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Keeping things in order: multivariate direct gradient analysis of a strongly fluctuating benthic community

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Keeping things in order: multivariate direct gradient analysis of a strongly fluctuating benthic community 23153

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Abstract

Two spatial surveys of the macrobenthos of an estuarine intertidal area, the Oosterschelde in the southwestern part of The Netherlands, were conducted in different years. In the period between the surveys changes in the hydrodynamics of the estuary took place as a result of the construction of a storm-surge barrier. The works reduced the tidal volume in the basin and as a consequence the altitude of the tidal flats decreased by approximately 0.1 to 0.2 m. Considerable differences in species densities were found between the two surveys, but these large differences could not be explained by changes in the 'spatial' environmental variables (such as altitude) that were taken into account in a direct gradient analysis. Unknown and 'only-to-time-related' (e.g. weather-related) factors had considerably influenced species abundance. This implies that the impact of the works on the macrobenthos could not be evaluated on the basis of observed species densities in the before-and after-the-works surveys. Generally, it implies that even if the levels of future 'spatial' environmental variables are known, direct gradient analysis based on a single survey cannot be used for prediction of future densities in absolute terms in such strongly fluctuating communities. Yet, the gradient analyses for the two years revealed rather similar estimates of the major environmental gradients. The same was true for the parameters that described the relative change in species densities in response to a change in the environmental gradient levels. Hence the most appropriate way of evaluating the changes that have occurred in the benthic community as a result of the works was in terms of the observed changes in the 'spatial' environmental gradient levels. The levels of the first environmental gradient, which was strongly related to the sediment structure, did not change between years. Levels of the second gradient, which could be interpreted as a tidal zone gradient, decreased. This suggests that the works particularly affected taxa that are strongly related to this second gradient, such as *Corophium* living in the upper tidal areas and *Nephtys* living in the lower tidal zone. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: canonical correlation analysis; direct gradient analysis; macrozoobenthos; estuarine intertidal communities; reduced rank regression

1. Introduction

Community ecologists are interested in the relationship between assemblages of organisms and the

environments they live in. A widely applied research method is to perform a single observational field survey in which data on species abundance and environmental conditions are gathered at a large number of sampling sites. Usually, as a next step, a regression model is formulated under the assumption that

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species abundance depends on the environment. 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 modestly noted as 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.

A more ambitious purpose is to use the estimated regression model for prediction of species abundance from knowledge of the environment (or vice versa) in the future, the past or in neighbouring areas. Examples of such extrapolations of statistical species–environment models are Moss et al. (1987), Nicholls (1989), and Ter Braak and Wiertz (1994). Extrapolation in time requires the assumption that a ‘true’ regression model exists that not just applies in the study period, but that must have been relevant in the past, and will be appropriate in the future. Time does not play a role, and, strictly speaking, it is presumed that a change in environmental conditions is instantaneously followed by a response in species abundance, a response towards the abundance as predicted by the ‘true’ regression model. Hence, the notion of a regression model that worked in the past and will work in the future supposes the community to be in a ‘steady state’, which is entirely determined by the ‘spatial’ environment.

However, even when the environment is constant, a community is not necessarily in a ‘steady state’. Interactions among species may bring about constant changes in the structure of the community, in terms of species abundance. The community might even show chaotic dynamics. Besides, some environmental factors, such as those related to weather, may only vary in time and not in space, at least not at the spatial scale of the study. Such ‘only-to-time-related’ factors are inevitably not included in the model, but nevertheless could have their effects on species abundance. Hence, species abundance is not necessarily constant, but may fluctuate around some long-term average driven by biotic interactions or ‘only-to-time-related’ environmental factors.

Such fluctuations can be more or less similar at a spatial scale much larger than the size of the study

area. Thus, when some 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 not tractable. Consider, for example, a ‘true’ model whose expected values (given by a function of the ‘spatial’ environment) are equal to the long-term average species abundance. Community dynamics at spatial scales larger than the scale of a single sampling site imply that in a single survey the errors, which are the differences between the observed density and the long-term average, are not independent from sampling site to sampling site. The errors could even be strongly correlated. Consequently, the estimated regression model from the data of a single survey will yield a strongly biased estimate of the ‘true’ model, and the estimated model is not generally suited for the purpose of prediction. Hitherto, the errors (‘noise’) in direct gradient analysis were usually regarded as ‘uninteresting’ (Gauch, 1982). ‘Noise’ was thought to be the result of measurement error, or ‘stochastic’ variations of observed abundance around the ‘ideal distribution’ (Palmer, 1993). As argued above, the assumption that the errors are uncorrelated among sampling sites may be valid when the ‘true’ model is only meant to give a description of the here and now. If the ‘true’ model is aimed for prediction at other times and in other places, the independence assumption is not generally true.

