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Sandy beach macroinfauna from the coast of Ancud, Isla de Chiloé, southern Chile

Macroinfauna de playas arenosas en la costa de Ancud, Isla de Chiloé, sur de Chile

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ABSTRACT

Six sandy beaches were sampled on the coast of Ancud, Isla de Chiloé, southern Chile (ca. 42° S) with the following purposes: 1) to study community structure and across shore zonation of the intertidal macroinfauna in relation to different beach types, and 2) to analyze how similar or different is the taxonomic composition and community structure of the macroinfaunal assemblages, compared to those inhabiting sandy beaches located further north of Canal de Chacao, the limit between Isla de Chiloé and the mainland coast. Sediment samples (0.1 m^2, 30 cm deep) were collected (April-May 1998) with plastic cylinders at fifteen equally spaced levels along three replicated transects (separated by 1 m) extending from above the drift line to the swash zone. The sediment was sieved through a 1 mm mesh and the organisms collected stored in 5% formalin until sorting. To define beach types, the Dean´s parameter was calculated from wave heights and periods, and sand fall velocity of sand particles from the swash zone. The calculations show that one of the sites was a dissipative beach, while the other five had reflective or low intermediate beach characteristics. The highest number of species and total macroinfaunal abundance occurred at the dissipative site (11 species and 59705 ind m^{-1}, respectively), the lowest at the most reflective site (3 species and 507 ind m^{-1}, respectively). In general, the abundance of organisms found were higher than those predicted by a worldwide model of sandy beach community structure. The talitrid amphipod *Orchestoidea tuberculata,* the cirolanid isopod *Excirolana hirsuticauda* and the anomuran decapod *Emerita analoga,* were the most abundant species at all beaches but one. Kite diagrams and cluster analyses show that in general, three faunistical belts occur across the intertidal of the beaches studied. The across shore distribution of the macroinfauna was more related to a sand moisture gradient than to grain size or sediment compactness. Taxonomic composition, community structure and across shore zonation of that macroinfauna were similar to that from beaches located further north of Canal de Chacao.

Key words: sandy beaches, macroinfauna, Isla de Chiloé.

RESUMEN

Se muestrearon seis playas arenosas en la costa de Ancud, Isla de Chiloé, sur de Chile (ca. 42° S) con los siguientes propósitos: 1) estudiar la estructura comunitaria y la zonación transversal de la macroinfauna intermareal en relación a tipos de playas, y 2) analizar cuan similares o diferentes en composición taxonómica y estructura comunitaria son esas macroinfaunas con aquellas que habitan playas arenosas localizadas al norte del Canal de Chacao, el límite entre la Isla de Chiloé y el continente. Se recolectaron muestras de sedimento (0.1 m^2, 30 cm de profundidad) (abril-mayo 1998) con cilindros plásticos en quince niveles igualmente espaciados entre sí y ordenados a lo largo de tres transectos replicados (separados por 1 m) y extendidos entre un nivel ubicado por sobre el nivel de la marea alta y la zona de resaca. El sedimento se filtró en mallas de 1 mm de abertura y el residuo se fijó en formalina al 5% hasta posterior sorteo en el laboratorio. Para definir tipos de playas, se calculó el parámetro de Dean en base a mediciones de altura y periodo de la ola y velocidad de sedimentación de las partículas de la zona de resaca. Esos cálculos muestran que una de las playas es disipativa, mientras que las otras cinco tienen características de playas reflectivas o intermedias bajas. Los valores más altos de riqueza de especies y abundancia de la macroinfauna total ocurrieron en la playa disipativa (11 especies y 59705 ind m^{-1}, respectivamente), los más bajos en el sitio más reflectivo (3 especies y 507 ind m^{-1}, respectivamente). En general, las abundancias de organismos fueron más altas que las predichas por un modelo mundial de estructura comunitaria de playas arenosas. El anfípodo talítrido *Orchestoidea tuberculata,* el isópodo cirolánido *Excirolana hirsuticauda* y el decápodo anomuro *Emerita analoga,* fueron las especies más abundantes en todas las playas con excepción de una. Gráficos de volantín y análisis de cluster muestran que en general ocurren tres cordones faunísticos a lo ancho del intermareal de las playas estudiadas. La distribución intermareal de la macroinfauna estuvo más relacionada a un gradiente de humedad de la arena que al tamaño del grano o compactación del sedimento. La composición taxonómica, estructura comunitaria y zonación transversal de esa macroinfauna son similares a las de playas localizadas en la costa chilena al norte del Canal de Chacao.

Palabras clave: playas arenosas, macroinfauna, Isla de Chiloé.

INTRODUCTION

Microtidal oceanic sandy beaches (< 2 m of tidal range, Leeder 1982) are categorized as reflective, intermediate and dissipative (Short 1996). Reflective beaches are characterized by a virtual absence of surf zone, coarse sands, small waves and steep profiles. On the other hand, dissipative beaches have a wide surf zone, fine sands, large waves and flat profiles. Intermediate beaches lie between both these extremes with bar-trough systems, rip currents and more variable conditions (Short, 1996, Short & Wright 1983). Thus, microtidal sandy beaches are described in terms of wave and sand characteristics, the so called beach morphodynamics. The dimensionless index, Dean´s parameter (or parameter Ω) reflects the interaccion among wave height, wave period and sand fall velocity of particles from the breaker zone (Short & Wright 1983), i.e., W = Hb/T x sand fall velocity, where Hb is the height in cm of breaking waves, T is the wave period in seconds and sand fall velocity (cm s^{-1}) comes from the mean grain size of sands and empirical data given by Gibbs et al. (1971). Dean´s values of ≤ 1, 1–6 and > 6 have been usually mentioned for reflective, intermediate and dissipative beaches, respectively (e.g., Short & Wright 1983).

Oceanic sandy beaches support a diverse and abundant macroinfauna, mainly represented by crustaceans, bivalves and polychaetes (Brown & McLachlan 1990). In recent years it has been shown that the community structure of the sandy beach macroinfauna is closely related to the beaches morphodynamic. Thus, species richness, abundance and biomass increase from reflective to dissipative conditions (e.g., Brown & McLachlan 1990). These paradigmatic relationships have been thoroughly analyzed by McLachlan et al. (1993, 1996, 1998) with data collected worldwide. It has been also shown that zonation patterns of the macroinfauna change according beach types; i.e., the complexity of the patterns or the number of faunal belts across shore, increase from reflective to dissipative beaches (Jaramillo et al. 1993, McLachlan & Jaramillo 1995).

The Chilean coast (18-56° S, ca. 4200 km in length) can be divided in two broad geomorphological regions: 1) a continuous shoreline without archipelagos and some small islands, extended between Arica and Isla de Chiloé (18-41° S), and 2) a shoreline characterized by the presence of archipielagos, fjords, islands of different sizes and many channels (41-56° S), due to the sinking of the longitudinal central valley of Chile under the sea. Exposed sandy beaches of different morphodynamic types are common in the first region. While in the northern coast of that area (ca. 18-30° S), these habitats alternate with rocky peninsulas, in south central Chile (ca. 38-41° S) sandy beaches alternate with intertidal sand flats located close to the mouth of plain river estuaries.

The community structure of the macroinfauna inhabiting the Chilean coast has been studied along the coasts of Iquique (Jaramillo 1987a), Antofagasta (Clarke & Peña 1988, Jaramillo et al. 1998), Caldera (Jaramillo et al. 1998), Chañaral (Castilla 1983), Coquimbo (Sánchez et al. 1982, Jaramillo 1987a, Jaramillo et al. 1998), Quinteros (Castilla et al. 1977), Valparaíso and San Antonio (Brazeiro 1999, Brazeiro et al. 1998), San Vicente (Hernández et al. 1998) and Valdivia (Jaramillo 1987b, 1994, Jaramillo & McLachlan 1993). Two of these studies have reported analyses of the relationships between the community structure of the macroinfauna and beach morphodynamic types. Jaramillo & McLachlan (1993) studied ten beaches along the coast of Valdivia finding a close relationship with the worldwide model described by McLachlan et al. (1993); i.e., increases in species richness, abundance and biomass of the macroinfauna from reflective to dissipative conditions. However, a reexamination of the results of that study leads us to suspect that the patterns do not necessarily fit the paradigmatic model, due to the fact that the possible influence of brackish water cannot be overruled; i.e., the reflective beaches with the lowest species richness and macroinfaunal abundances were the ones closest to the outlet of the Valdivia river estuary. There is also the possibility that lower species richness and abundance of the macroinfauna at the lower shore levels of some of those reflective beaches is the result of that closeness to the estuarine area. On the other hand, the higher species richness and macroinfaunal abundances reported by Jaramillo et al. (1998) at sandy beaches of northern Chile with higher Dean´s values, come from sites with intermediate features; i.e. that analyses did not included fully dissipative beaches.

