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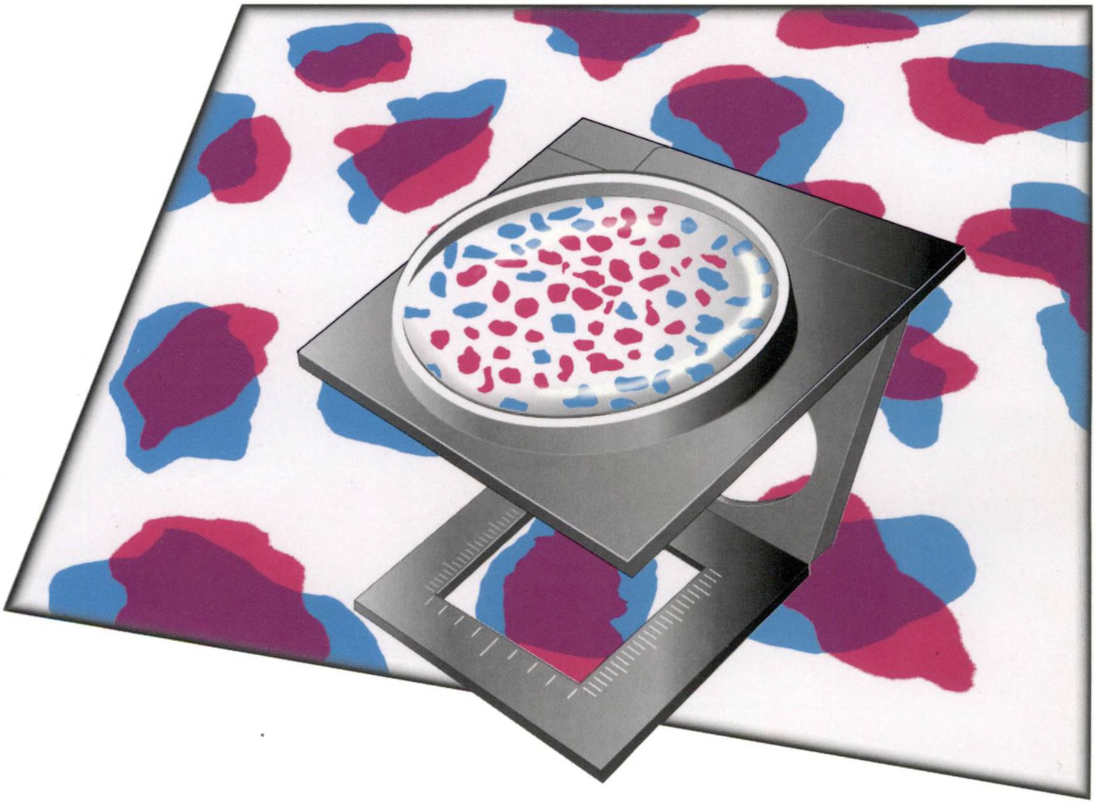

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SPECIES-ENVIRONMENT RELATIONSHIP IN MARINE SOFT-BOTTOM COMMUNITIES: REGRESSION MODELING AND THE IMPLICATIONS OF SCALE

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This report presents the results of a study commissioned by the
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ABSTRACT

A literature study was performed aiming to explore the relation between the spatial scale of marine benthic surveys and the observed goodness-of-fit of regression models relating animal abundance to the environment. A further objective was to tabulate the abiotic factors and processes that predominantly explain the variation in abundance and to examine whether or not the type of important factors differ in relation to the scale of the study. Single studies in which benthos-environment regression models were applied at different spatial scales and which would have allowed a within-study comparison of the goodness-of-fit in relation to scale, were not found. The paucity of studies that reported quantitative information and, if they did so, the use of a variety of incomparable statistical models resulted in very few observations and a lack of statistical power of the (between-study) relation between scale and goodness-of-fit. Most studies confirmed the importance of sediment characteristics and elevation (in case of intertidal areas) or water depth (in case of subtidal areas) in determining the benthos. Further studies on the importance of the spatial scale of marine benthos-environment surveys should be based on a unified analytical approach, which can only be realized if original data are available.

INTRODUCTION

Objectives

Rijkswaterstaat, which is part of the Dutch Ministry of Transport and Public Works, is co-responsible for the management of coastal and estuarine ecosystems in the Netherlands. The benthic soft-sediment fauna forms an essential element of these ecosystems. Human impact on this fauna, for example by means of infra-structural works, mining, and dredging, often works through changes in the abiotic environment. Knowledge of the relationships between the abiotic environment and the benthic fauna is therefore fundamental for a reliable impact assessment. The most commonly applied research method to estimate such relationships is to perform a spatial survey, in which data on species abundance and environmental conditions are gathered at a large number of sampling sites. Subsequently regression models are fitted, in which species abundance is supposed to depend on the environment. Two examples within the Dutch context of the use of known relationships between the abiotic environment and the benthic fauna for impact assessment are (1) the *a-posteriori* evaluation of the impact of the construction of the storm-surge barrier in the Oosterschelde on the abundance of the intertidal benthos, evaluated at the species level (Van der Meer 1999), and (2) the assessment of the impact of subsidence as a result of gas winning on the total macrozoobenthic biomass (Beukema 1998a, Beukema 1998b). In both cases the impact worked through changes in the elevation of the intertidal area.