The commonly used 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 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:

$$y_{ij} = \exp \left(c_j - \frac{(x_i - m_j)^2}{2\sigma_j^2} \right)$$

where the index $i = 1, \dots, n$ refers to the sites,

$j = 1, \dots, k$ 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, it is more convenient to write the model as $y_{ij} = \exp(b_{0j} + b_{1j}x_{1i} + b_{2j}x_{2i}^2 + b_{3j}x_{2i} + b_{4j}x_{2i}^2 + b_{5j}x_{1i}x_{2i})$.

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:

$$u_i = a_0 + \sum_{i=1}^q a_i x_{1i}$$

Estimation of the parameters of this constrained multivariate Gaussian response model is not straightforward. Usually, therefore, approximating methods such as canonical correspondence analysis 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 linearised form of the multivariate Gaussian response model, like the multivariate linear regression model using log-transformed species densities, may be more appropriate (Ter Braak and Prentice, 1988; Ter Braak, 1994a). Constrained forms of the multivariate linear regression model can be related to

the dimensionality-reduction techniques of canonical correlation analysis and redundancy analysis (Tso, 1981; Davies and Tso, 1982; Jongman et al., 1987; Van der Meer, 1991).

Studies on the reliability of multivariate direct gradient analysis have mainly focused on the performance of approximating methods. Most studies have been based on simulated data sets created by using the Gaussian response model (or slight modifications using asymmetric curves) and independent errors (Palmer, 1993). Studies that have used field data focused on observer differences (Leps and Hadincová, 1992), or on the stability of the parameter estimates by applying resampling techniques such as double-cross validation (Van der Meer, 1991). The 'steady-state' assumption, which is implicitly made when the Gaussian response model is used for the purpose of prediction, has been of no concern. So, emphasis has been placed more on the performance of the methods than on the crucial assumptions of the underlying model.

The present study focuses on the stability of direct gradient analysis of an estuarine intertidal macrobenthos community. Such communities are known for their large year-to-year variations in species abundance (Beukema, 1989; Coosen et al., 1994a). These variations may be due to the vagaries of the weather which have a 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 a strong influence on the structure of the community. The large variation in time and the small variation in space in intertidal benthic communities invalidate the use of direct gradient analysis, based on a single survey, for prediction of future densities in absolute terms. In the present study two surveys were conducted in the Oosterschelde estuary in the southwestern part of The Netherlands. In the study period a storm-surge barrier was constructed in the mouth of the estuary. Though the works may have affected the major environmental gradients and consequently species densities, the large year-to-year variation in benthos abundance makes it a priori impossible to evaluate the impact of the works solely on the basis of the observed macrobenthos densities in the two

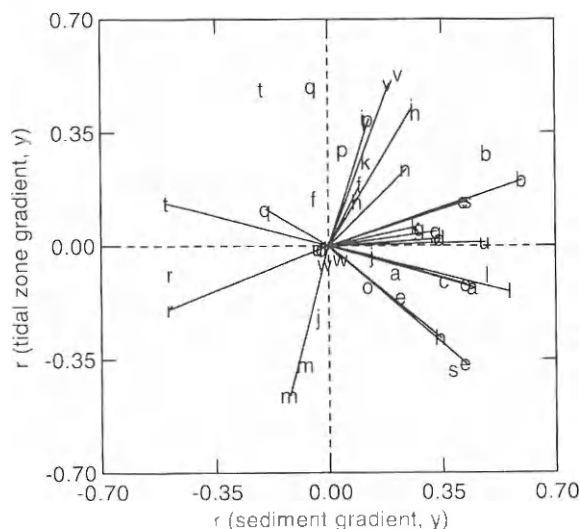


Fig. 3. The inter-set correlations r between the tidal zone gradient and the species densities y versus those for the sediment gradient. Estimates from the 1985 analysis are indicated by a letter connected to the origin. The 1989 data are only indicated by a letter. The gradients were based on the 1985 estimates of the canonical coefficients. Letters indicate the species; see Table 4. See text for further explanation.

accounted for by the first two canonical variates. So if a vector approaches the unit circle, then the species relates strongly to the first two variates. If the vector is short, then it does not. This explained variance is also given in Table 4. Its value is compared to the explained variance of the full-rank model, the well-known R^2 . Fig. 3 indicates that some species were mainly related to the sediment canonical variate. They seemed to 'prefer' either sandy (e.g., *Spio filicornis* and *Bathyporeia* sp.) or muddy (e.g., *Heteromastus filiformis* and *Hydrobia ulvae*) bottoms. Other species, which were especially related to the altitude variate lived high (*Corophium* sp.) or low (*Nephtys* sp.) in the tidal zone.

