Long-term macrofaunal studies in a subtidal habitat off Norderney (East Frisia, Germany) from 1978 to 1994. I. The late winter samples

Macrofaunal
Fabulina fabula
association
Long-term changes
Sublittoral
German Bight
Climate

Macrofaune
Association
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Évolution à long terme
Sublittoral
Golfe Allemand
Climat

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ABSTRACT

Macrofaunal samples were collected regularly during springtime from 1978 to 1994 in the subtidal zone off Norderney, one of the East Frisian barrier islands. Sampling was carried out from a research vessel by means of a 0.2 m^2 van-Veen grab at five sites with water depths of 10-20 m. Abundances, biomasses and species composition were analysed by cluster analysis and multidimensional scaling. The resulting patterns are discussed in terms of anthropogenic impact and varying meteorological conditions. Species survival is severely impaired by cold winters, whereas storms and hot summers have a minor impact. There is evidence that mild meteorological conditions and eutrophication have resulted in an increase in total biomass since 1989. In addition to environmental factors, the community is influenced by interspecific relationships, including competition.

RÉSUMÉ

Étude à long terme de la macrofaune dans un habitat subtidal au large de Norderney (Frise orientale) entre 1978 et 1994.
I. Échantillons de fin d'hiver.

Des échantillons de macrofaune ont été prélevés régulièrement au printemps entre 1978 et 1994 dans la zone subtidale au large de Norderney, l'une des îles allemandes de la Frise orientale. L'échantillonnage a été effectué en cinq stations, à l'aide d'une benne van Veen de 0,2 m^2 d'ouverture, par dix à vingt mètres de profondeur. Les résultats (abondance, biomasse et composition spécifique des espèces) ont été traités par analyse de groupement et hiérarchisation multidimensionnelle; ils sont discutés en termes d'impact des activités humaines et d'évolution des conditions météorologiques. La survie des espèces est fortement compromise par les hivers froids, alors que les tempêtes et les étés chauds n'ont qu'un effet minime. La douceur des conditions météorologiques et l'eutrophisation ont entraîné une augmentation de la biomasse globale depuis 1989. L'évolution de la communauté est influencée par les relations interspécifiques incluant la compétition.

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INTRODUCTION

The German Bight is known to be one of the most polluted marine regions of the world. As most of the benthic fauna is more or less sessile, the benthic communities have been considered as a possible "tool" for monitoring long-term changes in the ecosystem (Rees and Eleftheriou, 1989). A large number of such investigations of macrofaunal communities have been carried out. They deal with eutrophication (Beukema and Cadée, 1986; Rosenberg *et al.*, 1987; Rachor, 1990), with the disturbance and stress caused by varying natural conditions (Beukema *et al.*, 1978) or with catastrophic environmental events like cold winters (Ziegelmeier, 1970). In particular, cold winters (Beukema, 1979; Dörjes *et al.*, 1986) and strong gales (Rachor and Gerlach, 1978) cause severe damage to coastal benthic communities.

The Norderney long-term macrofaunal series was initiated by Dörjes in 1978, who sampled monthly until 1991. This unique data set from the coastal southern North Sea might elucidate the impact of natural (sedimentological and meteorological) and/or anthropogenic (eutrophication) factors on changes in the faunistic communities. Earlier publications (Dörjes *et al.*, 1986; Dörjes, 1992) deal mainly with the variability of species numbers off Norderney. The present communication deals with the late winter data (samples from February, March or April) for the years 1978 to 1994 only. Analyses of the spring, summer and autumn data sets will follow.

MATERIAL AND METHODS

The area of investigation is situated north of the island of Norderney, one of the barrier islands separating the tidal flats of the Wadden Sea from the North Sea. The five different sites (station 11-15) are situated in water depths between 12 m and 20 m (Fig. 1). A 0.2 m^2 van-Veen grab was used for sampling. At each station, one sample was taken and sieved over 0.63 mm mesh size. The samples were fixed in 4% buffered formaldehyde. After sorting, the organisms were preserved in 70% alcohol. Species numbers, abundances and biomasses are given per m^2. Due to poor conservation, some individuals could not be determined to species level (*e.g. Bathyporeia* spp.). The biomass was determined as mg ash-free dry weight (AFDW) per m^2.

Abiotic parameters such as water temperature and oxygen content were measured separately. Sediment composition was obtained from other investigations in the area (Dörjes, 1976; Dörjes *et al.*, 1986; Reineck, 1976). Fine sand with grain sizes between 0.63 and 250 μm has prevailed since 1978. Hagendorff (1993) found no difference in sediment composition or morphology according to echo soundings run during each sampling. Characteristic mean water temperatures in the area varied between 18.5 °C in July/August and 2.0 °C in January/February (Dörjes *et al.*, 1986). Higher average temperatures occurred during the hot summers 1982, 1983 and 1984. The winters 1978/1979, 1981/1982, 1984/1985 and 1985/1986 were colder than the long-term monthly average (Dörjes *et al.*, 1986) (Fig. 2). Air temperatures for the period of investigation, which confirm these local data, were made available by the Deutscher Wetterdienst, Offenbach (1978-1994).

