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E. Jaramillo

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Patterns of species richness in sandy beaches of South America

E. Jaramillo
Instituto de Zoologia, Universidad Austral de Chile, Valdivia, Chile

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Species richness of the intertidal macroinfauna of exposed sandy beaches around South America is reviewed in relation to geographic location. This macroinfauna is dominated by cirolanid isopods (*Excirolana*), bivalves (*Mesodesma* and *Donax*) and opheliid and spionid polychaetes. In general, the upper shore of tropical and subtropical beaches is characterized by crabs (Ocypodidae), whereas on temperate beaches it is dominated by talitrid amphipods and cirolanid isopods. The middle shore is primarily occupied by cirolanids and bivalves, and hippid crabs, bivalves and amphipods dominate the lower beach. Generally, species richness increases from upper to lower beach levels. Studies carried out on exposed sandy beaches of south-central Chile (*ca.* 40°S) show that different beach states harbour differences in species richness, with the greatest species richness on dissipative beaches, and the least on beaches with reflective characteristics, a pattern also observed in Uruguay.

Makroinfauna spesiesverskeidenheid van blootgestelde sandstrande van Suid Amerika word hersien en vergelyk ten opsigte van geografiese ligging. Die makroinfauna word oorheers deur Isopoda Cirolanidae (*Excirolana*), Bivalvia (*Mesodesma* en *Donax*) en Polychaeta Opheliidae en Spionidae. Oor die algemeen word die boonste deel van tropiese en subtropiese strande gekenmerk deur krappe (Ocypodidae) terwyl die gematigde strande oorheers word deur Amphipoda Talitridae en Isopoda Cirolanidae. Cirolanidae en Bivalvia word hoofsaaklik aangetref in die middelste gedeelte van die strand terwyl krappe (Hippidae), Bivalvia en Amphipoda die laer deel van die strand oorheers. Oor die algemeen neem verskeidenheid toe van die boonste na die laer dele van die strand. Studies wat gedoen is op blootgestelde strande in die suide van Chile (*ca.* 40°S) het getoon dat verskillende strandstadia ooreenkom met verskille in spesieverskeidenheid met die hoogste spesieverskeidenheid op verstrooide strande en die laagste op reflektiewe strande. Hierdie patroon is ook waargeneem op sandstrande van Uruguay.

Although sandy beaches constitute most of the coast of South America, research on these habitats has been limited, especially in tropical latitudes. The first community level studies were rather descriptive and devoted primarily to abundance data and zonation of the most representative species (e.g. Dahl 1952; Koepcke 1952; Osorio, Bahamonde & Lopez 1967; Dexter 1974; Scarabino, Maytia & Faedo 1974; Escofet, Gianuca, Maytia & Scaravino 1979). More recent studies have been based on quantitative sampling and analysis of physical factors affecting species richness and/or the dynamics of zonation patterns (Defeo, Jaramillo & Lyonnet 1992; Tarazona & Paredes 1992; Jaramillo & McLachlan 1993; Jaramillo, McLachlan & Coetzee 1993). However, an extensive study of species richness along this coastal zone which spans many zoogeographical provinces (Balech 1954) has not been carried out. Thus, the aim of this study was to provide a comparative analysis of the species richness on sandy beaches from different areas of the South American coast.

Materials and Methods

This study is based on three sets of data: (a) a review of the available published information on sandy beach macroinfauna around South America (Figure 1a); (b) 'snapshot' surveys carried out on ten sandy beaches of south-central Chile (*ca.* 40°S) in the late summer of 1991 (Figure 1b), and on two sites of the Atlantic coast of Uruguay in the late spring of 1991) (Figure 1c); and (c) a 17-month seasonal study on four sandy beaches of south-central Chile (Figure 1b).

Beaches studied in Chile and Uruguay were sampled during spring low tides. Three replicate samples (0,03 m², 30 cm deep) were collected with plastic cores at ten equally-spaced levels along a transect extending from above the drift line to the swash zone. The sediment was sieved through a 1-mm mesh and the macroinfauna was stored in 5% formalin until sorting. Cluster analysis was used to elucidate faunistic belts on selected beaches of south-central Chile and on two beaches from Uruguay. Dendrograms were constructed from Wiener similarity matrices (Saiz 1980) based on the Weighted Pair Group Method (Sokal & Sneath 1973).

Sediment samples were also collected for grain size analyses using a sampling tube (Emery 1938) and the moments computational method (Seward-Thompson & Hails 1973). The water content of sediments was estimated as the loss in weight of wet sands after drying (120°C for 96 h). Penetrability was measured by dropping a 33,6-g metal rod down a 1-m tube. The depth to which the rod penetrated into the sediment was measured four times at each station. The slope of each beach was determined by Emery's profiling technique (Emery 1961). Estimates of wave height, wave period and sand-fall velocity were used to calculate Dean's parameter (Ω), a measure of the morphodynamic state of a beach (Short & Wright 1983):

$$\Omega = H_b / W_s.T$$

where H_b is the breaker height in cm, W_s the sand velocity in cm s^{-1} (Gibbs, Mathews & Link 1971) and T the wave period in seconds.

