

COASTAL BEACH ECOSYSTEMS

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GLOSSARY

- accretionary** Accumulating sand.
- dissipative beaches** Wide, flat beaches.
- effluent line** Level on the beach face where the water table intersects the surface.
- macrotidal** Describing a spring tide range of more than 4 m.
- microtidal** Describing a spring tide range of less than 2 m.
- morphodynamics** Interactions between the physical structure and the water and sediment movement in a beach and surf zone environment.
- psammophilic** Sand-loving.
- reflective beaches** Narrow, steep beaches.
- transect** A linear series of samples, for example, across the intertidal zone.
- supralittoral** Immediately above the intertidal zone.

EXPOSED OCEAN BEACHES ARE HARSH AND DYNAMIC ENVIRONMENTS controlled by waves, tides, and sediment type. Global patterns of macrofauna biodiversity on sandy beaches are tightly coupled to these physical features of the beach environment and can be reliably predicted on the basis of beach type.

I. INTRODUCTION

The world has entered a biodiversity crisis. The rapid loss of species as a consequence of human alteration of the biosphere has attracted widespread attention among ecologists and spawned a voluminous literature concerning the cataloguing, description, prediction, rescue, and management of biodiversity. Marine ecologists have long been interested in explaining patterns in community diversity, especially in the benthos. Much of this effort has been directed at deciphering the role of biological interactions, such as competition, in maintaining diverse communities, and this debate has perhaps been most pronounced amongst workers interested in deep sea-floor and rocky shore environments. However, it has been suggested that competition is relatively unimportant in intertidal sediments (Peterson, 1979), where predation, recruitment, and other processes may exert greater influence on community structure (Reise, 1985).

Despite implicit assumptions of the underlying importance of physical environmental features and processes in influencing diversity in marine benthic com-

munities, it has been much more fashionable to look for biological explanations, especially in competitive interactions. This has perhaps been an oversight and abiotic factors have not been given adequate attention. This article addresses this shortcoming by examining a physically controlled ecosystem and determining to what extent biodiversity can be predicted by physical variables alone.

Sandy beaches dominate the ocean shorelines of all temperate and tropical continental coasts (Davies, 1972). Sandy beaches are devoid of any biological structures and their morphology and dynamics can be defined in terms of three interacting factors: waves, tides, and sand particle size. This simplicity should make understanding of such systems relatively elementary. However, relative to other shore types, beaches have been rather neglected by ecologists.

Here I describe the global range of wave-exposed, sandy beach types that can occur in response to changes in the values of their three defining variables, namely, waves, tides, and sand. I explore the extent to which the diversity and abundance of their intertidal macrobenthic communities can be explained by these factors, and then consider biological and biogeographic issues.

II. SANDY BEACH TYPES

Ocean beaches are defined by the interactions of the wave energy they experience, their tidal regimes, and the nature of the sand available for sorting and transport by the tides and waves. The simplest overall index of beach state is the beach slope, which is a product of the interaction among all three of these variables (Bascom, 1980; Short, 1996): beach face slopes flatten as wave energy increases, tide range increases, or particle size decreases, if other factors are kept constant. Thus the flattest beaches occur in macrotidal regions of high wave energy and fine sand, and the steepest beaches occur in microtidal regions with low wave energy and coarse sand. A range of beach morphodynamic types can be distinguished between these extremes.

In a microtidal regime, where beaches are wave dominated, three beach states can be recognized: reflective, intermediate, and dissipative. The reflective beach, characterized by a steep face and absence of a surf zone, occurs under a combination of coarse sand and gentle waves. The shoreward transport of sand, which occurs under these conditions, causes all sediment to be stored on the subaerial beach face; the reflective beach thus represents the accretionary extreme in beach states.

Waves surge up the beach face, where they may break before being reflected back to sea (Fig. 1).

Dissipative beaches, in contrast, are a product of large waves moving over fine sand. This results in a flat beach face and wide surf zone. Waves break far out and dissipate their energy while traversing the surf zone as bores before expiring as swash on the beach face. Dissipative beaches, with their sand spread out over extensive surf zones, thus represent the erosional extreme in beach states. Between these two extremes, intermediate beaches are distinguished by the presence of surf zones that are smaller than in the dissipative situation and generally 20–100 m wide. The intermediate surf zone characteristically has well-developed bars (sandbanks) and channels with rip currents (see Fig. 1).

Beaches are not locked into a single morphodynamic state and respond to changes in wave energy by moving towards dissipative conditions during storms (and spring tides, which are of maximum range and occur during the new and full moons) and towards reflective conditions during calm weather (and neap tides, which are of minimum range and occur during the first and third quarters of the moon); that is, sand erodes or accretes on the beach face as wave height (and tide range) rises or drops.

There is a useful index that conveniently describes the state of a microtidal beach, that is, the extent to which wave energy is dissipated or reflected. Dean's parameter, also known as the dimensionless fall velocity, is given by:

$$\omega \equiv \text{wave energy/sand fall velocity}$$

where wave energy is given by modal breaker height (cm) divided by modal wave period (seconds) and sand fall velocity is the sinking rate (cm per second) of the mean sand particle size on the beach. Values for ω that are <2 generally indicate reflective beaches and values >5 indicate dissipative beaches.

