

Macrofaunal community structure and zonation of an Ecuadorian sandy beach (bay of Valdivia)

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ABSTRACT. The sandy beach macrofauna of the Bay of Valdivia (Ecuador) was sampled in August-September 1999 along six replicate transects between the high and low water line. The sediment consisted of well-sorted, fine to medium sand. Taking into account the dimensionless fall velocity (Ω) and the relative tidal range, the beach was characterized as an exposed, low tide terrace - rip beach. The distribution of the macrofauna was mainly determined by the elevation on the beach. Thirty-one taxa were found throughout the study, varying between 10 and 22 taxa per transect. Molluscs were the most dominant taxon (overall average : 285 ind/m², max. : 2135 ind/m²), followed by crustaceans. The gastropod *Olivella semistriata* (overall average : 243 ind/m², max. 2131 ind/m²) was the most abundant species. The crustaceans were the most diverse taxon (10 spp.); *Haustorius* sp., *Excirolana braziliensis* and *Emerita rathbunae* were the most abundant species. Densities of polychaetes were low in comparison with the previous two taxa mentioned (overall average : 13 ind/m²). The total average density over the entire bay was 370 ind/m². Three zones of macrofaunal distribution along the tidal gradient could be distinguished : an upper beach, a middle beach and a lower beach assemblage. The upper beach assemblage consisted mainly of *Excirolana braziliensis* and ghost crabs. The middle beach assemblage had highest macrofaunal densities and was dominated by *Olivella semistriata* and *Haustorius* sp. The most diverse assemblage was found on the low beach, with representatives of different taxa, but with lower densities. These results are in conformity with other studies along the Pacific coast of South America and fit into the zonation scheme of DAHL (1952). Given that many other studies from South America were done at temperate latitudes, we conclude that, although differences in species composition were found, the general pattern of macrobenthos zonation on sandy beaches is similar in tropical regions.

KEY WORDS : Macrobenthos, sandy beach, Ecuador.

INTRODUCTION

Macrofaunal zonation on sandy beaches is a distinctive and well-described phenomenon of intertidal zones (MCLACHLAN & JARAMILLO, 1995). The existence of species zonation on exposed sandy beaches is thought to be mainly caused by species-specific responses to swash climate and sedimentology, with a less critical role of biological interactions (MCLACHLAN, 1983a; MCLACHLAN et al., 1993; MCLACHLAN & JARAMILLO, 1995).

Different generalizing zonation schemes for sandy beach macrofauna have been proposed (DAVENPORT, 1903; MORTENSEN, 1921; SCHULZ, 1937) with the schemes of DAHL (1952) and SALVAT (1964 and 1967) being the most commonly used. DAHL (1952) suggested a distinction between three zones, defined in terms of a typical crustacean fauna inhabiting each zone, while SALVAT proposed a four zone system based on physical conditions.

In all of the studies describing intertidal zonation within different South American Atlantic and Pacific regions, three zones have been recognized (MCLACHLAN & JARAMILLO, 1995 and references herein), supporting

Dahl's scheme. Several studies (CLARKE & PEÑA, 1988; DEFEQ et al., 1992; DEXTER, 1974, MCLACHLAN & JARAMILLO, 1995) showed that crustaceans are the most diverse taxon on South American sandy beaches. The upper parts of tropical and subtropical beaches are characterized by ocypodid crabs, while hippid crabs, bivalves and amphipods dominate the lower beach. Cirolanid isopods (*Excirolana* spp.) are abundant on the midshore, together with opheliid and spionid polychaetes; the bivalves *Mesodesma* spp. and *Donax* spp. are other characteristic organisms. To our knowledge, no information is available about sandy beach macrofauna in Ecuador. The studies of sandy beach macrofauna nearest to Ecuador were conducted to the south in Peru (8° S) by BOCANEGRA et al. (1985) and to the north in Colombia (1° 48' N) by RIASCOS & RALLÓN (2001), locations with different environmental conditions. Because the Ecuadorian coastal waters are divided by two opposite currents, the warm El Niño-current coming from the north, and the cold Humboldt-current coming from the south, and because of the tropical location of Ecuador, a different macrobenthic community structure might be expected.

In this study the intertidal zonation and assemblage structure of the macrofauna of the Bay of Valdivia (Ecuador; 1-2° S) were investigated. This bay was chosen because of the importance of the beach for harvesting shrimp larvae, which are used in one of Ecuador's largest economies.

