ADDENDUM 1

MACROFAUNAL COMMUNITY STRUCTURE AND ZONATION OF AN ECUADORIAN SANDY BEACH (BAY OF VALDIVIA).

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Published in *The Belgian Journal of Zoology* (2004) 134 (1): 15-22

Keywords: macrobenthos, sandy beach, Ecuador.

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/m^2, max.: 2,135 ind/m^2), followed by crustaceans. The gastropod *Olivella semistriata* (overall average: 243 ind/m^2, max. 2,131 ind/m^2) 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/m^2). The total average density over the entire bay was 370 ind/m^2. 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.

A1.1 Introduction

Macrofaunal zonation on sandy beaches is a distinctive and well-described phenomenon of intertidal zones (McLachlan and 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 and Jaramillo, 1995).

Different generalizing zonation schemes for sandy beach macrofauna were proposed (Davenport, 1903; Mortensen, 1921; Schulz, 1937) with the schemes of Dahl (1952) and Salvat (1964 and 1967) as 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 were recognized (McLachlan and Jaramillo, 1995 and references herein), supporting Dahl's scheme. Several studies (Clarke and Peña, 1988; Defeo *et al.*, 1992; Dexter, 1974, McLachlan and 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. Nearest studies to Ecuador of sandy beach macrofauna 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 and 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) was 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 economy.

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.

A1.2 Material and Methods

A1.2.1 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. A1.1). 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 in the Ecuadorian coast, with higher temperatures and precipitation levels during El Niño and lower temperatures during the subsequent La Niña.

A1.2.2 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. A1.1: 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. A1.2). At each station three replicate samples were collected by excavating a metal frame (sampling surface area: 0.1026 m^2) 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.

