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Community Structure and Zonation of the Macroinfauna along a Dissipative-reflective Range of Beach Category in Southern Chile

E. JARAMILLO and M. GONZALEZ



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Three oceanic sandy beaches, covering a full range of dissipative-reflective categories were sampled at southern Chile (ca. 39°S) during the summer of 1990. The purpose of this study was to analyse the abundance, species richness and zonation schemes of the macroinfauna in relation to physical characteristics (e.g. texture, slope) of that sites. In addition, we also sampled an estuarine protected beach located nearby. Furthermore, we analysed the body sizes of the crustacean species to assess between- and within-size variability. Principal component analysis showed that gravel percentage, mean grain size and slope were the most important variables accounting for by the spatial variability in the physical characteristics of the studied beaches. Maximum species richness (6) and abundances occurred at a dissipative and at an intermediate type of beach, respectively. Almost no macroinfaunal organisms were collected at the reflective beach of Matías. Kite diagrams and cluster analysis showed that the macroinfauna can be classified in four faunistical zones, each of one characterized by a particular species or duple of species. That zonation schemes are compared with other studies. Finally, body size comparisons detected that sizes of some species differed between and within beaches.

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Introduction

The morphology of exposed sandy beaches results from interactions between sediments and nearshore processes such as waves and longshore currents, in what has been called beach morphodynamics (e.g. Short, 1979). By combining wave energy and sediment size, sandy beaches have been categorized in several types, whose extremes are represented by dissipative and reflective beaches. Dissipative beaches have a wide surf zone (usually multibarred), waves break 100-200 m seaward of the beach face, and consequently, dissipate most of their energy before reaching the beach. On the contrary, reflective beaches are characterized by an almost virtual absence of surf zone. Thus, waves break directly on the beach resulting in coarser grains and steeper profiles than those usually

found at the dissipative beaches (Short, 1979, 1983, Wright et al., 1979).

The constantly changing harsh physical environment of exposed sandy beaches has typically been emphasized as a major structuring force for infaunal communities of these habitats (see e.g. review by McLachlan, 1983). Thus, variability in exposure to wave action, beach face slope and sediment particle size have been stressed as the most significant factors in determining observed patterns of abundance and distribution of macroinfauna (Jones, 1970; Fincham, 1974; Croker et al., 1975; Eleftheriou and Nicholson, 1975; Croker, 1977; Dexter, 1979; McLachlan et al., 1981). However, other physical factors such as sediment temperature (Jones, 1970; Vohra, 1971; Jaramillo, 1987), water content (Salvat, 1964; Sameoto, 1969; Hayes, 1977; Bally, 1983; Wendt and McLachlan, 1985; Jaramillo, 1987) and penetrability of the sediments (Craig, 1970, 1973; Jaramillo, 1987) have been also stressed as important factors in the spatial and temporal variability of the sandy beach macroinfauna.

Dissipative and reflective exposed sandy beaches alternate with estuarine protected beaches along the coast of southern Chile. This situation provides a wide between site variability in wave exposure and textural characteristics, a situation which in turn suggest a macroinfaunal variability. The numerically dominant intertidal organisms along this coast are crustaceans (i.e. Peracarida and Anomura), although bivalves [*Mesodesma donacium* (Lamarck)] and polychaetes (e.g. *Nephtys impressa* Baird) are also found, mostly at the lowest intertidal levels. The temporal variability of the zonation pattern of that organisms has been described for the dissipative beach of Mehuín (ca. 39° 23'S) (Jaramillo, 1987); however, no attempt has been made to analyse in this area of the Chilean coast the eventual spatial variability of community structure and zonation pattern of the macroinfauna along a gradient of sandy beach variability; neither, the eventual variability in body sizes along that gradient or across an intertidal gradient (within site variability) of tidal emersion. Thus, the objective of this study was to analyse the abundance, number of species and intertidal distribution of the macroinfaunal organisms along a gradient of beach category; i.e. from a reflective to a dissipative type of oceanic beaches. Furthermore, we compared the zonation patterns found at those beaches with the intertidal distribution of the macroinfauna inhabiting an estuarine protected beach. Finally, we analysed the spatial variability in body sizes of the crustacean species collected during this study. That comparisons provided the ground to analyse the role of wave exposure on the sandy beach macroinfauna of southern Chile.

Material and Methods

Study Area: The four beaches selected for study were Agua de las Niñas, Mehuín, Matías and Maiquillahue (Fig. 1). The most protected site was Agua de las Niñas, a beach located in the outlet area of Río Queule and protected from breaking waves by a subtidal sand bar located nearby. All the other beaches were fully exposed to breaking waves of the Pacific Ocean, especially the site sampled at Mehuín. Among these exposed sites, Mehuín can be classified as a dissipative beach, Maiquillahue as a reflective, and Matías as an intermediate type of beach (sensu Short, 1979).

Methods: During the summer of 1990 two 0.03m⁻² replicates of sediment, 20 cm deep, were collected at 5 and 3 m intervals on a transect extended between the predicted low tide level (MLWST) and the back border of each beach (defined by foredunes, cliffs or drift lines). The replicates were one meter

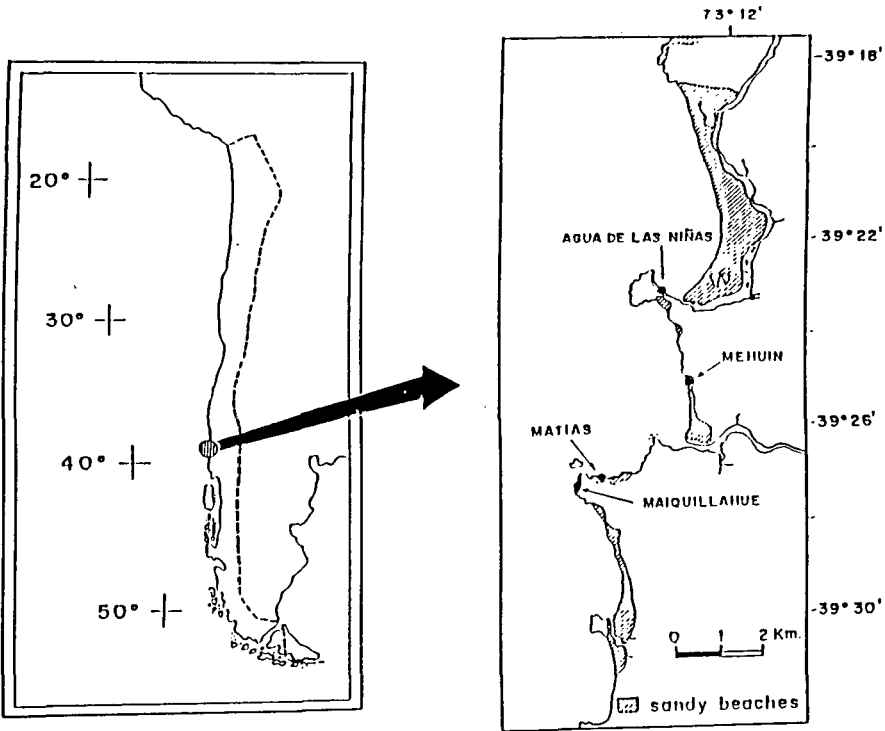


Fig. 1. Map of the Chilean coast showing the location of the beaches studied in this study.

apart each other. The sediment samples were sieved on a 1 mm mesh sieve and the residue preserved in 5% formalin. Later on, the animals were sorted from the sediments, identified and counted. Density values per 0.03 m^2 were calculated and used to draw kite diagrams and describe zonation patterns. To analyse the zonation of species, macroinfaunal samples (log transformed data) were subjected to numerical classification. The taxonomic similarity between pair of samples was calculated with Winer Index (Saiz, 1980) and a dendrogram was obtained after the Pair Group Method (Sokal and Sneath, 1973). This analysis was performed with the program ACOM (Navarro, 1984). Crustaceans were measured to the nearest 0.1 mm for body size comparisons among beaches and tidal levels. For talitrid amphipods, the body length was the distance from the rostrum tip to telson base, while in isopods the body length was the distance from rostrum tip to telson tip. The cephalothorax length of *E. analoga* was used as body size for that species.