Aim of the present study is to evaluate the scientific literature in which such species-environment models for the benthic fauna of soft-sediment coastal and estuarine ecosystems are used. Special emphasis will be placed on scale aspects, because the type of abiotic variables that appear to be important and the explanatory strength of the models may heavily depend on the scale of the study. In short, we will:

- provide an overview of scientific studies in which species-environment relationships have been quantified, but restricted to the benthic fauna of coastal and estuarine soft-sediment ecosystems;
- relate the fraction of the overall variation in the abundance of benthic species that is explained by the abiotic environment to the spatial scale (which may range from the scale of a region, for example including the Dutch Wadden Sea and the Dutch Delta, to the scale of an estuary, e.g. the Westerschelde, and further down to that of a single mudflat).
- tabulate the abiotic factors and processes that predominantly explain the variation in abundance and examine whether or not the type of important factors differ in relation to the scale of the study.

New analyses using original data are beyond the scope of the present study.

Scale

Organisms are not homogeneously distributed in space. Ecologists aim to understand these heterogeneous spatial patterns in terms of the processes that produce them (Levin 1992). Both physical factors and biological processes may generate and maintain spatial variation in population densities.

The relative role of particular physical features and processes in governing the spatial pattern of species abundance will depend on the scale that is used (Barry and Dayton 1991). Differences in species composition on a worldwide scale, e.g. between polar and tropical regions, can be explained by the uneven heating of the surface of the earth and the resulting temperature differences. On the other hand, it is most unlikely that temperature differences are relevant on a micro-scale of a few squared centimeters of ocean bottom. The importance of particular biological processes is also scale-dependent (Schneider 1994, McArdle et al. 1997, Schneider et al. 1997). Mathematical models, e.g. reaction-diffusion models and cellular automata models, suggest that spatial variation in population density on a local scale can be the result of biological processes such as limited dispersal of propagules (Okubo 1980, Murray 1989, Phipps 1992). Heterogeneity on a spatial scale larger than the mobility of an individual may be the result of periodic or chaotic dynamics which are not synchronized across different areas (Hassell et al. 1991).

The problem of understanding spatial patterns in animal abundance is as complex as ecology itself and an overwhelming variety of research methods has been applied to contribute to a further comprehension. In the present paper we therefore focus on a specific research approach, that is, as was said earlier, regression modeling on the basis of survey data. More specifically, we focus on the widely applied research method where (1) one or more observational field surveys in which data on species abundance and environmental conditions are gathered at a large number of sampling sites, are performed; and where (2) a regression model is formulated under the assumption that species abundance depends on the (spatial) environment. We also restrict ourselves to studies of coastal and estuarine soft-bottom communities.

As was said earlier, aim of the present study is to explore to what extent the observed species-environment relationships are scale-dependent. Does a relation exist between the spatial scale of the study and the estimated regression model? We review the existing literature on species-environment relationships in coastal and estuarine soft-bottom communities. We examine whether a relationship exists between the scale of a study and the explanatory strength of the regression model that has been used. We also look at the abiotic factors that play an important role and try to answer the question whether different sorts of factors contribute in small-scale studies compared to those in large-scale studies.

The Gaussian Response Model

In ecology fitting regression models that relate species abundance to environmental variables is known as direct gradient analysis (Whittaker 1967). The objective of direct gradient analysis may be noted as to providing a parsimonious description of the community (restricted in space and time to the study area and study period) in terms of a multivariate regression model that relates species abundance to environmental variables. The term multivariate refers to the fact that usually more than one species is involved.