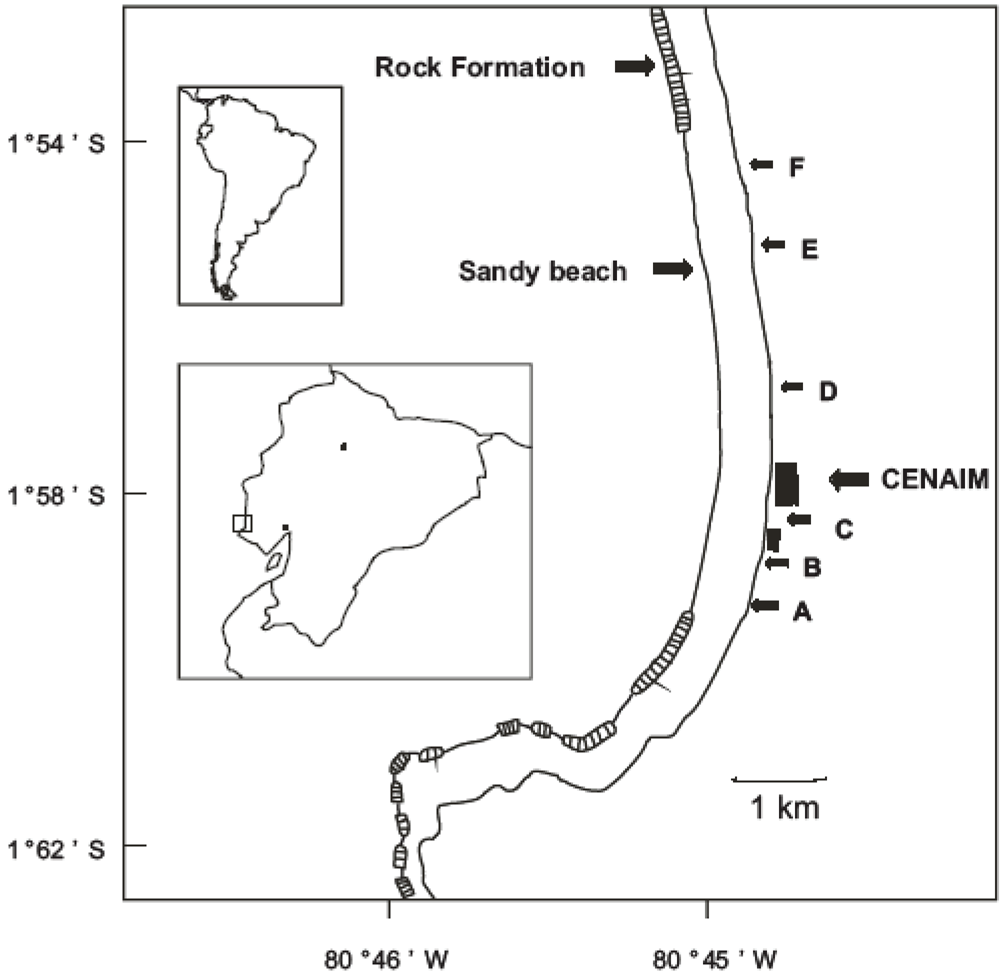

Fig. A1.1 - Geographical situation of the six sample transects (A-F) from the Bay of Valdivia, Ecuador (modified from Boothroyd *et al.*, 1994).

A1.2.3 Laboratory treatment

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

The sediment grain size distribution between 2 and 850 µm 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.

A1.2.4 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 to estimate 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 ($\Omega = H_b / w_sT$) (Dean, 1973) and the relative tide range ($RTR = MSR/H_b$) (Masselink and 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 and Weaver, 1949). Community analysis was done by means of Cluster-analysis (Clifford and Stephenson, 1975), Canonical Correspondence Analysis (CCA) (Ter Braak, 1988) and Indicator Species Analysis (Dufrêne and 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).

A1.3 Results

A1.3.1 Environment

The beach width ranged from 70 and 172 m, while the width of the intertidal zone ranged from 42 to 109 m. 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. A1.2). 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.

