Species – area relationships for sandy beach macrobenthos in the context of intertidal width

OCEANOLOGIA, 49 (1), 2007.
pp. 91–98.

KEYWORDS
Sandy beaches
Macrofauna
Benthos
Island biogeography

Anton McLachlan*
Atsu Dorvlo

College of Agricultural & Marine Sciences
and College of Science,
Sultan Qaboos University,
Sultanate of Oman;

e-mail: anton.m@squ.edu.om

*corresponding author

Received 27 November 2006, revised 22 January 2007, accepted 26 January 2007.

Abstract

The marine species richness (MSR) recorded in 159 sandy beach surveys was analysed in relation to beach width (W). MSR is the number of macrobenthic species collected in a standard intertidal transect survey, excluding insects. Beach width (W) was estimated by dividing the spring tide range [m] by the beach face slope, to give a value in [m]. The relationship between MSR and W was best described by a semilog (exponential) model, which was highly significant:

$$\mathrm{MSR} = -5.2 + 10.8 \log \mathrm{W}.$$

The fit of a power model ($\mathrm{MSR} = c\mathrm{W}^z$) was also significant. The steep slope of the curve for a power model ($z = 0.49$) suggests that beaches function as isolated rather than contiguous habitats and that the nature of the habitat becomes more benign as beaches widen. There are some latitudinal effects, with tropical beaches displaying a higher species-area relationship for any beach width than other regions.

1. Introduction

The relationship between area and species richness is one of the most widely accepted and intensively studied issues in ecology. The increase in the total number of species recorded as area increases has been documented

The complete text of the paper is available at http://www.iopan.gda.pl/oceanologia/

for a considerable range of habitats and taxa. The usual model for this relationship is a power function of the form:

$$S = c\,A^{z},$$

where S is species richness, A is area and c and z are constants (i.e. the intercept and slope of the log-log relationship). This model has also been applied in island biogeography theory to explain the increasing number of species on larger islands (MacArthur & Wilson 1967). In general, z values range from 0.1 to 0.4, the slope of the curve usually being around 0.3 for islands but lower for mainland samples, typically about 0.2. The species-area effect may be due to multiple factors such as: more diverse habitats with increasing area permitting habitat specialist species to be added; direct area effects as a result of larger areas supporting larger populations, with a smaller chance of extinction; the greater chance of receiving colonists in larger areas. Additional factors may include greater population densities and decreasing edge effects in larger areas (for review, see Connor & McCoy 2001). Colonisation and extinction rates are strongly affected by the distance from source populations.

These species-area relationships, i.e. the increasing number of species found in larger areas, whether isolated (islands) or contiguous (mainland), are different from species accumulation curves (Gray et al. 2004). Whereas the former are linear increases with area (usually as log/log plots), the latter are asymptotic and represent the increasing proportion of species richness collected within a habitat as sampling effort increases. Species accumulation curves are similar to rarefaction curves (Sanders 1968) and show remarkably high species richness in coastal and marine sediments (Gray 2002).

Species accumulation curves have been used by sandy beach ecologists in order to evaluate the accuracy of sampling protocols and to estimate the minimum sample area required to provide reasonable estimates of species richness on sandy beaches (Hartnoll 1983, Jaramillo et al. 1995, Brazeiro 2001, Schoeman et al. 2003). These studies have shown that large areas (at least 4 m^2) need to be sampled to estimate species richness during intertidal transect studies of sandy beach macrofauna and that most published accounts have been underestimates. Although these studies have given an idea of species accumulation curves on sandy beaches, they did not consider species-area relationships. Indeed, to the best of our knowledge there is no published analysis of species-area relationships on sandy beaches.

McLachlan & Dorvlo (2005; 2007, in press) analysed the available literature on beach transect studies and considered macroscale patterns, including species richness. However, they did not address species-area relationships, showing only an increase in species richness from narrow reflective beaches to wide dissipative beaches. Similarly, Brazeiro (1999) showed some weak effects of beach length, species richness tending to decrease when beach length dropped below 2 km. It is now well recognised that sandy beaches occur in a range of types, from narrow, steep reflective beaches to wide, flat dissipative beaches. The former are produced by low wave and tide energy and coarse sand, the latter by high wave and tide energy and fine sand, with a corresponding gradient from harsh conditions to benign conditions and increasing species richness, abundance and density (McLachlan & Brown 2006). Further, it has been shown that, whereas latitudinal effects do occur in the form of increasing species richness towards the tropics, they are weaker than the community response to physical features of the beach (Brazeiro 1999, McLachlan & Dorvlo 2005).