Results and Discussion

Species richness and beach types

Figures 2 & 3 show some physical characteristics of beaches with reflective and dissipative characteristics (*sensu*

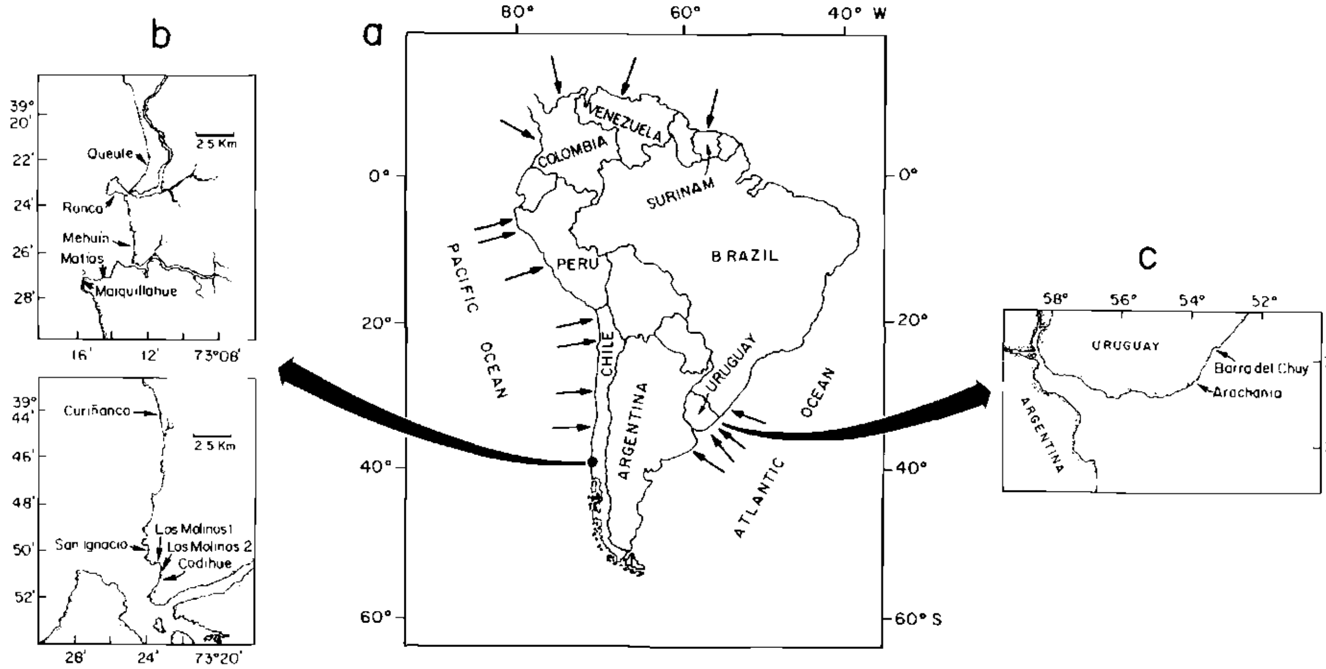

Figure 1 Map of the South American coast showing: (a) approximate locations of areas from which published information on sandy-beach intertidal communities was reviewed, (b) location of ten sandy beaches studied in south-central Chile, and (c) location of two sandy beaches studied on the Atlantic coast of Uruguay. Data collected at the beaches of Los Molinos 1, Los Molinos 2 and two sites in Mehuín (Mehuín 1 and Mehuín 2) were used in the seasonal study (17 months) in south-central Chile.

Short & Wright 1983) sampled in south-central Chile and the Atlantic coast of Uruguay. Beaches with reflective characteristics had mean grain sizes above 400 µm with particle sizes increasing from the lower shore. On the other hand, dissipative beaches had mean grain sizes lower than 300 µm, and the particle size was quite homogeneous throughout the intertidal zone (Figure 2). Due to the coarser grains in beaches with reflective features, the water content of the interstitial spaces drops more drastically across the intertidal zone than in the dissipative sites. Furthermore, the sediment packing (expressed here as penetrability of the sediments) is different (Figure 3).