The foregoing description of beach types adequately covers most microtidal situations, but increasing tide range complicates the picture and requires further explanation. Tides play a role essentially similar to that of waves in that increasing tide range tends to make beaches even more dissipative (Short, 1996). This occurs because increasing tide range allows the surf zone to work back and forth over a wider area. Indeed, fully reflective beaches will not occur when tide range exceeds 1–1.5 m. On beaches with larger tides reflective conditions can only occur at the top of the shore between the neap and spring high-water swash lines, an area reached by swash but not surf—this area is con-

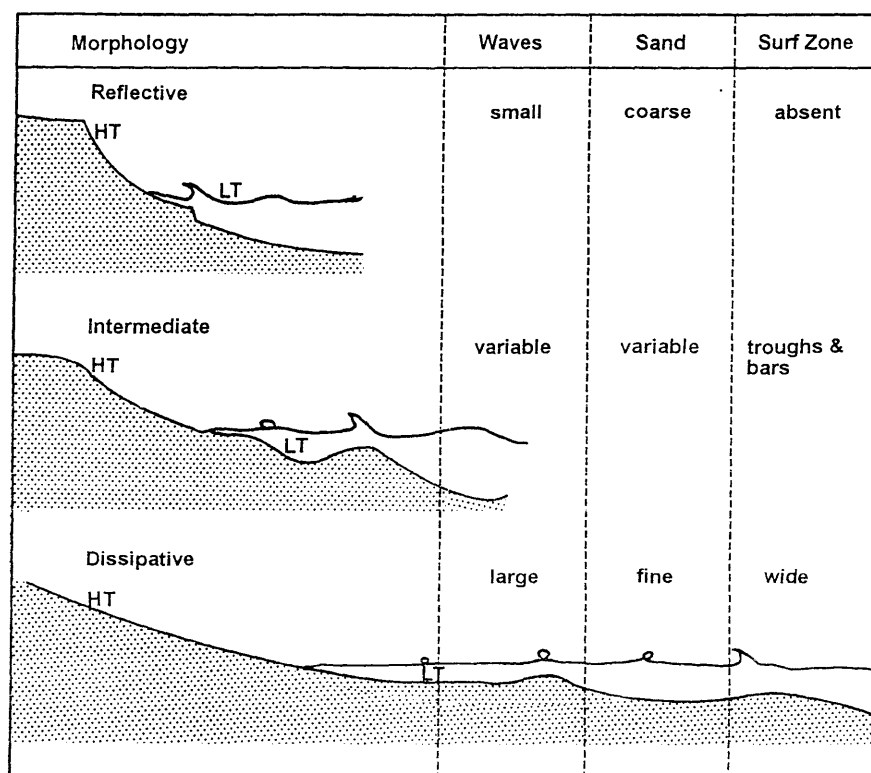


FIGURE 1 Three morphodynamic states of microtidal beaches (HT = high tide, LT = low tide).

trolled by swash processes and is accretionary and steep, in contrast to the rest of the shore, where shoaling and breaking wave and bore processes operate.

Under large tidal regimes (mean spring range >4 m) beaches are generally tide dominated, whereas in intermediate situations (tide range 2–4 m) they are mixed and either waves or tides can dominate. A useful index of the relative importance of waves and tides is the relative tide range (RTR), which is given by the mean spring tide range divided by the modal breaker height. By combining the dimensionless fall velocity and RTR, a two-dimensional model of beach states can be produced (Fig. 2).

Besides beach slope, omega, and RTR, another useful index of beach morphodynamic conditions is the beach state index (BSI; McLachlan *et al.*, 1993). BSI combines measures of wave energy, tide range, and sand fall velocity into one index:

$$BSI = \log[(\omega) \times (\text{maximum tide range}/0.8 \text{ m})]$$

This index is rendered dimensionless by dividing the tide range by an equilibrium tide range of 0.8 m. The BSI has values between 0 and 2; microtidal, reflective

beaches score <0.5, intermediate to dissipative beaches score 0.7–1.5, and macrotidal ultradissipative beaches and sand flats generally score >1.5.

III. SAMPLING BEACH MACROFAUNA

Community studies of beach macrofauna make use of standard beach transect surveys. These typically involve quantitative sampling across the intertidal zone by excavating quadrats and passing the sand through a screen of 1-mm mesh, the optimum mesh size. Other mesh sizes, for example, 0.5 mm or 2 mm, have also been used and can significantly influence the results. The finer mesh size is more effective in sampling larval stages of macrofauna and can collect some larger meiofauna, but it is not practical in coarser sands.

In the context of this article, each transect survey represents one datum point in the sense that beaches are compared as if they were units. Data should only be used from transect surveys where the total sampling effort (assessed as total area excavated, i.e., levels \times