A comprehensive analyses of community structure and zonation of the macroinfauna versus morphodynamic beach stages at the Chilean coast, should then be carried out avoiding such kind of outside interferences (such as brackish water influence) and including sites representig a broad range of morphodynamic beach stages. The north western coast of Isla de Chiloé is a unique place to carry out that sort of analyses since a broad range of morphodynamic beach stages are found in a small geographic area, and no major freshwater imputs are found close to those beaches. Moreover, the presence of Canal de Chacao around

41°S provides the opportunity to explore wether that geographic discontinuity is accompanied by differences in the faunal composition of the sandy beach macroinfauna south of the Chilean mainland. As reported by several authors, Isla de Chiloé and the adjacent shores represent a limit between two zoogeographic areas along the Chilean coast: a Magellanic Province from there further south, and a Peruvian Province or Transition Zone from about 40°S further north (Knox 1960, Dell 1971, Marincovich 1973). Consequently, the objective of this study was to find answers to the following questions: i)¿ How similar or different is the relationship, community structure of the macroinfauna - morphodynamic beach stages to the worlwide model (McLachlan et al. 1993, 1996) ?, and ii) ¿ Is there any difference in taxonomic composition, community structure and zonation of the macroinfauna inhabiting sandy beaches of Chiloé as compared with that of sandy beaches located further north of Canal de Chacao, Isla de Chiloé ?

MATERIAL AND METHODS

Study area

Figure 1 shows the exposed and protected coast of Ancud, Isla de Chiloé, southern Chile. While the beaches of Guabún (41°48'S, 74°01'W) and Mar Brava (41°54'S, 73°59'W) are located in the exposed coast of Isla de Chiloé (i.e., fully exposed to the Pacific Ocean), Huicha (41°50'S, 73°44'W), Gaviotas (41°51'S, 73°45'W), Lechagua (41°52'S, 73°51'W) and Ahuí (41°49'S, 73°51'W) are located in the less exposed coast of Golfo de Ancud (Fig. 1). The tides are semidiurnal with tide ranges close to 2 m.

Sampling procedures

Samplings were carried out during April and May 1998. Sediment samples (0.1 m^2, 30 cm deep) were collected with plastic cylinders at fifteen equally spaced levels along three transects (separated by 1 m) extending from above the drift line to the swash zone; i.e., the uppermost station was

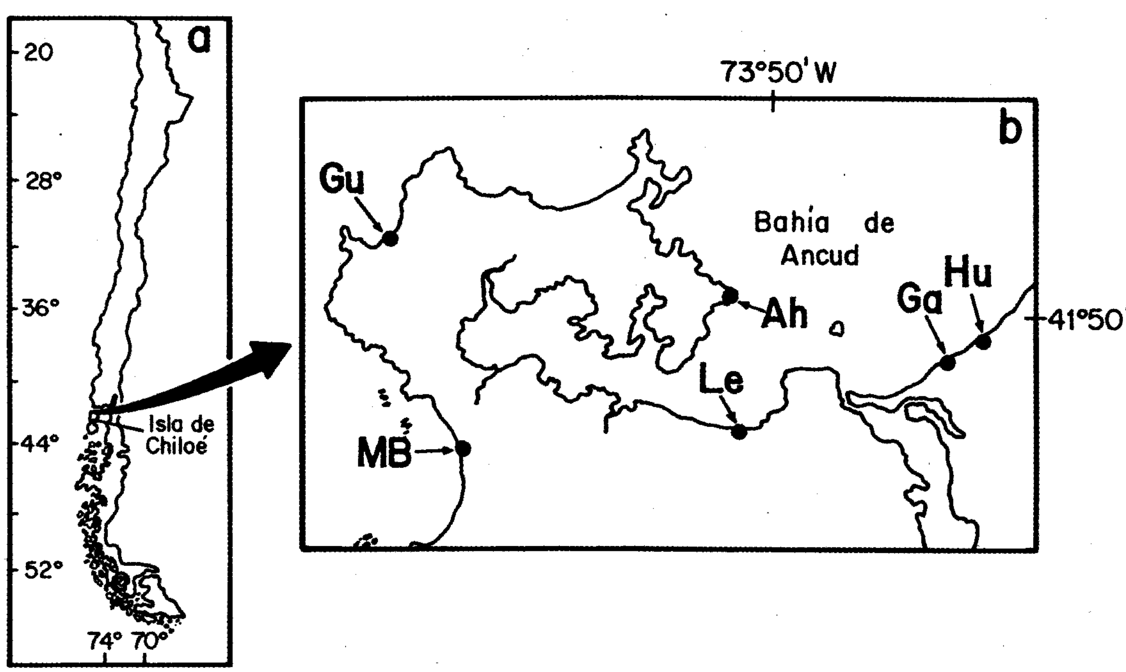

Figure 1. Map of the Chilean coast (a) and location of beaches studied at the coast of Ancud, Isla de Chiloé (b). The beaches are Guabún (Gu), Ahuí (Ah), Huicha (Hu), Gaviotas (Ga), Lechagua (Le) and Mar Brava (MB).

Mapa de la costa Chilena (a) y localización de las playas estudiadas en la costa de Ancud, Isla de Chiloé (b). Las playas son Guabún (Gu), Ahuí (Ah), Huicha (Hu), Gaviotas (Ga), Lechagua (Le) y Mar Brava (MB).

located above the drift line, the second on the drift line and the last at the lowest limit of the swash zone (indicated by bore collapse). The sediment was sieved through a 1 mm mesh and the organisms collected were stored in 5% formalin until sorting. Surface (about 5 mm) samples were collected for grain size analyses with a settling tube (Emery 1938). As a measurement of sediment compactness, the in situ shear strength of sediments at each sampling station was determined with a Pilcon hand vane tester (English Drilling Equipment Co. Ltd. England). The instrument comprises a torque head with a direct reading scale which is turned by hand. A non - return pointer indicates the reading. The vane (33 mm diameter) which is screwed into the rear of the torque head was pushed 5 cm into the sediment (the same extension of the vane). The readings are given in Kpa. Wave height was estimated by measuring the height of breaking waves with graduated poles against the horizon. The wave period (measured with a stop watch) was the time interval between breakers. The morphology (i.e., beach face slope at the site of the transect) at each beach was determined by Emery´s profiling technique (Emery 1961).

Analytical procedures

Mean grain size of sands was calculated according to the moments computational method (Seward - Thompson & Hails 1973). An index of sediment diversity was calculated with the Shannon diversity index (Brower & Zar 1977) as used by Etter & Grassle (1992) and Dugan & Hubbard (1996). From estimated mean wave height, wave period and sand fall velocity (Gibbs et al. 1971) of particles from the swash zone, Dean´s (Ω) dimensionless parameter was calculated to categorize the studied sites in beach types (Short & Wright, 1983).