Jaramillo & Gonzalez (1991), Defeo *et al.* (1992), Jaramillo & McLachlan (1993), Jaramillo *et al.* (1993) and McLachlan, Jaramillo, Donn & Wessels (1993) have shown that different beach types harbour differences in species richness. Figure 4 shows the relationships between number of macroinfaunal species and physical characteristics of ten beaches sampled in south-central Chile and two on the Atlantic coast of Uruguay. There is a general trend of decreasing species richness with increasing particle size and beach face slope (steeper beaches), and of an increase from reflective to dissipative conditions (from lower to higher Dean's parameter values). The best fit (R^2 = 0,83) was with Dean's parameter, a measure of beach type. These results are similar to those for sandy beaches in the USA, Australia and South Africa (McLachlan 1990). Studies carried out on sandy beaches of Colombia (Dexter 1974) and on other areas of the world have also reported low species richness in sandy beaches with reflective characteristics such as coarse sands (e.g. Gauld & Buchanan 1956; Dexter 1983; 1988; McLachlan 1985). However, although changes in beach type appear to result in predictable changes in macroinfaunal species richness, temporal studies carried out on four beaches of south-central Chile suggest that this pattern may

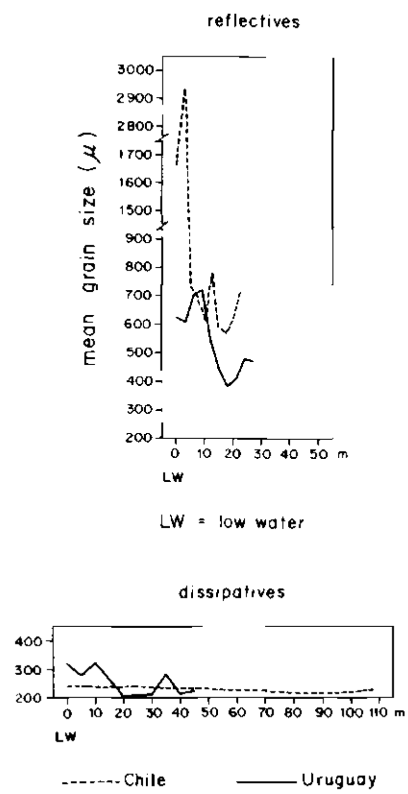

Figure 2 Intertidal variability in mean grain size of sediments across the intertidal zone of beaches with reflective and dissipative characteristics in south-central Chile and the Atlantic coast of Uruguay. Each line represents the values for a single beach.

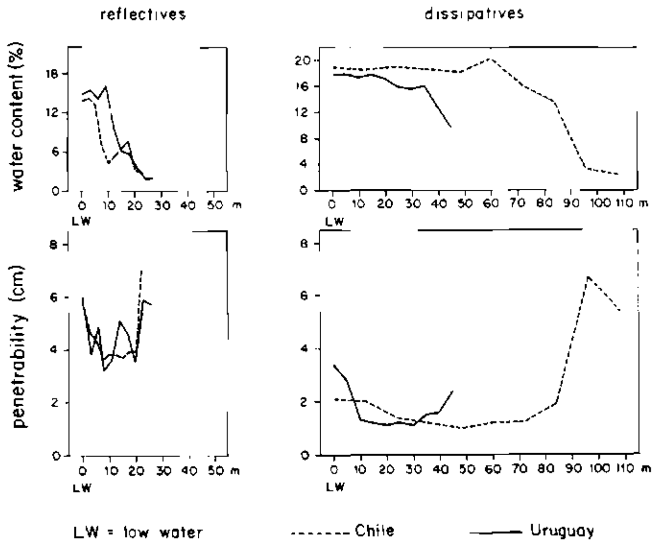

Figure 3 Intertidal variability in water content and penetrability of sediments across the intertidal zone of beaches with reflective and dissipative characteristics in south-central Chile and the Atlantic coast of Uruguay. Each line represents the values for a single beach.

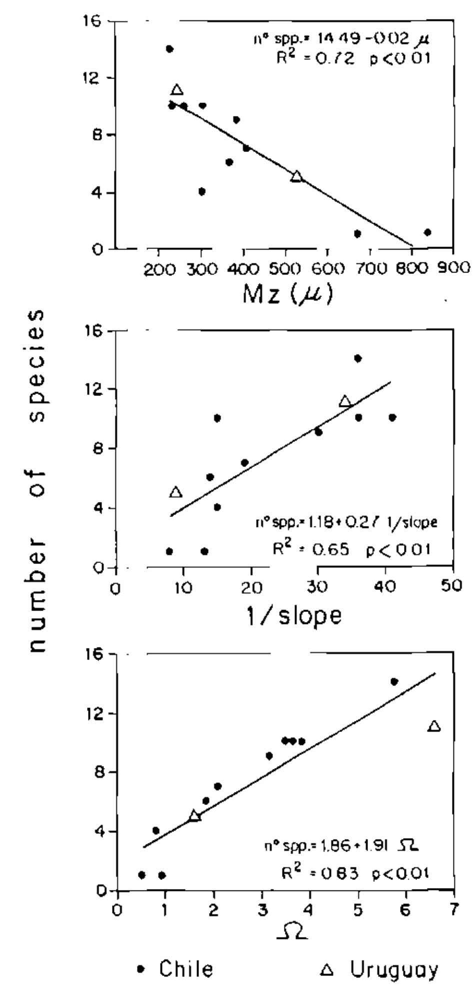

Figure 4 Number of species versus mean grain size (Mz), beach face slope and Dean's parameter (Ω). Beaches sampled in south-central Chile (n = 10) and on the Atlantic coast of Uruguay (n = 2) are combined in this analysis.

