

CHAPTER 1

CHANGES IN MACROFAUNAL ASSEMBLAGE STRUCTURE ALONG A MORPHODYNAMIC SANDY BEACH GRADIENT IN THE EASTERN TROPICAL PACIFIC.

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Paper in preparation

Keywords: macrofauna, surfing, sandy beaches, morphodynamics, zonation, swash.

Abstract

The macrofauna of seven beaches along the coast of Ecuador, in the tropical part of the Eastern Pacific, was sampled along transects. The beaches covered the entire range of beach types that occur in this part of the continent. The aim of the study was to identify the relation between morphodynamic state of beaches and several biological characteristics of the macrofauna: biodiversity, density, abundance, biomass, zonation and trophic structure.

The Ecuadorian beaches were characterized by a very diverse macrofaunal community; a total of 47 species were identified. This confirms the recent idea of a larger species pool existing in the tropics than in temperate regions. There was a very clear drop in species count when moving from the flat, dissipative beaches to the steep, reflective beaches. This was partly due to the absence of molluscs from the reflective beaches. Biomass and abundance (ind/m) likewise decreased towards reflective beach states, but not density (ind/m²), because reflective beaches harboured dense populations of interstitial polychaetes. Changes in biodiversity and, to a lesser extent, biomass could be linked to four environmental factors: sediment grain size, beach slope, number of effluent line crossings and swash width.

The zonation patterns confirmed the current state of knowledge on the topic, with four distinct zones on dissipative and intermediate beaches and only three zones on reflective beaches. This seems to be caused by the relatively wide swash zone compared to the intertidal width, combined with the absence of a surf zone on reflective beaches. The major distinction between the two groups of beaches was based on the presence of a rich middle and lower beach species association on the dissipative / intermediate beaches and the abundant interstitial community on the reflective beaches; the upper beach association was very similar on all beaches.

Six different feeding types were distinguished. Trophic diversity was markedly higher in the dissipative situation. Filter feeders were dominant on all beaches, followed by scavengers and carnivores. Deposit feeders peaked on the dissipative beaches; the reflective beaches were characterized by a high density of interstitial dwellers.

In conclusion, the dissipative and intermediate beaches were very similar in species composition, density, abundance and trophic structure. The reflective beaches were clearly different in all these aspects. It seems that there is a gradual change from dissipative to intermediate beaches yet an abrupt change from intermediate to reflective beaches.

2.1.1 Introduction

Exposed sandy beaches can be considered as very harsh ecosystems, where macrofaunal populations are mainly structured by the physical environment (Defeo and McLachlan, 2005). Conditions change with beach type, from a benign situation on flat, high energy, dissipative beaches to very harsh conditions on steep, reflective beaches (Short, 1999; McLachlan and Dorvlo, 2005), coinciding with a decrease in macrofaunal species richness, abundance and biomass from the dissipative to the reflective end of the beach spectrum. This has now widely been accepted as one of the paradigms in sandy beach ecology (McLachlan and Dorvlo, 2005; McLachlan and Brown, 2006). Many authors have described this pattern, though primarily in temperate regions (e.g. Australia: Hacking, 1997; Belgium: Degraer *et al.*, 2003; South-Africa: Soares, 2003; Uruguay: Defeo *et al.*, 1992; Chile: Jaramillo and McLachlan, 1993 and Brazeiro, 1999a; Brazil: Soares, 2003).

While the patterns are very clear and only few exceptions have been found, the underlying explanatory mechanisms remain highly debatable. Several hypotheses have been proposed, some of these concerning one physical factor, others multifactorial. Amongst the single factors, sand grain size and beach slope were the first to be identified as possible causes for changes in macrofaunal biodiversity and abundance (McLachlan *et al.*, 1981; McLachlan 1990). In the early 1990s McArdle and McLachlan (1991, 1992) showed a clear coupling between beach type and swash conditions, which resulted in the Swash Exclusion Hypothesis (McLachlan *et al.*, 1993). This hypothesis states that the decrease in species richness, abundance and biomass from dissipative to reflective beaches is caused by increasing harshness of the swash. At population level this was translated into the Habitat Harshness Hypothesis (HHH, Defeo *et al.*, 2001 and 2003), which predicts that on reflective beaches the harsh environment forces macrofauna to divert more energy towards maintenance, leaving less for reproduction and causing higher mortality – thus making it more difficult for populations to establish.

Brazeiro (2001) found that not only swash and sediment characteristics could influence sandy beach macrofauna, but also the accretion-erosion dynamics on beaches. He argued that those three factors act together and, as such, postulated the Multicausal Environmental Severity Hypothesis (Brazeiro, 2001). On the macroscale also indirect effects, such as the length of the beach and the tide range, could limit the occurrence of certain species (Brazeiro, 1999; Defeo and McLachlan, 2005). Finally, latitudinal effect should be taken into account: Soares (2003), for instance, demonstrated that the species pool is larger in the tropics than at temperate latitudes.

The Ecuadorian coast, with its wide variety in beaches over a relatively short distance, offers a great opportunity to test all those hypotheses in conditions which have not been investigated before: mesotidal tropical sandy beaches. For this study seven exposed beaches with contrasting morphodynamics were chosen. According to the paradigm described above, macrofaunal diversity, density, abundance and biomass are expected to decrease from dissipative to reflective beaches. This should go along with changes in swash and sediment conditions.

Although predictions have been made, the impact of morphodynamics on the zonation of the macrofauna, and especially on the trophic structure, has received much less attention than the impact on biodiversity, abundance and biomass. Jaramillo *et al.* (1993) could identify more zones on dissipative beaches than on reflective beaches, yet this study was done in a region with a microtidal regime (Chile). Similar results were found by Borzone *et al.* (1996), Brazeiro and Defeo (1996) and Nel (2001), again in microtidal conditions. With increasing tide range the intertidal widens and, as such, offers more space for macrofauna to be zoned over. One of the questions addressed in this paper is if zonation is altered by morphodynamics under mesotidal conditions.

Studies dealing with trophic links on sandy beaches are, unfortunately, almost always performed in a single beach type (reviewed in McLachlan and Brown, 2006). McLachlan and Brown (2006) noted a change in trophic groups from predominantly filter feeders on dissipative beaches to scavengers and carnivores on reflective beaches. Deposit feeders increase with finer sediments and flatter slopes (Ricciardi and Bourget, 1999) and under more sheltered conditions (McLachlan and Brown, 2006). The last aim of this study is to identify the changes in trophic structure groups over a range of beach types.

Thus, this paper seeks to identify and explain the impact of morphodynamics under tropical, mesotidal conditions on 1) sandy beach macrofaunal diversity, density, abundance and biomass, on 2) the zonation of the sandy beach macrofauna and on 3) the trophic structure of the macrofauna.

2.1.2 Material and Methods

2.1.2.1 Study sites and period

Seven beaches along the southwestern coastline of Ecuador (between 0°31'18 and 2°09'07 S and 80°26'34 and 80°47'29 W) were sampled for macrofauna (Fig. 2.1.1). All beaches are exposed to the Pacific Ocean and have a maximal tidal range of 2.6-3.0 m (mesotidal regime: Davies, 1964). Sampling took place between July 18th (Ballenita) and July 23rd (Portéte) 2004. During the dry season (May through November), the oceanographic features of the Ecuadorian coast are mainly under influence of the Humboldt Current, coming from the South.



Fig. 2.1.1 – Map of Ecuador with indication of the sampled beaches (for coordinates, see text).

2.1.2.2 Sampling strategy

Per beach one transect perpendicular to the shoreline was sampled. Transects were divided in nine (Ballenita) to 16 (San Clemente) sampling levels, equally spaced over the intertidal. The number of levels that were sampled depended on the intertidal width of the beach; only nine levels were sampled in Ballenita because of logistic reasons. Two to four of the sampling levels were placed in the active low tide swash zone. Three replicate samples, 2 m apart, were collected per sampling level, except for Ballenita, where only two replicates were taken because of the extremely coarse sand. The samples were collected by excavating a metal frame with a surface area of 0.1026 m² to a depth of 15 cm. To prevent migration of the animals during sampling of the levels in the swash zone, stations were isolated by simultaneously placing a wooden box (plywood, 100x50x50 cm lxxw) over each sampling spot (for a detailed description of this technique, see Chapter 2). The samples were sieved over a 1 mm mesh-sized sieve; the retained organisms were stored in an 8% formaldehyde-seawater solution.



Picture 2.1.1 – Sampling on the reflective beach of Ballenita.

At each station, one sediment sample was collected for grain size analysis, using a core with diameter of 3.6 cm, to a depth of 15 cm. Beach profiles were measured using a leveller, taking measurements every 2 meter. Wave height and wave period were estimated by monitoring 11 consecutive breaking waves. At high tide (low tide in San Pablo) the swash was recorded on videotape during 5 – 10 min, with plastic poles placed at 1 and 2 m intervals on the beach as reference. From the videotapes, swash time, swash width and swash period were identified (McArdle and McLachlan, 1991). Both at high (HT) and low tide (LT) the number of effluent line crossings in a 10 min period of time (EL-crossings) was counted.

2.1.2.3 Laboratory treatment

Samples were sorted for macrofauna and all specimens were identified to the lowest taxonomical level 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). Weight percentage of the coarser sediment ($>850 \mu\text{m}$) was measured by sieving and weighing dried sediment fractions. To calculate the median grain size over the full sediment spectrum, a conversion of weight percentage to volume percentage of the coarse sand ($>850 \mu\text{m}$) was performed.

Biomass (Ash-Free Dry Weight or AFDW) estimates for all molluscs, polychaetes and larger crustaceans (Anomura) were obtained by loss of mass on ignition (450°C for 4 h) of oven-dried samples (70°C for 48 h). For smaller crustaceans, assigned biomass values were calculated from determining the AFDW of a large number of specimens, using the same protocol as described above.

2.1.2.4 Statistical analyses

Beach profiles were constructed based on the measurements and the tide predictions for the nearby ports of La Libertad (Ballenita, Olon, Portéte, San Pedro and San Pablo), Manta (San Clemente) and Bahía de Cáracas (Briceño). Lowest swash point at low tide was assumed to be the low water level (Short, 1999) and is referred to as 0 m of elevation. Highest point of the intertidal was the lower swash limit at high tide. Intertidal width and beach slope were calculated from this highest point and the zero point. Swash characteristics (swash time, swash period and swash width) were retrieved from the videotapes. Swash velocity was calculated from swash time and swash width (McArdle and McLachlan, 1991).

Beach characterisation was done using two beach indices: ‘beach index’ (BI) and ‘beach deposit index’ (BDI) (McLachlan and Dorvlo, 2005). These indices were calculated as:

$$BI = \log\left(\frac{Sand \cdot Tide}{Slope}\right)$$

$$BDI = \left(\frac{1}{\tan B}\right)\left(\frac{a}{Mz}\right)$$

where *Tide* is the maximum spring tide range (meters), *Slope* or $\tan B$ is the beach slope, *a* is 1.03125 (mm), *Mz* is the mean sand particle size (mm) and *Sand* is the mean sand particle size in phi units +1. BI has dimension $\log \phi \cdot m$, BDI is dimensionless. Both indices increase from reflective to dissipative conditions.

Because of logistic reasons, not the same sampling effort could be achieved on all beaches. Hence, to analyse differences in macrofauna between beaches, we opted for measures that compensate for sampling effort. For biodiversity, these measures were Dominance (D), Evenness (E), estimated number of species (first-order jackknife estimation) and expected number of species. To assess the concentration of specimens, density (ind/m²), abundance (ind/m), and biomass (g AFDW/m and g AFDW/m²) were used.

For estimation of the species richness, the first-order jackknife algorithm (*Jack1*) was applied (with 999 random permutations). This has been demonstrated to be the most suitable estimator for sandy beach macrofaunal biodiversity sampled along transects (Brose and Martinez, 2004; Schoeman, pers. comm.), and is computed as:

$$Jack1 = S_{obs} + Q_1 \cdot \left(\frac{m-1}{m}\right)$$

with S_{obs} the observed number of species over the total sampling pool, Q_1 the number of singletons (species that occur in only one sample) and m the number of samples. A good property of the jack1 estimator is that a variance can be calculated (Heltshe and Forrester, 1983):

$$Var(Jack1) = \left(\frac{m-1}{m}\right) \cdot \left(\sum_{j=0}^{S_{obs}} j^2 \cdot f_j - \frac{Q_1^2}{m}\right)$$

with f_j the number of quadrates containing j singletons. The jack1 data were also used to construct a species-area curve.

The species diversity was also assessed as Expected number of Species (Hurlbert, 1971). ES(n)-values were used to construct rarefaction curves. The lowest number of specimens (325, Port  te) was used for maximum value of n.

Other biodiversity indices that were calculated are Dominance (D) and Evenness (E) (Magurran, 2004):

$$D = \sum p^2$$

$$E = \frac{\sum (p \cdot \ln(p))}{\ln(N_o)}$$

with p the relative density of a species in a sample and N_o the number of species in that sample. Dominance was also used in a cumulative dominance plot

To express the concentration of specimens, the data are listed in two measures: density and abundance. Density shows the occurrence of a species on a given surface and is given in individuals per square meter (ind/m^2). Abundance estimation was done using the IST (individuals per strip transect; ind/m) technique (Defeo, 1996). IST is calculated by multiplying the average sample density (ind/m^2) by the intertidal width in which the animals occur. The obtained value gives an estimate of the total population size present over the entire intertidal width (cross-shore) when considering one meter of beach length (alongshore). Biomass estimation was done using BST (biomass per strip transect: $\text{g AFDW}/\text{m}$; Defeo, 1996).