Macroinfaunal abundance values per running meter of beach were obtained by linear interpolation between sampling stations, after obtaining mean abundances per m^2 at each sampling station. The mean macroinfaunal abundances (ind. m^{-2}) estimated for each station were used to draw kite diagrams which are presented together with a zonation of the physical zones of the beach (i.e., dry, retention, resurgence and swash zone; see Salvat 1964). Biological relationships among the 15 stations sampled at each beach were assessed using cluster analyses and non-metric multidimensional scaling (MDS). Cluster analyses and MDS were based upon a similarity matrix calculated with the Bray Curtis similarity coefficient after double root transformation of abundance data as run by the PRIMER (Plymouth Routines in Multivariate Ecological Research) program (Carr 1997). MDS was used to graphically display two-dimensional ordination plots of the inter-relationships among stations, based on the mean abundance (ind. m^{-2}) of the major taxa estimated for each station. Thus, the stations which were closer in that biplots were most similar. The relationship between the macroinfaunal patterns and the location of each station across the intertidal was illustrated by the superimposition of letter codes representig the moisture zones of the intertidal (Salvat 1964). The usefulness of the MDS analyses (i.e. display of relationships between stations) was evaluated with the stress statistics: values <0.1 indicates that the depiction of relationships is good, while if stress values are >0.2 the depiction is poor (Clarke 1993). The matching of macroinfaunal abundances and physical data (physical zones, mean particle size and sediment compactness) was analyzed with the program BIOENV included in the PRIMER package. Basically, this program search for the best single variable or combination of variables that best explain the grouping of stations (Clarke & Warwick 1994).

Cluster analyses based upon a similarity matrix calculated with the Bray Curtis similarity coefficient as run by the PRIMER was used to compare the taxonomic composition of the macroinfauna at different areas of the Chilean coast. The data source for that analysis came from Brazeiro et al. (1998), Castilla (1983), Castilla et al. (1977), Clarke & Peña (1988), Hernández et al. (1998), Jaramillo (in press, 1987a, 1994), Jaramillo et al. (1993, 1998), Sanchez et al. (1982) and unpublished data from E Jaramillo.

RESULTS

Beach characteristics

Table 1 shows that Mar Brava and Lechagua were the longest beaches and had the widest intertidal and the flatest slopes (1/28 - 1/46). Guabún and Ahuí were the smaller ones with quite narrow and steep intertidal slopes (1/10 - 1/11). Lechagua and Mar Brava had the finest sediments (whole means = about 183 and 189 microns, respectively), while Gaviotas and Guabún had the coarsest sands (whole means = about 600 and 415 microns, respectively). As Table 1 shows, the steepest beaches had the coarsest sediments and viceversa. Sediment diversity was higher (i.e., more heterogeneous sands) at the beaches of

TABLE 1

Physical characteristics of the beaches studied. The averages of mean grain size and sediment diversity (with standard deviations in parentheses) are based upon the values calculated for the 15 stations sampled at each beach

Características físicas de las playas estudiadas. Los promedios del tamaño medio de la partícula y diversidad del sedimento (con desviación estándard en paréntesis) están basados en los valores calculados para las 15 estaciones muestreadas en cada playa

beach	beach length (km)	intertidal width (m)	1/slope	mean grain size (microns)	sediment diversity
Guabún	2,4	26,0	1/10	415.2 (44.2)	0.85 (0.03)
Ahui	0,2	32,5	1/11	259.0 (10.7)	0.69 (0.03)
Huicha	4,3	52,0	1/15	289.8 (59.7)	0.89 (0.06)
Gaviotas	4,6	32,0	1/9	599.5 (59.3)	0.68 (0.13)
Lechagua	5,1	84,0	1/28	182.7 (21.8)	0.72 (0.10)
Mar Brava	6,4	154,0	1/46	189.3 (6.2)	0.64 (0.03)

Guabún and Huicha (0.85-0.89) and lower (i.e., more homogeneous sands) at Mar Brava (Table 1). Figure 2 shows that at beaches with finer sands (Lechagua and Mar Brava), the mean grain size was more homogenous across the intertidal than at beaches with coarser sands. At the coarser sand beaches, the mean grain size was quite variable; usually, the coarsest grains occurred at the lower shore levels (Fig. 2). Figure 2 also shows that sediment compactness across the intertidal was usually higher at the beaches with finer sediments (Lechagua and Mar Brava). At all beaches but Lechagua, sediment compactness was higher at those stations located between the drift line and the effluent line (i.e., the retention zone).

Table 2 shows the spatial variability in wave heights, wave periods and Dean´s parameter (Ω). Waves were highest at Mar Brava and Guabún with a mean of 359.9 and 123.5 cm, respectively. Ahuí and Lechagua had the lowest waves (means of 51.4 and 76.7 cm, respectively). Lehagua and Mar Brava had the longest wave periods (means of 21.5 and 16.2 s, respectively), while Ahuí and Gaviotas had the shortest ones (means of 6.6 and 9.2 s, respectively). Dean´s values show that Mar Brava had dissipative characteristics ($\Omega>6$) while Gaviotas was a typical reflective beach ($\Omega=1.1$). The Dean´s values for the other beaches fall in the range of reflective (Ω close to 1) to low intermediate (values of Ω up to 3) beach characteristics (cf. Short & Wright 1983).

Community structure of the macroinfauna

Table 3 shows species richness and abundance of the total macroinfauna at each site. The highest number of species (11) occurred at the dissipative beach of Mar Brava; the lowest (3) at the reflective site of Gaviotas. At the other beaches, species richness varied between 4 and 9 taxa. No significant relationships ($P>0.05$) were found when species richness was regressed against mean size of sands, sediment diversity, beach face slope

TABLE 2

Wave characteristics and Dean´s parameter (Ω) for the beaches studied. The values are means with standard deviations in parentheses

Características del oleaje y parámetro de Dean (Ω) en las playas estudiadas. Los valores son promedios con desviación estándard en paréntesis

beach	wave height (cm)	wave period (s)	Ω
Guabún	123.5 (10.6)	10.1 (1.6)	1,9
Ahui	51.4 (12.9)	6.6 (1.7)	2,3
Huicha	85.6 (11.3)	11.3 (1.8)	1,5
Gaviotas	102.9 (7.3)	9.2 (1.4)	1,1
Lechagua	76.7 (4.8)	21.5 (2.8)	2,2
Mar Brava	359.9 (16.8)	16.2 (2.6)	10,4

and Dean´s parameter. The highest and lowest values of macroinfaunal abundances occurred at the beaches of Mar Brava and Gaviotas, respectively (Table 3). Abundances were significantly correlated ($p<0.05$) with beach face slope and Dean´s parameter; thus, abundance $m^{-1} = -11988.2 + 2384.3$ 1/slope ($r=0.92$) and abundance $m^{-1} = -4546.3 + 6186.6\ \Omega$ ($r = 0.99$), respectively.

The talitrid amphipod *Orchestoidea tuberculata*, the cirolanid isopod *Excirolana hirsuticauda* and the anomuran decapod *Emerita analoga* were the most abundant species at all beaches, except Lechagua (Table 4). *O. tuberculata* dominated at Ahuí and Huicha, *E. hirsuticauda* at Mar Brava, and *E. analoga* at Guabún and Gaviotas. Among the species collected at Lechagua, *E. analoga* also had a high representation; however, at this beach, a phoxocephalid amphipod and polychaetes (*Haploscolopos* sp. and *Nephthys impressa*) followed in abundances (Table 4).