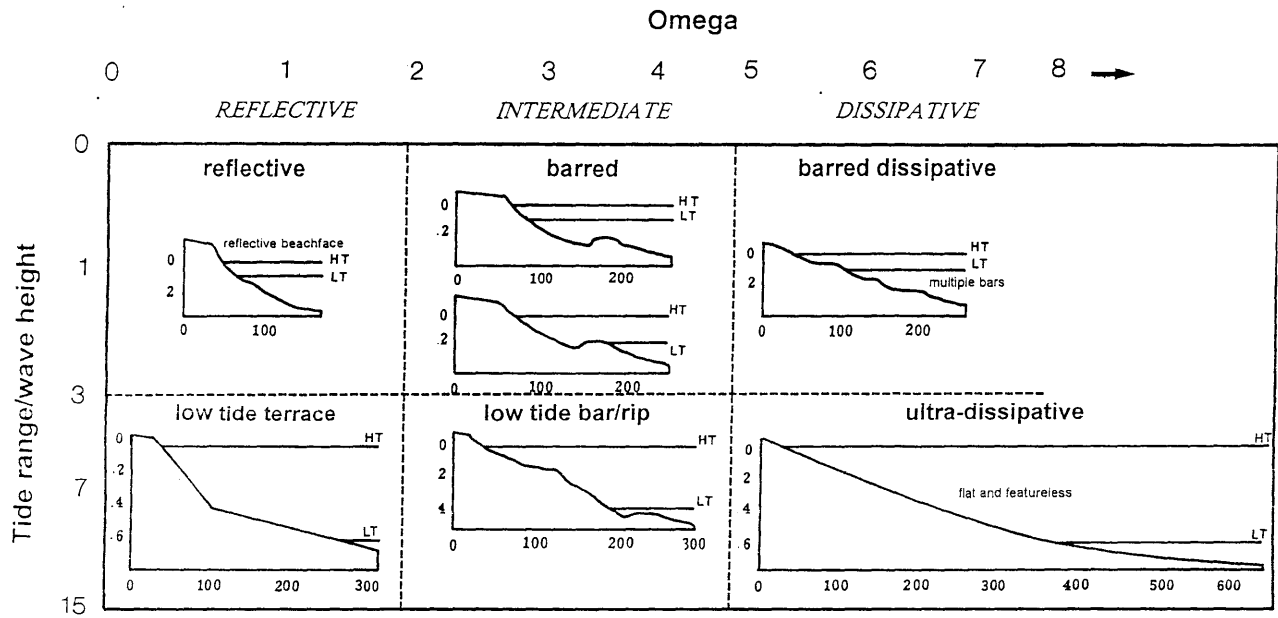


FIGURE 2 Two-dimensional model of beach states. (After Short, 1996.) Distances are in meters.

replicates \times quadrat size) per beach exceeded 2 m². Smaller sample sizes introduce problems of undersampling, as illustrated by species/area relationships in Fig. 3 (Jaramillo *et al.*, 1995). The absence of an asymptote in Fig. 3 means that total species richness is never sampled, but the curves indicate that, for microtidal beaches a sample area of 3 m² is effective; whereas macrotidal beaches require more. I will use richness rather than diversity indices because it is more conservative. Species richness (or number of species) in beach surveys is summed for all samples in a transect and abundance is usually calculated per running meter of transect, so results are expressed as the number of species per transect and the number of individuals per linear meter of transect.

IV. COMPOSITION AND ZONATION

The intertidal macrofauna of ocean sandy beaches is usually dominated by crustaceans, molluscs, and polychaetes, with other groups, such as insects, nemertean worms, echinoderms, anemones, and fishes, being of minor importance or restricted to the extreme upper or lower fringes. Crustaceans tend to be most successful in reflective conditions, where their great mobility enables them to cope with turbulence. Among the crustaceans, ocapodid crabs, hippid crabs, cirolanid isopods, a variety of amphipods, and psammophilic mysids are

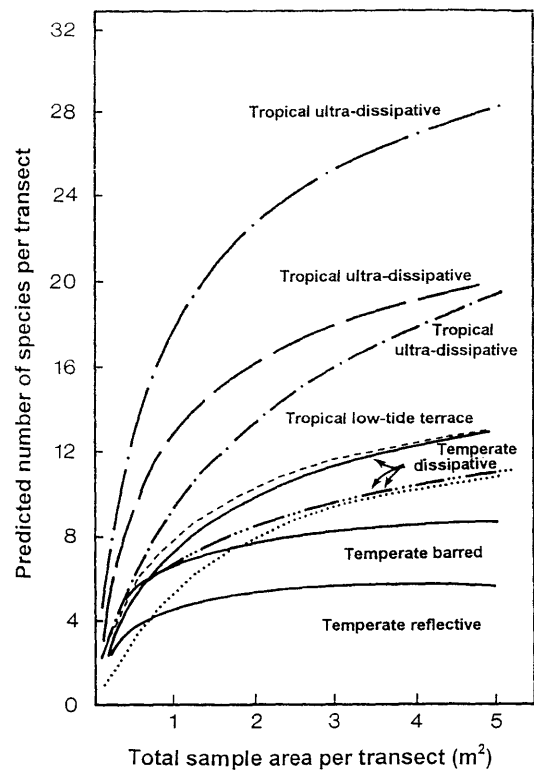


FIGURE 3 Species/area curves for sandy beach macrofauna. (After Jaramillo *et al.*, 1995.)

the most typical. Molluscs, both gastropods and bivalves, are successful over a wide range of beaches. Clams, in particular, may form large populations on high-energy dissipative beaches, where they can support commercial fisheries. Polychaetes tend to be the group that is most sensitive to beach state and are absent or scarce on reflective or coarse sand beaches. On lower-energy shores of fine sand, polychaetes can be particularly abundant and include predator/scavengers and deposit and suspension feeders.