This paper presents the distribution patterns of the macrofauna in order to set up a larger project on the influence of ENSO on macrobenthic communities of sandy beaches in Ecuador.

MATERIAL AND METHODS

Study site

The study area is located in the Bay of Valdivia, Ecuador (1°54'00" - 1°58'20" S and 80°46'00" - 80°45'30" W), approximately 50 km west of Guayaquil (Fig. 1). This 10 km long bay consists of 8 km of exposed sandy beaches with rock formations on either side.

The beaches have a semi-diurnal, mesotidal regime (DAVIES, 1964) with a tidal range of 2.5-3 m (average : 2.6 m). The modal breaker height (H_b) is 0.49 m. The modal wave period (T) is 14 s (unpublished pers. comm. S. GUARTATANGA).

The Ecuadorian coastal climate is characterised by two seasons : a dry-cool season (May-December) and a wet-warm season (January-April) and is influenced by currents in the Pacific Ocean. From July until October the area is subjected to the relatively cold (<22°C) Humboldt-current, heading North, while during the months January until April the warm (>25°C) El Niño-current, heading South, dominates.

Additional to the normal seasonality, with a periodicity of three to seven years the climatologic and oceanographic phenomenon ENSO dramatically alters the conditions along the Ecuadorian coast, with higher temperatures and precipitation levels during El Niño and lower temperatures during the subsequent La Niña.

Sampling and laboratory work

Sampling took place between 31 August and 5 September 1999. To cover habitat variability over the bay, six transects, distributed over the whole bay and perpendicular to the waterline, were sampled (Fig. 1 : A-F). Each transect was sampled at six stations : five stations were situated in the intertidal zone, while a sixth one was located on the dry beach. Sampling of the intertidal zone always started at high tide, following the receding water down the beach. To distribute the stations evenly across the intertidal gradient, the transect was sampled in the swash zone every 90 minutes (Fig. 2). At each station three replicate samples were collected by excavating a metal frame (sampling surface area : 0.1026 m²) to a depth of 15 cm. The samples were sieved alive over a 1 mm mesh-sized sieve. The organisms retained were stored in 8 % formaldehyde-seawater solution.

At each station, one sediment sample was collected for grain size analysis using a core with diameter 3.6 cm. In addition, the relative elevations of the different stations were measured using an altimeter. Distances between all sample sites were measured.

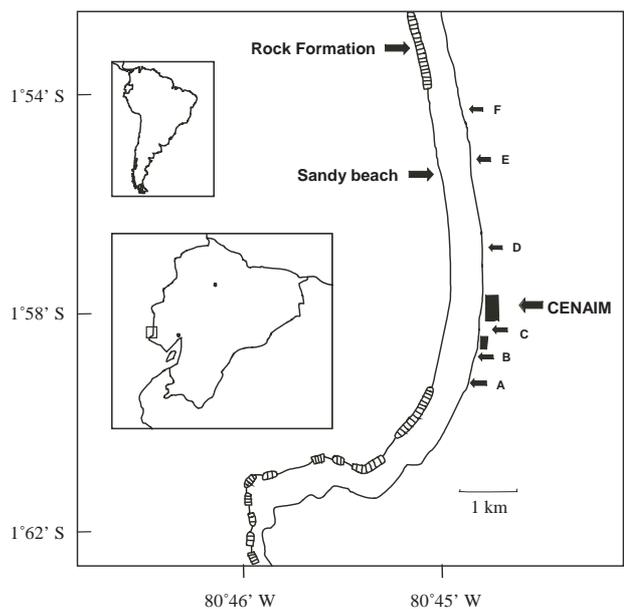


Fig. 1. – Geographical situation of the six sample transects (A-F) from the Bay of Valdivia, Ecuador (modified from BOOTHROYD et al., 1994).

Laboratory treatment

Macrobenthic organisms were counted and identified to species level, where possible.

The sediment grain size distribution between 2 and 850 μ m was determined with a laser COULTER LS and classified according to the Wentworth scale (BUCHANAN, 1984). The median grain size of the sand was largely biased by the mixture with shell fragments present in all samples, while the modal grain size remained unaffected. Hence, the modal grain size was preferred over median grain size as a good representation of the sediment's main characteristic.