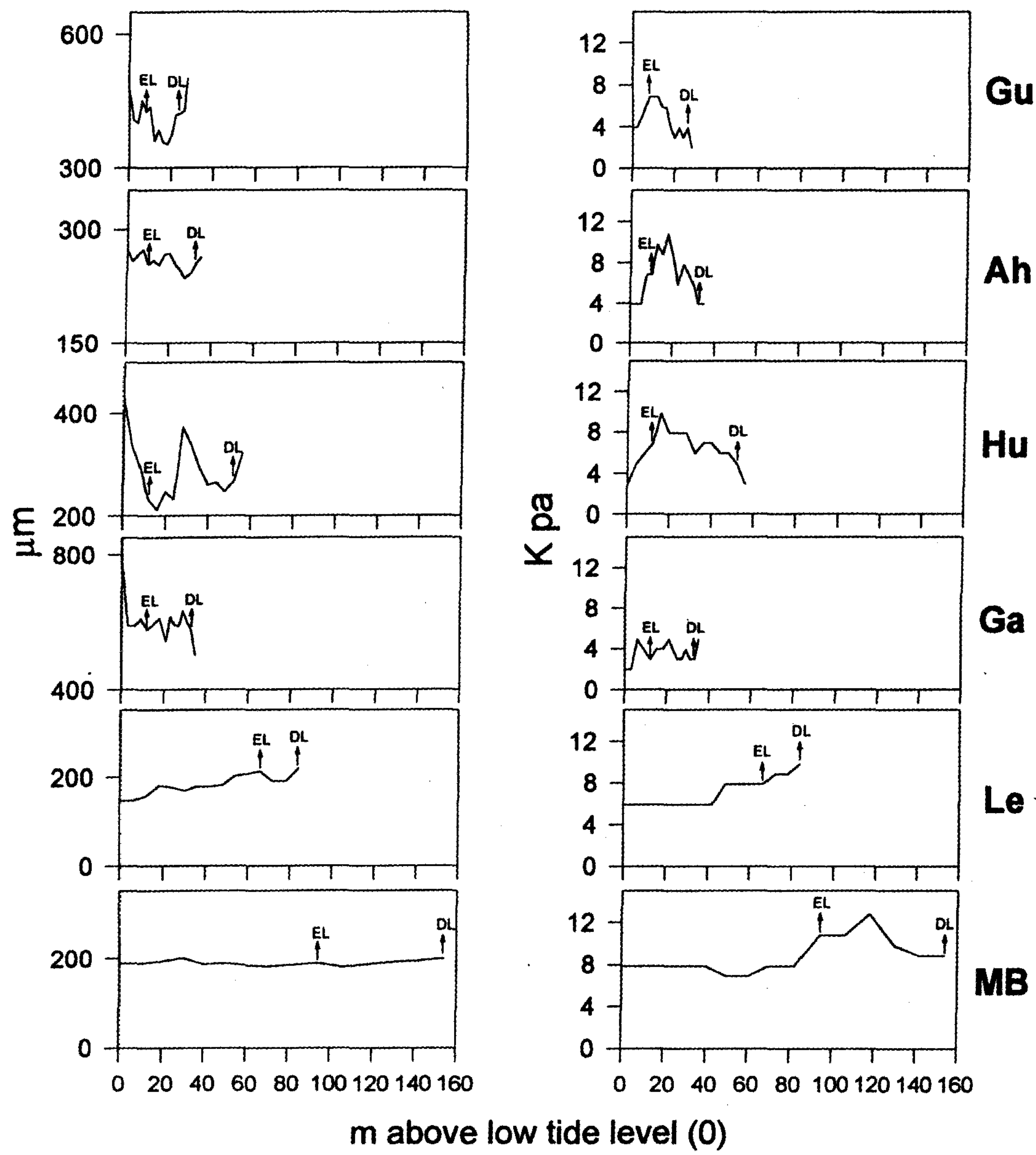

Fig. 2. Spatial variability of mean grain size (mm) and compactness of sediments (K pa) across the intertidal of the beaches studied. Codes for beaches as in Fig. 1. DL = drift line, EL = effluent line or upper limit of resurgence zone.

Variabilidad espacial del tamaño medio (mm) y compactación del sedimento (k pa) a lo ancho del intermareal de las playas estudiadas. Códigos para las playas como en la Fig. 1. DL = línea de marea alta, EL = línea de efluente o límite superior de la zona de resurgencia.

TABLE 3

Number of species and total abundance of the macroinfauna (n° m^{-1}) at the beaches studied. The values of abundances are means with standard deviations in parentheses

Número de especies y abundancia total de la macroinfauna (n° m^{-1}) en las playas estudiadas. Los valores de abundancia son promedios con desviación estándard en paréntesis

beach	n° of species	total abundance
Guabún	4	9 360.5 (3 046.5)
Ahui	9	6 816.6 (983.1)
Huicha	4	4 748.4 (2 430.8)
Gaviotas	3	507.5 (8.8)
Lechagua	8	11 662.5 (1463.8)
Mar Brava	11	59 705.0 (9 866.2)

Across shore abundance, diversity and zonation of the macroinfauna

Figures 3 to 5 show the across shore zonation of the macroinfauna of all the studied beaches. The uppermost beach levels (dry zone, drift line and uppermost levels of the retention zone) were occupied by *O. tuberculata* at all beaches. The isopod *E. braziliensis* was also present at the same shore levels in Guabún, Huicha and Mar Brava. *E. hirsuticauda* was the most abundant organisms at the middle beach levels (retention zone) in Ahuí and Mar Brava. This species and *E. analoga* occurred in similar abundances at the middle beach levels of Huicha and Gaviotas. The polychaete *Euzonus heterocirrus* also occurred at the middle beach levels of Mar Brava. The anomuran *E. analoga* was the most common organism at the lower beach levels (lowest levels of the resurgence zone and swash zone), even though at all beaches but Lechagua, its distribution extended up to the lowest levels of the retention zone. Other species collected at the lower shore levels were the polychaetes *N. impresa* and *Haploscolopos* sp. , the isopod *Macrochiridothea setifer* and juveniles of the bivalve *Mesodesma donacium* (mostly at the swash zone) (Fig. 3 to 5).

Figure 6 shows the grouping of stations resulting from cluster analyses. Even when linked at low similarity values, all the sations sampled at Guabún, Ahuí and Mar Brava were linked together (i.e., 11.7, 8.3 and 7.8% were the lowest grouping links at Guabún, Ahuí and Mar Brava, respectively). On the other hand, the clusters for Huicha, Gaviotas and Lechagua showed more marked faunal breaks. The two upper stations of Huicha had no similarity at all (0%) with the rest of the stations since *O. tuberculata* and *E.*

TABLE 4

Mean abundance of the macroinfauna per linear meter of beach at the study sites. One standard deviation in parentheses. CI = Crustacea Isopoda, CA = Crustacea Amphipoda, CDA = Crustacea Decapoda Anomura, P = Polychaeta, MB = Mollusca Bivalvia

Abundancia promedio de la macroinfauna por metro lineal de playa en los sitios de estudio. Una desviación estándard en paréntesis. CI = Crustacea Isopoda, CA = Crustacea Amphipoda, CDA = Crustacea Decapoda Anomura, P = Polychaeta, MB = Mollusca Bivalvia

taxa	category	Guabún	Ahui	Huicha	Gaviotas	Lechagua	Mar Brava
Excirolana braziliensis Richardson	CI	26.7 (23.1)		13.3 (23.1)			
Excirolana hirsuticauda Menzies	CI	620.0 (80.0)	1 166.7 (80.4)	226.7(61.1)	48.3 (36.2)	360.0 (261.5)	23 277.5 (7 480.5)
Excirolana monodi Carvacho	CI		108.3 (87.8)				
Macrochiridothea setifer Menzies	CI		82.3 (71.3)				818.3 (459.7)
Orchestoidea tuberculata Nicolet	CA	2 020.0 (100.0)	3 258.3 (428.9)	3 866.7 (2 335.9)	205.0 (22.9)	60.0 (60.0)	11 040.0 (623.5)
Huarpe sp. Barnard & Clark	CA						316.7 (283.5)
Phoxocephalidae Sars	CA					3 075.0(315.3)	
Lysianassidae Dana	CA						487.5 (339.8)
Amphipoda 1	CA		325.0 (237.4)				
Amphipoda 2	CA		262.5 (211.1)				
Emerita analoga Stimpson	CDA	6 693.8 (3 151.7)	1 270.8 (634.9)	641.7 (183.9)	254.2 (64.8)	3 480.0 (1 041.0)	8 820.0 (2 225.0)
Haploscoloplos sp. Monro	P		334.4 (246.4)			2 640.0 (626.4)	1 233.3 (376.3)
Euzonus heterocirrus Rozbaczylo & Zamorano	P						8 676.7 (1 158.5)
Gliceridae Grube	P					477.5 (366.3)	
Onuphidea Kinberg	P					165.0 (155.0)	
Nephthys impressa Baird	P					1 405.0 (256.1)	1 045.0 (45.0)
Lumbrinereis sp. Blainville	P		8.3 (14.4)				
Mesodesma donacium (Lamarck)	MB						3 910.0 (781.7)

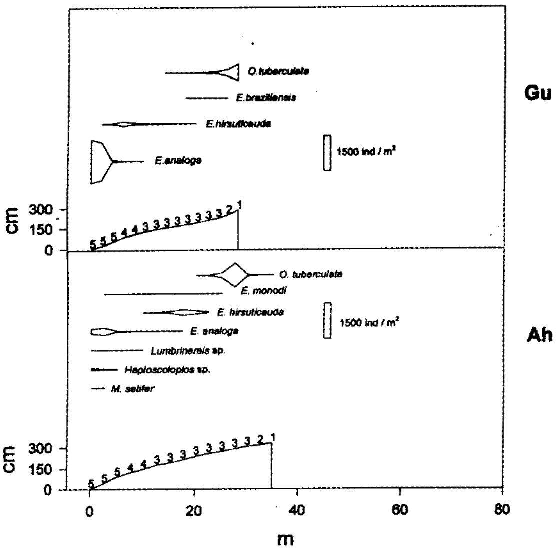

Fig. 3. Across shore zonation of the macroinfauna at the beaches of Guabún (Gu) and Ahuí (Ah). The beach face slope is shown for each beach. Numbers above that slopes indicate the physical beach zones: 1= dry zone, 2 = drift line, 3 = retention zone, 4 = resurgence zone, 5 = swash zone.

