

Local differences in macrozoobenthic response to enhanced food supply caused by mild eutrophication in a Wadden Sea area: Food is only locally a limiting factor

J. J. Beukema and G. C. Cadée

Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

Abstract

In the late 1970s food supply to herbivores suddenly doubled in the western half of the Dutch Wadden Sea probably as a consequence of increased nutrient concentrations. The response of zoobenthos was studied during 1970–1990 as part of a long-term monitoring program, including annual sampling at 15 fixed stations with very different environmental conditions (elevation, sediment grain size) on Balgzand, a 50-km² tidal flat area. The total zoobenthic stock in the affected area roughly doubled within 2 yr after the doubling of the stock of planktonic algae. However, the magnitude of the response differed from station to station. We tested the hypothesis that a strong positive response would occur particularly at stations where food could be limiting, i.e. where zoobenthic food demand was high relative to food supply. Biomass increases of zoobenthos in the order of a doubling were indeed restricted to the part of Balgzand characterized already in the 1970s by high biomass values. The zoobenthic biomass hardly increased in two areas of Balgzand with relatively low values for zoobenthic biomass and species richness. In these impoverished areas environmental conditions are harsh and the benthic communities are dominated by small opportunistic species. One of these areas is characterized by a high intertidal elevation (short daily inundation periods) combined with a sheltered location near the coast (resulting in muddy sediments), the other by severe exposure to currents and wind (resulting in mobile sands with low silt and organic-matter contents) due to its offshore position. We conclude that food limitation only existed in the midshore communities living under relatively mild abiotic conditions. Apparently, the benthic consumer populations benefitted from eutrophication-induced enhancement of their food supply by enlargement of their stocks only where they were not too stressed by unfavorable abiotic conditions.

As long as marine eutrophication is mild, it mainly results in enhanced productivity with higher concentrations of algae and increased stocks of consumers of these algae such as zoobenthos and zooplankton—the initial part of the relationship depicted by Pearson and Rosenberg (1978) and the initial “enrichment phase” of Gray (1992). If herbivores respond in this way, their food was apparently in short supply before the onset of the enrichment. Such food-limited conditions can occur only where consumer stocks (and their food demand) are high relative to food supply. In areas with a high food supply but low consumer stocks, food limitation is less obvious and accordingly a pronounced positive response to enhanced food supply is not to be expected.

Recent well-monitored developments in the Dutch Wadden Sea offer an opportunity to test this general hypothesis. In the late 1970s, primary production and algae stocks suddenly increased significantly in the western half of the Dutch Wadden Sea, an area of ~1,000 km² with tidal flats, shallow subtidal areas, and tidal streams. The probable cause of these increases were strong increases (more than twofold) of P and N concentrations during the 1980s as compared to the 1970s (Van der Veer et al. 1989; De Jonge and Essink 1991; De Jonge and Van Raaphorst 1995). Rates of primary production roughly doubled, both in the phytoplankton in the west-

ernmost inlet of the Wadden Sea (Cadée 1986; Cadée and Hegeman 1991) and in the microphytobenthos at a tidal flat close to this inlet (Cadée 1984). In spring and summer, cell numbers of phytoplankton and concentrations of chlorophyll were about twice as high in the 1980s as in the 1970s (Cadée 1986; Cadée and Hegeman 1991).

So far, it is not possible to predict accurately the response of a benthic system to changes in water column productivity (Heip et al. 1995). Not only might local and temporal variation caused by stressing abiotic factors (such as strong currents and wind; *see* Emerson 1989) disturb relationships between food supply and consumer abundance, the higher algae production itself might exert positive as well as negative effects. However, in the Dutch Wadden Sea negative effects such as reduced species richness or mass mortalities attributable to lack of oxygen have rarely been observed (Beukema 1989; Cadée 1990, 1996; De Jonge and van Raaphorst 1995). On the contrary, positive effects have prevailed: increases have occurred in the abundance of both zoobenthos (Beukema and Cadée 1986; Beukema 1991; De Jonge and Essink 1991) and zooplankton (Fransz et al. 1992). Shifts in species composition of the zoobenthos were minor, although the proportions of small animals and polychaetes increased (Beukema 1991). Thus, the eutrophication-induced enrichment can be characterized as mild, resulting in essentially positive effects on the zoobenthos.

The overall increase of food supply in the western part of the Wadden Sea took place in an area of heterogeneous abiotic conditions and significant place-to-place differences in the zoobenthic biomass. The Wadden Sea tidal flats show a

Acknowledgements

We thank our research assistants W. de Bruin, J. Hegeman, and J. Zuidewind for their dedicated help during more than two decades. We are grateful for comments and suggestions by several anonymous reviewers. This is NIOZ publication no. 3136.

wide range from high and sheltered mud flats near the coasts via mixed-sediment flats at intermediate elevation to low and exposed sand flats far offshore (De Glopper 1967; Beukema 1988; Hertweck 1994). The composition of the benthic fauna varies in relation to both intertidal elevation and sediment composition. At the two extremes of elevation and distance to the coast, the benthic macrofauna is characterized not only by a low number of species but also by low biomass values (Beukema 1976, 1988; Dankers and Beukema 1983). Along this gradient, effects of moderately increased amounts of organic material are likely to be highly diverse.

The existence of food limitation on Wadden Sea tidal flats is not only plausible from the overall increase of zoobenthic biomass after the increase of its food supply around 1980, organic-matter balance studies (De Wilde and Beukema 1984) also point to an annual food supply for herbivores that is not much higher than their annual food demand. There is also some direct evidence for the existence of food limitation in the Wadden Sea. In one year with abnormally low stocks of benthos, body weights of individual bivalves were exceptionally high (Beukema and Cadée 1996). On a smaller scale, growth rates in cockles in the Wadden Sea are reduced at extremely high densities (Jensen 1993; unpubl. obs. on Balgzand). Such reductions have also been found near mussel beds, where densities of food competitors are high (Kammernans 1993). Therefore, we expect that particularly in the high-biomass areas the zoobenthos could benefit from an enhancement of food supply as started in the late 1970s.

An extensive homogeneous dataset (more than 20 yr of uniform sampling at 15 fixed stations) on zoobenthos dynamics (in terms of numbers and biomass) is used to test the hypothesis that the enhanced primary production (and resulting higher concentrations of plankton algae) during the 1980s raised the biomass of zoobenthos particularly in those areas that were already rich in biomass and species number, i.e. in the moderate parts of the prominent environmental gradient.

Materials and methods

The Balgzand area—We worked on Balgzand and in the nearby Marsdiep, at ~53°N and 6°E in the Netherlands. The position of the 15 sampling stations on Balgzand and the phytoplankton station (plus a nearby microphytobenthos station) are indicated in Fig. 1a. All sampling stations on Balgzand are permanent and marked by iron poles. There are 12 1-km transects (numbered 1–12 in Fig. 1a) and three 900-m² plots (A, B, and C). The 15 stations cover almost the full range of intertidal levels and sediment types present in the westernmost part of the Wadden Sea (Fig. 1b; compare with Ente 1969).

Balgzand is a 50-km² tidal flat area, located in the westernmost part of the Wadden Sea. It is part of the tidal basin drained by the major tidal inlet Marsdiep (Fig. 1a). Balgzand and Marsdiep waters mix intensively, with flushing time of Balgzand water being only three tidal periods (Zimmerman 1978).

