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Global Patterns in Sandy Beach Macrobenthic Communities

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ABSTRACT

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The data from 161 quantitative sandy beach transect surveys from a wide variety of locations were examined to identify trends and relationships between total marine macrofauna species richness, abundance, and biomass and physical variables. Several physical variables were correlated, especially sand particle size and beach face slope, and spring tide range and beach face slope. Higher latitudes experienced larger waves, and flatter beaches had finer sands, larger waves, and larger tides. Strong correlations were found between species richness and beach slope, tide range, and sand particle size, as well as various indices of beach state. Tropical regions harbored significantly more species than other regions. A new Beach index (BI), based on tide range, beach face slope, and sand particle size, correlated well with species richness, explaining 56% of the variability in the data without considering latitude. Abundance and biomass were best correlated with log(1/beach face slope) and tended to be higher in temperate regions. General patterns are discussed; the new index is evaluated; and the roles of sand, tide, slope, and latitude are considered. It is concluded that for regional studies log(1/beach face slope) is the most useful index to compare beaches, whereas for wider comparisons covering areas of differing tide range, BI might be most useful. These patterns have implications for global biodiversity management on sandy beaches.

ADDITIONAL INDEX WORDS: *Species richness, biomass, tides, beach slope.*

INTRODUCTION

Ocean sandy beaches are environments in which physical structure can be defined in terms of three variables: sand grain size, wave climate, and tidal regime. The interactions between these three factors produce a wide range of beach morphodynamic types, which can broadly be considered to range from microtidal reflective beaches (narrow and steep) to macrotidal dissipative systems (broad and flat, which grade into tidal flats; SHORT, 1996). Because beach environments lack biological structures and are extremely dynamic in space and time, their intertidal macrofauna communities have been considered physically controlled in the sense of the Autecological Hypothesis. This hypothesis (NOY-MEIR, 1979) states that, in physically controlled environments, communities are structured by the independent responses of individual species to the physical environment, biological interactions being minimal. If this is the case, then community attributes should correlate closely with physical environmental parameters on sandy beaches.

The attributes of sandy beach macrobenthic communities that have been most widely used in macroscale comparative studies are species richness, abundance, and biomass. The earliest quantitative demonstration of a biological-physical relationship was a series of correlations between species richness and abundance on the one hand and sand particle size and beach face slope on the other, for a range of microtidal South African beaches (MCLACHLAN, WOODRIDGE, and DYE, 1981). This showed that the community increased in richness, density, and total abundance from steep beaches of coarse sand toward flatter beaches of finer sand. Subsequent work over a wider range of beach types and geographical areas confirmed this trend and related it to the beach morphodynamic type; it was shown that macrotidal dissipative beaches supported communities of greater richness, abundance, and biomass than microtidal reflective beaches (MCLACHLAN, 1990; MCLACHLAN, DE RUYCK, and HACKING, 1996; MCLACHLAN *et al.,* 1993).

The explanation for these patterns, in the context of the Autecological Hypothesis, was given as exclusion of species from the reflective end of the gradient of beach types by a harsh swash climate, the idea being refined to the Swash Exclusion Hypothesis (MCLACHLAN *et al.,* 1993). This refinement was based on the finding that swash climate, which the macrofauna experience on the beach face, is closely coupled to beach type (MCARDLE and MCLACHLAN, 1991, 1992). Subsequently, it was recognized that exclusion of species toward the reflective end of the beach gradient was likely to be a result of both harsh swash climate and coarse sands (MCLACHLAN, 2001). Support for these trends has come from a number of recent studies in Australia, Madagascar, South Africa, Brazil, and Chile (BRAZEIRO, 1999; HACKING, 1997; JARAMILLO, DUARTE, and CONTRERAS, 2000; SOARES, 2003). These studies have tended to show good correlations between

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community attributes and compound indices of beach state, with individual physical factors generally correlating less well.

The first index used to explain community changes (McLachlan, 1990) was Dean's dimensional fall velocity (Ω), which is a measure of how reflective or dissipative a microtidal beach is on the basis of wave energy and sand fall velocity (Short, 1996). Because this index does not take tides into account, and therefore is inadequate to cover macrotidal situations, another index was used to compare beaches subject to differing tide ranges; the Beach State Index (BSI) involved multiplying Dean's parameter by a tidal factor, and this gave good correlations when a wide range of beach types was considered (Hacking, 1997; McLachlan, De Ruyck, and Hacking, 1996; McLachlan *et al.,* 1993). More recently, Soares (2003) developed an index, the Beach Deposit Index (BDI), which is based on a measure of beach face slope multiplied by a measure of sand particle size; this proved successful for microtidal beaches under a wide range of conditions.

In an overview of this topic McLachlan (2001) identified three paradigms that define these community patterns on exposed sandy beaches and two hypotheses to explain the observed patterns. The paradigms are (1) the Autecological Hypothesis, (2) the beach morphodynamic models, and (3) the established patterns of species richness, abundance, and biomass increasing across the continuum from microtidal reflective to macrotidal dissipative beaches. The hypotheses to explain these patterns are (1) that latitude and beach length influence species richness and (2) that two physical factors, swash climate and sand particle size, define the immediate environment experienced by beach macrofauna and that increasing harshness in both of these factors excludes species from reflective systems. These ideas have found wide support. Latitudinal effects (*i.e.,* increasing species richness toward the tropics because of the larger species pool) have been confirmed by Hacking (1997), McLachlan *et al.* (1998), and Soares (2003), although earlier analyses, ignoring beach type effects, concluded otherwise (Dexter, 1992). Effects of beach length (*i.e.,* distance between headlands) are less clear and have been addressed by Brazeiro (1999). The roles of swash and sand in influencing the fauna have been demonstrated in many ways (Alexander, Stanton, and Dodd, 1993; Defeo, Gomez, and Lercari, 2001; Dugan, Hubbard, and Lastra, 2000; McLachlan *et al.,* 1995; Nel, 1995, 2001; Veloso, Caetano, and Cardoso, 2003), although much more remains to be done.

The mechanisms that explain the presence or absence of species across the continuum of beach types have elicited considerable discussion. It has been questioned whether the exclusion of species toward the reflective extreme is due to pre- or postsettlement processes (Soares, 2003). Brazeiro (2001) has argued that increasing environmental severity from harsh swash, coarse sediment, and accretion-erosion dynamics excludes species—the Multicausal Environmental Severity Hypothesis. Defeo, Gomez, and Lercari (2001) formulated the Habitat Harshness Hypothesis, which states that in harsh reflective beaches, organisms need to divert more energy toward maintenance and therefore have lower fecundity and higher mortality; thus, postsettlement processes are hypothesized to prevent some species from establishing populations on reflective beaches. Defeo, Gomez, and Lercari (2001) and Dugan and Hubbard (1996) tested these ideas on the mole crab *Emerita,* and Defeo and Martinez (2003) tested similar ideas, with mixed results, on the isopod *Excirolana* from beaches of different types. However, they had selected species typical of reflective beaches (*i.e.*, capable of maintaining populations across the whole morphodynamic spectrum); species typical of dissipative systems, such as polychaetes and many molluscs, would be expected to be more sensitive to harsh habitats.

The current status is therefore that the patterns of changing community richness across the continuum of beach types are widely recognized, and physical factors are accepted to play a major role in explaining this. However, the details are still being debated. The relative importance of sand, swash, tides, waves, beach slope, and latitude need refining, and none of the available indices of beach type seem suitable under all conditions. BSI has proved useful when areas of differing tide range are compared (Hacking, 1997), and the BDI index of Soares (2003) appears to be effective under microtidal conditions. Furthermore, most studies to date have concentrated on a limited geographic region, in which only part of the spectrum of conditions were present. The recent availability of comparable results of quantitative beach surveys from many regions, however, allows a database to be compiled that covers most beach types and latitudes to enable a broader comparison of global trends. The aim of this study was therefore to pool comparable data from quantitative beach surveys over the past 20 years to undertake a statistical analysis designed to clarify general patterns. This should identify the roles of the various individual physical factors controlling beach communities and confirm or develop the most useful index (or indices) for characterizing beaches in a way that enables useful predictions to be made.

METHODS

The literature back to 1980 was scanned for suitable results of quantitative beach transect studies that used similar techniques and provided sufficient information on the main physical factors (sand particle size, tide range, beach face slope, wave height) so that key parameters could be estimated. All such studies are one-off snapshot surveys, and the values for each beach are thus regarded as a single point in space and time. Techniques used by sampling teams were not identical, and surveys differed in quadrat size, quadrat number, and total sample area but all surveyed quantitative transects from the drift line down to the low tide swash. Considering the differences in sampling, that seasonality was ignored, the snapshot nature of the samples, and the difficulty of getting accurate values for some parameters, it is accepted that this data will have considerable noise. This is compensated for by obtaining the largest possible data set.