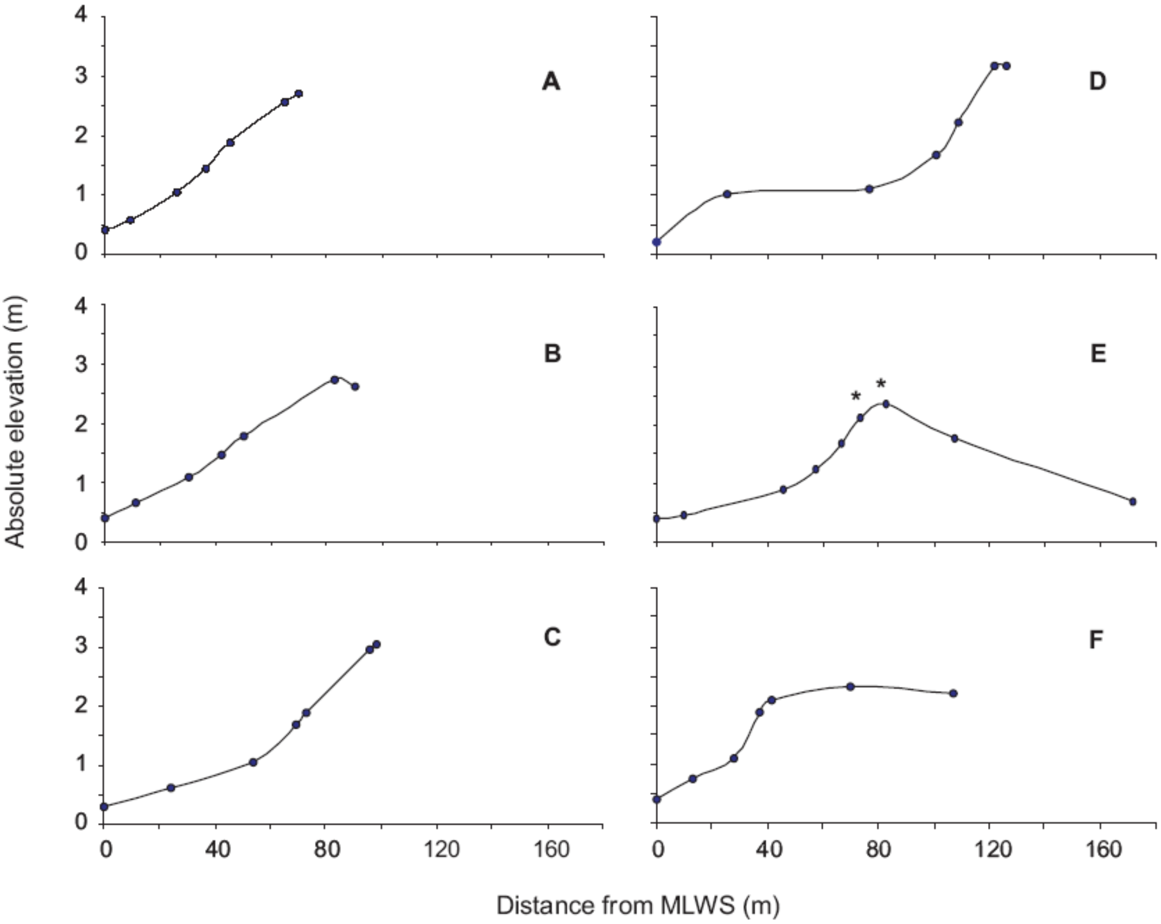

Fig. A1.2 - Beach profiles at the six transects (*: additional measure points; the most right point is the vegetation line).

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) ($r=-0.428$; $p<0.0001$).

A1.3.2 Macrofauna

A total of 31 macrofaunal taxa (10 taxa of crustaceans, 8 of molluscs, 8 of polychaetes and 5 others) were collected (Table A1.1: species list), ranging from 10 to 22 taxa per transect and varying between 0 and 10 taxa per station. H’ diversity index ranged from 0 to 2.87. Overall average macrobenthic density was 370 ind/m^2. Molluscs dominated the fauna (average: 285 ind/m^2, max. 2,135 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/m^2, max.: 2131 ind/m^2). Other abundant species were the gastropods *Mazatlania hesperia, Mazatlania* sp., the polychaetes *Nephtys* sp., *Hemipodus* sp. and *Lumbrineris* sp., the haustoriid amphipod *Haustorius* sp., the cirolanid isopod *Excirolana braziliensis,* the anomuran crabs *Emerita rathbunae* and *Lepidopa deamae* and spat of bivalves.