For all encountered taxa, their feeding type was checked in literature. Where no information was available, feeding type of other members of the same genus was chosen. The categories that were used are *scavengers*, *filter feeders*, *carnivores*, *deposit feeders*, *interstitial dwellers* and *non-feeders*. Non-feeders were zoea-larvae, a larval stage in which no feeding occurs; interstitial dwellers is not a feeding type *an sich*, yet it stands apart from the traditional foraging that occurs in sandy beach macrofauna. The Index of trophic diversity was calculated as (Heip *et al.*, 1985):

$$\text{trophic diversity} = \sum p^2$$

with p the relative density of each trophic group per beach. The trophic diversity decreases with increasing value of the index; minimal diversity is reached at a value of 1.

Correlation between environmental parameters and beach indices (*BDI*, *BI*, *median grain size*, *slope*, *intertidal width*, *swash velocity*, *swash period*, *HT* and *LT effluent line crossings* and *swash width*) were done through Spearman's rank correlation (Underwood, 1981).

Biological parameters (*diversity indices, species count, density, IST, biomass and BST*) were expressed as a function of beach indices (*BDI and BI*) and environmental parameters (*median grain size, slope, intertidal width, swash velocity and swash width*) with a first order General Linear Mixed Model (GLMM). The biological parameters were pooled per transect for each beach, and *transect nested in beach* was used as random factor in the models (McCullagh and Nelder, 1989).

Multivariate analyses were calculated with Primer 5.2 software package (Clark and Gorley, 2001). All analyses were performed on a reduced dataset, including only the species that contributed to at least 3% of a sample. Similarity matrices were generated by calculating Bray-curtis dissimilarities (biological data) or Normalized Euclidean distances (environmental data) on the fourth-root transformed data (Clark and Gorley, 2001). These matrices were then used for cluster analyses (by group averaging) and non-metric multidimensional scaling (MDS) for biological (between beach types and within beaches) or environmental data (between beach types). *Beach type* was chosen *a priori* to categorize the seven beaches in three different groups. The stress-factor on the MDS-plots indicates the correctness of the high-dimensional relationship between the points, and values below 0.20 are considered acceptable. Differences in macrofauna between beach types were tested with a nested two-way analysis of similarity (ANOSIM; *beach nested in beach type*). To identify the characterizing species causing differences in dissimilarities between beach types or zones (within one beach), the similarity-percentages procedure (SIMPER) was applied. Likewise, differences in feeding type composition between beaches were tested with the SIMPER procedure.

The 15 most common species were selected to identify species assemblages over all beaches. A Bray-curtis dissimilarity matrix (with all samples) was constructed, and MDS- and cluster-analysis (by group averaging) was performed (Clark and Gorley, 2001). Zoaе-larvae were deleted because they were too far apart from the other species.

2.1.3 Results

2.1.3.1 Physical environment

The seven beaches were chosen to cover the wide range of beach types present along the Ecuadorian coast. The steepest beach was Ballenita, with a slope of 1/7, whereas with a slope of 1/63 Briceño was the flattest beach (Table 2.1.1; Fig. 2.1.2). Only in Ballenita and Portéte the low tide swash crossed the low tide effluent line, resp. 25 and 15 times per 10 min. Ballenita also showed the shortest intertidal width and swash width, coarsest sediment and highest breaker wave height. Because of the extremely short intertidal width in Ballenita, the low tides swash covered 95% of the intertidal; this ratio was much lower on other beaches (Table 2.1.1). The most dissipative conditions were found in Briceño and Olon. San Clemente, San Pablo and San Pedro had similar intermediate conditions. Beach indices (BI and BDI) confirmed the trend from the reflective beaches of Ballenita and Portéte to the dissipative beaches of Briceño and Olon (Table 2.1.1). The high tide swash profile of the beaches is shown in Fig. 2.1.3. The position of the effluent line was very erratic in Ballenita, and the waves not only crossed the effluent line very often but also by a large margin. This was also the case in Portéte, be it to a lesser extent. In the other beaches, especially in Briceño en Olon, the effluent line stayed very constant, and, if the waves did cross the effluent line, this was only by less than five meters.

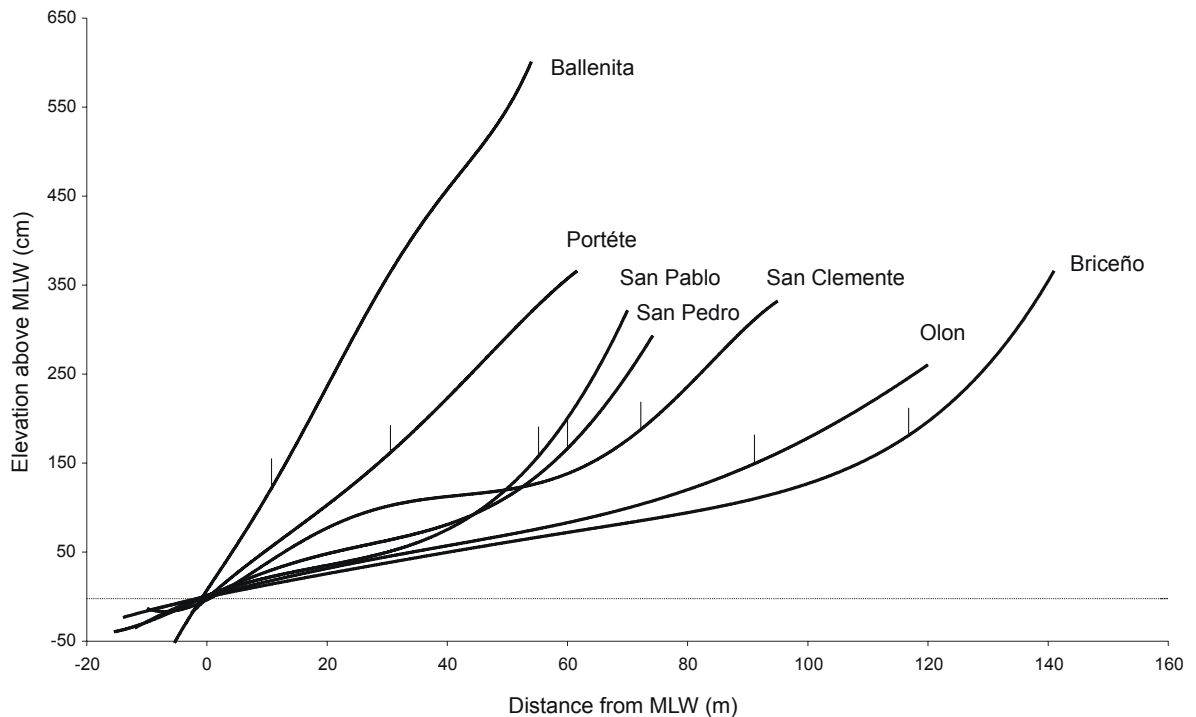


Fig. 2.1.2 - Profiles of the seven beaches, with indication of the high tide position (vertical lines). X-axis is the distance from the Mean Low Water (MLW) position, Y-axis the elevation above the MLW level.

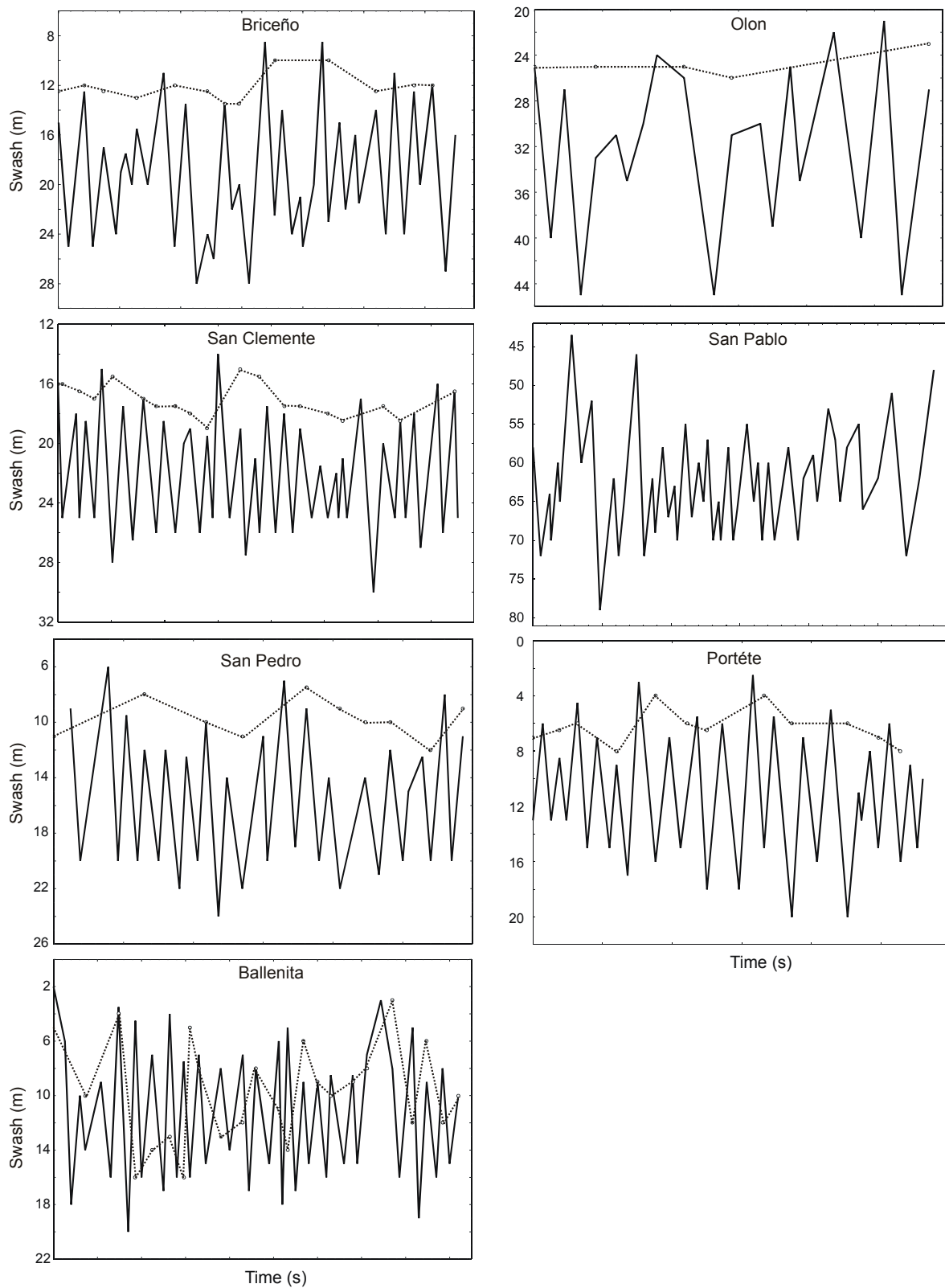


Fig. 2.1.3 - Swash profiles for the seven beaches. Open dots and dotted line indicate the positions of the effluent line. Position of the swash waves (Y-axis) is relative to a fixed point on the high beach. All series were measured at high tide, except for San Pablo.

Table 2.1.1 - Environmental parameters per beach. Average values \pm SE.

	Briceño	Olon	San Clemente	San Pablo	San Pedro	Portéte	Ballenita
Low tide EL-crossings (#/10 min)	0	0	0	0	0	15	25
High tide EL-crossings (#/10 min)	11	12	13	23	10	/	25
Breaker height (m)	0.78 \pm 0.06	0.54 \pm 0.05	0.39 \pm 0.04	0.78 \pm 0.06	0.68 \pm 0.05	0.45 \pm 0.03	1.78 \pm 0.33
Breaker period (s)	20	17	14	16	14	13	19
BDI	329	393	154	162	185	56	15
BI	2.73	2.78	2.45	2.49	2.52	2.11	1.62
Slope	1/63	1/59	1/38	1/36	1/34	1/19	1/7
Median Grainsize (μm)	194.3 \pm 5.0	190.5 \pm 9.9	248.1 \pm 2.42	229.4 \pm 6.0	206.6 \pm 3.4	444.0 \pm 18.6	536.4 \pm 17.7
Intertidal width (m)	118.0	91.0	73.0	55.5	59.5	30.5	11.0
Low tide swash width (m)	47.0	29.5	17.0	16.4	18.0	17.0	10.4
Swash velocity (m/s)	1.19 \pm 0.11	0.94 \pm 0.17	1.06 \pm 0.11	1.13 \pm 0.11	1.24 \pm 0.13	1.09 \pm 0.08	1.06 \pm 0.12
Swash period (s)	16.26 \pm 0.93	22.55 \pm 3.20	15.46 \pm 0.86	19.44 \pm 1.71	16.63 \pm 1.36	15.67 \pm 1.00	18.91 \pm 0.87
Swash width / Intertidal width	0.40	0.32	0.23	0.30	0.30	0.56	0.95

Multivariate analyses (MDS and cluster analyses, cluster not shown), based on environmental parameters, divided the seven beaches into three different groups (Fig. 2.1.4): two flat beaches (Briceño and Olon), characterized by fine sands, flat slope and long intertidal width; two steep beaches (Ballenita and Portéte) with EL-crossings at low tide, steep slopes, coarse sands and short intertidal width; and three intermediate beaches (San Clemente, San Pablo and San Pedro) with intermediate characteristics. This subdivision was confirmed by the multivariate ANOSIM test (Fig. 2.1.4).

