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An evaluation of the ABC-method (abundance/biomass comparison) as applied to macrozoobenthic communities living on tidal flats in the Dutch Wadden Sea

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Abstract

The ABC-method proposed by Warwick (1986) for detecting pollution effects on marine zoobenthic communities, was tested on distribution patterns of numbers and biomass among species in macrozoobenthos samples taken annually for 13 yr in a uniform way at 15 tidal-flat stations in the western part of the Dutch Wadden Sea. Along the margins of the tidal-flat area studied, where exposition to either drainage or water movements is extreme, the k-dominance plots for numbers were generally situated above those for biomass. In these areas values for biomass and species richness were relatively low and a few small-sized species such as *Corophium volutator* and *Hydrobia ulvae* were very numerous. In the central part of the area, where environmental conditions are less severe, values for biomass and species richness were higher. Biomass was dominated by large adults of *Mya arenaria, Mytilus edulis* and/or *Arenicola marina*. However, in only a restricted part of this area were plots for numbers consistently below biomass plots. In most of the central area high numbers of *H. ulvae* occasionally occurred, causing plots for numbers to be situated above those for biomass during such periods. There appears to be no reason to interprete a high abundance of *H. ulvae* as a sign of pollution or any other kind of disturbance or stress. It is concluded that the ABC method cannot be applied to tidal flat communities without reference to long-term and spatial series of control samples. In areas where such small-sized and sometimes numerous species as *H. ulvae* occur in strongly fluctuating numbers, the method appears useless for assessing the pollution status of a benthic community.

Introduction

Recently, Warwick (1986) proposed a method, called ABC method (short for abundance/biomass comparison, Warwick et al. 1987), for describing the pollution status of a marine benthic community. The numerical distribution of individuals among species and the distribution of biomass among species would exhibit a differential response to disturbance (by pollution or otherwise). Such a difference is to be expected from a dominance of r-selected or opportunistic species (with short life span, small body size and often high numerical densities) in disturbed areas, in contrast to the competitive dominance of K-selected or conservative species (with long life span, large adults and relatively constant and low numbers) in communities which are in equilibrium with a relatively stable environment. Thus, in disturbed areas there would be a numerical dominance of one or a few small-sized species which contribute only little to total biomass. In contrast, in more stable environments, a biomass dominance of one or a few large-sized species would exist and these species would contribute little to total numbers. Such situations can be described conveniently by using k-dominance curves (Lambshead et al. 1983) in which the species are ranked in order of dominance (separately both as to numbers and to biomass) on the X-axis (on a logarithmic scale) with percentage dominance on the Y-axis (on a cumulative scale). In a disturbed community (dominated by opportunistic species), the plot for numbers would lie above the biomass plot (Fig. 1 b), whereas in an equilibrium community (dominated by conservative species) the reverse situation would occur (like in Fig. 1 a).

The evidence presented so far (Warwick 1986, Warwick et al. 1987) appears convincing: both temporal and spatial series around grossly polluted sites exhibited the expected sequence of plot configurations, viz. before pollution and at long distances from a source of pollution the biomass plots were situated above the plots for numbers and the reverse configuration was found after pollution and at short distances from the source of pollution. Moreover, changes in plot configurations during recolonization after azoic conditions were the reverse as those resulting from progressive pollution. So far, "unpolluted" configurations have been observed in all undisturbed communities. However, only very few examples from intertidal communities have been presented (Warwick et al. 1987). Because intertidal communities are suspected to be more severely stressed and more frequently disturbed (compared to subtidal communities) by naturally fluctuating environmental conditions, the validity of the ABC method should be tested especially in intertidal areas.

An extensive homogeneous data set (13 annual and uniformly executed samplings at each of 15 fixed stations) is used to evaluate the ABC method for intertidal soft-bottom areas. Such a data set would, in particular, be useful to test the claim that this method can assess the pollution status of a benthic community without reference to a temporal or spatial series of control samples.

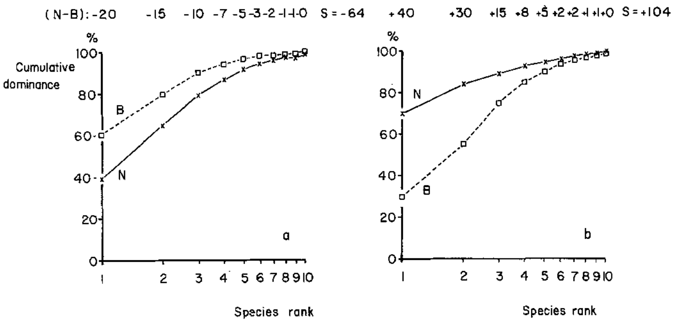

Fig. 1. Hypothetical k-dominance plots for species numbers (N, ×) and biomass (B, o). (a) A case of dominance of K-selected species (B-plot above N-plot, S (N−B) negative). (b) A case of dominance of r-selected species (N-plot above B-plot, S (N−B) positive)

Materials and methods

The 15 sampling stations were scattered in the 50 km^2 tidal-flat area known as Balgzand (Fig. 2a), which is located in the westernmost part of the Wadden Sea. Of these 15 stations, 3 are square plots of 900 m^2 each and 12 are transects of 1 km each. All stations are marked by permanent iron poles.