Mathematical analyses

Combining the relative elevation of the lowest station of each transect with the data from the tide table for La Libertad (INOCAR) allowed estimation of their absolute elevation (relative to the mean low water level at spring tide, MLWS), from which the absolute elevation of all higher stations was calculated and beach profiles were obtained. By means of these beach profiles, the mean slope between low and high water of every transect was calculated. In this study, beach width is defined as the distance between the low water line and the lowest edge of the terrestrial vegetation.

The morphodynamic state of each transect was assessed by calculating the dimensionless fall velocity ($\Omega = H_b / w_s T$) (DEAN, 1973) and the relative tide range ($RTR = MSR/H_b$) (MASSELINK & SHORT, 1993). Sediment fall velocity (w_s) was obtained from sediment particle size after GIBBS et al. (1971). Mean spring tidal range (MSR) was obtained from the tide table (INOCAR).

For each sample the species richness (N_0) (HILL, 1973) and diversity (Shannon-Wiener diversity index, H') were determined (SHANNON & WEAVER, 1949). Community analysis was done by means of Cluster-analysis (CLIF-

FORD & STEPHENSON, 1975), Canonical Correspondence Analysis (CCA) (TER BRAAK, 1988) and Indicator Species Analysis (DUFRÈNE & LEGENDRE, 1997). Correlations between environmental variables were analysed by means of the non-parametric Spearman rank correlation coefficient (CONOVER, 1971).

To visualize zonation patterns of density and the number of species (N_0), polynomial functions were fit to the data according to the distance-weighted least squares smoothing procedure, using STATISTICA 5.1 (STATSOFT, 1996).

RESULTS

Environment

The beach width ranged from 70 to 172m, while the width of the intertidal zone ranged from 42 to 109m. The beach slope varied between 1:25 and 1:54. Ω was found between 1.172 and 1.541; RTR had a value of 5.306.

Although all transects were situated on the same beach, some variation in beach profile was observed (Fig. 2).

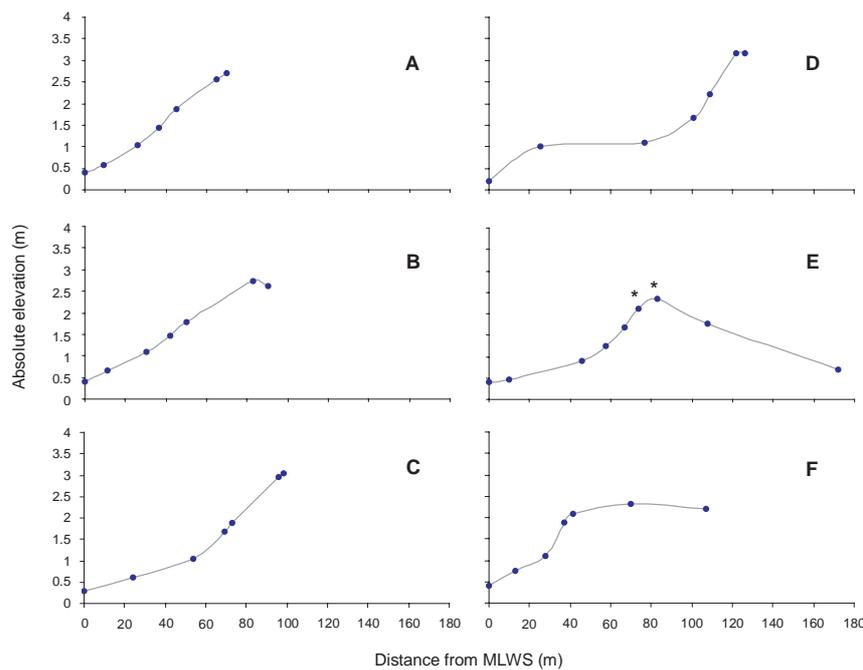


Fig. 2. – Beach profiles at the six transects (*: additional measuring points; the most right point is the vegetation line).

Furthermore, an alternation of ridges and runnels was present at transect F, while all other transects showed a quite featureless beach profile. Transects C and D showed a break in their slope. The upper part of transect C was steeper than the lower part (1:14 versus 1:39). The middle part of transect D had a gentle slope compared to the lower and upper part.