Not surprisingly, slope, median grain size, intertidal width and swash width were highly intercorrelated and correlated with the two beach indices, BDI and BI (Table 2.1.2). This was also the case with effluent line-crossings at low tide, yet not with effluent line-crossings at high tide. Swash velocity and swash period were not correlated with other environmental parameters, or with the beach indices.

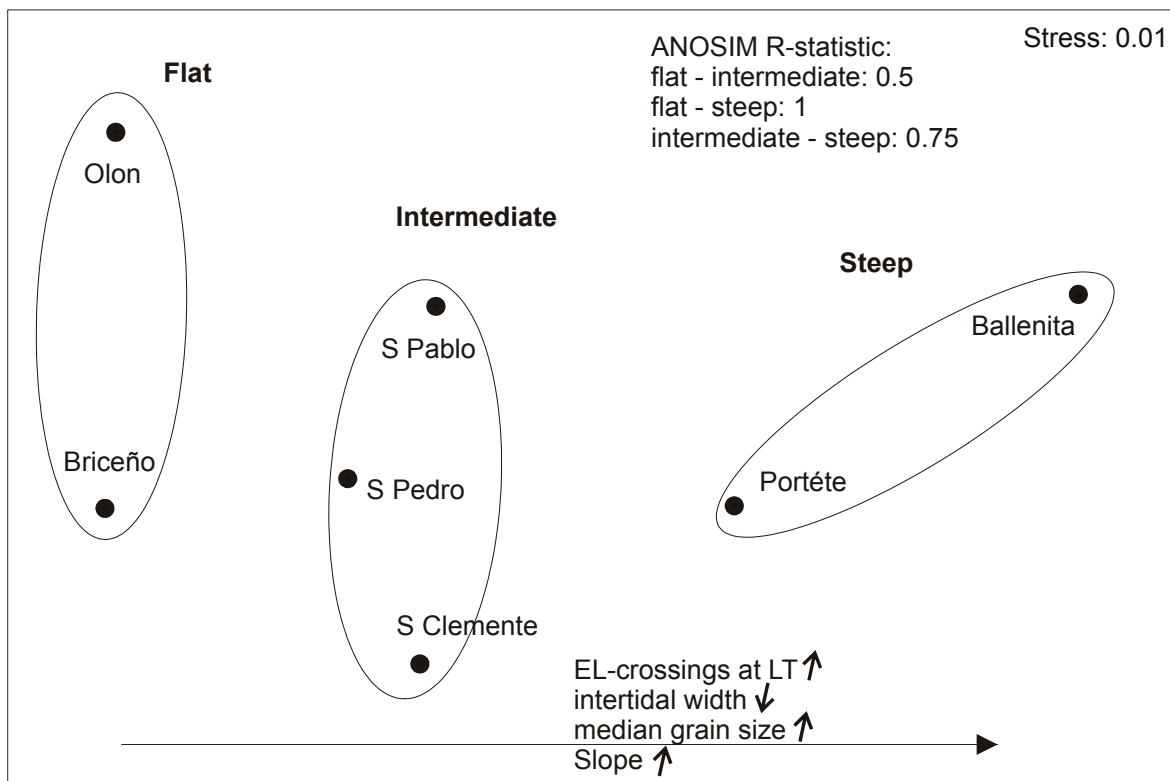


Fig. 2.1.4 - MDS-plot of the seven beaches (each point represents the pooled data per beach) based on the environmental variables, with indication of the statistical significance of the group division (ANOSIM-test). The environmental variables that were used for the analyses were: EL-crossings at high tide (HT) and low tide (LT), intertidal width, slope, median grain size, breaker height, breaker period, swash width, swash velocity and swash period.

Table 2.1.2 – Spearman's rank correlation values (r- and p-value) for the environmental parameters and beach indices. NS= non-significant at 0.05-level.

	High tide EL-crossings	BDI / BI	Slope	Median grain size	Intertidal width	Low tide swash width	Swash velocity	Swash period	Swash width / Intertidal width
Low tide EL-crossings	NS	-0.802 (0.0301)	0.802 (0.0301)	0.802 (0.0301)	-0.802 (0.0301)	NS	NS	NS	-0.802 (0.0301)
High tide EL-crossings	---	NS	NS	NS	NS	-0.829 (0.0416)	NS	NS	NS
BDI / BI		---	-0.857 (0.0137)	-1.000 (<0.0001)	0.857 (0.0137)	0.847 (0.0162)	NS	NS	NS
Slope			---	0.857 (0.0137)	-1.000 (<0.0001)	-0.883 (.0085)	NS	NS	NS
Median Grainsize				---	0.857 (0.0137)	0.857 (0.0137)	NS	NS	NS
Intertidal width					---	0.883 (.0085)	NS	NS	NS
Low tide swash width						---	NS	NS	NS
Swash velocity							---	NS	NS
Swash period								---	NS

Table 2.1.3 - Species list, with indication of the occurrence on the different beaches (x for more than one individual; o for one individual).

		Br	Ol	S Cl	S Pa	S Pe	Po	Ba
ISOPODA (C)	<i>Exciorolana brasiliensis</i> (RICHARDSON, 1912)	x	x	x	x	x	x	x
	<i>Exosphaeroma</i> sp. (STEBBING, 1900)	x	x		x	o	x	
AMPHIPODA (C)	<i>Haustorius</i> sp. (MÜLLER, 1775)	x	x	x	x	x	o	
	Pinnotheridae sp. (DE HAAN, 1833)	x	o					
	Amphipoda sp.1				o			
	Amphipoda sp.2						x	
	Platyischnopidae sp. (BARNARD, 1979)	x	x	x	x	x	o	
	Caprellidae sp. (LEACH, 1814)							o
ANOMURA (C)	<i>Emerita rathbunae</i> (SCHMIDT, 1935)	x	x	x	x	x	x	x
	<i>Lepidopa deamae</i> (BENEDICT, 1903)	x	x	x	x	x		
MYSIDA (C)	Mysini sp.	o						
	<i>Bowmaniella</i> cfr. <i>Braziliensis</i> (BACESCU, 1968)	x	x	o	x	x		
DECAPODA (C)	zoae-larva							x
BIVALVIA (M)	<i>Donax asper</i> (HANLEY, 1845)				o			
	<i>Donax dentifer</i> (HANLEY, 1843)	x	x	x		o		
	<i>Donax assimilis</i> (HANLEY, 1845)			x				
	<i>Donax ecuadorianus</i> (OLSSON, 1961)	o	x	x		o		
	<i>Donax obesulus</i> (REEVE, 1854)	x		x	o	o		
	<i>Donax spat</i> (LINNAEUS, 1758)	x	x	x	x	x		
	<i>Crassinela ecuadoriana</i> (ORBIGNY, 1842)	o	x			o		
	<i>Strigilla chroma</i> (SALISBURY, 1934)	x	x	x		x		
	<i>Tivela byronensis</i> (GRAY, 1838)	x	x	x	x			
GASTROPODA (M)	<i>Sinum cymba</i> (MENKE, 1828)					o		
	<i>Mazatlanian fulgurata</i> (PHILIPPI, 1846)		x	o	x	x		
	<i>Oliva undatella</i> (LAMARCK, 1811)	x	x	x	x	x		
	<i>Olivella semistriata</i> (GRAY, 1839)	x	x	x	x	x		
POLYCHAETA (A)	<i>Hemipodus armata</i> (HARTMAN, 1950)	x	x	x	x	x	x	x
	<i>Lumbrineris inflata</i> (MOORE, 1911)	x	x	x	x	x	o	
	<i>Magelona pacifica</i> (MORNO, 1933)	x	x	x	x			
	<i>Malacoceros indicus</i> (FAUVEL, 1928)					o		
	<i>Marphysa</i> sp. (QUATREFAGES, 1865)	o			o			
	<i>Nephtys</i> sp.1 (CUVIER, 1817)	x	x	x	x	x	o	
	<i>Nephtys</i> sp.2 (CUVIER, 1817)	x		x	x	x	o	
	<i>Pisione indica</i> (GRUBE, 1857)						x	x
	<i>Pisionella indica</i> (AIYAR & ALIKUNHI, 1941)	o		x	x		x	x
	<i>Saccocirrus sonomacus</i> (MARTIN, 1977)		o	o			x	x
	<i>Scolecopsis agilis</i> (BLAINVILLE, 1828)		o		x	x	o	
	<i>Scoloplos armiger</i> (MÜLLER, 1776)	x	x	o	x	x		
	<i>Sthenelais helenae</i> (KINBERG, 1855)	o	o		x			
NEMERTEA	Nemertea sp.1	x	x	x	x		o	
	Nemertea sp.2	x	o					
	Nemertea sp.3	o						
	Nemertea sp.4							o
ECHINODERMATA	Ophiuroidea sp.1	o	o	x	x			
	Ophiuroidea sp.2				x			
	<i>Encope grandis</i> (AGASSIZ, 1841)	x	x			x		
	<i>Mellita longifissa</i> (MICHELIN, 1858)	o	x			x		

2.1.3.2 Biodiversity vs. morphodynamics

A total of 47 macrofauna species were identified (Table 2.1.3; note that seven species were only found once), belonging to six higher taxonomical groups: crustaceans (13 species), polychaetes (13 species), bivalves (9 species), gastropods (4 species), nemerteans (4 species) and echinoderms (4 species). The lowest number of species was found in Ballenita (9 out of 47, or 19% of the total species pool; Table 2.1.4), the highest species richness in Briceño (33 out of 47, or 69% of the species pool). Although an equal number of crustacean and polychaete species were found in total, for all beaches polychaetes were the richest taxon, followed by crustaceans. Where the flat and intermediate beaches were rich in molluscs, no gastropods nor bivalves were found on the steep beaches of Ballenita and Portéte (Table 2.1.4). Echinoderms were also absent from the steep beaches.

A list of characterizing species per beach based on multivariate SIMPER analyses is given in Table 2.1.4. The cirrolanid isopod *Excirrolana braziliensis*, the mole crab *Emerita rathbunae* and the polychaete *Hemipodus armiger* were the only three species that were present on all seven beaches. On the steep beaches of Ballenita and Portéte the interstitial polychaetes *Pisionella indica*, *Pisione indica* and *Saccocirrus sonomacus* were characteristic. The intermediate and flat beaches shared the most characterizing taxa, such as the polychaetes *Lumbrineris inflata*, *Nephtys* sp.1, the amphipod *Haustorius* sp. but especially the gastropod *Olivella semistriata*.

Species richness estimation by using the jackknife 1 extrapolation yielded values between 12 species for Ballenita up to 43 species for Briceño (Table 2.1.4), yet no asymptotic values were obtained for Briceño, Portéte and San Pedro (Fig. 2.1.5). The trends, however, were confirmed by the expected number of species (ES) analysis (Fig. 2.1.6; Table 2.1.4). Dominance (D) was highest on the steep beaches (Table 2.1.4; Fig. 2.1.7), although Evenness (E) was surprisingly highest in Portéte as well.

The relationship between biodiversity data and the environmental characteristics is summarized in Table 2.1.5 and Fig. 2.1.8 and Fig. 2.1.9. There is a very clear increase in species richness with increasing value of the beach indices BDI (Fig. 2.1.8 and 2.1.9b) and BI (not shown), as well as with decreasing beach slope (not shown), increasing intertidal width (Table 2.1.5), and, to a lesser extent, with decreasing sediment grain size and decreasing number of effluent line-crossings (not shown). This also holds true when considering the different taxonomical groups separately as a function of BDI, except for number of polychaetes. Dominance (D) likewise showed a very clear decrease with

increasing BDI (Fig. 2.1.9a). This was not the case, however, for Evenness (E). Overall, species diversity was best explained by BDI, followed by BI and intertidal width.

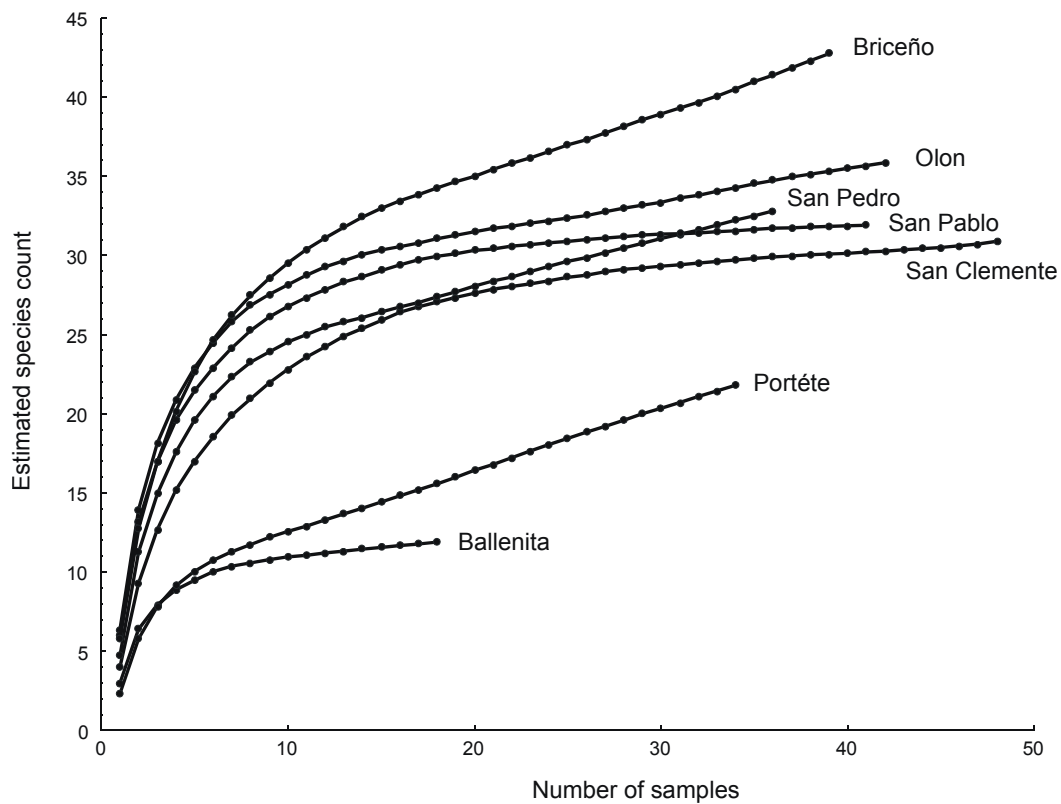


Fig. 2.1.5 – Species-area curve of the estimated species number (jackknife 1 estimator) per beach.