These 15 stations have been sampled at least annually (in late winter/early spring, mostly in March) for nearly 20 yr. Data from the last 13 yr have been used, because only since 1975 has the manner of sampling been completely uniform. The three square plots were sampled at least four times per year and data from these plots will be used to study seasonal effects.

Sampling procedures were described in detail in earlier papers (Beukema 1974, 1979). In short: cores were taken

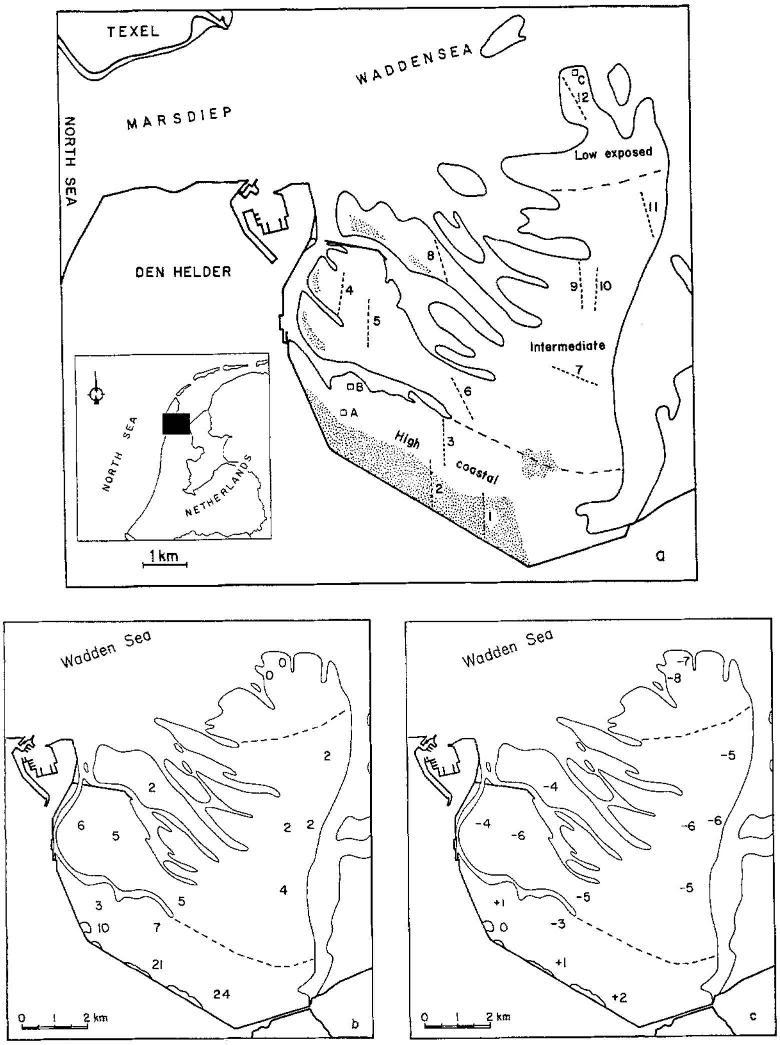

Fig. 2. The Balgzand tidal flat area (i.e., the area above LTL, roughly indicated by thin line), showing some environmental conditions. (a) Location of sampling stations (three squares: A, B and C and 12 transects: 1 to 12). (b) Mean percentage of silt (i.e. particles < 60 μm) in upper 5 cm of sediment. (c) Mean intertidal level expressed in dm difference to MTL. Approximate borders of three subareas are indicated by ---. Shaded area in (a) denotes area above MTL

and sieved in the field on 1 mm mesh screens. All samples were sorted in the laboratory while the animals were still alive, thereby facilitating complete extraction from the sieve residues. The total area sampled at each sampling was 0.9 m^2 along the 12 transects, 1.0 m^2 at the Squares A and B, and 1.7 m^2 at the sparsely populated Square C.

Abundance is expressed both in numbers per m^2 and in g m^{-2} AFDW (ash-free dry weight). For each of the 195 samples (13 yr × 15 stations), both numerical (N) and biomass (B) values were converted to percentages of the total of the sample and these percentages were ranked. To condense the configuration of the two plots into a single figure, the first (i.e., the highest) percentage for biomass was subtracted from the first number percentage (usually not referring to the same species!), the second B-percentage from the second N-percentage, etc. (following a suggestion of Janssen 1987). The sum of these (7 to 24) differences was called S (N−B) and was used to characterize the mutual position of the N and B plot. Two examples of the manner of calculation of S (N−B) are shown in Fig. 1. The value of this statistic reflects the area between the N- and B-plot. It is used as a dimensionless number, indicating as an index the mutual positions of the N- and B-plot. Thus, an N-plot situated (for the greater part) above a B-plot yields a positive value for S (N−B), and in the reverse configuration a negative value for S (N−B) is calculated.

Avarages of such S (N−B) values are shown (Fig. 3d) with one standard deviation to indicate the variability of the individual data. However, because the distribution of the individual data was far from normal at most stations and in most years, non-parametric tests were used to evaluate differences and trends. These tests are described in Siegel (1956).

