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Community and Population Responses of the Macroinfauna to Physical Factors over a Range of Exposed Sandy Beaches in South-central Chile

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Ten exposed sandy sites covering a range from reflective to dissipative beaches were sampled in south-central Chile to evaluate: (1) spatial changes in species richness, abundance and biomass of the intertidal macroinfauna in response to changes in mean grain size, beach face slope and beach type, and (2) spatial changes in abundance, biomass and body sizes of the most abundant species in response to changes in the physical factors. The number of species, abundance and biomass per beach in general decreased with increasing particle size and beach face slope (steeper beaches) and increased from reflective to dissipative conditions. The best fit for number of species was with Dean's parameter, a measure of beach type, whereas for abundance and biomass the best fits were found with particle size. The isopod *Excirolana braziliensis* and the anomuran *Emerita analoga* increased in abundance and biomass towards dissipative conditions, whereas *Excirolana hirsuticauda* showed the opposite trend in biomass and was significantly larger in beaches with steeper profiles. It is concluded that responses to changes in beach type are more pronounced at community level than within species populations.

Introduction

Variability in physical factors has been emphasized as the primary organizational force controlling macroinfaunal communities of exposed sandy beaches (see review by McLachlan, 1983). Thus, differences in community structure and intertidal distribution of the macroinfauna have been related to abiotic factors such as exposure gradients (Eleftheriou & Nicholson, 1975; Dexter, 1983, 1992; Jaramillo, 1987) grain size (Jones, 1970; Fincham, 1974; Dexter, 1979; McLachlan *et al.*, 1981; Jaramillo, 1987, Jaramillo & González, 1991), sediment temperature (Jones, 1970; Vohra, 1971; Jaramillo, 1987), water content (Salvat, 1964; Bally, 1983; Wendt & McLachlan, 1985; Jaramillo, 1987) and penetrability of the sediments (Craig, 1970, 1973: Jaramillo, 1987). However, few studies

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have found significant relationships between macroinfaunal abundances and single physical factors (Jaramillo, 1987).

Use of composite indices as measures of the beach environment has recently provided useful indications of community responses to the physical environment. McLachlan (1990) and McLachlan *et al.* (1981) found significant correlations between macroinfaunal community parameters and grain size, beach face slope and beach type; the latter two representing the result of several interacting factors. In a recent study, McLachlan *et al.* (1992) compared the responses of macroinfaunal communities to beach type through a wide geographical range (the west coast of the U.S.A, Australia, South Africa and south-central Chile) and found that beach type, defined by the dimensionless Dean's parameter, is a good predictor of species richness, abundance and biomass across different geographic regions. These studies examined community responses only.

In this paper we compare community and population responses to the above factors. To do this we examined responses of the macroinfaunal beach communities of south-central Chile to spatial changes in mean grain size, beach face slope and Dean's parameter and contrasted these with the responses in population abundances and body sizes of the most abundant species of the macroinfauna.

Materials and methods

Study area

The 10 beaches studied were located in the south-central area of the Chilean coast (approximately 39–40 °S; Figure 1) and were selected to illustrate different morphodynamic stages. All the sites were fully exposed to the breaking waves of the Pacific Ocean and most sites were near estuarine areas: however, none were located within 500 m of estuaries. Surf salinities along the beaches studied ranged approximately 25–32 , while the range for water temperature is close to 10–16 °C. The tides are semi-diurnal with a maximum range of 1·5 m.

