

Statistical Tools for Monitoring Benthic Communities

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With 12 Text-Figures and 6 Tables

Key words: Wadden Sea, monitoring, statistics, non-metric multidimensional scaling, minimal areas, diversity indices, conservation policy, economic development, multi criteria model for policy decisions.

Abstract

[PFEIFER, D. & BÄUMER, H.-P. & DEKKER, R. & SCHLEIER, U. (1998): Statistical tools for monitoring benthic communities. – *Senckenbergiana marit.*, **29** (1/6): 63–76, 12 figs., 6 tabs.; Frankfurt a. M.]

On the basis of long-term data from the monitoring program of the *Rijksinstituut voor Kust en Zee* (RIKZ), The Netherlands, we discuss how various statistical procedures can be successfully applied to the monitoring of benthic communities, especially in the Wadden Sea area. In particular, the following topics will be treated:

- (i) *Non-Metric Multidimensional Scaling* (NMDS) for visualization of trends and/or changes in species composition;
- (ii) *Minimal Areas* for checking the representativity of samples w.r.t. the number of species present;
- (iii) *Diversity* of species communities and its statistical estimation from samples including estimates for the estimation error in terms of their variance and standard deviation.

Although most of the underlying statistical techniques are in principal well-established [see, e.g. DIGBY & KEMPTON (1987) or SPELLERBERG (1991)] and applications in marine ecology are numerous, some new statistical results are added from an application-oriented point of view.

Kurzfassung

[PFEIFER, D. & BÄUMER, H.-P. & DEKKER, R. & SCHLEIER, U. (1998): Statistische Techniken für ein Monitoring benthischer Artengemeinschaften. – *Senckenbergiana marit.*, **29** (1/6): 63–76, 12 Abb., 6 Tab.; Frankfurt a. M.]

Anwendungen statistischer Techniken im Kontext eines Langzeit-Monitoringprogramms benthischer Artengemeinschaften insbesondere der Watten der südlichen Nordsee werden diskutiert auf der Grundlage zeitabhängiger Daten aus dem Monitoringprogramm des *Rijksinstituut voor Kust en Zee* (RIKZ), Niederlande. Dabei steht die anwendungsorientierte Behandlung der folgenden Themen im Vordergrund:

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- (i) *Nicht-metrische multidimensionale Skalierung* (NMDS) zur Visualisierung zeitabhängiger Entwicklungstendenzen und/oder Veränderungen in der Artenzusammensetzung;
- (ii) *Minimale Probenflächen*, um die Repräsentativität einer Probenahme in Hinsicht auf die Anzahl beobachteter Arten zu überprüfen;
- (iii) *Diversität von Artengemeinschaften* sowie Schätzer für Diversität, deren Varianz und Standardabweichung.

Obwohl die zugrundeliegenden statistischen Techniken überwiegend gut etabliert [siehe z.B. DIGBY & KEMPTON (1987) oder SPELLERBERG (1991)] und auf dem Gebiet der marinen Ökologie bereits zahlreiche Anwendungen veröffentlicht worden sind, sollen einige neue statistische Ergebnisse anwendungsorientiert präsentiert und zur Diskussion gestellt werden.

Non-Metric Multidimensional Scaling

A particular point of interest for environmental management is the comparison of communities over time, tracing changes or trends in species composition as possible indicators of environmental pollution or other exogenic effects on the system (see, e.g. SPELLERBERG 1991: Chapter 7). A usual way to visualize such complex objects as species communities – consisting frequently of several dozens of species – is to use non-metric multidimensional scaling (NMDS) [see, e.g. COX & COX (1994) for a comprehensive survey over the field; and LUDWIG & REYNOLDS (1988) or DIGBY & KEMPTON (1987) for ecological applications]. In short, the idea behind this technique is to project the high-dimensional points (vectors) of species abundances from the various sites and/or sampling times (henceforth called *monitoring units*) into a low-dimensional Euclidean space – typically IR^2 or IR^3 – such that the plot distances represent suitable *dissimilarities* between the monitoring units. Of course, it cannot be expected that such a representation will exist in all circumstances – therefore one has to confine oneself to approximate solutions in most cases. The usual measure to quantify the goodness-of-fit is *Stress* (see COX & COX 1994: Chapter 3) describing the weighted squared error in a monotonic regression for such a representation problem. From a practical point of view, the so-called *Shepard diagram* will usually provide a sufficient visualization of the goodness-of-fit. Here the NMDS distances are plotted against the “true” dissimilarities (or *similarities* which can however be easily converted into each other, e.g. by change of sign in connection with a suitable positive-linear transformation). A reasonably good fit is provided if the Shepard diagram displays a more or less monotonic relationship between the two variables which means that a large (small) dissimilarity between monitoring units is represented by a large (small) distance in the graph of the final configuration of monitoring units obtained by NMDS (henceforth called MDS plot) and vice versa.

However, the first step in NMDS is to decide on an appropriate measure for quantifying the substantive criteria or ideas of (dis)similarity. The many facets of the (dis)similarity measures proposed in the literature from an ecological as well as a statistical point of view and their fundamental importance for the results obtained by NMDS have led to a spirited discussion with disparate conclusions [see, e.g. FAITH & MINCHIN & BELBIN (1987) and CAO & WILLIAMS & BARK (1997) for ecological applications; 12 additional studies are cited in the last-mentioned paper]. This implies some controversy about which (dis)similarity measures are appropriate for NMDS in the context of ecological applications. Consequently, for each substantive problem investigated the (dis)similarity measure has to be chosen carefully.

With regard to the monitoring of benthic communities in the Wadden Sea area the question is brought into focus whether the observed seasonal variation is simply a uniform increase of the number of individuals of each species from winter (samples taken in March) to summer (samples taken in September) and/or a uniform decrease of the number of individuals of each species from summer to winter. Therefore, before we are going to investigate abundance data from the Netherlands monitoring program for the Wadden Sea carried out by NIOZ (*Nederlands Instituut voor Onderzoek der Zee*), provided kindly by RIKZ, we would like to discuss in short the effects of some usual (dis)similarity measures on MDS plots, namely the Pearson correlation, Spearman’s rank correlation, the cosine similarity, reversal Euclidean distance, and the Bray-Curtis similarity. For this purpose a working data set is constructed of a fictitious community of 10 species Spec 1 to Spec 10, recorded at 6 sites Site 1 to Site 6, showing the individual species abundances.

As can be seen from Tab. 1, Site 2 and Site 3 possess almost the same community structure as Site 1, with species abundances of roughly 2 and 4 times the size of Site 1, respectively. Hence, if the relative proportion of each species in the community is considered as a characteristic property of community structure, it seems reasonable to consider Site 1, Site 2, and Site 3 as “highly” similar. Site 4 is roughly the additive complement of Site 1, the sum of the abundances of both sites being almost equal to 17; hence a “larger” dissimilarity between Site 1 to Site 3, and Site 4 might be reasonable as well. Site 5 represents the case of an almost equi-distribution

Table 1. Abundance array assumed for a fictitious community of 10 species at 6 sites.

Species\Sites	Site1	Site2	Site3	Site4	Site5	Site6
Spec1	1	3	5	16	5	16
Spec2	1	4	4	15	6	9
Spec3	1	3	5	16	5	3
Spec4	1	2	6	14	7	3
Spec5	1	3	5	16	5	2
Spec6	2	5	9	15	5	2
Spec7	2	6	8	17	4	1
Spec8	4	10	18	13	5	1
Spec9	8	17	33	10	3	1
Spec10	16	33	66	1	5	1

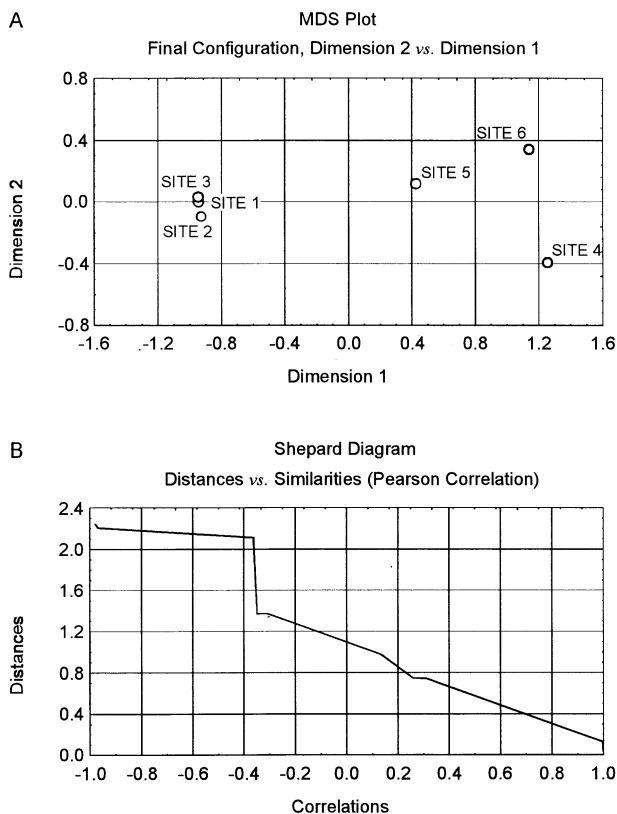


Fig. 1. NMDS ordination of the 6 sites (A) assumed for the fictitious abundance array given in Tab. 1 based on Pearson correlations (B).