Description of the area and its macrobenthic fauna

Various types of tidal flats were represented among the sampling stations (Fig. 2a), from soft muds to clean sands (Fig. 2b) and from high- to low-water level (Fig. 2c). The mean tidal range is from ~ −80 cm to ~ +60 cm (compared to MTL). The southwestern part of Balgzand is high (Transects 1 and 2 and part of 3 and the Squares A and B are situated above or around MTL) and silty (at Transects 1 and 2 and Square A silt, i.e., material smaller than 60 μm, constitutes more than 10% of the sediment). Contrastingly, the northeastern part is well below MTL and sandy (along Transects 8, 9, 10 and 11 the sediment contains ~2% of silt and at Transect 12 and Square C even less than 1%). The central part of Balgzand is intermediate in both respects (Fig. 2b, c).

Faunal composition of macrobenthos widely differs between these subareas of Balgzand. Along the southwest coast (Transects 1, 2 and 3, Squares A and B), the number of species is relatively low (Fig. 3b), no species with high biomass values are present and one or two small-sized species, viz. the crustacean *Corophium volutator* (Pallas) and the gastropod *Hydrobia ulvae* (Penn.), exhibit strong numerical dominance (Fig. 3a). At lower intertidal levels (further offshore), suspension-feeding bivalves (viz. *Cerastoderma edule* (L.), *Mytilus edulis* L. and *Mya arenaria* L.) become more prominent and dominate the biomass, together with the lugworm *Arenicola marina* (L.), causing high values for total biomass (Fig. 3c). Numbers in samples from this area were either not clearly dominated by any one species or by *H. ulvae* (Fig. 3a). In some years the numerical densities of this species amounted to tens of thousands per m^2 at the Transects 9, 10 and 11. Both species number (Fig. 3b) and particularly biomass (Fig. 3c) declined again in the far northeastern part of Balgzand. Particularly at Transect 12 and at Square C (situated close to a major tidal stream with strong currents) the fauna is numerically dominated by the small-sized polychaete worm *Scoloplos armiger* (O.F.M.) (Fig. 3a), whereas no biomass-dominating species is present. A species is called "dominant" when it has been the highest contributer to either numbers or biomass at a particular sampling station for at least 6 of the 13 yr.

The faunal differences between these parts of Balgzand are in accordance with a model proposed by Beukema (1976) for the relationship between local values for biomass and species richness of the tidal-flat macrozoobenthos of the Wadden Sea and prevailing environmental conditions at the sampling places. In short: maximal values for both biomass and species number occur at intermediate values for intertidal height and sediment composition. Both at extreme levels (near the HW or near the LW mark) and at extreme sediment compositions (either very high or very low proportions of fine material), the macrozoobenthic fauna is reduced in biomass as well as in species richness. Such extreme conditions usually occur at the fringes of large tidal flat areas. At Balgzand such marginal areas are: the high and silty 1 to 2 km wide strip along the southwest coast (the *Corophium volutator* zone) and the low, clean-sandy, exposed, northeastern part (*Scoloplos armiger* area). Seven of the 15 sampling stations at Balgzand are located in areas with extreme environmental conditions. The other 8 stations are characterized by less extreme values for both silt content of the sediment (Fig. 2b) and intertidal level (Fig. 2c). Accordingly, in this central part of Balgzand the number of species (Fig. 3b) and the biomass values (Fig. 3c) are higher. The response of biomass values appears particularly strong from the presence in this area of one or more species with large adults such as *Mya arenaria, Mytilus edulis, Cerastoderma edule* and *Arenicola marina* (the distribution pattern at Balgzand of the latter species is shown in Fig. 11 in Beukema and De Vlas 1979). It will be clear that such faunal differences are bound to affect the configuration of the N and B-plots.

Results

Spatial variation in N/B dominance

The 195 calculated values for S (N−B) varied from −210 to +186 (Fig. 6) and averaged +16. Among these 195 individ-

