

Sandy Beach Macrofauna Communities and their Control by the Physical Environment: A Geographical Comparison

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ABSTRACT

McLACHLAN, A., JARAMILLO, E., DONN, T. E., and WESSELS, F., 1993. Sandy beach macrofauna communities and their control by the physical environment. A geographical comparison. *Journal of Coastal Research*, Special Issue No. 15, 27-38, Fort Lauderdale (Florida), ISSN 0749-0208.

This paper examines changes in species richness, abundance, and biomass of the intertidal benthic macrofauna of wave exposed sandy beaches in response to changes in beach type from reflective to dissipative extremes. Trends in six different geographical areas are compared, making use of both published data and recent field data from the south central coast of Chile. A new index, based on the log of the dimensionless fall velocity, which incorporates measures of wave energy, sand fall velocity, and tidal range, provides a better estimate of beach type than the dimensionless fall velocity alone. Species richness is found to be controlled primarily by the physical environment, increasing predictably from reflective to dissipative beaches. This control appears to be a conservative feature of sandy beaches, differing little between different geographic provinces. Abundance and biomass follow similar patterns but are more variable and appear related also to surf zone productivity and wrack inputs, which in turn are influenced by wave energy. Although sand particle size and wave climate are both important, we argue that direct control on beach populations is via the swash climate, which changes significantly between different beach types. Morphology, body size, means of locomotion, and taxonomic composition of the fauna may demonstrate evolutionary consequences of adaptation to different swash climates.

ADDITIONAL INDEX WORDS: Sandy beach, macrofauna, species richness, abundance, biomass, swash.



INTRODUCTION

Exposed sandy beaches are amongst the harshest aquatic ecosystems on earth. Dynamic and apparently featureless, these environments consist only of water and sand and can be fully defined in terms of wave climate, sand particle size, and tide range. It is therefore not surprising that beaches have been likened to 'marine deserts' (McLACHLAN, 1983). As in the case of deserts, where animals are adapted primarily to coping with the physical extremes and biological interactions are of little importance (NOY-MEIR, 1979), the distribution and abundance of the fauna of sandy beaches might be expected to be controlled primarily by physical conditions.

Despite this seemingly obvious assumption, sandy beach researchers have had little success in identifying physical features controlling the

fauna or in demonstrating statistically significant relationships between beach fauna and the physical environment. Parameters relating to the sand, such as particle size, moisture content, and penetrability, have been singled out in most cases, but without any general trends emerging, except perhaps a tendency for the fauna to be richer in finer sands (SALVAT, 1964; HAYES, 1977; DEXTER, 1979, 1983; JARAMILLO, 1987). Indeed, it has been admitted that sand or waves alone are insufficient to characterize a beach (ELEFTHERIOU and NICHOLSON, 1975; BALLY, 1983). Macrobenthic diversity and abundance have, however, been negatively correlated with beach slope (McLACHLAN *et al.*, 1981), the latter being a product of sand particle size and wave energy interactions (DAVIES, 1972).

The recognition and description of a successional series of beach morphodynamic states, from reflective to dissipative, by Short and col-

leagues (SHORT and WRIGHT, 1983), has provided a major advance in the appreciation by biologists of sandy beach morphodynamics, the interactions between wave climates and sand storage, and the 'climatic features' of beaches relevant to the fauna. A good relationship has, for example, been found between overall beach state and faunal diversity and abundance (MCLACHLAN, 1990). Such patterns are especially relevant in this age of extinction, which has triggered widespread interest in biodiversity, its determinants and prediction (SOULE, 1986). Building on these ideas and models, this article explores patterns in beach faunal community parameters across different geographic regions and beach states.

METHODS

We make use of three sets of data:

- (1) published information in the form of pooled data from beach macrofauna surveys in warm temperate Western Australia, subtropical and warm temperate South Africa, and the temperate Oregonian Province in the USA (MCLACHLAN, 1990) provides the reference against which two other data sets are compared;
- (2) similar but separate surveys in subtropical, warm temperate, and temperate provinces in southern Africa (DONN, in preparation), these African beaches being selected to represent a wide range of habitat types, shoreline lengths, grain sizes, wrack and phytoplankton inputs; and
- (3) recent surveys of beaches in the transition region between warm and cold temperate provinces (BRATTSTROM and JOHANSEN, 1983) in southern Chile. The information provided here will be published elsewhere in full (JARAMILLO and MCLACHLAN, in preparation). It includes quantitative surveys of the macrobenthic communities of ten Chilean beaches ranging from fully reflective to dissipative conditions.

The study area for the Chilean data was the coast near Valdivia, where varying topography and aspect provide a wide range of beach types

and surf zone energy levels. Beaches in this area are mostly small pocket types, < 1 km in length and often associated with streams or estuaries. Ten sites were selected for study (Figure 1). No sites were located within 500 m of river mouths and we are confident that the lowest salinity experienced by any of these beaches during winter conditions of high runoff would not be below 25‰. Sea temperatures in this region range from 10–16°C and tides are semidiurnal subequal with a maximum range of 1.5 m.