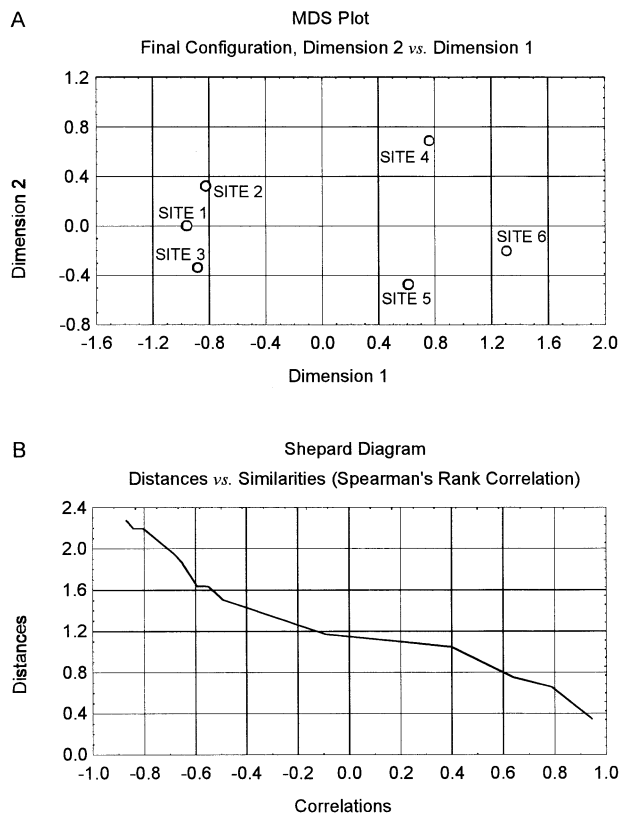
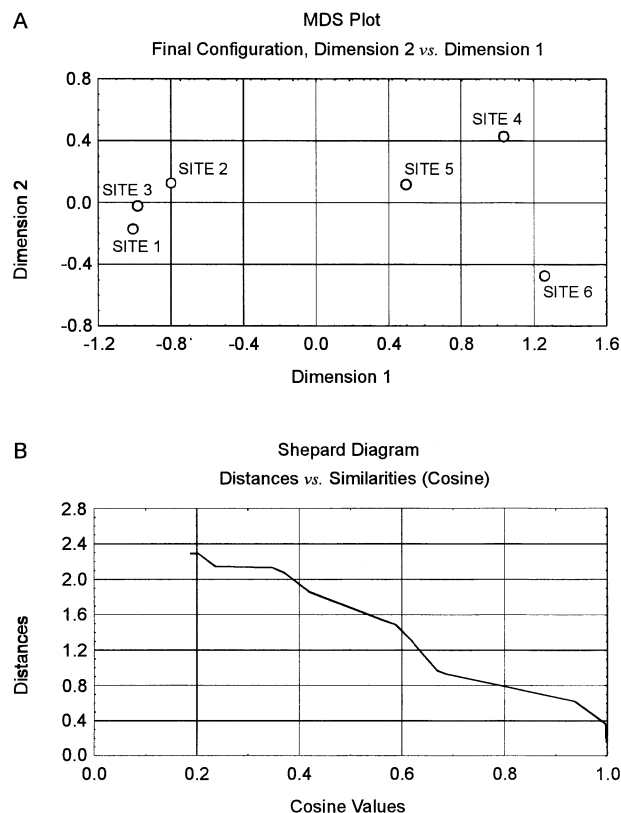


Fig. 2. NMDS ordination of the 6 sites (A) assumed for the fictitious abundance array given in Tab. 1 based on Spearman's rank correlations (B).

of species lying "in between" the other sites. Finally, Site 6 is practically a "reversed" version of Site 1 (with respect to the ordering of species), thus representing a kind of "extreme" dissimilarity between these two sites. Figs. 1A–5A show the output of the NMDS analyses with the five forementioned (dis)similarity measures for the fictitious community. As is expected from the Shepard diagrams (cf. Figs. 1B–5B) the corresponding stress values are very small (less than 10^{-3} in every case).

A comparison of these plots shows obviously that the more "qualitative" similarity measures as Pearson correlation, Spearman's rank correlation, and the cosine similarity reveal the structural properties of the fictitious community more clearly than do the more "quantitative" similarity measures as reversed Euclidean distance or the Bray-Curtis similarity. Although widely accepted in ecology, the Bray-Curtis similarity has the major drawback that it separates "similar" monitoring units if the difference is mainly due to multiples in abundance (cf. Site 1, Site 2, and Site 3 above) as is often the case when seasonal samples are considered (see also CAO & WILLIAMS & BARK 1997: 100). To be more precise, consider two monitoring units, one of which contains abundances which are K -times as large as the other ones. Then the Bray-

Fig. 3. NMDS ordination of the 6 sites (A) assumed for the fictitious abundance array given in Tab. 1 based on cosine similarities (B).



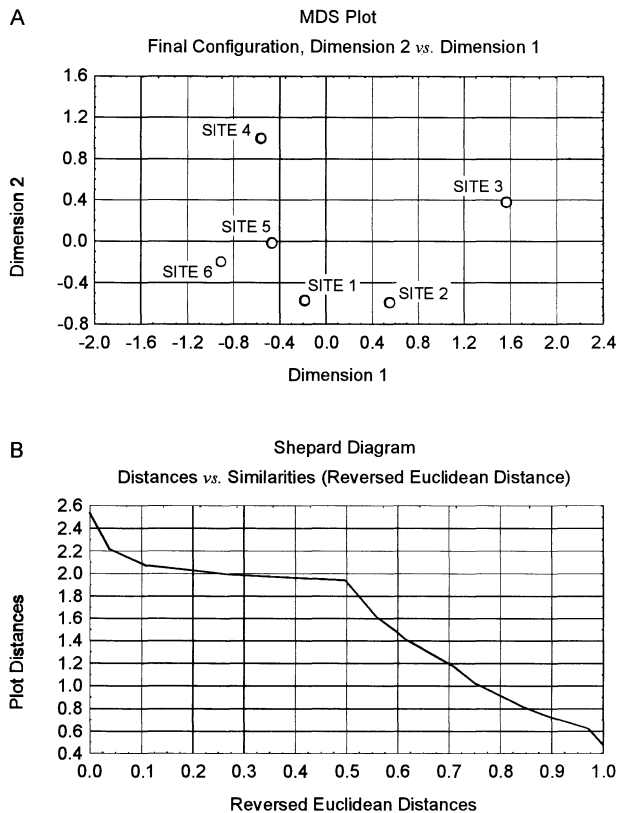


Fig. 4. NMDS ordination of the 6 sites (A) assumed for the fictitious abundance array given in Tab. 1 based on reversed Euclidean distances (B).

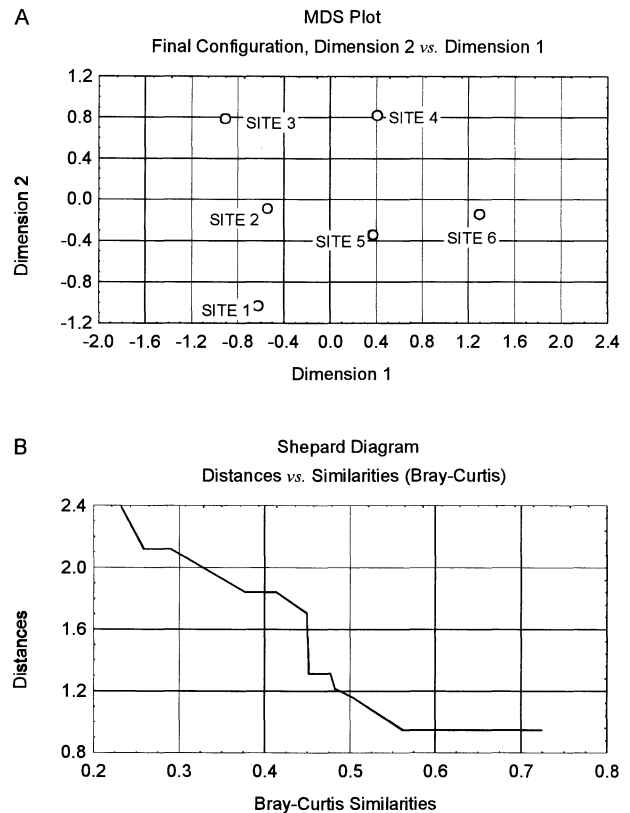


Fig. 5. NMDS ordination of the 6 sites (A) assumed for the fictitious abundance array given in Tab. 1 based on Bray-Curtis similarities (B).