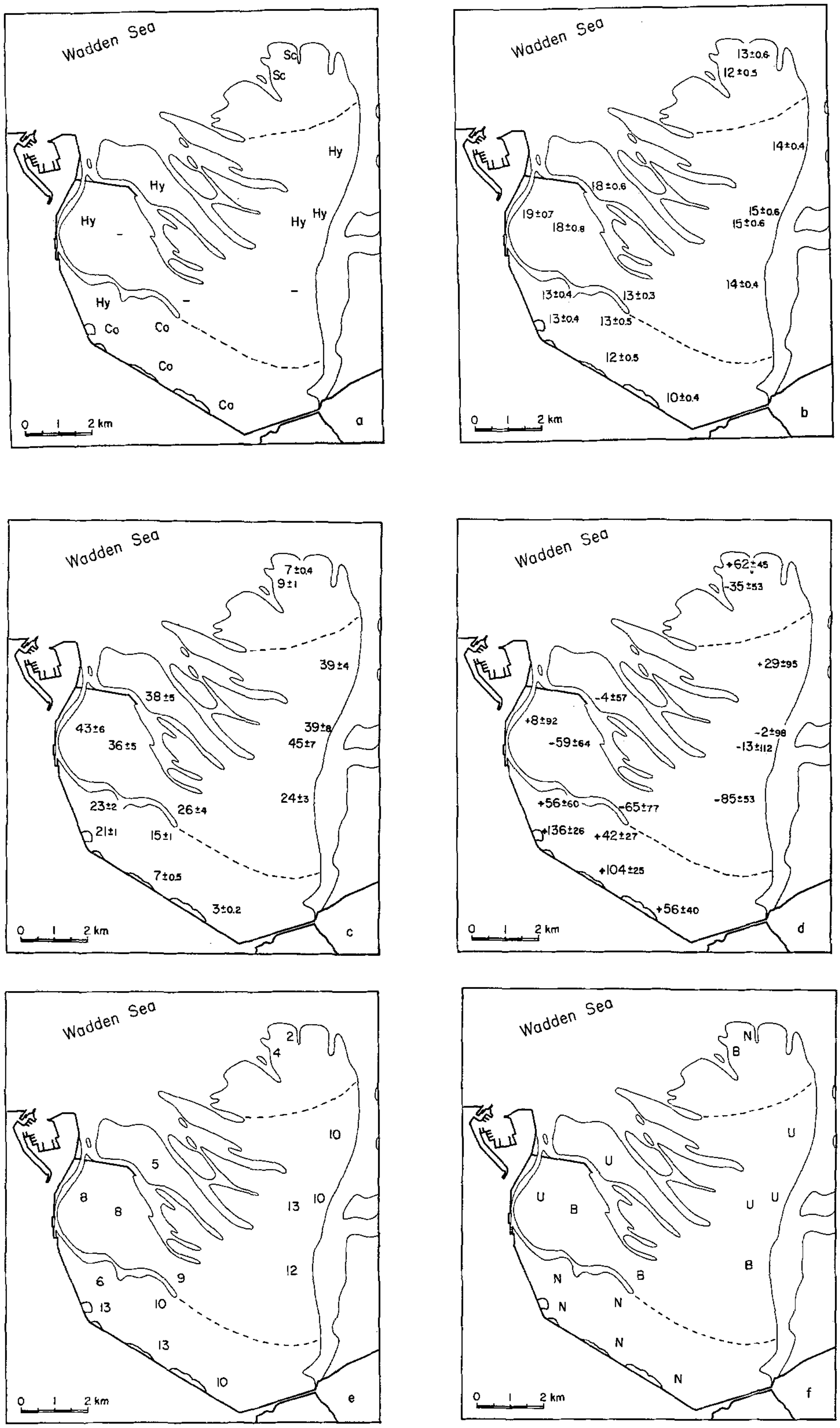

Fig. 3. Balgzand showing some characteristics of macrozoobenthos communities at each of 15 stations during 1975 to 1987 period. (a) Names of species that frequently dominated fauna numerically at sampling station (i.e., for at least 6 of 13 years it was more abundant than any other species): Hy = *Hydrobia ulvae*, Co = *Corophium volutator*, Sc = *Scoloplos armiger* and — = none. (b) Mean numbers of macrozoobenthic species found in samples of 0.9 m^2 (with 1 standard error, $n = 13$). (c) Mean values of total macrozoobenthos biomass in g AFDW per m^2 ($n = 13$, 1 SE). (d) Mean values of S(N−B) with 1 SD ($n = 13$, 9 out of 15 values that differed significantly from 0 indicated by bold signs). (e) Numbers of graphs (out of a total of 13 at each station) with non-crossing N- and B-plots. (f) Prevailing types of non-crossing plot configurations: N = N-plot invariably above B-plot, B = B-plot above N-plot in all or all but one case, and U = (nearly) equal numbers of two configuration types

ual plot configurations, 62 showed crossing N- and B-plots (in fact a few more, but possible crossings within the region of cumulative percentages of 99 to 100% were ignored). Estimates of S (N−B) from the clearly crossing plots were relatively close to zero (viz. between +94 and −74). Thus, in 133 plot configurations one of the two plots was clearly situated above the other, 79 times the N-plot was above the B-plot and 54 times the reverse occurred. The S (N−B) values from non-crossing plot configurations were generally either higher than +50 or lower than −40.

The various plot figuration types were not spread randomly over the area. Positive values (N-plots above B-plots) dominated in the high and silty strip along the southwest coast. At all five stations in this area the 13-yr averages were significantly positive ($P<0.01$, Wilcoxon signed-ranks test with $n=13$, 2-tailed, Fig. 3d). At four of the five stations in this subarea, crossings were few (Fig. 3e: numbers of non-crossing plots close to the maximum of 13). This high coastal subarea was thus characterized by N-plots above B-plots (Fig. 3f: N).

At only one other station, viz. Square C in the exposed northeastern part of Balgzand, the long-term average of S (N−B) was also significantly positive ($P<0.01$). However, crossing plots prevailed at this station. This was so at the nearby transect too (Fig. 3e). Thus, the low exposed subarea was characterized by crossing plots, without consistent prevalence of either N- or B-plots.

In the central part of Balgzand with more moderate environmental factors and high values for biomass and species richness, mean S (N−B) values were either significantly negative (at three stations, $P<0.02$) or not significantly different from 0 ($P>0.05$, Fig. 3d). Exactly at the three stations where the negative values prevailed (i.e., in nearly all years the B-plot was situated above the N-plot, denoted by B in Fig. 3f) none of the species exhibited a pronounced numerical dominance (Fig. 3a).