The morphology of each beach was determined by the Emery's (1961) profiling technique. The slope of the surveyed profiles was measured by the expression $a/L \times 100$, where a is the difference in height between the highest and lowest point (low tide line), and L is the distance between these two points. Two replicates of sediment were collected at each macroinfaunal sampling station for textural analysis. Samples were collected by inserting a 3.5 cm diameter metal core to a depth of 20 cm. Sediment samples were de-salted (tap water washing) and wet sieved through a - 1 phi (\emptyset) screen (2000 microns) to separate the gravel from sand fractions. Afterwards, the sand fractions were analysed for textural characteristics through an Emery's settling tube (Emery, 1938). Mean grain size, sorting, skewness, and normalized kurtosis ($1 / \text{kurtosis} + 1$) were calculated with a moments computational method (McBride, 1971), and using a program written by Pino (1982) for a Hewlett - Packard 41 CV. The results for each beach are expressed in \emptyset units ($\emptyset = -\log 2 \text{ mm}$). The slope of each station was measured with a clinometer ($n = 2$ measurements). The penetrability of the sediment was measured by dropping a 33.6 g metal rod down a 1 m tube. The depth to which the rod penetrated into the

Table 1. Physical characteristics of the beaches studied. Mean grain size and sorting values refer only to the sand fraction of each sample. Standard deviation in brackets.

Beach characteristics	Agua de las Niñas	Mehuín	Matías	Maiquillahue
Approximate length (m)	200	200	160	120
Width of transect studied (m)	60	45	40	15
Gravel (%)*	0.00	0.00	0.00	33.07
Mean grain size (ϕ)*	2.32 (0.10)	2.13 (0.03)	1.92 (0.32)	0.21 (0.29)
Sorting (ϕ)*	0.32 (0.02)	0.32 (0.02)	0.55 (0.11)	0.43 (0.05)
Skewness	-0.37 (0.16)	-0.72 (0.06)	-0.64 (0.38)	0.74 (0.33)
Normalized kurtosis	0.75 (0.02)	0.78 (0.01)	0.75 (0.05)	0.79 (0.02)
Beach face slope (%)**	4.25	4.76	6.70	17.6
Textural group***	fine	fine	medium	coarse

* = overall means based upon the gravel percentages, mean grain size and sorting values calculated for the individual stations sampled at each beach.

** = calculated through $a/L \times 100$ (see text)

*** = type of sand after Folk (1980) and based upon the mean grain size values reported in this table.

sediment was measured three times at each station, and the average calculated. Sediment temperatures were monitored at each station with a mercury thermometer accurate to 0.1°C. Temperatures were read at the surface (approximately 3 mm depth) and a depth of about 20 cm; the values reported here are the averages of these two readings. Variability of the physical characteristics of the stations, i.e. percentage of gravel, mean grain size, sorting, skewness, normalized kurtosis, slope, penetrability and temperature, were analysed by Principal Component Analysis (PCA). For this purpose, the program Principal Components of the statistical package Statgraphics 2.0 was used. This program was also used to examine the association among environmental variables and macroinfaunal abundances. Finally, the body size comparisons were carried out through one-way analyses of variance.

Results

The beaches: A summary of some physical characteristics of the beaches studied are given in Table 1. Textural characteristics and beach face slope showed a high between-site variability. Gravel sized particles (-1 to -2ϕ) were present only at the sediments of Maiquillahue, the beach with the coarsest sediments and the steeper slope. According to the overall mean grain size values of the sand fraction, Agua de las Niñas and Mehuín had fine sands, Matfás medium sands, and Maiquillahue coarse sands. In general, the sands of all beaches were well sorted sediments, with excess of coarse grains (negative skewness) at Agua de las Niñas, Mehuín and Matfás, and fine grains (positive skewness) at Maiquillahue. Sediments of all the studied beaches had similar values of normalized kurtosis (Table 1).

Fig. 2 shows that in Agua de las Niñas and Maiquillahue, sands of high intertidal stations had lower mean grain size values than that located at the lower intertidal. On the contrary, coarser sands were found at the higher intertidal of Matfás, while almost no variability in grain sizes was found at Mehuín. With the exception of Matfás, sorting values were quite homogeneous at all the other beaches. As shown in Fig. 3, the coarsest grains occurred at the steeper stations. Thus, the regression analysis carried out with slope and mean grain size values showed that both variables were inversely and significantly correlated. Station 13, located at the low tide level of Agua de las Niñas was excluded from that analysis due to its particular characteristics, i.e. steep slope and fine sand grains.

Mean sediment temperature increased gradually from low to high intertidal stations; the highest values fall in the range of 27.5 to 31.2°C (Fig. 4). The penetrability of the sediments also increased from low to high beach levels, with exception of Maiquillahue where high values were measured at low and high intertidal stations (Fig. 4).

In the PCA carried out with the physical characteristics of the studied beaches, the first two components accounted for by 63.4% of the total variance (component I = 42.0%, component II = 21.4%). Percentage of gravel, mean grain size, skewness and slope had the highest loadings in the first component, while penetrability and temperature loaded highest in the second component (Fig. 5). The distribution of station-points in the plane defined by the first two components is shown in Fig. 6. Stations sampled at Maiquillahue are clearly separated from all the other ones by component I because of their high percentages of gravel, textural and slope characteristics (i.e. coarser grains and steeper slopes). Stations from Agua de las Niñas, Mehuín and Matfás are separated by component II, because of their differences in penetrability and temperature. Thus, Fig. 6 shows the existence of a

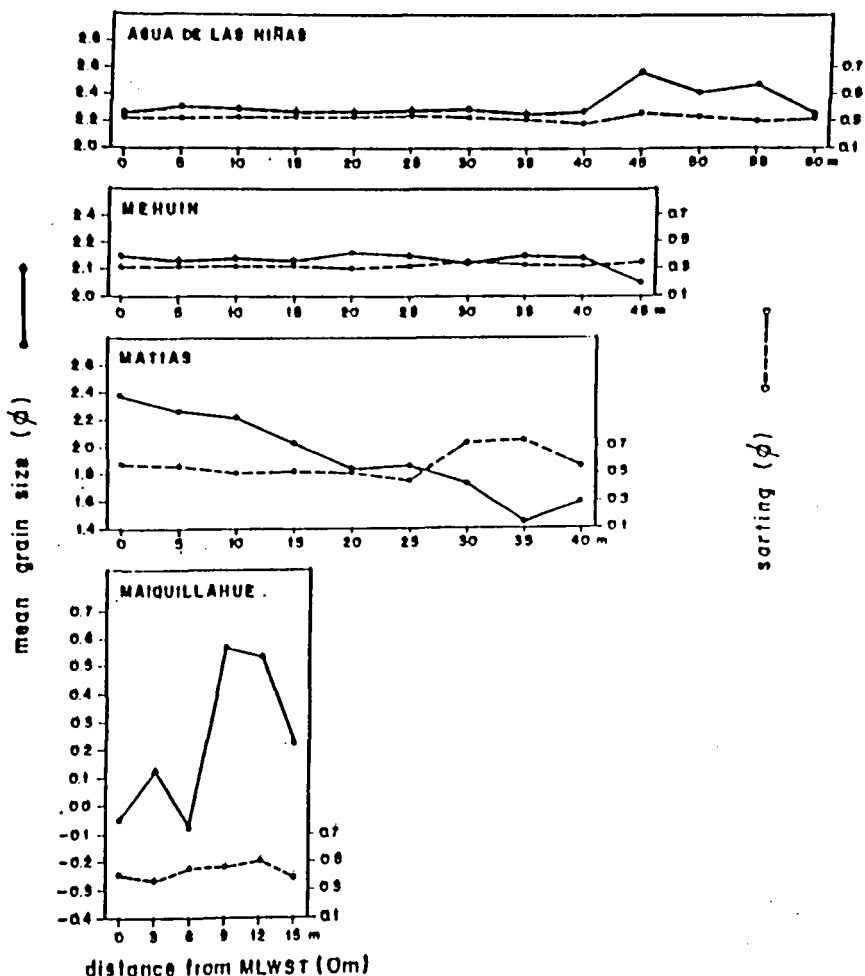


Fig. 2. Mean grain size and sorting of the intertidal sediments sampled at the beach studied. The values calculated for Maiquillahue refer only to the sand fraction of the sediments sampled there.

gradation from high intertidal stations, mostly located in the left lower quadrat, to mid and low intertidal stations (with lower temperatures and penetrabilities than the higher intertidal stations) which are mostly located in the left upper quadrat.