Only marine species were considered (*i.e.,* insects and arachnids were ignored but ocypodids and talitrids were included); hence, the term marine species richness was used.

Table 1. *Summary statistics of the database.*

Variable	N	Mean	SD	Minimum	Median	Maximum
Mean sand particle size (phi)	161	1.88	0.64	−0.50	1.90	3.30
Wave height (m)	161	1.07	0.71	0.10	1.00	3.60
Maximum spring tide range (m)	161	2.60	1.56	0.50	2.00	6.50
1/beach face slope	161	27.42	16.15	5.00	24.00	80.00
Log(beach face slope)	161	1.36	0.28	0.70	1.38	1.90
Log(maximum spring tide range)	161	0.35	0.23	−0.30	0.30	0.81
Marine species richness per transect	161	13.15	6.46	1.00	13.00	30.00
Log(Abundance per meter-wide transect)	161	3.96	0.95	0.48	3.98	5.87
Log(Biomass per meter-wide transect)	141	1.81	0.92	0.00	1.73	3.89
Relative tide range	161	4.36	4.54	0.00	2.30	23.00
Area (log [Tide/Slope])	161	1.71	0.44	0.65	1.68	2.60
Dean's parameter	161	3.52	2.54	0.16	3.09	15.15
BSI (Beach State Index)	161	0.96	0.38	0.14	0.95	1.72
BDI (Beach Deposit Index)	161	129.21	103.68	6.35	101.68	453.75
BI (Beach Index)	161	2.15	0.52	0.77	2.14	3.20

Biological data were for whole transects (*i.e.,* linear meter of intertidal zone from the low water mark to the drift line), not per square meter. Each beach was placed in one of four regions—tropical (1), subtropical (2), warm temperate (3), and cold temperate (4)—on the basis of the designation in the original source.

After completion of the matrix, the following indices were calculated: Dean's parameter (Ω), BSI, and BDI, as well as relative tide range (RTR; SHORT, 1996). Two new indices were tested: Area, a measure of intertidal area obtained by dividing tide range by the beach face slope, and Beach Index (BI), similar to Area but including a measure of sand particle size. Data on beach width were not available from all sources, hence, the use of Area as a measure of beach width. These indices were calculated as

$$\mathrm{RTR} = \frac{\mathrm{Tide}}{H_\mathrm{b}}$$

$$\mathrm{Dean} = \frac{H_\mathrm{b}\cdot 100}{W_\mathrm{s}\cdot T}$$

$$\mathrm{BSI} = \log\left(\frac{H_\mathrm{b}\cdot 100\cdot \mathrm{Tide}}{0.8\cdot W_\mathrm{s}\cdot T} + 1\right)$$

$$\mathrm{BDI} = \left(\frac{1}{\tan B}\right)\left(\frac{a}{Mz}\right)$$

$$\mathrm{Area} = \log\left(\frac{\mathrm{Tide}}{\mathrm{Slope}}\right)$$

$$\mathrm{Bl} = \log\left(\frac{\mathrm{Sand}\cdot \mathrm{Tide}}{\mathrm{Slope}}\right)$$

where Tide is maximum spring tide range (meters), H_b is significant breaker height (meters), W_s is sand fall velocity (cm/s), T is wave period (seconds), Slope or tan B is the beach slope, a is 1.03125 (millimeters), Mz is the mean sand particle size (millimeters), and Sand is mean sand particle size in phi units + 1 (see MCLACHLAN *et al.,* 1993; SHORT, 1996; SOARES, 2003). Tables from GIBBS *et al.* (1971) were used to calculate settling velocities from particle size. The indices are dimensionless except Area (log meters) and BI (log phi·m).

On completion of the database, the physical variables were first examined against each other and then the biological variables were examined against the individual physical parameters with Generalized Linear Models. Quadratic models were only used when analysis of variance indicated a significant improvement over the linear model. Stepwise multiple regression was used to identify the groups of parameters explaining the variance in the data. The biological variables were also regressed against the indices. Principal components analysis was used to investigate whether the number of parameters could be reduced. Cluster analysis was used to try to reduce the noise in the data by grouping the data points within regions, but no significant reductions were possible. Statistical analyses were performed with SPSS version 11.5 (SPSS, 2002).

RESULTS

The Data

From 14 sources, usable data were obtained for 161 beaches in 10 countries: four beaches in South Africa (DYE, MCLACHLAN, and WOOLDRIDGE, 1981); two beaches in Australia (MCLACHLAN, 1985); three beaches in the United States (MCLACHLAN, 1990); 10 beaches in Chile (MCLACHLAN *et al.,* 1993); six beaches in Australia (MCLACHLAN, DE RUYCK, and HACKING, 1996); 33 beaches in Australia (HACKING, 1997); 10 beaches in Oman (MCLACHLAN *et al.,* 1998); 10 (BORZONE, SOUZA, and SOARES, 1996) and three (VELOSO and CARDOSO, 2001) beaches in Brazil; five beaches in Uruguay (DEFEO, JARAMILLO, and LYONNET, 1992); six beaches in Chile (JARAMILLO, DUARTE, and CONTRERAS, 2000); nine beaches in New Zealand (STEPHENSON and MCLACHLAN, 2004); 52 beaches in South Africa, Madagascar, Brazil, and Chile (SOARES, 2003); and eight beaches in Belgium (DEGRAER, VOLCKAERT, and VINCX, 2003). Sites with an intertidal gradient flatter than 1/100 were considered tidal flats, not beaches; thus, two of the 35 sites originally studied by HACKING (1997) were not included in the analysis.

The summary statistics of the variables considered are shown in Table 1. The mean particle size was converted to phi units ($-\log_2$ mean millimeters) and ranged from −0.50