At the five other stations in the central subarea (with mean values of S (N−B) not differing significantly from zero), individual values fluctuated sharply from year to year (see the relatively high standard deviations in Fig. 3d). Among the non-crossing plots at these five stations, N-above-B and B-above-N configurations were about equally frequent (indicated by U for unstable in Fig. 3f). At these five stations, *Hydrobia ulvae* was the numerically dominant species in most years (Fig. 3a). In years with high numbers of this species (in the order of thousands or tens of thousands per m^2), the N-plots were clearly situated above the B-plots and accordingly the S (N−B) values were strongly positive. In years with low numbers of *H. ulvae*, the reverse was generally true. For the station where S (N−B) exhibited the highest variance (viz. Transect 9), the S (N−B) values were recalculated omitting data on numbers and biomass of *H. ulvae*. All S (N−B) values now dropped below 0 (Fig. 4), i.e., but for this one species all B-plots would have lain above the N-plots. The 13-yr mean value of S (N−B) would have been — 83 without *H. ulvae* instead of — 13 with this species included. The difference is statistically significant ($P<0.05$, $n=9$, Wilcoxon matched-pairs signed-ranks test).

From Fig. 1 it is easy to see how a single species can decisively affect the configuration of the N- and B- plots. At numerical densities of several thousands per m^2 (as may be reached frequently by populations of *Hydrobia ulvae* and *Corophium volutator* living on tidal flats), the starting point of the N-plot is around the 90% value. Such high starting points were never observed for B-plots (the highest were ~80%, but less than 5% were above 70% as contrasted to values for the N-plots of ~99% and more than 20%, respectively). Thus, high numbers in any one species (above ~1 000 per m^2) were bound to yield positive S (N−B) values.

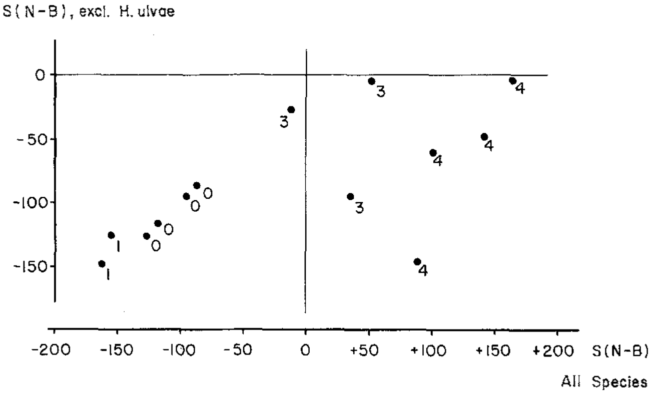

Fig. 4. The 13 values of S(N−B) found at Station 9 in two cases: including all species (hor. axis) and excluding *Hydrobia ulvae* (vert. axis). Log number of *H. ulvae* per m^2 is indicated for each sample (in rounded figures)

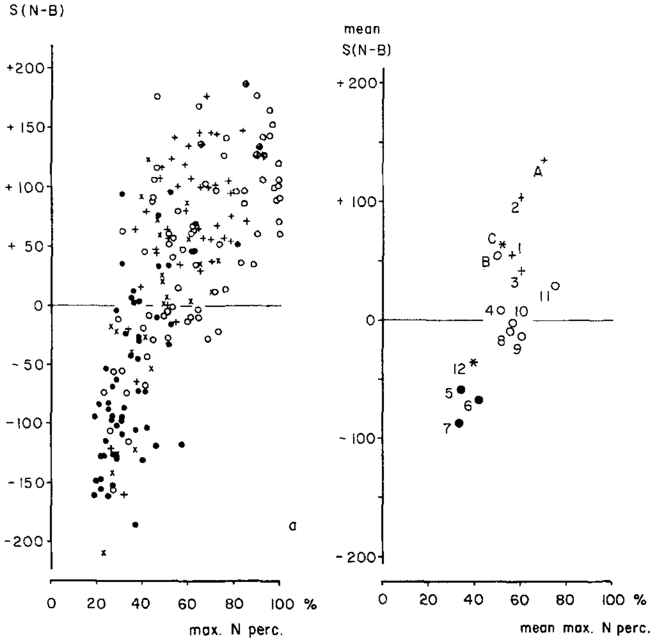

Fig. 5. Relationship between share of numerically dominant species (hor. axis, in % of total number of animals in sample) and configuration of N- and B-plots (vert. axis, expressed in S(N−B)). (a) All 195 samples separately included with an indication of most numerous species (o = *H. ulvae*, + = *C. volutator*, × = *S. armiger* and ● = another species). (b) 13-year averages for each of 15 stations (identified by letter or number shown in Fig. 2a; numerically dominant species indicated as in (a), but * = *S. armiger* and ● = none consistently (i.e., for at least 6 yr) dominant (cf Fig. 3a)

The relationship between the starting point of the N-plot and the resulting value of S (N−B) is shown in Fig. 5a. The estimates on the X- and Y-axis are not independent. Nevertheless, it is useful to investigate how a measure of community structure might depend on the behaviour of a single species. Whenever any species constituted more than ~70% of the total number of animals in a sample, the N-plot was situated above the B-plot (positive values for S (N−B)). On the other hand, when the most numerous species accounted for less than ~30% of the total numbers in a sample, the S (N−B) value was negative and the B-plot was situated above the N-plot (Fig. 5a). Whenever a species accounted for more than ~65% of the total numbers, this was nearly always either *Hydrobia ulvae* or *Corophium volutator*. High values of S (N−B), above ~ +100, were found almost exclusively for samples in which one of these two species was numerically dominant (Fig. 5a).