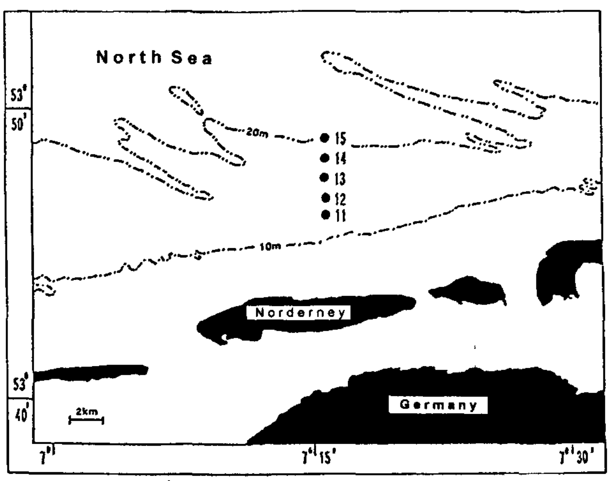

Figure 1

Area of investigation with sampling sites.

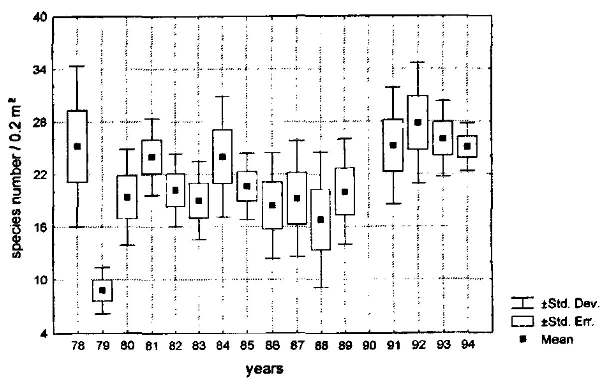

Figure 2

Mean species number per 0.2 m^2 between 1978 and 1994 (no samples were taken in 1990).

Species numbers and abundances are given as the means of the five samples taken per winter at stations 11 to 15. Diversity was calculated by using the Shannon-Weaver and Hill's (N_2) indices, evenness after Pielou (Clarke and Warwick, 1994; Heip *et al.*, 1988). A community analysis was carried out by means of cluster analysis, multidimensional scaling ordination (Clarke and Warwick, 1994; Field *et al.*, 1982), as well as correlation between faunistic and environmental data (BioEnv) (Clarke and Warwick, 1994) using the PRIMER software package of the Plymouth Marine Laboratory. Species accounting for less than 1% of total abundance or biomass were excluded. The Bray-Curtis similarity index and a double square-root transformation were used prior to analysis.

For biomass analyses, the species were separated into 21 groups on the basis of taxonomic and functional criteria. The groups were: Amphipoda (1), excluding the genus *Bathyporeia* spp. (2) and *Urothoe poseidonis* (3), Cumacea

(4), Decapoda (5), Mysidae (6), *Echinocardlum cordatum* (7) and other Echinodermata (8), Gastropoda (9), *Fabulina fabula* (10), *Donax vittatus* (11) and other Bivalvia (12), the Polychaeta groups *Nephtidae* (13), sediment and deposit feeding polychaetes (14), scavengers and predatory polychaetes (15), *Owenia fusiformis* (16), *Lanice conchilega* (17), *Magelona* spp. (18), *Pectinaria koreni* (19), Nemertini (20) and other taxa (21). In the following chapter, results are given as examples for five of these groups.

RESULTS

In total, 112 different taxa were found in 92 samples (43 Crustacea, 36 Polychaeta, 19 Mollusca, six Echinodermata and eight others). The mean number of species varied between nine species/0.2 m^2 in 1979 and 28 species/0.2 m^2 in 1992 (Fig. 2). In 1978 and between 1991 and 1994, species numbers were higher than during the period from 1980 to 1989. In 1979, the value for the species number was extremely low. The individual numbers varied between 88 Ind./0.2 m^2 and 673 Ind./0.2 m^2 (Fig. 3). The maxima in 1981, 1985 and 1993 are mainly caused by spatfalls of the sessile polychaete *Magelona* spp. and the bivalve *Fabulina fabula.*

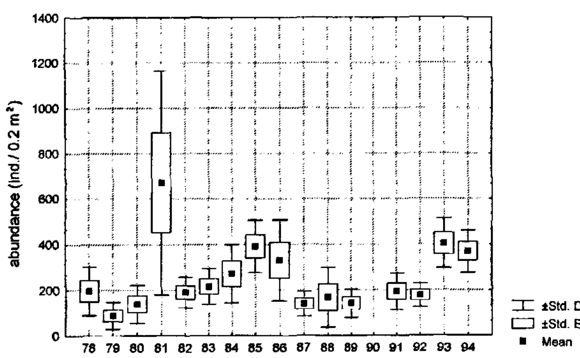

Figure 3

Mean abundances per 0.2 m^2 between 1978 and 1994 (no samples were taken in 1990).