Fine to medium sands (125-500 μm) dominated the sediment. The stations' modal grain size ranged between 171 μm and 262 μm , except for the lowest stations of the two northern-most transects (modal grain size: 325 μm). The fraction of silt and clay (<63 μm) was low (0-3.2 %) and was negatively correlated with the elevation ($r=-0.707$; $p<0.0001$) as was the fraction of coarse sand (>500 μm) ($r=-0.428$; $p<0.0001$).

Macrofauna

A total of 31 macrofaunal taxa (ten taxa of crustaceans, ten of molluscs, eight of polychaetes and five others) were collected (Table 1 : species list), ranging from ten to 22 taxa per transect and varying between nil and ten taxa per station. H' diversity index ranged from 0 to 2.87. Overall average macrobenthic density was 370 ind/m². Molluscs

dominated the fauna (average : 285 ind/m², max. 2135 ind/m²), followed by crustaceans (average : 66 ind/m², max. 413 ind/m²). The gastropod *Olivella semistriata* was the most dominant species of the whole beach (average : 243 ind/m², max. : 2131 ind/m²). Other abundant species were the gastropods *Mazatlaniania hesperia*, *Mazatlaniania* sp., the polychaetes *Nephtys* sp., *Hemipodus* sp. and *Lumbrineris* sp., the haustoriid amphipod *Haustorius* sp., the cirrolanid isopod *Excirrolana braziliensis*, the anomuran crabs *Emerita rathbunae* and *Lepidopa deamae* and spat of bivalves.

Along the whole beach, highest species richness (N_0) was situated at the lower beach (Fig. 3) : species richness generally decreased towards the upper beach. Highest densities (up to 2400 ind/m²) were found between 1.6 and 2.2 m above MLWS. The stations on the dry zone of the beach (>2.4 m) had the lowest densities (maximum : 100 ind/m²). Below 1.6 m, densities remained more or less equal (generally : 80-600 ind/m²) : no obvious density increase towards MLWS was observed.

Multivariate techniques, CCA, Cluster analysis and species indicator analysis consistently distinguished between three station groups (Fig. 4). Station elevation

TABLE 1
Species list (* not sampled and not counted in analyses)

		Family	Species
Annelida	Polychaeta	Maldanidae	Maldanidae sp.
		Lumbrineridae	<i>Lumbrineris</i> sp. (Blainville, 1828)
		Magelonidae	<i>Magelona</i> cf. <i>mirabilis</i> (Johnston, 1865)
		Pisionidae	<i>Pisione</i> sp. (Grube, 1857)
		Glyceridae	<i>Hemipodus</i> sp. (Quatrefages, 1865)
		Nephtyidae	<i>Nephtys</i> sp. (Cuvier, 1817)
		Spionidae	<i>Scolelepis</i> sp. 1 (Blainville, 1828)
		<i>Scolelepis</i> sp. 2 (Blainville, 1828)	
Crustacea	Decapoda	Albuneidae	<i>Lepidopa daemae</i> (Benedict, 1903)
		Hippidae	<i>Emerita rathbunae</i> (Schmidt, 1935)
		Paguridae	<i>Pagurus</i> sp. (Fabricius, 1775)
		Ocypodidae *	<i>Ocypode occidentalis</i> (Stimpson, 1860)
		Portunidae	<i>Arenaeus mexicanus</i> (Gerstaecker, 1856)
	Amphipoda	Haustoriidae	<i>Haustorius</i> sp. (Müller, 1775)
			<i>Bathyporeia</i> sp. (Lindström, 1855)
	Isopoda	Cirolanidae	<i>Excirrolana braziliensis</i> (Richardson, 1912)
		Sphaeromatidae	<i>Paracerceis</i> sp. (Hansen, 1905)
	Mysidacea	Mysidae	<i>Bowmaniella</i> sp. (Bacescu, 1968)
			<i>Metamysidopsis</i> sp. (Tattersall, 1951)
Echinodermata	Echinoidea	Mellitidae	<i>Mellita longifissa</i> (Michelin, 1858)
	Stelleroidae		Ophiurae sp.
Mollusca	Bivalvia	Donacidae	<i>Donax mancorensis</i> (Olssen, 1961)
			<i>Donax</i> sp. (Linnaeus, 1758)
	Gastropoda	Tellinidae	<i>Strigilla chroma</i> (Salisbury, 1934)
		Collumbellidae	<i>Mazatlaniania hesperia</i> (Pilsbry & Lowe, 1932)
			<i>Mazatlaniania</i> sp. (Dall, 1900)
		Olividae	<i>Olivella semistriata</i> (Gray, 1839)
		Terebridae	<i>Hastula luctuosa</i> (Hinds, 1844)
Vitrinellidae	<i>Anticlimax willetti</i> (Hertlein & Strong, 1951)		
Hexapoda	Insecta		Insecta sp.
Nemertea			Nemertea sp.