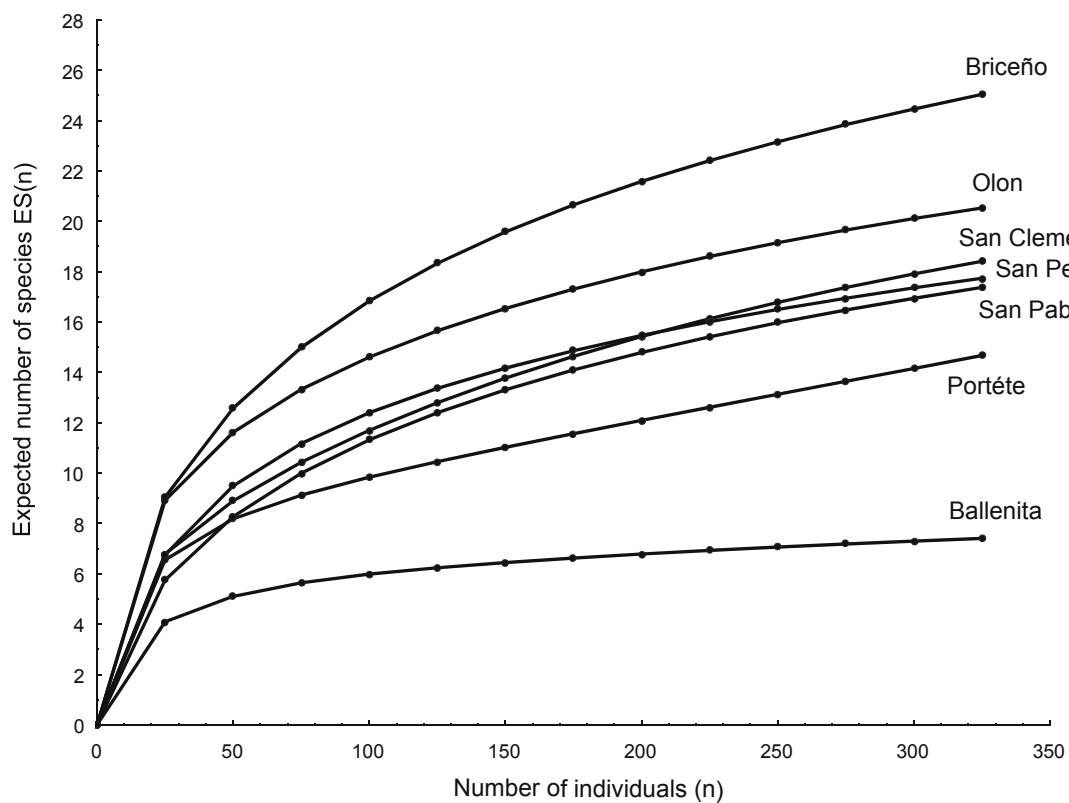


Fig. 2.1.6 – Rarefaction curves of the expected number of species for the pooled data per beach.

Table 2.1.4 - Biodiversity data for the seven beaches and characterizing species based on SIMPER analysis.

	Briceño	Olon	San Clemente	San Pablo	San Pedro	Portete	Ballenita
Number of species							
Crustacea	9	8	6	8	7	6	4
Bivalvia	7	6	7	3	6	0	0
Gastropoda	2	3	3	3	4	0	0
Polychaeta	9	8	8	10	7	8	4
Echinodermata	3	3	1	2	2	0	0
Total number of species (No)	33	30	26	27	26	15	9
% of the total species pool	69	67	54	54	52	33	19
Jack1 ± SD	42.7 ± 13.1	35.9 ± 5.0	30.9 ± 4.4	31.9 ± 3.5	32.8 ± 5.5	21.8 ± 7.4	11.9 ± 1.7
ES(325)	25.0	20.5	18.4	17.4	17.7	14.7	7.4
Evenness ± SE (E)	0.75 ± 0.03	0.74 ± 0.05	0.69 ± 0.03	0.58 ± 0.04	0.53 ± 0.04	0.77 ± 0.03	0.53 ± 0.07
Dominance ± SE (D)	0.39 ± 0.04	0.38 ± 0.04	0.58 ± 0.03	0.58 ± 0.04	0.58 ± 0.04	0.65 ± 0.05	0.64 ± 0.07
Characterizing species	<i>Lumbrineris</i> sp.	<i>Nephtys</i> sp.1	<i>Haustorius</i> sp.	<i>Olivella semistriata</i>	<i>Olivella semistriata</i>	<i>Pisone indica</i>	<i>Pisone indica</i>
	<i>Nephtys</i> sp.1	<i>Lumbrineris</i> sp.	<i>Donax spat</i>	<i>Nephtys</i> sp.1	<i>Nephtys</i> sp.1	<i>Pisone indica</i>	<i>Pisone indica</i>
	<i>Olivella semistriata</i>	<i>Exosphaeroma</i> sp.	<i>Olivella semistriata</i>	<i>Nephtys</i> sp.2	<i>Haustorius</i> sp.	<i>Emerita rathbunae</i>	<i>Excirrolana braziliensis</i>
	<i>Strigilla chroma</i>	<i>Strigilla chroma</i>	<i>E. braziliensis</i>	<i>Tivela byronensis</i>	<i>Lumbrineris</i> sp.	<i>Haustorius</i> sp.	<i>Hemipodus armiger</i>
		<i>Haustorius</i> sp.	<i>Nephtys</i> sp.1	<i>Emerita rathbunae</i>		<i>E. braziliensis</i>	

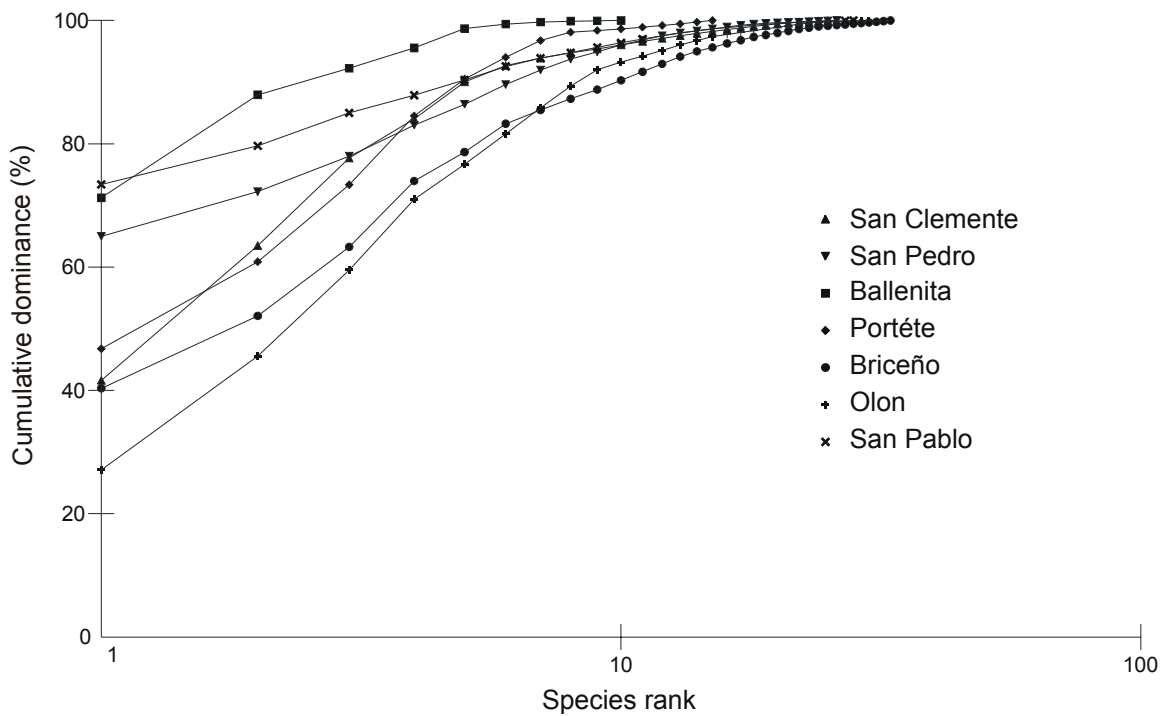


Fig. 2.1.7 - Cumulative dominance plot per beach. X-axis is the rank of species (log-scale).

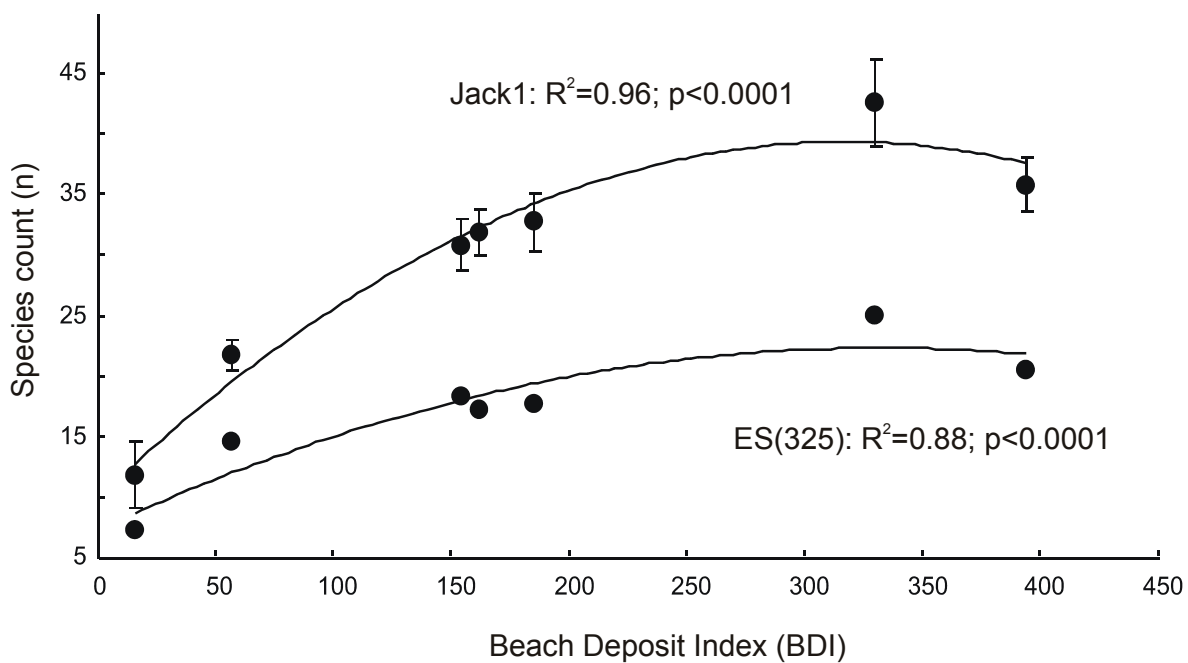


Fig. 2.1.8 – Species richness estimators – jack1 and ES(325) - as a function of the Beach Deposit Index (BDI). Lines represent second order linear regressions.

Table 2.1.5 – Biological parameters as a function of the Beach deposit index (BDI) and intertidal width. Estimate (Es), t-value and p-value of first order mixed models (with transects nested in beach as random factor); *DF* of intercept = 13. Italic/grey numbers indicate non-significant regression. Bold values indicate a more significant regression with intertidal width than with BDI. Regressions coloured in grey are shown in Fig 2.1.9.