Macroinfaunal distribution: The highest macroinfaunal abundances were registered at the beaches of Mehuín and Matías, which also had the highest number of species (Fig. 7). The lowest abundances occurred at Maiquillahue in which the talitrid amphipod *Orchestoidea tuberculata* Nicolet was the only species collected there. The cirrolanid isopod *Excirolana hirsuticauda* Menzies was the species with

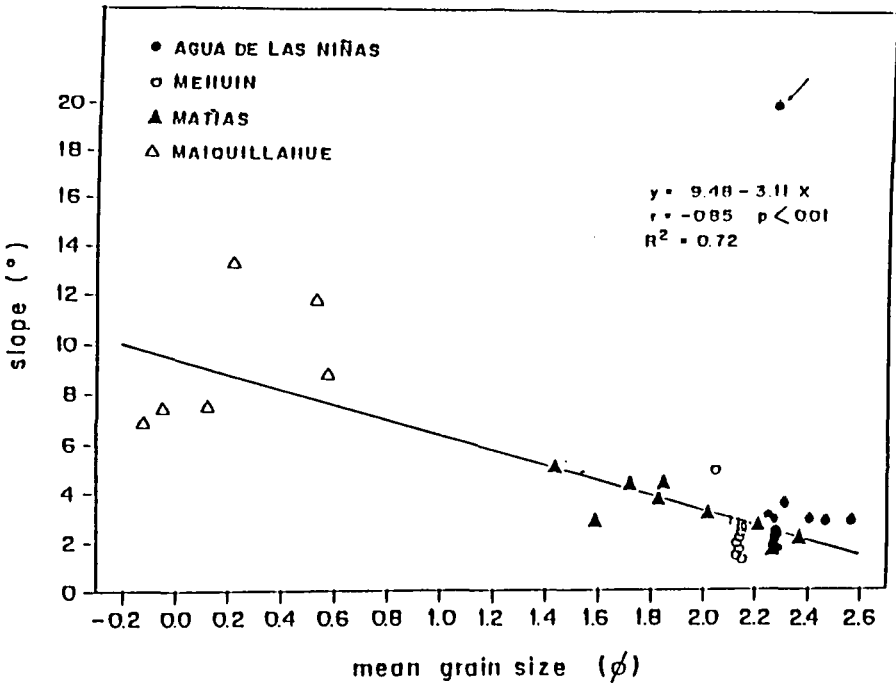


Fig. 3. Relationship between the spatial variability of the slope and mean grain size at the intertidal levels (i.e. stations) sampled at each beach.

the highest abundance at all the other beaches.

High beach levels were mainly occupied by *O. tuberculata* and the cirrolanid *Excirrolana braziliensis* Richardson. However, at Agua de las Niñas and Mehuín, the insect *Phalerisidia maculata* Kulzer was collected at higher beach levels than those occupied by the former two species (Fig. 7). *E. hirsuticauda* made up the main component of the mid beach levels, while the polychaete *Euzonus heterocirrus* Rozbaczylo & Zamorano and the anomuran crab *Emerita analoga* Stimpson were the dominant organisms of the low beach levels. Four major station groups were recognizable in the dendrogram produced by the cluster analysis (Fig. 8). Groups A and B included high beach levels; however, Group A was represented by stations with *P. maculata* as the only species collected there, while Group B was numerically dominated by *O. tuberculata* and *E. braziliensis*. Group C included stations dominated by *E. hirsuticauda* and located at the mid and low beach levels of Agua de las Niñas, and mid beach levels of Mehuín and Matías. Finally, Group D included stations located in the low beach levels of Mehuín and Matías and dominated by *E. analoga* and *E. heterocirrus* (cf. Fig. 7 and 8).

In the PCA carried out with the values of physical characteristics and macroinfaunal abundances, the first two components accounted for by 42.2% of the total variance (component I = 24.4%, component II = 17.8%). Percentage of gravel, mean grain size, skewness and slope loaded highest in the first component, while penetrability, temperature and *P. maculata* had the highest loadings

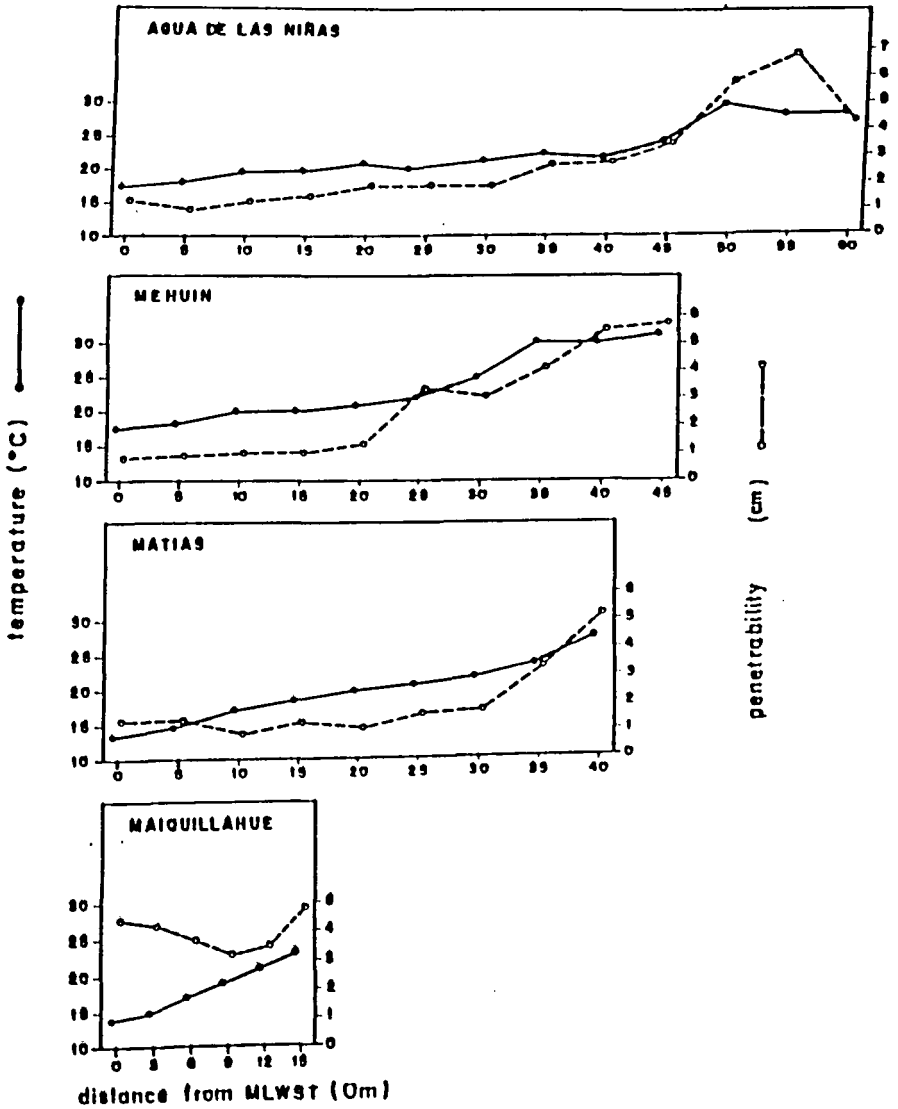


Fig. 4. Mean sand temperature and penetrability of the intertidal sediments sampled at the beaches studied.

in the second component (Fig. 9). In this analysis, the ordination of station-points in the plane defined by the first two components (Fig. 10) was similar to that obtained when PCA was carried out just with physical characteristics. Thus, macrofaunal abundances had no significant role in explaining the variability of the data collected.