Like all intertidal regions, sandy beaches display zonation of their macrofauna. Various models have been discussed, but the most applicable is that of Erik Dahl (see McLachlan and Jaramillo, 1995). This model identifies three zones on sandy beaches: a supralittoral zone characterized by ocypodid crabs in warm regions and talitrid amphipods in temperate areas; a littoral or midshore zone characterized by cirranid isopods and spionid and opheliid polychaetes; and a lower shore or sublittoral fringe with many groups, including hippid crabs, mysids, haustoriid and phoxocephalid amphipods, donacid clams, and nephtyid worms. The lower zone tends to reduce or even disappear in very reflective situations, but it can expand to a broad, species-rich terrace under dissipative conditions. The supralittoral zone, above the high-water mark or drift line, is present on all shores. Thus, on most shores there is a clear gradient of increasing species richness as one moves downshore, typically from one or two species in the supralittoral to many species on the lower shore. This

article focuses on between-beach diversity rather than variability within beaches.

V. GENERAL PATTERNS

McLachlan *et al.* (1981) were the first to demonstrate a relationship between beach type and biodiversity. Based on a survey of beaches around South Africa, they showed that the species richness of benthic macrofauna increased as beaches became flatter and particle size became finer (Fig. 4). They also demonstrated that faunal abundance increased exponentially as particle size decreased and beaches became flatter. At that time they were not aware of the beach state models that were first brought to the attention of ecologists two years later (Short and Wright in McLachlan and Erasmus, 1983). Since the South African coast is uniformly microtidal and subject to vigorous wave action throughout, these findings largely reflect the role of particle size in influencing microtidal beach state. The importance of beach slope, sand grain size, and wave exposure has also been stressed by other authors.

After taking into account the significance of morphodynamic models, a subsequent study that examined a wider range of beaches clearly showed a linear increase in species richness (and an exponential increase in abundance) per transect over a range of beach types from reflective to dissipative (Fig. 5; McLachlan, 1990). Taking this further, McLachlan *et al.* (1993) showed this trend to be global, based on data from four conti-

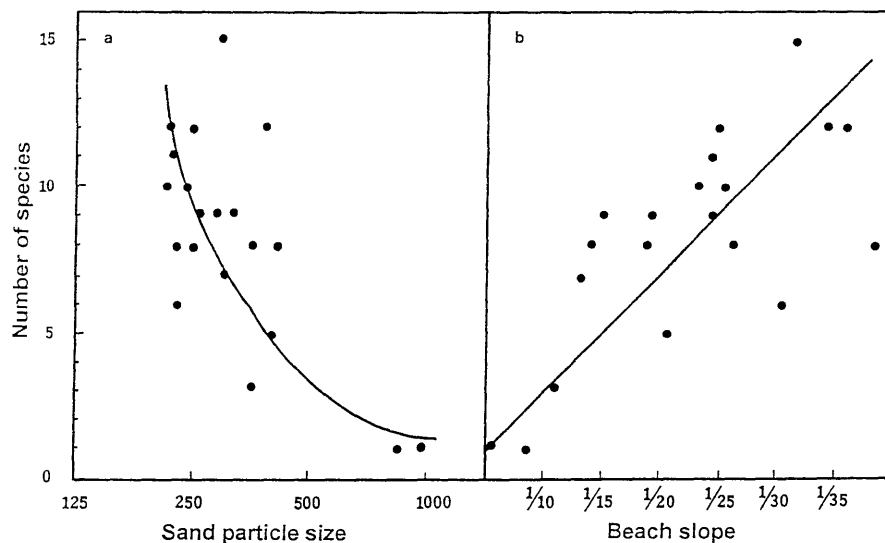


FIGURE 4 Species richness related to beach slope and grain size (in microns); early data from South Africa. (After McLachlan *et al.*, 1981.)