Curtis similarity between these units is $2/(K+1)$ which is close to zero for large values of K . A similar argument applies to reversed Euclidean distance. Therefore, in the analysis of the species abundances at different sampling sites and/or at several sampling times it has been proposed to apply the Bray-Curtis similarity after some transformation of the abundances (see, e.g. CLARKE 1993: 118; and CLARKE & WARWICK 1998: 279). But the severe transformations (e.g. fourth root) often applied reduce the values of abundances to the level of ranks in a substantive meaning. Especially in the monitoring of benthic communities, if abundances per m^2 are computed from the counts of individuals at a sampling area size of a few cm^2 then it seems suitable to look upon the resulting numerical values as qualitative information about the ranking of the species. Furthermore, the Bray-Curtis similarity is recommended in the ecological context because this measure complies with the criterion of "joint absences" (see, e.g. CLARKE 1993: 118). Especially for case studies of environmental impacts on benthic communities, the loss of some species at a few monitoring units may be considered to be important for an evaluation of the (dis)similarity of pairs of sampling sites or sampling times. Even the number of pairwise zeroes may be a relevant information in describing the (dis)similarity of pairs of monitoring units.

With regard to the problem mentioned above Spearman's rank correlation seems to be a good candidate among the three qualitative similarity measures. Note that the cosine similarity

will frequently not attain its minimum value zero when abundances are considered since the corresponding data vectors must be orthogonal in that case (Fig. 3B). This, however, occurs only if no species are simultaneously present in two monitoring units. On the contrary, for the Pearson correlation, there is frequently too little discrimination between monitoring units which differ mainly by multiples of abundances (Fig. 1A). The following analyses have, therefore, been based on Spearman's rank correlation as similarity measure.

For computational purposes as well as for the visualization of the results of NMDS the statistical software system STATISTICA FOR WINDOWS, version 5.0, was used.

The data set under consideration is a time series of monitoring units taken from three different transects in the sublittoral part of the western Wadden Sea of the Netherlands called S1, S2, and S3. These data have been documented and commented since 1991 in the NIOZ reports 1991-1, 1992-3, 1993-3, 1994-2, and 1995-1 by R. Dekker in commission of the *Rijksinstituut voor Kust en Zee* (RIKZ), Haren. Tab. 2 shows the abundances per m^2 of 33 "common" species between summer 1989 and summer 1994 (denoted by S1Z89, S2Z89, S3Z89, S1W90, S2W90, S3W90, ..., S3Z94). The winter samples were taken in March, the summer samples in September.

The following species are recorded in Tab. 2: **Coelenterata**: *Sagartia troglodytes*; **Mollusca**: *Hydrobia ulvae*, *Retusa obtusa*, *Mytilus edulis*, *Cerastoderma edule*, *Spisula subtruncata*, *Tellina tenuis*, *Tellina fabula*, *Macoma balthica*, *Ensis americana*

Mya arenaria; **Polychaeta:** *Harmothoe sarsi*, *Eteone longa*, *Anaitides mucosa*, *Microphtalmus similis*, *Nereis succinea*, *Nephtys hombergii*, *Scoloplos armiger*, *Spio filicornis*, *Polydora ligni*, *Pygospio elegans*, *Magelona papillicornis*, *Tharyx marioni*, *Capitella capitata*, *Heteromastus filiformis*, *Arenicola marina*,

Lanice conchilega; **Oligochaeta:** *without specification*; **Crustacea:** *Gammarus locusta*, *Corophium volutator*, *Crangon crangon*, *Carcinus maenas*; **Echinodermata:** *Asterias rubens*.

The three MDS plots (cf. Figs. 6A–8A) show the temporal developments of sites S1, S2, and S3 from winter 1990 to

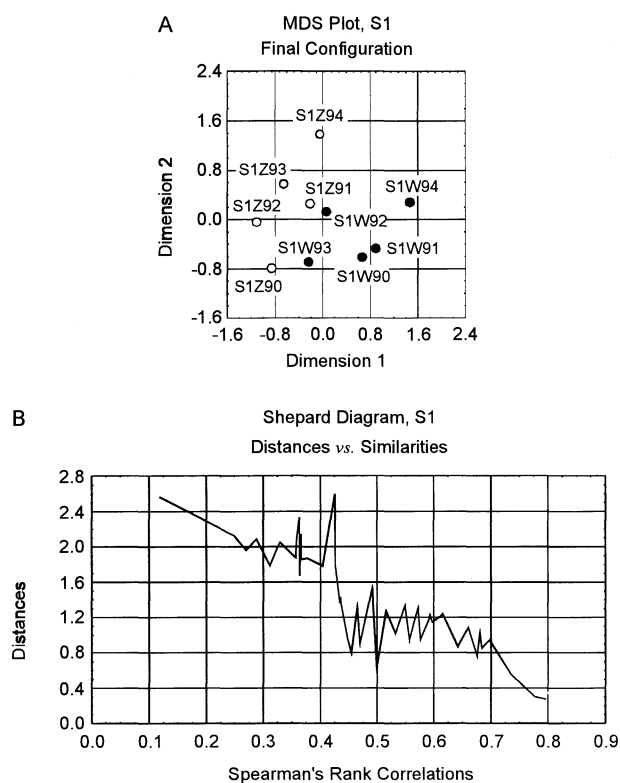


Fig. 6. Temporal development of the monitoring units at transect S1 from summer 1990 to winter 1994 given in Tab. 2. – (A) summer units in empty, winter units in solid circles. NMDS ordination based on Spearman's rank correlations (B).

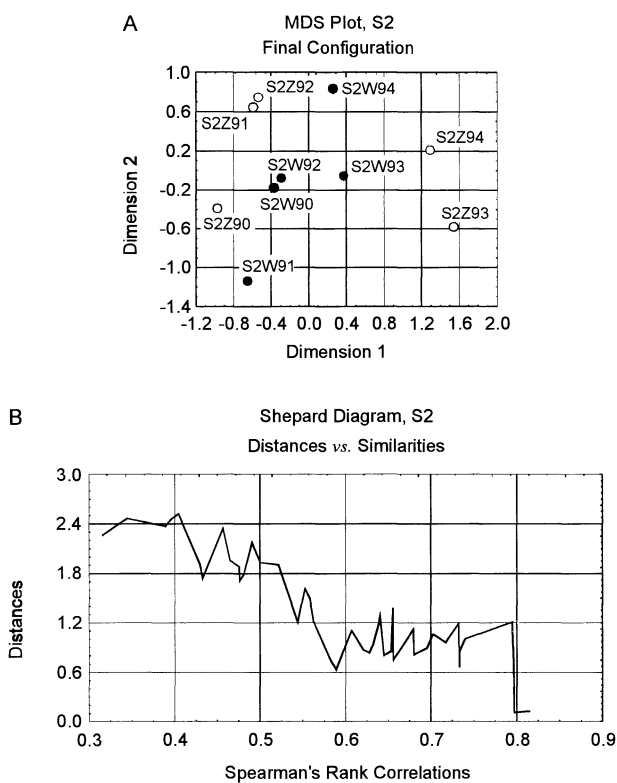


Fig. 7. Temporal development of the monitoring units at transect S2 from summer 1990 to winter 1994 given in Tab. 2. – (A) summer units in empty, winter units in solid circles. NMDS ordination based on Spearman's rank correlations (B).

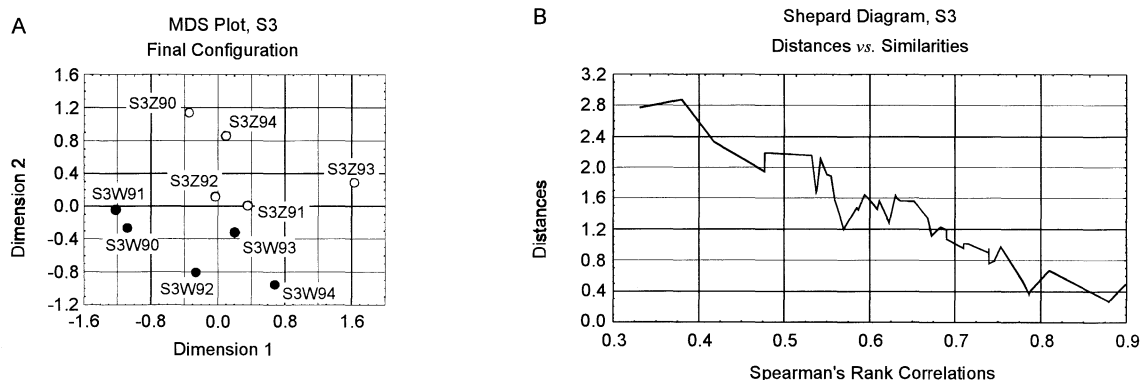


Fig. 8. Temporal development of the monitoring units at transect S3 from summer 1990 to winter 1994 given in Tab. 2. – (A) summer units in empty, winter units in solid circles. NMDS ordination based on Spearman's rank correlations (B).

