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Benthic response to sedimentation events during autumn to spring at a shallow-water station in the Western Kiel Bight

I. Analysis of processes on a community level *

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Abstract

The response of the benthos to the break up of anoxia in the Kiel Bight (Western Baltic Sea), and to three succeeding events of "external" food supply, consisting of a settled autumn plankton bloom, resuspended matter and macrophyte input during winter, and of a sedimented spring phytoplankton bloom, is described on a community level. The first input of oxygen broke up anoxic conditions and made stored food resources available to decomposition. This "internal" food supply, mainly consisting of protein (folin positive matter), was followed by a drastic increase in heat production and ATP-biomass and caused a period of low redox potential, which lasted for several weeks. During this phase, a plankton bloom (dinoflagellates and diatoms) settled to the sea floor. Although there was an immediate response of benthic activity, this food input was not completely consumed by the strongly disturbed benthic community. During winter resuspended matter and the input of macrophyte debris caused another maximum in benthic activity and biomass despite the low temperature. The response to sedimentation of cells from a diatom bloom during mid March was also without any time lag and was consumed within 5–6 wk. A comparison of the amount of particles collected in a sediment trap with the increase of organic matter in the sediment demonstrated that the sediment collected four times (autumn) and seven to eight times (spring) more than measured by the sediment trap. Strong indications of food limitation of benthic activity were found. During autumn and winter these indications were caused more by physical than by biological processes. The three events of "external" food supply caused a temporary shift in the type of metabolism towards fermentation processes and reduced the redox potential. In spring the development of the benthic community was still being strongly influenced by the events of the preceding summer and autumn.

Introduction

In recent years pelagic-benthic coupling has been found to be a highly dynamic process occurring over very short time scales. Especially the investigations of plankton blooms which, via sedimentation, represent a large food supply for the benthic system, have demonstrated the necessity of investigating sedimentation and the subsequent benthic response over time scales of days to a few weeks (Smetacek *et al.*, 1978; Smetacek, 1980; Graf *et al.*, 1982). This is particularly important in shallow water ecosystems, such as the Kiel Bight (Western Baltic Sea), where studies on benthic-pelagic coupling are additionally complicated by the close interaction of short-term weather conditions with the ecosystem, e.g. irradiance, wind, and horizontal advection.

The input of particulate organic matter to the benthic system is generally investigated by near-bottom sediment traps. However, large discrepancies have been found between the amount of matter collected in the trap and the benthic consumption immediately below (Wiebe *et al.*, 1976; Graf *et al.*, 1982). These authors explain the discrepancy with lateral advection and near-bottom transport of organic matter and show that a significant link in the chain of processes extending from production in the surface and incorporation of particles into the sediment is still to be identified. If, however, sedimentation of particles is strongly concentrated in certain periods of the year, it should be possible to measure the pelagic input directly in the sediment itself, even in the presence of a high background level of organic matter.

This report gives the first results of an interdisciplinary project carried out by the SFB 95. It will be followed by a paper dealing with the special role of benthic bacteria

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(Meyer-Reil, 1983). A report on the role of macrofauna, meiofauna, ciliates and benthic diatoms will be published later. This first part analyses pelagic-benthic coupling on a community level.

The response of the benthos to a settling phytoplankton bloom in spring 1980 was reported by Graf *et al.* (1982) and first results on the role of bacteria within this process have already been described by Meyer-Reil (1981). Consequently, our original intention was to investigate the response of the benthos to the settling autumn phytoplankton bloom of 1981. The project was extended, however, to the following spring because in 1981 there was unusually extensive anoxia in the Kiel Bight during the summer. Thus, the investigation of pelagic-benthic coupling ran into additional complexities.

Material and methods

From September 9, 1981 to April 26, 1982, 20 cruises with RV 'Littorina' to the 'Hausgarten', an area restricted for research in the Western Kiel Bight (Western Baltic Sea), were carried out. The sediment station was situated at a water depth of 18 m on the slope of the Kiel Bight channel system. The sediment is sandy mud. The dry weight of 1 cm^3 is 1.300 ± 0.064 g.

Temperature was measured with a TS probe (Electronic Switchgear, London). Redox potential of the sediment was measured with an Eh-electrode (Ingold, Pt-4800-M5, FRG) and a mV-meter (Knick, FRG). Water samples were taken from seven depths using 5-l Niskin bottles. The sediment trap (Zeitzschel *et al.*, 1978) collected particles at two-day intervals. The handling and the analysis of the water samples and that of trapped matter is described by Peinert *et al.* (1982). Chlorophyll *a* analyses were carried out as recommended by Edler (1979). For the trapped matter, chlorophyll *a* equivalents are given according to Peinert *et al.* (1982).

Sediment was collected using a Reineck grab (20×28 cm surface area). Subsamples were taken with Plexiglas corers with 5-cm diameter and, for direct calorimetry, with a plastic syringe (top cut off) with 2.3-cm diameter. The different sediment horizons were separated on board.