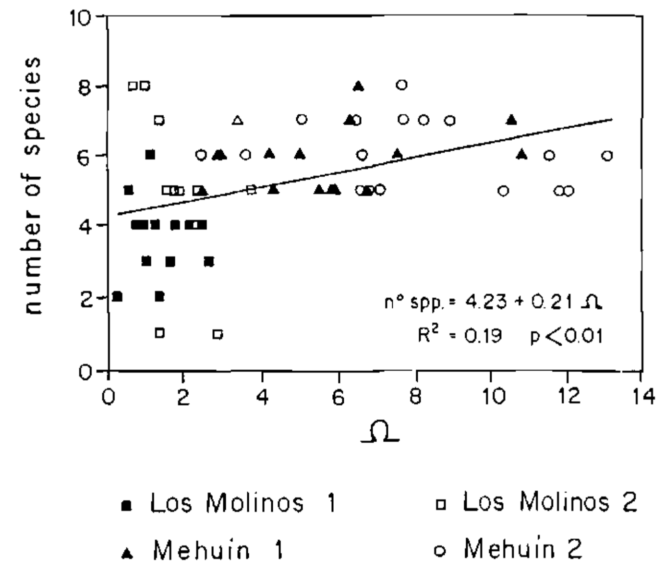

Figure 5 Temporal variability in number of species and Dean's parameter (Ω) in four sandy beaches of south-central Chile. LM1 = Los Molinos 1, LM2 = Los Molinos 2, ME1 = Mehuín 1 and ME2 = Mehuín 2. More dissipative conditions from LM1 to ME2.

be highly variable (Figure 5). This is probably a consequence of the fact that the higher species richness found under dissipative conditions is due to the presence of low shore species which are most affected by the changing physical conditions along exposed gradients.

Within-coast and between-coast comparative analyses also show that, in general, sites with dissipative conditions have more faunal belts across the shore. The within-coastal variability can be illustrated by the comparison of three beaches in south-central Chile. On a coastline stretching no more than 60 km, three faunal patterns are found (Figure 6): the first pattern in a reflective coarse sand beach with only talitrid amphipods occupying the zone above the drift line; a second in a reflective sand beach with fine sands and primarily represented by two faunal zones — an upper zone with talitrids and a middle-lower zone characterized by cirolanid isopods; and a third pattern found in fine-sand dissipative beaches with a higher number of faunal belts — talitrids and cirolanids on the upper shore, cirolanids on the middle, and anomurans, amphipods, idoteid isopods and juvenile bivalves on the lower shore. Figures 7 & 8 illustrate the between-coastal comparisons. In both areas, south-central Chile and the Atlantic coast of Uruguay, one or two faunal zone belts were differentiated in reflective conditions, whereas three were distinguished under more dissipative conditions. However, it is important to notice that even when two faunal zone belts were recorded on the reflective beach of Chile and Uruguay, they were not the same, i.e. on the beach of Uruguay the mid-shore levels were characterized by the absence of macroinfauna or had very low numbers.

The absence of macroinfauna on the middle and lower shore of a reflective beach in south-central Chile, and the paucity of organisms on similar levels of some reflective beaches of the Atlantic coast of Uruguay (Figure 8; Defeo *et al.* 1992), support the suggestion of McLachlan *et al.* (1992) that on fully reflective beaches the harsh swash climate