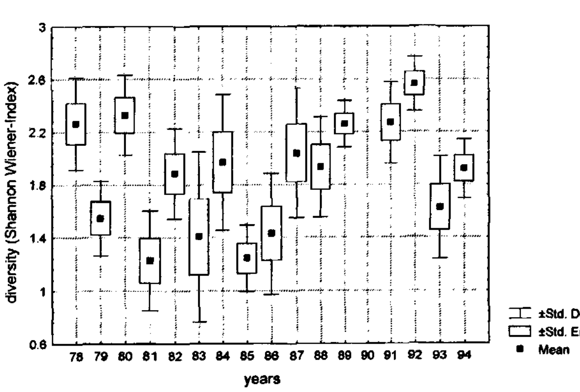

Figure 4

Mean diversity (Shannon-Wiener) between 1978 and 1994 (no samples were taken in 1990).

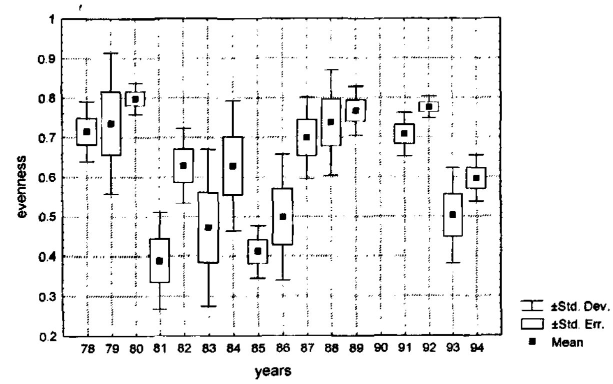

Figure 5

Mean evenness between 1978 and 1994 (no samples were taken in 1990).

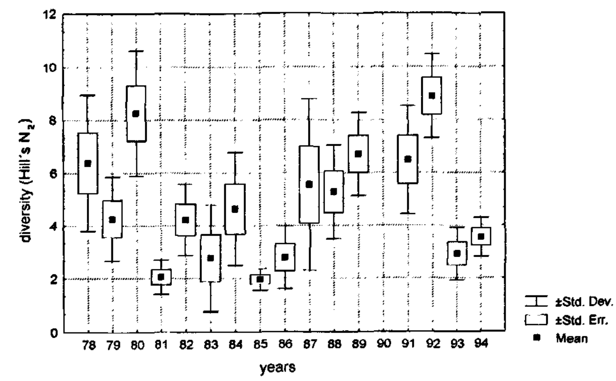

Figure 6

Mean diversity (Hill, N_2)/0.2 m^2, between 1978 and 1994 (no samples were taken in 1990).

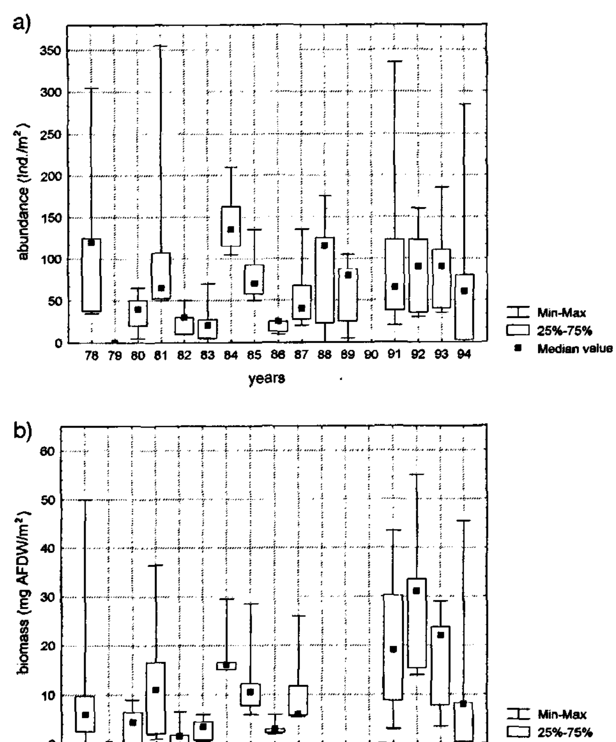

Figure 7

Median abundances (a) and biomasses (AFDW) (b) per m^2 of the genus Bathyporeia between 1978 and 1994 (no samples were taken in 1990).

Both diversity indices (Shannon-Wiener index, Hill's diversity N_2) showed similar temporal trends (Fig. 4, Fig. 6). Diversity decreased after 1980, fluctuated between 1981 and 1987, increased between 1988 and 1992 and decreased after 1993. Evenness (Fig. 5) showed the same pattern as the diversity indices.