Each beach was surveyed during spring low tide. A transect was marked out from above the drift line to below the swash line and ten equally spaced sampling levels identified, the uppermost above the drift line, the second on the drift line, and the last in the swash zone. The profile was surveyed with graduated poles, leveling against the horizon, to obtain the slope. At each level, four replicate cores of 0.03 m² were taken to 30 cm depth and sieved through 1 mm mesh. All macrofauna were retained, identified, counted, and shell-free biomass determined by drying at 80°C for 48 hrs. At each level, a sand sample was taken for particle size analysis by volume using a settling tube (EMERY, 1938).

Wave height and period were estimated using the horizon and a stopwatch at the time of sampling. For further analysis, however, the values used for wave height were based on both these observed values and 20 years experience of this coast and its seasonal range of wave heights (E.J.) and unpublished data of M. Pino (*personal communication*). From estimated modal significant breaker height, wave period, and sand fall velocity, the dimensionless fall velocity (GOURLAY, 1968; SHORT and WRIGHT, 1983) was calculated for each beach as a measure of its modal morphodynamic state:

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

where H_b is breaker height in cm, W_s the sand fall velocity in cm s⁻¹ (GIBBS *et al.*, 1971) and T the wave period in seconds.

The biological parameters of interest in this article are the species richness, total abundance per running meter, and total dry biomass per running meter of each beach. Abundance and biomass values per running meter of beach were obtained by linear interpolation between sampling points.

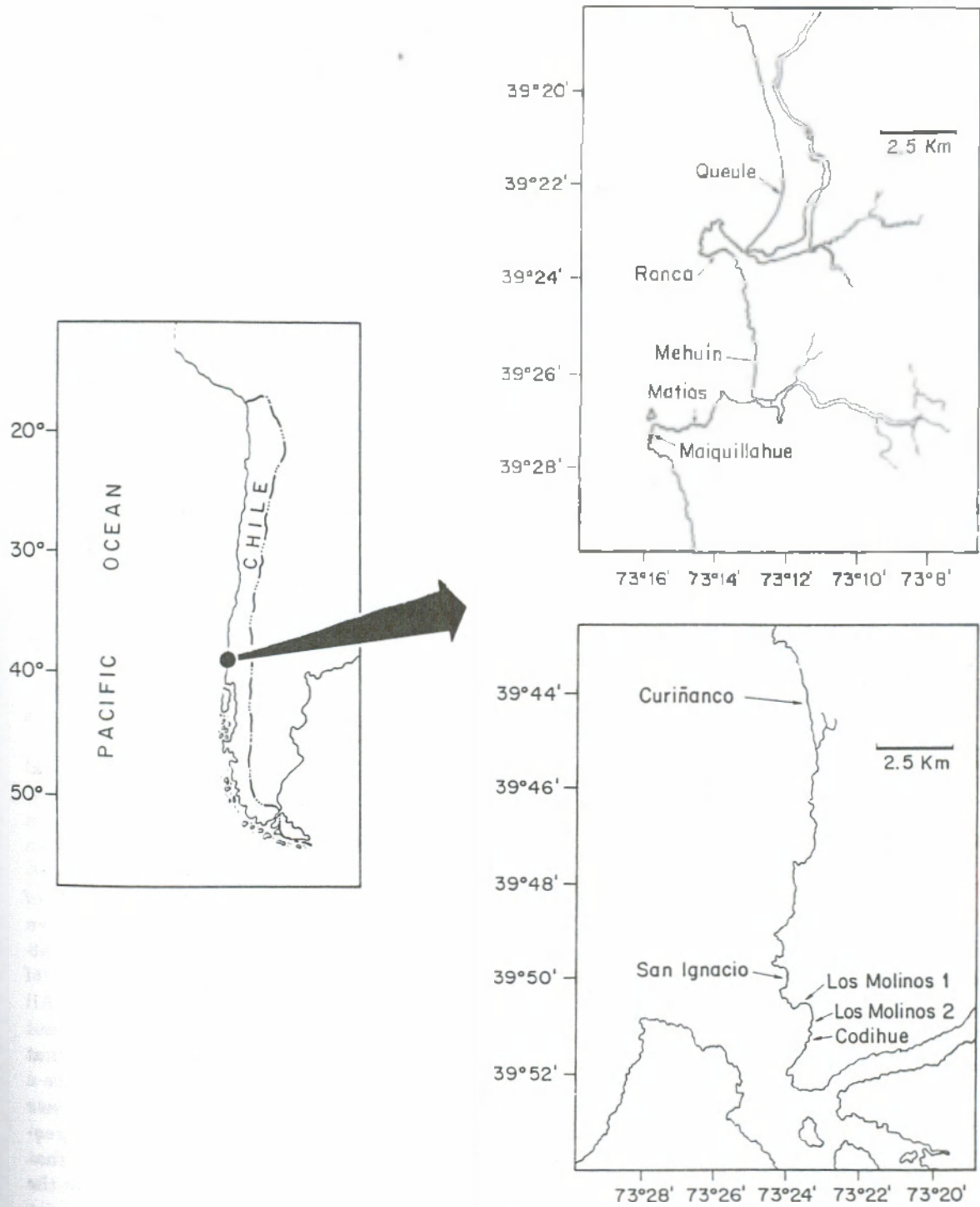


Figure 1. The Chilean coast near Valdivia showing the ten locations sampled.

