SANDY BEACH MACROINFAUNA FROM THE CHILEAN COAST : ZONATION PATTERNS AND ZOOGEOGRAPHY

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MACROFAUNE
PLAGES SABLEUSES
CHILI

RÉSUMÉ - La zonation de la macrofaune des plages sableuses est étudiée dans trois régions de la province Peruvo-Chilienne. Les niveaux inférieurs des trois zones sont caractérisés par *Emerita analoga* (Anomura), *Nephtys impressa* (Polychaeta) et *Mesodesma donacium* (Bivalvia). Dans les niveaux moyens, une réduction du nombre des espèces d'Isopodes Cirolanides du sud au nord est constatée jusqu'à leur absence dans certaines plages. Un Cirolanidé (*Excirolana brazilienzis*) et un Insecte (*Phalerisidia maculata*) sont présents dans la zone supérieure de toutes les plages étudiées. Les Crabes (*Ocypode gaudichaudii*) n'appartiennent qu'à la zone supérieure dans la partie nord du Chili, ainsi que des espèces d'Isopodes terrestres (*Tylos spinolosus*) dans le nord de la région centrale et un Amphipode (*Orchestoidea tuberculata*) dans toute dans toute la région centrale chilienne. Cette distribution géographique est analysée en fonction des conditions hydrographiques et climatiques particulières de la côte chilienne. L'hypothèse avancée repose sur l'absence de courant ou sur des barrières de température à la surface de l'eau ce qui favorise la similitude de la composition taxonomique dans les zones inférieures de toutes les plages étudiées. L'accroissement des précipitations du nord au sud et la différence de température de l'air et du sédiment, du sud au nord, expliquent les différences qui apparaissent dans les compositions taxonomiques de la macrofaune dans les zones supérieures.

MACROINFAUNA
SANDY BEACHES
CHILE

ABSTRACT - The zonation of the sandy beach macroinfauna was studied at three areas of the Peruvian-Chilean Province. The low beach levels (below MTL) of the three areas were characterized by : *Emerita analoga* (Anomura), *Nephtys impressa* (Polychaeta), and *Mesodesma donacium* (Bivalvia). The middle (MTL to MHWNT) and high (above MHWNT) beach levels showed significant changes in species composition whith latitude. At middle levels there is a decrease in the number of cirolanid isopod species (*Excirolana* spp.) from south to north, and at some northern beaches they were absent altogether. One cirolanid (*Excirolana brazilienis*) and an insect (*Phalerisidia maculata*), inhabited high beach levels of all the beaches studied. Ocypodid crabs (*Ocypode gaudichaudii*) were found only at high beach levels of northern Chile, oniscoid isopods (*Tylos spinulosus*) only at northern central Chile, and talitrid amphipodes (*Orhestoidea tuberculata*) at northern central and southern central Chile. The pattern of geographic distribution is analyzed in relation to some hydrographic and climatic conditions along the Chilean coast. It is hypothesized that the general absence of current or temperature barriers in the surface waters, allows similar species composition at low beach levels at all locations. On the other hand, an increase in rainfall from north to south, and differences in air and sediment temperatures from south to north, are associated with different taxonomic composition of fauna at high beach levels. The zonation patterns of the Peruvian-Chilean macroinfauna are very similar to those noted by Dahl (1952) and Trevallion *et al.* (1970).

INTRODUCTION

Investigations of the sandy beach macroinfauna of the Chilean coast are rather limited. The first mention of macroinfaunal zonation is that of Dahl (1952) who analyzed the intertidal distribution of Crustacea at Montemar (central Chile), Isla Tenglo (southern central Chile), and Punta Arenas (southern extreme of Chile). At northern central Chile, Sanchez *et al.* (1982) studied the community structure and zonation schemes of a semi-exposed beach and compared their zonation results with the schemes of Dahl (1952), Pichon (1967), and Trevallion *et al.* (1970). For this area of the Chilean coast, Castilla *et al.* (1977) and Castilla (1983) analyzed changes in the typical zonation pattern and community structure of sandy beaches affected by an oil spill and by copper mine tailings, respectively. Zonation of species living in sandy areas of central Chile were mentioned by Nuñez *et al.* (1974) and Osorio *et al.* (1967), while distributional patterns in southern central Chile were studied by Bertrán (1984), Epelde-Aguirre and Lopez (1975), and Jaramillo (1978). The last two studies also provided comparisons with world-wide zonation schemes. All of these earlier studies were carried out mainly in the central area of the Chilean littoral (from approximately 30 to 40°S). The Chilean coast is quite extensive (about 4,000 km) ranging from approximately 18°30'S to 55°S latitude, covering about 36 degrees of latitude. Zoogeographical boundaries were discussed by several authors (e.g. Balech, 1954; Brattstrom and Johanssen, 1983; Castilla, 1976; Dahl, 1960; Dell, 1971; Knox, 1960; Viviani, 1979). In general, most workers agree that two regions can be distinguished : a northern warm-temperate (from about 18 to 42°S latitude), the Peruvian or Peruvian-Chilean Province, and a southern cold-temperate (from about 42 to 55°S latitude) or Magellanic/Patagonic Province. A transitional zone has also been suggested, located approximately between 30 and 40°S, where many species from both regions co-exist (Balech, 1954; Brattstrom and Johanssen, 1983, and Dell, 1971).