Haustorids (Crustacea) of the genus *Bathyporeia* were temporally and spatially abundant; the species *B. elegans* and *B. guillamsoniana* were frequently found, while *B. pelagica, B. pilosa* and *B. tenuipes* were rare. Both abundances (Fig. 7*a*) and biomasses (Fig. 7*b*) showed similar temporal trends. Low median abundances were found in the late winters of the years 1979, 1982, 1983 and 1986. Biomass of the Bathyporeia species increased towards a maximum of 30 mg AFDW/m^2 in 1992.

The abundances of *Echinocardium cordatum* (Echinodermata) increased between 1981 and 1985 (Fig. 8*a*). Since 1989, abundances have shown rather high interannual variations. Since 1988, biomasses have increased, reaching 5 g AFDW/m^2 in 1989 and 1992 (Fig. 8*b*).

Fabulina fabula (Mollusca) was the dominant bivalve occurring in the sublittoral off Norderney. In 1981 and 1982, a spatfall was documented with abundances reaching 265 and 255 Ind./m^2 respectively (Fig. 9*a*) and low biomasses. In contrast, individual numbers did not exceed 100 Ind./m^2 during the years 1978-1980 and 1983-1989. From 1991, abundances increased and reached up to 220 Ind./m^2. Biomasses (Fig. 9*b*) reached up to 1 g/m^2 until 1990, and increased dramatically in 1992 and 1994.

Until 1989, abundances of *Donax vittatus* (Mollusca) were low (Fig. 10*a*), but they have increased in parallel with the biomasses since 1991 (Fig. 10*b*).

Abundances and biomasses of sediment-feeding polychaetes were highest in 1981 and 1985, reaching up to 2530 Ind./m^2 and 516 mg/m^2 respectively (Fig. 11*a*, Fig. 11*b*). *Magelona* spp., *Spiophanes bombyx* (selective surface deposit feeder) and *Scoloplos armiger* (selective sediment feeder) accounted for more than 90% of the total abundances of this functional group per year. Other abundant species were *Spio filicornis, Scolelepis bonnieri, Chaetozone setosa* and Capitellids (Fig. 11*c*).

Total biomasses

Fig. 12 shows a dramatic increase in total biomasses since 1989, ranging from median values below 2.4 g/m^2 in earlier years towards up to 11.5 g/m^2 in the 1990s. *E. cordatum* dominated the biomass in 1989 and 1992, *D. vittatus* since 1989. But *L. conchilega* (1989), the *Nephtys* species (1991, 1992), the sediment-feeding polychaetes (1993, 1994) and *F. fabula* (1992, 1994) have also increased in biomass during the 1990s.

Multivariate community analysis

The cluster analysis and the MDS-ordination of the communities are shown in Fig. 13*a* and 13*b* using median abundances. The greatest shifts within the community were observed between 1978 and 1981. The greatest distance

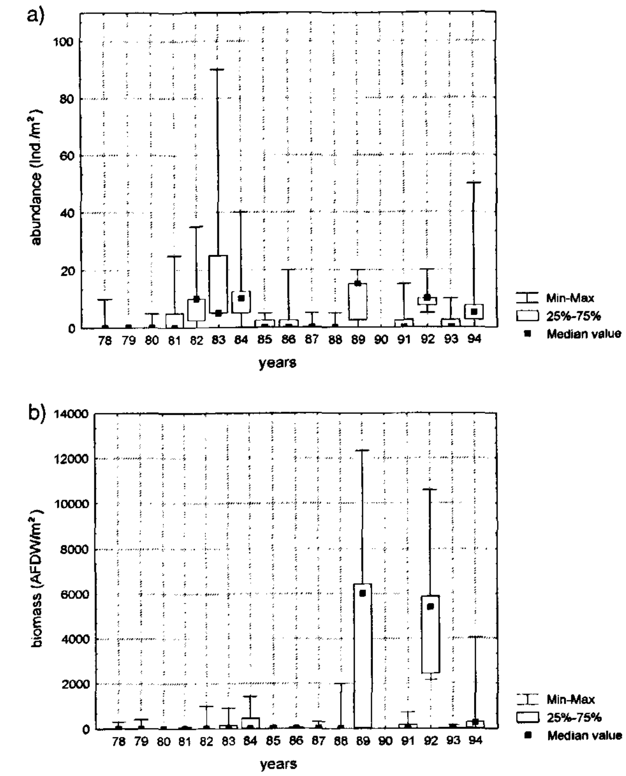

Figure 8

Median abundances (a) and biomasses (AFDW) (b) per m^2 of Echinocardium cordatum *between 1978 and 1994 (no samples were taken in 1990).*