As may be expected from the strong relationship shown in Fig. 5a, much of the spatial variation of the mean values of S (N−B) (see Fig. 3d) may be explained by the variation in the contribution to total numbers of the most numerous species, that determines the starting point of the N-plot. The 13-yr averages of S (N−B) were indeed well correlated ($r = +0.63$, $n = 15$, $P = 0.02$, Spearman rank correlation) with the 13-yr averages of the starting points of the N-plots (Fig. 5b). The six highest (> +40) mean values for S (N−B) were found either in the coastal strip (five stations) with invariably high numbers of *Corophium volutator* and/or *Hydrobia ulvae* or in the exposed far offshore area (two stations) with invariably high numbers of *Scoloplos armiger*. The three lowest (< −50) mean values for S (N−B) were observed in the part of the central area without a pronounced numerical dominance of any species (cf. Fig. 3a). Nearly all of the remaining group of six intermediate mean S (N−B) values belonged to the five sampling stations in the central area that were characterized by sharply fluctuating and often very high numbers of *H. ulvae*, which exhibited numerical dominance in all but a few years.

The results above show that in our area a few small-sized numerically-abundant species exerted a decisive influence on the configuration of the N- and B-plots as expressed in high S (N−B) values at high numerical densities of these species (Fig. 5a). A strong numerical dominance of small-sized species reduces the mean weight of the individuals in a sample, whereas an absence of clear numerical dominance results in a high mean individual weight. Therefore, a negative relationship is to be expected between the values of S (N−B) and the mean weight of the individuals in a sample. Such a negative correlation was indeed observed (Fig. 6).

Temporal variation in N/B dominance

At most stations, the 13 individual values of S (N−B) varied strongly between years (see the generally high standard deviations shown in Fig. 3d). Among the 195 values of S (N−B), 24% did not correctly indicate the sign of the long-term average. Even when the mean value of S (N−B) at a station differed significantly from zero (9 stations, see above), 12% of the individual (annual) figures showed the "wrong" sign. Consequently, predictability from individual samples was poor.

Significant long-term trends were not observed (Fig. 7a) as indicated by the relation between the annual 15-station averages and the year number (viz. $r = -0.21$, $n = 13$). At only one out of the 15 stations was a significant trend observed at the $P < 0.05$ level (Spearman rank correlations with $n = 13$), which number is to be expected when testing 15 cases of series of 13 random numbers.

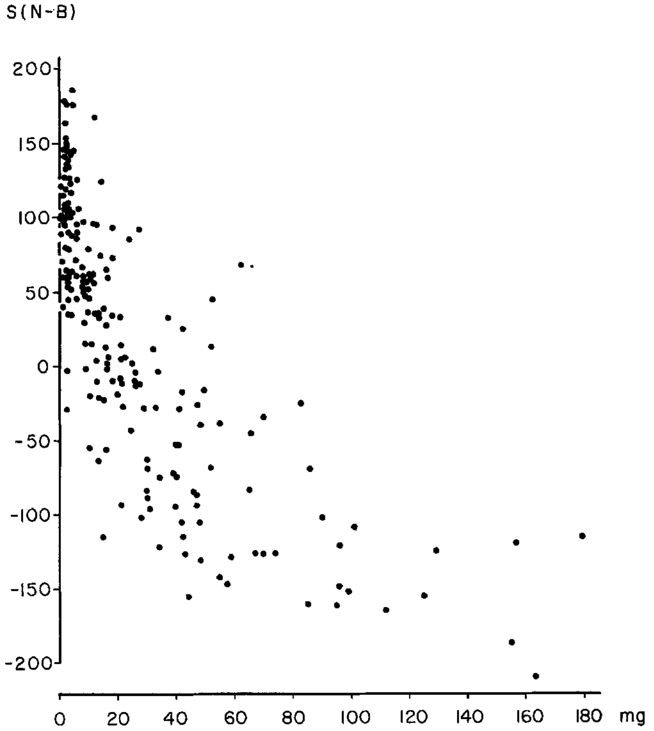

Fig. 6. Relationship between configuration of N- and B-plots (expressed in S(N−B), vert. axis) and mean weight (in mg AFDW) of individuals of all species in sample ($n = 195$)