The inter-set correlations between the species abundances from 1989 and the '1985' canonical variates (that is, the 1989 environmental data are 'standardised' using the 1985 means and variances and subsequently multiplied by the 1985 matrix of canonical coefficients A) are also provided by Fig. 3. These 1989 vectors do not exactly allow all interpretations that could be made for the 1985 vectors, because the '1985' canonical variates applied to the 1989 data are not uncorrelated. The explained vari-

Table 4

Explained variance between a species and all environmental variables Z_x , and the first two canonical variates u for the 1985 data (first three columns) and the 1989 data (last three columns)

| | Explained variance | | | | | |
|------------------------------------|--------------------|------------|------------|-------|------------|------------|
| | 1985 | | | 1989 | | |
| | Z_x | u_{1985} | u_{1989} | Z_x | u_{1989} | u_{1985} |
| (a) <i>Cerastoderma edule</i> | 0.28 | 0.22 | 0.10 | 0.26 | 0.06 | 0.05 |
| (b) <i>Hydrobia ulvae</i> | 0.48 | 0.40 | 0.27 | 0.46 | 0.38 | 0.34 |
| (c) <i>Macoma balthica</i> | 0.26 | 0.19 | 0.16 | 0.30 | 0.18 | 0.14 |
| (d) <i>Mya arenaria</i> | 0.30 | 0.12 | 0.21 | 0.04 | 0.00 | 0.00 |
| (e) <i>Mytilus edulis</i> | 0.37 | 0.31 | 0.13 | 0.18 | 0.07 | 0.07 |
| (f) <i>Retusa alba</i> | 0.09 | 0.04 | 0.06 | 0.08 | 0.02 | 0.02 |
| (g) <i>Scrobicularia plana</i> | 0.19 | 0.11 | 0.11 | 0.20 | 0.12 | 0.08 |
| (h) <i>Anatides maculata</i> | 0.27 | 0.20 | 0.10 | 0.09 | 0.02 | 0.03 |
| (i) <i>Arenicola marina</i> | 0.33 | 0.25 | 0.21 | 0.27 | 0.16 | 0.17 |
| (j) <i>Capitella capitella</i> | 0.21 | 0.02 | 0.04 | 0.14 | 0.05 | 0.05 |
| (k) <i>Eteone</i> sp. | 0.15 | 0.08 | 0.07 | 0.16 | 0.08 | 0.08 |
| (l) <i>Heteromastus filiformis</i> | 0.42 | 0.33 | 0.30 | 0.32 | 0.27 | 0.24 |
| (m) <i>Nephtys</i> sp. | 0.29 | 0.23 | 0.20 | 0.26 | 0.18 | 0.14 |
| (n) <i>Nereis</i> sp. | 0.25 | 0.11 | 0.17 | 0.38 | 0.29 | 0.26 |
| (o) <i>Polydora</i> sp. | 0.28 | 0.19 | 0.14 | 0.15 | 0.01 | 0.03 |
| (p) <i>Pygospio elegans</i> | 0.29 | 0.17 | 0.22 | 0.15 | 0.12 | 0.09 |
| (q) <i>Scoloplos armiger</i> | 0.11 | 0.05 | 0.01 | 0.35 | 0.25 | 0.24 |
| (r) <i>Spio filicornis</i> | 0.31 | 0.28 | 0.23 | 0.38 | 0.32 | 0.26 |
| (s) <i>Tharyx marione</i> | 0.32 | 0.20 | 0.25 | 0.36 | 0.31 | 0.28 |
| (t) <i>Bathyporeia</i> sp. | 0.34 | 0.27 | 0.27 | 0.46 | 0.37 | 0.26 |
| (u) <i>Carcinus maenas</i> | 0.29 | 0.23 | 0.14 | 0.04 | 0.00 | 0.00 |
| (v) <i>Corophium</i> sp. | 0.35 | 0.28 | 0.20 | 0.41 | 0.39 | 0.35 |
| (w) <i>Crangon crangon</i> | 0.05 | 0.00 | 0.00 | 0.06 | 0.01 | 0.00 |
| Redundancy | 0.27 | 0.19 | 0.16 | 0.24 | 0.16 | 0.14 |
| Explained total variance | 0.32 | 0.23 | 0.19 | 0.33 | 0.25 | 0.22 |
| $1 - (\text{Wilks lambda})^{1/k}$ | 0.17 | 0.10 | 0.07 | 0.18 | 0.10 | 0.08 |

The canonical variates are either based on the 1985 data (u_{1985}) or on the 1989 data (u_{1989}).

ance of the '1985' canonical variates for the 1989 data is given in Table 4. The reversed procedure, that is using the '1989' canonical variates, is visualised in Fig. 4. The results are very similar to those presented in Fig. 3. Generally, the explained variance of the 'own' canonical variates is somewhat higher than the explained variance of the 'other' canonical variates (Table 4). For most species the 1985 and 1989 vectors are rather similar.