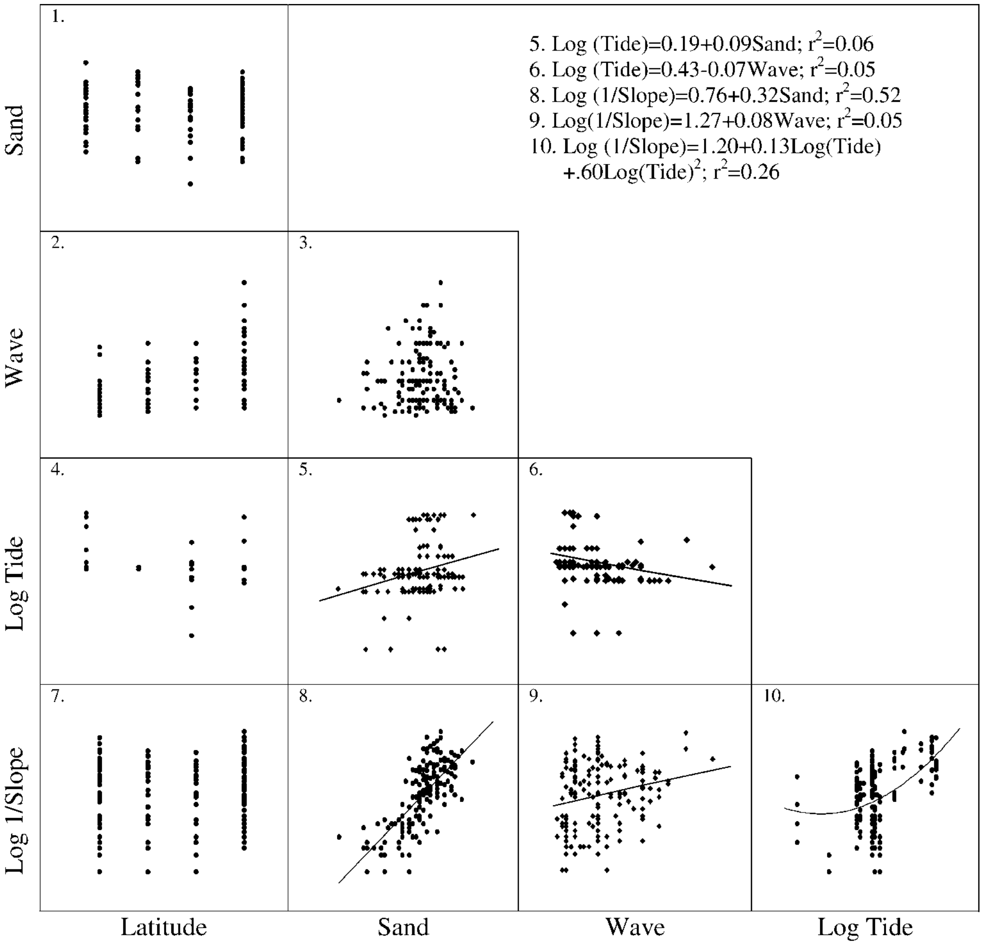


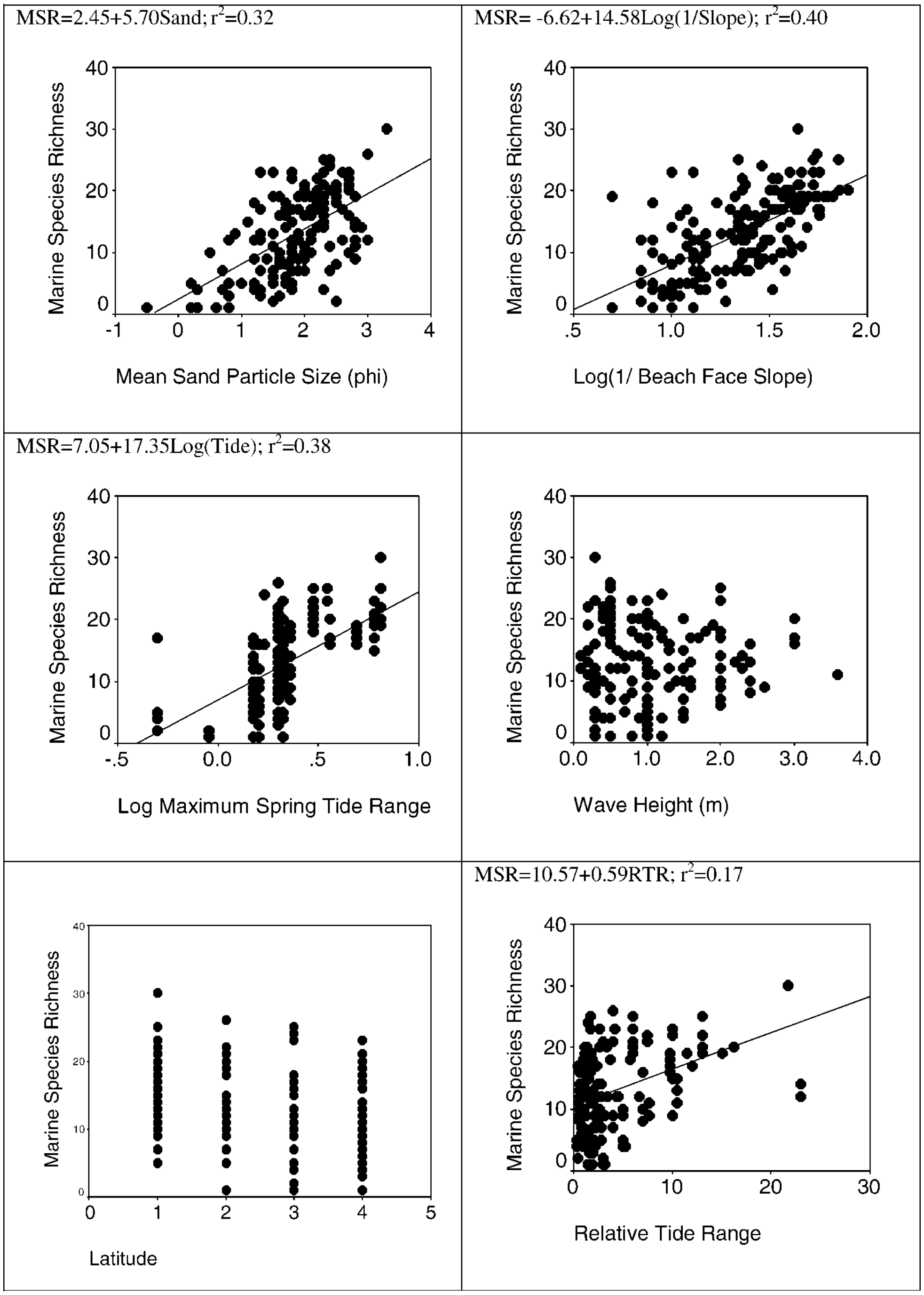
Figure 1. Scatter plots of relationships between physical parameters on 161 beaches. Where significant, regression lines are shown. 1, Tropical; 2, subtropical; 3, warm temperate; 4, cold temperate; sand, mean particle diameter in phi units; wave, wave height (m); log Tide, log(maximum spring tide range) (m).

to 3.30 phi; wave heights ranged between 0.1 and 3.6 meters. The greatest maximum spring tide range was 6.5 meters. The beach face slopes ranged between 1/5 and 1/80. Relative tide range values ranged from 0 to 23, Dean's parameter from 0.16 to 15.15, BSI from 0.14 to 1.72, and BDI from 6 to 453. The new index, Area, ranged between 0.65 and 2.65, and BI ranged from 0.77 to 3.20. The marine species richness (*i.e.,* the number of species collected in a single transect survey) ranged from 1 to 30 per beach transect, with a mean of 13. Log Abundance and log Biomass per meter transect ranged from 0.48 to 5.87 and 0 to 3.89, respectively. Only 141 of the 161 cases provided biomass data. A Kolmogorov-Smirnov test for normality showed that these variables are distributed normally.

When collecting physical data during transect surveys, there is a hierarchy of accuracy and reliability within which ecologists can obtain the information. Ranking the parameters in sequence from those that can be obtained most reliably and simply to those that are most difficult or variable orders them as follows: latitude, tide range, beach face slope, sand particle size, swash period, wave period, wave height. Thus, analyses involving wave data would be expected to be least reliable, whereas data on tide range, beach slope, and sand particle size are considered more reliable.

Physical Factors

Relationships between all physical variables are shown in Figure 1. Strongest correlations are found between mean sand particle size and log of the maximum spring tide range ($r = 0.25$), log(1/beach face slope) and mean sand particle size ($r = 0.72$), log of the maximum spring tide range and wave height ($r = -0.24$), log(1/beach face slope) and wave height ($r = 0.23$), and log(1/beach face slope) and log of the maximum spring tide range ($r = 0.51$). All relationships were linear except that between Slope and Tide, which was quadratic. Flat beaches tend to have finer sand, larger tides, and larger waves, and under large tidal regimes, waves tend to be smaller and the sand finer. A Kruskal-Wallis nonparametric test of wave heights indicates that higher latitudes experience larger waves.



MSR=2.45+5.70Sand; $r^2=0.32$

MSR= -6.62+14.58Log(1/Slope); $r^2=0.40$

MSR=7.05+17.35Log(Tide); $r^2=0.38$

MSR=10.57+0.59RTR; $r^2=0.17$

Figure 2. Scatter plots of relationships between marine species richness and six physical parameters. Where significant, regression lines are shown.

Species Richness

Plots of species richness against the physical parameters are given in Figure 2. Despite the inherent variability in the data, marine species richness correlates significantly with several parameters. Strongest correlations were for log of the inverse of the beach face slope ($r = 0.63$), log of the maximum spring tide range ($r = 0.62$), sand particle size ($r = 0.57$), and relative tide range, which can be considered an index of the relative role of waves and tides ($r = 0.41$). The trends were for marine species richness to increase with finer sand, flatter slope, lower latitude, and greater tide range. For wave height, variability in marine species richness was greatest at low wave heights and decreased toward greater wave heights. Similarly, variability decreased and marine species richness