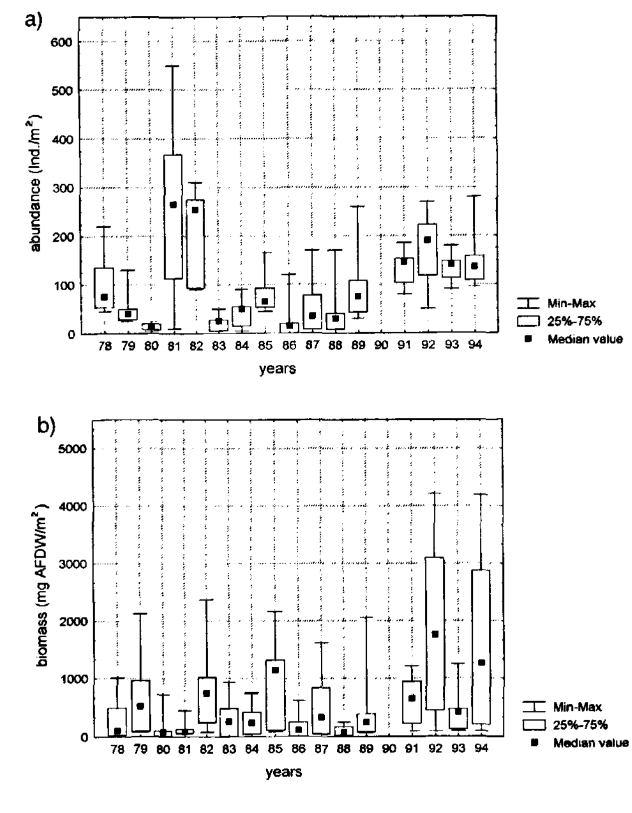

Figure 9

Median abundances (a) and biomasses (AFDW) (b) per m^2 of Fabulina fabula *between 1978 and 1994 (no samples were taken in 1990).*

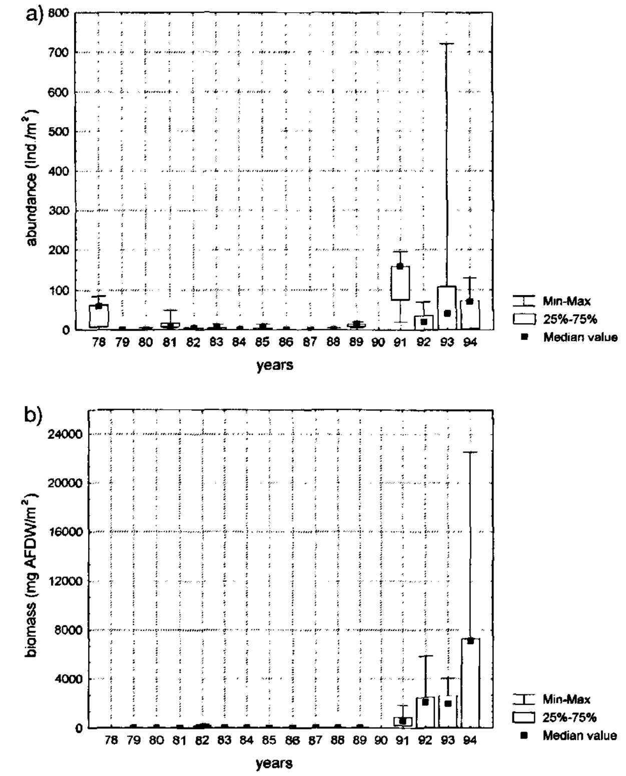

Figure 10

Median abundances (a) and biomasses (AFDW) (b) per m² of Donax vittatus *between 1978 and 1994 (no samples were taken in 1990).*

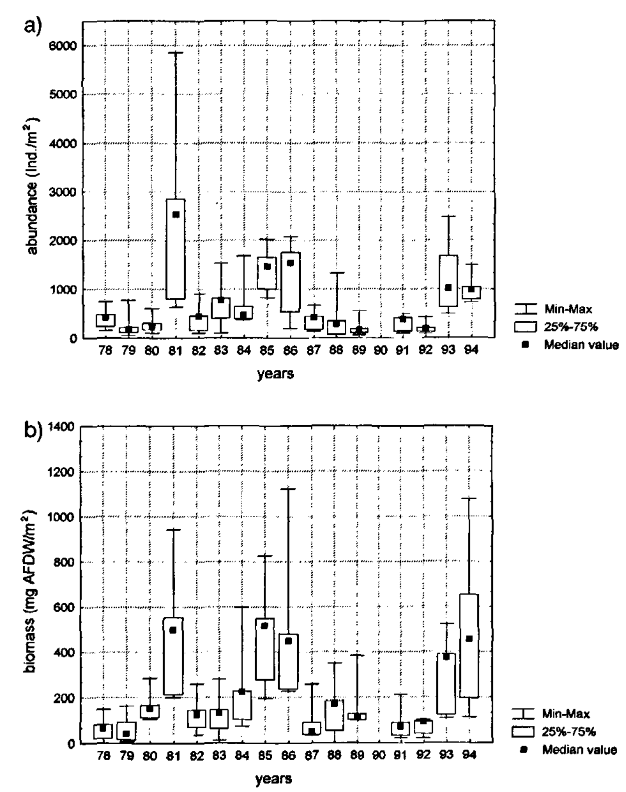

Figure 11

Median abundances (a) and biomasses (AFDW) (b) per m² of sediment-feeding polychaetes between 1978 and 1994 (no samples were taken in 1990) and abundances of dominant species per m² (c).

between two successive years was to be seen between 1980 and 1981. From 1981 to 1986, only minor changes occurred within the community, whereas between 1986 and 1989 shifts in community structure were similar to those between 1978 and 1981. Since 1991, a more stable period has been observed.