The purpose of this study was to analyze the species composition and zonation patterns of the sandy beach macroinfauna inhabiting three areas of the Peruvian-Chilean Province. Northern Chile corresponds approximately to an area between 18 and 25°S, northern central Chile between 25 and 35°S, and southern central Chile between 35 and 45°S.

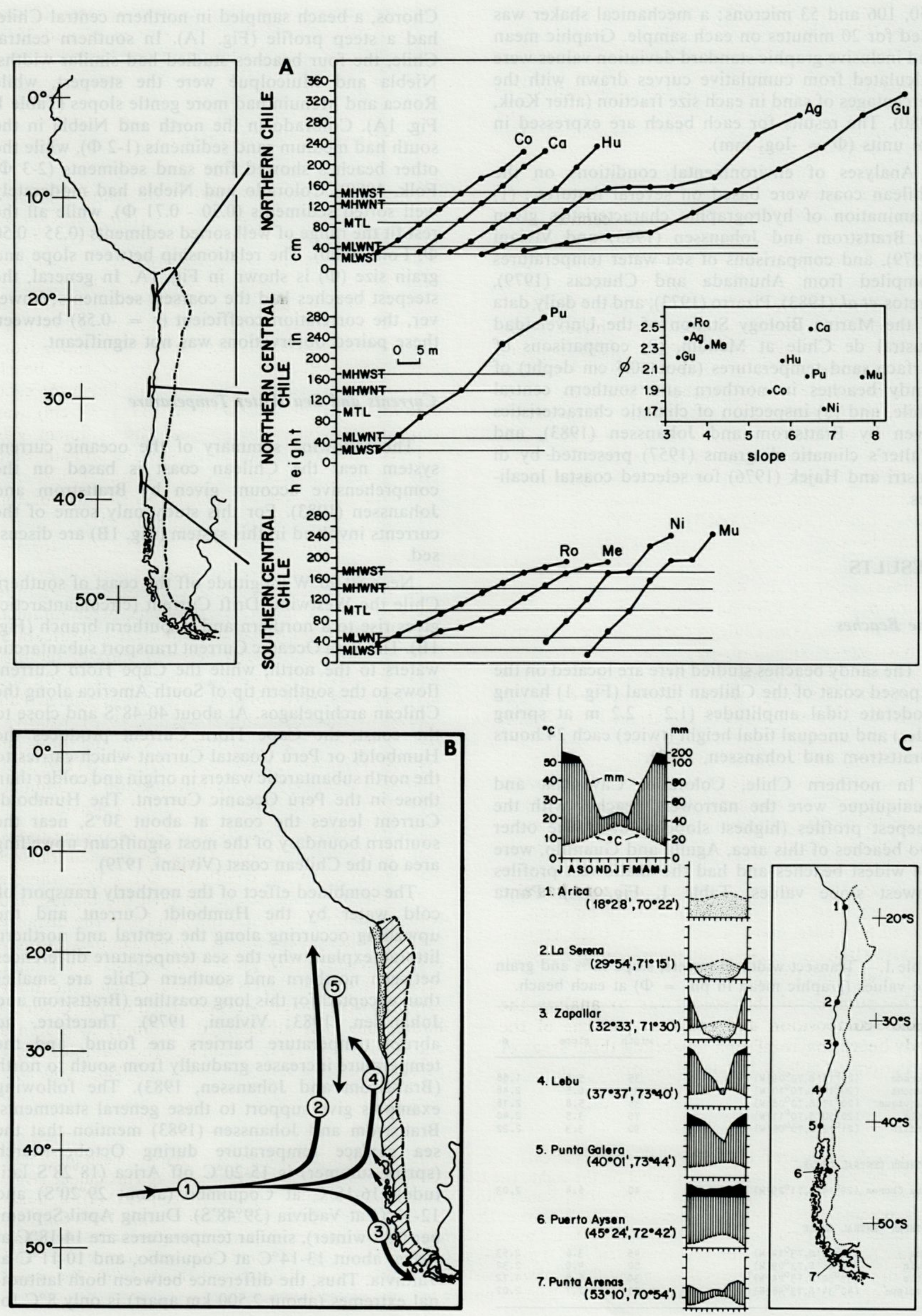
MATERIALS AND METHODS

The faunal data examined for this paper represent samples from ten sandy beaches along the Chilean coast (Fig. 1). Sites in northern and southern central Chile were sampled in the period January to December, 1977, while the site in northern central Chile was sampled during November, 1980. The macroinfauna were sampled during spring low tides at a series of stations along transects extending from low water level to the back border of each beach (defined by foredunes, cliffs or drift lines). At each station, a 0.1 m^2 box quadrat (33 x 33 cm) was pressed into the sand 15 cm. The sediment was washed through a 1 mm sieve, and the animals were removed and preserved in 10 % formalin. Ghost crab (*Ocypode gaudichaudii* Milne Edwards) distribution was recorded by the number of burrows.