Relationships between dependent variables (no, spp., abundance, biomass) (y) and the independent variable (Ω) (χ) were compared over all five data sets (z_i) using a dummy variable approach (KLEINBAUM and KUIPER, 1978). For each dependent variable a model of the form:

$$y_i = B_0 + B_1\chi_i + B_2z_{1i} + B_3z_{2i} + B_4z_{3i} + B_5z_{4i} \\ + B_6\chi_iz_{1i} + B_7\chi_iz_{2i} + B_8\chi_iz_{3i} + B_9\chi_iz_{4i}$$

where i represents the i^{th} data point of data set j , and the z_i are dummy variables defining the data sets. Using this approach the lines could be tested for parallelism and coincidence. Individual regression coefficients B were tested for significance using the approach of conditional errors; i.e., each coefficient was tested assuming that all other coefficients were already included in the model. The test for parallelism of the regression lines is:

$$H_0: B_6 = B_7 = B_8 = B_9$$

If regression lines are parallel, then a test for coincidence may be made using the full hypothesis:

$$H_0: B_2 = B_3 = B_4 = B_5$$

For comparison of slopes and elevations between individual regions a standard t-test was used.

RESULTS

Selected features of ten Chilean beaches (Table 1) indicate that the beaches covered a range from fully reflective to dissipative conditions and that generally sand particle size decreased, wave height increased, and species richness, abundance, and biomass tended to increase toward dissipative states. This agrees with the findings of JARAMILLO (1978, 1982) and JARAMILLO and GONZALEZ (1991) who surveyed the upper and mid intertidal levels of three of these beaches. These data will be discussed further together with the other available information.

A previous analysis of faunal changes in response to changes in beach morphodynamic states (McLACHLAN, 1990) indicated three major trends across a gradient from reflective to dissipative beaches: (1) an increase in intertid-

al macrobenthic species richness; i.e., increasing number of species with decreasing slope, particle size, or increasing the dimensionless fall velocity, with the latter giving the best fit, (2) a logarithmic increase in total abundance, in general, a $> 10^6$ increase for a $< 10^1$ increase in beach width (area), and (3) a logarithmic increase in total biomass. Although this analysis was based on pooled data from three continents, it included only 23 beaches (and among these beaches tide range increased from reflective to dissipative states), and thus raises the question as to whether the change in diversity with change in beach type is a conservative feature, i.e., does it occur in all cases? Further, is the rate of change constant or does it vary for different geographic areas? We examine these trends on a regional scale with respect to the Chilean data (for which all beaches experience the same tide range) and compare this to other available information.

Diversity/beach type plots (Figure 2) for the 'intercontinental' data of McLACHLAN (1990) as well as for data from the temperate transition zone of Chile and from three provinces in southern Africa, subtropical, warm temperate, and temperate, reveal similar responses in all cases. Multiple regression analysis showed general differences in slopes ($p < 0.001$), intercepts ($p < 0.001$), and coincidence ($p < 0.001$). However, further comparison between individual regions by t-test showed no significant differences between the regression lines for data from McLACHLAN (1990), Chile, and the South African east coast ($p = 0.41-0.70$), but significant differences in slopes and intercepts of lines for the south and west coasts of southern Africa ($p < 0.001$). The latter two produced flatter curves, but did not include the full range of beach types, reflective forms being absent. All data combined (Figure 2f) yield a significant common regression line, which suggests that changes in diversity with beach type may be a conservative feature and that this response does not differ widely in different zoogeographic regions. The implication of this is that morphodynamic state is a good predictor of the species richness likely to be encountered on a beach.

Total faunal abundance/beach type relationships (Figure 3) indicate an increase in abundance toward dissipative states in all cases, but display significant differences between the

Table 1. Summary of key environmental and macrofauna features of 10 Chilean beaches. Under type R = reflective, I = intermediate and D = dissipative. Ω = the dimensionless fall velocity for which <1 = reflective, >6 = dissipative and 2-6 = intermediate. Mz = mean particle size (μm), Hb = modal breaker height (m), T = mean wave period(s), slope = $1/\text{mean gradient from above the drift line to the low tide swash region}$. SR = species richness. Abundance (total numbers) and biomass (g) values per running meter of beach.

Beach	Type	Ω	Mz	Hb	T	Slope	SR	A	B
Maiquillahue	R	0.7	841	0.8	9	8	1	80	<1
LosMolinos1	R	0.9	304	0.3	8	14	4	31758	139
Codihue	R	1.0	674	1.0	9	13	1	80	<1
LosMolinos2	I	2.3	369	1.0	8	14	6	18925	491
San Ignacio	I	2.5	409	1.5	10	19	7	35811	1546
Matias	I	4.1	235	1.4	11	15	10	53706	1947
Curinanco	I	4.1	384	2.5	11	30	9	66783	643
Queule	I	4.3	262	1.6	11	41	10	7420	657
Mehuín	D	5.4	306	2.4	11	36	10	16742	3087
Rocas	D	7.2	229	2.3	11	36	14	41654	1409

regions. Multiple regression analysis and t -tests showed differences to be significant for slopes, intercepts, and coincidence between all the lines in Figure 3 ($p < 0.001-0.04$). Abundance is generally higher at lower intermediate and reflective beach states in Chile and southern Africa than in the data set from McLACHLAN (1990). Since Chile and the southern African west coast are rich upwelling regions with high productivity, elevated abundance levels are expected in these two areas. Pooling all data (Figure 3f) also results in a common regression line with a flatter response than found by McLACHLAN (1990). However, the fit of this common regression line for abundance/beach type relationships ($r^2 = 0.25$) is poorer than for species richness/beach type ($r^2 = 0.52$), indicating that factors other than beach state, for example productivity and availability of stranded kelp, also play a role. Thus, southern African east coast subtropical beaches, which have the lowest productivity (BATE *et al.*, 1990), display the lowest intercept.