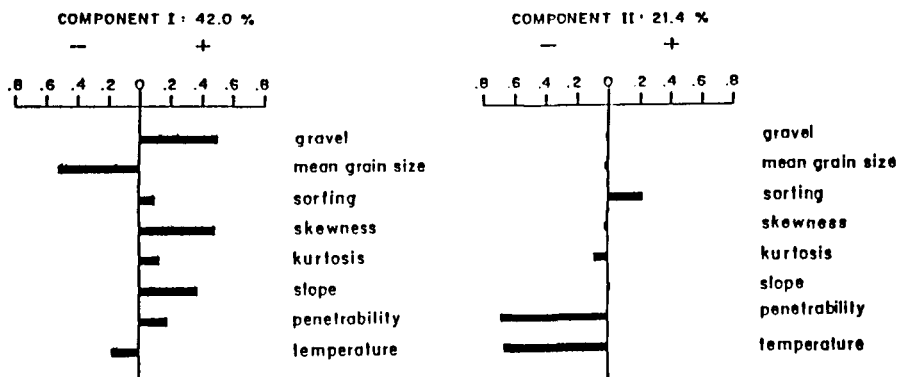


Fig. 5. Loads of each physical variable in relation to the first and second component.

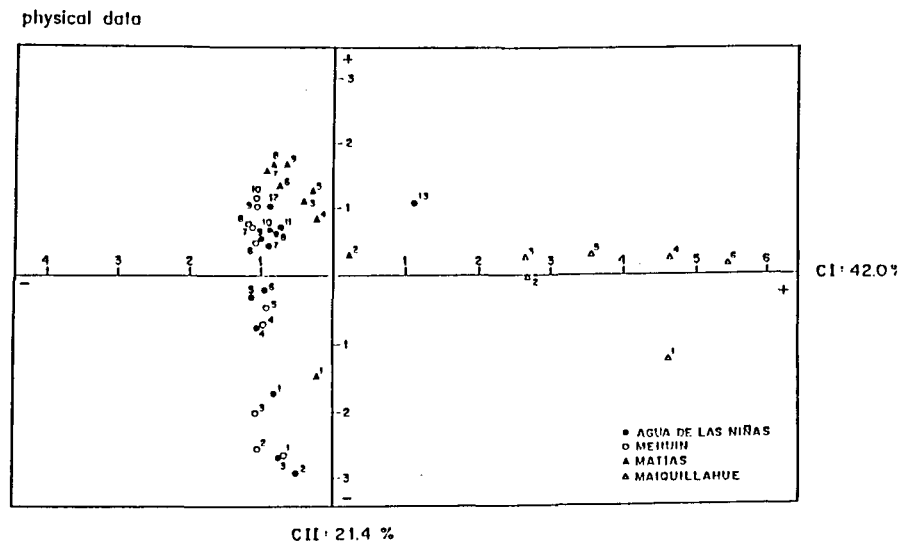


Fig. 6. Ordination of the intertidal levels sampled at each beach. The first component is represented by the horizontal axis while the second is represented by the vertical one. This analysis was carried out with the spatial variability of the physical variables shown in Fig. 5.

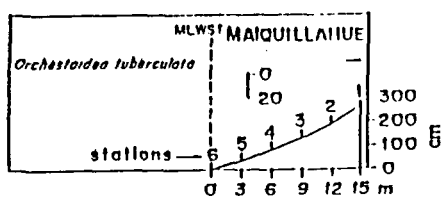
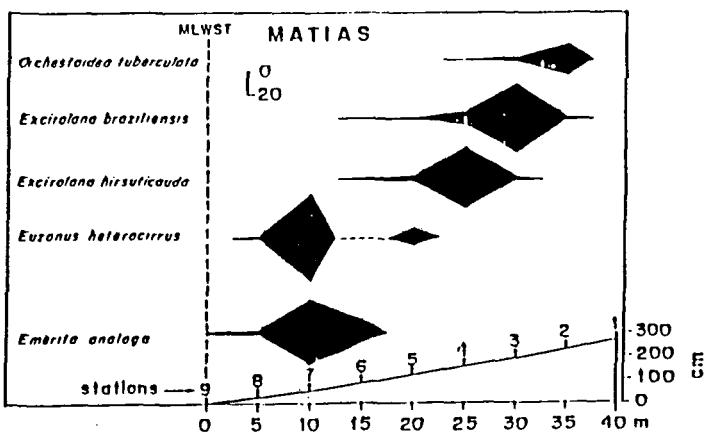
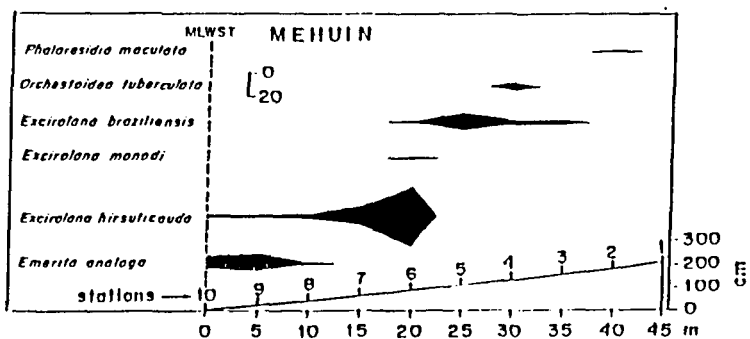
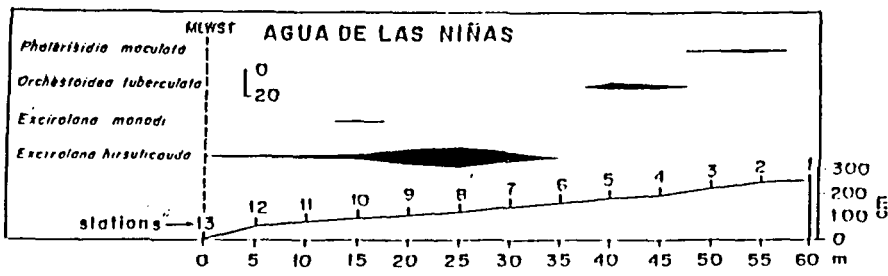
Body size comparisons: Fig. 11 shows the mean body sizes of the crustacean species collected at the beaches of Agua de las Niñas, Mehuín and Matías. Specimens of *O. tuberculata* collected at Matías were larger than those of Agua de las Niñas and Mehuín. No significant differences were found between the body sizes of *E. braziliensis* collected from Mehuín and Matías. *E. hirsuticauda* and *E. analoga* had their smallest sizes at Matías. Table 2 shows the body size variability of that species along the surveyed transects. Body sizes of *O. tuberculata* were not significantly different at Agua de las Niñas, while larger individuals of

Table 2. Body size comparisons between tidal level variability at the intertidal stations (st) in which the species were collected. Means followed by the same letter are not significantly different at the 0.05 probability level.

species	Agua de las Niñas			Mehuín			Matfás		
	st.	\bar{x}	(s.d.)	st.	\bar{x}	(s.d.)	st.	\bar{x}	(s.d.)
<i>O. tuberculata</i>	4	8.7	(2.8) A	*			2	14.3	(3.6) A
	5	11.1	(5.4) A				3	6.3	(3.4) B
<i>E. braziliensis</i>	**			3	5.8	(2.0) AA	2	7.9	(0.6)
				4	6.4	(2.1) A A	3	5.0	(1.1) A
				5	4.8	(1.2) AB	4	4.4	(0.7) A
<i>E. hirsuticauda</i>	7	6.9	(3.6) A	6	6.2	(2.0) A	3	6.9	(2.4) A
	8	6.1	(1.4) A	7	6.2	(1.5) A	4	5.0	(1.7) A
	9	5.1	(1.8) A	8	4.7	(1.0) A	5	6.7	(1.3) A
	10	6.6	(1.5) A	9	4.4	(0.1) A			
	11	6.5	(1.8) A	10	4.2	(1.3) A			
	12	4.3	(1.1) A						
<i>E. analoga</i>	**			8	7.0	(4.9) A	6	3.9	(1.0) A
				9	6.4	(3.8) A	7	6.1	(3.9) B
				10	8.2	(3.6) A	8	8.5	(2.5) B
							9	10.2	(2.0) B

* = species present at only one station

** = species not collected



distance from MLWST (0m)

Fig. 7. Intertidal distribution of the macroinfauna at the beaches studied.