Cluster analysis and MDS were also performed using median biomasses (Fig. 14*a*, *b*). Clear annual shifts in the biomass were recorded between the years 1978/1981 and 1987/1991. After 1980, biomass values were similar to those from 1978 and remained stable until 1987. Between 1988 and 1989, biomasses showed extreme changes. Since 1991, values have stabilized; however, there seems to be a transition between the 1980s and the 1990s. Distinct changes must have occurred within the communities, because abundances as well as biomasses in the 1990s were different from those in the 1980s.

Faunistic data from the years 1978 to 1994 were correlated with air temperatures of February and August as well as wind speeds of each year (Fig. 15). The maximum correlation (Spearman coefficient) was calculated to be r = 0.26 for temperatures in February.

DISCUSSION AND CONCLUSION

The area of investigation borders the *"Tellina" fabula* association, described by Salzwedel *et al.* (1985). As means or medians were calculated for samples taken at the five sites, no statements can be made about the spatial fluctuations in the macrofaunal communities.

The changes found in the macrofaunal communities cannot be explained by changes in sediment characteristics, since sediment grain size composition as well as morphology did not change over the investigation period (Reineck, 1976; Dörjes, 1976, 1992; Dörjes *et al.*, 1986; Hagendorff, 1993). In contrast with the more easterly parts of the German Bight, the shelf off Norderney is not affected by sediment inputs from the Elbe and Weser estuaries. According to Aigner and Reineck (1983), there are seasonal variations of the wave base at the shoreline of Norderney, but even in winter waves do not influence the sediments below 12 m.

Even if the correlation between the faunistic data and winter air temperatures was not significant, the method indicates cold winters as a major cause of changes in the communities compared *e.g.* with summer temperatures or storms; this is borne out by the decrease of species numbers after cold winters (1978/1979, 1981/1982, 1984/1985 and 1993/1994). The abundance of the polychaete *Magelona* spp. increased dramatically after the cold winter 1978/1979, while at the same time *F. fabula*, a possible competitor, decreased. In 1980 and 1986, *i.e.* years next to cold winters, high abundances of *S. bombyx* and *S. armiger* occurred. Ziegelmeier (1970) also correlated the dominance of sedentary polychaetes like *S. bombyx* with the absence of *F. fabula* after cold winters. Beukema *et al.* (1988) found low survival rates of *F. fabula* in the sublittoral after the cold winter 1978/1979. In our investigations, this species recovered during the year next to the one following the cold winter. The abundances and biomasses of the genus

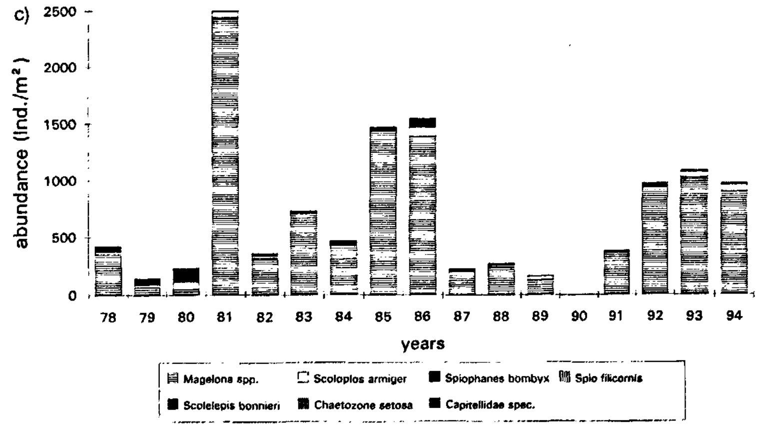

Figure 11 (*c*)

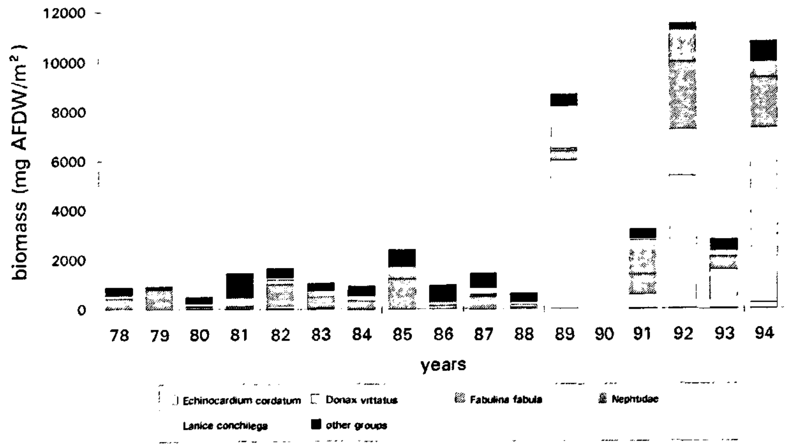

Figure 12

Total biomasses (AFDW mg/m²) for dominant species between 1978 and 1994 (no samples were taken in 1990).