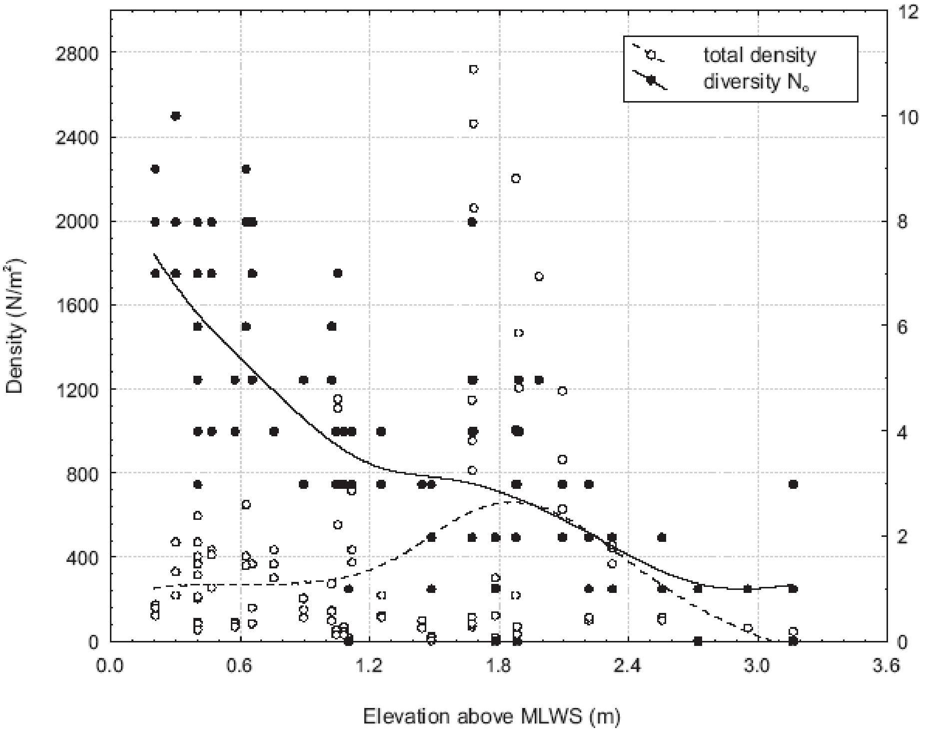

Fig. A1.3 - Total density and N_0 diversity set against elevation.

Along the whole beach, highest species richness (N_0) was situated at the lower beach (Fig. A1.3): species richness generally decreased towards the upper beach. Highest densities (up to 2,400 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. A1.4). Station elevation was the most determining variable as far as upper and middle beach zones are concerned, % mud and % very fine sand (< 125 µm) distinguished the lower beach fauna. The most important indicator species were *Excirolana braziliensis*, *Olivella semistriata*, *Haustorius* sp., Bivalvia spat and Nemertea sp.