Biomass/beach type relationships (Figure 4) show general differences in slopes ($p < 0.01$), and coincidence ($p < 0.01$) but not intercepts ($p > 0.10$). However, there are not differences in slopes or intercepts between individual regions ($p = 0.20-0.55$), except for the south coast of southern Africa where the slope ($p = 0.001$) and elevation ($p = 0.02$) of the line differed from the others. Less significant differences in the case of the biomass data than for the abundance data reflect higher variability in the biomass data. Nevertheless, subtropical beaches supported lowest values and cold temperate beaches the highest values. Pooled data (Figure 4f) give a

common regression with poorer fit ($r^2 = 0.18$) than in the case of species richness or abundance, indicating greater variability in these data due to the influence of factors other than beach type, *i.e.*, increased importance of factors such as surf zone productivity and kelp inputs.

The above regression analyses confirm that species richness, total abundance, and total biomass all increase from reflective to dissipative beaches in the six biogeographic provinces surveyed. Whereas the regression lines describing this relationship are fairly similar for all regions in the case of species richness, they differ significantly between regions in the case of total abundance. Despite more variable data sets, they also differ in the case of total biomass. These differences between regions may, however, be exaggerated because our measure of beach type (Ω) does not include tide range; but there are large differences in tide range between the six geographic areas which have been compared.

The use of the dimensionless fall velocity as a measure of beach state is thus not completely satisfactory since it does not take into account tides. Increasing tide range tends to make beaches more dissipative (WRIGHT *et al.*, 1982) although this is not a simple response, and tidal effects may be more complex under conditions other than sandy micro/mesotidal beaches. The effects of tidal range could be overcome by multiplying Ω by a dimensionless factor derived from the maximum tide range of a beach divided by the maximum tide range of a theoretical equilibrium tide. Furthermore, since Ω tends to respond logarithmically toward the dissipative extreme, a more normal distribution might be obtained by taking the log of Ω .