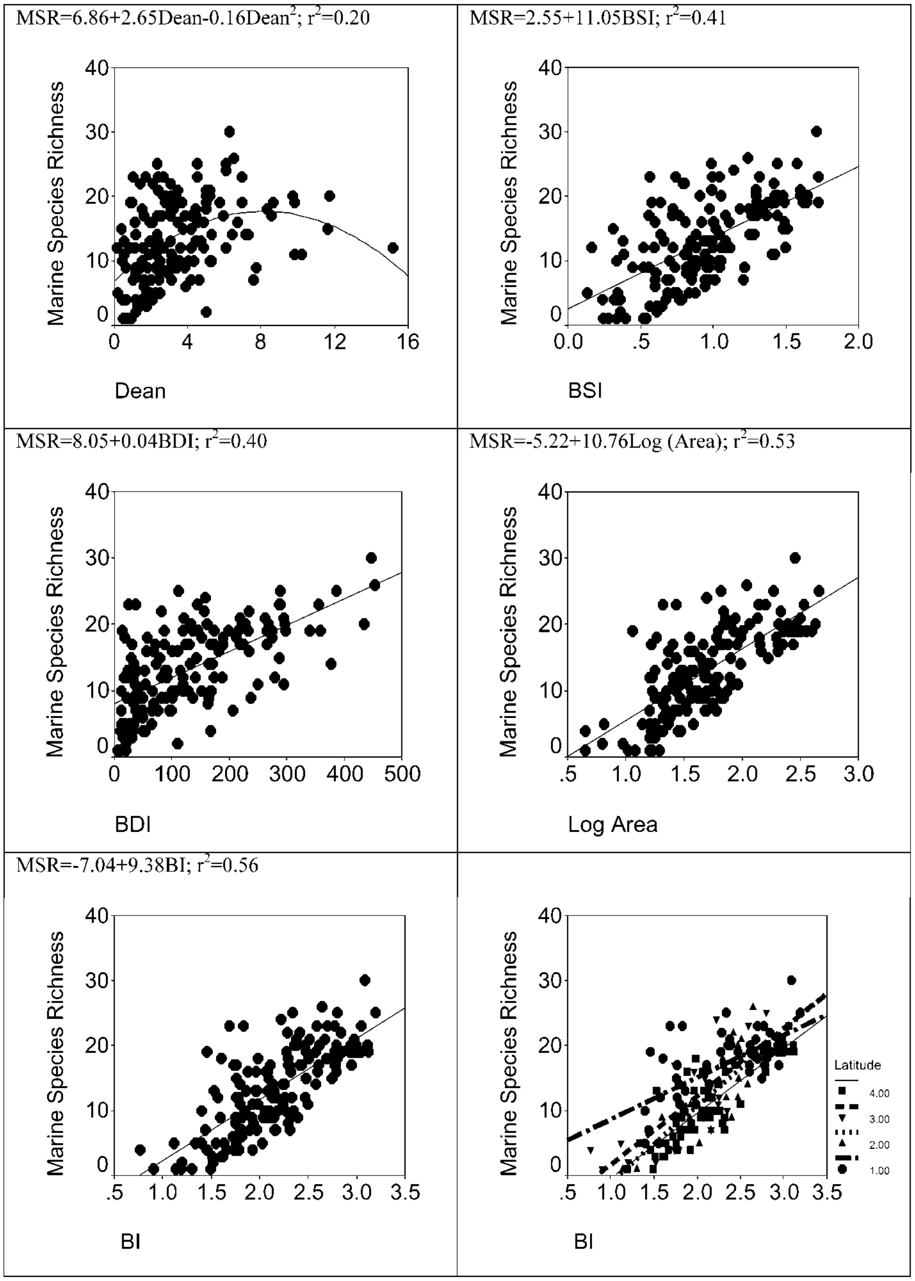


Figure 3. Scatter plots of relationships between marine species richness and four beach indices, as well as plots for four latitude regions against BI. 1, Tropical; 2, subtropical; 3, warm temperate; 4, cold temperate. Regression statistics are in Table 3.

tended to increase with greater relative tide range (*i.e.,* toward tide-controlled as opposed to wave-controlled beaches). Thus, under conditions of small waves or fully wave-controlled beaches, marine species richness is highly variable, but as beaches become either more high energy or more tide dominated (*i.e.,* more dissipative), the community becomes richer and less variable.

A principal components analysis was performed for the four variables mean sand particle size, wave height, maximum spring tide range, and beach face slope. The first two components explained 75% of the variance in marine species richness. The first component, which explained 47% of the variation, was highly correlated with beach face slope ($r = 0.88$), maximum spring tide range ($r = 0.79$), and mean sand particle size ($r = 0.69$). The second component was highly correlated with only wave height ($r = 0.92$). The principal components regression for the first two components resulted in $r^2 = 0.44$. Hence, the original parameters were used.

Marine species richness was modeled with a Poisson regression. Both the drop-in-deviance test and Wald's test sug-

Table 2. *Regresson equations for the response of marine species richness (MSR) to the Beach Index (BI) and the responses of log Abundance (LA) and log Biomass (LB) to Log (1/Slope) (LS) for the four latitudinal regions. See Figures 3, 5, and 7.* ** $p < 0.01$.

Latitude	Regression Equation	R^2
1 Tropical	$MSR = \exp(1.92 + 0.39BI)$	0.43**
2 Subtropical	$MSR = \exp(-0.15 + 1.20BI)$	0.59**
3 Warm temperate	$MSR = \exp(-0.10 + 1.22BI)$	0.68**
4 Cold temperate	$MSR = \exp(0.50 + 0.85BI)$	0.69**
1 Tropical	$LA = 1.53 + 1.79LS$	0.68**
2 Subtropical	$LA = -1.90 + 4.18LS$	0.74**
3 Warm temperate	$LA = 1.41 + 1.80LS$	0.39**
4 Cold temperate	$LA = 0.22 + 2.81LS$	0.50**
1 Tropical	$LB = -1.02 + 1.99LS$	0.60**
2 Subtropical	$LB = 1.23 + 0.18LS$	0.04
3 Warm temperate	$LB = -0.22 + 1.53LS$	0.22**
4 Cold temperate	$LB = 0.19 + 1.29LS$	0.09

gest that wave height is not an important physical parameter in estimating marine species richness. The best ($p < 0.001$) model for estimating marine species richness (MSR) is

$$\text{Log MSR} = 1.455 + 0.005(1/\text{Slope}) + 0.103\text{Tide} + 0.345\text{Sand} \qquad (r^2 = 0.51),$$

where Tide is the maximum spring tide range (meters) and Sand is the mean particle diameter in phi units. Interestingly, if two tidal flats of HACKING (1997) are included in this data set, Tide is selected as the first variable, followed by Sand and Slope.

Figure 3 gives the plots of species richness against the indices Dean, BSI, BDI, Area, and BI. These plots show that the correlations with marine species richness improved from Dean ($r = 0.14$) through BDI ($r = 0.64$), BSI ($r = 0.64$), and Area ($r = 0.73$) to BI ($r = 0.75$). For Dean, a quadratic model gave the best fit.

When latitude is considered, four separate regression lines are found for the four climatic regions according to BI (Table 2; Figure 3). All coefficients are significant except Slope for subtropical and cold temperate regions. Thus, BI is a good index to characterize a wide spectrum of beaches, but across climatic zones, latitude also plays a role. Tropical beaches support more species than temperate beaches. BI has the benefit of being based on three factors that are all relevant and easily measured.

Abundance

The responses of total community abundance (*i.e.,* total numbers per linear meter of intertidal area) to the physical factors and indices are shown in Figures 4 and 5. The responses are logarithmic and are mostly less clear than in the case of species richness, but nevertheless, some patterns do emerge. Log Abundance increases with finer sand ($r = 0.60$), flatter slope ($r = 0.73$), higher tides ($r = 0.41$), larger waves ($r = 0.25$), greater relative tide range ($r = 0.20$), and increase in the values of Dean ($r = 0.57$), BSI ($r = 0.62$), Area ($r = 0.66$), BI ($r = 0.70$), and BDI ($r = 0.71$). In the cases of Tide, Wave, relative tide range, Dean, and BDI, a quadratic fit was best, whereas the others were linear. There was no clear response to latitude. Of the indices, BI ($r = 0.70$) gave the best fit, followed by Area ($r = 0.66$) and BSI ($r = 0.62$) when linear models were used, but with a quadratic model, BDI ($r = 0.71$) gave the best fit. However, log(1/Slope) gave an even better correlation ($r = 0.73$) than any of the indices.

Stepwise forward selection (probability to enter 0.05) multiple regression selected Slope and Sand as the first two variables to explain variation in log Abundance,

$$LA = 0.65 + 2.10\log(1/\text{Slope}) + 0.24\text{Sand} \qquad (r^2 = 0.55),$$

where LA is the log of the total abundance per meter of transect and Sand is the mean particle diameter in phi units. If the two tidal flats of HACKING (1997) are included in the analysis, the order of inclusion changes to select Sand, Slope, Tide, and Wave variables in that order.

Separate treatment of the data from different latitudes when regressed against log(1/Slope) resulted in four regression lines (Table 2). With dummy variable techniques (GUJARATI, 1970), the effect of latitude and log(1/Slope) on log Abundance was studied. Overall, Chow's test (CHOW, 1960) shows a significant latitude effect ($F = 31.8$, $p < 0.001$). A detailed analysis indicates that the equations for tropical and warm temperate and for warm temperate and cold temperate regions are statistically similar (Table 3). All other pairs differ significantly.

Biomass

The responses of total community biomass (*i.e.,* total biomass per linear meter of intertidal area) to the physical factors and indices are shown in Figures 6 and 7. Few patterns emerge, but the following generalizations can be made. Log Biomass increases in response to log(1/Slope) ($r = 0.49$), Sand ($r = 0.44$), Wave ($r = 0.45$), and the indices Area ($r = 0.30$), BSI ($r = 0.36$), BI ($r = 0.40$), Dean ($r = 0.41$), and BDI ($r = 0.46$). For Slope, Wave, Dean, BI, and BDI, a quadratic model was best. For the linear model, BI ($r = 0.39$) gave the best fit of the indices, but with a quadratic model, BDI ($r = 0.46$) was better. Thus, as with Abundance, log(1/Slope) correlates better than any of the indices. There were no correlations with latitude, Tide, or relative tide range or any clear response to latitude.

Stepwise forward selection (probability to enter 0.05) multiple regression selected mean sand particle size and wave height as the first two variables to explain variations in log Biomass,

$$LB = 0.18 + 0.61\text{Sand} + 0.46\text{wave} \qquad (r^2 = 0.31),$$

where LB is log of the total biomass per meter of transect, Sand is mean particle size (phi units), and Wave is wave height (meters). If the two tidal flats of HACKING (1997) are included in the analysis, the order of inclusion changes to select Sand, Wave, and Slope, in that order.