The mean tidal range on Balgzand is roughly from -80 to +60 cm (compared to mean-tide level, MTL). Intertidal levels of each station were derived from a series of sounding charts kindly made available by the Rijkswaterstaat. Mud (silt plus clay) content of the top 5 cm of the sediment is

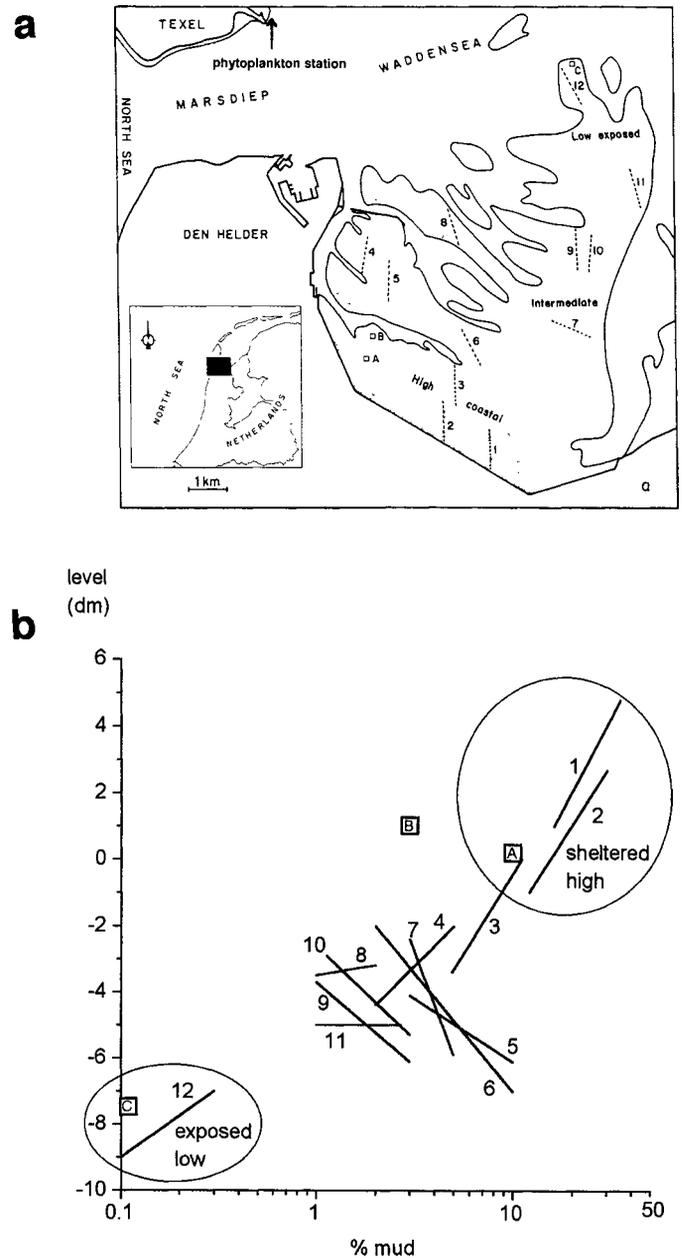


Fig. 1. (a) Map of the Balgzand tidal-flat area and location of the 15 sampling stations (three 900-m² squares: A, B, and C and 12 1-km transects: 1–12). The area above the mean low-tide level is roughly indicated by a thin line, the area above mean-tide level by shading. (b) The situation of the 12 transects and 3 squares in relation to the two main gradients: (vertical axis) intertidal level in dm above and below mean-tide level and (horizontal axis) sediment composition, expressed as percentages of mud (i.e. particles <60 μm) in the upper 5 cm of sediment. The ends of each transect line connect the most extreme environmental values (100-m averages) encountered along the transect.

defined as the percentage of total dry weight consisting of easily suspendible particles (those <50–60 μm). A combined plot (Fig. 1b) for elevation and sediment composition illustrates the main environmental gradient of the Balgzand intertidal area: from almost silt-free (clean) sand at low lev-

els to muddy sediments at high levels. Square C and transect 12 are situated in the extreme northern (offshore) part around low-tide level near a major tidal stream and their sediment consists of almost clean sand (suspensible fraction <1%). It is the most exposed part of Balgzand, where sediment movements by currents and waves are maximal and the surface shows megaripples. The transects 1, 2, and (part of) 3 and the square A are situated in the southwestern part of Balgzand, above or around MTL and close to the lee of the shore, where the sediment is muddy. The prevailing strong winds are westlies. All other transects are intermediate as to distance from the coast, intertidal level, sediment composition, and the incidence of sand ripples. Thus, the main environmental gradient on Balgzand (and in nearly all tidal flat areas along the mainland coasts of the Wadden Sea: De Glopper 1967; Hertweck 1994) runs from high (sheltered and muddy) coastal areas via intermediate tidal flats (with mixed sediments and moderate elevation) to low (exposed and sandy) areas far offshore.

Along transects 2, 3, 10, and 12, rates of primary production of microphytobenthos and concentrations of organic carbon and of Chl *a* (as a measure of algae abundance) in the top 1-cm layer of the sediment were estimated almost every month in 1974–1975. Methods and detailed results can be found in Cadée and Hegeman (1977) and Cadée (1978). Concentrations of both organic C and Chl *a* were closely related with other sediment parameters: silty (near-shore) sediments showed higher concentrations than sandy (offshore) sediments (Fig. 2). A long-term series of measurements of benthic primary production were made at a tidal flat near the Marsdiep phytoplankton station (Fig. 1a). Methods are described in Cadée and Hegeman (1974b) and results in Cadée (1984).

Starting from 1970, Chl *a* concentrations and primary production rates in the water column were estimated at a weekly to monthly frequency in the Marsdiep tidal inlet at the phytoplankton station (Fig. 1a). Methods are described in Cadée and Hegeman (1974a). All estimates showed a significantly increasing trend during the 1970–1990 period, as summarized in Fig. 3a and shown in detail in Cadée and Hegeman (1991, 1993) and Cadée (1992).

Zoobenthos—Macrozoobenthos was sampled at 15 sampling stations scattered over Balgzand (Fig. 1a). Data are used from the March samplings of the 20-yr period 1970–1989. Late winter is the season with the lowest biomass values (Beukema 1974). Sampling procedures have been described in detail in earlier papers (e.g. Beukema 1974). Per 1-km transect, 50 equally spaced samples of 0.018 m² each (total area 0.9 m² of sediment) were taken by core sampling to a depth of 30 cm (this is sufficient for all infaunal species). At the square stations, a total of 1 m² of sediment was taken, which was divided over nine randomly positioned cores of 0.1 m² plus nine cores of 0.01 m². All cores were sieved in the field on 1-mm mesh screens. Abundance of macrozoobenthic species is expressed both in numbers per square meter and in biomass units: g ash-free dry weight (AFDW) per m². The use of a 1-mm sieve will have caused an underestimate of the numbers of all small animals, particularly the juveniles of various species and adults of thin

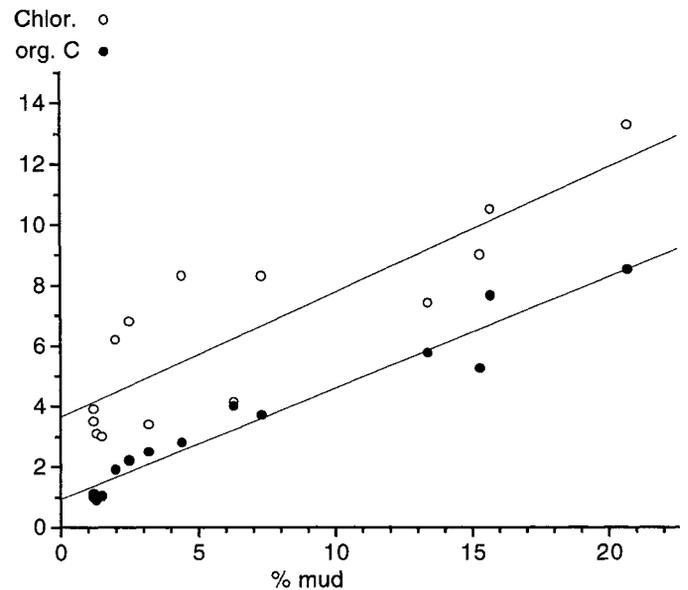


Fig. 2. Relationships for the upper sediment layer of Balgzand between sediment particle size (expressed in % of particles <50–60 µm) and (solid symbols) concentration of organic matter (in mg per g sediment) and (open symbols) concentration of functional Chl *a* (in µg per g sediment). Data were collected in 1974 and are enumerated in table 2 of Cadée and Hegeman (1977). The points at low mud contents originate from stations situated in the exposed offshore part of Balgzand (near Sta. 12), those with high mud contents from Sta. 2 and 3 in the coastal part of Balgzand (compare Fig. 1). The two lines indicate the best-fit regression relationships: For organic matter, $r^2 = 0.94$ ($P < 0.001$); for Chl *a*, $r^2 = 0.74$ ($P < 0.001$).