Sampling and analytical procedures

The beaches were sampled once during the spring low tides of March 1991. A transect was extended from above the drift line to below the swash line and 10 equally spaced sampling stations marked, the uppermost above the drift line, the second on the drift line and the last in the swash zone. At each station four 0·03 m^2 replicates (1 m apart) were taken with plastic cylinders to a depth of 30 cm and sieved through a 1 mm mesh. The residue was preserved in 5% formalin; the animals were later sorted from the sediments, identified, counted and weighed (shell-free dry weight after 48 h at 80 °C) for biomass determination. Abundance and biomass values per running metre of beach were obtained by linear interpolation between sampling points after obtaining mean abundances per m^2 at each point by averaging the four replicates. The most representative species were measured to the nearest 0·1 mm length: the talitrid amphipod *Orchestoidea tuberculata*, the cirolanid isopods *Excirolana braziliensis* and *E. hirsuticauda* and the anomuran crab *Emerita analoga*. For the amphipods, body length was the distance from rostrum tip to telson base, while in the isopods body length was the distance from rostrum tip to telson tip. The cephalothorax length of *Emerita analoga* was used as a measure of body size.

Wave height and period were estimated using the horizon and a stopwatch at the time of sampling. However, the final values used for wave height were based on these observed values together with personal experience of the seasonal range of wave heights (E.J.) and

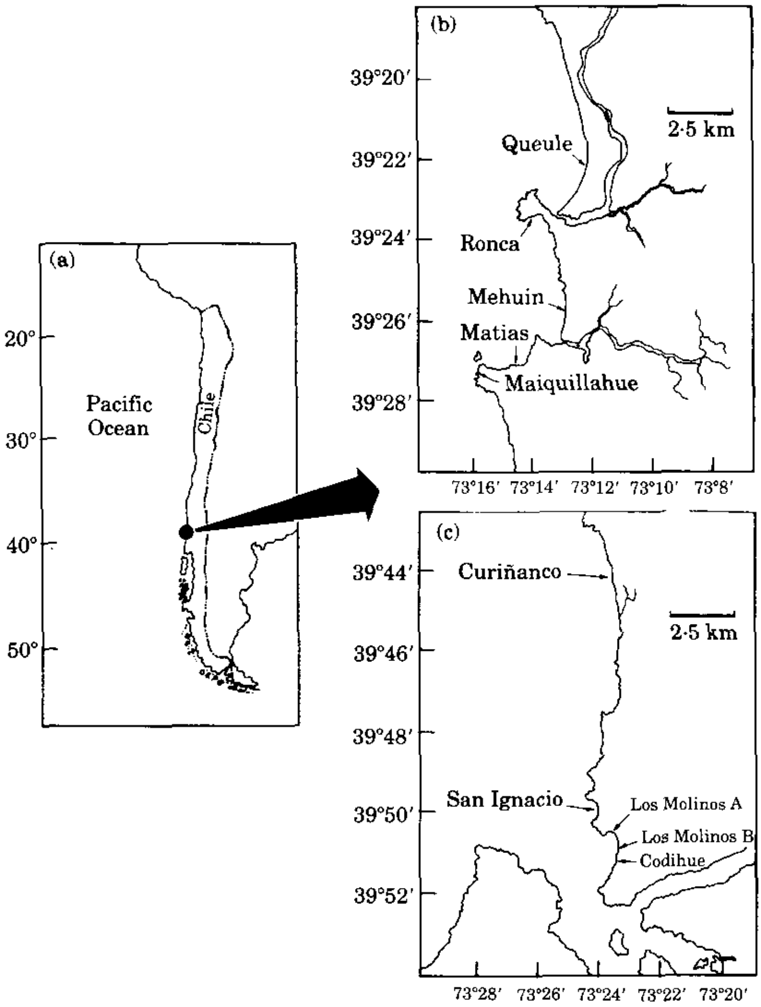

Figure 1. (a) Map of the Chilean coast showing the locations of the beaches studied in (b) and (c).

unpublished data (M. Pino, pers. comm.). From estimated modal significant breaker height, wave period and sand fall velocity, Dean's dimensionless parameter (Ω) (Short & Wright, 1983) was calculated for each beach as a measure of its morphodynamic state: $\Omega = H_a / W_s T$, where H_b is breaker height in cm, W_s the sand velocity in cm s^{-1} (obtained from particle size and Gibbs *et al.*, 1971) and T the wave period in seconds. The morphology (i.e. beach face slope) of each site was determined by Emery's profiling technique (Emery, 1961). Two replicate samples of sediment for grain size analyses were collected at each station by inserting a 3·5 cm diameter metal core to a depth of 10 cm. Grain size was analysed by a settling tube (Emery, 1938) and mean grain size and sorting were calculated according to the moments computational method (Seward-Thompson & Hails, 1973).