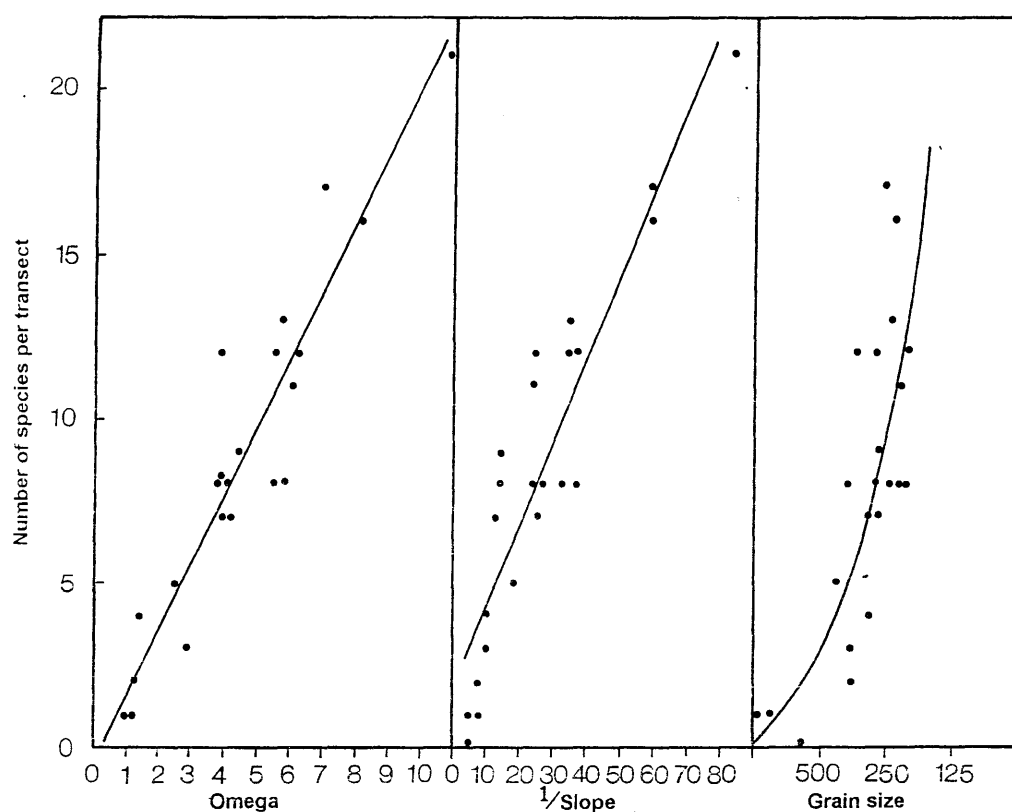


FIGURE 5 The first analysis of global patterns of species richness on sandy beaches. Grain size is in microns. (After McLachlan, 1990.)

nents (Fig. 6), and McLachlan *et al.* (1996) then examined an even wider data set, including macrotidal beaches, and showed excellent correlation using the BSI index. Further confirmation has come from data sets from Australia (Fig. 7; Hacking, 1997), New Zealand, Brazil, Madagascar, Spain, the United States and Oman.

The foregoing studies have confirmed that, for a diverse range of exposed sandy beach environments on five continents, intertidal macrofauna species richness per transect increases linearly with increasing values of BSI. Thus the number of species accommodated on an intertidal beach increases in response to increasing tide range, increasing wave energy, and decreasing sand particle size. In simple terms, this means that species richness increases as beaches become flatter and wider.

The width of sandy beaches ranges from as little as 10 m in reflective, microtidal situations to hundreds of meters in dissipative tidal flats, thus representing an order of magnitude range in the length of an intertidal transect. The total area sampled by various authors, however, has fallen within a much smaller range. Total

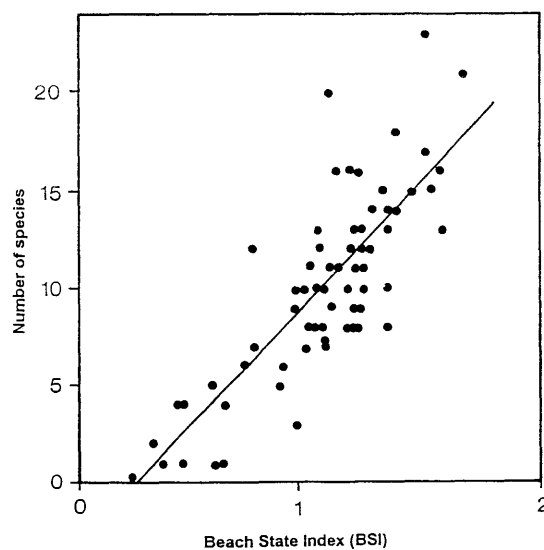


FIGURE 6 The first plot of species richness against BSI, based on data from four continents. (After McLachlan *et al.*, 1993.)

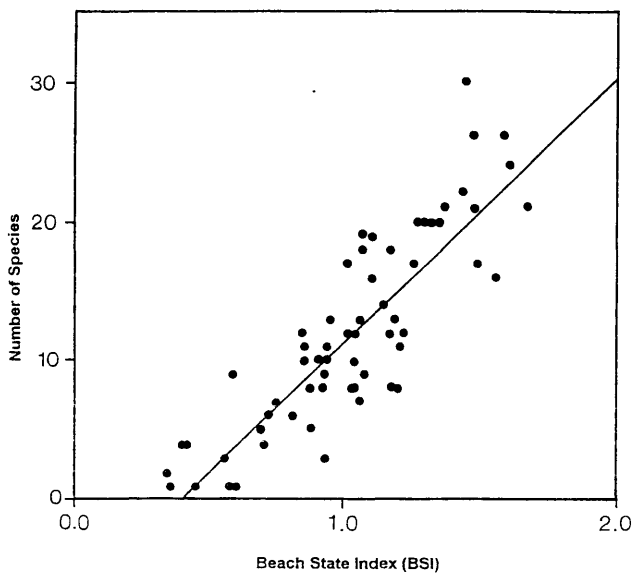


FIGURE 7 Compilation of species richness data from four continents, including wide-ranging surveys in Australia. (After Hacking, 1997.)

sample area per transect in the studies discussed here falls between 2 m² and 4.5 m², with most cases being around 3 m². The study by Jaramillo *et al.* (1995) concluded that a total sample area of 3 m² was sufficient to recover 90% of the species on microtidal beaches but would result in undersampling on wider beaches, such as macrotidal flats. This implies that actual richness on the latter beaches is higher than recorded in Figs. 5 and 6 and supports the suggestion of Hacking (1997) that the response of species richness to BSI may not be linear but may rather tend to be exponential over beaches with high BSI values. More work is needed to clarify this.