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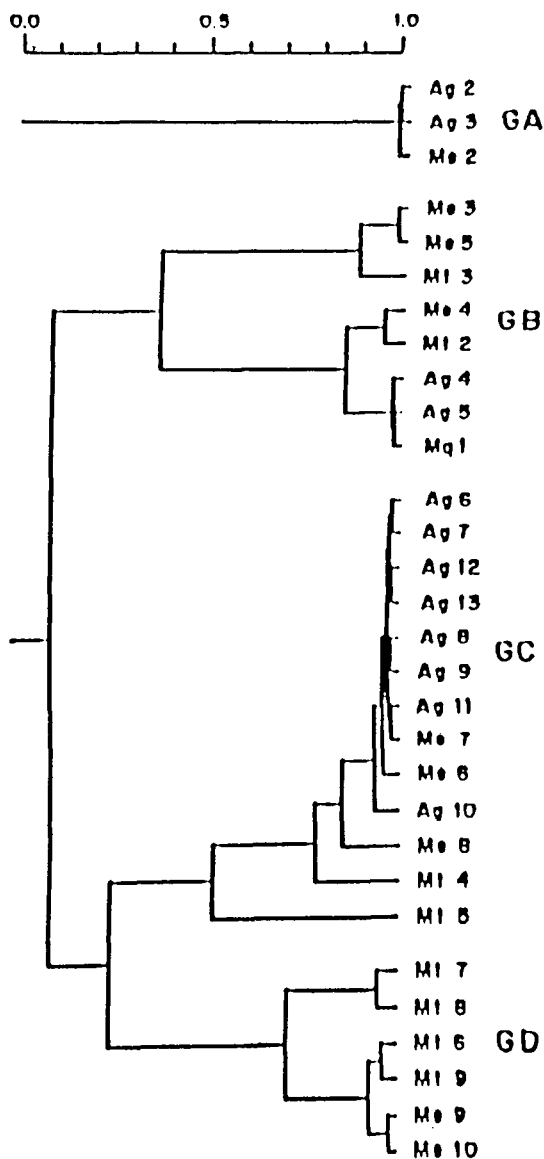


Fig. 8. Dendrogram showing clustering of stations in four main groups. A and B: high beach levels, C: middle beach levels and D: low beach levels. Number to the right of the dendrogram refer to station numbers as in Fig. 7, while letters refer to the beaches as follows: Ag: Agua de las Niñas, Me: Mehuín, Mt: Matías and Mq: Maiquillahue.

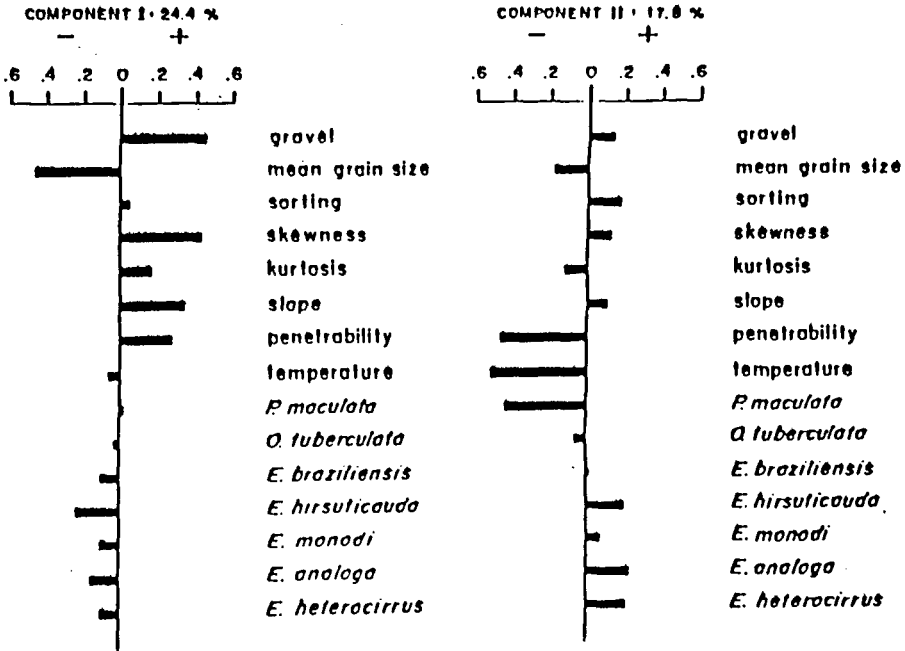


Fig. 9. Loads of each physical and biological variable (i.e. macrofaunal abundances) in relation to the first and second component.

this species were found at the highest station in which it occurred at Matfás. The smallest individuals of *E. braziliensis* occurred at the lowest station of Mehuín and Matfás, a trend which it was also apparent with *E. hirsuticauda*. However, no significant differences in body sizes were detected for this species. Finally, *E. analoga* was represented by the smallest sizes at the highest stations of its distribution at Matfás, while no significant differences in body sizes were found at Mehuín.

Discussion

The three oceanic sandy beaches analysed in this study covered a full range of dissipative to reflective category. Thus, the coarser grains and steeper slopes found at Maiquillahue chiefly defined its reflective character, while the finer sands, flatter slopes and a wide surf zone configured the dissipative character of Mehuín. Matfás, with intermediate values in grain sizes and slopes may be categorized as an intermediate type of beach, but close to the reflective category since it lacks a surf zone. Agua de las Niñas, an estuarine sandy beach protected from breaking waves had similar textural and morphological characteristics (i.e. slopes) to the dissipative beach of Mehuín. As shown by the results of Principal Component Analysis, that variables related to texture and profile morphology were more important in explaining the observed variability, than those of sediment

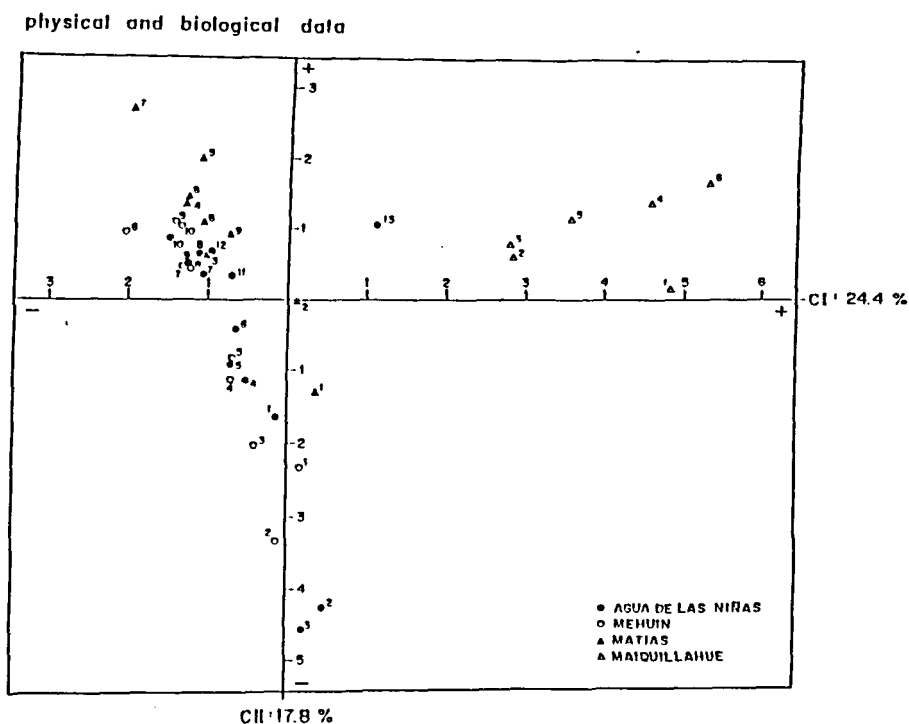


Fig. 10. Ordination of the intertidal levels sampled at each beach. The first component is represented by the horizontal axis, while the second is represented by the vertical one. This analysis was carried out with the spatial variability of physical and biological variables (i.e. macroinfaunal abundances) shown in Fig. 9.

temperature and penetrability. This is an obvious result due to the wide between-site variability observed along the range of beaches studied.