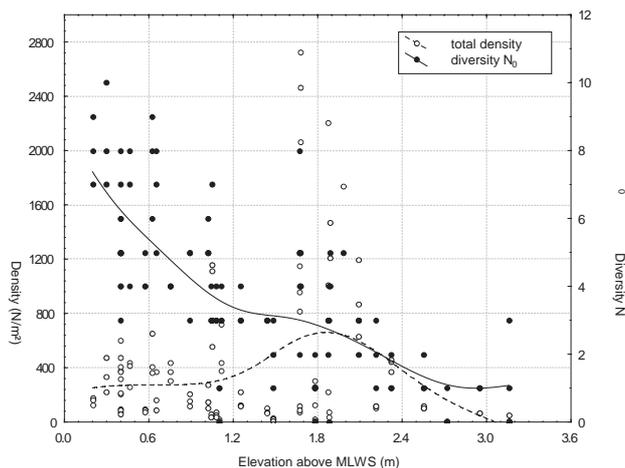


Fig. 3. – Total density and N0 diversity set against elevation.

was the most determining variable as far as upper and middle beach zones were concerned, % mud and % very fine sand (<125 µm) distinguished the lower beach fauna. The most important indicator species were *Excirrolana braziliensis*, *Olivella semistriata*, *Haustorius* sp., Bivalvia spat and Nemertea sp.

The first group of 47 replicates was found between 0.3 and 1.3 m above MLWS, the lower beach zone (Fig. 4 and table 2). The fine sand fraction (49 %) dominated the

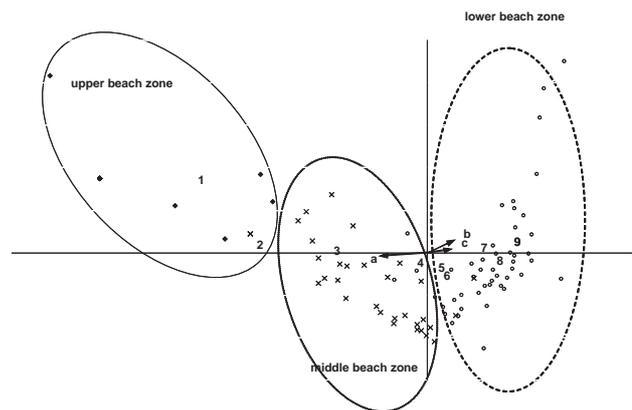


Fig. 4. – CCA-output with the three distinguished zones; group division is based on the outcome of all three applied multivariate techniques (eigenvalue axis 1: 0.500; axis 2: 0.183); a: elevation, b: % silt and clay (<63 µm), c: % very fine sand (63 – 125 µm); 1: *Insecta* sp., 2: *Excirrolana braziliensis*, 3: *Haustorius* sp., 4: *Olivella semistriata*, 5: *Nephtys* sp., 6: *Emerita rathbunae*, 7: *Nemertea* sp., 8: *Mazatlaniania* sp., 9: *M. hesperia*; ○: lower beach (47 stations), ×: middle beach (33 stations), ◆: upper beach (19 stations).

sediment. Relatively high percentages of mud (average : 1 %) and coarse sand (average : 9 %) were present. In total, 27 taxa were found, evenly divided over the molluscs, polychaetes and crustaceans (Fig. 5). Macrofaunal