The most favored regression model to describe the dependence of species on their environment is the Gaussian response model (Gauch and Chase 1974, Gauch et al. 1974). The regression model has a bell shape, i.e. it has the form of an optimum function and moreover can only give positive values for species abundance. The name Gaussian stems from the mathematical similarity to the Normal or Gaussian probability density function. In its simplest form, that is for a single environmental variable, the Gaussian response model is generally written as $y_{ij} = \exp\left(c_j - \frac{(x_i - m_j)^2}{2t_j^2}\right)$, where the index $i = 1, \cdots, n$ refers to the sites; $j = 1, \cdots, k$ to the species; y_{ij} is the abundance at site i of species j; x_i is the value of the environmental variable at site i; $\exp(c_j)$ is the maximum abundance of species j; m_j is the optimum for species j, that is the value of the environmental variable where species j has its maximum abundance; t_j is the tolerance of species j, which is a measure of the width of the response curve. For more than one environmental variable, for example for two environmental variables, it is more convenient to write the model as $y_{ij} = \exp\left(b_{0j} + b_{1j}x_{1i} + b_{2j}x_{1i}^2 + b_{3j}x_{2i} + b_{4j}x_{2i}^2 + b_{5j}x_{1i}x_{2i}\right)$. The latter equation already points to one disadvantage of fitting the Gaussian response model, that is the large number of parameters in which it may result. The results cannot be presented in one or a few graphical displays, which hampers interpretation. Alternatively, constraints can be set on the parameters such that the Gaussian response model can be written as $E(y_{ij}) = \exp\left(c_j - \frac{(u_i - m_j)^2}{2t_j^2}\right)$, where all species are supposed to respond to a single canonical variate u, which is a linear combination of the q environmental variables: $u_i = a_o + \sum_{l=1}^{q} a_l x_{li}$. Estimation of the parameters of this constrained multivariate Gaussian response model is not straightforward. Usually, therefore, approximating methods such as Canonical Correspondence Analysis (CCspA) are used. Ter Braak (1986) showed that under certain assumptions the results of Canonical Correspondence Analysis approximate the maximum likelihood estimates (assuming a Poisson-like distribution of species abundance) of the constrained multivariate Gaussian response model. Canonical Correspondence Analysis is now probably the most widely used multivariate direct gradient analysis method in community ecology (Palmer 1993).

When the environmental gradients are short compared to species tolerances the use of a linearized form of the multivariate Gaussian response model, like the multivariate linear regression model using logtransformed species densities, may be more appropriate (Ter Braak and Prentice 1988, Ter Braak 1994). Constrained forms of the multivariate linear regression model can be related to the dimensionality-reduction techniques of Canonical Correlation Analysis (CCltA) and Redundancy Analysis (RA) (Tso 1981, Davies and Tso 1982, Jongman et al. 1987, Van der Meer 1991).

Implicit regression models, indirect gradient analysis and other multivariate techniques

In some cases the same mathematical procedure can both be interpreted in terms of an ordination technique, providing a low-dimensional representation of the multi-dimensional species space (where originally each dimension represents a single species) or in terms of a regression model (Legendre et al. 1997). For example, Canonical Correspondence Analysis can be, as was shown above, interpreted as a restricted ordination technique or as an approximation to maximum likelihood fitting (assuming Poisson error) of a restricted Gaussian model (Ter Braak 1985, Ter Braak 1986). Similarly, Redundancy Analysis and Canonical Correlation Analysis can be regarded as reduced-rank linear regression models (Jongman et al. 1987, Van der Meer 1991). In some studies the ordination interpretation has been presented. We have, however, always interpreted the results, as far as possible, in terms of regression models.

Indirect gradient analysis is the ecological equivalence of (latent) factor analysis. The technique of factor analysis estimates for each site the values of one or more so-called latent factors, under the assumption of some specified type of relationship between the latent factor(s) and the species abundance data. These latent factor values are expected to represent environmental gradients. Examples of factor analytical techniques are Principal Component Analysis (PCA) and Correspondence Analysis (CA). Principal Component Analysis is based upon the assumption of a linear relationship between species abundance and environmental gradients (latent factors). Correspondence Analysis builds on the assumption of a unimodal relationship between species abundance and environmental gradients.

Many other multivariate techniques cannot easily be interpreted in terms of a regression model. One of the approaches which has recently been put on the foreground is based on the (harmonic rank) correlation between the species (dis)similarity matrix and the environment (dis)similarity matrix (Clarke and Ainsworth 1993). Additionally, the approach uses non-metric MultiDimensional Scaling (MDS) of the two (dis)simmilarity matrices to visualizese the relationship between species and environmental variables.

Goodness-of-fit

The present study focuses on the goodness-of-fit of multivariate regression models, which aim to relate species abundance to the environment. Generally, the goodness-of-fit term quantifies the explanatory power of the regression model, but the actual goodness-of-fit measure is necessarily strongly linked to the assumed error structure of the model. For example, for least-squares models (which are equivalent to the maximum likelihood method if the errors are Normally distributed) the usual goodness-of -fit measure is R^2, the fraction explained variance. This fraction is given by one minus the ratio of the residual sum of squares to the total sum of squares. For other assumptions about the error distribution, alternative goodness-of-fit measures have to be used. The class of generalized linear models uses the deviance as a generalization of the sum-of-squares and goodness-of-fit is expressed as percentage explained deviance.