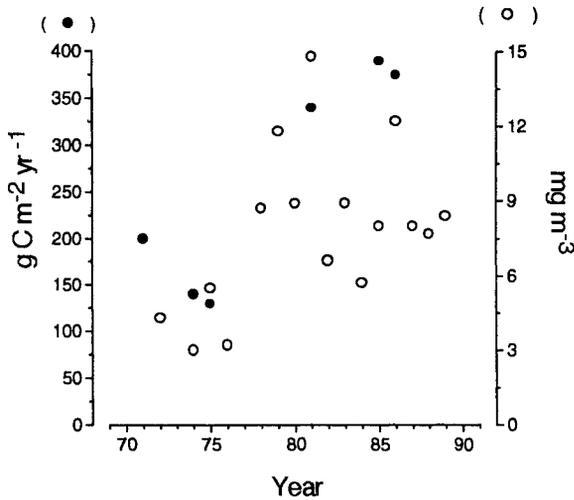
worms. However, the effect of these underestimates on biomass values is negligible. Limited numbers of samples sieved by finer meshes by R. Dekker (pers. comm.) indicated that in any part of Balgzand <5% of biomass is lost by using 1-mm meshes. As much higher proportions of numbers get lost by 1-mm sieving, we consistently use biomass rather than numerical abundance to study the effects of eutrophication. Changes in meiofauna biomass have not been studied. On Balgzand, meiofaunal biomass amounts to only ~5% of total benthic biomass (Witte and Zijlstra 1984).

Stations 6 and 8 (Fig. 1a) are located in areas with intensive fishing for benthic animals. At Sta. 6, several years of dredging around 1980 severely reduced the abundance of lugworms, *Arenicola marina* (L.), and adult gaper clams, *Mya arenaria* L., both dominating species with respect to biomass (Beukema 1995). At Sta. 8, a fishery for cockles (*Cerastoderma edule*) reduced the large stocks of adult cockles, particularly in the early 1980s. We omitted observations at these two stations from most of the further discussions.

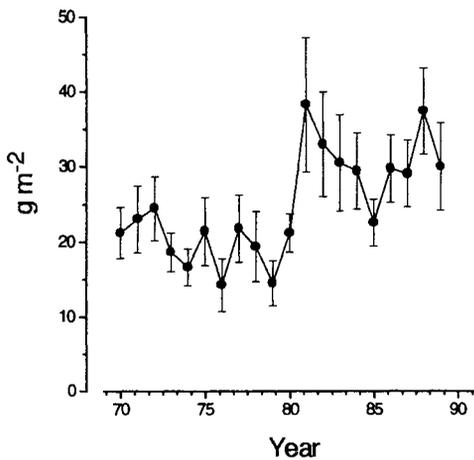
Results

Faunal composition—Beukema (1988) identified three macrozoobenthic assemblages on Balgzand: Area 1: A high and mostly muddy coastal area, with on average 12 macrozoobenthic species per 0.9 m² over the 1970s and 1980s. The fauna is numerically dominated by small deposit feeders

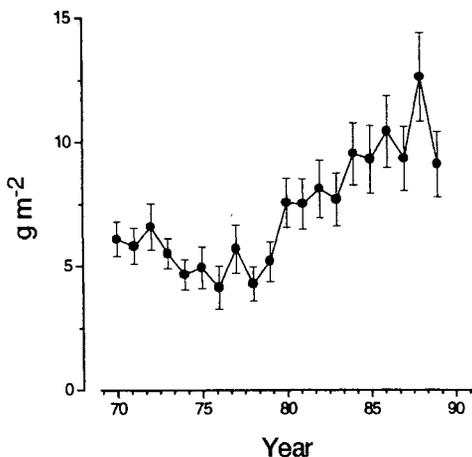
a: Food supply



b: B_{tot}



c: B_{dfw}



such as the amphipod *Corophium volutator* (Pallas) and the gastropod *Hydrobia ulvae* (Penn.). Biomass is dominated by rather big polychaetes (such as *Nereis diversicolor* O.F.M.) and bivalves [such as *Macoma balthica* (L.) and *Scrobicularia plana* Da Costa]. Area 2: A low and exposed northern area, also with a low number of species (on average 12 and 13 species per 0.9 m² in the 1970s and 1980s, respectively). It is composed of an almost completely different set of species: the polychaete worm *Scoloplos armiger* (O.F.M.) dominates in numbers and bivalves such as *Tellina (Angulus) tenuis* Da Costa and *Ensis directus* Conrad contribute substantially to the biomass in some years. Area 3: A larger intermediate area, where most species of the extreme zones co-occur. Species number is higher than in the two extreme areas (15 and 17 species per 0.9 m² in the 1970s and 1980s, respectively). Several large species reach maximal biomass values, e.g. *A. marina* (L.) (cf. fig. 11 of Beukema and De Vlas 1979), *Cerastoderma edule* (L.), *Mytilus edulis* L., and *M. arenaria* L. As a consequence, total zoobenthic biomass reaches maximal values in this area, particularly where *Mytilus* beds occur (parts of transects 4 and 5).

Areas 1 and 2 are characterized by higher proportions of r-selected or opportunistic species with short lifespan, small body size, and high numerical densities (Beukema 1988). According to Warwick (1986) and Warwick et al. (1987), these features are characteristic of disturbed and stressed communities.

Long-term changes in environmental conditions—The most significant and consistent change in the western part of the Wadden Sea during the last decades is certainly the higher level of primary production since about 1978. In the main tidal inlet of the western part of the Wadden Sea (Marsdiep, Fig. 1a), annual primary production in the water rose from a level of ~100 g C per m² in the 1970s to ~200 or more in later years (Fig. 3a). Concurrently, Chl *a* concentrations doubled (Fig. 3a), indicating a significantly denser stock of plankton algae in the 1980s than in the 1970s. Annual bloom periods lasted longer in the 1980s than in the 1970s, particularly for flagellates (with *Phaeocystis globosa* as a dominant species), but also for diatoms (Cadée 1992).

Not only was the pelagic food supply for herbivores enhanced in the 1980s, there is also evidence that benthic microalgae in the western part of the Wadden Sea were more plentiful and productive. Although the data series on primary production by microphytobenthos unfortunately ends after

←

Fig. 3. Changes in biomass (b, c) and food supply (a) of zoobenthos observed in the westernmost part of the Wadden Sea during the 1970–1989 period: (a) Annual averages of Chl *a* concentrations (in mg m⁻³, open symbols) and rates of primary production (in g C m⁻² per yr⁻¹, solid symbols) in the Marsdiep tidal inlet (after fig. 3 of Cadée and Hegeman 1991); (b) 15-station averages of total macrozoobenthic biomass on Balgzand (annual data of March samplings, expressed in g AFDW m⁻², with 1 SE); (c) 15-station averages of added biomass values of the main species (see text) of (mostly) deposit-feeding worms (B_{dfw}) on Balgzand (annual data for March samplings, expressed in g AFDW m⁻², with 1 SE).