Number of species, abundance and biomass of the whole macroinfauna and body sizes of the most representative species were regressed against mean grain size, beach face slope and beach type.

TABLE 1. Physical characteristics of the sandy beaches studied in south-central Chile

Beach	Mz (μm)	H_b (m)	T (s)	Slope	Ω
Maiquillahue	841	0·8	9	8	0·7
Codihue	674	1·0	9	13	1·0
Los Molinos A	304	0·3	8	14	0·9
Los Molinos B	369	1·0	8	14	2·3
San Ignacio	409	1·5	10	19	2·5
Matias	235	1·4	11	15	4·1
Curiñanco	384	2·5	11	30	4·1
Queule	262	1·6	11	41	4·3
Mehuin	306	2·4	11	36	5·4
Ronca	229	2·3	11	36	7·2

Mz, Mean particle size; H_b, modal breaker height; T, mean wave period; Slope, 1/mean gradient of the transect; Ω, Dean's parameter for which increasing values indicate changes from reflective ($\leqslant 1$) to more dissipative conditions (>5).

Results

Table 1 shows that the beaches studied covered a wide range of morphodynamic stages: the most reflective conditions ($\Omega \leqslant 1$) were found at Maiquillahue, Codihue and Los Molinos A, and the most dissipative state ($\Omega > 6$) was found at Ronca. Although Mehuin beach displayed typically dissipative characteristics it scored only 5·4. All the other beaches were intermediate (2·3–4·3). Generally, sand particle size and beach face slope decreased, whereas wave height increased towards dissipative conditions.

Number of species, abundance and biomass versus mean grain size, beach face slope and beach type plots (Figure 2) showed a general decreasing trend with increasing particle size and beach face slope (steeper beaches) and an increasing trend with increasing Dean value. The best fit for number of species was with Dean's parameter, whereas for abundance and biomass the best fits were found with particle size (Figure 2).

A total of 18 species were collected during this study, 14 of which were crustaceans, namely: *O. tuberculata, Bathyporeiapus magellanicus, Phoxocephalopsis mehuinensis, Tryphosella schellenbergi, Huarpe* sp. and *Ampelisca* sp. (Amphiopoda), *Excirolana braziliensis, E. hirsuticauda* and *E. monodi, Macrochiridothea setifer* and *Chaetilia paucidens* (Isopoda), *Emerita analoga, Lepidopa chilensis* and *Bellia picta* (Decapoda). Polychaetes were represented by *Nephtys impressa* and *Euzonus heterocirrus*, and Insecta and Bivalvia by *Phalerisidia maculata* and *Mesodesma donacium* juveniles, respectively. The most abundant species were *O. tuberculata, Excirolana braziliensis, E. hirsuticauda* and *Emerita analoga*, the last one contributing 40–95% of the total biomass.

Orchestoidea tuberculata, Excirolana braziliensis and *Emerita analoga* increased in abundance towards dissipative conditions (finer sands, flatter beach face slopes and higher Dean values); *Excirolana hirsuticauda* showed the opposite pattern (Figure 3). However, the above trends were significant only for the regressions between the abundances of *Excirolana braziliensis* and mean grain size and beach type (Figure 3). Plots relating biomass of these species to physical parameters (Figure 4) showed similar trends to the abundance data. Again, only a few of the regressions were significant, namely: biomass of *E. braziliensis* against mean grain size and beach type, biomass of *E. hirsuticauda* against beach face slope and biomass of *Emerita analoga* against beach type (Figure 4). Generally, the best fits (i.e. highest r^2) were between these biological parameters and beach type.