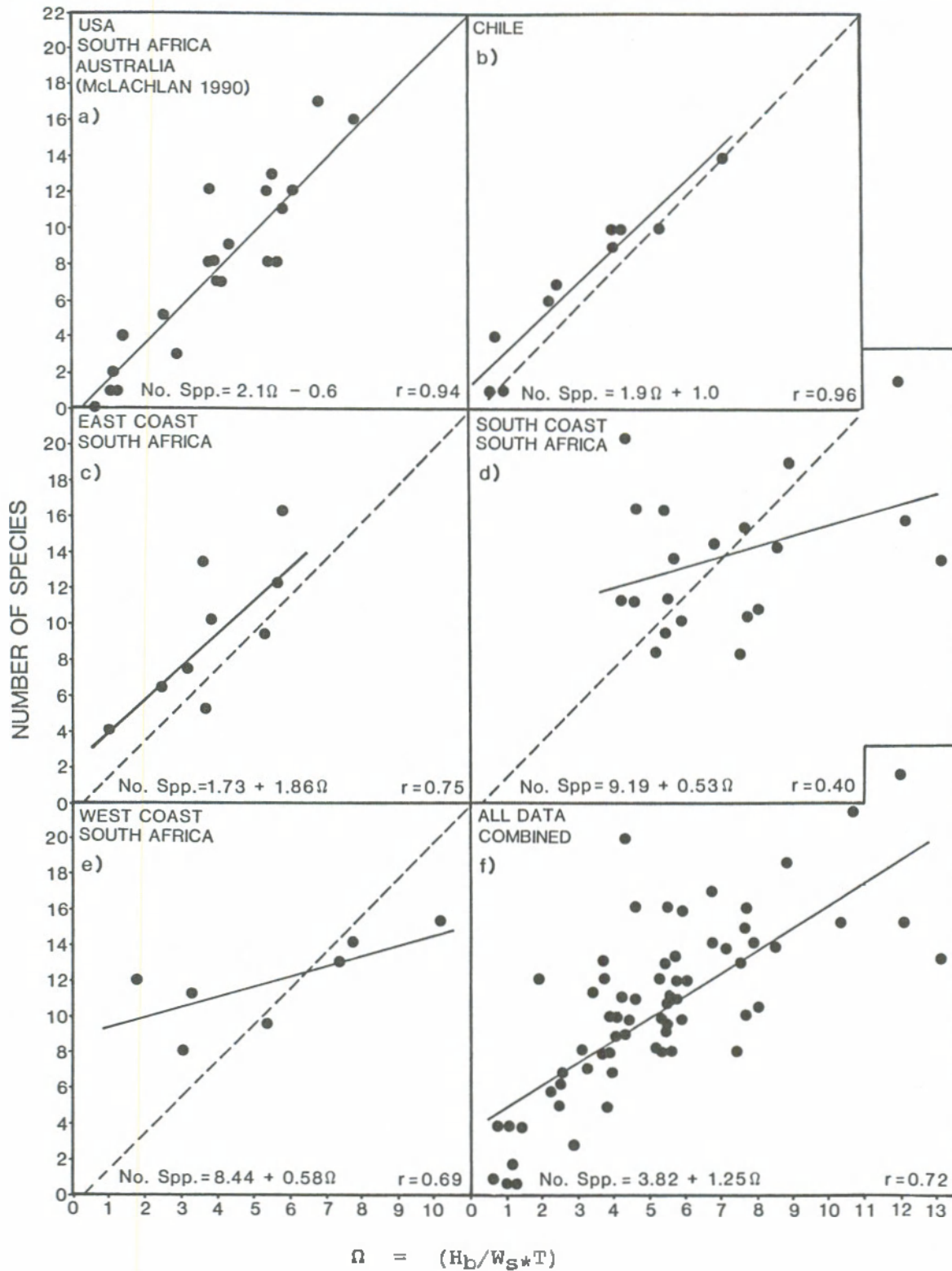


Figure 2. Species richness versus beach type for beaches in (a) Australia, southern Africa, and the USA, (b) southern Chile, (c) subtropical southern Africa, (d) warm temperate southern Africa, (e) temperate southern Africa, and (f) all areas combined. Broken lines in (b) - (f) indicate line (a).

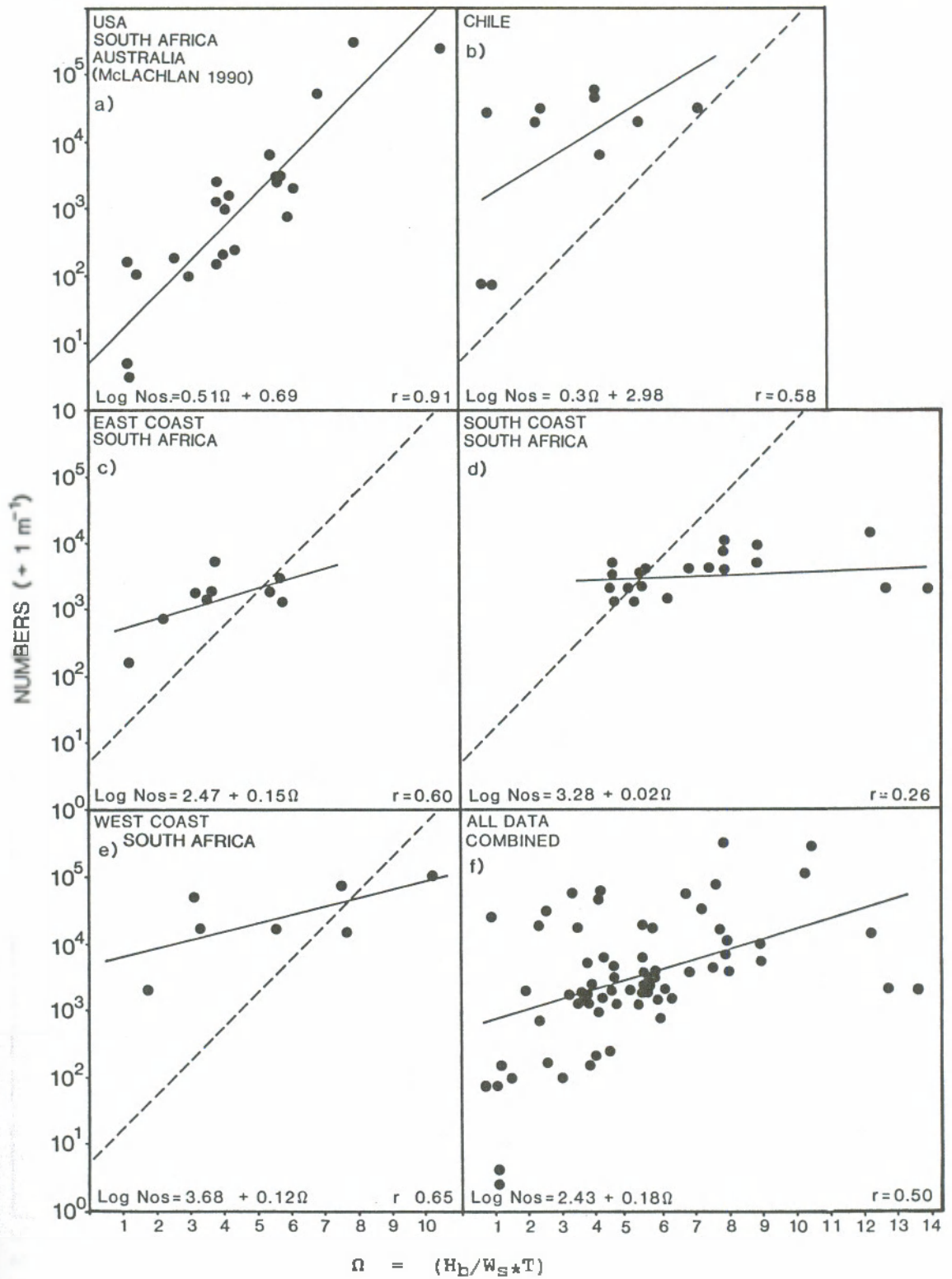


Figure 3. Relationships between total faunal abundance and beach type. Details as for Figure 2.