Classification

In short, studies were categorized as follows:

1) univariate models, dependent variable is species abundance;
2) univariate models, dependent variable is a community attribute (e.g. some diversity measure, total abundance, etc.);
3) linear direct gradient analysis, i.e. CcltA or RA;
4) non-linear direct gradient analysis, i.e. CCspA;
5) linear indirect gradient analysis, i.e. a multivariate latent factor model (PCA) combined with univariate models to relate the latent factors to observed environmental variables;
6) non-linear indirect gradient analysis, i.e. a multivariate latent factor model (CA) combined with univariate models to relate the latent factors to observed environmental variables;
7) harmonic rank correlation between the species (dis)similarity matrix and the environment (dis)similarity matrix, in combination with MDS.

The scale of macrobenthos surveys

Usually, not much attention is paid to interpreting the results of a benthos survey (i.e. the explanatory strength of the regression model and the type of environmental variables that appeared to be important) in terms of the scale of the study. We are not aware of any study in which benthos-environment regression models are applied at different spatial scales within a single area, allowing a comparison of the goodness-of-fit. One noticeable exception (although qualitative) is Flach (1996), who observed that the larger scale patterns in the distribution of *Corophium* in the Wadden Sea are determined by physical factors, such as sediment composition and elevation. The smaller scale patterns are related to biological interactions, i.e. clusters of juveniles around burrows of adult females.

The scale of a sampling survey consists of two parts, the unit and the frame (Cochran 1977). The unit is the smallest item that is sampled in the survey. In benthos surveys it is the area of the sampling device. The frame is the list of all possible units. Stated otherwise, the total study area (the frame) can be thought of as comprising a finite number (and usually large) of small non-overlapping areas (the units), each of the size of the sampling device. Instead of using the statistical terms frame and unit, other terms are in use as well, extent and grain (Wiens 1989), field of view and grain (Van der Meer 1997), maximum outer scale and minimum inner scale, or range and resolution (Schneider 1994).

MATERIAL AND METHODS

A computerized literature survey was performed using *Online Contents*, a database containing the contents of 12,500 scientific and non-scientific journals and magazines. It is possible to search for literature published since September 1992. We searched for the following keywords (or combinations of): (marine) (macro) benthos, macrofauna, multivariate (analyses), intertidal (as initially we wanted to restrict our analysis to intertidal areas), scale pattern, benthos or benthic survey, distribution pattern(s) and spatial scale. This literature survey yielded 37 titles, but only two papers could be used. Only these papers (ref. 5 and ref. 14) reported a quantitative analysis of the relation between the benthic community of an intertidal area and abiotic factors.

In recent published, possibly not yet computerized, literature we found one suitable paper (ref. 14). A study of 48 internal reports, mainly concerning marine benthos of Dutch coastal systems and estuaries and the North Sea, revealed 4 studies from which we could abstract useful data.

A second computerized survey was performed using the *DIALOG* data search engine. We looked for in the following archives, *Oceanic Abstracts* (references available since 1964) and *Aquatic Sciences and Fisheries Abstracts* (references available since 1978). The following combinations of keywords were used: benthos or benthic, combined with marine and multivariate and intertidal or inter-tidal and macrofauna or macrozoobenthos combined with intertidal and multivariate. This survey yielded in total 60 titles. From the abstracts, we selected 26 papers from which at last only 14 had enough quantitative detail to be suitable for our analysis (ref. 1-4, 6-12, 15, and 16). From these 14 references, two are dealing with a subtidal environment (ref. 3 and 13).

Because literature about marine intertidal benthos and abiotic structuring factors seemed to be scarce (only 16 refereed papers and 4 internal reports) we decided to extend our survey to subtidal regions. Again a computerized survey in the *Oceanic Abstracts* and *Aquatic Sciences and Fisheries Abstracts* archives was performed using the *DIALOG* data search engine. The above mentioned keywords were used but instead of intertidal, the keywords subtidal or sub-tidal were used. This search yielded only 7 titles, from which one (ref. 3) was already known. From the remaining six references, two did not provide the required quantitative information.

The lists of literature references within the selected papers and reports yielded a few more titles that were suitable for further study.

For each study, grain (m^2) is defined as the sampled surface area per station, and extent (km) as the maximum distance between stations.