Separate treatment of the data from different latitudes, when regressed against log(1/Slope), resulted in four regression lines (Table 2). With dummy variable techniques (GUJARATI, 1970), the effects of latitude and log(1/Slope) on log Abundance was studied. Overall, Chow's test (CHOW, 1960)

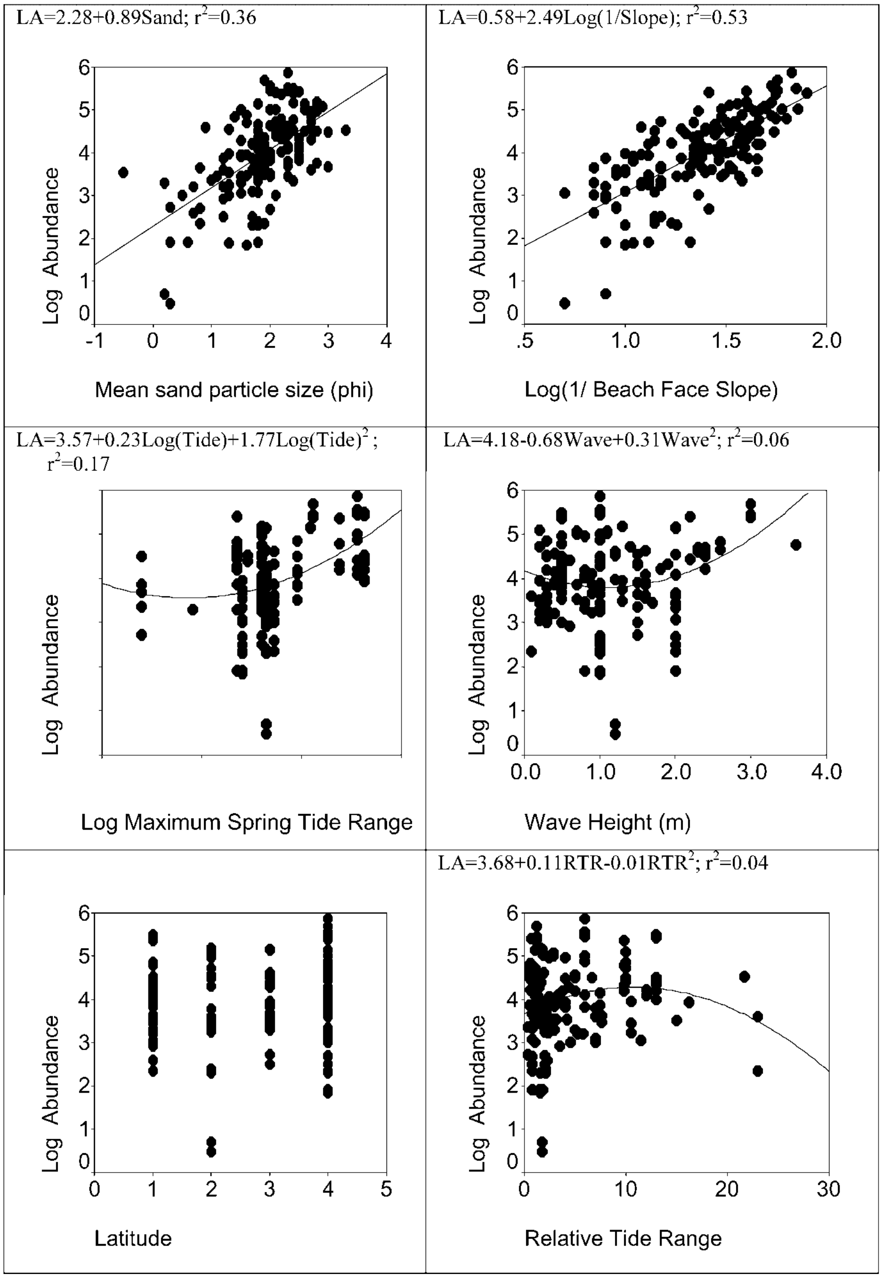


Figure 4. Scatter plots of relationships between log(total abundance per transect) and six physical parameters. Where significant, regression lines are shown.

shows a significant latitude effect ($F = 6.582$, $p < 0.001$). A detailed analysis indicates that only the equations for tropical and subtropical regions are statistically different (Table 3). All the other pairs are similar.

DISCUSSION

The use of snapshot sampling in sandy beach ecological studies has been widely criticized (see DEFEO and RUEDA, 2002). However, for the understanding of large-scale patterns, intensive long-term sampling in a few areas would be meaningless, and a large number of snapshot samples covering a wide range of conditions is more appropriate. This was the approach adopted here, and it is considered valid for the questions being investigated; namely, What physical factors control sandy beach community structure on a global scale? and What indices can best predict beach features that these communities respond to?

Sampling effort and season is clearly important in assess-

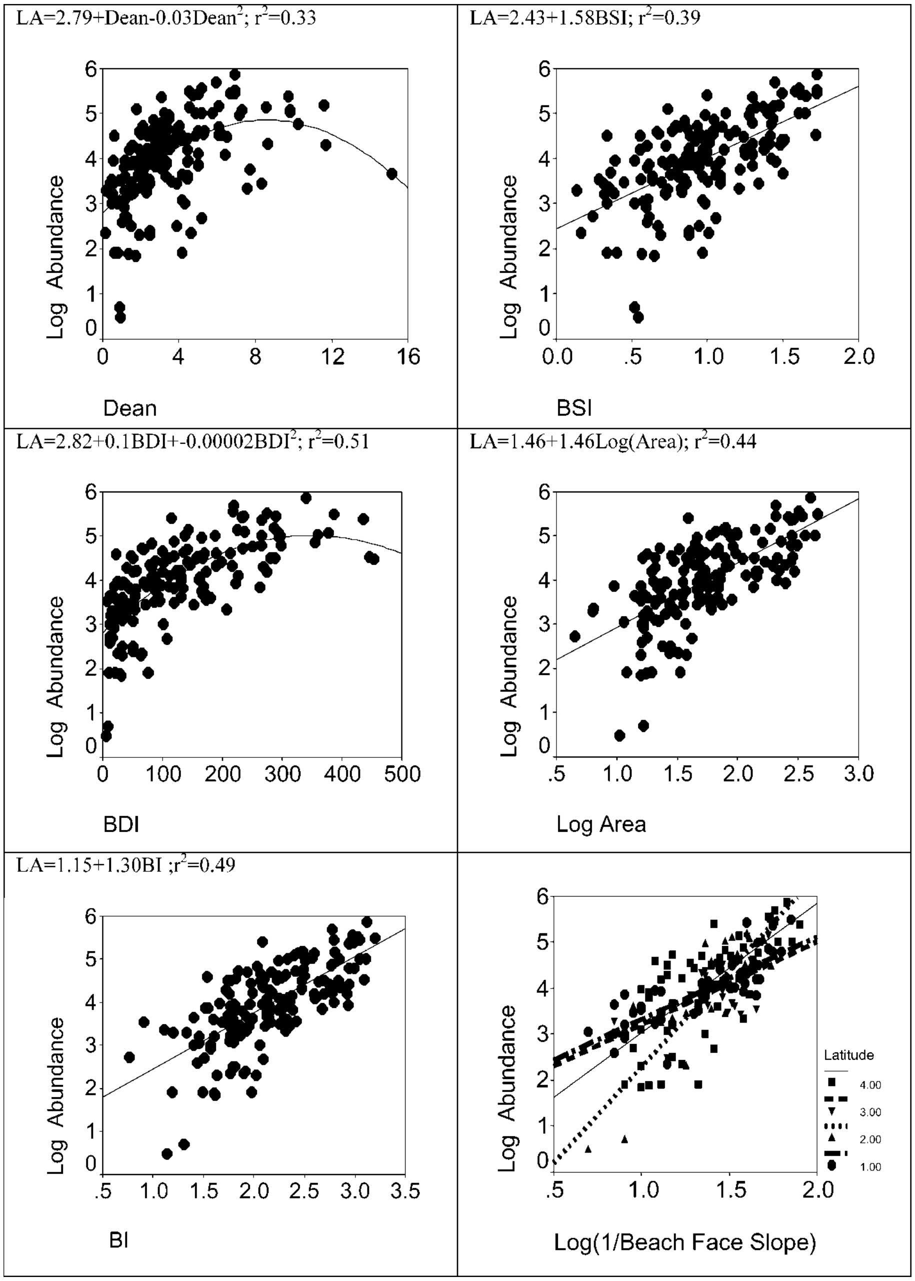


Figure 5. Scatter plots of relationships between log(total abundance) and four beach indices, as well as plots for four latitude regions against log(1/Slope). 1, tropical; 2, subtropical; 3, warm temperate; 4, cold temperate. Regression statistics are in Table 3.

ing the community, and total sample area influences the results through the species area curve (Jaramillo, McLachlan, and Dugan, 1995). This has not been taken into account here, and we acknowledge that it will contribute to noise in the data because total sample area ranged from 1 to 4.5 square meters in the studies used. However, all investigations followed the same general strategy of transect sampling.