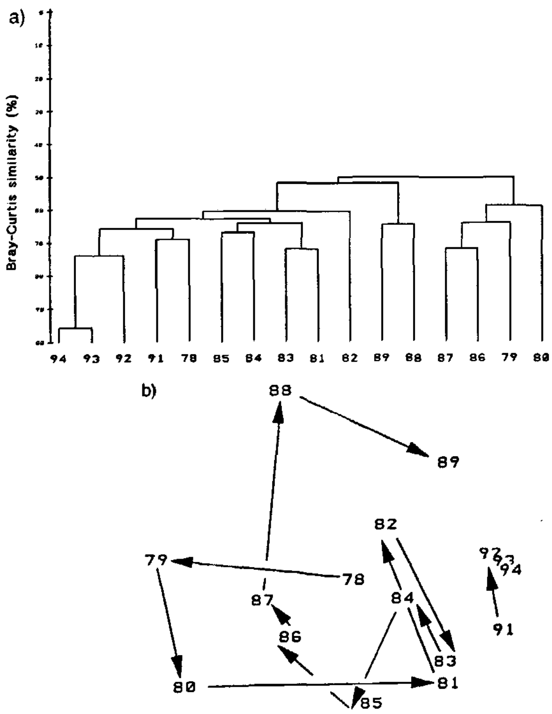

Figure 13

Dendrogram of cluster analysis (a) and multidimensional scaling ordination (MDS) (b) for median abundances between 1978 and 1994 (no samples were taken in 1990).

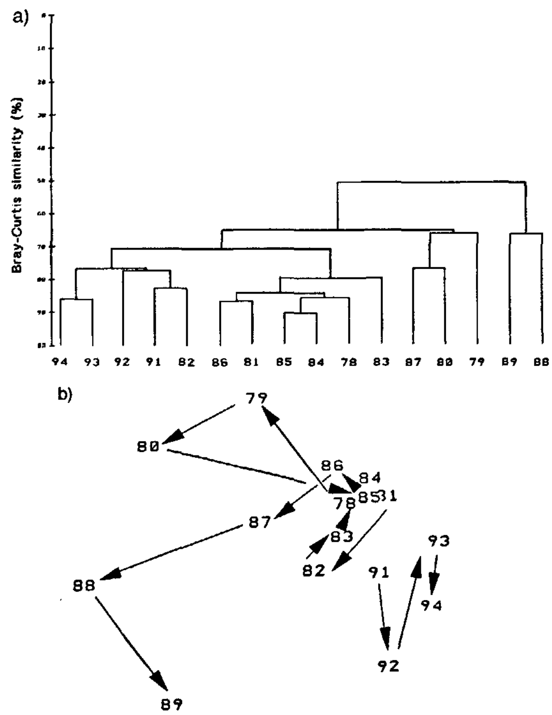

Figure 14

Dendrogram of cluster analysis (a) and multidimensional scaling ordination (MDS) (b) for median biomasses from between 1978 and 1994 (no samples were taken in 1990).