1981, the values found around 1980 were clearly higher than those observed before (Cadée 1984).

We are not aware of any other consistent and(or) substantial changes during the 1970–1990 period in the western part of the Dutch Wadden Sea. The turbidity of the Marsdiep water hardly changed during this period (Cadée and Hegeman 1991). The tidal range (as measured in Den Helder, see Fig. 1a) hardly changed, with the averages for the 1971–1980 and 1981–1990 periods being 138 and 139 cm, respectively (Ministerie Verkeer Waterstaat 1994). Mean strength of tidal currents, therefore, will have been similar over the two periods. During the last century, mean sea level and mean levels at high and low water tended to increase by ~2 cm per decade. The differences between the 1970s and 1980s were higher (viz. 6–7 cm). Probably as a consequence of more westerly winds in the 1980s than in the 1970s, a few percent more water will have remained on average within the tidal basin in the 1980s. Mean water temperatures (measured at Den Helder) were slightly higher (10.6 vs. 10.3°C) in the 1980s than in the 1970s (Ministerie Verkeer Waterstaat 1994), but in view of the strong year-to-year variability (9.5–11.5°C) this difference is not of any ecological significance. The benthic fauna on the tidal flats of the Wadden Sea is particularly affected by the character of the winter (Beukema 1979, 1992). Both in the 1970s and the 1980s there were three exceptionally mild winters with fewer than 3 d with maximal temperatures below 0°C. Total numbers of such cold days amounted to 90 in the 1970s and to 97 in the 1980s.

Changes in intertidal height of the Balgzand sampling stations were only slight during the 1970–1989 period and did not change the general pattern shown in Fig. 1b. Successive sounding charts show that the highest areas became even higher (roughly keeping pace with the trend of high-water levels becoming higher) and low areas even lower (cf. also fig. 10 of Dapper and van der Veer 1981). Sediment composition at the sampling stations on Balgzand regularly changed with the season (the upper layer of the bottom becomes muddier during calm periods, particularly in summer), and these changes were more significant than those from year to year. The latter did not show a marked trend (Ente 1969; Dapper and van der Veer 1981; unpubl. recent data). If anything, silt content slightly declined at the muddiest stations, but again the order of the sampling stations shown in Fig. 1b did not change and the shifts were insignificant as compared to seasonal changes and consistent station-to-station differences.

Long-term changes in zoobenthos—On average, zoobenthic biomass on Balgzand was significantly higher during the 1980s than during the 1970s (Fig. 3b, $P < 0.001$, Wilcoxon test). This was particularly so in all species of deposit-feeding polychaetes (Beukema 1989, 1991). The added biomass values of the major species of this group showed a consistently increasing trend during most of the 1970–1990 period, resulting in a much higher biomass of this group in the 1980s than in the 1970s (Fig. 3c, $P < 0.001$, Wilcoxon test). Similar changes were observed in the major species of bivalves with flexible feeding strategies (viz. *M. balthica* and *S. plana*). The biomass values of the major species of sus-

pension-feeding bivalves (*C. edule*, *M. edulis*, and *M. arnaria*) showed more variability but also an increasing trend (Beukema 1991). Only the carnivores did not significantly increase in biomass, but their biomass values were low and variable (Beukema 1991). Thus, all important deposit- and suspension-feeding species showed biomass values that were higher during the 1980s than during the 1970s (important species are those that contributed on average at least 0.1 g AFDW m⁻² to total annual biomass).

Note that the course of biomass change in zoobenthos (Fig. 3b) is closely related to their food as measured in the nearby Marsdiep tidal inlet (Fig. 3a), although with a time lag of almost 2 yr. A significant correlation ($r = +0.74$, $P < 0.01$, Spearman rank test with $n = 15$) is observed between the mean Chl *a* concentration in year n and zoobenthos biomass early in year ($n + 2$).

Local changes in total biomass—At all 13 unfished stations (solid symbols in Fig. 4) mean biomass values were higher in the 1980s than in the 1970s (Fig. 4a: $P < 0.01$ at 10 stations, $0.01 < P < 0.05$ at 2 stations, and $P > 0.05$ at 1 station; t -tests with $n = 20$). The magnitude of the increase, however, differed from place to place. The changes were small (<4 g AFDW m⁻² or <50%) in the two extreme areas (Fig. 4a)—the exposed northern part (Sta. C and 12) and the sheltered, high, and muddy coastal part of Balgzand (Sta. 1, 2, 3, and A). Changes were also small (or even negative) at Sta. 6 and 8 (open symbols in Fig. 4), but these changes were seriously affected by intensive fishing.

The remaining seven stations (B, 4, 5, 7, 9, 10, and 11) showed much elevated biomass values in the 1980s, with differences exceeding by far the standard errors (Fig. 4a). At three of these stations (9, 10, and 11), biomass values of the 1980s were on average even more than twice the averages of the 1970s (Fig. 4b).

Comparison of Figs. 1a and 4 clearly shows that stations geographically close to one another are also clustered in Fig. 4, i.e. they show a similar increase in biomass during the 1970–1989 period. The framed groups of two to four single-station values shown in Fig. 4 thus really represent specific parts of Balgzand: extreme (either exposed/low/sandy or sheltered/high/muddy) and fished areas with little biomass change vs. a large nonfished central part with less extreme environmental conditions going with substantial biomass increase. Maximal biomass increase (Sta. 9, 10, and 11) occurred in an area rather close to the exposed part of Balgzand. The position in Fig. 4 of the lower value of the elevated-biomass group (Sta. B) is close to those of the sheltered area, in accordance with its location on Balgzand (Fig. 1a), and its exclusion from the group of sheltered stations is rather arbitrary.

At the 13 nonfished stations, the rise in biomass from the 1970s to the 1980s was sharper at stations with high than at those with low initial (1970s) biomass. This was so both for absolute increase (Fig. 4a: $r = +0.88$, $P < 0.001$) and for relative increase (Fig. 4b: $r = +0.68$, $P < 0.02$). Rise in biomass was also sharper at stations with high rather than with low initial species number (Fig. 4c: $r = +0.79$, $P < 0.01$ for absolute changes and Fig. 4d: $r = +0.54$, $P < 0.1$ for relative changes). Two-tailed Spearman rank tests with n

of 13 were used for statistical evaluation of these correlations.

The two areas (exposed and sheltered) with only a slight increase in biomass were characterized by extreme types of sediment (Fig. 4e, f; compare Fig. 1b): clean sands with <1% mud and mixed sediments with >7% mud, respectively. Maximal increases were observed in the area with relatively sandy sediments (mud contents of ~2%). If we exclude the two exposed stations with very low mud contents (<1%), the relative biomass increase became smaller as the mud contents increased (Fig. 4e: $r = -0.87$, $P < 0.01$; Fig. 4f: $r = -0.82$, $P < 0.01$; Spearman rank tests for the 11 nonfished stations with mud contents >1%). Thus, maximal biomass increase between the 1970s and 1980s occurred where mud contents were just high enough (i.e. where exposure to waves and currents was just low enough) to make conditions suitable for a relatively high number of species (see location of top cluster in Fig. 4c, d) with a relatively high biomass already at the start of the enrichment period (see location of top cluster in Fig. 4a, b).