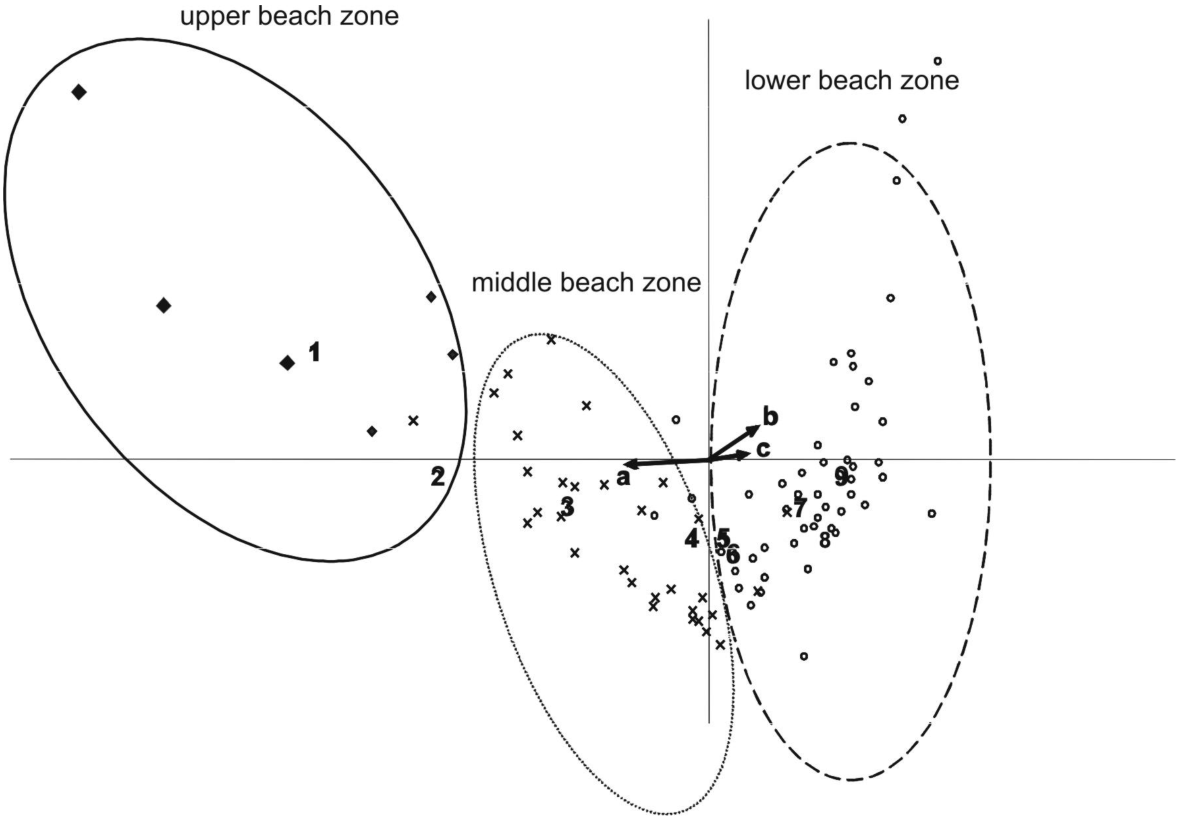

Fig. A1.4 - CCA-output with the three distinguished zones; group division is based on the outcome of all three applied multivariate techniques (eigenvalue axis 1: 0.500; axis 2: 0.183); a: elevation, b: % silt and clay (< 63 µm), c: % very fine sand (63 – 125 µm); 1: Insecta sp., 2: *Excirolana braziliensis*, 3: *Haustorius* sp., 4: *Olivella semistriata*, 5: *Nepthys* sp., 6: *Emerita rathbunae*, 7: *Nemertea* sp., 8: *Mazatlania* sp., 9: *M. hesperia*; **O**: lower beach (47 stations), **x**: middle beach (33 stations), ♦: upper beach (19 stations).

Table A1.1 - Species list (* not sampled and not counted in analyses).

		Family	**Species**
Annelida	Polychaeta	Maldanidae	Maldanidae sp.
		Lumbrineridae	*Lumbrineris* sp. (BLAINVILLE, 1828)
		Magelonidae	*Magelona* cf. *mirabilis* (JOHNSTON, 1865)
		Pisionidae	*Pisione* sp. (GRUBE, 1857)
		Glyceridae	*Hemipodus* sp. (QUATREFAGES, 1865)
		Nephtyidae	*Nephtys* sp. (CUVIER, 1817)
		Spionidae	*Scolelepis* sp. 1 (BLAINVILLE, 1828)
			Scolelepis sp. 2 (BLAINVILLE, 1828)
Crustacea	Decapoda	Albuneidae	*Lepidopa daemae* (BENEDICT, 1903)
		Hippidae	*Emerita rathbunae* (SCHMIDT, 1935)
		Paguridae	*Pagurus* sp. (FABRICIUS, 1775)
		Ocypodidae *	*Ocypode occidentalis* (STIMPSON, 1860)
		Portunidae	*Arenaeus mexicanus* (GERSTAECKER, 1856)
	Amphipoda	Haustoriidae	*Haustorius* sp. (MÜLLER, 1775)
			Bathyporeia sp. (LINDSTRÖM, 1855)
	Isopoda	Cirolanidae	*Excirolana braziliensis* (RICHARDSON, 1912)
		Sphaeromatidae	*Paracerceis* sp. (HANSEN, 1905)
	Mysidacea	Mysidae	*Bowmaniella* sp. (BACESCU, 1968)
			Metamysidopsis sp. (TATTERSALL, 1951)
Echinodermata	Echinoidea	Mellitidae	*Mellita longifissa* (MICHELIN, 1858)
	Stelleroidae		Ophiurae sp.
Mollusca	Bivalvia	Donacidae	*Donax mancorensis* (OLSSEN, 1961)
			Donax sp. (LINNAEUS, 1758)
		Tellinidae	*Strigilla chroma* (SALISBURY, 1934)
	Gastropoda	Collumbellidae	*Mazatlania hesperia* (PILSBRY & LOWE, 1932)
			Mazatlania sp. (DALL, 1900)
		Olividae	*Olivella semistriata* (GRAY, 1839)
		Terebridae	*Hastula luctuosa* (HINDS, 1844)
		Vitrinellidae	*Anticlimax willetti* (HERTLEIN & STRONG, 1951)
Hexapoda	Insecta		Insecta sp.
Nemertea			Nemertea sp.