VI. LATITUDINAL AND OTHER EFFECTS

McLachlan (1990) suggested that, because wave energy is highest in temperate areas, these regions would enjoy a preponderance of dissipative beaches and hence greater species richness. Subsequently, Dexter (1992) proposed that tropical beaches harbor less diverse faunas than temperate beaches. However, this was based on empirical data and did not consider the role of morphodynamics. More recent work comparing beaches of the same morphodynamic state has indicated that tropical beaches may in fact support greater species richness than temperate beaches of the same type; ex-

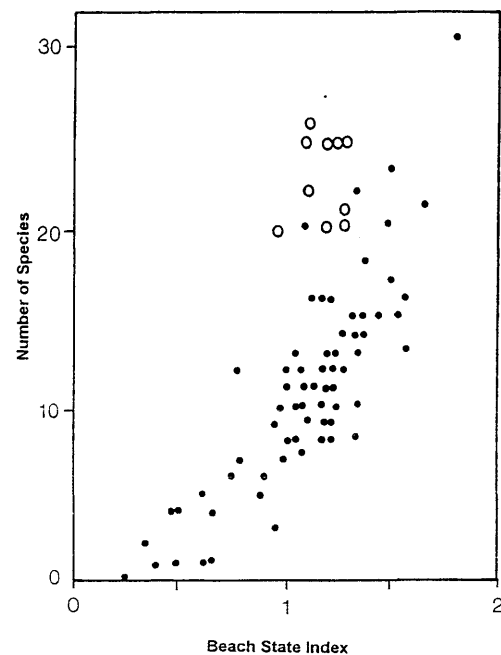


FIGURE 8 Data from tropical beaches in Oman (O) plotted against global data showing elevated species richness. (After McLachlan *et al.*, 1999.)

ceptional species richness has been reported for beaches in Queensland and Oman (Fig. 8). Thus, in addition to the three physical factors listed earlier, latitude also appears to play a role in determining species richness. Certainly, tropical beaches do not seem to be poorer in species than temperate beaches of similar types.

A final factor of importance to intertidal beach macrofauna communities may be beach length. In Australia, it has been shown that angling activity and success, and thus intertidal bait organism communities, may become richer as beach length increases; a non-linear relationship between beach length and species richness has been found for Chilean beaches, and studies showing clam abundance increasing with beach length also support this. Experience suggests that short "pocket" beaches are often impoverished and this factor deserves further study.

VII. CAUSATIVE FACTORS

For ocean beaches, the number of species recorded in a single transect survey ranges from 1 to 40, if insects are excluded. Reflective beaches with coarse sand, dynamic swash action, and rapid drainage may be devoid of intertidal species and harbor only supralittoral forms,

whereas more dissipative beaches and flats may harbor 20–40 species at least. Loss of species under reflective beach conditions occurs mainly in the lower intertidal, not the supralittoral zone. It is in the lower intertidal zone where most species are added as the shore flattens towards the dissipative or tidal flat extreme. So the question must be raised: Why are so many species excluded towards the reflective beach extreme?

Considering only between-beach patterns, that is, if whole beaches are compared, the physical environment impinging directly on beach fauna differs primarily in two sets of variables. These two variables are (1) the movement of water over and through the beach face, which has been termed the swash climate, and (2) the sediment particle size range. This ignores the normal intertidal gradient of exposure, which is relevant to any within-beach study.

On most beaches, waves do not break directly in the intertidal but rather in the surf zone. It is only after transformation to bores and crossing the surf zone that wave energy reaches the beach face as swash. Thus, intertidal fauna experience the effects of waves, tides, and the surf zone transformation of these forces as the swash “climate” on the beach face. McLachlan (1990) suggested that it was not the beach state or morphodynamic type itself that was important for the fauna, but rather the swash climate associated with it.

There is a consistent relationship between beach type and swash climate features. Dissipative beaches are characterized by swash with extended periods and lengths, variable speeds, most swash activity below the effluent line (water table outcrop), and fairly laminar swash flow. Reflective beaches display the opposite swash features: the swash climate is extremely harsh; there are high swash speeds throughout the tidal cycle; and waves break directly in the intertidal, resulting in considerable turbulence and increased probability of animals being stranded above the effluent line where unsaturated sand might make burrowing difficult. Swash drainage through the sand is also rapid on reflective beaches and there is little inundation time for feeding. Physical stress in the swash zone on the beach face thus increases from dissipative to reflective beaches.

The “swash control hypothesis” suggested that swash climate controlled beach macrofaunal community structure (McLachlan, 1990). McLachlan *et al.* (1993) refined these ideas to define the “swash exclusion hypothesis”: the swash climate associated with dissipative beaches is considered sufficiently accommodating and varied to enable most psammophilic macrofauna species to maintain viable populations; however, as beach type changes through intermediate states toward re-

flective conditions, the increasingly inhospitable swash climate excludes more and more species until, in the fully reflective situation, only supralittoral forms (tali-trid amphipods, ocyrodid crabs, insects), which live “outside” the area affected by swash, remain. Swash also has important indirect effects on the macrofauna since animals move, feed, and reproduce in the water moving over the beach face. Swash patterns and percolation of water through the beach face above the effluent line are closely coupled.