Table 2. Species abundances per m² for summer (Z) as well as winter (W) samples taken from 1989 to 1994 at 3 different transects called S1, S2, and S3 in the sublittoral part of the western Wadden Sea of the Netherlands. – Data of the Nederlands Instituut voor Onderzoek der Zee, Den Burg, Texel.

	S1Z89	S2Z89	S3Z89	S1W90	S2W90	S3W90	S1Z90	S2Z90	S3Z90	S1W91	S2W91
<i>Sagartia</i>	5.0	0.0	0.0	8.0	0.0	0.0	1.0	2.0	7.0	2.0	0.0
<i>Hydrobia</i>	75366	68699	152667	96961	61546	142674	160713	67930	226292	169093	25536
<i>Retusa</i>	0.3	66.0	0.0	0.0	2.0	0.0	1.0	143.0	0.0	0.0	32.0
<i>Mytilus</i>	25.0	5.0	0.0	1.0	0.0	0.0	0.0	0.0	18.0	0.0	0.0
<i>Cerastod.</i>	10.0	37.0	25.0	0.0	14.0	1.0	120.0	11.0	214.0	0.0	0.0
<i>Spisula</i>	0.0	0.3	0.0	0.0	0.0	0.0	37.0	1.0	1.0	0.0	0.0
<i>Tellina ten.</i>	3.0	3.0	0.0	3.0	3.0	0.0	50.0	23.0	1.0	1.0	16.0
<i>Tellina fab.</i>	7.0	0.0	0.0	3.0	0.0	0.0	83.0	6.0	3.0	0.0	0.0
<i>Macoma</i>	180.0	74.0	122.0	146.0	59.0	173.0	98.0	87.0	153.0	69.0	56.0
<i>Ensis</i>	0.2	0.0	0.0	0.0	0.0	0.0	220.0	1.0	0.0	0.0	0.0
<i>Mya</i>	1.0	2.0	8.0	6.0	1.0	25.0	9.0	0.0	20.0	0.0	0.0
<i>Harmothoe</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Eteone</i>	13.0	0.3	1.0	1.0	0.0	3.0	8.0	0.0	1.0	0.0	0.0
<i>Anaitides</i>	125.0	2.0	0.3	40.0	4.0	21.0	12.0	0.0	0.0	3.0	2.0
<i>Microph.</i>	5.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	0.0	0.0
<i>Nereis</i>	15.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	9.0	0.0	0.0
<i>Nephtys</i>	113.0	54.0	8.0	114.0	31.0	14.0	166.0	45.0	14.0	95.0	42.0
<i>Scoloplos</i>	178.0	42.0	2.0	24.0	23.0	4.0	10.0	41.0	1.0	8.0	78.0
<i>Spio</i>	142.0	3.0	0.3	24.0	191.0	44.0	1388.0	188.0	28.0	10.0	30.0
<i>Polydora</i>	15.0	0.0	0.0	0.0	0.0	0.0	38.0	1.0	18.0	0.0	0.0
<i>Pygospio</i>	19.0	0.0	0.0	2.0	10.0	23.0	0.0	13.0	3.0	4.0	6.0
<i>Magelona</i>	7.0	0.0	0.0	1.0	0.0	2.0	4.0	3.0	6.0	1.0	0.0
<i>Tharyx</i>	17.0	0.0	4.0	22.0	1.0	40.0	31.0	0.0	51.0	14.0	0.0
<i>Capitella</i>	162.0	0.0	1.0	16.0	8.0	22.0	148.0	7.0	86.0	2.0	2.0
<i>Heterom.</i>	157.0	1.0	20.0	33.0	1.0	962.0	57.0	1.0	543.0	49.0	10.0
<i>Arenicola</i>	1.0	0.3	1.0	5.0	3.0	11.0	2.0	0.0	1.0	3.0	2.0
<i>Lanice</i>	0.0	0.3	0.3	0.0	1.0	1.0	37.0	2.0	38.0	0.0	0.0
<i>Oligoch.</i>	91.0	0.0	2.0	39.0	3.0	7.0	19.0	0.0	20.0	4.0	0.0
<i>Gammarus</i>	1.0	0.3	0.0	0.0	0.0	0.0	1.0	6.0	6.0	0.0	1.0
<i>Corophium</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
<i>Crangon</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Carcinus</i>	18.0	1.0	0.3	0.0	2.0	0.0	1.0	0.0	1.0	2.0	0.0
<i>Asterias</i>	4.0	1.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	7.0	0.0

	S3W91	S1Z91	S2Z91	S3Z91	S1W92	S2W92	S3W92	S1Z92	S2Z92	S3Z92	S1W93
<i>Sagartia</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
<i>Hydrobia</i>	210812	260582	15360	192728	120749	21497	65576	104662	56587	290731	200858
<i>Retusa</i>	0.0	0.0	378.0	0.0	0.0	40.0	0.0	28.0	433.0	0.0	3.0
<i>Mytilus</i>	0.0	1.0	0.0	11.0	0.0	0.0	0.0	0.0	9.0	27.0	0.0
<i>Cerastod.</i>	0.0	48.0	398.0	469.0	4.0	6.0	32.0	2.0	1666.0	71.0	0.0
<i>Spisula</i>	0.0	2.0	2.0	2.0	1.0	0.0	0.0	4.0	4.0	0.0	3.0
<i>Tellina ten.</i>	0.0	2.0	21.0	0.0	1.0	6.0	1.0	3.0	34.0	0.0	3.0
<i>Tellina fab.</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
<i>Macoma</i>	104.0	63.0	45.0	98.0	79.0	47.0	127.0	47.0	40.0	121.0	40.0
<i>Ensis</i>	0.0	3.0	1.0	8.0	0.0	0.0	0.0	0.0	4.0	1.0	2.0
<i>Mya</i>	3.0	10.0	446.0	439.0	1.0	121.0	36.0	2.0	286.0	47.0	0.0
<i>Harmothoe</i>	0.0	0.0	0.0	0.0	1.0	0.0	1.0	1.0	1.0	4.0	2.0
<i>Eteone</i>	3.0	2.0	3.0	1.0	0.0	1.0	1.0	3.0	1.0	0.0	0.0
<i>Anaitides</i>	3.0	0.0	1.0	1.0	3.0	1.0	2.0	0.0	0.0	0.0	0.0
<i>Microph.</i>	0.0	0.0	0.0	2.0	0.0	0.0	0.0	6.0	1.0	0.0	0.0
<i>Nereis</i>	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0
<i>Nephtys</i>	15.0	63.0	67.0	32.0	71.0	51.0	30.0	50.0	64.0	30.0	39.0
<i>Scoloplos</i>	4.0	7.0	309.0	0.0	14.0	118.0	0.0	12.0	29.0	1.0	4.0
<i>Spio</i>	9.0	18.0	132.0	3.0	14.0	18.0	1.0	39.0	97.0	17.0	44.0
<i>Polydora</i>	4.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Pygospio</i>	12.0	0.0	11.0	4.0	0.0	18.0	13.0	0.0	68.0	4.0	1.0
<i>Magelona</i>	1.0	1.0	1.0	0.0	1.0	1.0	0.0	4.0	3.0	0.0	4.0
<i>Tharyx</i>	60.0	9.0	0.0	13.0	3.0	1.0	1.0	1.0	2.0	6.0	1.0
<i>Capitella</i>	67.0	22.0	7.0	27.0	22.0	10.0	10.0	10.0	56.0	94.0	14.0
<i>Heterom.</i>	529.0	6.0	0.0	333.0	18.0	3.0	147.0	0.0	1.0	48.0	2.0
<i>Arenicola</i>	4.0	2.0	0.0	6.0	4.0	1.0	2.0	1.0	1.0	4.0	1.0
<i>Lanice</i>	0.0	0.0	3.0	1.0	1.0	1.0	0.0	8.0	1.0	2.0	1.0
<i>Oligoch.</i>	24.0	88.0	1.0	30.0	16.0	0.0	2.0	61.0	2.0	22.0	6.0
<i>Gammarus</i>	0.0	1.0	1.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0
<i>Corophium</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0
<i>Crangon</i>	0.0	8.0	11.0	2.0	2.0	2.0	1.0	2.0	2.0	3.0	0.0
<i>Carcinus</i>	1.0	0.0	0.0	2.0	1.0	4.0	1.0	1.0	1.0	0.0	2.0
<i>Asterias</i>	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0