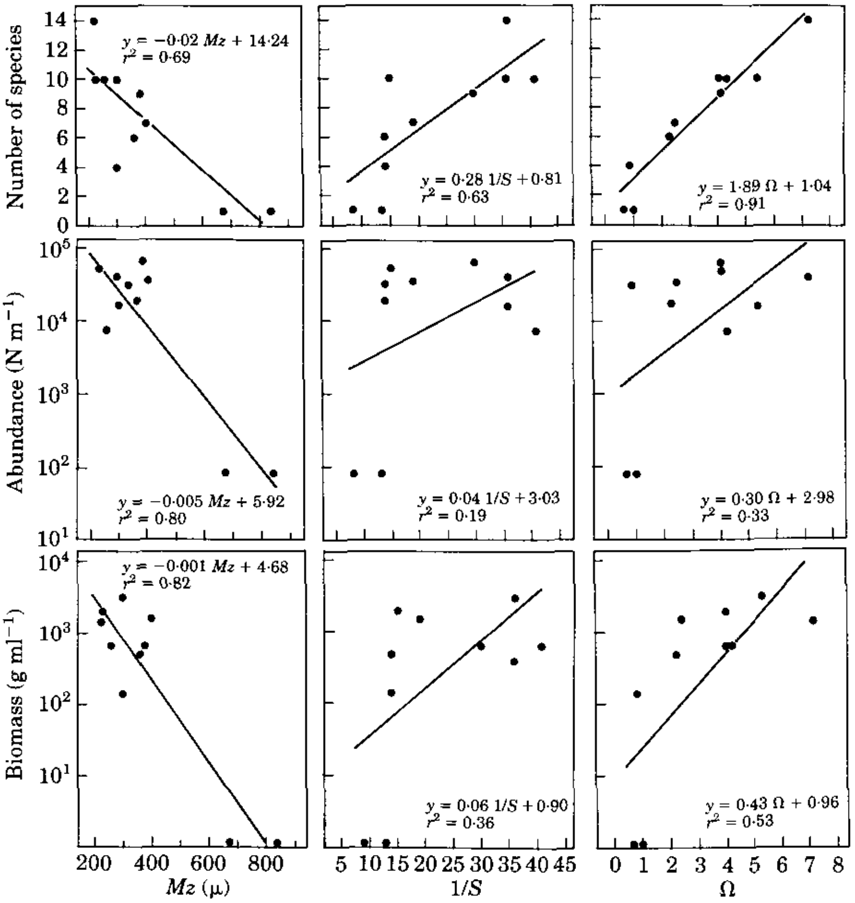

Figure 2. Number of species, abundance and biomass versus mean grain size (*Mz*), beach face slope ($1/S$) and Dean's parameter (Ω). The critical r value at $P = 0{\cdot}5$ (d.f. $= 8$) is $0{\cdot}63$ ($r^2 = 0.40$).

Figure 5 shows the relationships between the body sizes of these species and mean grain size, beach face slope and beach type. *Orchestoidea tuberculata* tended to be larger in size with an increase in grain size and beach face slope (beaches with characteristics close to reflective conditions); however, these trends were not significant. *Excirolana braziliensis* and *Emerita analoga* showed few trends, while *Excirolana hirsuticauda* was significantly larger in beaches with steeper profiles (Figure 5).