For the chemical analyses, sediments from three different grabs were combined, whereas for calorimetry three slides of the parallel grabs were carefully placed in one calorimeter chamber.

ATP-concentration, electron-transport (ETS-)-activity and heat production were measured according to Pamatmat *et al.* (1981). ETS-activity is given in $\mu l\ O_2$. For the recently suggested unit electrochemical microequivalents (μeq) (Packard *et al.*, 1983) the results have to be converted into $\mu \cdot$mol and multiplied by four. Unlike in earlier investigations, direct calorimetry was run at *in-situ* temperature (± 1 C°) and ETS-activity at 10 °C. Thermograms of anoxic and suboxic sediments were not evaluated before a constant heat flow was observed (6–7 h) (c.f. Pamatmat, 1982). Protein and carbohydrate were assayed as described by Meyer-Reil (1983).

Results and discussion

Physical environment

During summer, the oxygen tension in the bottom water of the Western Kiel Bight is generally low. Hydrogen sulfide, however, can only be observed in the deeper parts of the Kiel Bight channel system. The station investigated had originally been chosen to avoid anoxic conditions. During 1981, however, large areas of Kiel Bight became anoxic (Ehrhardt and Wenck, in press).

To distinguish oxic from anoxic conditions, the redox potential in the sediment was measured (Fig. 1). The first autumn storms in early October broke up the anoxic conditions and increased the redox potential from Eh = −160 mV on September 23 to Eh = +420 mV on October 8. This break, however, was only observed at the sediment surface; the deeper horizons of the sediment were less affected. From October 28 to December 3 the redox potential of the top centimeter of the sediment was within the range of Eh = +100 mV to Eh = +300 mV. In Fig. 1, this range is marked by dashed lines and is termed suboxic. In the sediments of the study site, Eh = +100 mV is the upper limit for the occurrence of free hydrogen sulfide (Reimers, 1976). Jørgensen and Fenchel (1974) also indicated an Eh = +100 mV as the lower limit for free oxygen. Accordingly Eh = +300 mV is typical for oxic conditions.

The final termination of the suboxic conditions occurred during early December and produced oxic conditions down to sediment depth 5 cm. Although the hydrographical processes transporting oxygen rich water to the sediment surface are not yet completely understood, it is

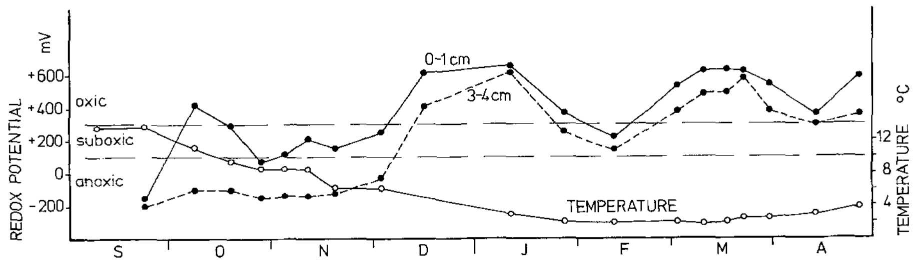

Fig. 1. Redox potential in the sediment and temperature of the sea floor. The range between Eh = +100 mV and Eh = +300 mV is marked with dashed lines and termed suboxic

probable that the final break was induced by heavy northwest storms during the last few days of November, which after some delay in time were followed by an inflow of saline rich bottom water from the Great Belt, causing a lateral exchange of water masses (cf. Wittstock, 1982). A comparable displacement of bottom water, however, was not found when the first hydrographical change in early October occurred.

The process of terminating the summer anoxic period as described above, i.e. a first autumnal break followed by a suboxic period lasting several weeks and a final break in early winter, seems to be typical for the area. The same pattern was observed in the years 1971 to 1973 by oxygen measurements in the near bottom water of the Western Kiel Bight (v. Bodungen, 1975).

The decrease of the redox potential following the first break may have been caused by both a chemical oxygen demand for the oxidation of hydrogen sulfide and also, as will be demonstrated, by increased biological activity. The latter would also explain the temporary reduction of the redox potential from late January to mid February and during early April.

The temperature development in the near-bottom water is typical for a boreal region. Temperature decreased from 13.9 °C on September 23 to 2 °C on January 27 and increased slowly at the end of the investigation period. For the Western Kiel Bight the temperature curve is well within the range given for the statistical mean recorded over many years (Krey *et al.*, 1978).

Food supply to the benthos

During recent years the importance of the phytoplankton spring bloom for benthic nutrition has been postulated (Hobro *et al.*, as cited by Jansson, 1978; Skjoldal and Lännergren, 1978; Walsh, 1981). Studies in the pelagic system of the Kiel Bight have demonstrated that large amounts of freshly produced matter during both spring and autumn bloom do not enter the pelagic food web but rather settle to the sea floor, representing up to 2/3 of the yearly input from the pelagic to the benthic system (Smetacek, 1980). The consequence of such a food input on the benthic system during spring was described by Graf *et al.* (1982).