The coupling between beach state and swash climate is clear, but there is no published study undertaking a simultaneous examination of swash climate and fauna. However, recent work in New Zealand shows a strong correlation between community parameters and swash climate. Further, it has been demonstrated that the hallmarks of bivalves that are able to survive on reflective beaches are small size and high density, both adaptations for stability under turbulent conditions. The harsh swash climate on reflective beaches thus appears to select for relatively small size and high body density in bivalves, but may select for larger size and mobility in crustaceans.

It is now clear that swash is not the only physical factor of importance to beach macrofauna; sand particle size also plays a role. Ongoing work shows that small body sizes tend to be excluded in coarse sediments and various authors have demonstrated how sand particle size influences burrowing rate in a variety of sandy beach species—in most cases coarse sand makes burrowing difficult or impossible. Sandy beach isopods, for example, have been shown to select finer substrates. Coarse sand can cause vicious abrasion, especially of bivalve shells, and it reduces sand saturation by raising permeability and hastening drainage.

In the only study to examine faunal community response to swash and sediment factors over a range of each types, Gary Stephenson and I have concluded that both sediment particle size and swash climate directly influence the number of species of macroinfauna on wave-exposed sandy beaches in northern New Zealand. Since both factors are closely related to beach type, this explains the good correlations between beach type and macroinfaunal species richness. In general, conditions of fine sediment and long swash periods, with limited swash activity above the effluent line, appear most conducive to developing rich faunas. The key characteristic of this type of swash may, in fact, be its low degree of turbulence and laminar flow over fine, saturated sand, enabling even delicate forms to survive. Thus Stephenson and I propose that the swash exclusion hypothesis should be modified to a hypothesis of physical exclusion

of species by coarse sand, turbulent swash, and low effluent lines as one moves towards the reflective beach condition.

VIII. BIOLOGICAL FACTORS

There is little evidence of biological factors controlling intertidal beach macrofauna. Predation by birds, fishes, and invertebrates is well documented, indeed quantified (Brown and McLachlan, 1990), but it has not been demonstrated to influence species richness. The absence of an underlying base of competition probably precludes this. In such dynamic, three-dimensional environments, with highly mobile faunas, competition is limited and indicated in only a few exceptional cases.

One biological factor that can add to species richness is the input of seaweed wrack to a beach, if the input is not so great as to cause disturbance, smothering, and deoxygenation. In cases of moderate input, many wrack-associated species may be added to the usual beach fauna. A well-developed drift line can also add many insects. Progressing along the gradient from reflective, wave-dominated beaches to macrotidal flats where tidal factors are more important than waves, increasing stability of the substrate leads to the formation of permanent burrows and more complex communities with greater scope for biological interactions. At some point, as yet not defined, in the continuum between beaches and tidal flats, biological factors are likely to become more important than outlined here for wave-exposed beaches.

IX. DISCUSSION

Three paradigms provide perspective for our current understanding of the factors controlling the large-scale patterns of species richness of sandy beach intertidal benthic macrofauna.

The Autecological Hypothesis The autecological hypothesis of I. Noy-Meir states that inhabitants of physically controlled environments respond independently to the physical environment. This implies that the presence or absence of a species on a beach will be little influenced by biological factors.

Beach Morphodynamic Models Beach morphodynamic states can be defined by three physical factors: wave energy, tide range, and sand particles size. Increases in wave and tide energy and decreases in sand

particle size all result in beaches becoming wider, flatter, and more dissipative.

Richness and Abundance Coupled to Beach State Intertidal sandy beach macrofauna increase linearly (probably) in species richness and exponentially in abundance in response to the increasing dissipativeness of beaches, that is, from microtidal reflective systems through high-energy dissipative systems to ultradissipative tidal flats.

Beyond these paradigms, two further hypotheses can be erected to explain the known patterns of sandy beach macrofauna biodiversity:

Latitude and Beach Length Tropical beaches support more species than do temperate beaches of the same type, and long beaches appear to support greater abundance and more species than do short (or pocket) beaches. The former trend may be due to the greater species pool available to colonize beaches in the tropics, whereas the latter trend reflects the more favorable surf circulation patterns on long beaches, which promote greater retention of particulate primary production, better recruitment of planktonic larvae, and larger and therefore more resilient adult populations. Long beaches are also more persistent, that is, unlikely to erode away completely during storms, as can happen on pocket beaches.

Swash and Sand Control Two physical factors define the immediate environment experienced by the beach macrofauna and may therefore control species richness: the swash climate and sand particle size. Reflective beaches have harsh swash climates in the sense of high turbulence, short swash periods, and rapid swash drainage, resulting in low effluent lines; beaches at the other extreme have more benign swash climates in the form of long-period swash/tidal bores with laminar flow over the beach face and low turbulence, keeping much of the beach saturated because of the slow drainage. All beach fauna can burrow into saturated sand and, in terms of grain size, fine to medium sands seem optimal for most beach fauna. Coarse sand appears to exclude small or delicate forms by crushing and abrasion and most species experience decreasing burrowing efficiency in coarse sands. Thus harsh swash climates and coarse sand associated with reflective beaches appear to exclude many species. The degree of exclusion of species by these factors will increase from the dissipative/macrotidal to the reflective/microtidal end of the continuum of beach morphodynamic types.