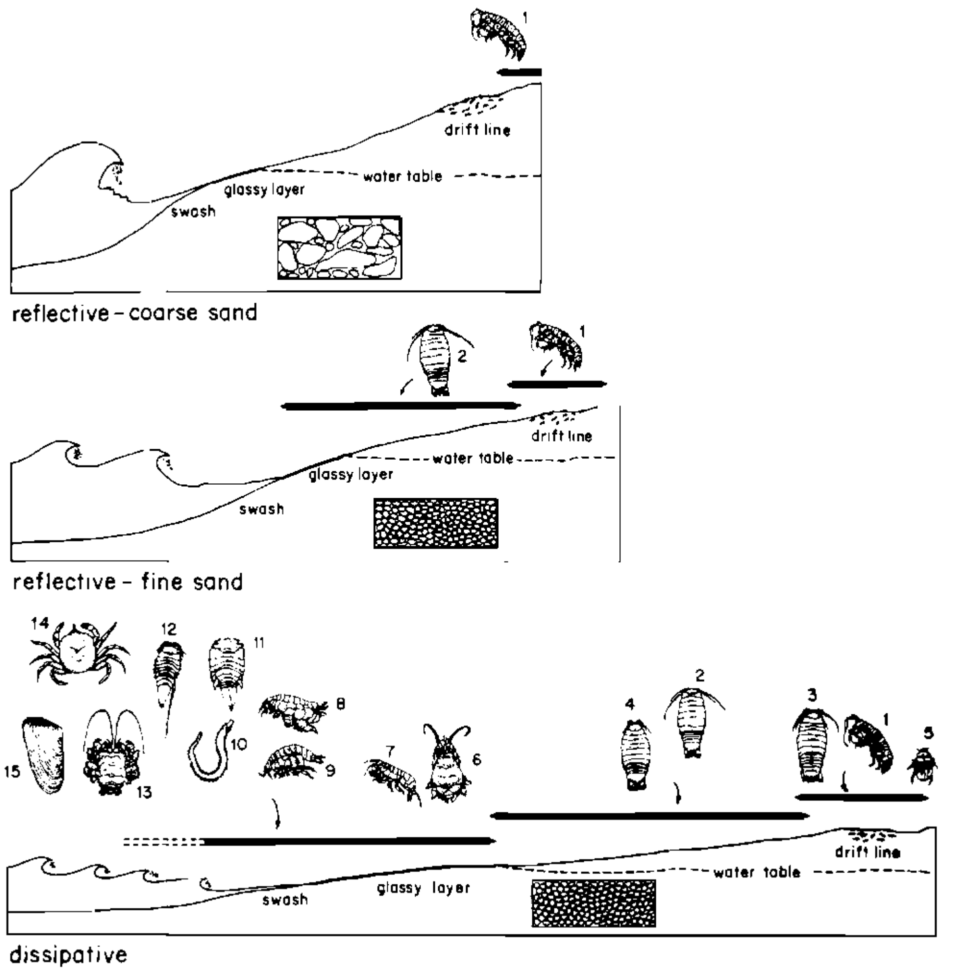

Figure 6 Diagrammatic representation of the zonation patterns of the intertidal macroinfauna on sandy beaches of south-central Chile (after Jaramillo *et al.* 1993): (a) a reflective coarse-sand beach, (b) a reflective fine-sand beach and (c) a dissipative beach. Just the most typical species are represented. 1 = *Orchestoidea tuberculata* (Amphipoda); 2 = *Excirolana hirsuticauda;* 3 = *Excirolana braziliensis;* 4 = *Excirolana monodi* (Isopoda); 5 = *Phalerisidia maculata* (Coleoptera); 6 = *Emerita analoga* (Anomura); 7 = *Bathyporeiapus magellanicus;* 8 = *Huarpe* sp.; 9 = *Phoxocephalopsis mehuinensis* (Amphipoda); 10 = *Nephtys impressa* (Polychaeta); 11 = *Macrochiridothea setifer;* 12 = *Chaetilia paucidens* (Isopoda); 13 = *Lepidopa chilensis* (Anomura); 14 = *Bellia picta* (Brachyura) and 15 = *Mesodesma donacium* (Bivalvia).

excludes the establishment of intertidal macroinfaunal species. McLachlan (1985), Gauld & Buchanan (1956) and Dye, McLachlan & Wooldridge (1981) also reported the absence or paucity of macroinfauna in the middle and lower intertidal zone of beaches with reflective conditions in Australia, Ghana and Natal, South Africa.

Species composition in different areas

Dexter (1974) studied five beaches along the Atlantic and Pacific coasts of Colombia (about 3–12°N). The cirolanid isopod *Excirolana braziliensis* inhabited the upper and middle shore; the ocypodid crab *Ocypode quadrata* also occurred at one of the sites studied (presumably on the upper shore) and the spionid polychaete *Scolelepis agilis* was present in the intertidal zone, being most abundant toward the lower beach. The lower shore of these beaches was primarily occupied by the polychaetes *Hemipodus armatus* (Glyceriidae) and *Nephtys singularis* (Nephtyidae), phoxocephalid amphipods, two species of the anomuran crab *Emerita*, and several species of *Donax* (Bivalvia).

Perez *et al.* (1980) studied the zonation of the macroinfauna inhabiting sandy beaches in Venezuela, around 10–11°N. They found that the upper shore was occupied by *Ocypode quadrata*, cirolanid isopods (probably *Excirolana*) and amphipods (probably talitrids). Cirolanids, polychaetes, *Emerita brasiliensis* and *Donax* dominated the middle shore, whereas the lower beach was occupied by bivalves (*Donax* and *Tivela*), the echinoid *Mellita quinquiesperforata* and the starfish *Astropecten marginatus*. Dahl (1952) also examined a sandy beach in Venezuela (about 10°N); he found ocypodid crabs on the upper shore and cirolanid isopods on the middle shore. He also mentioned that anomuran crabs (Hippidae) probably occur in the swash zone of the beach he studied. Rodriguez (1959) analysed the sandy shore communities of Isla Margarita (about 11°N) located in the Caribbean off the coast of Venezuela. His results were similar to those described by Perez *et al.* (1980) but with talitrid amphipods on the upper shore.

Swennen & Duiven (1982) studied two coarse sandy beaches in Surinam (about 6°N) and found that *Ocypode quadrata* inhabited the high-tide mark of these beaches.