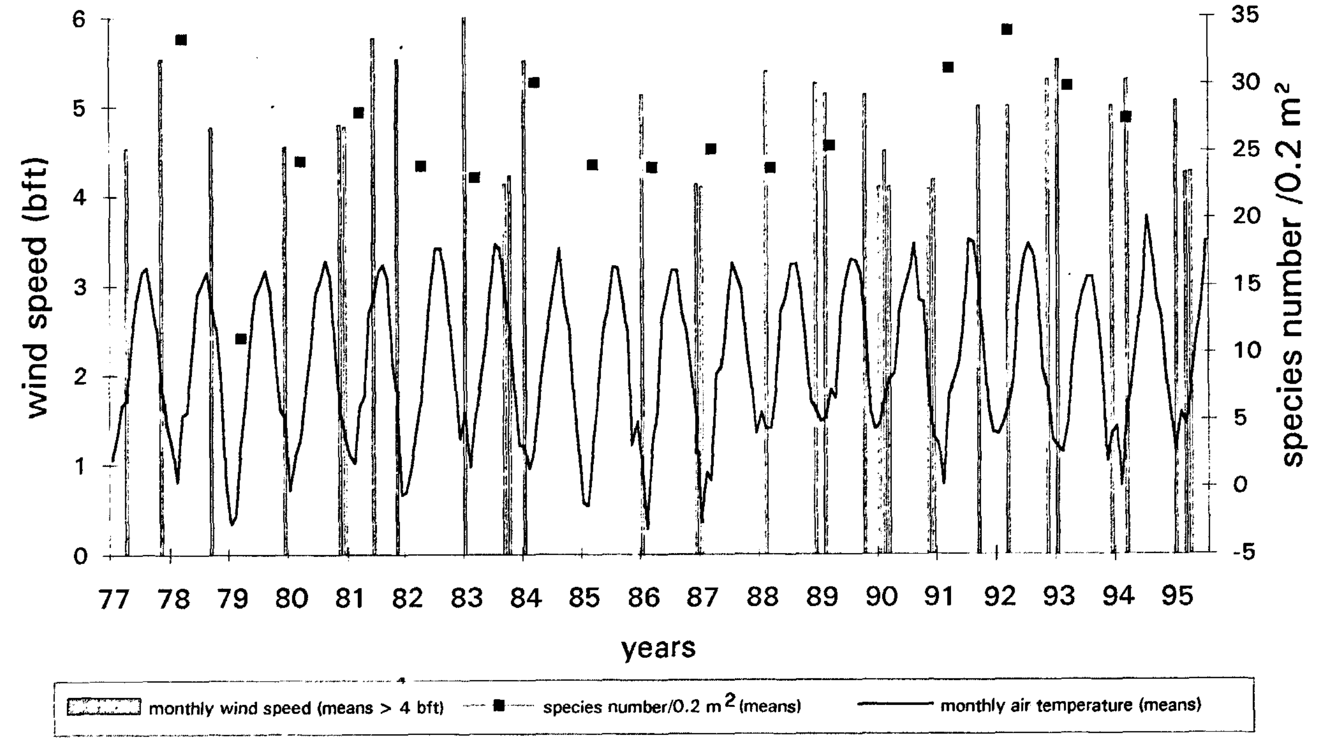

Figure 15

Mean monthly air temperatures, winds (means > 4 bft) and mean species numbers per 0.2 m^2 between 1978 and 1994 (no samples were taken in 1990).

Bathyporeia were also low during years following cold winters (1979, 1982, 1983 and 1986). The higher biomasses between 1991 and 1993 were mainly due to higher numbers of *B. guillamsoniana*.

With an exception in 1981/1982, the cold winters 1978/1979, 1984/1985 and 1987/1988 lead to a decrease in diversity. The extreme decrease between 1980 and 1981 can be explained in terms of interspecific competition. Due to high numbers of short-living opportunistic species, diversity increased in 1980 and was reduced by a succession of long living species during the following years.

Storms appear to have only minor effects on the communities, although in 1982 and 1983 species numbers declined, probably due to severe storms; in contrast, since 1989 species numbers have increased despite intense storms.

Hot summers in 1982 and 1983 did not influence species numbers in the following winters. Mild winters between 1987 and 1992 (Damm *et al.*, 1993) might have induced changes in the communities. *E. cordatum* is known to suffer during cold winters (Beukema, 1985). Therefore, the high biomasses of *E. cordatum* found in 1989 and 1992 were probably caused by a synergistic effect of mild winters and eutrophication, which is documented for the German Bight by an increase in nutrients and phytoplankton biomass (Hickel *et al.*, 1993). Rosenberg *et al.* (1987) also discussed increased food availability as a reason for higher biomasses of *E. cordatum*, and Rachor (1990) described an increase in biomasses of this species in the German Bight. Increasing abundances and biomasses since 1991 lead to the conclusion that *F. fabula* and *D. vittatus* also profited from mild winter conditions and eutrophication. Dörjes (1979) described a high temporal fluctuation of the latter species in the area of investigation, considering this to be due to sediment mobility caused by wave action. This is in contrast with the rather stable sediment composition (Reineck, 1976; Dörjes *et al.*, 1986; Hagendorff, 1993), the minor influence of winter waves below 12 m (Aigner and Reineck, 1983), and the increase of the population during a period of severe storms in the early 1990s.

The MDS plots reflect the shifts within the communities since 1978. After the cold winter 1978/1979, the communities returned to a rather stable condition during the 1980s, which was followed by a transitional period at the end of the decade, leading to a more stable situation again since the early 1990s.

Apart from the effect of the above-mentioned local meteorological events during the period of investigation, other factors might have influenced the ecosystem on a broader scale. Dickson *et al.* (1988) described an increase of northerly winds between 1950-1980, as well as a decrease of westerly winds during this period (Fransz *et al.* 1991), both of these phenomena having reversed since 1980. In parallel, Austen *et al.* (1991), Evans and Edwards (1993), and Buchanan (1993) found a transition in phyto- and zooplankton as well as benthic biomass off the Northumberland coast, which correlated with the inflow of changing Atlantic water masses and coincided with the changes in our area of investigations between 1980 and 1987. Such changes in 1980 were also found for Phoronids in the German Bight (Niermann, in press). The question arises as to which factors other than the mild winters might have caused the changes in the communities since 1988.

This study presents only preliminary results of the long-term series. Further analyses of the data will show whether the spring, summer and autumn data follow the same trends as the late winter data, and might confirm the hypothesis of the natural and anthropogenic impacts on the coastal region of the North Sea since the late 1970s.

Acknowledgements

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