RESULTS

Studies and scales

The literature survey yielded eventually 32 studies (Warwick 1971, Lie 1978, Moore 1978, Poore and Mobley 1980, Hogue and Miller 1981, Whitlatch 1981, Esselink and Van Belkum 1986, Raffaelli et al. 1986, De Gee and Dekker 1987, Pearson and Rosenberg 1987, Gray et al. 1988, Zwarts 1988, Austen and Warwick 1989, Elliott and O'Reilly 1991, Meire et al. 1991, Raffaelli et al. 1991, Van der Meer 1991, Defeo et al. 1992, Gee et al. 1992, Buhl-Mortensen and Høisæter 1993, Jaramillo and McLachlan 1993, Sun et al. 1993, Jaramillo 1994, Haynes and Quinn 1995, Soetaert et al. 1995, Bachelet et al. 1996, Mclachlan 1996, Legendre et al. 1997, Netto and Lana 1997, Oug 1998, Oug et al. 1998). Macrobenthos studies were much more common than meiobenthos studies (Table 1). Most of the studies were performed in intertidal areas in the temperate zone (Table 2). The grain of the macrobenthos studies ranged from 0.015 to 3.3 m^2 (apart from one outlier, where the grain was 250 m^2), and the extent from 0.025 to 450 km (Table 1, Fig. 1). If only the macrobenthos studies are taken into account, the relative variability in grain (*SD(log grain)* = 0.57,

$n = 25$) was smaller than the relative variability in extent (*SD(log extent)* = 1.08, $n = 25$). No significant correlation ($r = 0.10$, $n = 25$, $P = 0.62$) between grain and extent was observed (Fig. 1). The relatively low variability in grain is presumably the result of the use of standardized sampling equipment and procedures.

Table 1. An overview of the 32 selected studies. Grain in m^2, extent in km, category refers to the type of analysis (see text), habitat (Hab) refers to intertidal (I) or subtidal (S).

Nr	**Grain**	**Extent**	**Category**	**Reference**	**Group**	**Hab**	**Latitude**
1	2.00E-03	2000	_2_4___	Soetaert & Vincx, 1995	Meio	I	47ºN
2	1.90E+00	0.05	_2____7	Haynes & Quinn, 1995	Macro	I	38ºS
3	2.16E-01	18	_____6_	Bachelet et al., 1996	Macro	S	44º40'N
4	4.00E-02	0.025	______7	Netto & Lana, 1997	Macro	I	25º33'S
5	3.10E-07	.00007	12_____	Sun *et al.*, 1993	Meio	I	29º15'N
6	9.54E-02	45	_____6_	Meire *et al.*, 1991	Macro	I	51º50'N
7	9.00E-01	50	_2_____	Jaramillo, 1994	Macro	I	39º35'S
8	3.30E-01	200	_2__5_7	Defeo *et al.*, 1992	Macro	I	34ºS
9	6.25E-02	11	____5__	Moore, 1978	Macro	I	53º30'N
10	3.42E-03	12	______7	Austen & Warwick, 1989	Meio	I	52ºN
12	2.50E-01	0.5	1______	Legendre *et al.*, 1997	Macro	I	37º02'S
13a	4.00E-01	450	___4___	Oug *et al.*, 1998	Macro	S	61ºN
13b	4.00E-01	20	___4___	Oug *et al.*, 1998	Macro	S	61ºN
14	3.30E+00	25	_2___6_	McLachlan, 1996	Macro	I	27ºS
15	1.45E-02	30	1_3____	Van der Meer, 1991	Macro	I	51º50'N
16	5.00E-02	6	_____6_	Raffaelli *et al.*, 1986	Macro	I	57º50'N
17	1.00E-01	80	_2_____	Elliott & O'Reilly, 1991	Macro	S	56º05'N
18	2.50E-01	0.06	_____67	Raffaelli *et al.*, 1991	Macro	I	57º15'N
19	4.88E-02	1.5	_2_____	Whitlatch, 1981	Macro	I	41º42'N
21	2.88E-03	10	______7	Warwick, 1971*	Meio	I	50°40'N
22	1.00E-01	13	______7	Pearson & Rosenberg, 1987*	Macro	S	55º40'N
23	2.80E-05	0.0012	_2_____	Hogue & Miller, 1981	Meio	I	44º38'N
24	9.00E-01	50	12_____	Jaramillo & McLachlan, 1993	Macro	I	39º35'S
25	4.00E-01	17	___4___	Oug, 1998	Macro	S	69º40'N
27	4.00E-01	15	_____67	Gray *et al.*, 1988	Macro	S	59º05'N
28	2.50E+02	117	_2_4___	Buhl-Mortensen & Høisæter, 1993	Macro	S	60º50'N
29	4.00E-03	320	______7	Gee *et al.*, 1992	Meio	S	54º06'N
30	6.00E-01	10	_2__5__	Lie, 1978	Macro	S	60º15'N
31	5.00E-02	2	__3____	Poore & Mobley, 1980	Macro	S	37º55'S
101	7.07E-02	40	1______	Zwarts, 1988	Macro	I	53º24'N
102	4.38E-02	4	1______	Esselink & Van Belkum, 1986	Macro	I	53º18'N
103	2.00E-01	50	_2_____	De Gee & Dekker, 1987	Macro	S	53º05'N

* See also Clarke & Warwick, 1993.