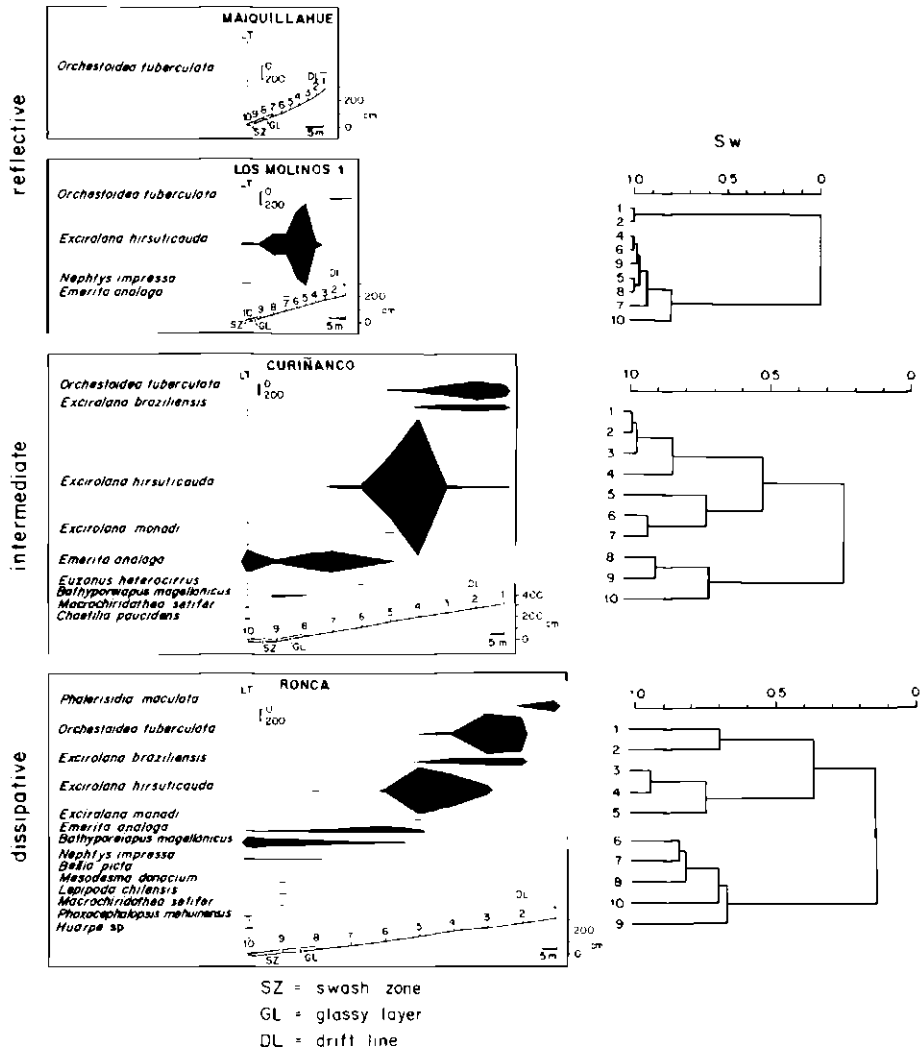

Figure 7 Intertidal distribution of the macroinfauna, and clustering of stations in beaches sampled in south-central Chile. The beach at Maiquillahue was omitted from the classification analysis.

Apart from one juvenile of the brachyuran *Hepatus pudibundus*, no macroinfauna was found across the intertidal zone.

Gianuca (1983) and Escofet *et al.* (1979) studied the zonation of the macroinfauna on dissipative beaches of southern Brazil (about 32°S). They found that the upper shore levels were characterized by the presence of *Ocypode quadrata*, the talitrid *Orchestoidea brasiliensis* and the tenebrionid *Phaleria brasiliensis*. The bivalve *Mesodesma mactroides*, the amphipod *Cheus micros*, the isopod *Excirolana armata*, and the polychaetes *Spio gaucha* (Spionidae) and *Euzonus furciferus* (Opheliidae) were typical species of the middle shore, while *Mesodesma mactroides* and *Donax gemmula*, the polychaete *Hemipodus olivieri*, the gastropods *Olivancillaria vesico auricularia* and *Buccinanops duartei*, *Emerita brasiliensis*, the idoteid isopod *Macrochiridothea giambiagiae*, and the brachyuran crab *Callinectes sapidus* were primarily found on the lower shore (swash zone).

The Atlantic sandy beaches of Uruguay (about 34–35°S) have been studied by Scarabino *et al.* (1974), Escofet *et al.* (1979) and Defeo *et al.* (1992). Defeo *et al.* (1992) found that *Orchestoidea brasiliensis* and the cirolanid isopod *Excirolana braziliensis* were typical species of the upper shore. *Ocypode quadrata* has been found in some areas close to southern Brazil (Scarabino *et al.* 1974). *Orchestoidea brasiliensis* and *Excirolana braziliensis* also occurred on the highest levels of the middle shore in which *Excirolana armata* and the polychaete *Euzonus furciferus* were common organisms. *Emerita brasiliensis*, *Mesodesma mactroides* and *Donax hanleyanus* characterized mainly the lower shore; gastropods such as *Olivancillaria vesico auricularia* and *Buccinanops duartei* are also found on some dissipative beaches. Sandy beaches studied in northern Argentina (*ca.* 37°S) (Escofet *et al.* 1979) show a similar pattern of species zonation to that mentioned for Uruguay, but *Ocypode quadrata* has not been found in this area of the Argentinian coast.