Density values for 1 m^2 were calculated (except for *Ocypode gaudichaudii*) and used to draw kite diagrams and describe zonation patterns. To analyze the zonation of species associations, macroinfaunal samples were subjected to numerical classification. The taxonomic similarity between pairs of samples was calculated with Jaccard's Index (Saiz, 1980), and dendrograms were obtained after the Weighted Pair Group Method (Sokal and Sneath, 1973). Multivariate analyses were performed with the program ACOM (Navarro, 1984) on a DECSYSTEM-2020 computer at the Centro do Información y Computación, Universidad Austral de Chile, Valdivia.

Beach profiles were constructed according to the method for Emery (1961). The slope of each transect was measured by the coefficient a/L x 100, where a is the difference in height between the highest and lowest station (low water line) and L is the distance between these two points. Sand samples (15 cm deep) were taken for grain size analysis at the high, middle, and low levels of each beach. The three samples were mixed, washed, dried at 105°C for 24 hours, and then subsampled randomly to obtain a cumulative 100 gram sample. The samples were passed through a series of sieves of 2,000, 1,000, 500,

Fig. 1.— A, Study areas showing beach profiles at each site. The relationship between grain size (graphic mean in Φ) and slope (%) is shown in the inserted panel on the right. The beaches are Colorado (Co), Cavancha (Ca), Huaiquique (Hu), Aguila (Ag),, Guanillo (Gu), Punta Choros (Pu), Ronca (Ro), Mehuin (Me), Niebla (Ni) and Muicolpue (Mu); B, Some of the oceanic currents off the Chilean coast. 1 : Westwind Drift Current; 2 : Peru Oceanic Current; 3 : Cape Horn Current; 4 : Humboldt or Peru Coastal Current and 5 : Peru Counter Current. The dotted area indicates the region of the upwelling system. Based on Brattstrom and Johanssen (1983) and Viviani (1979); C, Walter's climatic diagrams (temperature and rainfall) of selected coastal localities along the Chilean coast (figures taken from di Castri and Hajek, 1976). The scales of this representation are shown in the inserted diagram on the left side of the figure.


A
B
C
0°
10°
20°
30°
40°
50°
NORTHERN CHILE
NORTHERN CENTRAL CHILE
SOUTHERN CENTRAL CHILE
height in cm
MHWST
MHWNT
MTL
MLWNT
MLWST
Co
Ca
Hu
Ag
Gu
Pu
Ro
Me
Ni
Mu
0 5 m
slope
°C
mm
1. Arica (18°28', 70°22')
2. La Serena (29°54', 71°15')
3. Zapallar (32°33', 71°30')
4. Lebu (37°37', 73°40')
5. Punta Galera (40°01', 73°44')
6. Puerto Aysen (45°24', 72°42')
7. Punta Arenas (53°10', 70°54')
J A S O N D J F M A M J
20°S
30°S
40°S
50°S

250, 106 and 53 microns; a mechanical shaker was used for 20 minutes on each sample. Graphic mean and inclusive graphic standard deviation values were calculated from cumulative curves drawn with the percentages of sand in each size fraction (after Kolk, 1980). The results for each beach are expressed in phi units ($\Phi = -\log_2$ mm).

Analyses of environmental conditions on the Chilean coast were based on several features : (1) examination of hydrographic characteristics given by Brattstrom and Johanssen (1983) and Viviani (1979), and comparisons of sea water temperatures compiled from Ahumada and Chuecas (1979), Bretos *et al.* (1983), Pizarro (1973), and the daily data of the Marine Biology Station of the Universidad Austral de Chile at Mehuin, (2) comparisons of surface sand temperatures (about 0.5 cm depht) of sandy beaches in northern and southern central Chile, and (3) inspection of climatic characteristics given by Brattstrom and Johanssen (1983), and Walter's climatic diagrams (1957) presented by di Castri and Hajek (1976) for selected coastal localities.

RESULTS

The Beaches

The sandy beaches studied here are located on the exposed coast of the Chilean littoral (Fig. 1) having moderate tidal amplitudes (1.2 - 2.2 m at spring tides) and unequal tidal height (twice) each 24 hours (Brattstrom and Johanssen, 1983).

In northern Chile, Colorado, Cavancha and Huaiquique were the narrowest beaches with the steepest profiles (highest slope values). The other two beaches of this area, Aguila and Guanillo, were the widest beaches and had the shallowest profiles (lowest slope values, Table I, Fig. 1A). Punta Choros, a beach sampled in northern central Chile, had a steep profile (Fig. 1A). In southern central Chile, the four beaches studied had similar widths. Niebla and Muicolpué were the steepest, while Ronca and Mehuín had more gentle slopes (Table I, Fig. 1A). Colorado in the north and Niebla in the south had medium sand sediments (1-2 Φ), while the other beaches showed fine sand sediments (2-3 Φ, Folk, 1980). Colorado and Niebla had moderately well sorted sediments (0.50 - 0.71 Φ), while all the rest fit the range of well sorted sediments (0.35 - 0.50 Φ, Folk, 1980). The relationship between slope and grain size (Φ) is shown in Fig. 1A. In general, the steepest beaches had the coarsest sediments; however, the correlation coefficient (r = -0.58) between these paired observations was not significant.