TABLE 2
Characteristics of the three distinguished zones

		Lower beach zone	Middle beach zone	Upper beach zone
Elevation (m above MLWS)		0.3-1.3	1.0-2.1	1.8-3.2
Sediment	% silt and clay (<63µm)	1.3	0.4	0.1
	% very fine sand (63-125µm)	8.1	3.9	3.1
	% fine sand (125-250µm)	48.5	50.5	57.0
	% medium sand (250-500µm)	31.3	37.9	37.0
	% coarse sand (500-800µm)	9.0	6.3	2.0
Average N ₀		5.38	3.47	1.42
Number of species	All taxa	27	15	7
	Mollusca	8	3	2
	Polychaeta	7	4	1
	Crustacea	9	7	3
Average density (ind/m ²)	All taxa	268	662	154
	Mollusca	221.0	577.0	2.6
	Polychaeta	18.8	11.2	0.5
	Crustacea	14.5	111.0	148.0
Percentage of all taxa within zone (%)	Mollusca	82.5	82.5	1.7
	Polychaeta	7.0	1.6	0.3
	Crustacea	5.4	15.9	96.0
Dominant taxa (>2%)		<i>Olivella semistriata</i> Bivalvia spat <i>Mazatlanian hesperia</i> <i>Mazatlanian</i> sp. <i>Emerita rathbunae</i> <i>Nephtys</i> sp. Nemertea sp.	<i>Olivella semistriata</i> <i>Haustorius</i> sp.	<i>Excirrolana braziliensis</i> Insecta sp.

density (average : 268 ind/m²) was dominated by molluscs (83 %), mainly *Olivella semistriata* (48 %). Other abundant macrofauna comprised spat of bivalves (28 %), *Mazatlanian* sp. (4 %), *Emerita rathbunae* (3 %), nemertean (3%), *Nephtys* sp. (2 %), and *Mazatlanian hesperia* (2 %).

The second group (33 replicates) was situated between 1.0 and 2.1 m above MLWS, the middle beach zone. Sediment was mainly composed of fine sand (50.5 %), with 0.4 % of mud and 6.0 % of coarse sand on average. Fifteen taxa, of which seven were crustaceans, were present. This zone was characterized by a high density (average : 662 ind/m²). Molluscs, especially the gastropod *Olivella semistriata* (82 %), dominated the macrofauna (Fig. 5). The amphipod *Haustorius* sp. was the second most abundant species (13 %).

The third group (19 replicates) was found between 1.8 and 3.2 m above MLWS (upper beach zone), including the upper intertidal and supralittoral zone (high tide mark at 2.4 m above MLWS). Sediment was dominated by fine sand (average : 57.0 %) with low mud and coarse sand contents (average : 0.1 and 2.0 %, respectively). Seven taxa were found, with an average macrofaunal density of 154 ind/m². This zone was dominated by crustaceans (96 %), mainly *Excirrolana braziliensis* (Fig. 5). Next to crustaceans, several insect species were present. *Excirrolana braziliensis* was found both on the dry beach and at the highest intertidal station. The insects were only present on the dry beach, together with high numbers of ocypodid crabs.

The mole crabs *Emerita rathbunae* and *Lepidopa deamae* were found across the entire intertidal gradient.

DISCUSSION

This study was initiated as a pilot study for macrofauna research on Ecuadorian sandy beaches. Because only one beach was sampled, generalization of the results to all Ecuadorian beaches cannot be made. Further, since the beach was only sampled in one short period, no inference about seasonal trends can be made. It has to be emphasized that the macrobenthic community structure and zonation pattern, which are obtained by data collected in a short period of time, do not necessarily represent the distribution during the rest of the year (HAYNES & QUINN, 1995; BRAZEIRO & DEFEO, 1996). In this study, the macrofaunal zonation during the dry, cool season is documented.

Sampling took place during a very strong La Niña phase of the ENSO cycle, and the preceding year was one of the strongest El Niño years ever recorded (CHAVEZ et al., in press). There is some evidence that ENSO, and more specifically a strong El Niño, has a substantial influence on macrobenthic communities of sandy beaches (TARAZONA et al., 1988; TARAZONA & PAREDES, 1992). It is thus very likely that the situation encountered in this study was altered by the abnormal climatologic conditions of the two preceding years. Regardless of these shortcomings, if interpreted with caution, the present study provides a first overview on the community structure and zonation of Ecuadorian sandy beach macrofauna.