Studies carried out along the Chilean coast (Osorio *et al.* 1967; Sanchez, Castilla & Mena 1982; Jaramillo 1978; 1982; 1987; Jaramillo *et al.* 1993; Clarke & Peña 1988) show significant changes in species composition with latitude, primarily on the upper and middle shore. On sandy beaches of south-central Chile (*ca.* 40°S), the upper shore is occupied by tenebrionid beetles (*Phalerisidia maculata*), talitrid amphipods (*Orchestoidea tuberculata*) and cirolanid

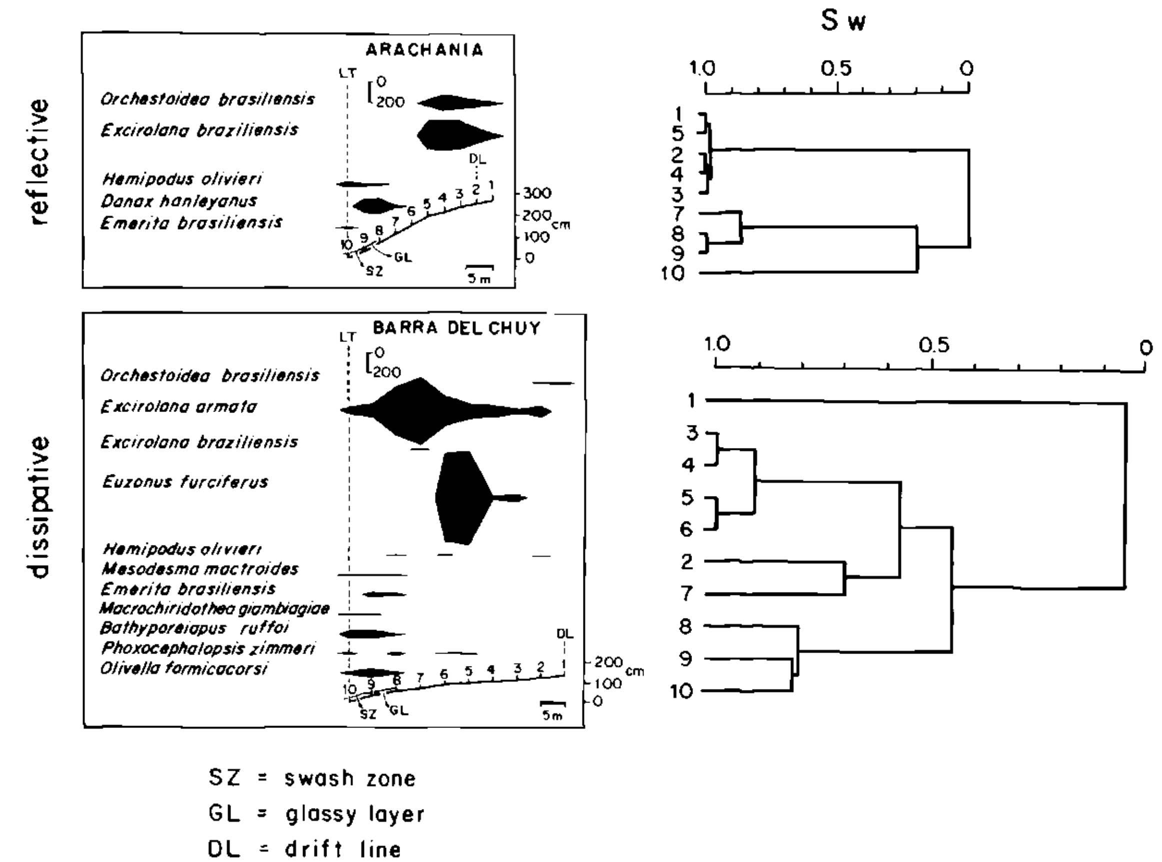

Figure 8 Intertidal distribution of the macroinfauna, and clustering of stations in beaches sampled on the Atlantic coast of Uruguay.