Table A1.2 - 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%)		*O. semistriata* Bivalvia spat *M. hesperia* *Mazatlania* sp. *E.rathbunae* *Nephtys* sp. Nemertea sp.	*O. semistriata* *Haustorius* sp.	*E. braziliensis* Insecta sp.

The first group of 47 replicates was found between 0.3 to 1.3 m above MLWS, the lower beach zone (Fig. A1.4 and Table A1.2). The fine sand fraction (49 %) dominated the sediment. A relatively high percentage of mud (average: 1 %) and coarse sand (average: 9 %) was present. A total of 27 taxa was found, evenly divided over the molluscs, polychaetes and crustaceans (Fig. A1.5). Macrofaunal density (average: 268 ind/m^2) was dominated by molluscs (83 %), mainly *Olivella semistriata* (48 %). Other abundant macrofauna comprised spat of bivalves (28 %), *Mazatlania* sp. (4 %), *Emerita rathbunae* (3 %), nemerteans (3%), *Nephtys* sp. (2 %), and *Mazatlania 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. A1.5). 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/m^2. This zone was dominated by crustaceans (96 %), mainly *Excirolana braziliensis* (Fig. A1.5). Next to crustaceans, several insect species were present. *Excirolana 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.

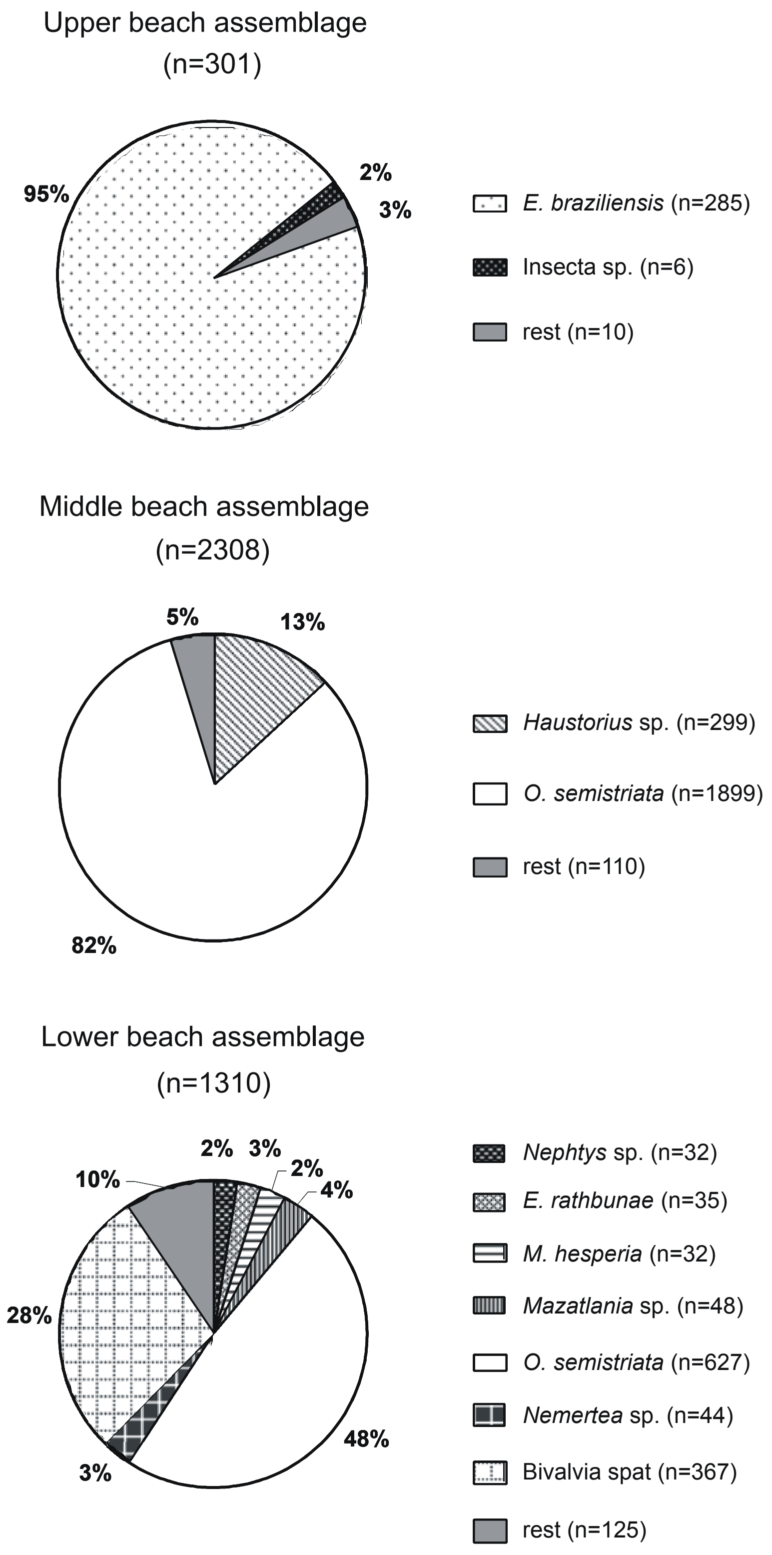

Fig. A1.5 - Taxon distribution for the three distinguished assemblages.

A1.4 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 at one date, 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, are not necessarily representing the distribution during the rest of the year (Haynes and Quinn, 1995; Brazeiro and 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.*, 2002). 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 and 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.

A1.4.1 Environment

According to the morphodynamic classification scheme of Masselink and Short (1993), all investigated transects can be classified as low tide terrace - rip beaches (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. A1.2) show that it could be dangerous to only sample one transect when investigating the macrofauna of a sandy beach.

A1.4.2 Macrofauna: General