Environment

According to the morphodynamic classification scheme of MASSELINK & SHORT (1993), all investigated transects can be classified as low tide terrace-rip beaches

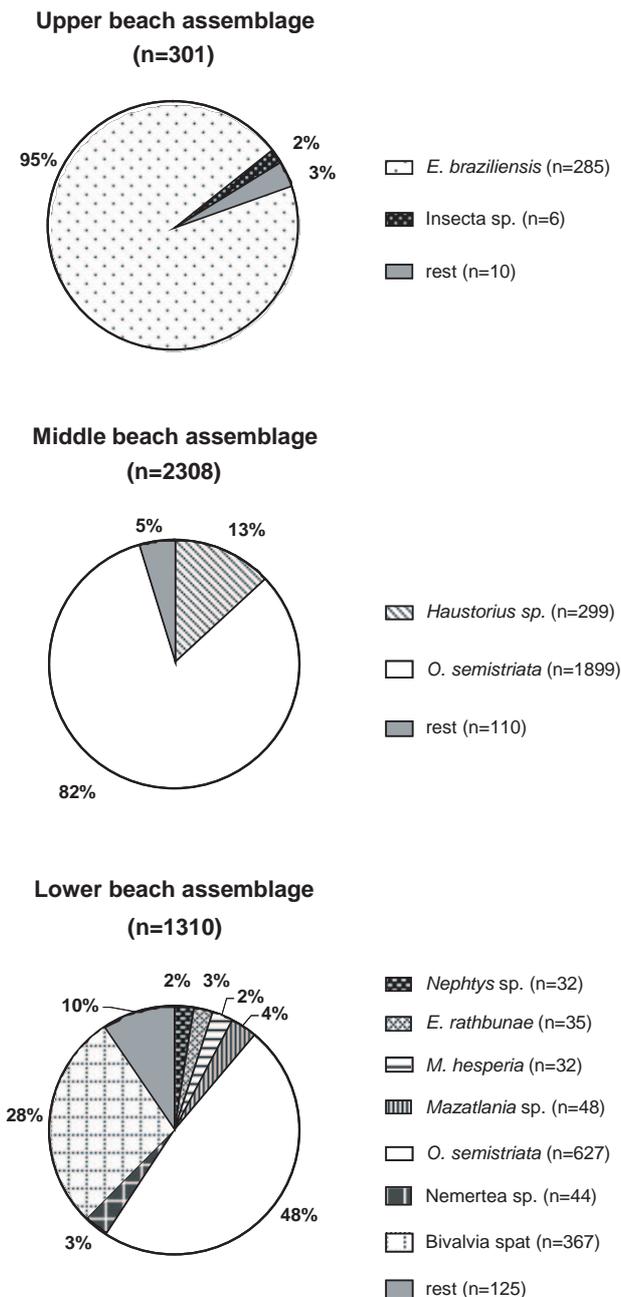


Fig. 5. – Taxon distribution for the three distinguished assemblages.

(Ω : 0-2; RTR: 3-7). Although differences between the different transects exist, the six transects were regarded as replicates of the same beach, rather than transects along six different beaches. Therefore, the zonation patterns might be less clear, but can be considered as representative for the whole bay (DEGRAER et al., 1999). The differences in beach profile for the six sampled transects of the same beach (Fig. 2) show that it could be dangerous to only sample one transect when investigating the macrofauna of a sandy beach.

Macrofauna : General

Molluscs, crustaceans and polychaetes have been reported to be the three most abundant macrofaunal taxa

on sandy beaches worldwide (SOURIEA, 1957; PICHON, 1967; DEXTER, 1969; MCLACHLAN, 1983b). Crustaceans tend to dominate exposed beaches, polychaetes sheltered beaches, while molluscs reach maximum densities in intermediate situations (DEXTER, 1983). The investigated beach had a high richness of crustaceans (ten taxa) but was, in terms of density, dominated by molluscs. Especially the gastropod *Olivella semistriata* proved to be very abundant in this study (66 % of the overall macrofauna). So far, this genus has only been found in low numbers on sandy beaches in Peru (SUAREZ CALVANAPÓN, 1981), Columbia (RIASCOS & RALLÓN, 2001) and the Pacific coast of Mexico (CUPUL-MAGANA & TÉLLEZ-DUARTE, 1997). The high numbers found might be an overestimation of the actual density of this species, since this gastropod is thought to appear in high density patches (RIASCOS & RALLÓN, 2001). Still, preliminary research on other sandy beaches in Ecuador supports the statement that *O. semistriata* is a very dominant species (VANAGT, unpublished). It thus seems that this species is more abundant towards the Equator.