Local changes in biomass of two major functional groups—Two functional groups make up the major part of total biomass on the Balgzand tidal flats, viz. the suspension-feeding bivalves (with main species of *C. edule*, *M. edulis*, and *M. arenaria*) and the (mostly deposit-feeding) polychaetes (with main species of *A. marina*, *N. diversicolor*, *S. armiger*, and *Heteromastus filiformis* (Clap.)). On the whole, the relationship between sediment composition and biomass change from the 1970s to the 1980s was similar in the two groups (compare Fig. 5a and b for worms with Fig. 5c and d for bivalves) and resembled that for total biomass (Fig. 4e, f). In both groups, biomass changes were again small in the most exposed as well as in the most sheltered areas, whereas biomass increases were maximal in the area with a sediment containing ~2% mud (Fig. 5). At the two stations with lower (<1%) mud contents, most of the main species of the two groups were regularly present, but they never established stocks with high biomass values. At the two muddiest stations, which were also the stations with the highest elevation, typical suspension feeders were almost entirely lacking. Therefore, we omitted these two stations (1 and 2) from Fig. 5c and d.

A more detailed comparison of Fig. 5a and b with Fig. 5c and d reveals some differences in the responses of deposit and suspension feeders: (1) Deposit feeders showed higher maximal increases than did suspension feeders (compare Fig. 5b and d, and also Fig. 3c with b). (2) There is a clear difference for the two fished stations. At the cockle-fished Sta. 8, the effect of fishing was clear only in the bivalve biomass (Fig. 5c, d), whereas the worms had apparently remained unaffected and even reached their maximal increase at this station (Fig. 5a, b). Cockle fishing affects only the top layer of the sediment and is highly efficient in removing cockles but causes little damage to most worms (De Vlas 1987). At the lugworm-fished Sta. 6, the fishery influence was visible in both groups, but more clearly in the bivalves than in the worms: reductions in the gaper clams (*M. arenaria*) exceeded those in the targeted lugworms (*A. marina*) (Beukema 1995). (3) The relationship between biomass in-

creases and mud content appears to be closer in this group (Fig. 5a, b) than in the suspension feeders (Fig. 5c, d). The negative relationship observed above between biomass change and mud content of the sediment (at mud contents >1%) can be traced back in particular to the changes in the group of deposit feeders (Fig. 5a: $r = -0.84$ or -0.82 , Spearman rank test with n of 13 or 11, including or excluding the fished stations, respectively, $P < 0.01$ both; Fig. 5b: $r = -0.76$ or -0.74 , $P < 0.01$). In the suspension feeders this relationship is less clear ($r = -0.51$ and -0.41 for Fig. 5c and Fig. 5d, respectively; $P > 0.05$, $n = 9$: unfished stations only). Apparently, the fate of deposit feeders is more intimately linked with the local sediment composition, whereas that of suspension feeders is primarily dependent on intertidal elevation (Beukema, 1976). The exceptional environmental conditions at Sta. B (Fig. 1b) and the position of the points for this station in Fig. 5 are illustrative. Sta. B is exceptional for Balgzand because it combines a high elevation (just above MTL) with a sandy sediment (only ~3% mud). As a consequence of its high elevation, it is a marginal habitat for suspension feeders—they grow slowly at this station or are almost absent. Therefore, a significant increase of suspension-feeding bivalves cannot be expected at Sta. B. The response of the deposit feeders at this station matches those of other stations with a similar sediment composition (Fig. 5a, b). Thus, the relationship between sediment composition and biomass change appears to be a direct and causal one in the deposit feeders, but will be indirect (via the generally positive correlation between intertidal elevation and mud content, see Fig. 1b) in suspension feeders.

Discussion

Around 1978, benthic and pelagic primary production and Chl *a* concentrations suddenly increased to a level twice as high as before in the main inlet of the western part of the Wadden Sea (Fig. 3a). After a few years, average biomass values of zoobenthos on Balgzand (part of the catchment area of this inlet) had also doubled (Fig. 3b). We think that this response of the benthos was caused by the increase of small algae, viz. by a higher availability of food for most benthic animals. About 55% of the zoobenthic biomass on Balgzand consists of filter feeders (feeding directly on pelagic algae) and another 25% are deposit feeders (taking part of their food from pelagic algae settled on the sediment). Most of the food of the ~15% of animals with a mixed feeding type also consists of such algae. Thus ~90% of the total benthic stock (in weight units) depends for its food directly and (almost) entirely on small algae (either suspended or at the sediment surface).

The biomass increases of these herbivores took place after a time lag of one or two years. Similar time lags were observed by Johnson and Wiederholm (1992) in the response of bottom animals (amphipods in a lake) to interannual variability in food availability (diatom biovolume), by Buchanan (1993) in the response of numbers in some benthic species to the changes in phytoplankton abundance off the Northumberland coast, by Josefson et al. (1993) in the response of benthic abundance and biomass to river runoff (correlated