Various methodologies

Goodness-of-fit measures can only be compared within each of the seven methods categories separately.

Results of simple or multiple regression of species abundance versus environmental variables (category 1) were reported in 5 studies. This low number of studies does not permit any conclusions, although the available data indicate a negative relationship between extent and maximum explained variance (Max R^2). See Table 3. The lack of data also holds for the relationship between community attributes and environmental variables (category 2), which were reported in 13 studies. Species richness, which was the most frequently reported community attribute (i.e. in 7 studies), did not show any relation with scale (Table 4).

Table 2. Latitude and habitat of the 32 selected studies. Meiobenthos studies between brackets. Amsterdam, Holland is located at 53° N, Lisbon, Portugal at about 40° N, and Durban, South-Africa or Perth, Australia at about 30° S.

	Intertidal	**Subtidal**	**Total**
> 40º N	8 (4)	10 (1)	18 (5)
30º S to 40º N	2 (1)	0	2 (1)
< 30º S	5	1	6
Total	15 (5)	11 (1)	26 (6)

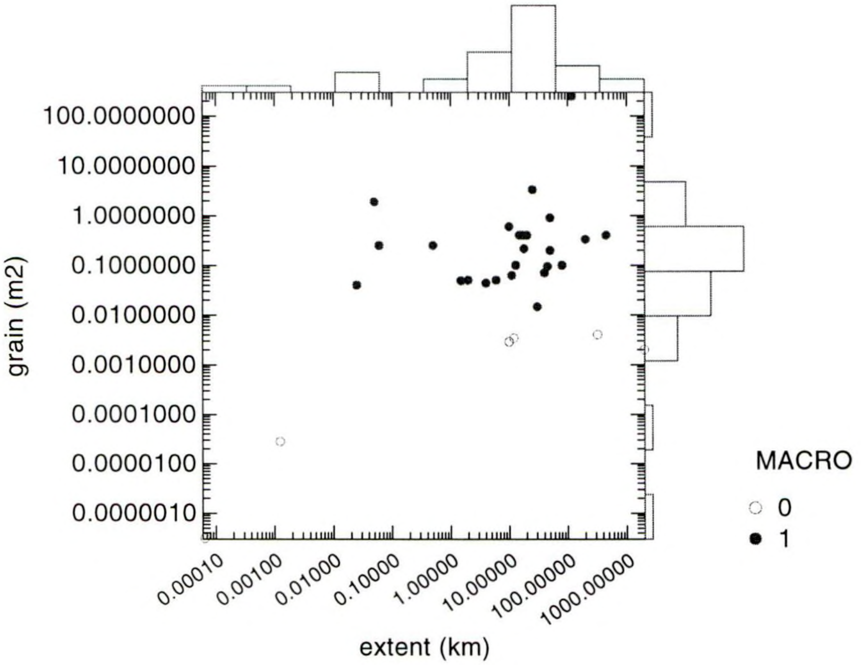

Fig. 1. Relation between extent (km) and grain (m^2) of a benthos study. Filled dots refer to macrobenthos studies, open dots to meiobenthos studies.

Table 3. Maximum R^2 of five studies in which species abundance was related to environmental variables. Type refers to multiple (M) or simple (S) linear regression.

Nr	Grain	Extent	Type	Independent variables	Max R^2
12	0.25	0.5	M	Shell hash, elevation, shear stress, energy dissipation, water coverage, wave stirring	0.69
102	0.0438	4	S	Silt, altitude	0.70
15	0.0145	30	M	Median grain, altitude and other environmental variables	0.48
101	0.07068	40	M	Silt, altitude	0.39
24	0.9	50	S	Mean grain size, beach slope, Dean's parameter	0.43

Table 4. Maximum R^2 of seven studies in which species richness was related to environmental variables. Type refers to multiple (M) or simple (S) linear regression.

Nr	Grain	Extent	Type	Independent variables	Max R^2
19	0.0488	1.5	S	Total particle diversity, food particle diversity, % organic matter	0.34
30	0.6	10	S	Median grain	0.12
14	3.3	25	S	Beach slope, sand particle size, sand sorting	0.85
7	0.9	50	S	Median grain, 1/beach slope, Dean's parameter	0.83
24	0.9	50	S	Mean grain size, beach slope, Dean's parameter	0.91
103	0.2	50	M	Median grain size, silt content, sediment sorting, depth, distance to shore, distance to MLWL	0.02
17	0.1	80	M	Water depth, median particle diameter (MPD),silt and clay content (%SC), sediment sorting (SC), salinity, area	0.42

Direct gradient analysis (categories 3 and 4) was applied in six studies. Two studies used a linear technique, i.e. Canonical Correlation Analysis, and four studies a non-linear method, Canonical Correspondence Analysis. One of the latter studies (nr. 1) did not report any goodness-of-fit measure, and the remaining three studies do not allow any suggestions for possible relationships (Table 5).