The results of this study agree with others in which grain size is assumed to be the dominant factor controlling sandy beach community structure (e.g. Colman & Segrove, 1955; Jones, 1970; Croker, 1977; Dexter, 1979; McLachlan et al., 1981). Thus, the obvious grain size differences found among the beaches studied correlate well with the differences found in macroinfaunal community structure. The most obvious difference between the macroinfaunas, was the marked contrast in abundance and number of species collected in the reflective beach of Maiquillahue as compared with the other beaches. The paucity of macroinfauna at that beach, agrees with the findings of Gauld & Buchanan (1956), Dye et al., (1981) and McLachlan (1985) who reported that reflective beaches of Ghana and South Africa were characterized by an impoverished macroinfauna. As shown by several authors (e.g. McLachlan et al., 1981; Dexter, 1983), species richness and macroinfaunal abundance are negatively correlated with particle size. Another important difference among the sites studied was that polychaetes were collected only at the intermediate beach of Matías. As reported by several authors (e.g.

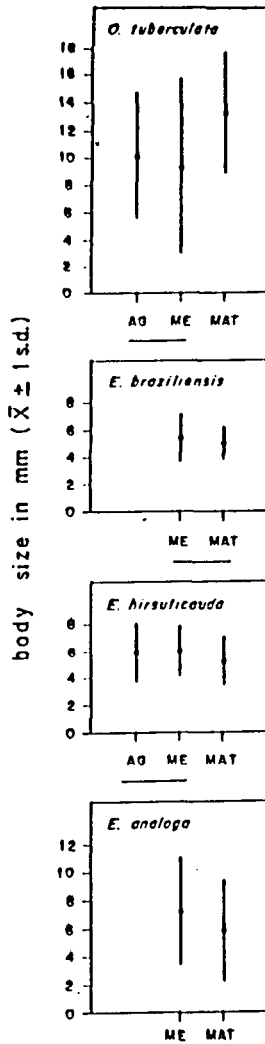


Fig. 11. Inter-beach comparisons of the body sizes of *O. tuberculata*, *E. braziliensis*, *E. hirsuticauda* and *E. analoga*. AG: Agua de las Niñas, ME: Mehuín and MAT: Matías.

McIntyre, 1970; Seed and Lowry, 1973; Croker, 1977; Dexter, 1983; McLachlan, 1983), the abundance of sandy beach polychaetes increase along a gradient of decreasing wave exposure. But other factors than those related to wave exposure should be invoked here to explain the high abundances of the spionid *E. heterocirrus* at Matías. That, because in a beach with lower exposure (i.e. finer sands and flatter slopes) such as Mehuín, polychaetes were absent. Finally, *E. analoga* was only collected at Mehuín and Matías. While this species has been casually found at this area, it has never been collected at protected estuarine beaches of southern

Chile (Jaramillo, 1987). Low salinity tolerances shown by *E. analoga* in laboratory experiments, suggests that its absence from that estuarine beaches, is due to the lower salinities of these habitats as compared with the exposed sandy beaches of e.g. Mehufn and Matfas (Jaramillo, 1987). In addition, the absence of a surf zone at that estuarine areas, may in turn indicate an absence of an adequate food source in suspension, precluding the establishment of this suspension – feeder at that sites.

Several zonation schemes have been proposed for sandy beach habitats. While Dahl (1952), Pichon (1967) and Trevallion et al. (1970) based their schemes in biological factors (i.e. the intertidal distribution of the macroinfauna), Salvat (1964) used physical characteristics; i.e. the water content of the sediments. Thus, Dahl (1952) proposed three faunistical zones: the higher one characterized by talitrid amphipods in temperate areas and ocypodid crabs in warm areas (the subterrestrial fringe), the middle one dominated by cirolanid isopods (the midlittoral zone), and the lower zone, mainly characterized by amphipods and anomurans (the sublittoral zone). Salvat (1964) defined the zones of drying (the water spray zone), retention (water is trapped at the interstitial space), resurgence (water moves in the sand, but that is not saturated) and saturation (the sediment is saturated of water). Dahl's subterrestrial fringe corresponds to the Salvat's drying zone; the midlittoral zone of Dahl is equivalent to the retention and resurgence zones of Salvat, and Dahl's sublittoral fringe corresponds to the Salvat's saturation zone (MacLachlan, 1983). Recently, classification and ordination techniques have been used to look up into the number of such faunistical zones. In that way four zones have been distinguished in sandy beaches of South Africa (Bally, 1983; Wendt & McLachlan, 1985) and Namibia (Donn & Cockcroft, 1989), while in northern Chile just three zones were determined (Clarke & Peña, 1988).

The kite diagrams representing the intertidal distribution of the macroinfauna and the cluster analysis carried out with the samples collected in this study, showed that the stations sampled can be classified in four groups, each one numerically dominated by a particular species or duple of species. Thus, *P. maculata* can be considered as a typical species of the subterrestrial fringe – drying zone; *O. tuberculata* and *E. braziliensis* dominated at the high beach levels of the midlittoral zone (retention zone), *E. monodi* and *E. hirsuticauda* were numerically dominant at the low levels of the midlittoral zone (resurgence zone), while *E. analoga* and *E. heterocirrus* were typically found at sublittoral fringe or saturation zone. It should be emphasized, however, that species which dominated at some particular tidal level also extended their distribution to another ones; e.g. *O. tuberculata* was also found at the uppermost stations sampled (i.e. drying zone) of Matfas and Maiquillahue, while *E. hirsuticauda* the dominant taxon at the midlittoral zone, was also collected at the saturation zone of Agua de las Niñas and Mehufn. Furthermore, the zonation pattern outlined before may change considerably with season and tidal period (i.e. spring versus neap tides). As a matter of fact, no specimens of *P. maculata* are usually found at that beaches during winter time (unpublished data). Also, Jaramillo (1987) has described at seasonal downshore migration of the peracarid assemblage at the beach of Mehufn; e.g. during the summer time, species characteristics of the high beach levels occurred at lower tidal levels than those previously occupied during winter and early spring. Thus, temporal variability might be a key factor in the configuration of

that zonation schemes.