		BDI				Intertidal width		
		<i>DF</i>	Es	t-value	p-value	Es	t-value	p-value
Biodiversity	Dominance	5	-0.001	-8.44	0.0004	-0.002	-3.93	0.0111
	Eveness	5	0.001	1.23	0.2721	0.002	1.43	0.2116
Species count	Total	5	0.060	5.49	0.0027	0.192	5.78	0.0022
	Crustacea	5	0.011	5.45	0.0028	0.040	4.43	0.0068
	Bivalvia	5	0.021	3.34	0.0207	0.066	4.95	0.0043
	Gastropoda	5	0.010	2.84	0.0362	0.029	2.38	0.0629
	Polychaeta	5	0.008	1.76	0.1380	0.026	1.78	0.1348
Density (ind/m²)	Total	5	-0.497	-0.93	0.3952	-3.264	-1.82	0.1286
	Crustacea	5	-1.153	-1.87	0.1211	-2.784	-2.13	0.0861
	Bivalvia	5	0.226	1.69	0.1522	0.914	1.78	0.1348
	Gastropoda	5	1.090	1.89	0.1169	3.192	1.68	0.1546
	Polychaeta	5	-0.855	-2.36	0.0651	-13.039	-3.45	0.0183
Biomass (g/m²)	Total	5	0.644	2.27	0.0722	1.902	1.98	0.104
	Crustacea	5	-0.019	-1.01	0.3568	-0.085	-1.17	0.2955
	Bivalvia	5	0.139	1.95	0.1085	0.574	3.17	0.0247
	Gastropoda	5	0.579	1.93	0.1121	1.744	1.75	0.1398
	Polychaeta	5	-0.031	-0.89	0.4143	-0.067	-0.81	0.4528
IST (ind/m)	Total	5	57.554	2.19	0.0802	61.532	0.40	0.7061
	Crustacea	5	-6.169	-0.34	0.7446	5.407	0.09	0.9287
	Bivalvia	5	20.667	2.03	0.0979	77.805	1.84	0.1250
	Gastropoda	5	64.789	2.25	0.0742	190.600	2.00	0.1013
	Polychaeta	5	-110.71	-2.34	0.067	-289.09	-3.12	0.0263
BST (g/m)	Total	5	51.378	4.31	0.0076	168.030	3.86	0.0119
	Crustacea	5	0.991	0.88	0.4209	4.038	0.93	0.3954
	Bivalvia	5	0.124	2.16	0.0831	0.517	3.39	0.0195
	Gastropoda	5	0.351	2.56	0.0508	1.091	2.31	0.0687
	Polychaeta	5	2.740	2.22	0.0768	8.33	2.00	0.1021

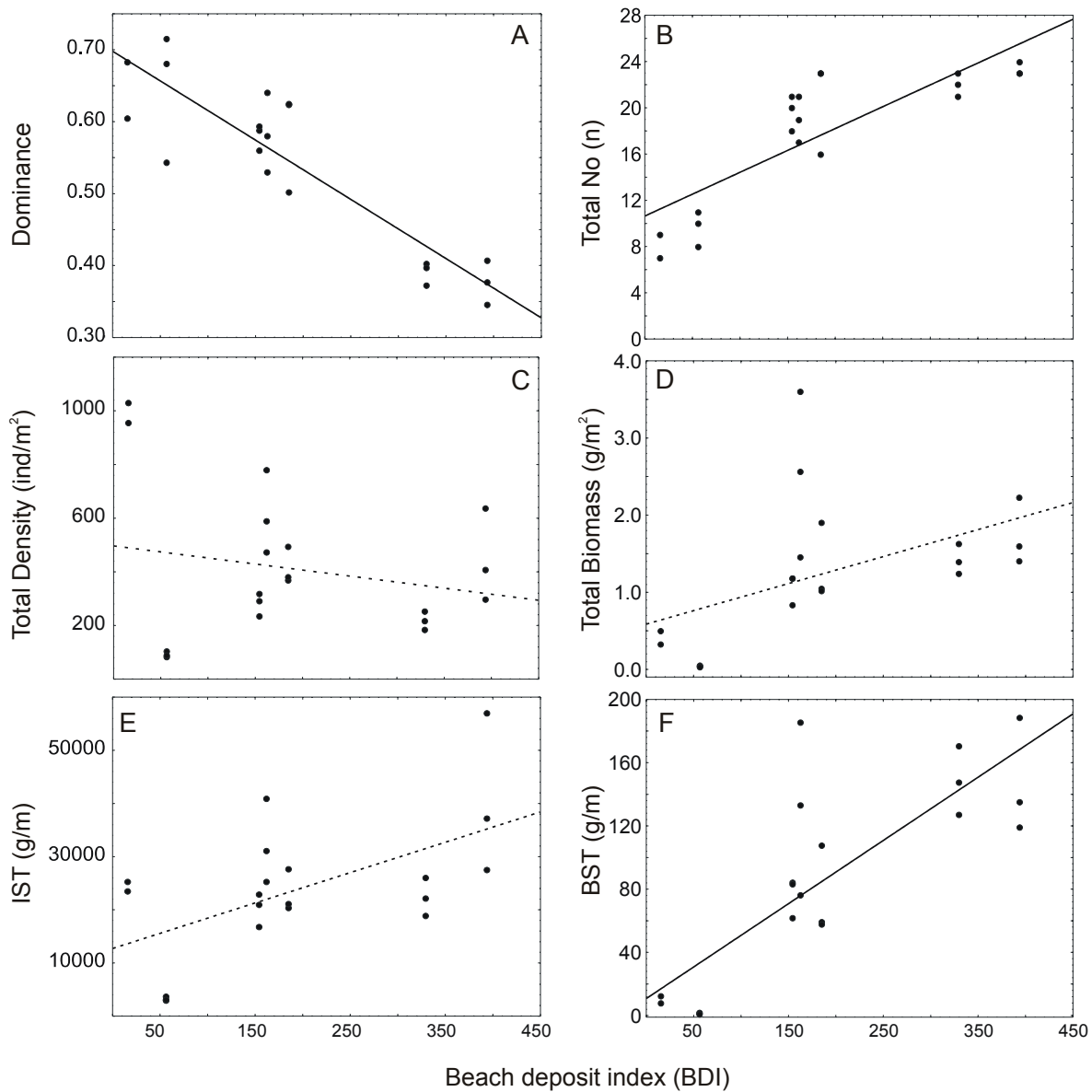


Fig. 2.1.9 – Biological parameters in function of the Beach deposit index (BDI). Each point represents the pooled data of one transect. For regression details, see Table 2.1.5; dotted lines are non-significant regressions. A) Dominance; B) Total number of species; C) Total density; D) Total biomass; E) Total abundance (expressed in IST); F) Total biomass expressed in BST

2.1.3.3 Density, abundance and biomass vs. morphodynamics

Although the beach of Ballenita had the lowest number of species, it harboured the highest densities of macrofauna, due to the presence of high numbers of crustaceans but especially polychaetes (Table 2.1.6). By far the lowest densities were found in Portéte. Crustaceans were dominant in Olon, polychaetes dominated the steep beaches of Ballenita and Portéte and gastropods were the dominant taxon in Briceño, San Clemente, San Pablo and San Pedro. Echinoderm densities were always very low (less than 16 ind/m²).

Olon harboured by far the highest total abundance, followed by San Pablo (Table 2.1.6). In Portéte the macrofaunal abundance was almost one order in magnitude lower than on any of the other beaches. With 27,569 ind/m gastropods in San Pablo were by far the most abundant taxon, although a high gastropod abundance was also found in San Pedro. Abundance of crustaceans was much higher in Olon than on any other beach; the same could be said about the polychaete abundance in Ballenita.

Biomass numbers ranged from 0.04 to 2.54 g AFDW/m² or 1.5 to 166.7 g AFDW/m (Table 2.1.6). Where highest average densities were found in Ballenita, its average biomass numbers were much lower compared to the other beaches, except Portéte. The high densities of polychaetes in Ballenita were mainly composed of very small interstitial forms, which resulted in extremely low average polychaete biomass numbers (0.14 g AFDW/m²). Only gastropods (in Olon, San Pablo and San Pedro) reached a biomass exceeding 1 g AFDW/m².

Whereas biodiversity measures showed very clear linear correlations with the environmental parameters, this was – apart from a few exceptions – not so much the case for density nor biomass data (Table 2.1.5). Beach deposit index (BDI) and intertidal width were still the best predictors, but significant results were only found for total BST (Fig. 2.1.9f), BST and biomass of bivalves, BST of gastropods (all increasing with increasing BDI or intertidal width) and for polychaete density and abundance (decreasing with increasing BDI or intertidal width). Total biomass (g/m²) and abundance (ind/m) increased with increasing BDI, but the trend was not significant (Figs. 2.1.9d and e). With total density (ind/ m²), there were no trends at all.

Table 2.1.6 - Density, abundance and biomass (AFDW) data for the seven beaches. Average values \pm SE.

		Briceño	Olon	San Clemente	San Pablo	San Pedro	Portéte	Ballenita
Density / Abundance								
Total	ind./m ²	219 \pm 53	448 \pm 184	420 \pm 281	614 \pm 147	414 \pm 94	92 \pm 25	994 \pm 420
	ind./m	24404 \pm 5948	42683 \pm 17525	21430 \pm 6720	36842 \pm 8836	23942 \pm 5430	3323 \pm 884	25053 \pm 10582
	ind./m ²	32 \pm 9	226 \pm 70	59 \pm 12	55 \pm 23	69 \pm 16	25 \pm 6.00	229 \pm 89
Crustacea	ind./m	3570 \pm 1028	21563 \pm 6691	4518 \pm 925	3314 \pm 1357	3959 \pm 930	8898 \pm 216	5758 \pm 2237
	ind./m ²	29 \pm 7	119 \pm 77	88 \pm 30	43 \pm 13	10 \pm 3	absent	absent
Bivalvia	ind./m	3235 \pm 745	11301 \pm 7374	6731 \pm 2296	2618 \pm 763	595 \pm 202	absent	absent
	ind./m ²	95 \pm 30	58 \pm 31	120 \pm 43	459 \pm 105	283 \pm 65	absent	absent
Gastropoda	ind./m	10626 \pm 3403	5485 \pm 2918	9129 \pm 3281	27569 \pm 6301	16369 \pm 3774	absent	absent
	ind./m ²	58 \pm 6	41 \pm 4	13 \pm 2	52 \pm 6	37 \pm 4	67 \pm 19	764 \pm 330
Polychaeta	ind./m	6526 \pm 654	3892 \pm 427	975 \pm 178	3147 \pm 359	2113 \pm 245	2434 \pm 668	19253 \pm 8315
	ind./m ²	4 \pm 1	4 \pm 1	1.0 \pm 0.5	3 \pm 1	16 \pm 5	absent	absent
Biomass								
Total	g/m ²	1.42 \pm 0.45	1.75 \pm 0.74	1.07 \pm 0.40	2.54 \pm 0.95	1.32 \pm 0.41	0.04 \pm 0.01	0.41 \pm 0.18
	g/m	158.8 \pm 50.0	166.7 \pm 70.7	81.4 \pm 30.4	152.7 \pm 57.0	76.5 \pm 23.4	1.5 \pm 0.4	10.5 \pm 4.5
Crustacea	g/m ²	0.05 \pm 0.02	0.09 \pm 0.03	0.14 \pm 0.11	0.08 \pm 0.03	0.06 \pm 0.02	0.02 \pm 0.00	0.28 \pm 0.12
	g/m	5.6 \pm 1.9	8.6 \pm 2.8	10.9 \pm 8.7	4.8 \pm 1.6	3.6 \pm 1.2	0.6 \pm 0.2	7.0 \pm 3.1
Bivalvia	g/m ²	0.58 \pm 0.23	0.44 \pm 0.17	0.44 \pm 0.16	0.00 \pm 0.00	0.01 \pm 0.01	absent	absent
	g/m	65.0 \pm 25.3	41.5 \pm 16.6	33.7 \pm 12.2	0.2 \pm 0.1	0.8 \pm 0.7	absent	absent
Gastropoda	g/m ²	0.61 \pm 0.17	1.10 \pm 0.52	0.45 \pm 0.12	2.33 \pm 0.90	1.16 \pm 0.36	absent	absent
	g/m	67.7 \pm 19.2	105.0 \pm 49.5	34.6 \pm 9.0	140.0 \pm 54.0	67.2 \pm 20.6	absent	absent
Polychaeta	g/m ²	0.18 \pm 0.03	0.12 \pm 0.02	0.03 \pm 0.01	0.13 \pm 0.02	0.09 \pm 0.02	0.03 \pm 0.01	0.14 \pm 0.06
	g/m	20.5 \pm 3.6	11.6 \pm 1.7	2.2 \pm 0.5	7.8 \pm 1.3	5.0 \pm 0.9	0.9 \pm 0.3	3.5 \pm 1.4

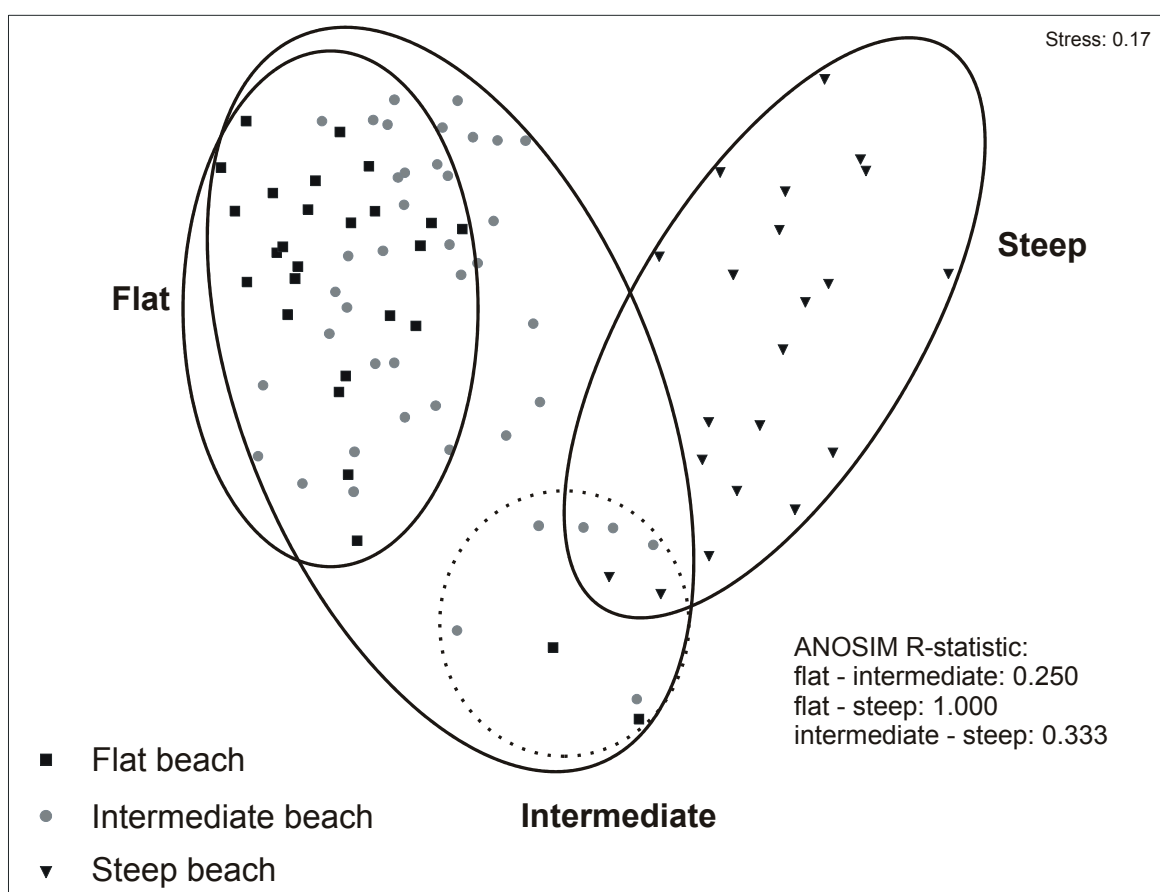


Fig. 2.1.10 - MDS-plot of the seven beaches (each point representing one sampling level) based on the density data, with indication of the statistical significance of the group division (two-way nested ANOSIM-test). Global R-statistic for the ANOSIM-test was 0.275. The dotted circle highlights the high beach stations of all beaches