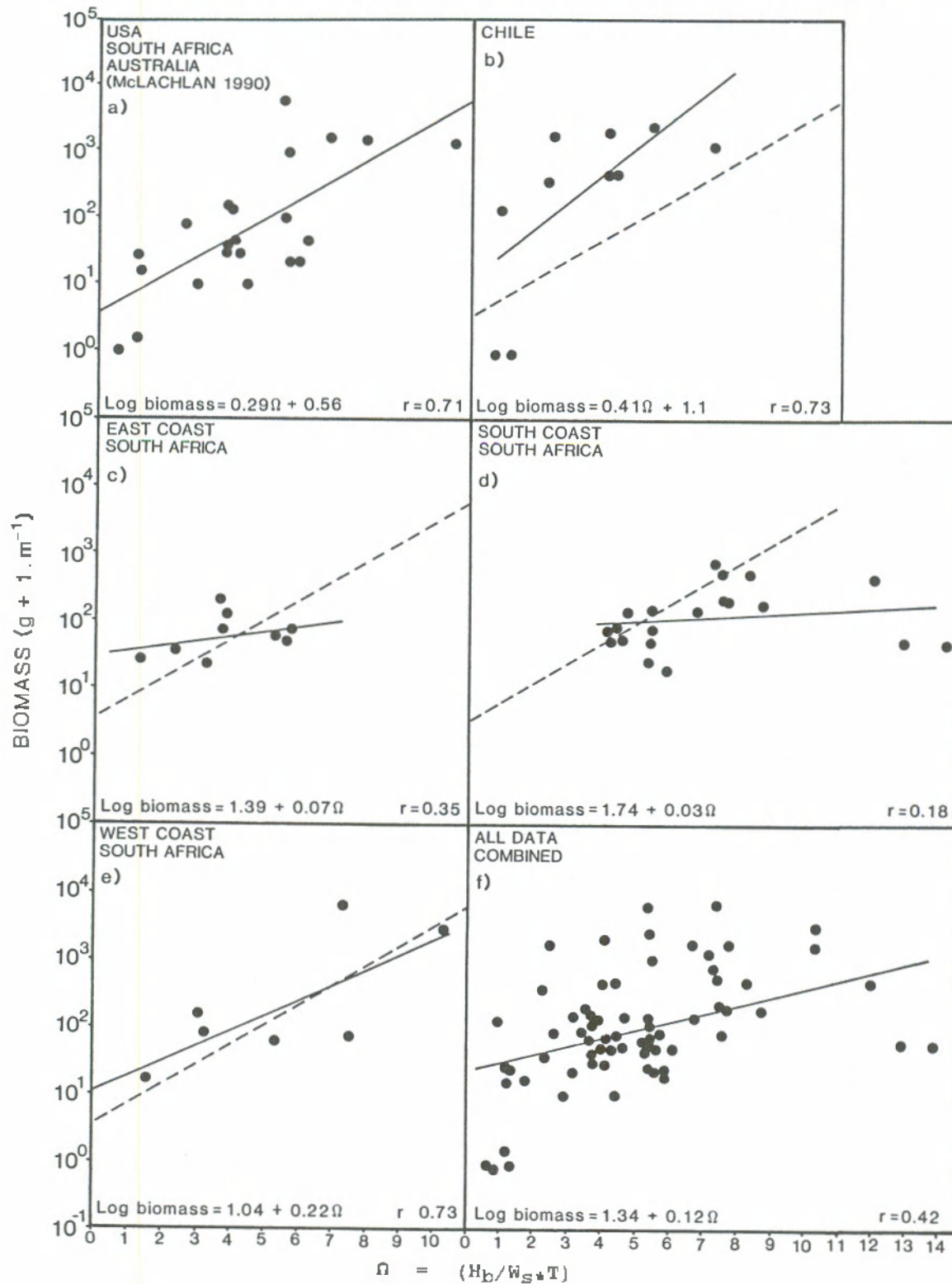


Figure 4. Relationships between total faunal biomass and beach type. Details as for Figure 2.

To overcome the above problems with the dimensionless fall velocity, and allow more appropriate comparison of data from different geographic areas experiencing different tide ranges, we have used a modification of the dimensionless fall velocity which we call the beach state index (BSI):

$$\text{BSI} = \log (H_w M / W_s T E) + 1).$$

where M is the maximum tide range and E the maximum theoretical equilibrium tide (for the earth covered in water = 0.8 m). This index includes measures of wave energy, sand fall velocity, and tide range. Data on sand properties and tide range are readily available to ecologists and only the wave climate information might pose problems for other workers wishing to compare their data with ours. In most cases, however, reasonable estimates of wave height and period can be obtained using a ranging pole against the horizon and a stopwatch. Examination of our data and the general features of the 69 beaches covered suggests a breakdown according to this index as follows:

- < 0.5 = reflective beaches
- 0.5–1.0 = low to medium energy intermediate beaches
- 1.0–1.5 = high energy intermediate/dissipative beaches
- 1.5–2.0 = fully dissipative beaches
- > 2.0 = ultra dissipative macrotidal beaches