Species richness appears to be a conservative trait of sandy beach macrobenthic communities. It increases in a clear and predictable way from narrow, reflective systems to broad, dissipative and macrotidal beaches. Thus, positive responses in species richness were found to sand particle size, reciprocal of the slope, and tide range, all indicative of changes toward dissipativeness. Latitude also plays a role, with tropical beaches displaying greater richness than temperate beaches of the same type. Although the response to wave height was not significant, the scatter plot (Figure 2) shows that increasing wave energy (*i.e.,* increasing dissipativeness) results in more uniformly rich communities, as opposed to variable

Table 3. *Analysis of effects of latitude and log(1/slope) on log(Abundance) and log(Biomass).*

Parameter	Estimate	SE	t	p
Dependent variable: log(Abundance), $r^2 = 0.26$				
Intercept	1.41	0.79	1.77	0.079
Tropical	0.13	0.88	0.15	0.883
Subtropical	−3.30	1.03	−3.19	0.002
Cold temperate	−1.18	0.89	−1.32	0.188
Tropical log(1/Slope)	−0.01	0.63	−0.15	0.988
Subtropical log(1/Slope)	2.38	0.74	3.23	0.002
Cold temperate log(1/Slope)	1.01	0.73	1.57	0.118
Log (1/Slope)	1.80	0.57	3.17	0.002
Dependent variable: log(Biomass), $r^2 = 0.26$				
Intercept	−1.02	0.54	−1.87	0.064
Subtropical	2.25	1.11	2.03	0.045
Warm temperate	0.80	1.18	0.68	0.500
Cold temperate	1.21	0.80	1.52	0.132
Subtropical log(1/Slope)	−1.82	0.84	−2.18	0.031
Warm temperate log(1/Slope)	−0.46	0.84	−0.55	0.583
Cold temperate log(1/Slope)	−0.70	0.57	−1.24	0.219
Log(1/Slope)	1.99	0.39	5.10	0.000

communities at low wave energy. This result can be interpreted as meaning that, under low wave energy, any beach type can occur (depending on sand particle size and tide range), whereas at high wave energy, all beaches tend toward dissipative states. To some extent the same holds for tides.

It is clear that no single physical factor can account for the recorded changes in species richness (Brazeiro, 2001) on a larger scale, hence, the development of various indices of beach state. These have been found to be useful, especially Dean's parameter and BSI, but they have limitations. Of the indices previously described, BSI and BDI gave the best correlations. BDI incorporates a measure of intertidal area and measures of the two factors that impinge directly on the fauna: sand particle size and swash climate, the latter assessed as slope (McArdle and McLachlan, 1991, 1992). However, this index only applies to microtidal beaches and does not accommodate tides, which this study has shown to be the second factor selected by stepwise multiple regression analysis to explain patterns in richness. When only linear models are used, the new index, Area, provides better predictability than BSI or BDI for species richness and abundance, but BI provides better predictability than any of the other indices for all three variables: species richness, Abundance, and Biomass. When latitude is also considered, it is clear that BI can explain most of the macroscale patterns of species richness, that left being mainly noise in the data.

This analysis has confirmed the paradigm that species richness increases from microtidal reflective toward macrotidal dissipative beaches (*i.e.,* with finer sands and larger waves and tides). What is the underlying explanation for this, and is the presence or absence of a species on a beach a result of pre- or postsettlement processes? Our findings support the idea that sand and swash limit the fauna (*i.e.,* that coarse sand and harsh swash climates toward microtidal reflective conditions can exclude species, although these may not be the only key factors). Thus, elements of the Swash Exclusion Hypothesis, the Multicausal Environmental Severity Hypothesis, and the Habitat Harshness Hypothesis are all supported. We do not know whether this exclusion is because settlement was prevented or because of an inability to survive after settlement. In this respect, the approach of Defeo, Gomez, and Lercari (2001) in investigating population responses along the beach morphodynamic gradient is insightful but would be even more useful if the species selected were typical of dissipative conditions so that their exclusion down the gradient toward reflective beaches could be monitored.

Another gap in our understanding concerns the direct role of tides, as highlighted by the multiple regression and the new index. Tides are the cause of intertidal zones, and expansion of the tide range expands the intertidal zone, with wave effects being secondary. Perhaps this fundamental role of tides, creating the primary habitat gradient along which intertidal species establish their niches, has been overlooked on sandy beaches and needs more attention. It might have been neglected because most workers studied regions subject to fairly uniform tide ranges. Another area of neglect has been the subtropics, which have received less attention from sandy beach ecologists than other latitudes.

The response of abundance to changes in physical factors and indices is logarithmic, as recorded previously. Other than this, the response is similar to, but more varied than, the response of species richness. Biomass is the most variable of the three community measures considered and responds logarithmically to changes in physical factors. Previous studies have found it to correlate positively with measures of wave energy (McLachlan, 1990; McLachlan *et al.,* 1993), and wave height was included in the multiple regression for Biomass in this study. However, in the cases of both Abundance and Biomass, the best correlation was with log (1/Slope), not wave height. For Abundance and Biomass, BI gave the best correlation among the indices when a linear model was used, but with a quadratic model, BDI proved better, although this was much weaker for Biomass than Abundance and not as strong as the correlation with Slope. Slope can be considered an integrated measure of beach type, beach area, and swash climate.

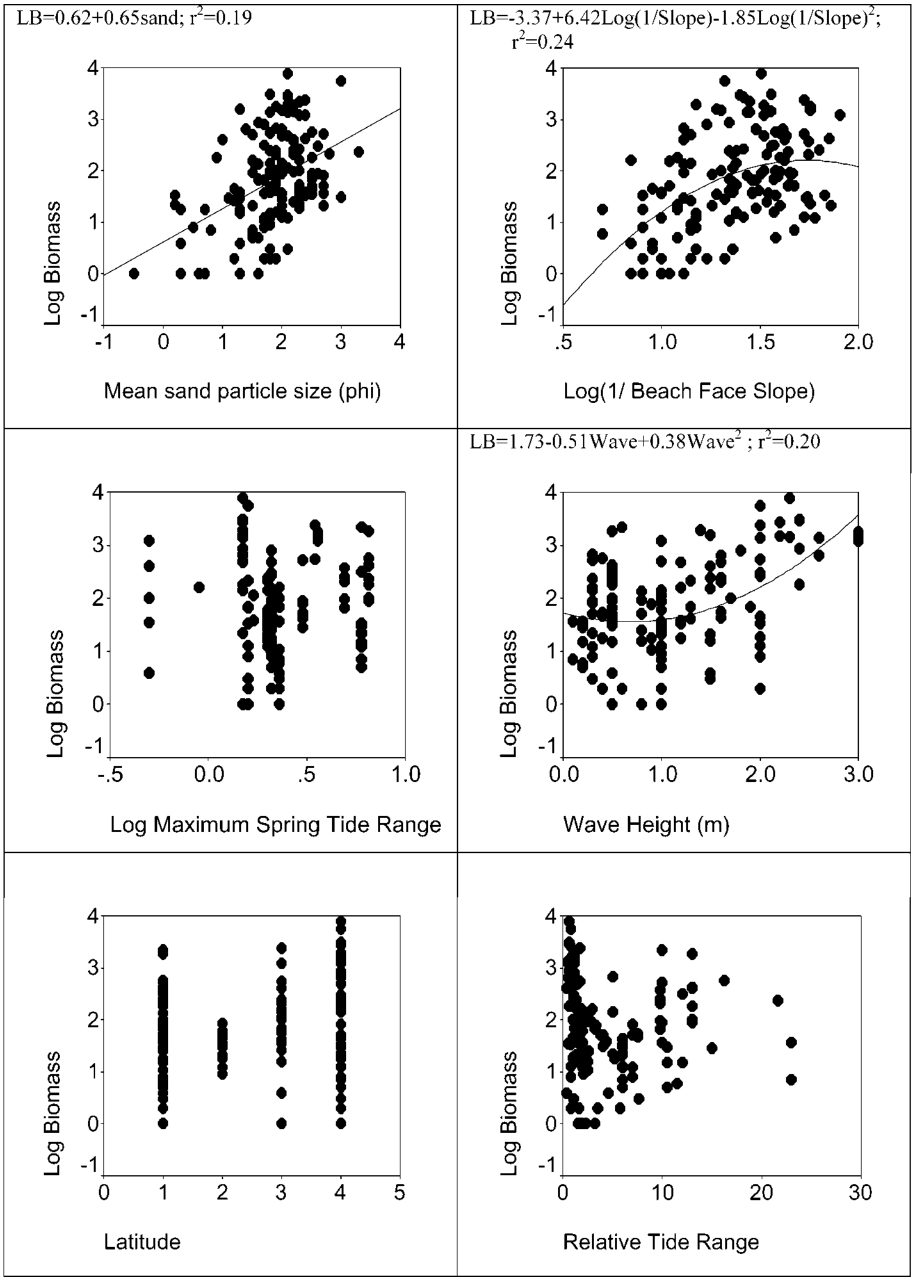


Figure 6. Scatter plots of relationships between log(total biomass per transect) and six physical parameters. Where significant, regression lines are shown.