	S2W93	S3W93	S1Z93	S2Z93	S3Z93	S1W94	S2W94	S3W94	S1Z94	S2Z94	S3Z94
<i>Sagartia</i>	1.0	0.0	0.0	2.0	0.0	1.0	0.0	0.0	0.0	2.0	0.0
<i>Hydrobia</i>	34097	99289	529346	108941	261912	348661	86327	130923	408799	128246	116261
<i>Retusa</i>	138.0	0.0	1.0	48.0	0.0	0.0	8.0	0.0	0.0	48.0	0.0
<i>Mytilus</i>	16.0	20.0	0.0	273.0	400.0	2.0	0.0	3.0	0.0	894.0	282.0
<i>Cerastod.</i>	896.0	39.0	6.0	524.0	71.0	0.0	6.0	22.0	62.0	213.0	456.0
<i>Spisula</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
<i>Tellina ten.</i>	16.0	1.0	0.0	16.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Tellina fab.</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Macoma</i>	40.0	91.0	47.0	51.0	93.0	51.0	26.0	66.0	33.0	54.0	73.0
<i>Ensis</i>	2.0	0.0	0.0	2.0	0.0	0.0	1.0	0.0	4.0	17.0	8.0
<i>Mya</i>	100.0	36.0	4.0	8.0	26.0	3.0	7.0	24.0	1.0	100.0	400.0
<i>Harmothoe</i>	0.0	3.0	0.0	0.0	3.0	1.0	0.0	0.0	0.0	0.0	0.0
<i>Eteone</i>	0.0	0.0	0.0	0.0	0.0	1.0	0.0	3.0	0.0	4.0	4.0
<i>Anaitides</i>	0.0	0.0	0.0	19.0	12.0	8.0	3.0	2.0	0.0	13.0	0.0
<i>Microph.</i>	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
<i>Nereis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	61.0	16.0
<i>Nephtys</i>	41.0	26.0	12.0	20.0	18.0	16.0	8.0	2.0	8.0	14.0	2.0
<i>Scoloplos</i>	7.0	2.0	2.0	7.0	1.0	12.0	6.0	2.0	0.0	61.0	7.0
<i>Spio</i>	18.0	9.0	7.0	6.0	4.0	0.0	0.0	0.0	0.0	317.0	127.0
<i>Polydora</i>	0.0	0.0	0.0	56.0	142.0	0.0	0.0	0.0	0.0	13.0	17.0
<i>Pygospio</i>	26.0	18.0	0.0	7.0	6.0	0.0	47.0	43.0	0.0	282.0	12.0
<i>Magelona</i>	0.0	0.0	7.0	0.0	3.0	4.0	0.0	0.0	2.0	1.0	2.0
<i>Tharyx</i>	3.0	3.0	3.0	3.0	2.0	0.0	1.0	1.0	0.0	2.0	9.0
<i>Capitella</i>	12.0	37.0	4.0	29.0	19.0	1.0	12.0	1.0	0.0	110.0	30.0
<i>Heterom.</i>	1.0	9.0	0.0	1.0	2.0	0.0	0.0	2.0	1.0	19.0	188.0
<i>Arenicola</i>	0.0	4.0	1.0	0.0	6.0	1.0	0.0	3.0	2.0	0.0	2.0
<i>Lanice</i>	0.0	0.0	3.0	16.0	21.0	0.0	0.0	0.0	0.0	6.0	9.0
<i>Oligoch.</i>	0.0	30.0	3.0	2.0	57.0	6.0	2.0	51.0	3.0	0.0	49.0
<i>Gammarus</i>	2.0	1.0	3.0	143.0	22.0	0.0	0.0	9.0	0.0	37.0	0.0
<i>Corophium</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Crangon</i>	0.0	3.0	4.0	3.0	3.0	0.0	0.0	1.0	2.0	3.0	2.0
<i>Carcinus</i>	1.0	2.0	0.0	100.0	30.0	0.0	2.0	6.0	1.0	11.0	7.0
<i>Asterias</i>	0.0	0.0	0.0	23.0	14.0	1.0	0.0	0.0	1.0	2.0	0.0

summer 1994 (winter units are marked in black, summer units in white). The corresponding stress values are 0.12, 0.14, and 0.08, respectively (see also Figs. 6B–8B). These MDS plots show quite clearly that in each year the summer community structure is noticeably different from the winter community structure, for all three sampling sites S1, S2, and S3. This means mainly that there is neither a uniform increase of the number of individuals of each species from winter to summer nor a uniform decrease in number from summer to winter. However, for each season itself, a clear similarity of the community structure is visible. Particular attention should be given to the Shepard diagrams showing no negative rank correlations between the monitoring units.

The MDS plot showing all units simultaneously (Fig. 9A) displays clearly three groups of data points separating the sampling sites S1, S2, and S3 from each other. Note that if we would disregard the point S1Z94 then all three groups would be strictly separated without overlap (the population density for S1Z94 is indeed comparably low which is the major reason for its outlying position in the MDS plot). In spite of the rela-

tively high natural and seasonal variation in the data, the last MDS plot reveals quite well that there exist explicit structural differences between the three monitoring units S1, S2, and S3 (even though the stress value of 0.22 as well as the Shepard diagram indicate that not all pairwise similarities correspond perfectly to the plotted pairwise distances). With respect to time, each unit seems to behave relatively stable with the exception of unit S1 in summer 1994. This is due to the fact that in this particular year the samples of this transect were sorted alive and not sorted after preservation as usual. The consequence of this different procedure is that a number of smaller polychaetes are lost/overlooked during the sorting procedure of the samples which leads to the outlying position of point S1Z94.

The above example shows that NMDS can be a fruitful statistical tool in monitoring programs, either to check regularly the “stability” of a complex system or to detect temporal particularities which might indicate environmental or other exogenic effects on the system.

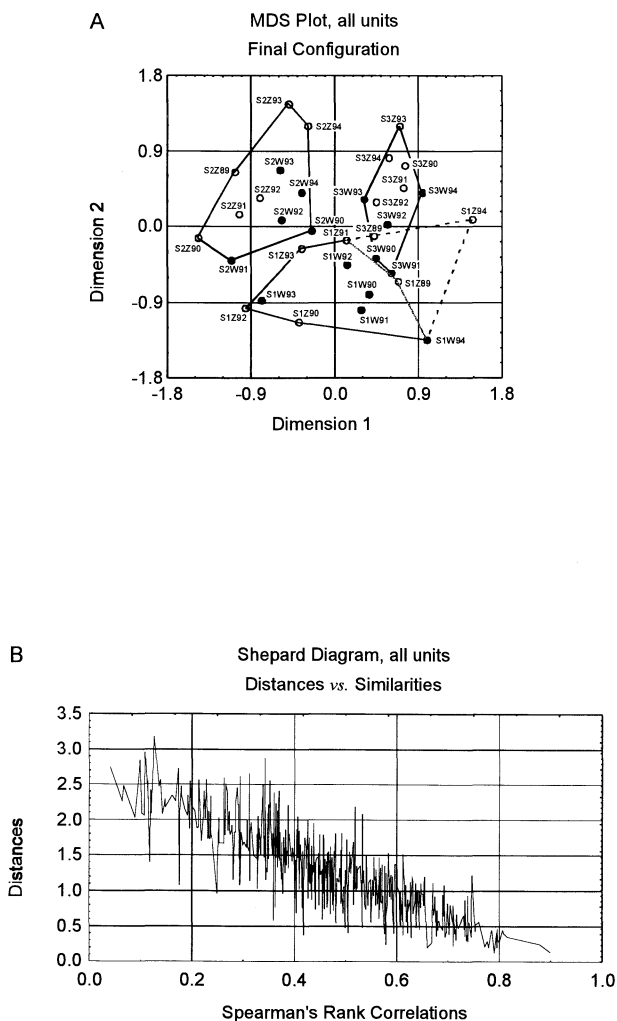


Fig. 9. Temporal development of all the monitoring units given in Tab. 2. – (A) summer units in empty, winter units in solid circles. NMDS ordination based on Spearman's rank correlations (B).