Table I.— Transect width in meters, slope in % and grain size values (graphic mean in phi = Φ) at each beach.

		width	slope	ø
NORTHERN CHILE				
Colorado	(20°11'S,70°09'W)	35	5.5	1.88
Cavancha	(20°14'S,70°10'W)	30	6.5	2.48
Huaiquique	(20°17'S,70°08'W)	35	5.8	2.18
Aquila	(20°50'S,70°11'W)	75	3.5	2.40
Guanillo	(21°12'S,70°06'W)	90	3.3	2.22
NORTHERN CENTRAL CHILE				
Punta Choros	(29°14'S,71°29'W)	40	6.4	2.03
SOUTHERN CENTRAL CHILE				
Ronca	(39°23'S,73°14'W)	45	3.6	2.53
Mehuín	(39°26'S,73°09'W)	50	4.0	2.32
Niebla	(39°52'S,73°24'W)	30	6.8	1.72
Muicolpué	(40°34'S,73°46'W)	30	7.7	2.02

Currents and Sea Water Temperature

The following summary of the oceanic current system near the Chilean coast is based on the comprehensive account given by Brattstrom and Johanssen (1983). For this study only some of the currents involved in this system (Fig. 1B) are discussed.

Near 80-90°W longitude off the coast of southern Chile the Westwind Drift Current (circumantarctic) gives rise to a northern and a southern branch (Fig. 1B). The Perú Oceanic Current transport subantarctic waters to the north, while the Cape Horn Current flows to the southern tip of South America along the Chilean archipelagos. At about 40-48°S and close to the coast, the Cape Horn Current produces the Humboldt or Perú Coastal Current which carries to the north subantarctic waters in origin and colder than those in the Perú Oceanic Current. The Humboldt Current leaves the coast at about 30°S, near the southern boundary of the most significant upwelling area on the Chilean coast (Viviani, 1979).

The combined effect of the northerly transport of cold water by the Humboldt Current and the upwelling occurring along the central and northern littoral, explain why the sea temperature differences between northern and southern Chile are smaller than excepted for this long coastline (Brattstrom and Johanssen, 1983; Viviani, 1979). Therefore, no abrupt temperature barriers are found, and the temperature increases gradually from south to north (Brattstrom and Johanssen, 1983). The following examples give support to these general statements. Brattstrom and Johanssen (1983) mention that the sea surface temperature during October-March (spring-summer) is 15-20°C off Arica (18°28'S latitude), 16-18°C at Coquimbo (about 29°20'S) and 12-16°C at Vadivia (39°48'S). During April-September (fall-winter), similar temperatures are 14-18°C at Arica, about 13-14°C at Coquimbo, and 10-11°C at Valdivia. Thus, the difference between both latitudinal extremes (about 2,500 km apart) is only 8°C for both seasonal periods. These values are quite similar to those from other sources. Mean sea surface temperature at Huaiquique (20°17'S) varied between 15 and 17.5°C during 1979-80; however, higher temperatures have been mesured (up to 25°C) here (Bretos *et al.*, 1983; Viviani, 1979) during years when El Niño, a tropical south-flowing current affects especially northern and central Chile. At Montemar (32°58'S), Bahía de Concepción (36°40'S) and Mehuín (39°26'S), the mean values fluctuate in a similar manner between approximately 12 and 14°C over a number of years (Ahumada and Chuecas, 1979; Pizarro, 1973 and data from the Marine Biology Station of Universidad Austral de Chile).

Climate

From approximately 18 to 30°S latitude (Arica to Coquimbo), there is a very low and irregular rainfall (di Castri and Hajek, 1976). Brattstrom and Johanssen (1983) consider this area the dry zone of Martin (1923) with a desert coast and a mean monthly air temperature of 18-22°C in the summer and about 12-17°C in the winter. The area between 30 and 38°S latitude (Coquimbo to Isla Mocha) corresponds closely to Martin's (1923) warm zone where the mean temperature for the warmest month varies from about 15 to 22°C, and for the coldest month from 10-13°C. Furthermore, Brattstrom and Johanssen (1983) state that the yearly rainfall increases from about 110 mm at Coquimbo to 760 mm at Talcahuano (Isla Quiriquina) and still higher farther south. Finally, Brattstrom and Johanssen (1983) claim that the area between about 38 to 56°S (Isla Mocha to Cabo de Hornos) closely corresponds to the rainy zone and the Patagonia-Tierra del Fuego zone of Martin (1923). The mean annual temperature here decreases approximately linearly from 12.5°C at about 38°30'S south to 5.4°C at Cabo de Hornos.

These climatic characteristics are graphically displayed by Walter's climatic diagrams. In this display (Fig. 1C, left side) the abcissa represents the monthes of the year, while the two ordinate axes represent temperature and rainfall. Aridity (dotted area) is indicated when the rainfall curve lies below the temperature curve. The humid period is conventionally represented by vertical lines, with the exception of periods exceeding 100 mm rainfall which are black; the dry period is represented by a dotted surface (di Castri and Hajek, 1976). Arica is typical of the dry zone, with aridity during the entire year. La Serena, Zapallar, and Lebu are located in the warm zone delimited by Brattstrom and Johanssen (1983), where the arid period decreases from north to south, coincidental with an increase of the humid period. Aridity ceases south of Lebu; Punta Galera and Puerto Aysen show an excess of rainfall during at least half of the year. These two localities and Punta Arenas are included in the so-called rainy zone.

