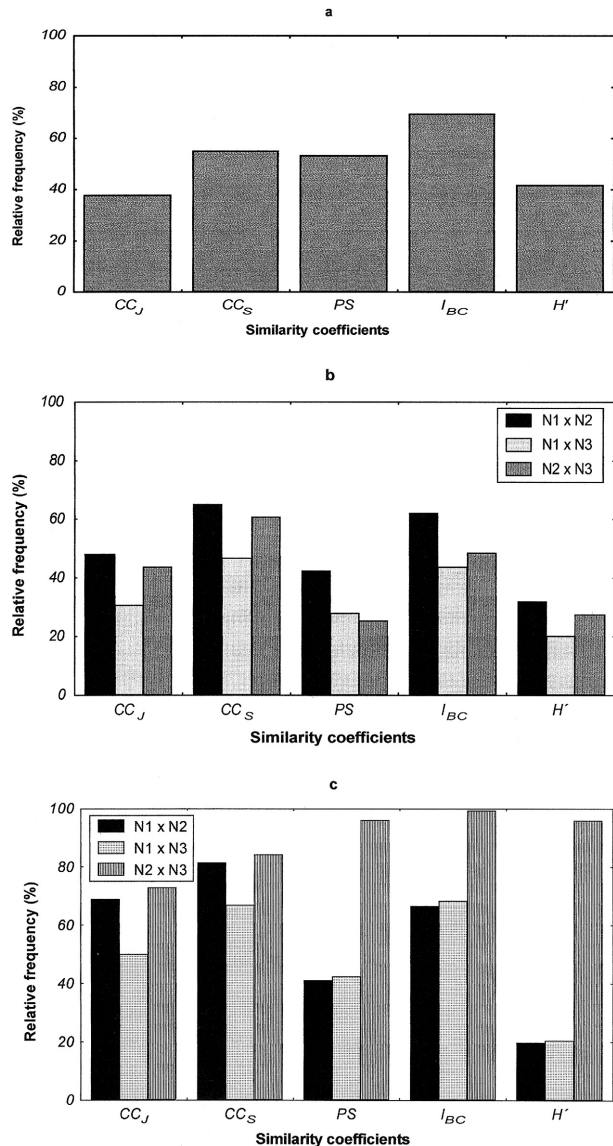

FIG. 2. – Similarities in the malacofauna between the locations (**a**) and in the locations (**b**: St. I and **c**: St. II), with respect to species richness (CC_J and CC_S) and proportional composition of species (PS, I_{BC} and H').

DISCUSSION

The spatial distribution of benthic fauna at the intertidal level is reported as being strongly affected by the variation in physico-chemical conditions (Reise, 1985; Peterson, 1991; Wilson, 1991). As a result of the physical regime imposed by the tides, a decrease in the species richness generally occurs from subtidal bottoms towards the high tide level (McIntyre and Eleftheriou, 1968; Johnson, 1970). The high degree of fauna similarity normally observed between the intertidal level and the immediately-adjacent infralittoral zone results, according

to Reise (1985), from tidal, nocturnal and/or seasonal migrations to and from the tidal flats and, according to Holland and Polgar (1976), also from passive transport by the carriage (through the action of waves and tides) of animals from the sublittoral to the intertidal zone. This would explain the occasional presence in the present study of various species, particularly represented by recruits and young, at the lower level of the flats.

As a result of the decrease in wave strength and tidal current energy in the direction of the upper intertidal zone along extensive banks of low slope, there generally occurs a decrease both in grain size and in sediment aeration from the lowest to the highest tidal levels. Boehs (2000) has described frequent conditions of hypoxia and even anoxia in the interstitial water in the belt corresponding to N1 in the present study, particularly at St. I. These conditions, together with the greater time of exposure to the air at the upper levels in these environments, make the organisms more vulnerable to physiological stress and are probably responsible for the high degree of dissimilarity, both in species richness and (principally) in relative abundance, of the molluscs between the upper and the lower levels, especially at St. I. At this site, the slope is more pronounced than at St. II (Boehs, 2000), and this is presumed to lead to a greater exposure time during low tides at N1. According to Underwood and Denley (1984), the air exposure may cause thermal shock, desiccation, osmotic imbalance and a temporary cessation in feeding and aerobic respiration. Peterson and Black (1988) have also demonstrated a decrease in growth of bivalves when these are transplanted from the lower to the upper levels on a tidal plain, with the decline in growth being greatest for those "specialist" species from the lowest levels, based on the hypothesis, proposed by Peterson (1991), of a relationship between zonation and relative tolerance to physiological stress in the organisms. In this context, the Lucinidae *Codakia costata*, *Ctena pectinella* and *Divaricella quadrisulcata*, constant species at St. I and restricted to the lowest tidal level (N3), are reported by Rios (1994) to occur from the intertidal zone to 100 m in depth. Thus, this intertidal level is most probably their limit of tolerance of intertidal conditions.