Minimal Areas

Another important point of interest in ecological monitoring programs is the representativity of the samples that are taken with respect to the number of species present at the particular observation site. This problem is closely related to the so-called *species-area-curve* which plots the (average) number of species detected against sampling area size. In most ecological applications, this relationship appears nearly linear on a log-log-scale before the theoretically expected plateau corresponding to the overall number of abundant species is reached (see, e.g. VALIELA 1995: Chapter 10). In a recent paper (PFEIFER & BÄUMER & SCHLEIER 1996) a more rigorous mathematical explanation of this effect is discussed, based on spatial point process models of Poisson type for the individual species. In this setting, a “minimal area” is – in a certain sense – the “smallest” observation area which is necessary to detect all abundant species. Due to the model assumptions, the resulting minimal area is independent of the shape of the particular sampling device. If, in practice, sampling would be repeatedly performed using devices of a comparably “small” size covering a unit area of 1 cm², say, then, with regard to

spatial randomness, the model assumptions are approximately fulfilled, and the minimal area size would roughly correspond to the *number of samples* necessary to obtain all abundant species. Note that by this kind of procedure, the minimal area size is a *random variable* whose distribution and moments like the expectation (= average size) μ and standard deviation σ can be explicitly calculated on the basis of the (true) average abundances $\lambda_1, \dots, \lambda_s$ of species per unit area. In particular, if we denote by $S(x)$ the species-area-curve and by W the size of the minimal area then

$$S(x) = \sum_{i=1}^s (1 - e^{-\lambda_i x}), \quad P(W \leq x) = \prod_{i=1}^s (1 - e^{-\lambda_i x}), \quad x \geq 0$$

$$\mu = \sum_{i=1}^s (-1)^{i-1} \sum_{1 \leq i_1 \dots \leq i_k \leq s} \frac{1}{\lambda_{i_1} + \dots + \lambda_{i_k}}, \quad \text{and}$$

$$\sigma^2 = 2 \sum_{i=1}^s (-1)^{i-1} \sum_{1 \leq i_1 \dots \leq i_k \leq s} \frac{1}{(\lambda_{i_1} + \dots + \lambda_{i_k})^2} - \mu^2$$

Table 3. Estimates of the average minimal area size μ , its standard deviation σ , and the average number of species $S(\mu)$ detected in an area of size μ with regard to the 6 sites assumed for the fictitious abundance array given in Tab. 1.

Parameters\Sites	Site1	Site2	Site3	Site4	Site5	Site6
μ	2.33	0.84	0.48	1.02	0.63	2.15
σ	1.18	0.46	0.24	0.98	0.29	1.14
$S(\mu)$	9.49	9.52	9.50	9.64	9.49	9.50

In order to check the representativity of a particular sample taken, the calculation of μ and σ could be performed with the abundance data obtained; a comparison of μ with the actual sampling size s then indicates whether the sample is really "representative" or not. For instance, if $\mu > s$ then one would on average need a larger sampling area than s in order to re-obtain the same number of species as in the original sample. This situation occurs for instance if a larger number of "rare" species is included in the sample. In general, the influence of "common" species on the average sampling area size is insignificant. If, on the contrary, $\mu < s$ then a smaller sampling effort would do equally well.

Note that although μ is the average sampling area size in order to detect *all* abundant species, sampling with an area size of μ will by mathematical reasons not necessarily guarantee that all species are actually included in the sample. However,

the *average number* of species detected will differ only slightly (by less than 1) from the overall number of species.

Programs to calculate the average minimal area size μ and its standard deviation σ have been developed by the first two authors and are available as DOS-versions on PC as well as MAPLE-versions on PC and workstations.

Tab. 3 shows the calculation results for the fictitious sampling sites Site 1 to Site 6 from Tab. 1. Remember that $S(\mu)$ denotes the average number of species detected if the sampling area is actually μ .

The results in Tab. 3 show clearly that the sampling size for Site 1 and Site 5 is too small due to the occurrence of relatively many "rare" species. On the other hand, the sampling effort for Site 3 could be reduced by 50% without losing too much information. The samples of Site 2 and Site 4 can be considered as being sufficiently large in order to be "representative". Note, however, that the variability of the minimal area size is comparably large with the exception of Site 3 and Site 5.

Figs. 10–11 show the output of the DOS version for the minimal area calculation for Site 1 and Site 2.

Tab. 4 contains the minimal area calculations for all monitoring units of the RIKZ data for sites S1 to S3, from summer 1989 to summer 1994. Fig. 12 shows the result of the minimal area calculation for unit S3W91 as an example.

The foregoing analysis shows that in all cases the average minimal area size μ is above the actual sampling area of 2.7 m² and 0.9 m², respectively. However, in many cases it is not above $\mu - \sigma$, such that on average, between two and three (presumably of the "rare") species might be overlooked in this case. The comparably large values of μ and $\mu - \sigma$ for summer

```

data input file? site1.txt

number n of species observed: 10

expected minimal area size  $\mu$ :      2.3304
[in multiples of reference area]

standard deviation  $\sigma$ :          1.1821
[in multiples of reference area]

expected number of species detected: 9.49 for sampling area  $\mu$ 
                                     8.2 for sampling area  $\mu - \sigma = 1.1482$ 
corresponding species-area-curve [log-log-scale]  number of species

```

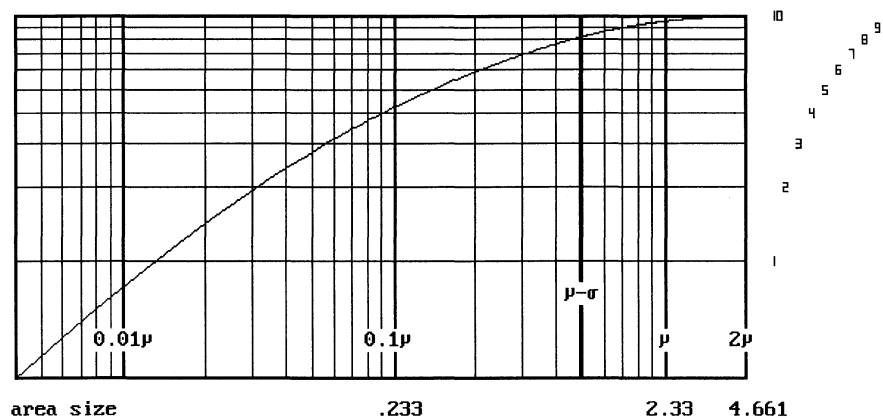


Fig. 10. Minimal area calculation for Site 1 of the 6 sites assumed for the fictitious abundance array given in Tab. 1. – Output of the DOS version of the programme.

data input file? site2.txt
 number n of species observed: 10
 expected minimal area size μ : .843
 [in multiples of reference area]
 standard deviation σ : .4591
 [in multiples of reference area]
 expected number of species detected: 9.52 for sampling area μ
 8.1 for sampling area $\mu - \sigma = .3839$
 corresponding species-area-curve [log-log-scale] number of species

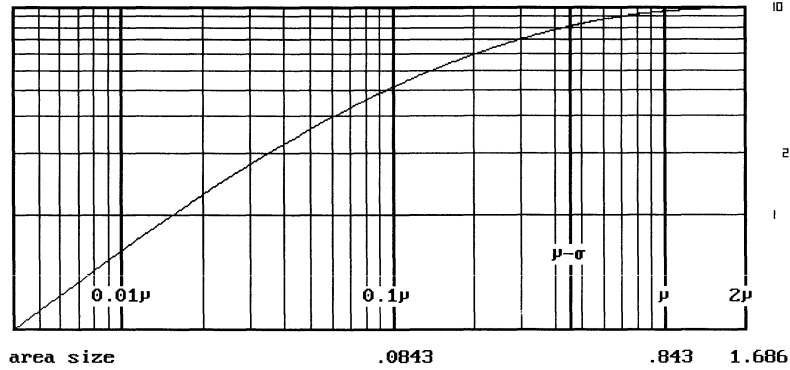


Fig. 11. Minimal area calculation for Site 2 of the 6 sites assumed for the fictitious abundance array given in Tab. 1. – Output of the DOS version of the programme.

data input file? s3w91.txt
 number n of species observed: 18
 expected minimal area size μ : 1.8907
 [in multiples of reference area]
 standard deviation σ : 1.1225
 [in multiples of reference area]
 expected number of species detected: 17.54 for sampling area μ
 16.17 for sampling area $\mu - \sigma = .7682$
 corresponding species-area-curve [log-log-scale] number of species

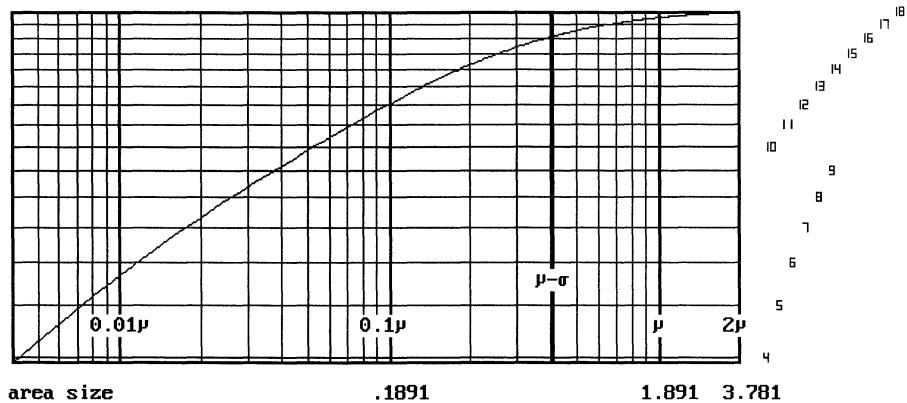


Fig. 12. Minimal area calculation for the monitoring unit S3W91 given in Tab. 2. – Output of the DOS version of the programme.