Sand Temperature

The data obtained during the autumn of 1977 from beaches of northern Chile (Colorado, Cavancha, Huaiquique, Aguila and Guanillo) show that the sand temperature values were similar to those measured during summer at the sandy beach of Mehuín in southern central Chile. At these beaches, temperatures ranged from approximately 18 to 45°C, with values above 33°C at the highest beach levels, i.e. above MHWST. At Mehuín, sediment temperatures varied between approximately 14 and 19°C in May 1978, 17 and 29°C in April 1979, and 21 and 34°C in April 1980. During the autumn of 1979 and 1980, the temperature values measured at the highest beach levels of Mehuín were quite similar to those

Table II.— Number of species and density values (number per 1 m²) of the total macroinfauna and the dominant species. Mean densities are in relation to the number of stations with animals. The ghost crab *Ocypode gaudichaudii* is included in the number of species living in the sandy beaches of northern Chile, but not in the density figures.

	no. spp.	total density $\bar{x}$	highest density	tidal level (station)	dominant species	density $\bar{x}$	highest density	tidal level (station)
NORTHERN CHILE								
Colorado	3	29	56	above MHWST (1)	*P. maculata*	30	56	above MHWST (1)
Cavancha	5	43	83	MLWST (7)	*E. analoga*	56	65	MLWST (7)
Huaiquique	6	140	250	MLWST (8)	*E. analoga*	158	176	MLWST (8)
Aguila	7	149	704	MLWST (13)	*E. analoga*	477	602	MLWST (13)
Guanillo	6	103	231	MLWNT (9)	*E. analoga*	95	185	MLWNT (9)
NORTHERN CENTRAL CHILE								
Punta Choros	8	874	1500	above MHWST (1)	*E. hirsuticauda*	1111	1389	MLWNT (5)
SOUTHERN CENTRAL CHILE								
Ronca	8	71	204	MHWNT (5)	*E. hirsuticauda*	69	185	MHWNT (5)
Mehuín	8	189	417	MHWNT-MTL (6)	*E. hirsuticauda*	118	352	MHWNT-MTL (6)
Niebla	4	94	287	MHWNT-MTL (5)	*E. hirsuticauda*	84	194	MLWNT (7)
Muicolpué	6	145	389	MTL (5)	*O. tuberculata*	111	222	MTL (5)

measured at the middle levels of the beaches in northern Chile.

The Macroinfauna

The highest number of species and total densities were found in sandy beaches of northern central and southern central Chile (Table II). In northern Chile (with the exception of Colorado) the highest densities per station, and the highest density of the dominant species, as the anomuran crab *Emerita analoga* (Stimpson)(Hippidae), occurred near the low water line (Table II). At Punta Choros, the highest density per station was estimated for the highest level of that beach, while in southern central Chile, stations located at the middle levels (MHWNT to MTL or MTL) of Mehuin and Muicolpué yielded the highest densities (Table II). The isopod *Excirolana hirsuticauda* Menzies (Cirolanidae) was the most abundant species in both of these areas with the exception of Muicolpué in the south, where the amphipod *Orchestoidea tuberculata* Nicolet (Talitridae) was the most abundant species.

The zonation of the species from each area of the Chilean coast is shown in Fig. 2. The insect *Phalerisidia maculata* Kulzer occurred on the high beach levels of all the beaches studied. The ghost crab *Ocypode gaudichaudii* Milne Edwards (Ocypodidae) occurred only in northern Chile. Tylid isopods (*Tylos spinulosus* Dana) were not collected in northern Chile, nor in southern central Chile, but only at Punta Choros in northern central Chile. Talitrid amphipods (*Orchestoidea tuberculata*) were absent at northern Chile, and cirolanid isopods were more diverse at southern central Chile (*Excirolana hirsuticauda, Excirolana braziliensis* Richardson and *Excirolana monodi* Carvacho). *Emerita analoga,* the polychaete *Nephtys impressa* Baird (Nephtyidae), and the