In an analysis of published data on intertidal macrofauna biomass on rocky and sedimentary shores Riccardi and Bourget (1999) found that linear combinations of physical variables explained up to 44% of the variance in total biomass on sedimentary shores, grain size being the best single predictor, but correlations with wave height, beach slope, and exposure were also significant. Biomass reached a peak on mudflats and fine-grained beaches and was generally higher in temperate regions. They interpreted their results in terms of two factors, wave energy and shore stability, because fine sands (*i.e.,* stable beaches) and flat slopes indicate dissipative beaches. This matches our results very closely, although our data set is different.

The significance of slope in the formulation of the indices BDI, Area, and BI and in the multiple regressions for marine species richness and abundance lies not only in its relationship to intertidal width or area, but probably also in its correspondence to intertidal environmental conditions. Clearly,

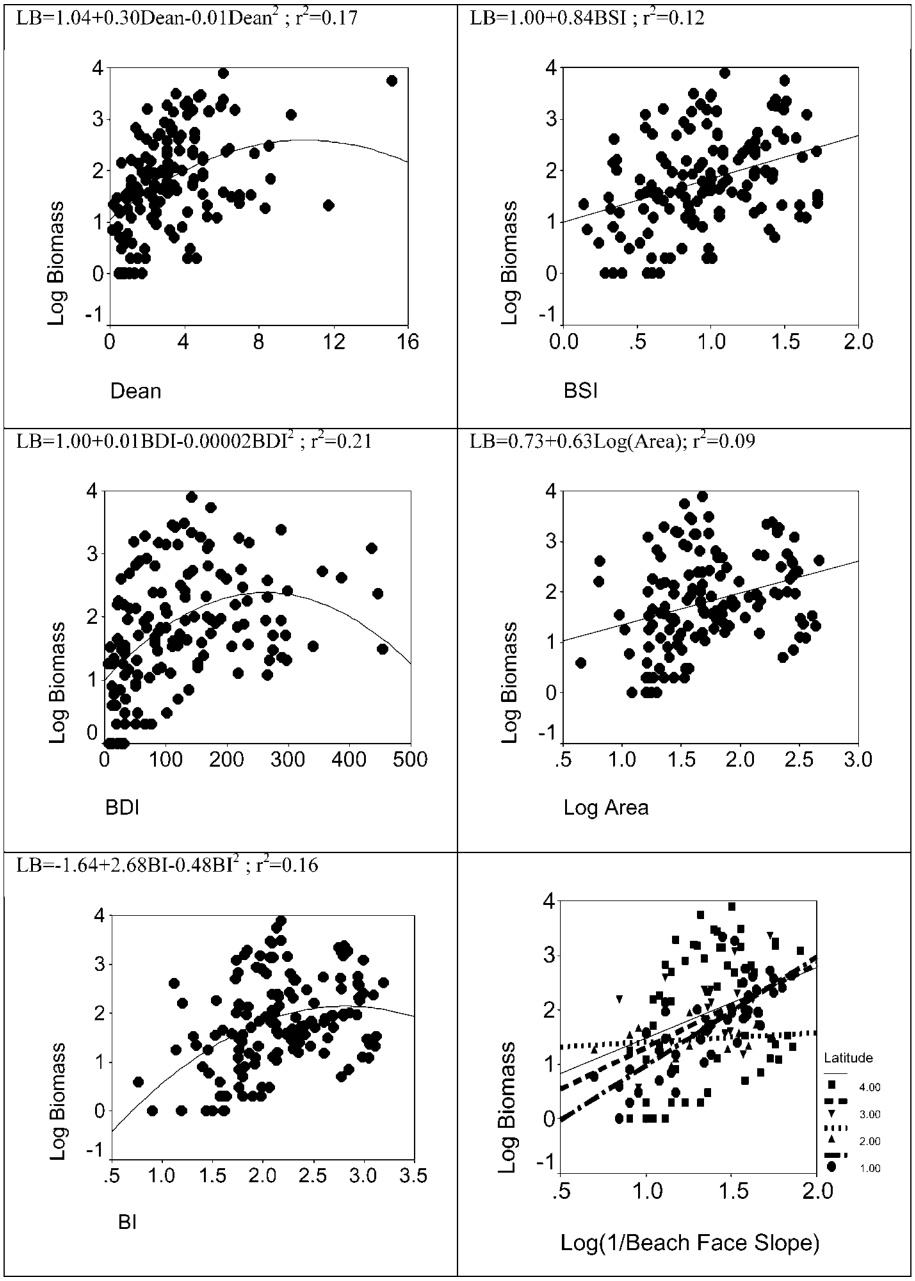


Figure 7. Scatter plots of relationships between log(total biomass) and four beach indices, as well as plots for four latitude regions against log(1/Slope). 1, tropical; 2, subtropical; 3, warm temperate; 4, cold temperate. Regression statistics are in Table 3.

slope *per se* does not affect faunas directly. Rather, slope correlates well with swash climate (BRAZEIRO, 2001; MCARDLE and MCLACHLAN, 1991, 1992). Swash climate on the beach face becomes less harsh as beach face slope flattens, which is exhibited as longer swash periods, less swash activity above the effluent line, and less turbulence. We therefore interpret the strong correlation between marine species richness and this new index, BI, to the combination of the dimensions of the intertidal zone (tide and slope) and the measures of swash climate (slope) and sand particle size. The results of this study mark a full circle in our study of the relationships between sandy beach communities and the physical environment by confirming the first quantitative analysis that demonstrated good correlation between species richness/abundance and beach face slope and sand particle size (MCLACHLAN, WOODRIDGE, and DYE, 1981).

How does this new index, BI, couple to beach type? Some typical examples of different beach types illustrate this.

Beach 1 Sand 125 μm, Tide range 5 m, Slope 1/80, macrotidal ultradissipative,
BI = log(4 × 5 × 80) = 3.20

Beach 2 Sand 500 μm, Tide range 1 m, Slope 1/10, microtidal reflective,
BI = log(2 × 1 × 10) = 1.30

Beach 3 Sand 250 μm, Tide range 2 m, Slope 1/25, micro/mesotidal intermediate,
BI = log(3 × 2 × 25) = 2.17.

Thus, values for BI below 1.5 indicate microtidal reflective beaches, and values above 3 indicate macrotidal dissipative beaches. The maximum likely value is

Sand 63 μm, Tide 8 m, Slope 1/100,

BI = log(5 × 8 × 100) = 3.60,

and the minimum likely value is

Sand 1800 μm, Tide 0.5 m, Slope 1/5,

BI = log(0.1 × 0.5 × 5) = 0.11.

For practical purposes, ecologists will want to use linear models, and BI will be best for large-scale comparisons of species richness, whereas for regional studies and analysis of patterns in abundance and biomass, the logarithm of (1/slope) will be most useful if tide range is uniform.

This analysis has confirmed the role of latitude in influencing marine species richness. There are also latitudinal effects in the other two community parameters. As found by Brazeiro (1999), latitude effects are weaker than effects of the physical variables. Nevertheless our data lend support to earlier findings (Hacking, 1997; McLachlan *et al.,* 1998; Soares, 2003) of a greater species pool in the tropics. Abundance and biomass, however, tend to increase toward temperate regions, where there is a greater preponderance of dissipative beaches because of higher wave energy. Seasonality might also be greater in temperate beaches, a factor we have not considered.

The foregoing results have shown that the number of species recorded in a beach transect survey increases with increasing tide range, finer sand, and flatter slope. If slope is taken as a measure of swash climate, and latitude effects are also considered, this information can be brought together in an expansion of existing hypotheses of exclusion of species by swash, sand, and instability (Brazeiro, 2001; McLachlan, 2001; McLachlan, *et al.* 1993). On a global scale, the number of species recorded in a beach transect study is primarily determined by four physical factors: it is maximum (1) where beaches experience large tides and (2) at low latitudes under conditions of (3) fine sand and (4) benign swash climates (*i.e.,* flat slopes). Species richness decreases away from these conditions because smaller tides allow fewer intertidal niches, the species pool decreases with higher latitudes, and coarse sand and harsh swash climates exclude some species. This can be considered a hypothesis of physical control at the large scale. On finer scales and toward dissipative beach states, biological factors might become more important in structuring sandy beach macrobenthic communities.