Table 4. Size of the sampling areas in [m²], estimates of the average minimal area size μ , its standard deviation σ , the average minimal area minus one times its standard deviation $\mu - \sigma$, the average number of species detected in an area of size μ and $\mu - \sigma$, resp., and the number of species actually observed with regard to all monitoring units given in Tab. 2.

	S1Z89	S2Z89	S3Z89	S1W90	S2W90	S3W90	S1Z90	S2Z90	S3Z90	S1W91	S2W91
actual sampling area	2.7	2.7	2.7	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
μ	6.49	7.65	7.00	1.91	2.16	1.90	2.31	2.15	2.59	1.74	1.70
σ	1.15	3.99	3.91	1.12	1.14	1.12	1.19	1.15	1.22	1.01	1.03
$\mu - \sigma$	5.34	3.66	3.09	0.79	1.02	0.78	1.12	1.00	1.37	0.73	0.67
$S(\mu)$	27.58	18.49	15.50	18.52	17.51	17.52	26.49	18.50	25.47	16.54	13.53
$S(\mu - \sigma)$	27.44	17.25	14.25	17.21	16.15	16.25	25.32	17.20	24.19	15.00	12.17
species detected	28	19	16	19	18	18	27	19	26	17	14

	S3W91	S1Z91	S2Z91	S3Z91	S1W92	S2W92	S3W92	S1Z92	S2Z92	S3Z92	S1W93
actual sampling area	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
μ	1.89	2.00	2.31	2.37	2.61	2.47	2.63	2.50	2.64	1.90	2.23
σ	1.12	1.08	1.18	1.15	1.21	1.20	1.20	1.18	1.15	1.12	1.11
$\mu - \sigma$	0.77	0.92	1.13	1.22	1.40	1.27	1.43	1.32	1.49	0.78	1.12
$S(\mu)$	17.53	19.52	19.49	23.49	19.48	19.48	17.48	22.49	25.48	18.52	19.51
$S(\mu - \sigma)$	16.16	18.10	18.21	22.12	18.17	18.20	16.14	21.13	24.12	17.20	18.05
species detected	18	20	20	24	20	20	18	23	26	19	20

	S2W93	S3W93	S1Z93	S2Z93	S3Z93	S1W94	S2W94	S3W94	S1Z94	S2Z94	S3Z94
actual sampling area	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
μ	1.93	1.70	1.68	1.42	1.70	2.60	1.67	2.02	2.18	1.72	1.06
σ	1.11	1.02	1.02	0.88	1.02	1.21	1.04	1.07	1.13	1.15	0.58
$\mu - \sigma$	0.82	0.68	0.66	0.54	0.68	1.39	0.63	0.95	1.05	0.57	0.48
$S(\mu)$	17.52	18.55	15.56	23.55	23.55	15.47	13.54	17.52	12.50	25.54	21.50
$S(\mu - \sigma)$	16.21	17.02	13.89	21.93	22.00	14.17	12.14	16.05	11.15	24.08	20.22
species detected	18	19	16	24	24	16	14	18	13	26	22

1989 are due to the fact that because of the larger sampling area, more “rare” species were found.

It is, of course, also possible to restrict minimal area calculations solely to certain “key species” which should be comprised in the sample with preference, if they actually occur at the sampling site.

Summarizing, one can say that with the present sampling area of 0.9 m² for the monitoring units S1, S2, and S3, the

“common” species will usually be sufficiently well represented in the samples whereas the less frequent species will occasionally not be detected, although they might be present at the sampling site. The question of presence/absence of “rare” species can thus not be sufficiently answered, if a zero value for the corresponding abundance is observed.

Diversity

Here we shall restrict ourselves to indices of diversity based on the proportional abundances $p = (p_1, \dots, p_s) \in \mathcal{P}$ of species (see, e.g. MAGURRAN 1988; or VALIELA 1995: Chapter 10),

where s denotes the total number of abundant species. Likewise, we shall not enter any of the controversial debates about the usefulness of diversity indices in ecology. Rather, we shall

discuss some of the *mathematical* foundations of diversity including statistical estimations and estimates of the corresponding statistical estimation errors (see also ENGEN 1978).

Some of the commonly accepted mathematical "axioms" of the diversity $D(\mathbf{p})$ can be summarized as follows.

- (D1) $D(\mathbf{p}) \geq 0$ for all $\mathbf{p} \in \mathcal{P}$ (choice of scale).
- (D2) $D(\mathbf{p}) = 0$ if and only if $s=1$, i.e. if the community consists only of one single species.
- (D3) $D(\mathbf{p}) = D(\mathbf{p}')$ for all permutations \mathbf{p}' of \mathbf{p} (invariance against numbering of species).
- (D4) $D(\mathbf{p}) \leq D\left(\frac{1}{s}, \dots, \frac{1}{s}\right)$ for all $\mathbf{p} \in \mathcal{P}$, i.e. diversity attains its maximum in case of an equi-distribution of species.
- (D5) $D(\mathbf{p}, 0) = D(\mathbf{p})$ for all $\mathbf{p} \in \mathcal{P}$, i.e. diversity does not change if the community "contains" an irrelevant species with zero abundance.
- (D6) $D\left(\frac{1}{s-1}, \dots, \frac{1}{s-1}, 0\right) \leq D\left(\frac{1}{s}, \dots, \frac{1}{s}\right)$ if $s > 1$, i.e. diversity is smaller for an equi-distributed community with less species than for an equi-distributed community with more species.

Unfortunately axioms (D1) to (D6) do not yet determine a diversity index uniquely. Frequently indices of the form

$$D(\mathbf{p}) = \sum_{i=1}^s f(p_i), \mathbf{p} \in \mathcal{P}$$

are considered in practice with some concave function f on the interval $(0,1)$ which fulfills the conditions $f(0) = f(1) = 0$. For instance, with $f(p) = -p \ln(p)$, one obtains the *Shannon entropy* $D_E(\mathbf{p})$, or, with $f(p) = p(1-p) = p - p^2$, one obtains *Simpson's index* $D_S(\mathbf{p})$. Characteristic differences between these diversity indices are given by their growth behaviour in the case of equi-distributed communities: while in the first case,

$D_E\left(\frac{1}{s}, \dots, \frac{1}{s}\right) = \ln(s)$ for s tending to infinity, we have, in the second case,

$D_S\left(\frac{1}{s}, \dots, \frac{1}{s}\right) = 1 - \frac{1}{s}$ tending to 1 for s tending to infinity.

Therefore, only moderately large or small numerical values for the diversity will be obtained for these indices (cf. MAGURRAN 1988: 35). In PFEIFER & BÄUMER & SCHLEIER & DE VALK (1995) a different index was therefore proposed which allows for an adjustment of the desired magnitude of diversity when s is large. The so-called γ -index is defined by $f(p) = p^\gamma(1-p)$ for $0 < \gamma < 1$ or

$$D_\gamma(\mathbf{p}) = \sum_{i=1}^s p_i^\gamma(1-p_i), \mathbf{p} \in \mathcal{P}$$

For γ -values close to zero, we obtain

$$D_\gamma(\mathbf{p}) \approx D_0(\mathbf{p}) = s - 1, \mathbf{p} \in \mathcal{P},$$

i.e. the number of abundant species up to 1, while for γ -values close to 1, we obtain

$$D_\gamma(\mathbf{p}) \approx D_1(\mathbf{p}) = D_S(\mathbf{p}), \mathbf{p} \in \mathcal{P},$$

i.e. Simpson's index. Note that Simpson's index measures in some sense the deviation of the species proportions from equi-distribution since also

$$D_S(\mathbf{p}) = 1 - \frac{1}{s} - \sum_{i=1}^s \left(p_i - \frac{1}{s}\right)^2, \mathbf{p} \in \mathcal{P}.$$

For benthic communities, applications of Shannon's entropy or Simpson's index will usually lead to extremely low numerical values for the diversity if e.g. the species *Hydrobia ulvae* is present; cf. the RIKZ data above. We therefore recommend to use the γ -index in such cases with γ -values close to zero, e.g. $\gamma = 0.1$.