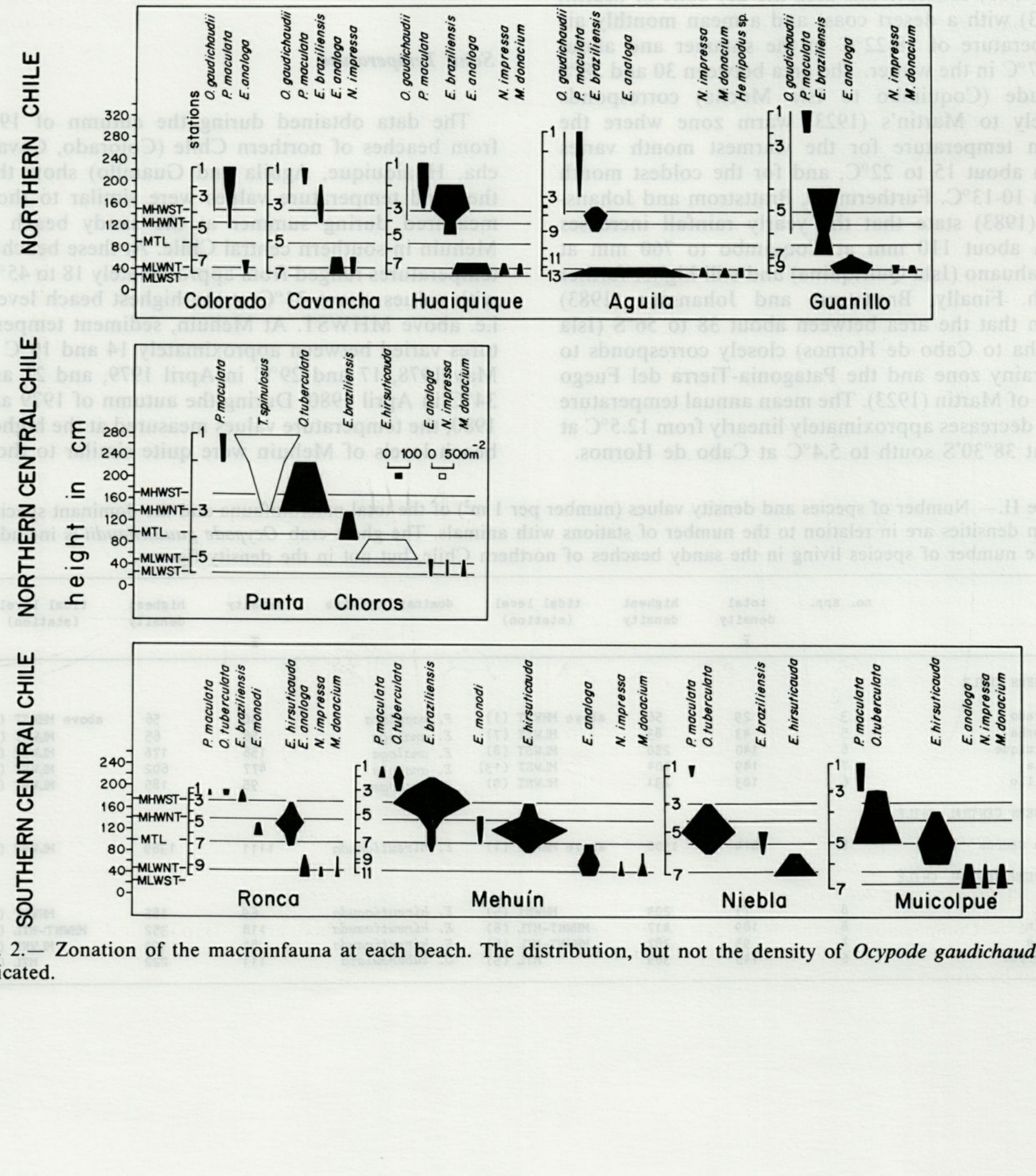


Fig. 2. Zonation of the macroinfauna at each beach. The distribution, but not the density of *Ocypode gaudichaudii* is indicated.

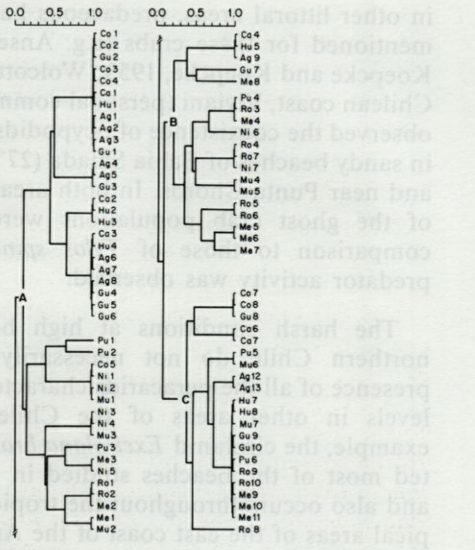


Fig. 3.— Dendrogram showing clustering of stations in three main groups. A : high beach levels; B : middle beach levels and C : low beach levels. Numbers to the right of the dendrogram refer to station numbers as in Fig. 4, while letters refer to the beaches as in Fig. 1.

clam *Mesodesma donacium* (Lamark) were collected at the low levels (below MTL) of most of the beaches.

Three major station groups, linked by a very low value of similarity (0.04), are recognizable in the dendrogram produced by the cluster analysis (Fig. 3). The groups (A,B and C) represent tidal levels, while the subgroups within them represent groups of stations from different geographical areas. Group A includes levels inhabited by insects, ocypodids, talitrids, cirolanid (*E. Braziliensis*) and tylid isopods. Group B has cirolanids as the main component and group C includes *E. analoga, N. impressa* and *M. donacium.*

DISCUSSION

The analysis of the zonation patterns and cluster analysis of the macroinfauna from the Chilean coast show that significant changes in species composition occur at middle and high beach levels, while similar species occur at low beach levels (Fig. 4). At middle