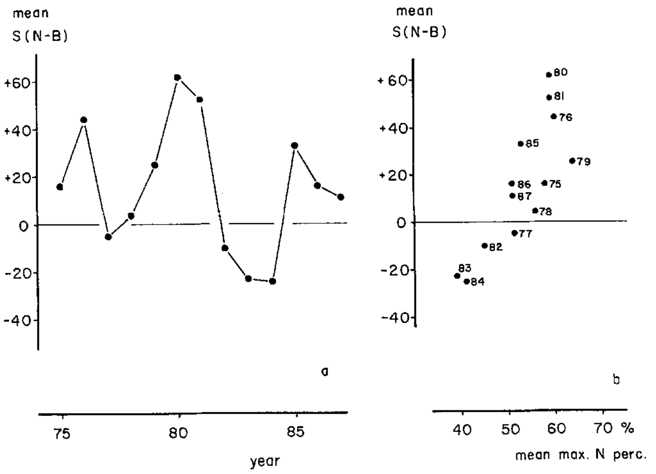

Fig. 7. Year-to-year variation in configuration of the N- and B-plots expressed in mean values ($n = 15$) of S(N−B). (a) Mean values for each of 13 yr 1975 to 1987. (b) These 13 means (vert. axis) plotted against mean share (%) of numerically most abundant species (hor. axis). Year indicated

Similar to the station-to-station variation (Fig. 5b), the between-year variation in the mean values of S (N−B) proved to be governed largely by the variation in the numbers of the numerically dominant species (Fig. 7b). The higher the starting points of the N-plots on average in a particular year, the higher the N-plots were on average situated relative to the B-plots ($r = +0.85$, $n = 13$, $P < 0.01$, Spearman rank correlation). Thus, the abundance in any year of *Hydrobia ulvae* and *Corophium volutator* largely determined the mean annual configuration of the N- and B-plots. Year-to-year variation was generally higher in N-plots than in B-plots. The species with high numerical densities (which determine the start of the N-plot and most of the difference with the B-plot) generally fluctuated strongly, whereas the weights of the biomass-dominating species were relatively stable (their large adults exhibiting low rates of mortality and growth, Beukema 1974, Beukema and De Vlas 1979).

The abundance of *Hydrobia ulvae* was high in 1979, 1980 and 1981 and low in 1982, 1983 and 1984. These changes in abundance of this one species are clearly reflected in the means of S (N–B) of these periods (Fig. 7a, b).

All data presented above concern samples taken in late winter/early spring. Summer data are available from the three square stations. Values for S (N–B) tended to be higher in summer than in winter. These differences were statistically significant at two out of the three stations ($P<0.01$, $n=13$, Wilcoxon matched-pairs signed-ranks test). In summer, numbers of numerous and small-sized species such as *Hydrobia ulvae* and *Corophium volutator* were much (up to 10 times) higher than in winter and more frequently reached high levels (thousands and tens of thousands). Moreover, in *Macoma balthica* young-of-the-year were more abundant in summer and could also occasionally reach densities of several thousands per m^2 (Beukema 1982, Fig. 2). Thus, in summer the N-plots often started at a much higher level, whereas the B-plots had hardly changed (because the latter depend mainly on adult and large-sized animals).

Discussion

High variability was observed in the configuration of the N- and B-plots, both spatially (Fig. 3d) and with time, i.e., between seasons and years (Fig. 7). In none of the 13 years of observation did all 15 plots exhibit the same type of configuration. At only two of the 15 stations did all 13 annual plots exhibit the same type (viz. with all N-plots above the B-plots), so the results appear to reveal little consistency. Moreover, the N-above-B-type configuration prevailed. Of the total of 195 pairs of plots obtained by winter sampling, 114 exhibited N-plots above B-plots (which, according to Warwick, indicates a polluted situation). If sampling had taken place in summer, this figure would have been even higher. Does this characterize Balgzand as a polluted area, with particularly strong pollution effects during the 1979 to 1981 period (Fig. 7a)?

Before considering this question, one should note that despite the high variability, the data set obtained in the area reveals some system. Most of the variability in the S (N–B) statistic was found to be related to the dynamics of a few small-sized, short-living and numerically highly variable species. A few such species (viz. *Corophium volutator* and *Scoloplos armiger*) were dominant especially in the marginal parts of Balgzand, where the benthic community will indeed be more stressed than in other parts of Balgzand (or than in most subtidal areas). Such marginal areas include: (1) the highest tidal flats (coastal subarea), where (aquatic) animals are exposed to long periods of emergence, to the high silt content of the sediment with high turbidity in the overlying water and anoxic conditions close to the surface; and (2) the lowest tidal flats situated in the offshore part of the area, where the (mostly shallowly buried) animals are exposed to strong currents and wave action, and hence unstable sediment conditions.

At the seven sampling stations in these stressed areas, 76 of the 91 plot configurations exhibited the N-plot above the B-plot. In the remaining part of the area (eight stations), where such adverse conditions are less prominent, the macrobenthic fauna has a higher biomass (Fig. 3c) and species number (Fig. 3b). In this subarea, the N-above-B configuration occurred significantly less frequently (38 out of 104 cases, $P<0.001$, χ^2-test). Thus, the ABC method appears to be sound as judged from spatial variability. However, the occurrence in the less-stressed area of high numbers of a small-sized species, viz. the small gastropod *Hydrobia ulvae*, was not at all rare and caused high values of S (N–B) during such periods, as shown in Fig. 4.