Discussion

Our results indicate that community parameters describing the richness of macroinfauna inhabiting exposed sandy beaches of south-central Chile increased towards dissipative conditions, as observed for sandy beaches in the U.S.A, Australia and South Africa (McLachlan *et al.*, 1992). Beaches with the most reflective conditions harboured the lowest species richness values and abundances. Previous studies have also reported low

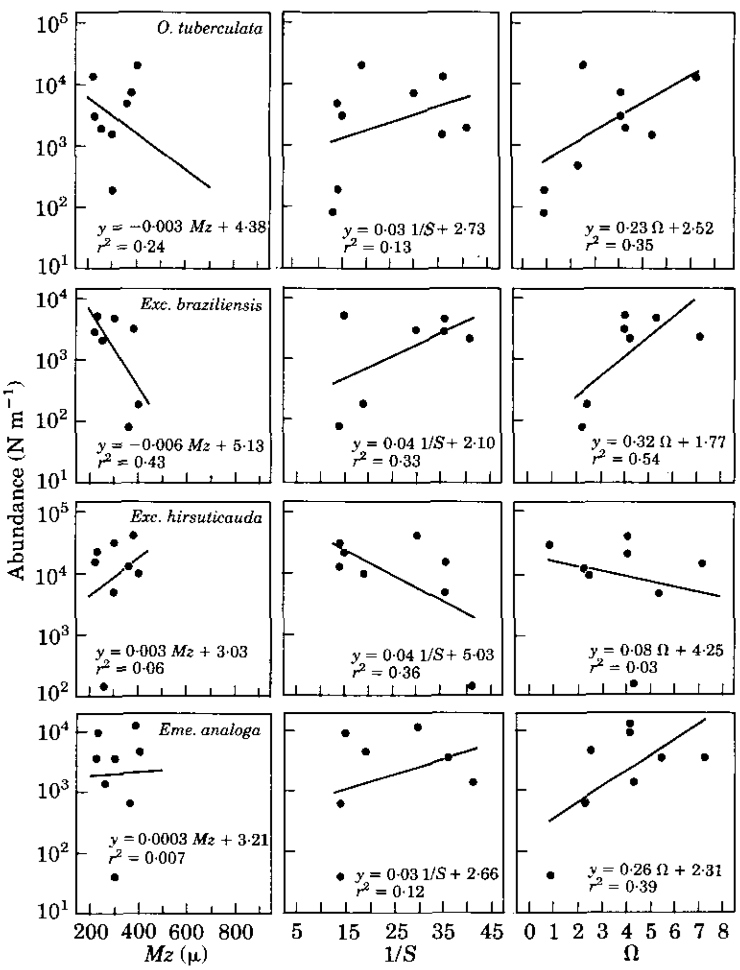

Figure 3. Abundances of *Orchestoidea tuberculata, Excirolana braziliensis, Excirolana hirsuticauda* and *Emerita analoga* versus mean grain size (Mz), beach face slope ($1/S$) and Dean's parameter (Ω). The critical r value at $P = 0{\cdot}05$ (d.f. = 8) is 0·63 ($r^2 = 0{\cdot}40$).

values for these community parameters in sandy beaches with reflective characteristics (Gauld & Buchanan, 1956; Dexter, 1983; McLachlan, 1985; Jaramillo & González, 1991).

While beach type, as defined by Dean's parameter, was the best predictor for species richness, mean grain size was the best predictor for the spatial variability of abundance and biomass of the macroinfauna communities. In contrast, McLachlan (1990) found that beach type was a better predictor for macroinfaunal abundances than grain size. These differences between McLachlan's (1990) findings and ours might be a consequence of the limited geographical area studied here. Wave action, which, together with particle size, defines beach type, displays less variation than grain size in this restricted area and might thus result in increased importance of grain size variability in this case. Both grain size and wave action differed widely over the areas studied by McLachlan (1990), resulting in a more sensitive response by Dean's parameter than either particle size or wave action individually.