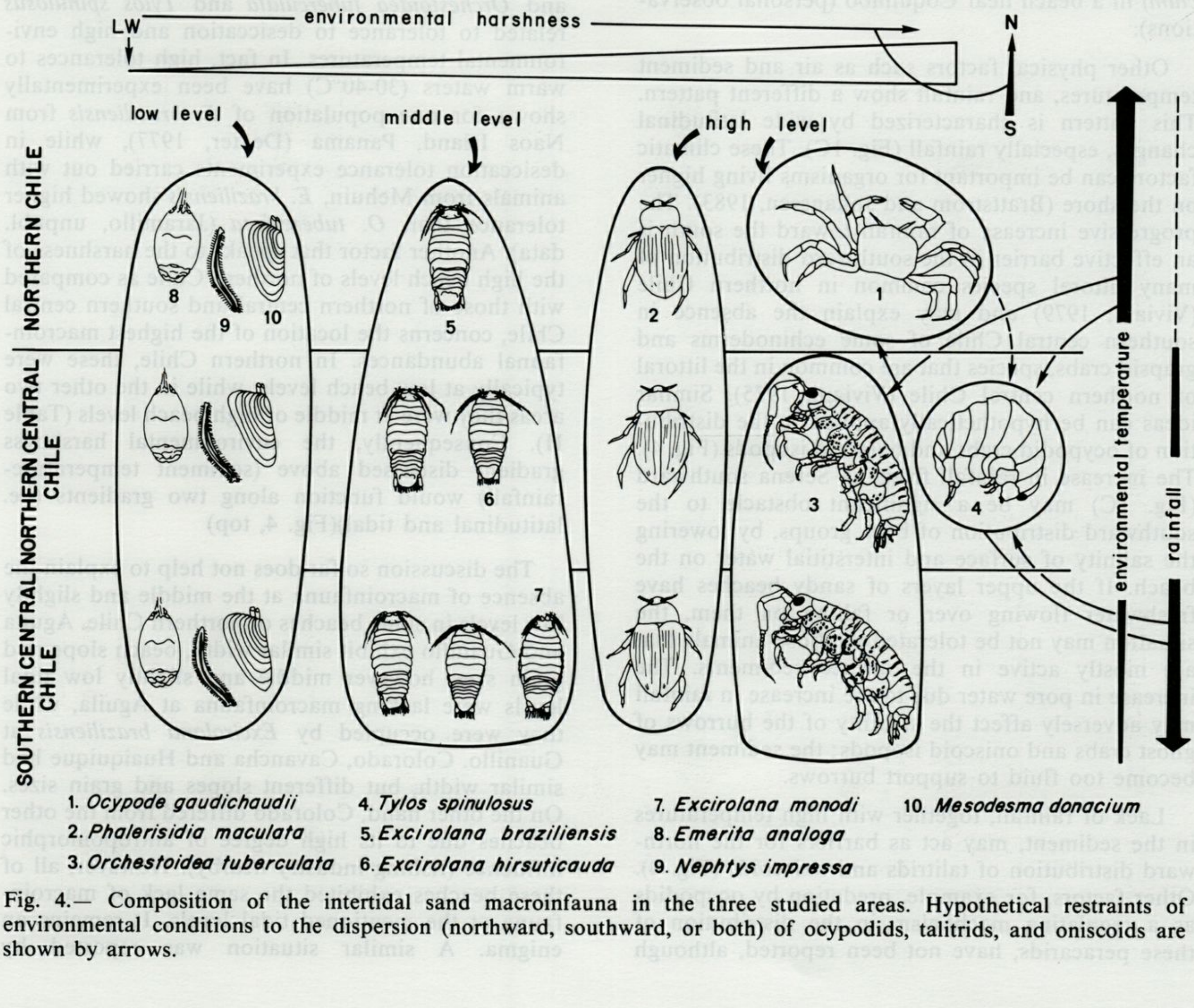


Fig. 4. Composition of the intertidal sand macroinfauna in the three studied areas. Hypothetical restraints of environmental conditions to the dispersion (northward, southward, or both) of ocypodids, talitrids, and oniscoids are shown by arrows.

beach levels, there is a northward reduction in the number of cirolanid isopod species, and an absence of cirolanids at some beaches in northern Chile. At high beach levels, talitrid amphipods occur in southern central and northern central Chile, while in northern Chile ocypodid crabs occupy similar levels. On the other hand, oniscoid isopods only occur in the northern central area of the Chilean coast.

The hydrographic analyses of Brattstrom and Johanssen (1983) and Viviani (1979) show that no abrupt sea water temperature or current barriers are typically found on the Chilean coast. This may explain why the same species, *Emerita analoga, Nephtys impressa* and *Mesodesma donacium*, characterize the low beach levels in sands that are water saturated most of the time. These abiotic factors could readily favor widespread distribution of benthic animals with pelagic larvae. The presence of upwelling waters bringing higher primary production to the northern coast (Viviani, 1979), may explain the higher abundance of *E. analoga* in northern Chile (Fig. 1B). Higher abundances than those presented here were also observed for this species and another suspension feeder (*M. donacium*) in a beach near Coquimbo (personal observations).