The zonation schemes reported for the crustacean assemblage studied here are similar to that reported for Castilla et al. (1977) for exposed sandy beaches of central Chile (ca. 32°S); i.e. the same species were collected at both areas of the Chilean coast and at similar intertidal levels. However, the distribution of *E. analoga* at the beaches studied for Castilla et al. (1977) included not only the low intertidal levels, but also part of the midlittoral zone. On the other hand, our results differ from others found at another Chilean sandy beaches. For example, Clarke & Peña (1988) found that in a protected beach of northern Chile (ca. 23°S) the cirrolanid isopods did not appear at the midlittoral zone, which was occupied by *E. analoga* and polychaetes. Similar situation was reported by Sanchez et al. (1982) for an exposed beach of central Chile (ca. 30°S), in which the midlittoral zone was primarily occupied by polychaetes and oedocerotid amphipods. Finally, Epelde – Aguirre & Lopez (1975) distinguished just two faunistical belts, without an indication of the characteristic cirrolanid belt found in this study. However, the most striking difference between the last three studies and our study is that related to the number of cirrolanid species that were collected in some of the beaches studied here. Two species were collected at Agua de las Niñas and Matías, while three cirrolanid coexisted at Mehuín. At any of these beaches, that species had their maximum abundances at different tidal heights. A similar gradient in zonation of cirrolanid isopods was described by Jones (1971) from the coast of Kenya; there he found that *Eurydice geniculata* Jones had a distribution centered on the upper beach levels (HWN to MHW), while *E. orientalis* (Dana) showed a maximum density just below MLWN. Similarly, Pichon (1967) found that in Madagascar *E. natalensis* (Vanhoffen) occurred at the subterrestrial fringe-drying zone, while *E. orientalis* was distributed further down in the midlittoral zone. The former distributional schemes represent common examples of closely related species partitioning available space. Both horizontal and vertical space partitioning have been suggested as reducing, or avoiding potential competition between peracarids of oceanic sandy beaches (Jones, 1979; Croker, 1967; Croker & Hatfield, 1980). But, as far as cirrolanid isopods is concerned, no strong evidence has been presented to validate that suggestion. For example, in coexistence experiments carried out with the sympatric species *E. braziliensis* and *E. hirsuticauda* Jaramillo (1987) did not find evidence for ongoing competition between these species; i.e. mortality rates were similar in single or mixed cultures. Body size differences have been found in the intertidal distribution of several sandy beach species. This phenomenon has been observed in gastropods (Edwards, 1969), bivalves (e.g. Wade, 1967; McLachlan & Hanekom, 1979; Tarifeño, 1980; Arntz et al., 1987), hippid crabs (Efford, 1965; Philip, 1974; Haley, 1982), haustoriid amphipods (Hager & Croker, 1979), talitrid amphipods (Craig, 1973) and cirrolanid isopods (Glynn et al., 1976; Dexter, 1977). Causes of zonation by sizes have been attributed to several factors, among them beach morphology (e.g. Cubit, 1968; Perry, 1980; Bowman & Dolan, 1985), reproductive behaviour (Efford, 1965), intraspecific competition (Haley, 1982) and sand desiccation tolerance (Hager & Croker, 1979). It is difficult to assess the causes which originate between-beach differences in the body size of some of the crustaceans studied here. For example, while *O. tuberculata* was significantly larger at a coarser beach (Matías versus Agua de las Niñas), *E. hirsuticauda* was significantly smaller. Other

body size comparisons (i.e. within beach-variability) showed that some of the crustacean species studied here were zoned by sizes; i.e. *E. braziliensis* and *E. analoga*. Due to the fact that almost no differences were found in the textural characteristics among the tidal levels occupied by *E. braziliensis* it can be hypothesized that differences in the distribution of sizes are related to differences in sand desiccation related factors. A similar hypothesis can not be invoked to explain the apparent concentration of juveniles of *E. analoga* in the higher distributional level of this species. On the contrary, wave disturbance might well be the factor causing the differential size distribution shown by *E. analoga*: i.e. larger animals could stand better (by burrowing deeper) the energy liberated by the breaking waves of the lower shore.

In conclusion, the macroinfauna of the beaches studied showed similar characteristics to that of other littoral areas around the world; i.e. number of species increased from high to low beach levels; that species can be zoned in distinct faunistical zones, and finer and flatter slope sediments had higher species richness and abundances than coarser and steeper sediments (i.e. more exposed substrates). Thus, wave exposure related factors, such as grain size and slope were the most important ones in defining the observed patterns.

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References

- ARNTZ, W.E., BREY, T., TARAZONA, J. and ROBLES, A., 1987. Changes in the structure of a shallow sandy-beach community in Perú during an El Niño event. *S. Afr. J. Mar. Sci.*, 5: 645-658.
- BALLY, R., 1983. Intertidal zonation on sandy beaches of the west coast of South Africa. *Cah. Biol. Mar.*, 24: 85-103.
- BOWMAN, M.L. and DOLAN, R., 1985. The relationship of *Emerita talpoida* to beach characteristics. *J. Coast. Res.*, 1: 151-163.
- CASTILLA, J.C., SANCHEZ, M. and MENA, O., 1977. Estudios ecológicos en la zona costera afectada por contaminación del "Northern Breeze". I. Introducción general y comunidades de playas de arena. *Medio Ambiente, Chile*, 2: 53-64.
- CLARKE, M. and PEÑA, R., 1988. Zonación de la macroinfauna en una playa arenosa del norte de Chile. *Estud. Oceanol., Chile*, 7: 17-31.
- COLMAN, J.S. and SEGROVE, F., 1955. The fauna living in Stoupe Beck Sand, Robin Hood's Bay (Yorkshire, North Riding). *J. Anim. Ecol.*, 24: 426-444.
- CRAIG, P.C., 1970. The behaviour and distribution of the intertidal sand beetle, *Thinopinus pictus* (Coleoptera: Staphyllinidae). *Ecology*, 51: 1012-1017.
- CRAIG, P.C., 1973. Behaviour and distribution of the sand-beach amphipod *Orchestoidea corniculata*. *Mar. Biol.*, 23: 101-109.
- CROKER, R.A., 1967. Niche diversity in five sympatric species of intertidal amphipods (Crustacea: Haustoriidae). *Ecol. Monogr.* 49: 746-751.
- CROKER, R.A., 1977. Macroinfauna of northern New England marine sand: Long-term intertidal community structure. In: Coull, B.C. (ed.), *Ecology of Marine Benthos*. Belle W. Baruch Library in Marine Science # 6, Univ. of S. Carolina Press: 439-450.