Zonación transversal de la macroinfauna en las playas de Guabún (Gu) y Ahuí (Ah). Para cada playa se grafica el perfil o inclinación de la misma. Los números ubicados arriba de esos perfiles indican las zonas físicas de la playa: 1= zona de secado 2 = línea de marea alta, 3 = zona de retención, 4 = zona de resurgencia, 5 = zona de batido de las olas.

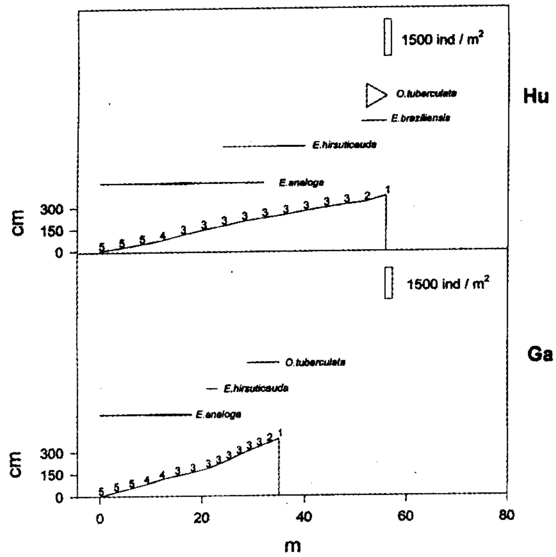

Fig. 4. Across shore zonation of the macroinfauna at the beaches of Huicha (Hu) and Gaviotas (Ga). Details as for Figure 3.

Zonación transversal de la macroinfauna en las playas de Huicha (Hu) y Gaviotas (Ga).Detalles como en la Figura 3.

braziliensis only occurred at stations 1 and 2 (cf. Fig. 4). Due to the fact that no species overlaped at Gaviotas, the cluster for this site resulted in three separate groups (i.e., no macroinfaunal similarity at all), each one characterized by the presence of a single species (cf. Fig. 4). Station 2 of Lechagua (no macroinfauna was collected at station 1 of this site) has no similarity (0%) with the rest of the stations since *O. tuberculata* was collected just at this level (cf. Fig. 5). A trend to group according to the physical zones where the stations were located was also observed in the cluster analysis for each beach (Fig. 6). In general, stations located at the dry zone and drift line linked with stations of the upper levels of the retention zone; those of the lower levels of the retention zone linked to some of the resurgence zone, and most of the ones located at the middle and lower levels of the resurgence zone linked to those located at the swash zone (Fig. 6).

The macroinfaunal relationships between sampling stations resulting from MDS analyses are depicted in the plots shown in Fig. 7 and 8. The

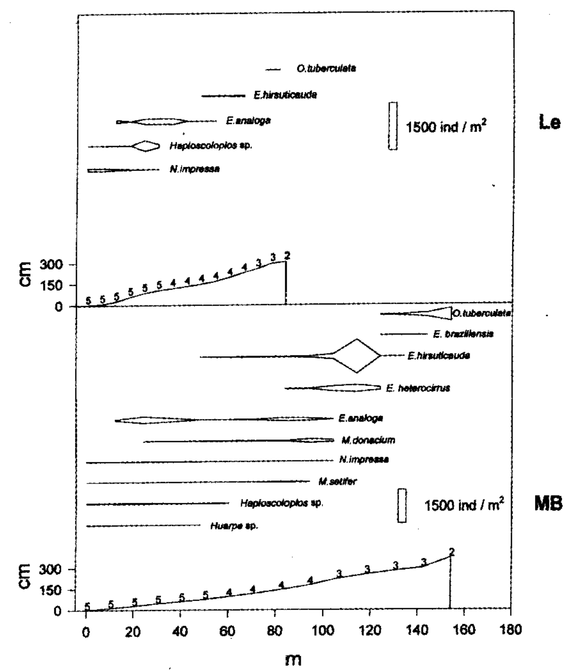

Fig. 5. Across shore zonation of the macroinfauna at the beaches of Lechagua (Le) and Mar Brava (MB). Details as for Figure 3.

Zonación transversal de la macroinfauna en las playas de Lechagua (Le) y Mar Brava (MB).Detalles como en la Figura 3.