Molluscs, crustaceans and polychaetes were 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 (10 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 was only found in low numbers on sandy beaches in Peru (Suarez Calvanapon, 1981), Columbia (Riascos and Rallón, 2001) and the Pacific coast of Mexico (Cupul -Magana and 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 and Rallón, 2001). Still, preliminary research on other sandy beaches in Ecuador supports the statement of *O. semistriata* being 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 and 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 and Peña, 1988; Defeo *et al.*, 1992; Dexter, 1974, McLachlan and Jaramillo, 1995), that crustaceans are the most diverse taxon on South American beaches along the Pacific coast. Cirolanid isopods, especially *Excirolana 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/m^2) and *Emerita rathbunae* (average: 6 ind/m^2) were abundant crustaceans as well. These latter two crustaceans groups were also found on many other South American beaches (e.g. Peru: Suarez Calvanapon, 1981; Chile: Jaramillo *et al.*, 1993 and Uruguay: Giménez and 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 Calvanapon, 1981), Chile (Clarke and 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 and 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.

A1.4.3 Macrofauna: Zonation

In the Bay of Valdivia, three beach zones were distinguished: upper, middle and lower zone. The presence of three zones was already demonstrated for several sandy beaches around the world (McLachlan and 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. *Excirolana 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 and Jaramillo, 1995). In the present study, however, the most abundant species within the middle beach zone is the gastropod *Olivella semistriata*. Although polychaetes are rarely abundantly present in the middle beach zone of South American beaches, some species might be (e.g. opheliids, spionids and nephtyids) (McLachlan and 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 and Jaramillo, 1995), as is 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.