The seven beaches were divided into three groups based on multivariate analyses of the environmental data. This could only partly be repeated when considering the density data of the macrofauna (MDS in Fig. 2.1.10; cluster analysis not shown). The two steep beaches were clearly separated from the other beaches; while the two flat beaches clustered together, this cluster was found entirely within the cluster of intermediate beaches. This was confirmed by the multivariate ANOSIM test, which was highly significant for the steep beaches vs. the other beaches but had a low R-value (0.250) for flat vs. intermediate beaches. Note that the stations positioned high on the beach (level 1 and 2) grouped together (Fig. 2.1.10), clearly caused by the dominance of one species, *Excirolana braziliensis*, in this zone on all seven beaches (see also further).

SIMPER analysis using the three different beach types as grouping variable showed that the steep beaches were mainly characterized by the interstitial polychaetes *Pisionella indicans* and *Pisione indicans* and the absence of *Olivella semistriata*.

Differences between the intermediate and flat beaches were not found in presence/absence of dominant species yet in their densities: the intermediate beaches had high numbers of *Olivella semistriata* compared to the high numbers of *Excirolana braziliensis*, *Haustorius* sp., *Nephtys* sp.1 and *Donax*-species on the flat beaches.

2.1.3.4 Zonation and community analyses

Cluster analyses and MDS-plotting was used to define zonation of the macrofauna per beach. The samples collected in the swash zone were defined as a separate zone *a priori* (see Chapters 2 and 3). The MDS-graphs per beach, with grouping based on the cluster analyses, are shown in Fig. 2.1.11.

On the two steep beaches, Ballenita and Portéte, only two zones could be distinguished: an upper beach zone characterized by *Excirolana braziliensis* and a lower beach zone with interstitial polychaetes, *Hemipodus armata* and *Exosphaeroma* sp. The swash zone confirmed its status as a separate zone with high numbers of *Emerita rathbunae*. The dominant interstitial polychaete *Pisionella indica* was present over the entire intertidal.

On all other beaches three zones were identified: an upper beach, middle beach and lower beach zone. The upper beach zone typically consisted of *Excirolana braziliensis* and *Donax*. The middle beach zone was dominated by *Haustorius* sp. and nephtyids. The lower beach zone was richest in species, but without any typical taxa.

The swash zone, inhabited by *Olivella semistriata*, could be found very close to or within the lower beach species association (Fig. 2.1.11).

Over all beaches, five different species associations were identified: an upper beach association, a middle beach association, a lower beach association, a swash zone association and a *steep beach* association (Fig. 2.1.12). This division was confirmed by a cluster analysis.

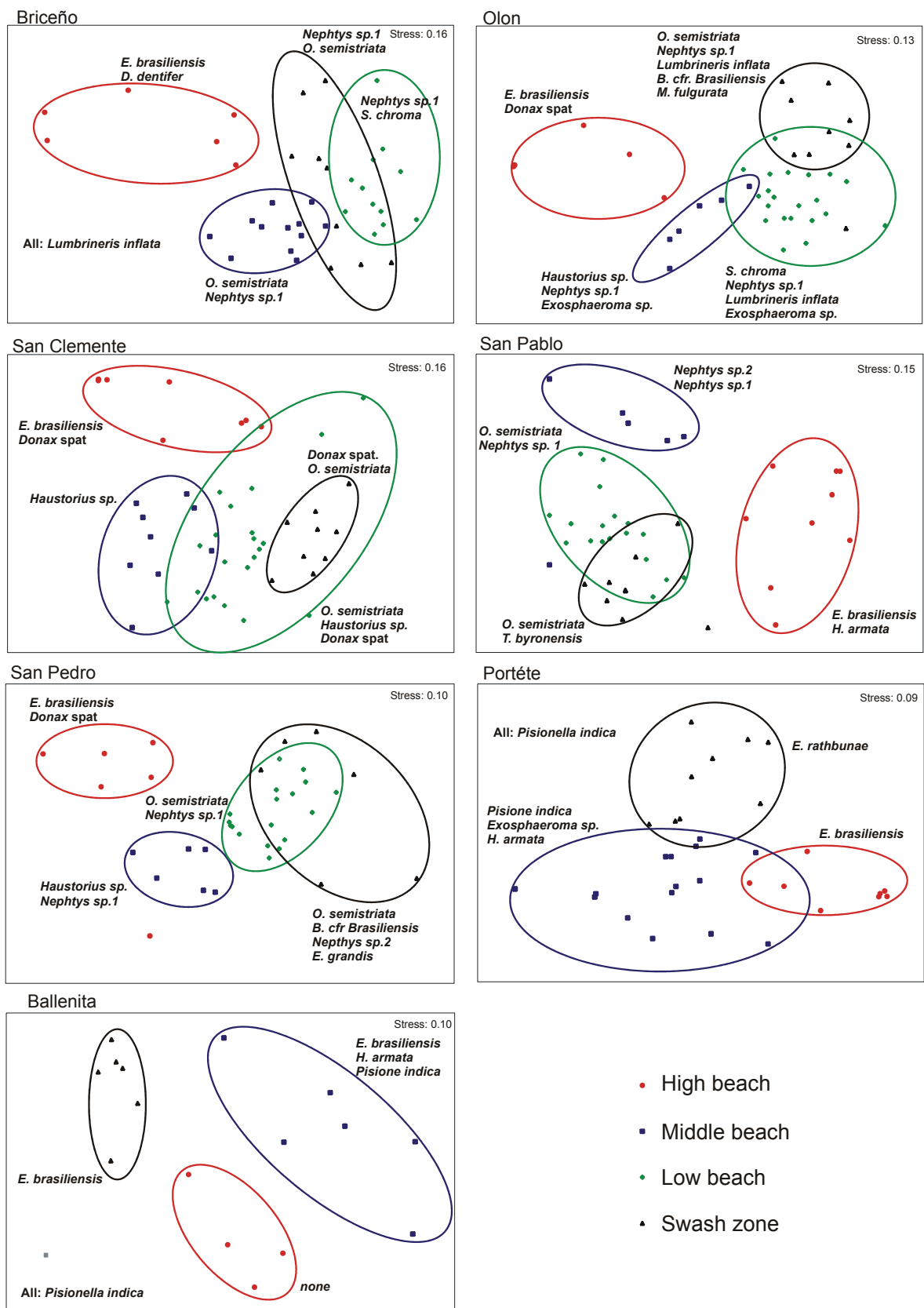


Fig. 2.1.11 - MDS-plot per beach with indication of the different zones (each point representing one sample) based on the density data. Division of zones is done *a posteriori* based on the MDS-plots and cluster analysis; swash zone is defined *a priori*. Indicator species based on the multivariate SIMPER analysis. Colour codes as indicated on the figure.

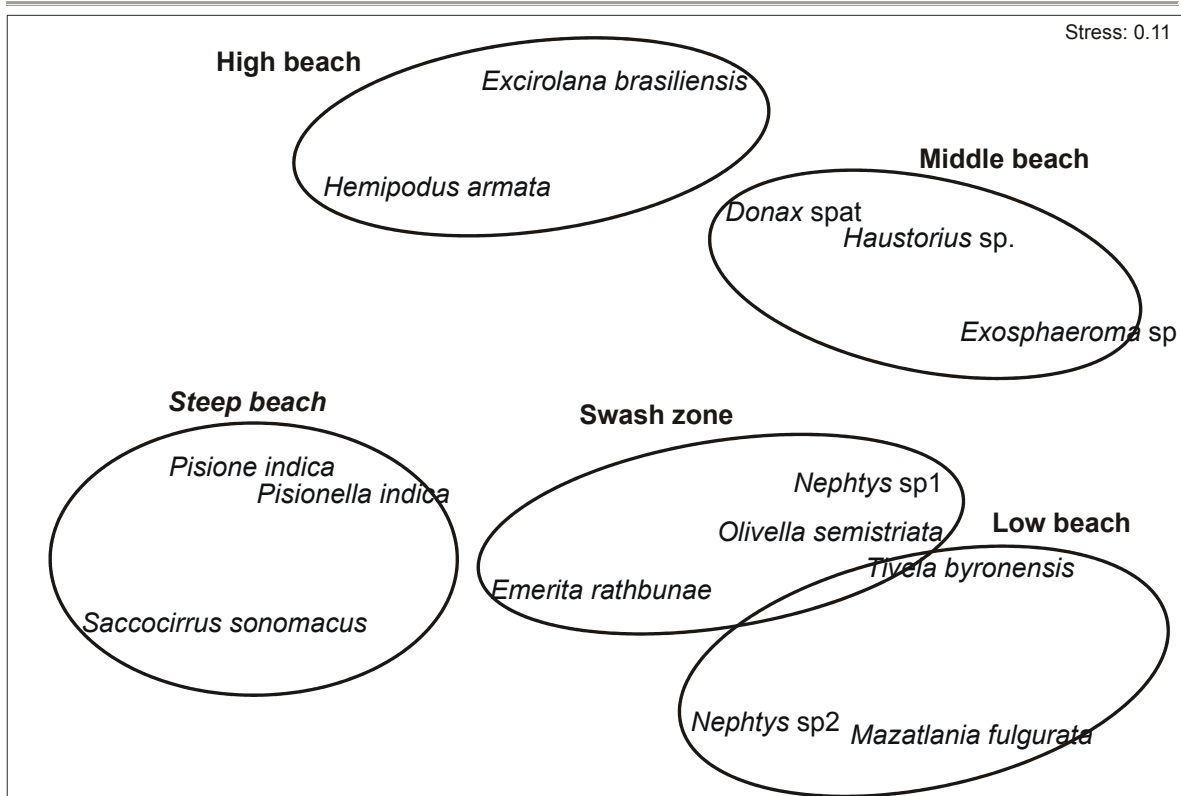


Fig. 2.1.12 - MDS-plot of the five different macrofaunal communities found over all beaches. This division was confirmed by cluster analysis.

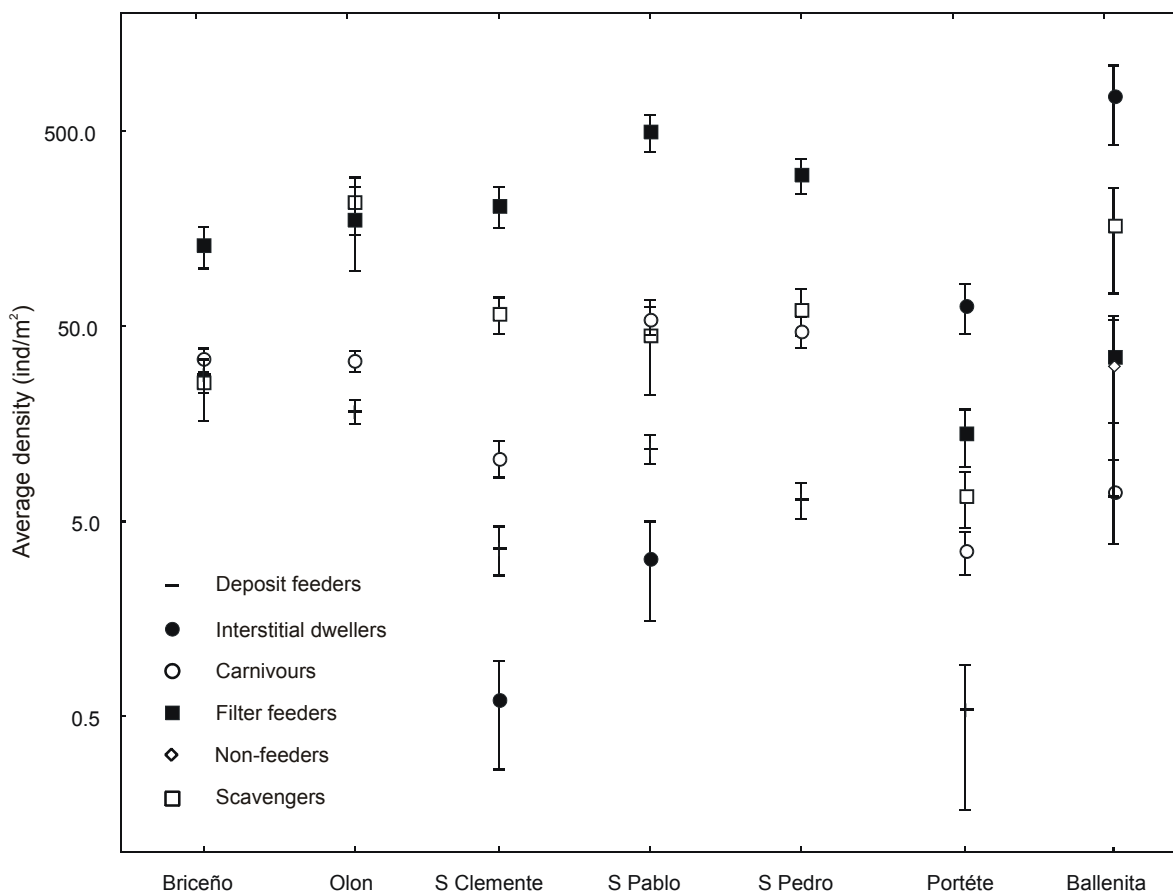


Fig. 2.1.13 - Average density \pm SE (log-scale) of the different trophic types at the seven beaches.