isopods (*Excirolana braziliensis*). Tenebrionid beetles, talitrid amphipods and oniscid isopods (*Tylos spinulosus*) occupy similar shore levels on sandy beaches of north-central Chile (*ca.* 30°S). The same taxa, plus *Excirolana braziliensis* and ocypodid crabs, are found in similar levels on sandy beaches at Antofagasta (about 23°S, Clarke & Peña); further north (*ca.* 20°S), only *Phalerisidia maculata* and ocypodid crabs are found on the upper shore (Jaramillo 1987). *Excirolana braziliensis*, *Excirolana hirsuticauda* (the most abundant species) and *Excirolana monodi* occupy the mid-shore in south-central Chile. The first two isopods also occur on similar shore levels in north-central Chile, while only *Excirolana braziliensis* occupies the mid-shore in northern Chile. The anomurans *Emerita analoga*, *Lepidopa chilensis* and *Blepharipoda spinimana*, the brachyuran crab *Bellia picta*, the amphipods *Bathyporeiapus magellanicus* (Oedicerotidae), *Phoxocephalopsis* sp. (Haustoriidae), idoteid isopods (*Chaetilia paucidens*, *Macrohiridothea* spp.) and the polychaete *Nephtys impressa* typically inhabit the lower shore (swash zone) of beaches located along the Chilean coast. Spionid, opheliid and glyceriid polychaetes have also been mentioned as common inhabitants of the middle and lower shores of some Chilean beaches (Sánchez *et al.* 1982; Clarke & Peña 1988; Jaramillo *et al.* 1993).

Penchaszadeh (1971), Bocanegra, Carbajal, Oliva & Ancieta (1985), Tarazona, Arntz, Canahuire, Ayala & Robles (1985), Tarazona, Paredes & Igreda (1986) and Tarazona & Paredes (1992) studied sandy beaches in Peru (about 8–12°S). The upper shore was characterized by *Ocypode gaudichaudii*, *Excirolana braziliensis* and one species of *Phaleria* (Coleoptera). The middle shore was primarily occupied by *Excirolana braziliensis* and the polychaete *Hemipodus triannulatus*, although *Emerita analoga* and *Nephtys multicirrata* were also found on the lower levels of the middle shore. *Emerita analoga*, *Donax obesulus*, *Mesodesma donacium*, *Nephtys multicirrata* and *Nephtys monilibranchiata*, some spionid polychaetes, the brachyuran *Bellia picta* and the anomurans *Lepidopa chilensis* and *Blepharipoda spinimana* were typical of the lower shore (swash zone).

Based on the intertidal distribution of crustaceans inhabiting some South American beaches, Dahl (1952) proposed a zonation scheme: a subterrestrial fringe occupied by talitrid amphipods in temperate areas and ocypodid crabs at lower latitudes, a mid-littoral, chiefly characterized by cirolanid isopods, and a sublittoral fringe, with amphipods on temperate beaches and hippid crabs in warmer areas. The zonation schemes described earlier for sandy beaches of South America are roughly similar to Dahl's zonation scheme. The coexistence of talitrid amphipods and ocypodid crabs (southern Brazil and Uruguay), the occurrence of talitrids and cirolanid isopods on the upper shore, and the presence of anomuran crabs (Hippidae) on the lower shore of tropical and temperate beaches are the primary differences.

In conclusion, this study shows that crustaceans are the most diverse group on the sandy beaches of South America. Among them, the cirolanid isopods (*Excirolana*) are the most typical organisms, primarily on the middle shore.

Together with them, bivalves (*Mesodesma* and *Donax*) and opheliid and spionid polychaetes are also found. In general, the upper shores of tropical and subtropical beaches are primarily characterized by crabs (Ocypodidae), whereas this zone on temperate beaches is dominated by talitrid amphipods and cirolanid isopods. Hippid crabs, bivalves and amphipods dominate the lower beaches. With the exception of the most reflective beaches, the diversity of the macroinfauna increases from upper to lower beach levels and towards dissipative conditions. Thus, beach type variability must be taken into account when diversity patterns of the intertidal macroinfauna are discussed (e.g. McArdle & McLachlan 1991). Large scale events, such as the periodic occurrences of El Niño might influence species richness patterns along the eastern coast of South America. Tarazona *et al.* (1985), Arntz, Brey, Tarazona & Robles (1987) and Tarazona & Paredes (1992) have shown that El Niño in 1976–1977 and 1982–1983 had significant effects on the species richness of sandy beaches on the coast of Perú. While *Mesodesma donacium* and *Emerita analoga* were the dominant species of the lower shore before El Niño, they disappeared or decreased dramatically in abundance on some beaches thereafter; instead *Donax obesulus* represented most of the biomass during and just after El Niño. Furthermore, the decrease in the abundance of bivalves which occurred during El Niño 1982–1983 allowed for the invasion of macroinfaunal species not present before; for example, spionid polychaetes (*Dispio* and *Scololepis*) became members of the lower shore during that period. Clarke & Peña (1988) mentioned that *Ocypode gaudichaudii* (typically found further north) was seen on the upper shore of a sandy beach of Antofagasta (north of Chile) during and after the El Niño 1982–1983. Clearly, more research is needed to elucidate the role of meso- (variability in beach morphodynamics) and macro-scale (e.g. El Niño) events, as well as the influence of sampling strategies on the faunal diversity patterns recorded for the sandy beaches of South America and elsewhere.

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