Table 5. Extracted variance by the first canonical variate (*EV* 1), a goodness-of-fit measure, of three studies which used Canonical Correspondence Analysis to relate species abundance to environmental variables.

Nr	Grain	Extent	Type	Independent variables	*EV* 1
25	0.4	17	S	water depth, TOC, gravel, sorting, fine sand	0.21
13b	0.4	20	S	C/N ratio, water depth, polycyclic aromatic hydrocarbons, effluent impacted sediment	0.20
28	250	117	S	sill depth, C/N, %Carbon, %Clay	0.35
13a	0.4	450	S	water depth, distance from river, polycyclic aromatic hydrocarbons, distance from pollution source, effluent impacted sediment, sand-mixed sediment	0.08

Indirect gradient analysis (categories 5 and 6) was applied in nine studies. Three studies used a linear technique, i.e. Principal Component Analysis, and six studies a non-linear method, Correspondence Analysis. Only two of the latter studies reported a correlation coefficient between one of the canonical axes and one or more environmental variables. Clearly, this does not permit any suggestions for possible relationships.

The harmonic rank correlation between the species (dis)similarity matrix and the environment (dis)similarity matrix (category 7) was reported in four studies. Again, the number of studies is not sufficient for any conclusions (Table 6).

Table 6. Harmonic rank correlation between the species (dis)similarity matrix and the environment (dis)similarity matrix in four selected studies.

Nr	**Grain**	**Extent**	**Independent variables**	***r***
4	0.04	0.025	Spartina biomass, fines, water content, organic content	0.80
21	0.00288	10	H2S, salinity, median particle diameter (MPD)	0.80
22	0.1	13	C, Cd, N content of sediment	0.79
29	0.004	320	silt/clay fraction (SCF),depth	0.77

For each category separately, sample sizes were unfortunately too low to allow conclusions. Using a non-parametric procedure, however, combines the results. We categorized for each analytical method both the extent and the goodness-of-fit in two classes: lower than the median and higher than the median. If the number of studies within a category was uneven, the median was put in one of the two classes by equal chance. The combined results can be arranged in a two-by-two table, and the final result did not point to any association at all (Table 7).

Table 7. The association between extent and goodness-of-fit (for each analytical category all figures are clategorized as lower or higher than the median).

	Goodness-of-fit lower than median	Goodness-of-fit higher than median	Sum
Extent lower than median	3	6	9
Extent higher than median	4	5	9
Sum	7	11	18

Environmental variables

The type of environmental variables that were related to the benthic fauna did not seem to vary systematically with scale (Table 8). For the intertidal studies, elevation and a variable characterizing sediment composition (most often median grain size) were the most often mentioned physical factors correlating with the benthic fauna. For the subtidal studies, water depth instead of elevation was mentioned. Two studies (nrs. 13 and 22) also considered pollution-related variables, e.g. polycyclic aromatic hydrocarbons, distance from pollution source, effluent impacted sediment. Few studies (mainly those concerned with exposed beaches, i.e. nrs. 7, 8, 14 and 24) mentioned variables directly related to the morpho-dynamic state of the environment, e.g. variables like shear stress, beach slope and Dean's parameter (a combination of breaker height, sinking velocity of sand and wave period).

Table 8a. Environmental variables that best correlated with the benthic fauna, subdivided in general, sediment and water-related variables. Intertidal areas.

Nr	Grain	Extent	General	Sediment	Water
5	3.1E-07	65e-6	elevation		
23	0.000028	.00124	elevation		
4	0.04	0.025		water, organic matter	
2	1.9	0.05	elevation		
18	0.25	0.06	elevation		
12	0.25	0.5	elevation, shear stress, energy dissipation, water coverage, wave stirring		
19	0.0488	1.5		total particle diversity, food particle diversity, organic matter	
102	0.0438	4	elevation	silt	
16	0.05	6	elevation	median grain, silt	
21	0.00288	10		median grain, H2S	salinity
9	0.0625	11		silt	
10	0.00342	12			salinity
14	3.3	25	beach slope	mean grain, sorting	
15	0.0145	30	elevation	median grain	
101	0.07068	40	elevation	silt	
6	0.0954	45	inundation time	median grain, silt	chlorinity,O2 saturation, POC, suspended matter, total P, total N, dissolved Si, dissolved Cd
24	0.9	50	beach slope, Dean's parameter	mean grain	
7	0.9	50	beach slope, Dean's parameter	median grain	
8	0.33	200	beach slope, Dean's parameter	mean grain	
1	0.002	2000		median grain, silt	salinity

Table 8b. Environmental variables that were taken into account in the selected studies, subdivided in general, sediment and water-related variables. Subtidal areas.