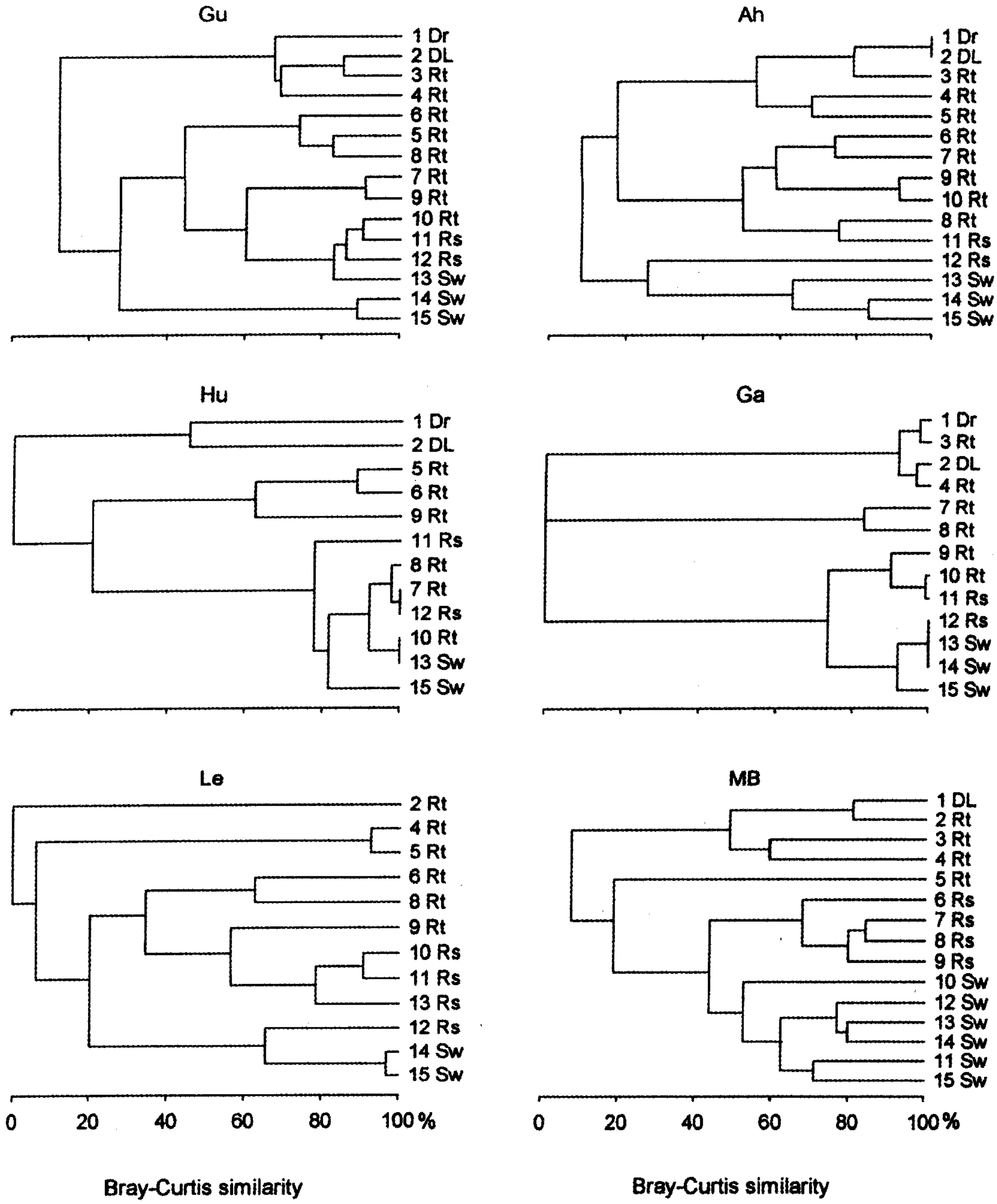

Fig. 6. Cluster analysis of the faunal relationships among the stations sampled at each beach. The numbers correspond to the stations and the letters to the physical zones of the beach: D = dry zone, DL= drift line, Rt = retention zone, Rs = resurgence zone, Sw = swash zone.

Análisis de agrupamiento de las relaciones faunísticas entre las estaciones muestreadas en cada playa. Los números corresponden a las estaciones y las letras a las zonas físicas de la playa: D = zona de secado, DL = línea de marea alta, Rt = zona de retención, Rs = zona de resurgencia, Sw = zona de batido de la ola.

values of the stress statistic (<0.04) indicate that the depiction of the relationship for each beach is good (Clarke 1993). Each MDS plot reveals a gradient of macroinfaunal change from the upper to the lower beach levels. The superimposition of codes for the physical zones of the beach on each point (station) of the MDS plots suggests that the main axis of macroinfaunal variability is related to a moisture gradient. Table 5 displays the outcome of the BIO-ENV procedure included in the PRIMER package. The inclusion of a single environmental variable, rendered the best correlation

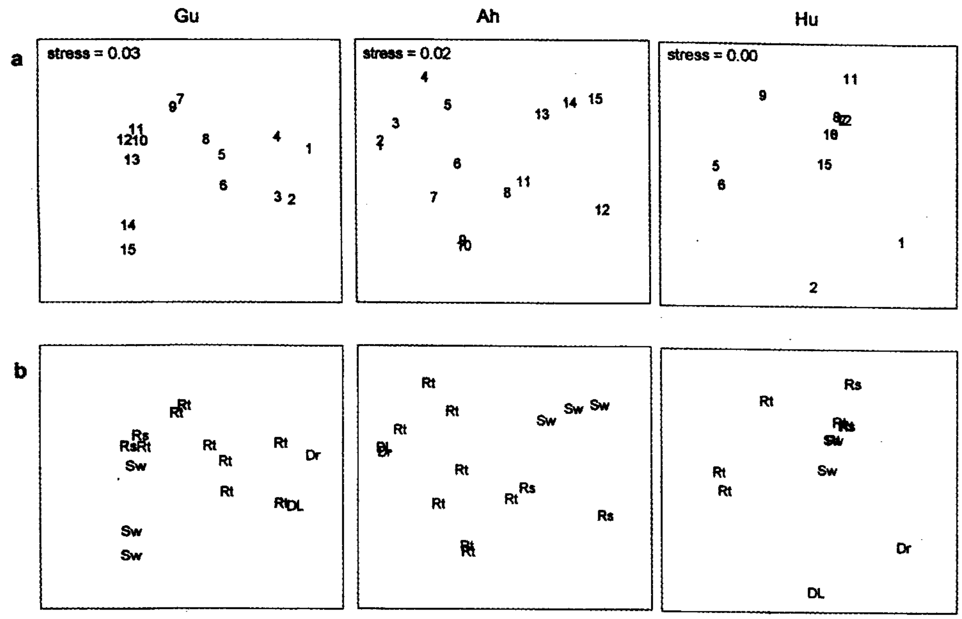

Fig. 7. a) MDS plots of Bray-Curtis similarities from root root transformed macroinfaunal abundances at the stations sampled at the beaches of Guabún, Ahuí and Huicha. b) MDS of macroinfaunal data with superimposed codes representing a moisture gradient across the intertidal: D = dry zone, DL= drift line, Rt = retention zone, Rs = resurgence zone, Sw = swash zone.

a) gráficos MDS basados en similitudes de Bray-Curtis sobre las abundancias de la macroinfauna transformadas por doble raíz cuadrada en las estaciones muestreadas en las playas de Guabún, Ahuí y Huicha. b) gráficos MDS de la macroinfauna con códigos superimpuestos que representan un gradiente de humedad a lo ancho del intermareal: D = zona de secado, DL = línea de marea alta, Rt = zona de retención, Rs = zona de resurgencia, Sw = zona de batido de las olas.

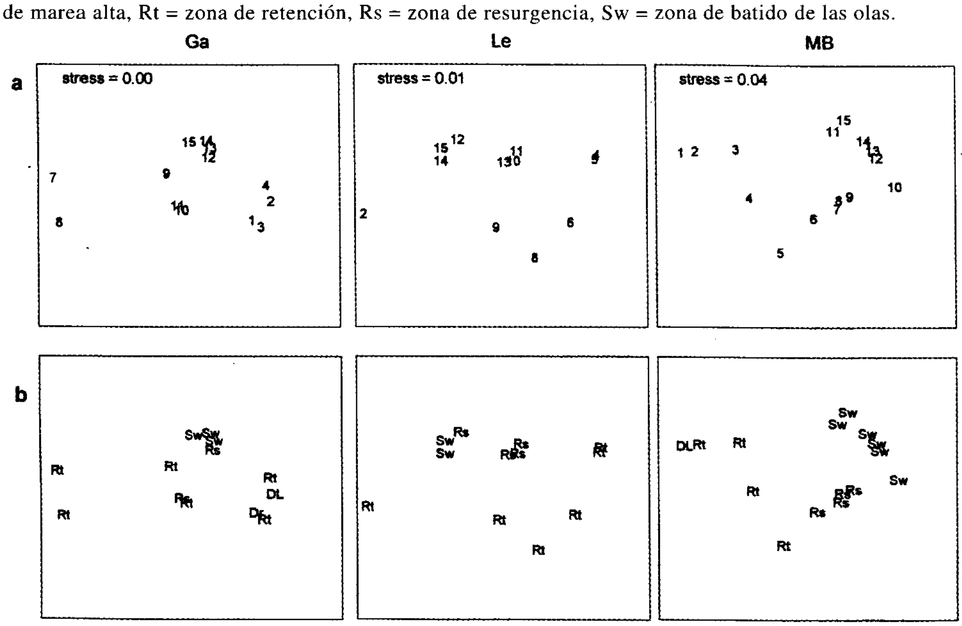

Fig. 8. a) MDS plots of Bray-Curtis similarities from root root transformed macroinfaunal abundances at the stations sampled at the beaches of Gaviotas, Lechagua and Mar Brava. b) MDS of macroinfaunal data with superimposed codes representing a moisture gradient across the intertidal: D = dry zone, DL = drift line, Rt = retention zone, Rs= resurgence zone, Sw = swash zone.

a) gráficos MDS basados en similitudes de Bray-Curtis sobre las abundancias de la macroinfauna transformadas por doble raíz cuadrada en las estaciones muestreadas en las playas de Gaviotas, Lechagua and Mar Brava. b) gráficos MDS de la macroinfauna con códigos superimpuestos que representan un gradiente de humedad a lo ancho del intermareal: D = zona de secado, DL = línea de marea alta, Rt = zona de retención, Rs = zona de resurgencia, Sw = zona de batido de las olas.