2.1.3.5 Feeding types vs. morphodynamics

All encountered species were ascribed to one of the following feeding types: scavengers, filter feeders, carnivores, deposit feeders, interstitial dwellers and non-feeders. The most diverse group were the filter feeders. There were only three interstitial dwellers and one non-feeding taxon. Deposit feeders were absent from the beach of Ballenita (Table 2.1.7); scavengers but especially interstitial dwellers were dominant on this beach (Fig. 2.1.13). Interstitial dwelling was also the most dominant feeding type in Port  te. All other beaches were dominated by filter feeders, both in number of species and in densities (Table 2.1.7). Olon also had high numbers of scavengers (Fig. 2.1.13). Carnivores and deposit feeders were not found in high densities on any of the beaches.

Just as with the density data, the beaches grouped into two different clusters in the multivariate analyses: steep vs. intermediate and flat (MDS Fig. 2.1.14; cluster analysis not shown). Feeding type occurrence was not significantly different between the flat and intermediate beaches (Fig. 2.1.14). The steep beaches were characterized by interstitial dwellers and scavengers. Flat beaches harboured more deposit feeders than intermediate beaches, although both beach types were dominated by filter feeders and carnivores. On average flat beaches showed a higher trophical diversity (0.40-0.41) than intermediate or steep beaches (0.56 - 0.68).

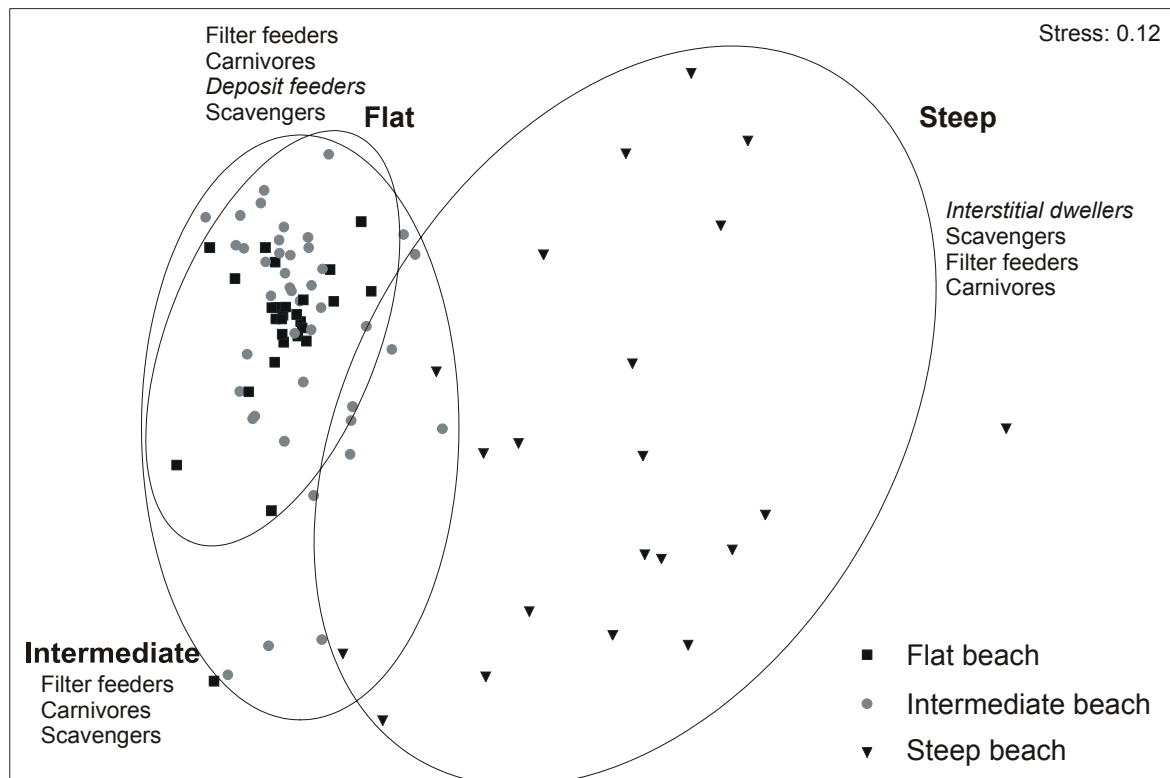


Fig. 2.1.14 - MDS-plot of the seven beaches (each point representing the pooled data for one sampling level) based on the trophic groups. Division in three groups was confirmed by cluster analysis, with *flat* found entirely in the *intermediate* cluster. Indicator feeding types are listed, based on the multivariate SIMPER analysis; *italic* feeding types are unique for one beach type.

Table 2.1.7 - Number of species and density (ind/m² ± SE) per feeding type of the seven beaches.

	Briceño	Olon	San Clemente	San Pablo	San Pedro	Porté	Ballenita
Number of species							
Scavenger	4	4	2	4	4	4	4
Filter feeder	11	10	10	6	10	1	2
Carnivour	5	5	6	6	6	4	1
Deposit feeder	4	5	4	5	3	2	0
Interstitial dweller	1	1	2	1	0	3	3
Non-feeder	0	0	0	0	0	0	1
Average density							
Scavenger	26 ± 9	218 ± 71	58 ± 12	45 ± 23	61 ± 16	7 ± 2	164 ± 91
Filter feeder	130 ± 31	177 ± 82	209 ± 50	498 ± 106	299 ± 60	14 ± 5	35 ± 19
Carnivour	34 ± 5	33 ± 4	11 ± 2	54 ± 9	47 ± 8	4 ± 1	7 ± 3
Deposit feeder	28 ± 6	18 ± 3	4 ± 1	12 ± 2	6.5 ± 1.3	0.5 ± 0.4	absent
Interstitial dweller	0.2 ± 0.2	0.2 ± 0.2	0.6 ± 0.3	3 ± 2	absent	64 ± 18	757 ± 331
Non-feeder	absent	absent	absent	absent	absent	absent	31 ± 25
Index of tropical diversity	0.41	0.40	0.59	0.68	0.56	0.55	0.61

2.1.4 Discussion

2.1.4.1 Physical environment

Given the tidal range present along the Ecuadorian coast (mean spring range around 2.5 m), the beaches that were investigated for this study represent the full spectrum of possible beach types. A mesotidal regime indeed prevents the formation of extremely reflective or ultra-dissipative beaches (Masselinck and Short, 1993). The Beach Index (BI) values were positioned around the average value that was found by McLachlan and Dorvlo (2005) for a large number of beaches worldwide (this study: 1.62 – 2.78; McLachlan and Dorvlo (2005): 0.77 – 3.20 with a mean of 2.15). Neglecting the factor tide (Beach Deposit Index, BDI), we came very close to covering the full spectrum described by McLachlan and Dorvlo (2005): 15 – 393 for this study compared to their 6 – 454.

It was very difficult to find reflective beaches in the conditions present along the Ecuadorian coast. Ecuador's coastal waters are characterized by a significant swell, fed by a constant input of large waves from the Pacific Ocean. This favours the formation of relatively flat, high energy beaches, especially combined with a meso- or macrotidal regime (Short, 1999). Consequently the two steep beaches we sampled are not textbook reflective beaches. Portéte is a very small pocket beach (beach length of about 200 m), yet fully exposed. Ballenita is a very steep, coarse sanded beach, but is known for its extremely high breakers and the absence of a surf zone (this study and Cornejo, pers. comm.), uncharacteristic to reflective beaches (Short, 1999). A last particularity of Ecuadorian beaches is the very long breaker period (13 – 20 s in this study). For open oceanic beaches this usually is in the range of 7 - 13 s (McArdle and McLachlan, 1992; McLachlan *et al.*, 1993).

2.1.4.2 Macrofauna on Ecuadorian beaches

This is only the second paper describing the macrofauna of exposed beaches in Ecuador, the other being from one single beach (Addendum 1). Moreover, information on the sandy beach macrofauna of the tropical coast of the Eastern Pacific in South-America is almost non-existing, and none of the studies from the region consider the beach morphodynamics (Dexter, 1974; Riascos and Rallon, 2001; Addendum 1).

Considering the fact that we did not sample above the drift line and as such neglected the supralittoral fauna, which by some authors is regarded as beach fauna (McLachlan and Brown, 2006), the number of macrofaunal species we encountered was

very high (47 species over 7 beaches). Degraer *et al.* (2003), for instance, found 35 species (also excluding the supralittoral fauna) on eight beaches along the Belgian coast. These were all very flat, dissipative beaches, which should normally support a very rich fauna (Defeo and McLachlan, 2005; McLachlan and Brown, 2006). Along the same coastline of the present study, but much more to the south in Chile, Jaramillo and McLachlan (1993) could only find 18 macrofaunal species, including species from above the drift line, although they extensively sampled ten beaches with contrasting morphodynamics.

The only equally high, or even higher, number of species found in beach surveys are all from tropical regions. Soares (2003) found 53 species on beaches in Madagascar and 42 in tropical part of Brazil, but he sampled more beaches (11 resp. 10). The highest recorded species richness comes from North-East Australia where Hacking (1997) identified 61 species from 15 sandy beaches. The results from Ecuador clearly justify Soares' hypothesis that tropical regions have a larger species pool than temperate regions (Soares, 2003), thereby contradicting Dexter (1992), who claimed that the number of species found per beach decreases with decreasing latitude.

Most investigated beaches were dominated by polychaetes in terms of number of species, closely followed by crustaceans and molluscs. Crustaceans dominated in San Pedro; molluscs were the most diverse taxon in San Clemente, but were absent from Ballenita and Portéte. Crustaceans are generally dominating the species diversity on South-American beaches (McLachlan and Jaramillo, 1995; Soares, 2003), especially on exposed shores (Dexter, 1992). Polychaetes, in contrast, seem to prefer sheltered beaches, with mollusc diversity being highest on intermediate beaches (Dexter, 1992). These trends are thus not supported by our findings. Although the Ecuadorian beaches are highly exposed and tend more towards the reflective end of the beach spectrum, more polychaete than crustacean or mollusc species were found per beach, even though the total number of species encountered over all seven beaches was as high for polychaetes as for crustaceans and molluscs.

Not only the species richness on the Ecuadorian beaches was very high, but also the abundance and, to a lesser extent, biomass values were rather high (3,323 – 42,683 ind/m and 1.5 – 166.7 g/m). McLachlan and Brown (2006) regard values between 100 and 10,000 ind/m and 10 and 1,000 g/m as typical. However, the values mentioned by McLachlan and Brown (2006) are Dry Weight, whereas we used Ash-Free Dry Weight (Crisp, 1984), so for better comparison their values should be reduced by a factor 4 to 10

(depending on the proportion of molluscs). Much higher values, however, can be obtained. In Chile, for instance, Jaramillo and McLachlan (1993) found abundance values up to 100,000 ind/m with a biomass of nearly 5,000 g DW/m. Interestingly, in Chapter 3 we recorded abundance values for the gastropod *Olivella semistriata* on the beach of San Pedro (from this study) of nearly 100,000 ind/m. We argued that, because of the very specific zonation in the swash of this species, standard transect sampling of the full intertidal could cause an under- or overestimation of the population size (Chapter 2 and 3). It might well be that the two or three swash stations we used in the present study are not sufficient to locate the peak density of *Olivella semistriata* in the swash, with an underestimation of the population size as a consequence.

Where polychaetes, on average, dominated in terms of species diversity, this was only the case in Ballenita for abundance and in Portéte for biomass. Most beaches were dominated, both in abundance and biomass, by gastropods. This was almost solely because of the very high numbers of the surfing gastropod *Olivella semistriata*. Molluscs dominating the biomass on beaches is a well-documented phenomenon (Soares, 2003; McLachlan and Brown, 2006), although this is nearly always because of bivalves (McLachlan *et al.*, 1996; Defeo, 2003).

Where *Olivella semistriata* is by far the most dominant species on the intermediate and flat beaches, the steep beaches were dominated by the interstitial polychaete *Pisionella indicans*. Note that this species, and other interstitial polychaetes of considerable size (*Saccocirrus sonomacus* and *Pisione indicans* from this study), is sometimes regarded as part of the meiofauna (McLachlan and Brown, 2006). The division of macro- and meiofauna, however, is arbitrary and the fact that we recorded high numbers of these polychaetes despite sieving over a 1 mm mesh-size, where even 0.5 mm is also used for macrofauna (e.g. Brazeiro and Defeo, 1996; James and Fairweather, 1996; Defeo and Martinez, 2003) justifies the inclusion of the interstitial polychaetes in our macrofauna dataset.