Other physical factors such as air and sediment temperatures, and rainfall show a different pattern. This pattern is characterized by wide latitudinal changes, especially rainfall (Fig. 1C). These climatic factors can be important for organisms living higher on the shore (Brattstrom and Johanssen, 1983). The progressive increase of rainfall toward the south is an effective barrier in the southward distribution of many littoral species common in northern Chile (Viviani, 1979) and may explain the absence in southern central Chile of some echinoderms and grapsid crabs, species that are common in the littoral of northern central Chile (Viviani, 1975). Similar ideas can be hypothetically applied to the distribution of ocypodid crabs and oniscoid isopods (Fig. 4). The increase in rainfall from La Serena southward (Fig. 1C) may be a significant obstacle to the southward distribution of both groups, by lowering the salinity of surface and interstitial water on the beach. If the upper layers of sandy beaches have freshwater flowing over or falling on them, the situation may not be tolerated by those animals that are mostly active in the surface sediments. The increase in pore water due to the increase in rainfall may adversely affect the stability of the burrows of ghost crabs and oniscoid isopods; the sediment may become too fluid to support burrows.

Lack of rainfall, together with high temperatures in the sediment, may act as barriers for the northward distribution of talitrids and oniscoids (Fig. 4). Other factors, for example, predation by ocypodids as a regulating mechanism in the distribution of these peracarids, have not been reported, although in other littoral areas, predaceous habits have been mentioned for these crabs (e.g. Ansell *et al.*, 1972; Koepcke and Koepcke, 1953; Wolcott, 1978). On the Chilean coast, Viviani (personal communication) has observed the coexistence of ocypodids and oniscoids in sandy beaches of Bahía Salada (27°38'S, 70°58'W) and near Punta Choros. In both areas, the densities of the ghost crab populations were very low in comparison to those of *Tylos spinulosus* and no predator activity was observed.

The harsh conditions at high beach levels of northern Chile do not necessarily preclude the presence of all the peracarids characteristics of these levels in other areas of the Chilean coast. For example, the cirolanid *Excirolana braziliensis* inhabited most of the beaches studied in northern Chile and also occurs throughout the tropical and subtropical areas of the east coast of the Americas (Glynn *et al.*, 1975). This species was restricted to the high or highest middle levels in most of the beaches in northern Chile, and in two sites (Colorado, Cavancha), it did not occupy the middle levels at all. The presence of *E. braziliensis* in northern Chile suggests that significant differences exist between this species and *Orchestoidea tuberculata* and *Tylos spinulosus* related to tolerance to desiccation and high environmental temperatures. In fact, high tolerances to warm waters (30-40°C) have been experimentally shown for one population of *E. braziliensis* from Naos Island, Panama (Dexter, 1977), while in desiccation tolerance experiments carried out with animals from Mehuín, *E. braziliensis* showed higher tolerance than *O. tuberculata* (Jaramillo, unpubl. data). Another factor that speaks to the harshness of the high beach levels of northern Chile as compared with those of northern central and southern central Chile, concerns the location of the highest macroinfaunal abundances. In northern Chile, these were typically at low beach levels, while in the other two areas they were at middle or high beach levels (Table II). Consequently, the environmental harshness gradient discussed above (sediment temperature-rainfall) would function along two gradients (i.e. latitudinal and tidal)(Fig. 4, top)

The discussion so far does not help to explain the absence of macroinfauna at the middle and slightly low levels in some beaches of northern Chile. Aguila and Guanillo exhibit similar width, beach slope and grain size; however middle and slightly low tidal levels were lacking macroinfauna at Aguila, while they were occupied by *Excirolana braziliensis* at Guanillo. Colorado, Cavancha and Huaiquique had similar width, but different slopes and grain sizes. On the other hand, Colorado differed from the other beaches due to its high degree of antropomorphic influence (fishing industry nearby). However, all of these beaches exhibited the same lack of macroinfauna at the mentioned tidal levels. It remains an enigma. A similar situation was reported by

Epelde-Aguirre and Lopez (1975) for the middle beach levels of Playa Blanca in southern central Chile.

Several attempts have been made to build zonation schemes for worldwide application, or at least, for littoral sandy areas over wide latitudinal ranges. Among them, those of Dahl (1952) and Trevallion *et al.* (1970) are the most comprehensive schemes. The zonation patterns described above for the Peruvian-Chilean Province are very similar to those noted by Dahl and Trevallion *et al.*, but with some important differences. The presence of cirolanid isopods at higher beach levels (Dahl's subterrestrial fringe) of all the beaches studied, talitrid amphipods in the middle beach levels (Dahl's midlittoral) of southern central Chile, cirolanids in the lower beach levels (Dahl's sublittoral) of the same area, and anomuran crabs (Hippidae) in the lower beach along all the shores studied, are the main differences with the scheme of Dahl (1952). Similar differences were also found in other studies carried out on the Chilean coast (Castilla *et al.*, 1977; Epelde-Aguirre and Lopez, 1975; Jaramillo, 1978; Sanchez *et al.*, 1982) and in other areas of the world. More similarities are found when zonation patterns are compared with Trevallion's *et al.* (1970) scheme. In the specific case of the littoral studied here, the main difference with Trevallion's scheme is the absence of bivalves of the genus *Donax*, gastropods and echinoids from the Chilean coast.

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