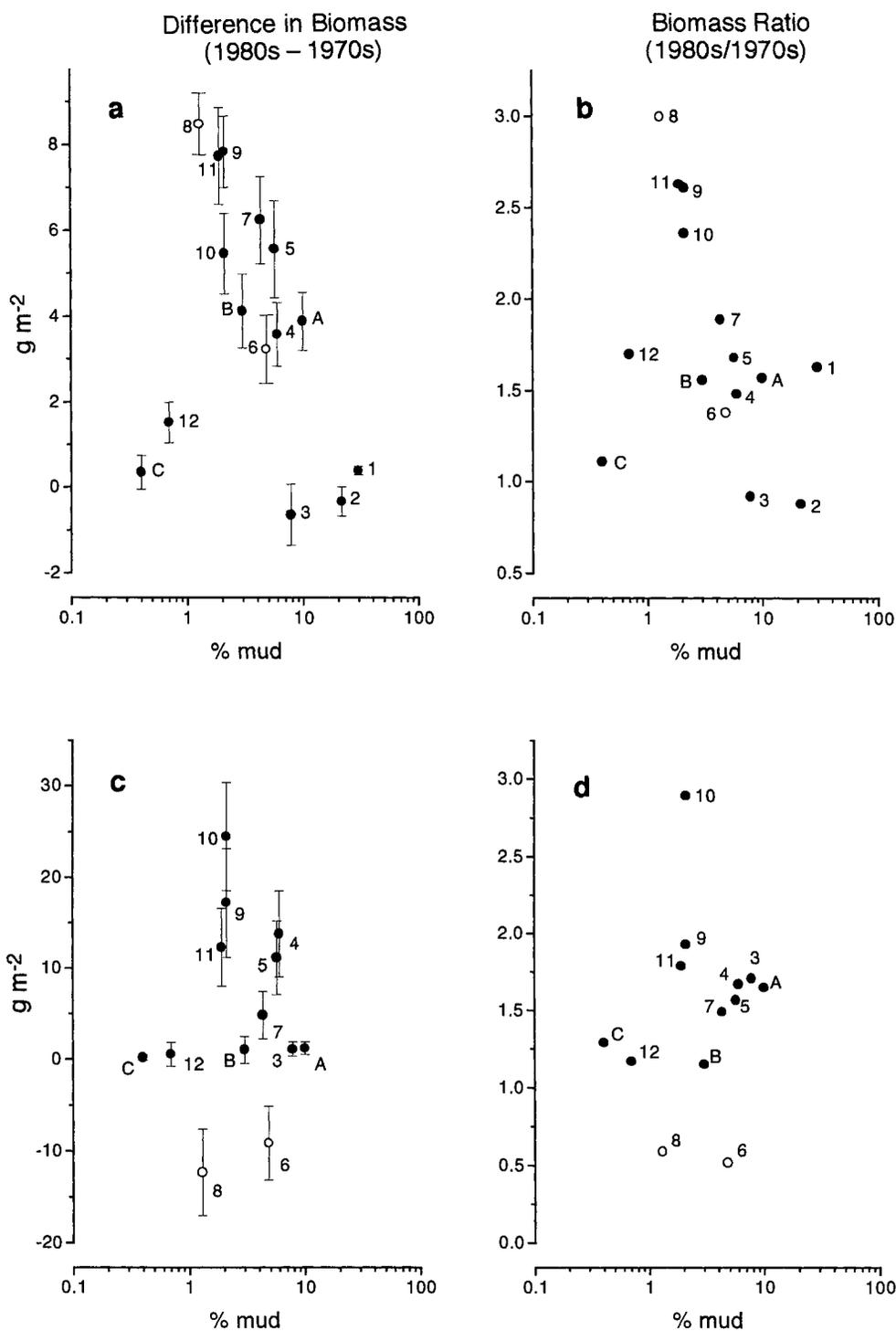


Fig. 5. Absolute (a, c) and relative (b, d) differences in biomass of the groups of (mostly deposit-feeding) worms (a, b) and suspension-feeding bivalves (c, d) between the 1980s and the 1970s at each of the 15 sampling stations on Balgzand, arranged in order of increasing mud content of the sediment. Absolute differences with 1 SE ($n = 20$) (see further legend of Fig. 4).

with Chl *a* concentration) in the Kattegat, and by Hagerman et al. (1996) in the response of total benthic biomass in the Skagerak-Kattegat area to Chl *a* concentrations in the overlying water. Consumer species can positively respond to higher food supplies either or both by higher numbers and

accelerated growth. Both responses have been observed in worms (Dauer and Conner 1980). Growth responses will be almost immediate, but the increases in numbers and particularly in biomass will need more time. On Balgzand, most species responded by an increase in abundance rather than

in growth rate (Beukema 1991). In such cases a time lag is expected as most species need one or two years to reach substantial weights after birth and can only then add substantially to biomass.

The close correspondence of the geographic areas of nutrient and organic matter enrichment and benthic biomass increase (Beukema et al. 1996) is further evidence that the increase of the zoobenthic biomass that started around 1980 was caused by the locally enhanced levels of primary production and algae concentrations. The doubling of benthic biomass was limited to the part of the Wadden Sea that receives large amounts of freshwater (with high concentrations of nutrients and algae and their remains) sluiced from Lake IJssel (De Jonge and Essink 1991; De Jonge and van Raaij 1995).

Although alternative explanations are not obvious, it should be noted that several large and rather sudden changes took place at the end of the 1970s in an extensive area encompassing the North Sea (Austen et al. 1991; Evans and Edwards 1993; Lindeboom et al. 1995). At all marine trophic levels (phytoplankton, zooplankton, fish, and birds), declining trends more or less simultaneously reversed around 1980 (Aebischer et al. 1990). Perhaps, some changes observed in the western part of the Wadden Sea were part of these large-scale changes. Alternative environmental factors that might control zoobenthic biomass (e.g. weather, sediment composition, sea level, current speeds, predators) did not change between the 1970s and 1980 and certainly did not change rather suddenly around 1980 and exclusively in the western part of the Dutch Wadden Sea. Therefore, it makes little sense to elaborate on alternative hypotheses based on changes in such other factors. Particularly the local nature of the changes described in the present paper (involving only the western half of the Dutch part of the Wadden Sea) points to a more local primary cause, in this case the enriching influence of freshwater originating from Lake IJssel (Beukema et al. 1996).

Within the Balgzand area, we observed significant place-to-place differences in the magnitude of the increase of the zoobenthic stocks (Figs. 4, 5). Just as the two fishery-disturbed stations (open symbols in Figs. 4 and 5), the two most exposed and the four most sheltered stations showed lower-than-average increases. We may have slightly underestimated all biomass increases, because small-sized species were not completely retrieved in the 1-mm sieved samples and particularly the smaller sized species increased more than the large-sized species (Beukema 1991). Moreover, the sieving losses may have been somewhat higher in the exposed subarea than in other parts of Balgzand (R. Dekker pers. comm.). Such inaccuracies, however, can explain only an insignificantly small part (<10%) of the biomass increases and of the differences in these increases between the three subareas. Thus, major responses of the zoobenthic biomass were indeed limited to the middle (nonextreme) part of the main environmental gradient (Fig. 4e, f), where both species numbers (Fig. 4c, d) and biomass (Fig. 4a, b) were already relatively high before the enrichment started. The strong positive response to enhanced feeding conditions in this large central part of Balgzand indeed indicates that food was a limiting factor there in the 1970s. The maximal increase of

zoobenthos was observed in an area where the sediment contains ~2% mud (Figs. 4e, f, 5), i.e. near the off-shore edge of the area with intermediate environmental conditions. In this area the sediment will be just sufficiently stable to harbor a dense and diverse benthic fauna. For two reasons, an overall increase in primary production would be most effective in enhancing the food supply just there: the concentration and production of benthic algae were relatively low in the 1970s in this area with a relatively low mud content (Fig. 2), and the pelagic food reaches this area by tidal currents that traverse only small and scarcely populated tidal flats and have not yet been depleted of food (Peterson and Black 1987, 1991).

If we accept the hypothesis that the overall doubling of food supply caused the general doubling of the benthic biomass around 1980 on Balgzand, the lack of a significant zoobenthos response in the two extreme parts of the area remains to be explained. The supposition that these areas did not have a full share in the general increase of algae concentrations can be refuted because of the thorough mixing of the water in the Balgzand area (Zimmerman 1978). Neither was the degree of depletion of algae concentrations in the water flowing over the Balgzand tidal flats higher in the 1980s than in the 1970s, as the ratio of algae concentrations to zoobenthic biomass remained unchanged (both factors roughly doubled). Moreover, the fauna in these two subareas was (and is) scant and food demands have always been relatively low. Food limitation is particularly improbable in the sheltered coastal area where the sediment is muddy and concentrations of Chl *a* and organic C in the upper sediment layer are relatively high (Fig. 2), due to a dense stock of diatoms (with a benthic primary production that is higher than anywhere else on Balgzand) and high rates of sedimentation of fresh organic matter (Cadée and Hegeman 1977; Cadée 1996). As a result, annual amounts of >200 g C m⁻² were available there already in the 1970s. Such a food supply exceeds by far the demands of the macrozoobenthos with a biomass of only ~2 g C m⁻² at Sta. 1 and 2 and ~5 and 8 g C m⁻² at Sta. 3 and A, respectively. Thus, food demands of macrozoobenthos were in this area much lower than food supply, making it improbable that food was ever really limiting in these coastal areas. The same holds for the exposed area, where the zoobenthic biomass rarely exceeded 5 g C m⁻² so that the pelagic food supply of ~100 g C m⁻², present already in the 1970s (Cadée and Hegeman 1974a,b; 1977), always surpassed the demands.

Faunal abundance in these extreme parts of Balgzand must be limited by other factors than food supply. The stressed nature of the zoobenthic community in these areas (according to results obtained by application of the ABC method, *see* first section of the results) points to unfavorable environmental conditions, causing a persistent poverty in terms of both species richness and biomass. Although stress is often associated with pollution, this is not true for the Balgzand area (Beukema 1988). Other harsh conditions must exert stressing effects in subareas 1 and 2.

In the coastal area, the short immersion times and softness of the sediment will cause the scarcity and slow growth of true suspension feeders (Beukema 1976); the softness of the sediments makes conditions unfavorable for the largest de-

posit feeder, the lugworm *A. marina* (Beukema and Flach 1995). The few remaining species will be limited in their abundance particularly by the short immersion times, as for example shown for the higher part of the area in *Corophium* species by Beukema and Flach (1995).