Other typical species were the cirrolanid isopod *Excirolana braziliensis*, omnipresent throughout the whole of South-America (McLachlan and Jaramillo, 1995), the mole crab *Emerita rathbunae*, which replaces the well-known *E. analoga* in the tropical part of the Eastern Pacific, and the amphipod *Haustorius* sp. The presence of several beach clams of the genera *Donax* and *Tivela* seems to be ubiquitous (McLachlan and Brown, 2006). *Nephtys* and *Lumbrineris* were the most widespread polychaete genera in our study.

2.1.4.3 Macrofauna and beach morphodynamics

There was a very clear linear increase in biodiversity moving from the steep, reflective beaches to the flat, dissipative beaches. This pattern is very well-documented from sites all over the world, independent of latitude or tidal range (e.g. Defeo *et al.*, 1992; Jaramillo and McLachlan, 1993; Hacking, 1997; Brazeiro, 1999; Degraer *et al.*, 2003; Soares, 2003). Together with biodiversity, also abundance and biomass tend to increase when moving towards the dissipative end of the beach spectrum (Defeo and McLachlan, 2005; McLachlan and Dorvlo, 2005). We found a decrease in density (ind/m²) and no clear pattern for abundance (ind/m). However, if the interstitial polychaetes are left out of the dataset (see higher), the trend of increasing abundance from steep to flat beaches becomes visible. For biomass, values were lower in Portéte than in Ballenita, although the latter is a more reflective beach. However, both beaches supported a much lower biomass than the other five beaches.

The increase in biodiversity, abundance and biomass was mainly because molluscs were absent from the two steep, reflective beaches. Crustacean density, abundance nor biomass, on the other hand, showed a relation with beach type; polychaete (including interstitial forms) density and abundance decreased where biomass increased from reflective to dissipative beach states (non-significant trends; see Table 2.1.5).

For all taxa, density and biomass numbers were lowest in Portéte, although Ballenita is a more reflective beach and has fewer species. Portéte, however, is a very short pocket beach. Brazeiro (1999) showed that to support sustainable populations beaches should be at least 2 km in length, below which species richness could drop significantly. In the case of Portéte, it seems that the length of the beach was not so much limiting for the number of species that could settle on the beach. It is clear, however, that no large populations had developed on this short beach.

Looking at the species composition, the two steep beaches noticeably harbour a unique, but poor community, with species that were not found on the other beaches. Between the flat and intermediate beaches, on the other hand, there is a gradual shift in species composition and the species group is fairly similar. The beach of Portéte harboured the typical interstitial steep beach community, as well as some of the intermediate/flat beach polychaetes and crustaceans and could as such be considered as a transitional state. This might explain the relatively high species count, despite the very short beach length. It would be interesting to see if there exists a beach state at which

also molluscs could survive, without losing the interstitial community. This could theoretically lead to an unusually high biodiversity under rather reflective conditions.

2.1.4.4 Zonation and beach morphodynamics

One of the paradigms in sandy beach ecology is that zonation of populations is physically controlled, with the exception of sheltered, dissipative beaches where biological interactions can occur (McLachlan and Brown, 2006). With increasing tide range and flattening of the slope the number of zones that could be identified, grows (Defeo and McLachlan, 2005). On dissipative and intermediate beaches three or four zones are generally present (reviewed in McLachlan and Jaramillo, 1995): a supralittoral zone, a littoral zone and one or two sublittoral zones. On reflective beaches the sublittoral zone, which is an upward extension of the surf zone, is normally absent (McLachlan and Brown, 2006).

Since we did not sample above the drift line the supralittoral zone is not included in this study. Starting from the drift line we could identify three different zones (upper, middle and lower beach) on all but the two reflective beaches, where only two distinct zones were present. The swash zone, although physically distinguished from the low intertidal, did not show up as a clear different zone on the dissipative and intermediate beaches, yet it did differ considerably from the middle beach zone on the steep beaches.

Thus, if we assume that a supralittoral community with its distinct zone is present on all exposed beaches (McLachlan and Jaramillo, 1995; in this study ocy podid crabs were observed on all beaches), on the exposed mesotidal beaches of Ecuador three (reflective beaches) or four (intermediate and dissipative) zones are present. Moreover, it seems that, at least on reflective beaches, the swash zone harbours a separate community. In Chapters 2 and 3 we advocated to treat – and sample – the swash fauna as a separate community. The subdivision of the lower beach or sublittoral zone into two different zones is normally only possible on dissipative beaches (McLachlan and Brown, 2006). Most studies, however, have been performed in microtidal conditions. A small intertidal range indeed leaves little room for several distinct zones. In Ecuador the mesotidal regime seems to allow for a clearer zonation in the lower intertidal. Similar results were also found on macrotidal beaches (Degraer *et al.*, 2003).

On steep, reflective beaches the low tide swash zone covers more than half of the intertidal width (56 and 95% in this study). So, even at low tide, more than half of the intertidal part of the beach is still secured of regular swash input. This leaves only a limited area to be zoned; this is probably one of the reasons why there is a reduced number of

macrofaunal zones on reflective beaches. Additionally, there is no surf zone on reflective beaches (Short, 1999) and as such, no sublittoral beach community exists (McLachlan and Brown, 2006).

It has to be noted that identifying zonation is a tricky and often subjective science (Brazeiro and Defeo, 1996; Brazeiro, 2001; McLachlan and Brown, 2006). Especially on microtidal beaches zonation can change considerably over time (Brazeiro and Defeo, 1996), although this is also the case on macrotidal beaches in temperate regions where seasonality plays a very important role (McLachlan and Jaramillo, 1995; Degraer *et al.*, 1999). Group division, based on multivariate tests such as correspondence analysis, cluster analysis and multi-dimensional scaling, is not tested for significance and should be treated with caution (Brazeiro, 2001). Therefore, our findings concerning zonation should be considered as indicative.

2.1.4.5 Macrofauna and beach morphodynamics: underlying factors?

While the patterns of macrofaunal distribution on the macroscale (*sensu* Defeo and McLachlan, 2005) may be clear, the underlying causal links are not. Several physical factors such as beach slope, sediment grain size and swash characteristics have been considered as principal functioning forces in the distribution of macrofauna on sandy beaches (McLachlan *et al.*, 1981; McLachlan *et al.*, 1993; Brazeiro, 2001; Defeo *et al.*, 2001; Nel *et al.*, 2001). The state-of-the-art in beach ecology seems to support Brazeiro's Multicausal Environmental Severity Hypothesis (2001) of sediment grain size, swash characteristics and accretion-erosion dynamics acting together as driving forces in the distribution of sandy beach macrofauna, and more specifically in limiting the occurrence of species towards reflective beaches due to increasing environmental severity with coarse sands, heavy swash action and a fast-changing beach profile.

Since we did not monitor the beaches over time we could not check the influence of accretion-erosion dynamics on the macrofauna in Ecuador. It was very clear, however, that the reduction in species richness coincided with an increase in sand grain size. There was a very strong linear, negative correlation between grain size and all species richness variables (total and per taxon). These results were not repeated for density of biomass, because values were lowest for Portéte although the sand was finer on this beach than in Ballenita.

Interestingly, the results for the swash parameters differed considerably from earlier reports in the literature. We could not find a correlation between slope and swash velocity or swash period, where McArdle and McLachlan (1992) and Brazeiro (2001) did. On the other hand swash width and number of effluent line crossings did follow the same pattern as described by McArdle and McLachlan (1991, 1992). Not surprisingly we could thus only demonstrate a clear relationship between species richness and swash width and effluent line crossings but not with swash velocity or period. McArdle and McLachlan (1991) predicted that an increase in number of effluent line crossings and swash velocity as well as a decrease in swash period and swash width would correspond with a drop in species richness. This was later confirmed by Brazeiro (2001) for number of effluent line crossings, swash velocity and swash period, and is now confirmed by our results for swash width.

Beach slope is one of the best predictors of species richness and the number of species seems to decrease consistently with steepening of the beach slope (e.g. McLachlan, 1990; Defeo *et al.*, 1992; Brazeiro, 2001; Nel, 2001; Bayed, 2003; McLachlan and Dorvlo, 2005). Its direct impact on structuring or limiting macrofauna, however, is generally questioned, since changes in slope concur with changes in sediment grain size, the latter being acknowledged as the forcing factor (Defeo *et al.*, 1992; Borzone *et al.*, 1996; Rodil and Lastra, 2004). The beach of Portéte offered a unique opportunity to distinguish between slope and grain size, since the upper two or three centimetres of the sand bed consisted of very fine sand (median grain size of 283 μm), the sort of sand expected on a relatively flat beach, yet on a beach with a steep slope (1/19). Underneath the fine top sediment layer was very coarse sand, so with an average grain size of 444 μm the overall sand was coarse. Several mollusc species (*Olivella semistriata*, *Mazatlaniana fulgurata*, *Strigilla chroma* and some of the *Donax* species) that only burrow superficially and as such would stay in the upper layer of fine sand were present on the intermediate beaches but not in Portéte. Hence, since grain size cannot be the limiting factor in this case, another factor must act as restrictive for the presence of these species. Two possibilities are beach slope and swash action. Swash parameters, however, were very similar to those of the intermediate beaches (especially San Clemente). It thus seems that beach slope itself prevented the molluscs from settling on the steep beach of Portéte.

Field studies can, of course, not prove any causal links between factors and patterns. To do that, field or laboratory experiments are needed. The different factors that

are thought to structure the macrofauna should be investigated one at a time. This has proven to be very difficult (Chapter 5), and therefore field campaigns have been and will continue to be a valuable tool to describe patterns and identify possible causal links.

2.1.4.6 Trophic structure and beach morphodynamics

The trophic structure of a community is a good measure for the complexity of the habitat, with a more diverse community expected in stable conditions (MacArthur, 1955; Watt, 1964). In sandy beach terms this means that dissipative beaches should host a fauna with a higher trophical diversity. This is exactly what we found on the beaches in Ecuador. The trophic diversity was clearly higher on the two dissipative beaches; there was no difference, however, between the intermediate and reflective beaches.

The configuration of the trophic structure depends on the food web of the ecosystem. Since primary production is very limited on exposed sandy beaches, the fauna inhabiting the beach largely depends on external input of nutrients at the base of the food web (McLachlan and Brown, 2006). Filter feeding of material that is in suspension is logically the dominant feeding type on beaches (Steele, 1976; Ansell *et al.*, 1978; Ricciardi and Bourget, 1999; McLachlan and Brown, 2006), as was the case in our study. Other ways of addressing the exogenous food supply is through deposit feeding and (herbivorous) scavenging. Sandy beach carnivores predate on both beach macroinfauna and hyperbenthos (McLachlan, 1990). Finally we also included 'non-feeding' as a feeding type for the zoeae larvae present in large numbers in Ballenita and 'interstitial dwellers' for the interstitial polychaetes since these could be considered as part of a interstitial food web, which is basically independent from the macrofaunal food web (McLachlan and Brown, 2006). The reason why interstitial species flourish on reflective beaches is to be found in the large amount of water that is filtered through coarse sands (Short, 1999), providing much more organic matter to the interstitial space than on intermediate and reflective beaches.

Deposit feeders were absent from the steep beaches and reached their highest numbers on the flat beaches of Briceño and Olon. Deposit feeding is indeed only possible under more stable conditions (McLachlan and Brown, 2006) and Ricciardi and Bourget (1999) demonstrated a significant decrease in deposit feeder biomass with steepening of the beach slope. There were no clear trends for scavengers or carnivores, which is in

contrast to what Bayed found for mesotidal exposed beaches in Morocco (2003): an increase in carnivore diversity and density with decreasing importance of filter feeders.

Note that we did not find any wrack on the beaches. Wrack can play an important role in the sandy beach faunal composition (Dugan *et al.*, 2003) and can be the most important source of carbon for the sandy beach food web (Hayes, 1974; Robertson and Hansen, 1981; Griffiths *et al.*, 1983; Dugan *et al.*, 2003). Beaches subjected to large wrack inputs can harbour a dominant population of scavengers in the supra- and midlittoral (Colombini and Chelazzi, 2003).

2.1.5 Conclusions

- 1) During this study the full spectrum of beach types along the Ecuadorian coast was sampled for macrofauna. Ecuador offers a unique environment with a mesotidal regime and tropical coastal waters.
- 2) With 47 species collected on 7 sites the Ecuadorian beaches prove to be very rich in species.
- 3) Biodiversity decreased from dissipative to reflective beaches; similar trends were found for biomass and abundance but not for density.
- 4) Changes in biodiversity could be linked to four environmental factors: sediment grain size, beach slope, number of effluent line crossings and swash width.
- 5) On the reflective beaches three different zones were identified; the intermediate and dissipative beaches had one more zone: the lower beach or sublittoral zone.
- 6) The two dissipative beaches had a highest diversity in trophic groups, indicating a more stable environment. Filter feeders were dominant on all beaches; deposit feeders only reached significant densities on the dissipative beaches. The reflective beaches were characterized by a unique interstitial fauna.
- 7) Overall, the dissipative and intermediate beaches seem very similar in species composition, density, abundance and trophic structure. The reflective beaches were clearly different in all these aspects. It seems that there is a gradual change from dissipative to intermediate beaches yet an abrupt change from intermediate to reflective beaches.