The aim of this study was to consider the relationship between the species richness of marine intertidal macrofauna and area, as expressed by beach width, using the data set of McLachlan & Dorvlo (2005). These data, including the results of 161 sandy beach transect studies, enable an analysis of species-area relationships over a wide range of beach types and latitudes. More specifically, we aim to see whether the species-area relationship on sandy beaches conforms to the usual power (log-log) model, whether the slope of the relationship is indicative of the island or the mainland pattern, and whether there are any latitudinal effects.

2. Material and methods

We used the data set gathered by McLachlan & Dorvlo (2005) for 161 sandy beach transect studies from 14 sources, and this reference should be consulted for full details of these data. Two transects were excluded because they were considered tidal flats and not ocean beaches, leaving 159 transect studies for analysis. These 159 transect studies covered a full range of beach morphodynamic types from microtidal reflective beach to macrotidal dissipative, beach width spanning two orders of magnitude from 5 m to nearly 500 m. The beaches cut across all latitudes from tropical to cold temperate.

Only two parameters were considered in our initial analysis – the number of marine species recorded in each study (termed marine species richness, MSR, showing inventory richness) and an estimate of beach width; latitude was considered later. Marine species richness is the number of macrobenthic species (excluding insects) collected in a standard transect survey conducted by excavating quadrats across the intertidal zone from above the drift line down to the low tide swash zone. Polychaetes, crustaceans and molluscs were the main contributors to marine species richness in all cases.

The original data did not report beach width in all cases, so McLachlan & Dorvlo (2005) developed an index to estimate this, based on the maximum spring tide range in metres and the beach face slope. We refer to this index as beach width (W = tide/slope), since this index represents the distance along one dimension (the intertidal beach from the low to the high tide marks) and is expressed in [m]. For these data, the maximum spring tide range fell between 0.5 m and 6.5 m and the slope between 1/5 and 1/80. To obtain the area of a beach we would need to multiply beach width by the length of the beach, but such data are not available. However, assuming that beach lengths were roughly similar for beaches in all width categories, and considering that beach area would then be directly proportional to length, we use this as a proxy for area.

All data came from quantitative intertidal transects where beaches were sampled once between the low tide swash level and the drift line during spring low tides. There is no nestedness in these samples; all are independent and each transect is considered to represent a point in space and time, not the whole beach. However, these data have considerable noise for the following reasons: a) it is inherent in the nature of sandy beach sampling; b) different studies employed slightly different sampling strategies; c) standard transect surveys record only 50–70% of the total complement of species actually present along the transect (Jaramillo et al. 1995, Schoeman et al. 2003).

To explore patterns in these data we considered a variety of different plots of MSR against W on untransformed data and log transformed data using ordinary linear regression and a quadratic model. When considering latitude the data were divided into four groups based on sea temperature: tropical, subtropical, warm temperate and cold temperate. ANOVA was used to test for differences between the regressions for different latitudes.

3. Results

The species-area relationships for the data set for 159 beach transect surveys are presented as four plots of species richness against beach width (Fig. 1). It must be borne in mind that the effects of undersampling, i.e. underestimates of species richness, will be greater on wider beaches, so that the true relationship between species richness and beach width will be slightly steeper than illustrated in Fig. 1. The untransformed data (Fig. 1a) suggest an asymptotic relationship. However, Fig. 1b shows that the semilog or exponential model gives a remarkably close fit ($r^2 = 0.53$, $p > 0.001$), considering the noise inherent in these data. The usefulness of this semilog model may be a consequence of the use of width (one dimension) rather than area (two dimensions). The log-log transformed data can generate a power relationship (Fig. 1c), which is also highly significant ($r^2 = 0.47$, $p > 0.001$)