Some of the most representative species also showed trends of increasing abundance (*Excirolana braziliensis*) and biomass (*Excirolana braziliensis* and *Emerita analoga*)

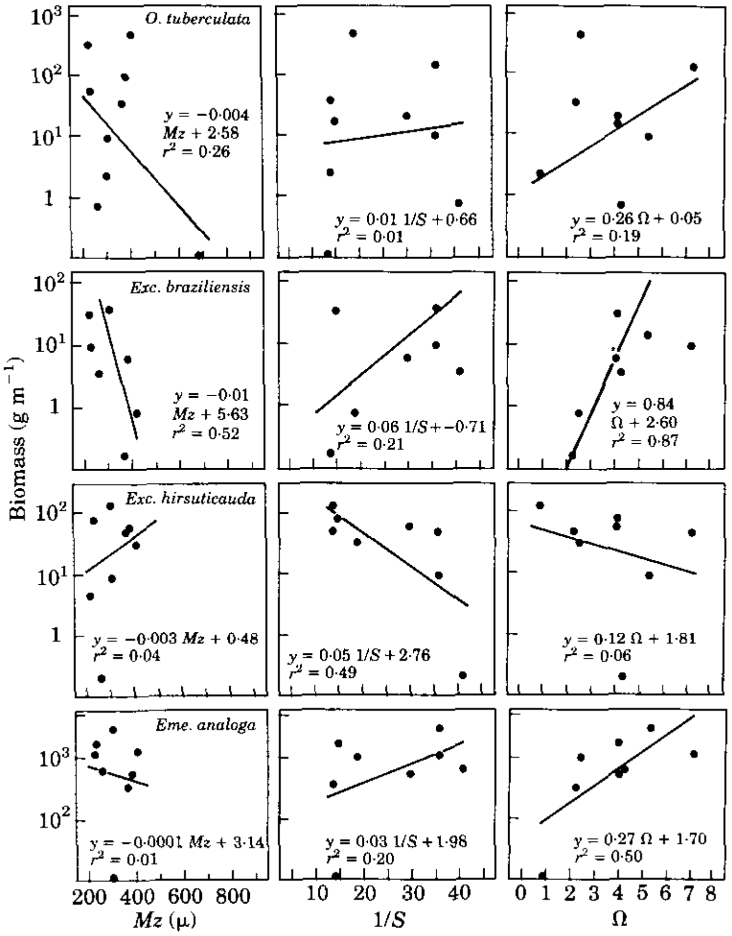

Figure 4. Biomass of *Orchestoidea tuberculata*, *Excirolana braziliensis*, *Excirolana hirsuticauda* and *Emerita analoga* versus mean grain size (Mz), beach face slope ($1/S$) and Dean's parameter (Ω). The critical r value at $P = 0{\cdot}05$ (d.f. = 8) is 0·63 ($r^2 = 0.40$).

towards dissipative conditions, each type being the best predictor for the spatial variability in these parameters. One species (*Excirolana hirsuticauda*) showed the opposite trend in biomass. Thus, the regression analyses indicated poorer fits than observed at the community level, implying that at the finer level of individual species there is greater variability in responses to these physical changes. But it is also possible that a larger data set including seasonal variability in beach and population abundance and biomass of these species may render stronger relationships.

The isopod *E. hirsuticauda* tended to be larger in size in beaches with steeper profiles (more reflective conditions). McLachlan *et al.* (1992) suggested that, whereas crustaceans decrease in size, bivalves increase in size from reflective to dissipative conditions over a range of beaches studied in the U.S.A, Australia and South Africa. These trends imply an adaptation to the harsher physical conditions found on reflective beaches where the wave energy does not dissipate before reaching the beach face. It has been widely shown for sandy beach bivalves that differences in body size confer differences in burrowing rates