If the data on species richness, abundance, and biomass (Figures 2–4) are recalculated using the BSI index, differences due to differing tide range are reduced and the zoogeographic provinces appear more similar; for the species richness data there are no differences in slopes ($p > 0.10$), elevations ($p > 0.10$), or coincidence ($p > 0.25$) of the lines in general and differences between individual regions decrease ($p = 0.03$ – 0.80); for the abundance data the lines still differ in all three respects ($p < 0.001$) but p values for comparisons between individual regions increase to 0.001 – 0.02 ; and for biomass data the lines are parallel ($p > 0.10$) and with equal elevations ($p > 0.25$) but are not coincident ($p < 0.001$) and p values for individual regions increase to 0.14 – 0.73 , respectively. Use of the BSI index thus indicates a more similar

response of species richness, abundance, and diversity to changes in beach type by communities from the different regions.

The effect of replottting the common curves for species richness and abundance using the modified index of beach state is illustrated in Figure 5. This shows an improved fit in both cases: r^2 increases from 0.52 to 0.67 for species richness and from 0.25 to 0.94 for abundance, respectively. For biomass the equation is:

$$\log(b + 1)m^{-1} = 0.6 + 1.3\text{BSI} \dots r = 0.48$$

also increasing the coefficient of determination from 18% to 23%.

We conclude from the above analyses using the BSI that dissipative beaches generally support richer faunas than reflective beaches and that species richness, abundance, and biomass respond to changes in beach type in a remarkably consistent manner, although abundance and biomass may be more variable than species richness. This implies that primary physical control is of overriding importance for beach communities and that zoogeographic considerations are secondary. It would, however, be ideal to have more data from other areas, particularly in the tropics, in order to test these trends over the widest possible range of conditions. Unfortunately, we are unable to make use of most published beach survey data since no authors have provided sufficient information for us to characterize their beaches or calculate the dimensionless fall velocity.

DISCUSSION

How does beach morphodynamic state control macrobenthic communities and can key factors be identified? We believe that neither sand nor wave energy are of direct (proximate) importance as controlling factors, other than for extreme instances such as the presence of very coarse sand. Most sandy beach animals can operate over a wider range of particle sizes than they encounter in nature and substrate selection studies have confirmed rather catholic tastes in grain size (BROWN, 1983; JARAMILLO, 1987). Furthermore, from Table 1 and figures 2–4 can be seen that large changes in fauna occur across beaches with essentially similar grain sizes but differing wave energy, *i.e.*, different morphodynamic states.