- CROKER, R.A., HAGER, R.P. and SCOTT, K.J., 1975. Macroinfauna of northern New England marine sand. II. Amphipod - dominated intertidal communities. *Can. J. Zool.*, 53: 42-51.
- CROKER, R.A. and HATFIELD, E.B., 1980. Space partitioning and interactions in an intertidal sand-burrowing amphipod guild. *Mar. Biol.*, 61: 79-88.
- CUBIT, J., 1968. Behaviour and physical factors causing migration and aggregation of the sand crab *Emerita analoga* (Stimpson). *Ecology*, 50: 118-123.
- DAHL, E., 1952. Some aspects of the ecology and zonation of the fauna on sandy beaches. *Oikos*, 4: 1-27.
- DEXTER, D.M., 1977. Natural history of the Pan-American sand beach isopod *Excirolana braziliensis* (Crustacea: Malacostraca). *J. Zool., London*, 183: 103-109.
- DEXTER, D.M., 1979. Community structure and seasonal variation in intertidal Panamanian sandy beaches. *Estuarine Coastal Mar. Sci.*, 9: 543-558.
- DEXTER, D.M., 1983. Community structure of intertidal sandy beaches in New South Wales, Australia. In: McLachlan, A. and T. Erasmus (eds.), *Sandy beaches as Ecosystems*. W. Junk Publishers, The Hague: 461-472.
- DONN, T.E. and COCKCROFT, A.C., 1989. Macrofaunal community structure and zonation of two sandy beaches on the central Namib coast, South West Africa/Namibia. *Madoqua*, 16: 129-135.
- DYE, A.H., McLACHLAN, A. and WOOLRIDGE, T., 1981. The ecology of sandy beach in Natal, South Africa. *S. Afr. J. Zool.*, 16: 200-209.
- EDWARDS, D.C., 1969. Zonation by size as an adaptation for intertidal life in *Olivella biplicata*. *Am. Zoologist*, 9: 399-417.
- EFFORD, I.E., 1965. Aggregation in the sand crab, *Emerita analoga* (Stimpson). *J. Anim. Ecol.*, 34: 63-75.
- ELEFThERIOU, A. and NICHOLSON, M.D., 1975. The effects of exposure on beach fauna. *Cah. Biol. Mar.*, 16: 695-710.
- EMERY, K.O., 1938. Rapid method of mechanical analysis of sand. *J. Sedimen. Petrol.*, 8: 105-111.
- EMERY, K.O., 1961. A simple method of measuring beach profiles. *Limnol. Oceanogr.*, 6: 695-710.
- EPELDE-AGUIRRE, A. and LOPEZ, M.T., 1975. Zonación en el sustrato arenoso de Playa Blanca, Bahía de Coronel, y observaciones sobre crustáceos poco frecuentes. *Bol. Soc. Biol. de Concepción, Chile*, 49: 161-170.
- FINCHAM, A.A., 1974. Intertidal sand-dwelling peracarid fauna of Stewart Island. *N.Z.J. Mar. Freshwat. Res.*, 8: 1-14.
- FOLK, R., 1980. *Petrology of Sedimentary Rocks*. Hemphill Publishing Co., Austin, TX: 182 pages.
- GAULD, D.T. and BUCHANAN, J.B., 1956. The fauna of sandy beaches in the Gold Coast. *Oikos*, 7: 293-301.
- GLYNN, P.W., DEXTER, D.M. and BOWMAN, T.E., 1976. *Excirolana braziliensis*, a Pan-American sand beach isopod: taxonomic status, zonation and distribution. *J. Zool., London*, 175: 509-521.
- HAGER, R.P. and CROKER, R.A., 1979. Macroinfauna of northern New England marine sand. IV. Infaunal ecology of *Amphiporeia virginiana* Shoemaker, 1933 (Crustacea: Amphipoda). *Can. J. Zool.*, 57: 1511-1519.
- HALEY, S.R., 1982. Zonation by size of the Pacific mole crab, *Hippa pacifica* Dana (Crustacea: Anomura: Hippidae), in Hawaii. *J. Exp. Mar. Biol. Ecol.*, 58: 221-231.
- HAYES, W.B., 1977. Factors affecting the distribution of *Tylos punctatus* (Isopoda, Oniscoidea) on Beaches in Southern California and Northern México. *Pacif. Sci.*, 31: 165-186.
- JARAMILLO, E., 1987. Community ecology of Chilean sandy beaches. Ph. D. dissertation, University of New Hampshire, Durham, N.H.: 216 pages.
- JONES, D.A., 1970. Factors affecting the distribution of the intertidal isopods *Eurydice pulchra* Leach and *Eurydice affinis* Hansen in Britain. *J. Anim. Ecol.*, 39: 455-472.
- JONES, D.A., 1971. The systematic and ecology of some sand beach isopods (Crustacea: Eurydicidae) from the coast of Kenya. *J. Zool., London*, 165: 201-207.
- JONES, D.A., 1979. The ecology of sandy beaches in Penang, Malaysia, with special reference to *Excirolana orientalis* (Dana). *Estuarine Coastal Mar. Sci.*, 9: 677-682.
- McBRIDE, E.F., 1971. Mathematical treatment of size distribution data. In: Carver, R.E. (ed.), *Procedures in Sedimentary Petrology*. Wiley-Interscience, John Wiley & Sons, Inc. New York: 109-127.
- McINTYRE, A.D., 1970. The range of biomass in intertidal sand with special reference to the bivalve *Tellina tenuis*. *J. Mar. Biol. Ass. U.K.*, 48: 113-142.

- McLACHLAN, A., 1983. Sandy beach ecology: a review. In: McLachlan, A. and T. Erasmus (eds.), *Sandy Beaches as Ecosystems*. W. Junk Publishers, The Hague: 321-330.
- McLACHLAN, A., 1985. The biomass of macro- and interstitial fauna on clean and wrack-covered beaches in Western Australia. *Estuarine Coastal Shelf Sci.*, 21: 587-599.
- McLACHLAN, A. and HANEKOM, N., 1979. Aspects of the biology, ecology and seasonal fluctuations in biochemical composition of *Donax serra* in the East Cape. *S. Afr. J. Zool.*, 14: 183-193.
- McLACHLAN, A., WOOLDRIGE, T. and DYE, A.H., 1981. The ecology of sandy beaches in Southern Africa. *S. Afr. J. Zool.*, 16: 219-231.
- NAVARRO, R., 1984. Programa computacional para el análisis numérico de comunidades. *Medio Ambiente, Chile*, 7: 82-87.
- PERRY, D.M., 1980. Factors influencing aggregation patterns in the sand crab *Emerita analoga* (Crustacea: Hippidae). *Oecologia* (Berlin), 45: 379-384.
- PHILIP, K.P., 1974. The intertidal fauna of the sandy beaches of Cochin. *Proc. Ind. Nat. Sci. Acad. B*, 38: 317-328.
- PICHON, M., 1967. Contribution a l'étude des peuplements de la zone intertidale sur sables fins et sables vaseux non fixes dans la région de Tular. *Recl. Trav. Stn. mar. Endoume Suppl.*, 7: 57-100.
- PINO, M., 1982. Interpretación granulométrica a través de componentes principales de la dinámica de acreción - erosión en playa Pichicullín, Mehuín, Provincia de Valdivia. III Congreso Geológico Chileno: 36-68.
- SAIZ, F., 1980. Experiencias en el uso de criterios de similitud en el estudio de comunidades. *Arch. Biol. Med. Exp.*, 13: 387-402.
- SALVAT, B., 1964. Les conditions hidrodynamiques interstitielles de sediments meubles intertidaux et la répartition verticale de la faune endogée. *C.R. Acad. Sc. Paris*, 259: 1576-1579.
- SAMEOTO, D.D., 1969. Comparative ecology, life histories, and behaviour intertidal sand-burrowing Amphipods (Crustacea: Haustoriidae) at Cape Cod. *J. Fish. Res. Bd. Canada*, 26: 361-388.
- SANCHEZ, M., CASTILLA, J.C. and MENA, O., 1982. Variaciones verano - invierno de la macrofauna de arena en playa Morrillos (Norte Chico, Chile). *Stud. Neotrop. Fauna Environm.*, 17: 31-49.
- SEED, R. and LOWRY, B.J., 1973. The intertidal macrofauna of seven sandy beaches of County Down. *Proc. Roy. Irish Acad. B*, 73: 217-230.
- SHORT, A.D., 1979. Three dimensional beach stage model. *J. Geol.*, 87: 553-571.
- SHORT, A.D., 1983. Sediments and structures in beach-nearshore environments, South East Australia. In: McLachlan, A. and T. Erasmus (eds.), *Sandy Beaches as Ecosystems*. W. Junk Publishers, The Hague: 145-155.
- SOKAL, R.R. and SNEATH, P.H.A., 1973. *Numerical Taxonomy*. W.H. Freeman and Company, San Francisco: 549 pages.
- TARIFEÑO, E., 1980. Studies on the biology of the surf clam *Mesodesma donacium* (Lamarck, 1818) (Bivalvia: Masodesmatidae) from Chilean sandy beaches. Ph. D. dissertation, University of California, Los Angeles, CA: 229 pages.
- TREBALLION, A., ANSELL, A.D., SIVADAS, P. and NARAYANAN, 1970. A preliminary account of two sandy beaches in South West India. *Mar. Biol.*, 6: 268-279.
- VOHRA, F.C., 1971. Zonation on a tropical sandy shore. *J. Anim. Ecol.*, 40: 679-708.
- WADE, B.A., 1967. Studies on the biology of the West Indian Beach clam *Donax denticulatus* Linné. 1. Ecology. *Bull. Mar. Sci.*, 17: 149-174.
- WENDT, G.E. and McLACHLAN, A., 1985. Zonation and biomass of the intertidal macrofauna along a South African sandy beach. *Cah. Biol. Mar.*, 26: 1-14.
- WRIGHT, L.D., CHAPPELL, J., THOM, B.G., BRADSHAW, M.P. and COWELL, P., 1979. Morphodynamics of reflective and dissipative beach and inshore systems: Southeastern Australia. *Mar. Geol.*, 32: 105-140.