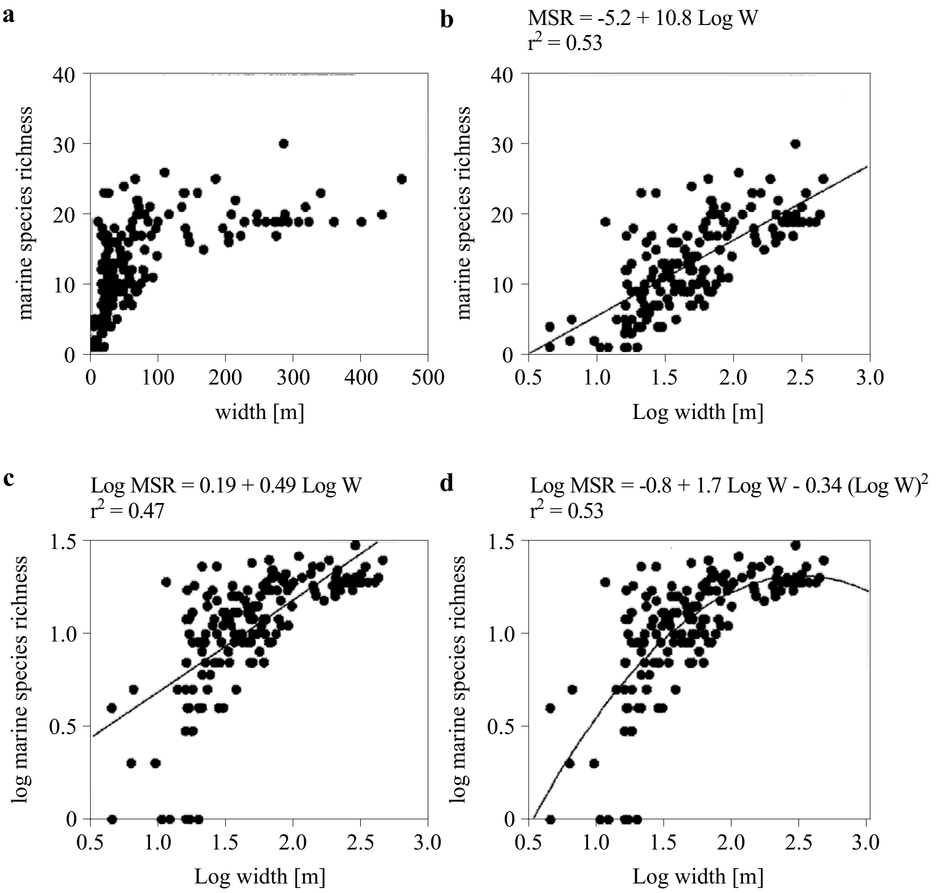

Fig. 1. Four plots of marine species richness against beach width

and a quadratic curve (Fig. 1d), which also gives a good fit ($r^2 = 0.53$) but is clearly not appropriate as it indicates species richness declining on the widest beaches.

The best fit to these data is the exponential model first proposed by Gleason and since supported by several authors (Palmer 1990). This semilog model was used to compare latitudinal regions. This comparison showed no differences in slopes or intercepts between regression lines for data from subtropical, warm temperate and cold temperate regions; however, the tropical data are significantly different in intercept and slope (ANOVA, $p < 0.05$). The tropical data show generally more species per beach width than the other regions. Higher species richness on tropical beaches has been confirmed in previous studies in the southern hemisphere (Soares 2003, unpublished) and globally (McLachlan & Dorvlo 2005).

4. Discussion

In the power model for these data the slope z is 0.49, well above the value of 0.2 expected for mainland habitats and even above the 0.3 expected for islands. This suggests that not only do beaches function as islands, i.e. are isolated from each other, but that there are additional effects of increasing beach width. We believe these additional effects are due to the changing nature of the habitat as beaches become wider and more dissipative: the intertidal environment becomes less harsh due to milder swash climates and finer sand, thereby enabling more species to establish populations. This supports well-documented evidence for more benign conditions on dissipative beaches (McLachlan & Brown 2006).