Competition for space and food are reported to have a lesser effect on the distribution of organisms and the consequent zonation in soft sediments (Peterson, 1979; Black and Peterson, 1988; Wilson, 1991), while diverse biological interactions, together with physical conditions, undoubtedly affect the distribution of organisms in these environments. Thus, for example, the exclusive finding of *Turbonilla interrupta* in the occurrence belt of *Crassostrea* sp. at St. I may be related to the ectoparasitism (Rios, 1994) that this species exerts over the oysters. While *Sphenia antillensis* also occurred at St. II (where the oysters were absent), it was always found to be associated with these organisms at St. I as epizoites. Oysters (probably due to the unavailability of other kinds of hard substrates for their attachment in the non-vegetated belts) were observed at the intermediate and lower levels of St. I, adhering mainly to empty shells of *Anomalocardia brasiliana*, which were abundant in this belt. *Neritina virginea* and *Chione subrostrata* were also more abundant in the belts containing deposits and fragments of shells, and, though the cause of this association is unknown, it has been observed previously by Rios (1994) in other regions.

The feeding habits of the molluscs also appear to affect their spatial distribution. According to Rhoads and Young (1970), the distribution of gastropods, be they predators, herbivores or detritivores, is directly conditioned by the pattern of food belts, which may explain the preferential distribution of some of the species in the lower belt of the flats where, due to a greater submersion time and the carriage of detritus from the higher tidal levels, the availability of food tends to be greater than on the upper belts. Thus, carnivorous species such as *Thais haemastoma, T. mariae*, *Anachis catenata*, *Natica micra* and *Epitonium albidum*, necrophages such as *Nassarius vibex* and those that feed on algae and detritus, such as *Bittium varium* and *Cerithium atratum*, were restricted or more abundant in this belt along the banks. With reference to the bivalves, according to Rhoads and Young (1970), due to their filtration feeding habits these molluscs can potentially occupy wider belts in the intertidal region, as was shown in both of the flats analysed.

The spatial intertidal distribution of organisms may also be affected by the spatial variability in the settling of larvae and by the intensity variation of predation by marine consumers with intertidal elevation (Peterson, 1991). In the present study we found, particularly for *Anomalocardia brasiliana*, *Lucina pectinata, Tagelus divisus* and *T. plebeius*, the clear presence of recruits and young in the upper belt of the shallows, which suggests areas of preferential settling for the larvae and an eventual horizontal migration along the intertidal area. At least in the case of *A. brasiliana*, which, contrary to what was observed on the upper levels, exhibited a clear

dominance of larger individuals on the lower levels of the flats, according to Monti *et al*. (1991), a negative density-dependent interaction between larvae and adults (influenced by the high population densities) occurs, reflected in its horizontal distribution across the intertidal zone. With respect to predation, according to Peterson (1991), sluggish predatory invertebrates (such as predatory gastropods and seastars) probably do exert greater pressure lower on the shore, where they can specifically predate small molluscs, including recruits. Thus, the preferential settlement on upper intertidal levels probably contributes to the successful settling of some molluscs.

Low salinity generally occurring in the inner sections of estuaries has been noted (Tommasi, 1970; Capitoli *et al*., 1978; Wu and Richards, 1981) as the principal limiting factor for the occupation of marine species. Consequently, a decreasing gradient of species richness is generally observed towards the internal sectors of estuaries, mainly occupied by estuarine or typically euryhaline species, e.g. *Anomalocardia brasiliana*. At St. II, where the salinity was lower and more fluctuating than at St. I (Boehs, 2000), those species reported as typically estuarine such as *Thais mariae*, *Mytella charruana* and *Tagelus plebeius* (Tommasi, 1970; Rios, 1994) were found to occur, whilst they were absent at the entrance to the bay (St. I). Furthermore, the strong development of some species at St. II, such as *A. brasiliana* and *Macoma constricta*, is probably favoured by the low densities of other species (i.e. reduced competition). The marked dominance of *A. brasiliana* on both of the flats also is also assumed to be favoured by the high resistance (Hiroki, 1977) exhibited by this tropical clam to anoxic conditions.

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