It has been stated that community structure in harsh

environments is in nonequilibrium, characterized by the decoupling of loose biotic interactions and the independent response of species to environmental variations. Thus populations and communities in stressful environments may respond primarily to the abiotic environment, that is, be highly stochastic and thus loosely structured. This is a restatement of the idea of a physically controlled community and the autecological hypothesis and appears to be highly relevant to the case of sandy beaches. The dynamic, three-dimensional nature of wave-exposed ocean beaches, their shifting populations, and the absence of biological structures (they are even devoid of permanent burrows in most cases) leave limited scope for biological controls of community structure. Furthermore, the evidence presented here has shown that an index based only on the three physical variables that define a beach (tides, waves, and sand) has high predictive power to estimate the species richness likely to be encountered on ocean beaches. Latitude, beach length, and biological interactions may contribute additionally, to a small extent, to explain some of the variability in the data, but their roles have yet to be conclusively demonstrated in high-energy beach environments.

Several lines of research could improve our understanding of patterns of sandy beach biodiversity and their control.

1. The BSI is a simple index developed partly by ecologists and fitted to a few data sets. Collaborative work between ecologists and geomorphologists, using all the data available at present and investigating new regions, could lead to refinement of this to an even more appropriate index (or indices) with greater predictive power.
2. Comparative work contrasting similar beaches in the tropics and temperate latitudes is needed to confirm conclusively whether tropical beaches do indeed support higher diversity and what controls this.
3. Once these processes are better understood, useful predictions could be made of global beach diversity patterns based purely on the global distribution of tide and wave regimes and sedimentology. This capability would be useful in predicting and identifying areas of high diversity and in planning coastal conservation strategies.

X. CONCLUSIONS

In the case of wave-exposed, ocean sandy beaches, the species richness of the intertidal (and immediately su-

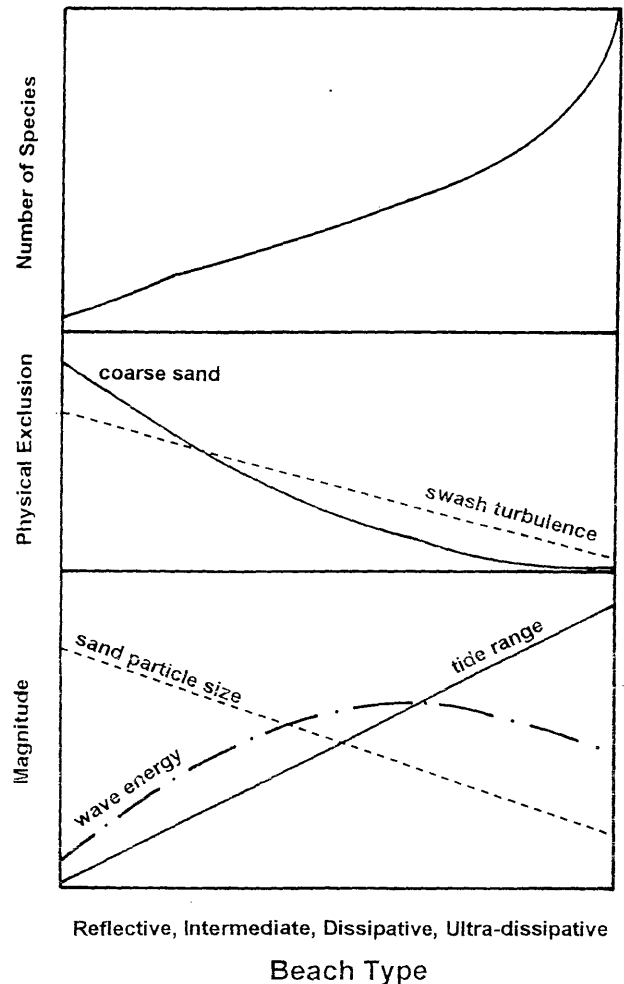


FIGURE 9 Simplified diagrammatic model of changes in defining variables (wave energy, tide range, and sand particle size), levels of physical stress induced by the substrate and swash, and species richness over a continuum from microtidal reflective to macrotidal ultra-dissipative sandy beaches.

pralittoral) macrobenthic fauna is strongly controlled by, and predictable on the basis of, the physical nature of individual beach environments rather than global biogeographic patterns. Beaches that tend toward the ultra dissipative/tidal flat extreme—the product of large tide ranges, vigorous wave action, and fine sand—harbor most sandy beach species likely to be encountered in a region. Progressing from this end of the beach continuum towards reflective conditions, that is, decreasing tide range or wave energy or increasing sand particle size, results in beaches becoming steeper and narrower and the increasing exclusion of species. On highly reflective beaches, intertidal macrofauna may be absent and only supralittoral forms remain. These relationships are illustrated in simplified form in Fig. 9.

The mechanisms by which species are increasingly excluded as one moves towards reflective conditions appear to relate primarily to two environmental variables, the swash climate and sand particle size. Decreasing swash period, increasing swash turbulence, lower effluent lines, and coarse sand exclude delicate, less robust, and slower-moving species. At present our knowledge of how biogeographic factors influence species richness on sandy beaches is limited, but it appears that tropical beaches may support more species than do temperate beaches of similar morphodynamic type. There is considerable scope for further research to clarify these patterns and to decipher cause and effect relationships.

See Also the Following Articles

ESTUARINE ECOSYSTEMS • INTERTIDAL ECOSYSTEMS • LAKE AND POND ECOSYSTEMS • MARINE ECOSYSTEMS • RIVER ECOSYSTEMS

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