TABLE 5

Combinations of the three environmental variables resulting in the best matches of macroinfaunal abundance and abiotic similarity matrices. The values are Spearman rank correlations. The variables which rendered that correlation values are presented in parenthesis

Combinación de las tres variables ambientales que resultan en la mejor correlación entre abundancias de la macroinfauna y matrices de similitud abiótica. Los valores corresponden a correlación de Spearman. Se presentan en paréntesis las variables que corresponden a esos valores de correlación

	1 variable		2 variables		3 variables	
Guabún	0,415	(zones)	0,396	(zones + sand size)¡	0,368	(zones + sand size + sed compacteness)
Ahuí	0,518	(zones)	0,511	(zones + sand size)	0,499	(zones + sand size + sed compacteness)
Huicha	0,343	(sed compactness)	0,320	(zones + sed compacteness)	0,066	(zones + sand size + sed compacteness)
Gaviotas	0,239	(zones)	0,061	(zones +sand size)	0,020	(zones + sand size + sed compacteness)
Lechagua	0,485	(zones)	0,613	(zones + sed compacteness)	0,627	(zones + sand size + sed compacteness)
Mar Brava	0,766	(Zones)	0,669	(zones + sed compacteness)	0,550	(zones + sand size + sed compacteness)

value between macroinfaunal patterns and physical variables at all beaches but Lechagua (i.e., r = 0.485 with a single variable versus r = 0.627 with three variables). The single environmental variable which best groups the stations is physical zones at all beaches but Huicha, where sediment compactness best explained the variability in macroinfaunal abundances across the intertidal.

Inter-region comparisons

The dendrogram depicted in Figure 9 shows that the taxonomic composition of the sandy beach macroinfauna of Chiloé,is quite similar to that inhabiting sandy beaches at the coast of Valdivia, about 300 km north (Bray-Curtis similarity index: 83.3% between both coasts). As a matter of

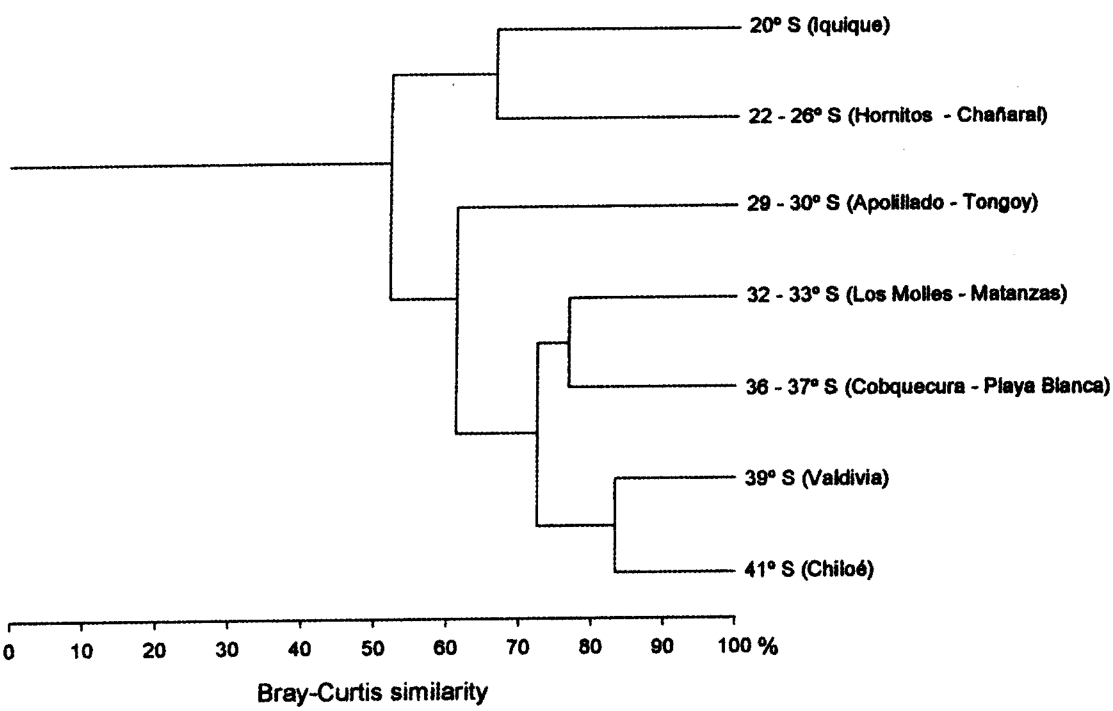

Fig. 9. Cluster analysis of the taxonomic relationships among the macroinfauna of sandy beaches located at seven coastal regions of Chile.

Análisis de agrupamiento de las relaciones taxonómicas entre la macroinfauna de playas arenosas localizadas en siete regiones costeras de Chile.

TABLE 6

Taxonomic composition of the sandy beach macroinfauna at seven coastal areas of the Chilean coast. IC: Insecta Coleoptera, CI: Crustacea Isopoda, CA: Crustacea Amphipoda, CDM: Crustacea Decapoda Macrura, CDA: Crustacea Decapoda Anomura, CDB: Crustacea Decapoda Brachyura, MB: Mollusca Bivalvia, P: Polychaeta

Composición taxonómica de la macroinfauna de playas arenosas en siete áreas de la costa Chilena. IC: Insecta Coleoptera, CI: Crustacea Isopoda, CA: Crustacea Amphipoda, CDM: Crustacea Decapoda Macrura, CDA: Crustacea Decapoda Anomura, CDB: Crustacea Decapoda Brachyura, MB: Mollusca Bivalvia, P: Polychaeta

	20°S (Iquique)	22-26° S (Hornitos-Chañaral)	29-30° S (Apolillado-Tongoy)	32-33°S (Los Molles-Matanzas)	36-37°S (Cobquecura-Playa Blanca)	39° S (Valdivia)	41°S (Chiloé)
Eriopis conexa IC				X			
Phalerisida maculata IC	X	X	X	X	X	X	X
Tylos spinulosus CI			X				
Excirolana braziliensis CI	X	X	X	X	X	X	X
Excirolana hirsuticauda CI		X	X	X	X	X	X
Excirolana monodi CI		X		X	X	X	X
Macrochiridothea mehuinensis CI					X	X	X
Macrochiridothea lilianae CI						X	X
Macrochiridothea setifer CI				X	X	X	X
Chaetilia paucidens CI		X	X	X	X	X	X
Cheus sp. CA			X			X	
Lysianasidae CA	X				X		
Phoxorgia sp. CA				X	X	X	X
Phoxocephalidae CA				X			X
Orchestoidea tuberculata CA		X	X	X	X	X	X
Phoxocephalopsis mehuinensis CA						X	X
Bathyporeiapus magellanicus CA			X	X	X	X	X
Phoxocephalopsis sp. CA			X	X	X	X	X
Tryphosella schellenbergi CA						X	
Ampelisca sp. CA						X	
Huarpe sp. CA						X	X
Ogyrides tarazonai CDM	X	X					
Emerita analoga CDA	X	X	X	X	X	X	X
Lepidopa chilensis CDA	X	X	X	X	X	X	
Blepharipoda spinimana CDA	X		X				
Ovalipes puntatus CDB			X				
Ocypode gaudichaudii CDB	X	X					
Bellia picta CDB			X			X	
Mesodesma donacium MB	X		X	X	X	X	X
Donax peruvianus MB		X					
Gliceridae P	X	X	X		X	X	X
Polydora sp. P			X				
Scololepis sp. P				X			
Scololepis cirratulus chilensis P			X	X	X		
Nephtys monilibranchiata P			X				
Nephtys impressa P	X	X	X	X		X	X
Leitoscoloplos sp. P	X	X	X			X	X
Sthenelais sp. P				X			
Hemipodus sp. P	X		X				
Euzonus heterocirrus P		X	X	X	X	X	X
Lumbrinereis sp. P	X	X		X			X
total number of species	14	16	23	21	18	25	22

fact, the number of species found at both areas (25 at Valdivia and 23 at Chiloé) and the species themselves, are almost the same (Table 6). That similarity decreases further north; i.e., a gradual change in taxonomic composition occurs from 39-41°S till 18°S in the north (Fig. 9). For example, 64 and 75% of the species found at the coast of Iquique (20°S) and at that of Hornitos and Chañaral (29-30°S) are also found at the coast of Chiloé.