The high z value questions the metapopulation model, which suggests connectivity between beaches by exchange of larvae (Defeo & McLachlan 2005). Connectivity between populations on different beaches is an important issue that requires more investigation. Also requiring further consideration is the extent to which the relationship between species richness and beach width is a) an area effect and b) due to changing conditions in the habitat. Separating these two influences will not be simple as they are not independent. Further, a study considering total beach area, where beach length is also taken into account, would be useful. However, to do this a massive sampling effort would have to be undertaken to cover a whole beach; this would not be feasible without a huge team of workers.

The conclusions from this analysis are that:

1) sandy beach intertidal macrofauna display increasing species richness in response to increasing beach width, similar to the species-area relationships described for many other environments;
2) the best model to describe this is an exponential or semilog model;
3) a power curve of the form $\mathrm{S} = c\,\mathrm{A}^z$ also gives a good fit, with a steep slope z of 0.49 indicating that beaches function as island habitats with good degrees of isolation;
4) this high z value also suggests that the nature of these habitats changes, becoming more benign and accommodating proportionately more species towards wider (more dissipative) beaches;
5) there are latitudinal trends, with the tropics displaying more species for any beach width than other regions;
6) further work is needed to separate area effects across the range of beach widths from the effects of changing habitat harshness across the range of beach types.

Acknowledgements

We thank Beth Umali for preparing the manuscript and Reg Victor, John Gray and David Schoeman for insightful comments on the manuscript.

References

Brazeiro A., 1999, *Community patterns in sandy beaches of Chile: richness, composition, distribution and abundance of species*, Rev. Chil. Hist. Nat., 72, 93–105.

Brazeiro A., 2001, *Relationships between species richness and morphodynamics in sandy beaches: what are the underlying factors?*, Mar. Ecol. Prog. Ser., 224, 35–44.

Connor E. F., McCoy E. D., 2001, *Species-area relationships*, [in:] *Encyclopedia of biodiversity*, S. Levin (ed.), Acad. Press, London, 397–411.

Defeo O., McLachlan A., 2005, *Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis*, Mar. Ecol. Prog. Ser., 295, 1–20.

Gray J. S., 2002, *Species richness of marine soft sediments*, Mar. Ecol. Prog. Ser., 244, 285–297.

Gray J. S., Ugland K. I., Lambshead J., 2004, *On species accumulation and species-area curves*, Global Ecol. Biogeogr., 13, 567–568.

Hartnoll R. G., 1983, *The species-area relationship on a sandy beach*, [in:] *Sandy beaches as ecosystems*, A. McLachlan & T. Erasmus (eds.), Dr. W. Junk, The Hague, 473–479.

Jaramillo E., McLachlan A., Dugan J., 1995, *Total sample area and estimates of species richness in exposed sandy beaches*, Mar. Ecol. Prog. Ser., 119, 311–314.

MacArthur R., Wilson E. O., 1967, *The theory of island biogeography*, Princeton Univ. Press, New Jersey, 203 pp.

McLachlan A., Brown A. C., 2006, *The ecology of sandy shores*, 2nd edn., Acad. Press, New York, 373 pp.

McLachlan A., Dorvlo A., 2005, *Global patterns in sandy beach macrobenthic communities*, J. Coast. Res., 21 (4), 674–687.

McLachlan A., Dorvlo A., 2007, *Global patterns in sandy beach macrobenthic communities: biological factors*, J. Coast. Res., (in press).

Palmer M. W., 1990, *The estimation of species richness by extrapolation*, Ecology, 71, 1195–1198.

Sanders H. L., 1968, *Marine benthic diversity: a comparative study*, Am. Nat., 102, 243–282.

Schoeman D. S., Wheeler M., Wait M., 2003, *The relative accuracy of standard estimates for macrofaunal abundance and species richness derived from selected intertidal transect designs used to sample exposed sandy beaches*, Estuar. Coast. Shelf Sci., 58 (SI), 5–16.

Soares A. G., 2003, *Sandy beach morphodynamics and macrobenthic communities in temperate, subtropical and tropical regions – a macroecological approach*, Ph. D. thesis, Univ. Port Elizabeth, South Africa, (unpublished).