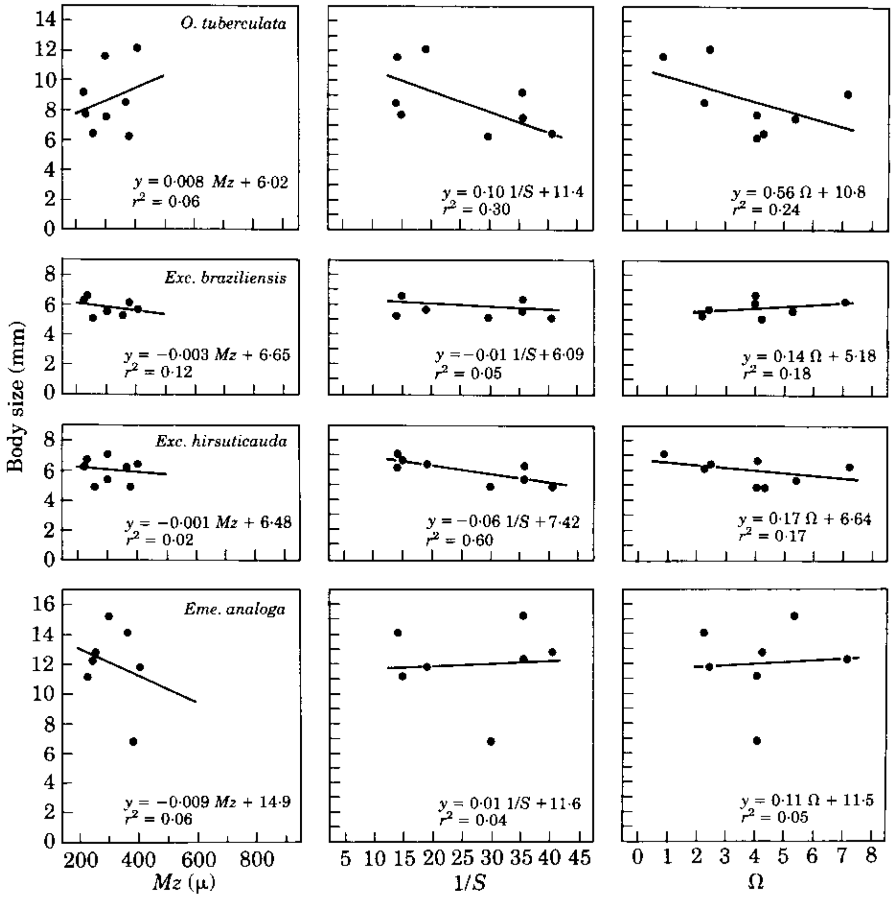

Figure 5. Body sizes of *Orchestoidea tuberculata, Excirolana braziliensis, Excirolana hirsuticauda* and *Emerita analoga* versus mean grain size (Mz), beach face slope ($1/S$) and Dean's parameter (Ω). The critical r value at $P = 0{\cdot}05$ (d.f. $= 8$) is $0{\cdot}63$ ($r^2 = 0{\cdot}40$).

and abilities to remain in the swash: Stanley (1970), Ansell (1983), McLachlan and Young (1982) and Donn and Els (1990) found that within species, burrowing rate shows a linear relationship with shell length, with the largest animals excavating the slowest. These findings may explain the trend of decreasing body size of bivalves towards reflective conditions as suggested by McLachlan *et al.* (1992); that is, the harsher swash climate of beaches with the most reflective conditions would exclude large-sized bivalves, due to the fact that they cannot respond fast enough either to excavate or feed in short-period swash (McLachlan, 1990). Moreover, Trueman *et al.* (1966) and Stanley (1970) have shown that bivalves with broad, heavy shells burrow less easily than those with thin shells.

Thus, it is not only body size (e.g. body length) that should be taken into account, but also morphometric relationships describing body shapes. In this way, it should be possible to determine which body volumes or shapes are better adapted to particular swash climates. Such analyses need to be linked with experimental studies in which different body sizes, masses and shapes are subjected to different swash climate conditions. This could indicate whether some particular body form is better suited to move, swim or burrow under the variety of swash conditions which characterize the different beach types (McArdle & McLachlan, 1992).

In conclusion, this study has shown that changes in beach type along the coast of south-central Chile result in predictable community responses of the intertidal macroinfauna. These responses must represent the summed responses of the individual community constituents, since species populations showed less clear trends than communities.

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