The bivalve *Donax* sp. only appeared in low numbers in Valdivia Bay, but has been reported to be very abundant at other sandy beaches from the same geographical area (DEXTER, 1974; PEREZ NIETO, 1980; RIASCOS, 2002). There might be a negative correlation between *Donax* and *Olivella semistriata*-populations. Another possibility is that *Donax* was negatively influenced or *O. semistriata* positively influenced by the strong El Niño one year before sampling or by the strong La Niña during the sampling campaign. This hypothesis is supported by the fact that another common bivalve of South American Pacific beaches, *Mesodesma* spp., was absent on the Ecuadorian beach. TARAZONA & PAREDES (1992) reported that in Peru *Mesodesma donacium* might disappear almost entirely after a strong El Niño.

This study shows, in agreement with different other studies (e.g. CLARKE & PEÑA, 1988; DEFEO et al., 1992; DEXTER, 1974, MCLACHLAN & JARAMILLO, 1995), that crustaceans are the most diverse taxon on South American beaches along the Pacific coast. Cirolanid isopods, especially *Excirrolana braziliensis*, were abundant in Valdivia Bay. This species is widely spread along the coasts of Central and South America, but shows a high spatial variability in density, attributed to variable beach temperatures (ZUÑIGA et al., 1985). Next to *E. braziliensis*, *Haustorius* sp. (average: 27 ind/m²) and *Emerita rathbunae* (average: 6 ind/m²) were abundant crustaceans as well. These latter two crustaceans groups were also found on many other South American beaches (e.g. Peru: SUAREZ CALVANAPÓN, 1981; Chile: JARAMILLO et al., 1993 and Uruguay: GIMÉNEZ & YANNICELLI, 1997). Ghost crabs (*Ocypode occidentalis*) appeared in high numbers above the drift line on the investigated beaches, as was the case in Valdivia Bay. They were not sampled because of the applied sampling technique.

Polychaete species of the genera *Hemipodus*, *Lumbrineris* and *Nephtys*, which were the most abundant polychaete taxa in this study, have been reported from Peru (SUAREZ CALVANAPÓN, 1981), Chile (CLARKE & PEÑA, 1988) and Columbia (DEXTER, 1974). Spionid polychaetes were only found in very small numbers. Opheliid polychaetes

(e.g. *Euzonus furciferus*), which were found on several other South American beaches (CLARKE & PEÑA, 1988; GIANUCA, 1983; ESCOFET et al., 1979) were not registered in the present study.

In general, taxon composition in Valdivia Bay was similar to other South American sandy beaches. Some differences, mainly in molluscs, were found, possibly due to the location near the Equator with its tropical conditions.

Macrofauna : Zonation

In the Bay of Valdivia, three beach zones were distinguished: upper, middle and lower zone. The presence of three zones has already been demonstrated for several sandy beaches around the world (MCLACHLAN & JARAMILLO, 1995 and references herein).

Generally, the upper beach zone of South American sandy beaches is dominated by a low number of species. Cirolanid isopods (e.g. *Excirrolana braziliensis*) are often encountered (DEXTER, 1974; BOCANEGRA et al., 1985), together with large numbers of air-breathing ghost crabs (*Ocypode occidentalis*). This is typical for the transition zone between the marine and the terrestrial environment (JARAMILLO, 1987).

Compared with the upper beach zone, a higher diversity of very abundant macrofaunal species is found at the middle beach. Again, crustaceans tend to be characteristic for this zone along many South American beaches (MCLACHLAN & JARAMILLO, 1995). In the present study, however, the most abundant species within the middle beach zone was the gastropod *Olivella semistriata*. Although polychaetes are rarely abundantly present in the middle beach zone of South American beaches, some individual species might be (e.g. opheliids, spionids and nephtyids) (MCLACHLAN & JARAMILLO, 1995). In Valdivia Bay, few polychaetes were found in the middle beach zone.

The lower beach zone of all exposed South American beaches is characterized by a large number of abundant species (MCLACHLAN & JARAMILLO, 1995), as was the case in the intermediate beach in our study. The lower beach zone is often regarded as an intertidal extension of the subtidal habitat. The higher diversity of the lower beach zone could be a reflection of the high subtidal diversity (DEGRAER et al., 1999). Also, the short period of exposure to the air allows more species to inhabit the lower beach zone.

It has to be emphasized that no sharp boundaries between the different zones were found, partly because of the morphodynamic differences between the replicate transects. Moreover, zonation on sandy beaches has to be seen as an artificial division of a continuum, with an overlap between adjoining zones (DEGRAER et al., 1999).

In general, the zonation pattern of the macrobenthic assemblages on the investigated tropical beach was similar to other beaches at different latitudes in South America and the rest of world.

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