In this analysis, we have not considered biological interactions for several reasons: biological data, such as primary production values for the sampled locations, were not available; conclusive support for biological interactions on sandy beaches is not generally available; data on predation mechanisms are limited; and the scale of our study reduces the potential significance of most biological factors. However, we recognize that biomass, in particular, could be strongly influenced by inshore productivity.

The predictability of macrofauna community response to beach types globally has wide implications for the management and conservation of biodiversity on sandy beaches. On the large scale, beaches with high biodiversity potential could be identified from a knowledge of tide, wave, and sediment regimes without need for surveys. At a more local level, beaches could be compared and prioritized for conservation with the use of these indices. Our results on the role of sand particle size also indicate the importance in beach nourishment of selecting appropriate particle size for borrow material.

Sandy beach intertidal macrofauna species richness is mainly controlled by the physical environment on the large scale. Most environmental factors play some role: sand, tides, waves, beach face slope, and latitude. In concert, they determine the nature of the intertidal gradient and the swash climate and, therefore, which species are able to establish permanent populations. The roles of latitude and beach length require more study, as does the relative importance of pre- and postsettlement processes. It will be necessary to move beyond the correlative approach toward an experimental analysis of cause and effect to address these issues and to understand patterns on finer scales.

LITERATURE CITED

Alexander, R.R.; Stanton, R.J., and Dodd, J.R., 1993. Influence of sediment grain size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of selected Neogene clams. *Palaios* 8, 289–303.

Borzone, C.A.; Souza, J.R.B., and Soares, A.G., 1996. Morphodynamic influence on the structure of inter and subtidal macrofauna communities of subtropical sandy beaches. *Revista Chilena de Historia Natural,* 69, 565–577.

Brazeiro, A., 1999. Community patterns in sandy beaches of Chile: richness, composition, distribution and abundance of species. *Revista Chilena de Historia Natural,* 72, 93–105.

Brazeiro, A., 2001. The relationship between species richness and morphodynamics in sandy beaches: which are the underlying factors? *Marine Ecology Progress Series,* 224, 35–44.

Chow, G.C., 1960. Tests of equality between different sets of coefficients in two linear regressions. *Econometrica,* 28, 591–605.

Defeo, O. and Martinez, G., 2003. The habitat harshness hypothesis revisited: life history of the isopod *Excirolano braziliensis* in sandy beaches with contrasting morphodynamics. *Journal of the Marine Biological Association of the United Kingdom,* 83, 331–340.

Defeo, O. and Rueda, M., 2002. Spatial structure, sampling design and abundance estimates in sandy beach macrofauna: some warnings and new perspectives. *Marine Biology,* 140, 1215–1225.

Defeo, O.; Gomez, J., and Lercari, D., 2001. Testing the swash exclusion hypothesis in sandy beach populations: the mole crab *Emerita brasiliensis* in Uruguay. *Marine Ecology Progress Series,* 212, 159–170.

Defeo, O.; Jaramillo, E., and Lyonnet, A., 1992. Community structure and intertidal zonation of the macrofauna on the Atlantic coast of Uruguay. *Journal of Coastal Research,* 8, 830–839.

DEGRAER, S.; VOLCKAERT, A., and VINCX, M., 2003. Macrobenthic zonation patterns along a morphodynamic continues of macrotidal, low tide bor/rip and ultra-dissipative sandy beach. *Estuarine Coastal and Shelf Science,* 56, 459–468.

DEXTER, D.M., 1992. Sandy beach community structure: the role of exposure and latitude. *Journal of Biogeography,* 19, 59–66.

DUGAN, J.E. and HUBBARD, D.M., 1996. Local variation in populations of the sand crab *Emerita analoga* on sandy beaches in southern California. *Revista Chilena de Historia Natural,* 69, 579–588.

DUGAN, J.E.; HUBBARD, D.M., and LASTRA, M., 2000. Burrowing abilities and swash behaviour of three crabs, *Emerita analoga* Stimpson, *Blepharipoda occidentalis* Randall, and *Lepidopa californica* Efford (Anomura, Hippoidea), of exposed sandy beaches. *Journal of Experimental Marine Biology and Ecology,* 255, 229–245.

DYE, A.; MCLACHLAN, A., and WOOLDRIDGE, T., 1981. The ecology of sandy beaches in Natal. *South African Journal of Zoology,* 16, 200–209.

GIBBS, R.J.; MATTHEWS, M.D., and LINK, P.A., 1971. The relationship between sphere size and settling velocity. *Journal of Sedimentary Petrology,* 41, 7–18.

GUJARATI, D.N., 1970. Use of dummy variables in regression analysis: a generalization. *American Statistician,* 24, 18–21.

HACKING, N., 1997. Sandy Beach Macrofauna of Eastern Australia: a Geographical Comparison. Armidale, Australia: University of New England, Doctoral thesis, 292p.

JARAMILLO, E.; DUARTE, C., and CONTRERAS, H., 2000. Sandy beach macroinfauna from the coast of Ancud, Isla de Chiloe, Southern Chile. *Revista Chilena de Historia Natural,* 73, 771–786.

JARAMILLO, E.; MCLACHLAN, A., and DUGAN, J., 1995. Total sample area and estimates of species richness in exposed sandy beaches. *Marine Ecology Progress Series,* 119, 311–314.

MCARDLE, S. and MCLACHLAN, A., 1991. Dynamics of the swash zone and effluent line on sandy beaches. *Marine Ecology Progress Series,* 76, 91–99.

MCARDLE, S. and MCLACHLAN, A., 1992. Sandy beach ecology: swash features relevant to the macrofauna. *Journal of Coastal Research,* 8, 398–407.

MCLACHLAN, A., 1985. The biomass of macro- and interstitial fauna on clean and wrack-covered beaches of Western Australia. *Estuarine Coastal and Shelf Science,* 21, 587–599.

MCLACHLAN, A., 1990. Dissipative beaches and macrofauna communities on exposed intertidal sands. *Journal of Coastal Research,* 6, 57–71.

MCLACHLAN, A., 2001. Coastal beach ecosystems. *In:* LEWIN, R. (ed.), *Encyclopedia of Biodiversity.* New York, New York: Academic Press, pp. 741–751.

MCLACHLAN, A.; DE RUYCK, A.M.C., and HACKING, N., 1996. Community structure on sandy beaches: patterns of richness and zonation in relation to tide range and latitude. *Revista Chilena de Historia Natural,* 69, 451–467.

MCLACHLAN, A.; WOODRIDGE, T., and DYE, A.H., 1981. The ecology of sandy beaches in southern Africa. *South African Journal of Zoology,* 16, 219–231.

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,* 15, 27–38.

MCLACHLAN, A.; JARAMILLO, E.; DEFEO, O.; DUGAN, J.; DE RUYCK, A., and COETZEE, P., 1995. Adaptations of bivalves to different beach types. *Journal of Experimental Marine Biology and Ecology,* 187, 147–160.

MCLACHLAN, A.; FISHER, M.; AL-HABSI, H.N.; AL-SHUKAIRI, S., and AL-HABSI, A.M., 1998. Ecology of sandy beaches in Oman. *Journal of Coastal Conservation,* 4, 181–190.

NEL, P., 1995. The effect of sand particle size on sandy beach macrofauna. Port Elizabeth, South Africa: University of Port Elizabeth, Master's thesis, 98p.

NEL, P., 2001. Physical and biological factors structuring sandy beach macrofauna communities. Cape Town, South Africa: University of Cape Town, Doctoral thesis, 202p.

NOY-MEIR, I., 1979. Structure and function of desert ecosystems. *Israel Journal of Botany,* 28, 1–19.

RICCARDI, A. and BOURGET, E., 1999. Global patterns of macroinvertebrate biomass in marine intertidal communities. *Marine Ecology Progress Series,* 185, 21–35.

SHORT, A.D., 1996. The role of wave height, slope, tide range and embaymentisation in beach classification: a review. *Revista Chilena de Historia Natural,* 69, 589–604.

SOARES, A.G., 2003. Sandy beach morphodynamics and macrobenthic communities in temperate, subtropical and tropical regions—a macroecological approach. Port Elizabeth, South Africa: University of Port Elizabeth, Doctoral thesis, 152p.

SPSS, 2002. *Statistical Package for the Social Sciences,* Version 11.5. Chicago, Illinois: SPSS Inc.

VELOSO, V.G. and CARDOSO, R.S., 2001. The effect of morphodynamics on the spatial and temporal variation of the macrofauna of three sandy beaches on the Rio de Janeiro State, Brazil. *Journal of the Marine Biological Association of the United Kingdom,* 81, 1–7.

VELOSO, V.G.; CAETANO, C.H.S., and CARDOSO, R.S., 2003. Composition, structure and zonation of intertidal macrofauna in relation to physical factors in microtidal sandy beaches in Rio de Janeiro State, Brazil. *Scientia Marina,* 67, 393–402.