Duration of immersion varied strongly in the 1970–1990 period, with concomitant fluctuations in the zonation of benthic species, but mean values for the two 10-yr periods were similar (both mean sea level and mean bottom level became slightly higher during the 1970–1990 period, see second section of the results). Neither did the silt content of the sediments at the sampling stations change consistently. In the muddy coastal area, the oxygenated top layer of the sediment is generally thinner than in sandier parts of Balgzand. Perhaps the eutrophication caused a general decline of oxygen conditions, effects of which could have been more serious in the coastal areas. If so, added stress by oxygen shortage may have contributed to the lack of response to higher food supply in these areas. Unfortunately, no direct evidence is available on this point. Periods with high mortality in a few sensitive species were observed only twice during the 1970–1989 period and were restricted to small (~1 km²) areas, only one of them being located in the muddy coastal area (Beukema 1989).

In the exposed offshore area, the environmental conditions are unfavorable because of unstable sediments due to strong tidal currents and high waves that cause moving sand ripples of various size and remove nearly all mud and organic matter. It may be considered a marginal habitat for nearly all species thriving in other parts of Balgzand. Only a few specialists, particularly some small-sized crustaceans and worms, show their maximal abundance on tidal flats in such extreme areas (most of these species are common in sandy subtidal areas). A recent immigrant, *E. directus* (Conrad), is found here, but it only occasionally reaches high biomass values (Beukema and Dekker 1995). Again, no evidence is available of a consistent change in the most important environmental characteristics during the 1970–1990 period.

The most plausible hypothesis to explain the general increase of the zoobenthic biomass around 1980 is the enhancement of food supply that started just before 1980 (and was in its turn caused by mild eutrophication), whereas the most plausible hypothesis to explain why these biomass increases lagged behind in the extreme parts of Balgzand is permanent stress by harsh abiotic factors. Rather than food supply, such harsh abiotic conditions are the true limiting factors in such marginal habitats. This seems to be generally true in the marine environment, both on rocky shores (Menge and Sutherland 1987) and in near-shore soft-sediment areas (Beukema and Flach 1995). This explanation is also in line with the general conclusions derived from the comparison of the situation in a high number of estuaries, that “the system-wide biomass and secondary production (of macrobenthic suspension feeders) are limited by the planktonic primary production of the system, whereas the local biomass is highly dependent on hydrodynamic conditions” (Heip et al. 1995, p. 1). We extend this conclusion to all benthic animals feeding primarily on microalgae.

In conclusion, the richer food supply starting around 1980 was fully effective only in areas where environmental con-

ditions were relatively benign. In such areas zoobenthic communities were already relatively rich in species number and biomass long before the enhancement of food supply started. On the other hand, in areas with harsh conditions, the fauna was and remained relatively impoverished and stressed, not being able to profit fully from the enhanced food supply. Consequently, local conditions determined the outcome of this large-scale “experiment” of an enhanced supply of primary food to the heterogeneous environment of the tidal flats over an area of about 1,000 km². Of course, a natural experiment lacks the controls and duplicates of real and well-planned experiments. The phenomena observed during the last few decades in the Wadden Sea were probably unique and may never be repeated. Despite these limitations, they offered an opportunity to study and understand changes at the ecosystem level on a scale not easily reproduced by any experimental setup.

References

- AEBISCHER, N. J., J. C. COULSON, AND J. M. COLEBROOK. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* **347**: 753–755.
- AUSTEN, M. C., J. B. BUCHANAN, H. G. HUNT, A. B. JOSEFSON, AND M. A. KENDALL. 1991. Comparison of long-term trends in benthic and pelagic communities of the North Sea. *J. Mar. Biol. Assoc. U.K.* **71**: 179–190.
- BEUKEMA, J. J. 1974. Seasonal changes in the biomass of the macrobenthos of a tidal flat area in the Dutch Wadden Sea. *Neth. J. Sea Res.* **8**: 94–107.
- . 1976. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. *Neth. J. Sea Res.* **10**: 236–261.
- . 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: Effects of a severe winter. *Neth. J. Sea Res.* **13**: 203–223.
- . 1988. An evaluation of the ABC-method (abundance/biomass comparison) as applied to macrozoobenthic communities living on tidal flats in the Dutch Wadden Sea. *Mar. Biol.* **99**: 425–433.
- . 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. *Helgol. Meeresunters.* **43**: 405–415.
- . 1991. Changes in composition of bottom fauna of a tidal-flat area during a period of eutrophication. *Mar. Biol.* **111**: 293–301.
- . 1992. Expected changes in the Wadden Sea benthos in a warmer world: Lessons from periods with mild winters. *Neth. J. Sea Res.* **30**: 73–79.
- . 1995. Long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. *Neth. J. Sea Res.* **33**: 219–227.
- , AND G. C. CADÉE. 1986. Zoobenthos responses to eutrophication of the Dutch Wadden Sea. *Ophelia* **26**: 55–64.
- , AND ———. 1996. Consequences of the sudden removal of nearly all mussels and cockles from the Dutch Wadden Sea. *P.S.Z.N. I: Mar. Ecol.* **17**: 279–289.
- , AND R. DEKKER. 1995. Dynamics and growth of a recent invader into European coastal waters: The American razor clam, *Ensis directus*. *J. Mar. Biol. Assoc. U.K.* **75**: 351–362.
- , AND J. DE VLAS. 1979. Population parameters of the lugworm, *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.* **13**: 331–353.
- , K. ESSINK, AND H. MICHAELIS. 1996. The geographic