Nr	Grain	Extent	General	Sediment	Water
31	0.05	2	water depth	medium sand, fine sand, silt, clay, sorting	ortho-phosphate, ammonia, carbonate
30	0.6	10		median grain	
22	0.1	13			
27	0.4	15	water depth		
25	0.4	17	water depth	gravel, fine sand, sorting, TOC	
3	0.216	18	water depth	median grain, gravel, silt, organic matter, zostera debris	salinity
13b	0.4	20	water depth		
103	0.2	50	water depth, distance to shore, distance to MLWL	median grain, silt, sorting	
17	0.1	80	water depth, area	median grain, silt and clay, sorting	salinity
28	250	117		clay, carbon	
29	0.004	320	water depth	silt/clay fraction	
13a	0.4	450	water depth	sand-mixed sediment	distance from river

DISCUSSION

Lack of power of the present study

The number of appropriate studies that we were able to select was unfortunately rather small. The main reason is that very often authors do not report quantitative information on the goodness-of-fit of their models, but only provide the parameters of the model or just visually display the relationship. A timely example is the recent study on the effect of subsidence as a result of gas exploitation in the Wadden Sea. A relationship between elevation and total benthic biomass was fitted and subsequently used to assess the impact of changes in the elevation of the mudflats on total biomass (Beukema 1998a, Beukema 1998b). The goodness-of-fit of the applied model was, however, not mentioned. Staying within the Dutch context, the impressive handbook on the ecology of the Wadden Sea shows a wealth of (graphical) information on the relationship between the abundance of macrozoobenthic species and various environmental factors (Dankers and Beukema 1983). Goodness-of-fit figures were, however, not presented. A further problem that we experienced was related to the variety of approaches that were applied in the selected studies for modeling the benthos-environment relationship. The accompanying goodness-of-fit measures of this variety of models cannot be compared. For each analytical method only very few studies were available (with a maximum of seven studies which used linear regression models to relate species richness to environmental variables). Inevitably this resulted in a lack of statistical power. The combined procedure, although it might be labeled as ad-hoc, did not point to any association between scale and goodness-of-fit. Nevertheless, further studies on the importance of the spatial scale of marine benthos-environment surveys should be based on a unified analytical approach, which can only be realized if original data are available.

Abiotic variables

Although the relative importance of various abiotic variables in relation to scale remained obscure, most studies confirmed the general importance of sediment characteristics and elevation (in intertidal areas) or water depth (in subtidal areas) in determining the benthos. Some studies (mainly on exposed beaches) pointed to the relevance of morpho-dynamics, by showing the effect of variables like shear stress and Dean's parameter. However, these variables are often strongly correlated with sediment characteristics. For example, in one study (nr. 14) the Pearson correlation coefficient between beach slope and mean particle size was 0.99 (as we calculated on basis of the data presented). In another study (nr. 24) this coefficient appeared to be equal to 0.78. This interdependency between environmental variables, which is usually encountered in field studies, makes it almost impossible to be conclusive on the mechanisms underlying the observed correlations. Observational studies like we are concerned with in the present study, should report these interdependencies. Yet, only one study (Van der Meer 1991) explicitly described these interdependencies between abiotic variables. Another point of concern is that studies were usually silent on the reasons of including specific abiotic variables in the study.

The scope of benthos-environment regression models

Finally, we will from a more general perspective, discuss the applicability of regression models relating benthos to the environment. Surveys of the macrobenthos of soft-sediments are usually conducted over a short time span. Usually, only a single survey is performed. Are these models only relevant to the here and now of the study? This would mean that the models could only be used for interpolation. Or are the models also applicable in the future, the past and in other areas? This would enable some sort of extrapolation. The answer to this question relates to the biological assumptions that can or cannot be made. For example, what can we say about the presumed interaction between time and environment? In other words what can we say about the time-invariance of the regression parameters?

Surveys of the macrobenthos of soft-sediments are usually snap-shots in time, but benthic communities (particularly in the estuarine environment) are known for their large temporal variations in species abundance (Beukema 1989, Coosen et al. 1994). These variations may be due to the vagaries of weather, which have strong impact on the recruitment success of many species (Beukema 1989). Unknown variations in the environmental conditions during the pelagic phase of the larvae may also contribute to the large variations in recruitment that are usually observed. Variation in recruitment seems to have strong influence on the structure of the community. Thus, when only a single point in time is considered, it might be that at all sites in the study area the observed abundance of a species is much lower than the long-term average density. At other times the observed abundance could be much higher at all sites. Time plays a role, and the notion of a single 'true' regression model that worked in the past and will work in the future, is then not tractable.

In conclusion, it would be highly recommendable that future studies on the goodness-of-fit of regression models relating esturarine benthos to its environment should not only consider the role of spatial scale but the effects of temporal scales as well.

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