Acknowledgements

This study was made possible by ESPOL (Escuela Superior Politécnica del Littoral) in Guayaquil, Ecuador. Financial support for co-author T.V. comes from the Fund for scientific research – Flanders (FWO). The following people are acknowledged for their assistance in the field and in the laboratory: Bart Bulckaen, Micheline De Mey, Daniëlle Schram, Dirk Van Gansbeke and Guy Desmet. Valuable comments on this manuscript were made by Mariano Lastra.

A1.5 Critical note

The paper from Addendum 1 was published in 2004 and is reproduced here in its original form. Data collection of this chapter was done in 1999, three years before the start of this thesis. During the last two years of this PhD, however, we have come to several conclusions that question the outcome of some of the aspects of Chapter 1. These points of auto-criticism are listed in this critical note.

First of all, the sampling design used in Addendum 1 was not appropriate for the given circumstances and the goals of the study. Sampling the intertidal with the falling tide, with the sampling stations positioned in the upper swash zone, is a strategy that is commonly used on sheltered beaches along the Belgian coast (Elliott *et al.*, 1997; Degrear *et al.*, 1999, 2003). When the sandy beach research was transferred to the exposed sandy beaches of Ecuador's Pacific coast, the same strategy was applied. In contrast to sheltered beaches, exposed sandy beaches harbour a very mobile fauna, which often migrates up and down the intertidal with the swash (McLachlan and Brown, 2006; Chapter 1, 2 and 3). Positioning the sampling stations in the swash zone at different times during the tidal cycle will thus lead to an overestimation of the population size of swash migratory species (Chapter 2). This was demonstrated for *Olivella semistriata* by Mercx (2005): sampling with the falling tide renders a population size which is much larger than sampling the intertidal at the time of low tide. Thus, although all studies from the bay of Valdivia (Chapter 1, 2 and 3) agree that *O. semistriata* is the most abundant species from this beach, the numbers in Addendum 1 should be treated with care.

Secondly, the main goal set for Addendum 1, identifying zonation on an Ecuadorian sandy beach, is not correctly achieved by sampling with the falling tide. McLachlan and Brown (2006) explicitly state that sandy beach zonation should be assessed at low tide. Although Mercx (2005) demonstrated that the zonation results of sampling with the falling tide or sampling at the time of low tide do not differ significantly, the overestimation of mobile fauna could blur zonation patterns. Moreover, in Chapter 1 and 2 we argue that mobile swash fauna should be treated as a different zone. As such, the middle beach zone from Addendum 1, dominated by the surfer *Olivella semistriata*, is false. Still, the patterns are very alike those of found in Chapter 1, where a more appropriate sampling design was used.

Thirdly, the upper beach zone was not treated correctly in Addendum 1. We did not sample above the drift line, thereby neglecting the supralittoral fauna. Although this should not be problematic *an sich* (Chapter 1, Degraer *et al.*, 2003), the supralittoral community does form one of the three or four separate zones recognized on sandy beaches (McLachlan and Jaramillo, 1995; McLachlan and Brown, 2006). In Addendum 1 the qualitatively sampled ocypodid crab *Ocypode occidentalis*, one of the typical members of the supralittoral community, was placed in the upper beach zone, together with *Excirolana braziliensis*. These two species, however, inhabit a different zone, the former being an air-breather and the latter a true marine species (McLachlan and Brown, 2006). The upper beach zone remains valid, but *Ocypode occidentalis* should be moved to an additional – not sampled - supralittoral zone. The number of zones present in the bay of Valdivia is thus not three but four, as was also found in Chapter 1.

Finally, some of the taxa have been identified differently since the publication of Addendum 1. *Mazatlania* sp. and *M. hesperia* are one and the same species, namely *M. fulgurata. Paracerceis* sp. has been identified as *Exosphaeroma* sp. The *Pisione*-species is *P. indica* and *Donax mancorensis* was re-identified as *D. obesulus*.

The remaining value of this paper lies in its baseline description of the macrofaunal species composition and distribution on a typical intermediate Ecuadorian sandy beach.