DISCUSSION

The sandy beaches studied included one site with dissipative characteristics (Mar Brava), and five which displayed reflective or low intermediate beach features. Thus, the beach stages analyzed cover a wide range of morphodynamic beach types (cf. Short & Wright 1983, Short 1996). The results of this study show that the highest species richness and macroinfaunal abundances occurred at the dissipative beach (highest Dean´s), while the lowest values for that community attributes were found at the reflective site with the lowest Dean´s (Gaviotas). Our results are similar to the conclusions presented for other sandy beach studies; either at the Chilean coast (Jaramillo & McLachlan 1993, Jaramillo et al. 1998) or elsewhere (Defeo et al. 1992, McLachlan et al. 1993, 1996); that is, beaches located toward the dissipative side of the full spectrum generally support richer and more abundant macroinfaunas than beaches close or at the reflective side of that spectrum.

In an attempt to compare the results of this study with data from other coasts, we compare our results with that coming from a worldwide analyses published by McLachlan et al. (1996) and that included data from sandy beaches of South Africa, Australia, USA and Chile. McLachlan et al. (1996) confirmed earlier results (McLachlan et al. 1993), asserting that the good fit of data collected from four continents to single regression models of species richness and macroinfaunal abundances as a function of beach type, is primarily determined by morphodynamic type. Due to the fact that in such comparisons, coastal areas with different tide ranges are compared we had to convert our Dean´s values to Beach State Index (BSI) which integrates that parameter with tide ranges (McLachlan et al. 1993). Thus, Table 7 shows the BSI values for each of the beaches of Chiloé. The comparisons of species richness rendered quite variable results: the observed number of species at Guabún, Huicha and Gaviotas was equal or similar to the predicted richness; that of Ahuí and Lechagua was higher, while the observed number for Mar Brava was lower than predicted. On the other hand, the total population abundance of the macroinfauna at the beaches of Chiloé was15-105 higher than those predicted by that model at similar BSI values. The above comparisons allow us to suggest that morphodynamic beach state is not always a straitght predictor of the community structure of the sandy beach macroinfauna. As a matter of fact, the results of a seasonal study carried out by Jaramillo (in press) in sandy beaches of northern, central and southern Chile, show that intermediate beaches usually support richer and more abundant macroinfaunas than dissipative sites. Jaramillo & Lastra (in press) concluded that the lack of matching between community struc-

TABLE 7

Beach State Index, observed and predicted number of species and total abundances of the macroinfauna at the beaches studied. The predicted values come from the equations given my McLachlan et al. (1996). These are: n° of species = 12.8 BSI - 3.5 (r = 0,82) and log abundance = 2.55 BSI + 0.39 (r = 0,77)

Indice del Estado de Playa, valores observados y predichos del número de especies y abundancia total de la macroinfauna para las playas estudiadas. Los valores predichos provienen de las equaciones dadas por McLachlan et al. (1996). Estas son: n° de especies = 12.8 BSI - 3.5 (r = 0,82) y log abundancia = 2.55 BSI + 0.39 (r = 0,77)

		number of species		total abundances (ind. m^{-1})	
	BSI	observed	predicted	observed	predicted
Guabún	0,61	4	4	9361	89
Ahuí	0,68	9	5	6817	130
Huicha	0,54	4	3	4784	57
Gaviotas	0,45	3	2	508	34
Lechagua	0,66	8	5	11663	119
Mar Brava	1,25	11	13	59705	3844

ture of the macroinfauna-beach morphodynamic beach types at the Chilean coast may well be related to the high representation in density and biomass of the suspension feeder anomuran crab *Emerita analoga*, a widely distributed species along most of the sandy beaches of the Chilean coast. This is similar to the conclusion of Dugan & Hubbard (1996) who found that the abundance of that species in sandy beaches of California was higher than the worldwide trend predicted by McLachlan et al. (1993).

The macroinfaunal zonation observed in this study is similar to that found in other sandy beaches of the Chilean coast (Castilla et al. 1977, Sanchez et al. 1982, Clarke & Peña 1988, Jaramillo 1987a, Jaramillo et al. 1993, 1998). That zonation is reminiscent of the zonation scheme suggested by Dahl (1952) for sandy beaches worldwide. He characterized the upper, middle and lower beach levels based upon characteristic crustaceans: ocypodid crabs and talitrid amphipods in the upper shore, cirolanid isopods in the middle shore and hippid crabs and amphipods in the lower shore. However, our results differ to Dahl´s scheme in some aspects: presence of cirolanid isopods in the upper shore and hippid crabs (*E. analoga*) in the middle shore of some beaches. It must be pointed out however, that such kind of comparisons must be handled with care, since Dahl´s result (1952) and ours, both represent snapshot samplings.

The across shore distribution of the intertidal macroinfauna at the beaches of Ancud, do not seem to be related to the across shore distribution of mean grain size of sands. This is clearly seen for example at the reflective beach of Gaviotas, where increases in grain size did not result in changes in species distribution or abundance. Thus, sediment size (in the range of sizes studied) doesn't seem to control the macroinfaunal distribution. This assertion is supported by sediment selection laboratory studies, which have shown rather broad trends in grain size for the sandy beach macroinfauna of southern Chile (Jaramillo 1987b). The presence of *Emerita analoga* in the lower shore levels of Gaviotas contradicts earlier studies (McLachlan & Jaramillo 1995) which suggested that reflective beaches in southern Chile lacked macroinfauna at those levels. However, the conclusions of McLachlan & Jaramillo (1995) were based upon a sampling carried out at a beach close to a brackish water zone. As shown by Jaramillo (1987 b), water salinities lower than 20 ppt significantly affected the survival of *Emerita analoga*. On the other hand, sandy beaches with quite homogeneous size particles (Lechagua and Mar Brava) showed quite notorious breakes in the distribution of the species. The cluster analysis of the beaches studied and the results of the BIO-ENV procedure showed that the zonation of the macroinfauna at most beaches was correlated (in varying degrees) to the location of the moisture zones proposed by Salvat (1964). The beach levels located at the dry zone - drift line and uppermost beach levels of the retention zone were characterized by *O. tuberculata* and *E. braziliensis*; those beach levels which included most of the retention zone were mostly occupied by *E. hirsuticauda* and *E. heterocirrus* (just in Mar Brava), and the resurgence and swash zone were typically occupied by *E. analoga* at most beaches but Lechagua. The lower beach levels of Lechagua (swash zone) were mostly occupied by spionid polychaetes, a typical condition of quite sheltered sandy beaches resembling intertidal sand flats elsewhere (e.g., Eleftheriou & McIntyre, 1976). Thus, Lechagua with the finest sands and flatest slope after Mar Brava, and one of the sites with the lowest breakers, most probably represents the morphodynamic link between dissipative beach stages and ultra dissipative intertidal sand flats.

In conclusion, the results of this study show, that even when species richness and macroinfaunal abundances were higher at the dissipative site and lower at the reflective beach, supporting the paradigmatic model of macroinfaunal community structure vs. morphodynamic beach types, there are facts that show that beach types are not always good predictors of community attributes on exposed sandy beaches. On the other hand, the taxonomic composition of the macroinfauna inhabiting the intertidal of sandy beaches located at Isla de Chiloé, is similar to that of sandy beaches located further north (cf. Jaramillo 1994, Jaramillo et al. 1998). Species such as the amphipod *O. tuberculata*, the isopods *E. braziliensis* and *E. hirsuticauda* and the anomuran *E. analoga*, are species commonly found at sandy beaches along all the Chilean coast. Also, the community structure of the macroinfauna of the coast of Ancud, was similar to that of sandy beaches located further north; i.e., similar species (*E. hirsuticauda*, *E. analoga*) were the most abundant organisms at sandy beaches of different latitudes. The above results allow us to conclude that the composition and distribution of the sandy beach macroinfauna, follows a continuoum without faunistical breakes further south of Canal de Chacao, the geographic feature which interrups the continuous coastal line of the Chilean coast at about 41° S. This conclusion is only valid for the wave dominated beaches studied at the exposed coast, since a gradual change from wave to tide dominated beaches occurs when moving west from the exposed coast to the most sheltered areas of the northern archipelagos of Chiloé.

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