4. Discussion

The abundance of marine intertidal soft-sediment benthos may vary considerably from year to year

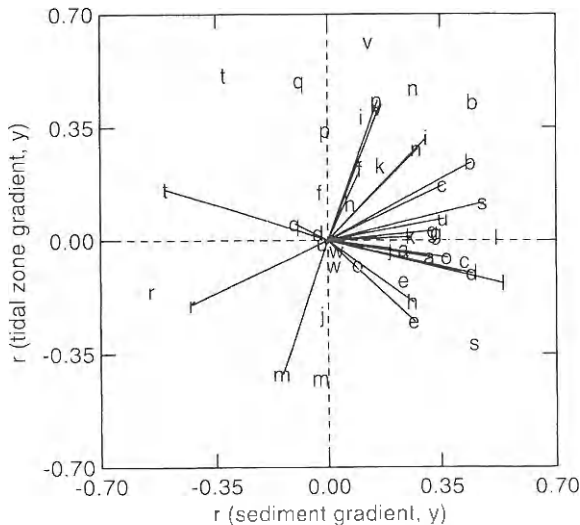


Fig. 4. The inter-set correlations r between the tidal zone gradient and the species densities y versus those for the sediment gradient. Estimates from the 1989 analysis are indicated by a letter connected to the origin. The 1985 data are only indicated by a letter. The gradients were based on the 1989 estimates of the canonical coefficients. Letters indicate the species; see Table 4. See text for further explanation.

(Beukema, 1989; Coosen et al., 1994a). Hence one may wonder what the use is of applying multivariate direct gradient analysis to a single survey from such a community where densities are so strongly fluctuating. What is the use of species–environment relationships that are only applicable on a very limited time–space scale? This question, which is rarely posed by the proponents of multivariate direct gradient analysis, is the theme of the present article.

This study confirmed that large differences in density and biomass of marine intertidal macrobenthos occur from year to year. The density of almost all species, and particularly of the molluscs, was much smaller in 1989 than in 1985. On the contrary, total biomass was much larger in 1989. This was mainly due to a high mortality of adult molluscs in the winter of 1984/1985 and a succeeding large recruitment of almost all mollusc species in the spring of 1985, resulting in large numbers of small individuals in the August 1985 survey (Coosen et al., 1994b). Spring 1987 showed another strong recruitment of cockles and other molluscs (Coosen et al., 1994b). In 1989 most of the individuals of the 1987 year-class were dead, but those which survived had grown to a large

individual size (Coosen et al., 1994b). The August 1989 survey can be characterised by small numbers of large individuals. Clearly, no statistical model of the species density–environment relationship based on the single 1985 survey would be able to predict accurately the 1989 densities in absolute terms.

Relative densities (in terms of “for this species a plot with such or such an environment will contain twice as many individuals as a plot with this or that environment”) were, however, much more consistent from year to year. This consistency was also apparent in the first two canonical variates u as found in both years (although reversed) and in most of the inter-set correlations between the standardised log-transformed species densities and the canonical variates u (Figs. 3 and 4). However, some inconsistencies (e.g., for *Bathyporeia* sp. and *Tharyx marione*) occurred, and there was a loss of explained variance when using the ‘other’ canonical variates (Table 4). One possible reason for such inconsistencies is the occurrence of different age-classes, each with its specific environmental preference, in the two years.

The species–environment relationship as estimated from the data of a single survey may explain part of the spatial variation, that is the total variance in species densities among sites. The present study showed that, in spite of the large year-to-year fluctuations in species densities which seem to be typical of marine intertidal communities, such relationships may have a more general validity in terms of relative species densities than just the time of the study. Yet, generally this does not need to be true. For example, the community dynamics may be caused by factors (varying only in time) that interact with the environmental variables (mainly varying in space) which were taken into account in the estimated species–environment relationship. For example, high numbers in the upper tidal zone relative to the lower tidal zone may occur after a severe winter, and the opposite may be true after a mild winter, or vice versa. Then, serious instabilities in time in the estimated relationship between relative densities and the environment can be expected.

During the study period changes in the hydrodynamics of the study area took place as a result of the construction of a storm-surge barrier. The works reduced the tidal volume in the basin and as a consequence the altitude of the tidal flats decreased by ap-

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