The most significant disturbance noted during the 13-yr period of observation was the severe winter of 1978 to 79 with high rates of mortality in several species (Beukema 1979, 1985). The 1979 samples were taken immediately after this exceptional winter. The plots for 1979, however, did not show any clear anomaly that could be attributed to the severity of this winter. The relatively high mean S (N–B) value for 1979 (Fig. 7) can be explained satisfactorily by the high numbers of *H. ulvae*. There is, however, no evidence that these numbers were affected by the low winter temperatures (because the high numbers were already present in the summer of 1978). A clear effect of this cold winter was the highly successful recruitment in several species during the subsequent summer, resulting in relatively high numbers of young (and consequently small) animals in the samples taken in early 1980. However, the even higher numbers of *Hydrobia ulvae* and *Corophium volutator* affected the configuration of the plots decisively in this year too.

Corophium volutator was abundant in all years in a relatively narrow coastal zone. Numbers in *Hydrobia ulvae* were more erratic and extremely high in some years. The strong fluctuations in numbers of this species may be caused by its ability to migrate by floating during calm weather (Anderson 1971, Barnes 1981). Immigration of *H. ulvae* to tidal flat areas on Balgzand was observed by Dekker (1979). These animals might originate from nearby dense subtidal populations (Dekker 1988). Outbursts of this species on tidal flats so far appear to be unpredictable.

A significant characteristic of the 1975 to 1987 period is the consistent increase in both numbers and biomass in about half of the species during this period, probably as a consequence of eutrophication (Beukema and Cadée 1986). As both numbers and biomass were affected in the same way, no clear effects on the configuration of the N- and B-plots are to be expected. Indeed, no significant long-term trends could be discerned in the S (N–B) values (Fig. 7a).

The question remains whether possible effects of pollution in the area would be discernible by the ABC method. Although the Balgzand area is slightly polluted since the seawater is diluted by ~10% of fresh and polluted water from the river Rhine, no solid evidence is available that pollution has affected numbers or biomass of the macrozoobenthos. Fortunately, the zonation and other characteristics of the macrobenthic fauna recently observed at Balgzand can be compared with those found in other tidal-flat areas in the Wadden Sea long before the present levels of pollution were reached. Thamdrup (1935), Linke (1939) and Jepsen (1965) all observed, on high tidal flats near the coasts of Denmark and Germany, low-biomass and low-diversity communities with high numerical densities of *Corophium volutator* and mostly also *Hydrobia ulvae*. Both Linke (1939) and Smidt (1951) observed high numbers (tens to even hundreds of thousands per m^2) of *H. ulvae* in more offshore tidal flats with rich benthic communities. On more exposed far offshore tidal flats, both Linke (1939) and Jepsen (1965) observed a low-biomass community with high numbers of *Scoloplos armiger*. Thus, several characteristics of the abundance and distribution of the recent Balgzand macrobentic fauna were also observed in similar tidal-flat areas during earlier periods (before the pollution from river output was serious). Apparently, the characteristics affecting the configuration of the N- and B-plots at Balgzand are normal ones for tidal-flat communities in the Wadden Sea. Thus, no added effects of pollution can be discerned with any confidence from the results obtained.

Few data sets of both numbers and biomass obtained from the same samples are available from other intertidal or shallow subtidal areas. So far, the applicability of the ABC-method to such areas has hardly been tested (Warwick et al. 1987, Warwick and Ruswahyuni 1987). Data sets published in Smidt (1951, Table 18) may be used to calculate S (N–B) values for eight samples taken in the summer of 1942 along two transects close together in the Danish Wadden Sea. These values were relatively high, averaging +25, due to high numbers of young-of-the-year in most samples. The summer of 1942 followed a severe winter and also the foregoing winters were severe. Numbers of old animals (and thus biomass values) will have been relatively low (Smidt 1951) and numbers of young animals relatively high (Beukema 1982). As a consequence, N-plots were mostly (viz. in six out of eight cases) situated above B-plots. It is unlikely that pollution was cause of this prevailing configuration, but the disturbance of the preceding severe winters will have contributed.

The size of the smallest organisms included in the samples appears to be of crucial importance for the configuration of the N- and B-plots (Fig. 6). The two species which showed very high numbers in many samples (viz. *Hydrobia ulvae* and *Corophium volutator*) both had individuals just big enough to be caught for the greater part by a 1 mm sieve. A slightly coarser sieve would have retained only the largest individuals and numbers would have declined to such an extent that most positive S (N–B) values would have turned negative (compare Fig. 5a and Fig. 6).

The ABC-method appears to be of limited value in tidal flat areas such as Balgzand. At only three of the 15 stations did the configuration of the N- and B-plots almost invariably point to a non-polluted situation. At several nearby stations with similar environmental conditions and a similar fauna (except for the occasionally high numbers of *Hydrobia ulvae*) the N-plots exhibited an erratic behaviour with a high proportion of configurations pointing to "polluted" conditions. Because there is no evidence that a high density of *H. ulvae* points to pollution or to any other type of disturbance, a naive use of the ABC-method would lead to erroneous conclusions. Similarly, the usually observed configuration of the plots in the marginal subareas will point to a stressed but not necessarily polluted situation. Thus, the claim stated by Warwick (1986) that the pollution status of a marine macrobenthic community can be assessed by this method without reference to a spatial or temporal series of control samples appears to be unjustified for tidal flat communities.

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