- scale of synchronized fluctuation patterns in zoobenthos populations as a key to underlying factors: Climatic or man-induced. *ICES J. Mar. Sci.* **53**: 964–971.
- , AND E. C. FLACH. 1995. Factors controlling the upper and lower limits of the intertidal distribution of two *Corophium* species in the Wadden Sea. *Mar. Ecol. Prog. Ser.* **125**: 117–126.
- BUCHANAN, J. B. 1993. Evidence of benthic pelagic coupling at a station off the Northumberland coast. *J. Exp. Mar. Biol. Ecol.* **172**: 1–10.
- CADÉE, G. C. 1978. On the origin of organic matter accumulating on tidal flats of Balgzand, Dutch Wadden Sea. *Hydrobiol. Bull.* **12**: 145–150.
- . 1984. Has input of organic matter into the western part of the Dutch Wadden Sea increased during the last decades? *Neth. Inst. Sea Res. Publ. Ser.* **10**: 71–82.
- . 1986. Increased phytoplankton primary production in the Marsdiep area (western Dutch Wadden Sea). *Neth. J. Sea Res.* **20**: 285–290.
- . 1990. Lokale sterfte van kokkels op het wad tijdens een *Noctiluca* bloei (Local mortality of *Cerastoderma edule* on a tidal flat during a *Noctiluca* bloom). *Het Zeepaard* **50**: 119–128.
- . 1992. Phytoplankton variability in the Marsdiep, the Netherlands. *ICES Mar. Sci. Symp.* **195**: 213–222.
- . 1996. Accumulation and sedimentation of *Phaeocystis globosa* in the Dutch Wadden Sea. *J. Sea Res.* **36**: 321–327.
- , AND J. HEGEMAN. 1974a. Primary production of phytoplankton in the Dutch Wadden Sea. *Neth. J. Sea Res.* **8**: 240–259.
- , AND ———. 1974b. Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.* **8**: 260–291.
- , AND ———. 1977. Distribution of primary production of the benthic microflora and accumulation of organic matter on a tidal flat area, Balgzand, Dutch Wadden Sea. *Neth. J. Sea Res.* **11**: 24–41.
- , AND ———. 1991. Phytoplankton primary production, chlorophyll and species composition, organic carbon and turbidity in the Marsdiep in 1990, compared with foregoing years. *Hydrobiol. Bull.* **25**: 29–35.
- , AND ———. 1993. Persisting high levels of primary production at declining phosphate concentrations in the Dutch coastal area (Marsdiep). *Neth. J. Sea Res.* **31**: 147–152.
- DANKERS, N., AND J. J. BEUKEMA. 1983. Distributional patterns of macrozoobenthic species in relation to some environmental factors, p. 69–103. *In* W. J. Wolff [ed.], *Ecology of the Wadden Sea*, v. 1. Balkema.
- DAPPER, R., AND H. W. VAN DER VEER. 1981. Onderzoek naar de ruimtelijke variatie van de bodemsamenstelling op het Balgzand. *Ned. Inst. Onderz. Zee, Interne Verslagen* **9**: 1–21.
- DAUER, D. M., AND W. G. CONNER. 1980. Effects of moderate sewage input on benthic polychaete populations. *Estuarine Mar. Sci.* **10**: 335–346.
- DE GLOPPER, R. J. 1967. Over de bodemgesteldheid van het wadengebied. *Van Zee tot Land* **43**: 1–67.
- DE JONGE, V. N., AND K. ESSINK. 1991. Long-term changes in nutrient loads and primary and secondary producers in the Dutch Wadden Sea, p. 307–316. *In* M. Elliott and J.-P. Ducrot [eds.], *Estuaries and coasts: Spatial and temporal inter-comparisons*. ECSA 19 Symposium. Olsen & Olsen.
- , AND W. VAN RAAPHORST. 1995. Eutrophication of the Dutch Wadden Sea (western Europe), an estuarine area controlled by the river Rhine, p. 129–149. *In* A. J. McComb [ed.], *Eutrophic shallow estuaries and lagoons*. CRC Press.
- DE VLAS, J. 1987. Effects of cockle fisheries on the macrobenthos in the Wadden Sea, p. 215–227. *In* S. Tougaard and S. Asbirk [eds.], *Proc. 5th Int. Wadden Sea Symp.*, Esbjerg.
- DE WILDE, P. A. W. J., AND J. J. BEUKEMA. 1984. The role of the zoobenthos in the consumption of organic matter in the Dutch Wadden Sea. *Neth. Inst. Sea Res. Publ. Ser.* **10**: 145–148.
- EMERSON, C. W. 1989. Wind stress limitation of benthic secondary production in shallow, soft-sediment communities. *Mar. Ecol. Prog. Ser.* **53**: 65–77.
- ENTE, P. J. 1969. De bodemgesteldheid en de bodemgeschiktheid van het Balgzand en de Breehorn. *Rijksdienst IJsselmeerpolders, Flevovericht* **66**: 1–29.
- EVANS, F., AND A. EDWARDS. 1993. Changes in the zooplankton community off the coast of Northumberland between 1969 and 1988, with notes on changes in the phytoplankton and benthos. *J. Exp. Mar. Biol. Ecol.* **172**: 11–29.
- FRANZ, H. G., S. R. GONZALES, G. C. CADÉE, AND F. C. HANSEN. 1992. Long-term change of *Temora longicornis* (Copepoda, Calanoida) abundance in a Dutch tidal inlet (Marsdiep) in relation to eutrophication. *Neth. J. Sea Res.* **30**: 23–32.
- GRAY, J. S. 1992. Eutrophication in the sea, p. 3–15. *In* G. Colombo et al. [eds.], *Marine eutrophication and population dynamics*. Olsen & Olsen.
- HAGERMAN, L., A. B. JOSEFSON, AND J. N. JENSEN. 1996. Benthic macrofauna and demersal fish, p. 155–178. *In* B. Barker Jørgensen and K. Richardson [eds.], *Eutrophication in coastal marine ecosystems*, v. 52. Coastal and Estuarine Studies.
- HEIP, C. H. R., N. K. GOOSEN, P. M. J. HERMAN, J. KROMKAMP, J. J. MIDDELBURG, AND K. SOETAERT. 1995. Production and consumption of biological particles in temperate tidal estuaries. *Oceanogr. Mar. Biol. Annu. Rev.* **33**: 1–149.
- HERTWECK, G. 1994. Zonation of benthos and Lebensspuren in the tidal flats of the Jade Bay, southern North Sea. *Senckenb. Mar.* **24**: 157–170.
- JENSEN, K. T. 1993. Density-dependent growth in cockles (*Cerastoderma edule*): Evidence from interannual comparisons. *J. Mar. Biol. Ass. U.K.* **73**: 333–342.
- JOHNSON, R. K., AND T. WIEDERHOLM. 1992. Pelagic-benthic coupling—the importance of diatom interannual variability for population oscillations of *Monoporeia affinis*. *Limnol. Oceanogr.* **37**: 1596–1607.
- JOSEFSON, A. B., J. N. JENSEN, AND G. ÆRTEBJERG. 1993. The benthos community structure anomaly in the late 1970s and early 1980s—a result of a major food pulse? *J. Exp. Mar. Biol. Ecol.* **172**: 31–45.
- KAMERMANS, P. 1993. Food limitation in cockles (*Cerastoderma edule* (L.)): Influences of location on tidal flat and nearby presence of mussel beds. *Neth. J. Sea Res.* **31**: 71–81.
- LINDEBOOM, H. J., W. VAN RAAPHORST, J. J. BEUKEMA, G. C. CADÉE, AND C. SWENNEN. 1995. (Sudden) changes in the North Sea and Wadden Sea: Oceanic influences underestimated? *Dtsche. Hydrogr. Z. Suppl.* **2**: 87–100.
- MENGE, B. A., AND J. P. SUTHERLAND. 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* **130**: 730–757.
- MINISTERIE VERKEER WATERSTAAT. 1994. Tienjarig overzicht 1981–1990 (presentatie van afvoeren, waterstanden, watertemperaturen, golven en kustmetingen). Ministerie Verkeer Waterstaat, Direct.-Gen. Rijkswaterstaat, Den Haag, p. 1–217.
- PEARSON, T. H., AND R. ROSENBERG. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Annu. Rev.* **16**: 229–311.
- PETERSON, C. H., AND R. BLACK. 1987. Resource depletion by active suspension feeders on tidal flats: Influence of local density and tidal elevation. *Limnol. Oceanogr.* **32**: 143–166.

- , AND ———. 1991. Preliminary evidence for progressive sestonic food depletion in incoming tide over a broad tidal sand flat. *Estuarine Coastal Shelf Sci.* **32**: 405–413.
- VAN DER VEER, H., W. VAN RAAPHORST, AND M. J. N. BERGMAN. 1989. Eutrophication of the Dutch Wadden Sea: External nutrient loadings of the Marsdiep and Vliestroom basin. *Helgol. Meeresunters.* **43**: 501–515.
- WARWICK, R. M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. *Mar. Biol.* **92**: 557–562.
- , T. H. PEARSON, AND RUSWAHYUNI. 1987. Detection of pollution effects on marine macrobenthos: Further evaluation of the species abundance/biomass method. *Mar. Biol.* **95**: 193–200.
- WITTE, J. IJ., AND J. J. ZIJLSTRA. 1984. The meiofauna of a tidal flat in the western part of the Wadden Sea and its role in the benthic ecosystem. *Mar. Ecol. Prog. Ser.* **14**: 129–138.
- ZIMMERMAN, J. T. F. 1978. Tidal flushing of the Balgzand tidal flat area, Dutch Wadden Sea. *Hydrobiol. Bull.* **12**: 151–152.

Received: 7 November 1995

Accepted: 30 January 1997