In practical situations, such as monitoring, it is not possible to determine the *exact* diversity of the whole community. Rather, the diversity has to be estimated on the basis of samples, i.e. on the basis of *empirical proportional abundances* $\hat{\mathbf{p}}$. A statistically reasonable estimate for the true diversity then is $D(\hat{\mathbf{p}})$ which, however, is usually *biased* by the concavity of the defining function f . By application of a Taylor series expansion, a bias correction can approximately be performed using the formula

$$E[D(\hat{\mathbf{p}})] \approx D(\mathbf{p}) + \frac{1}{2n} \sum_{i=1}^s p_i f''(p_i)$$

where n denotes the overall number of individuals in the sample [for a detailed mathematical analysis in the general context of diversity, see PFEIFER & BÄUMER & SCHLEIER & DE VALK (1996)]. Likewise by Taylor series expansion, for the variance σ^2 of $D(\hat{\mathbf{p}})$, we obtain the approximation

$$\sigma^2 \approx \frac{1}{n} \left[\sum_{i=1}^s p_i f'(p_i)^2 - \left(\sum_{i=1}^s p_i f'(p_i) \right)^2 \right].$$

For the Shannon entropy and Simpson's index, we thus obtain

$$E[D_E(\hat{\mathbf{p}})] \approx D_E(\mathbf{p}) - \frac{s-1}{2n}, \quad \sigma^2 \approx \frac{1}{n} \left[\sum_{i=1}^s p_i \ln^2(p_i) - D_E^2(\mathbf{p}) \right],$$

$$E[D_S(\hat{\mathbf{p}})] \approx \frac{n-1}{n} D_S(\mathbf{p}), \quad \sigma^2 \approx \frac{4}{n} \left[\sum_{i=1}^s p_i^3 - \left(\sum_{i=1}^s p_i^2 \right) \right]$$

The bias correction for both indices can thus be performed via

$$\hat{D}_E(\mathbf{p}) = D_E(\hat{\mathbf{p}}) + \frac{s-1}{2n}, \quad \hat{D}_S(\mathbf{p}) = \frac{n}{n-1} D_S(\hat{\mathbf{p}}),$$

where $\hat{D}_E(\mathbf{p})$ and $\hat{D}_S(\mathbf{p})$ now denote the estimates to be used in practice. (Note that in MAGURRAN (1988) a typographical error has occurred on p. 35, relation (2.18)). Likewise, the variance and standard deviation, respectively of these estimates can be estimated by the above formulas, if the empirical proportions of abundances are used instead of the true (but unknown) proportions. This is justified by the law of large numbers because for all $i=1, \dots, s$ \hat{p}_i converges to p_i almost surely with increasing n .

Tabs. 5–6 contain the estimated diversities together with the estimated standard deviations σ for the fictitious samples from Site 1 to Site 6 above, and the monitoring units S1 to S3 from RIKZ, during summer 1989 to summer 1994. For the γ -index, the value of 0.3 was used in the first case, and 0.1 in the second case. Note that because of the high number of individuals observed, a bias correction has no relevant numerical

Table 5. Estimates of diversity indices $D(\boldsymbol{p})$ and estimates of their standard deviation σ with regard to the 6 sites assumed for the fictitious abundance array given in Tab. 1. – The minimal and maximal value for each diversity index are shaded lightly and darkly, resp.

Parameters \ Sites	Site1	Site2	Site3	Site4	Site5	Site6
$\hat{D}_E(\boldsymbol{p})$	1.85	1.92	1.82	2.24	2.37	1.89
σ	0.12	0.08	0.07	0.02	0.08	0.11
$\hat{D}_S(\boldsymbol{p})$	0.737	0.783	0.759	0.887	0.893	0.752
σ	0.054	0.030	0.025	0.002	0.005	0.049
$\hat{D}_{0.3}(\boldsymbol{p})$	3.82	3.99	3.90	4.34	4.48	3.87
σ	0.21	0.12	0.09	0.06	0.03	0.20

effects for the RIKZ data due to the occurrence of *Hydrobia ulvae* throughout. For the first data set, the minimal values for the diversity are each shaded light, while the maximal values for the diversity are shaded dark. For the RIKZ data, the three minimal and maximal values for the diversity are shaded each.

As was expected from the data given in Tab. 1, the diversities of Site 1 to Site 3 differ only marginally for all three indices since the corresponding proportional abundances \boldsymbol{p} are very close to each other. Note that in the MDS plots, the points which represent these monitoring units are also the closest in distance w.r.t. Pearson correlation, Spearman's rank correlation, and the cosine similarity measure. The proportional abundances at Site 6 are also very similar to those of Site 1 to Site 3, however in reverse order, so that the diversity is again nearly the same (cf. Axiom (D3) above), while the distances

Table 6. Estimates of diversity indices $D(\boldsymbol{p})$ and estimates of their standard deviation σ for all monitoring units given in Tab. 2. – The three lowest and highest estimated values for each diversity index are shaded lightly and darkly, resp.

	S1Z89	S2Z89	S3Z89	S1W90	S2W90	S3W90	S1Z90	S2Z90	S3Z90	S1W91	S2W91
$\hat{D}_E(\boldsymbol{p})$	0.129	0.035	0.011	0.042	0.045	0.064	0.109	0.065	0.044	0.015	0.081
σ	0.003	0.001	0.001	0.001	0.002	0.001	0.019	0.002	0.001	0.001	0.004
$\hat{D}_S(\boldsymbol{p})$	0.0339	0.0084	0.0025	0.0099	0.0114	0.0186	0.0308	0.0168	0.0108	0.0032	0.0213
σ	0.0009	0.0005	0.0001	0.0004	0.0006	0.0005	0.0006	0.0007	0.0003	0.0002	0.0013
$\hat{D}_{0.1}(\boldsymbol{p})$	11.52	6.70	5.04	7.26	6.77	6.76	10.62	7.42	9.28	5.80	5.90
σ	0.11	0.14	0.12	0.07	0.09	0.07	0.08	0.09	0.09	0.07	0.08

	S3W91	S1Z91	S2Z91	S3Z91	S1W92	S2W92	S3W92	S1Z92	S2Z92	S3Z92	S1W93
$\hat{D}_E(\boldsymbol{p})$	0.031	0.013	0.542	0.058	0.019	0.142	0.048	0.025	0.259	0.016	0.008
σ	0.001	0.001	0.101	0.001	0.001	0.006	0.002	0.001	0.004	0.001	0.001
$\hat{D}_S(\boldsymbol{p})$	0.0079	0.0027	0.2001	0.0152	0.0042	0.0404	0.0123	0.0054	0.0914	0.0034	0.0017
σ	0.0002	0.0001	0.0043	0.0004	0.0002	0.0019	0.0006	0.0003	0.0017	0.0001	0.0001
$\hat{D}_{0.1}(\boldsymbol{p})$	6.30	6.69	9.56	8.57	6.92	8.57	6.69	8.18	10.68	6.53	6.44
σ	0.07	0.08	0.10	0.09	0.10	0.11	0.10	0.10	0.11	0.07	0.09

	S2W93	S3W93	S1Z93	S2Z93	S3Z93	S1W94	S2W94	S3W94	S1Z94	S2Z94	S3Z94
$\hat{D}_E(\boldsymbol{p})$	0.207	0.030	0.002	0.091	0.031	0.003	0.014	0.017	0.003	0.124	0.104
σ	0.005	0.001	0.000	0.002	0.001	0.000	0.001	0.001	0.000	0.002	0.002
$\hat{D}_S(\boldsymbol{p})$	0.0724	0.0066	0.0004	0.0244	0.0072	0.0006	0.0029	0.0036	0.0005	0.346	0.0286
σ	0.0020	0.0003	0.0001	0.0006	0.0002	0.0001	0.0002	0.0002	0.0001	0.0007	0.0007
$\hat{D}_{0.1}(\boldsymbol{p})$	7.80	7.11	4.64	9.62	8.57	4.70	4.96	6.24	3.74	10.57	8.92
σ	0.08	0.07	0.06	0.07	0.07	0.08	0.07	0.08	0.07	0.07	0.06

between Site 6 and the group of points representing Site 1 to Site 3 in Figs. 1A–3A are the largest occurring.

The highest diversity for all three indices is simultaneously reached at Site 5 which comes close to an equi-distribution of species, followed by Site 4 with a similar community structure, except for species 10.

For the RIKZ data, similar results hold true. The lowest diversity values here are observed for site S1 since summer 1993; note that the point corresponding to S1Z94 (absolute minimum of diversities) is also outlying in the MDS plot, and that the points corresponding to S1Z93 and S1W94 are on the boundary of the S1-group of points in the MDS plot. This is

in contrast to the earlier years up to summer 1990 for this site where at least the γ -index reaches two of its largest values.

In general, the highest diversity values are reached in summer (with one exception for the Shannon entropy in winter 1993), in particular at site S2.

Summarizing, one can thus say that the characteristic differences visualized in the MDS plot between sites S1, S2, and S3 are confirmed by the foregoing analysis showing a gradual development for site S1 over the years towards a less diverse community, a highly diverse and stable community at site S2, and a moderately diverse community at site S3.

Acknowledgement

We thank Dr. K. ESSINK, RIKZ, for giving permission to use and publish part of the RIKZ monitoring data in this paper. We are most grateful to Dr. K. R. CLARKE of the Plymouth Marine Laboratory and

to an anonymous referee for their constructive criticisms and valuable comments.

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Submitted: 19.02.1997

Reviewed: 15.07.1997

Accepted: 20.11.1997