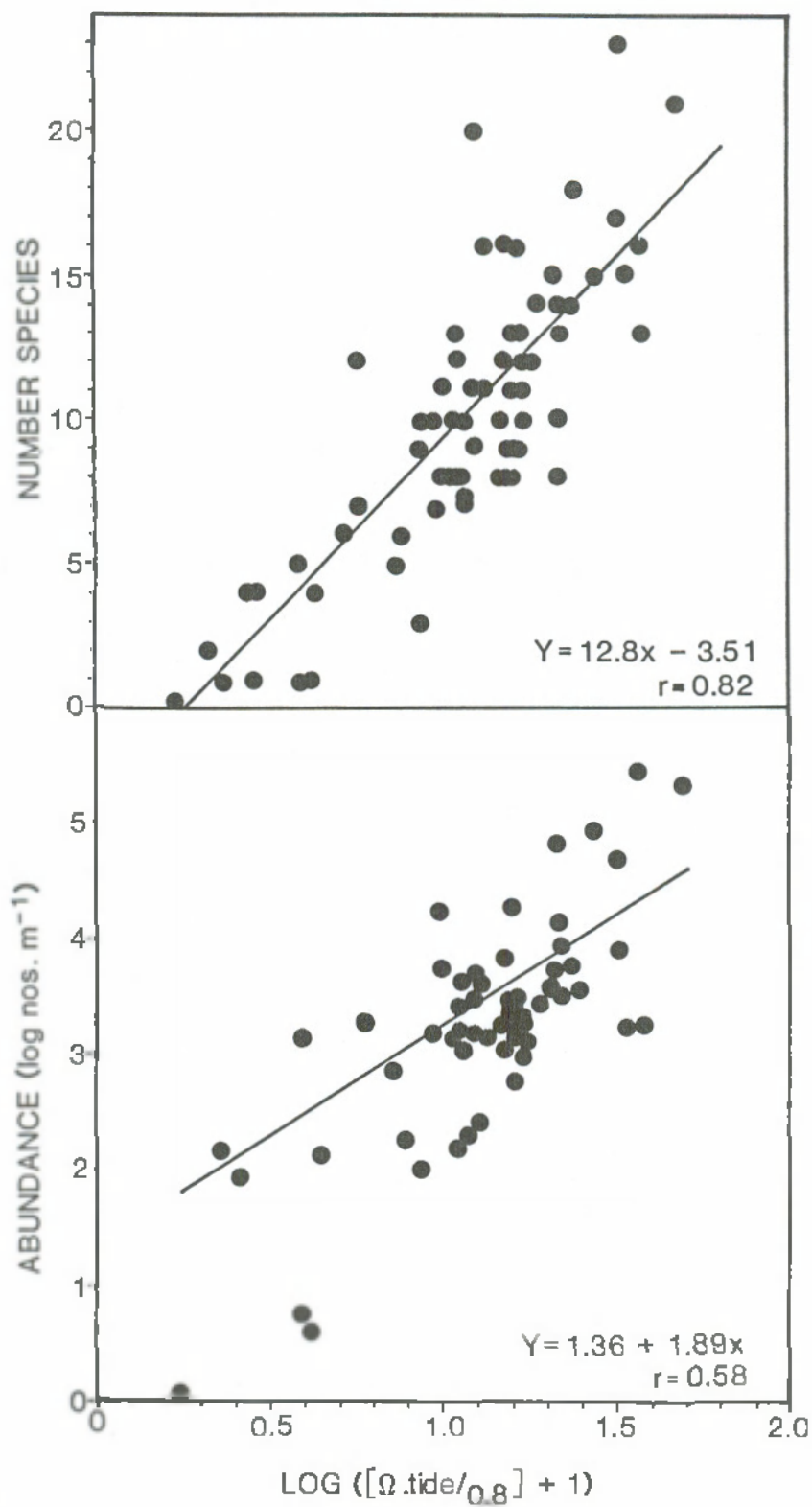


Figure 5. Species richness and abundance plots using a transformed dimensionless fall velocity, the BSI.

Similarly, wave height *per se* seems unimportant, since for most beach types waves break in the surf zone, far from the beach, and are considerably modified by the surf zone and beach slope before being experienced by the fauna as swash on the beach face. Beach slope is an integrated measure of wave energy levels and sand particle size and is thus a better measure than either of these parameters alone, relating closely to swash climate (EMERY and GALE, 1951; MCARDLE and MCLACHLAN, 1991a), but it varies widely on short time scales and gives a poorer fit against faunal parameters than a measure of the overall morphodynamic state of a beach (BSI). Furthermore, slope itself is not directly limiting since even the steepest beach slopes (1/5 - 1/10) present no mechanical problems to locomotion by the macrofauna. Rather, these parameters (sand particle size, wave energy, and beach slope) are the ultimate factors affecting the fauna through their combined effects on beach face climate.

The total morphodynamic state of a beach, resulting from the interaction of the above factors and expressed quantitatively as Ω or BSI, has correlated well with beach macrofaunal community parameters. However, it is not the beach state or type itself that is important for the fauna, but the swash climate associated with it. There is a consistent relationship between beach type and swash climate features (MCARDLE and MCLACHLAN, 1991a, b), dissipative beaches being characterized by swash with extended periods and lengths, variable speeds, and most swash activity below the effluent line, whereas reflective beaches display the opposite swash features. Swash climate on reflective beaches is extremely harsh, providing little feeding time and having high swash speeds throughout the tidal cycle; waves break directly in the intertidal resulting in a high probability of animals being stranded above the effluent line where unsaturated sand might make burrowing difficult (BROWN, 1983). Physical stress in the swash zone on the beach face thus decreases from reflective to dissipative beaches.

The 'swash control hypothesis' suggested that swash climate controlled beach macrofaunal community structure (MCLACHLAN, 1990). We refine this to the 'swash exclusion hypothesis,' suggesting that the swash climate associated with dissipative beaches is sufficiently accommodating and varied to enable virtually all

macrofauna species encountered on exposed beaches to maintain viable populations, but, as beach type changes through intermediate states toward reflective conditions, the increasingly inhospitable swash climate excludes more and more species until, in the fully reflective situation, only supralittoral forms (talitrid amphipods, ocypodid crabs, insects), which live 'outside' the swash climate, remain. This needs to be tested experimentally.

MCLACHLAN (1990) noted a change in mean body size over his series of beaches, with smaller animals occurring on dissipative than reflective beaches. However, re-analysis of his data reveals that, whereas crustaceans decrease in size, molluscs increase in mean body mass from reflective to dissipative beaches. Such trends in the southern African and Chilean beaches will be explored in detail in separate papers. Body size as well as shape, morphology, and means of locomotion must display some adaptations to the swash climate and convergent evolution in forms adapted to the same beach types may be expected.

CONCLUSIONS

Sandy beaches from six different zoogeographic provinces and four continents all fit a similar pattern, with macrofaunal species richness, abundance, and biomass changing predictably in response to changes in beach morphodynamic type, all increasing toward more dissipative conditions. This implies overriding control by the physical environment, in particular the swash climate, which is coupled to beach type. Presumably certain taxonomic groups, their morphological and their behavioral adaptations have evolved in response to different swash climates. We suggest that dissipative beaches require minimal adaptations of these sorts, as reflective conditions are approached, increasingly hostile swash climates demand increasing specialization and more species are excluded. Such adaptations to swash climates warrant further study.

ACKNOWLEDGMENTS

This work was made possible by travel grants to A.M. from the FRD, UPE, and ICR, South Africa and FONDECYT research grant 904-88 to E.J. We thank students and colleagues who

assisted with field work and laboratory analysis, in particular Claudia Añazco, Sonia Fuentealba, Sandra Silva, Marcia Gonzalez, Jacqueline Muñoz, Pedro Quijoñ, Antonio Loew, Luis Filun, Victor Poblete, Mario Pino, and Claudio Pavez, as well as Maggie Hawkins for artwork. An de Ruyck is thanked for assistance with statistical treatment of the data.

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