During autumn 1981, the plankton population maintained a high ATP-biomass level from September to early November with peak values above 1.4 μg ATP l^{-1}. Phytoplankton growth was terminated by heavy storms followed by sedimentation of cells in late November (Figs. 2 and 3). At the beginning of the investigation period, the mixed phytoplankton population was dominated by the armoured dinoflagellates *Ceratium tripos* and *C. fusus*, whereas at the end diatoms became more important in terms of biomass. There was, however, no distinct separation of these populations, as recorded in 1973 (Smetacek, 1980).

From the integrated POC values of the water column, we presume that the autumn bloom started to settle at the end of October, and in fact, there was a significant increase of the protein content of the top centimeter of the sediment (Fig. 4). Unfortunately, no sediment trap data are available for this period as the trap was lost. During November there is a steady vertical flow of freshly produced cells to the sediment, as indicated by the high amount of chlorophyll *a* equivalents collected by the sediment trap and the low C:chlorophyll *a* ratios of the collected matter (< 100:1).

During mid November, high chlorophyll *a* concentrations in the water column concomitant with high primary production rates (Peinert, unpublished data) might be related to a nutrient release from the sediment following the first break (v. Bodungen, 1975). The storms at the end of November were followed by sedimentation of the entire phytoplankton population within 5 to 6 d (Fig. 3).

During the period of December 16 to March 2 sediment traps were not employed. The plankton standing stock was followed in terms of ATP-biomass. As depicted in Fig. 2, it was very low during this period.

The spring bloom in 1982 started in early March and was mainly composed of the diatom *Detonula confervacea* as in other years (Smetacek, 1975; Peinert *et al.*, 1982). During mid March it reached its maximum ATP-biomass (4 μg l^{-1}) and settled out of the water column within a few days shortly thereafter (Fig. 3). The amount of chlorophyll

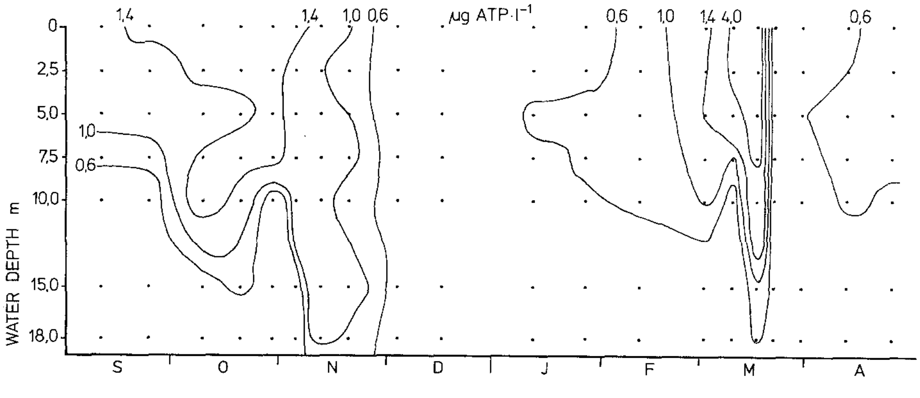

Fig. 2. Isopleth diagram of ATP-biomass in the water column, describing the biomass development of the autumn and spring plankton bloom

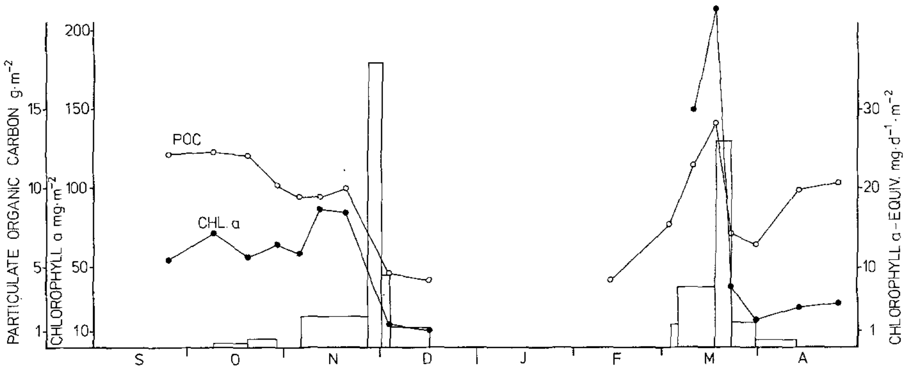

Fig. 3. Particulate organic carbon and chlorophyll *a* in the water column (integrated for 18 m) compared to sedimentation rate of particles collected by a bottom near sediment trap as analysed in terms of chlorophyll *a* equivalents. For the period Dec. 17 to Feb. 10 no values are available

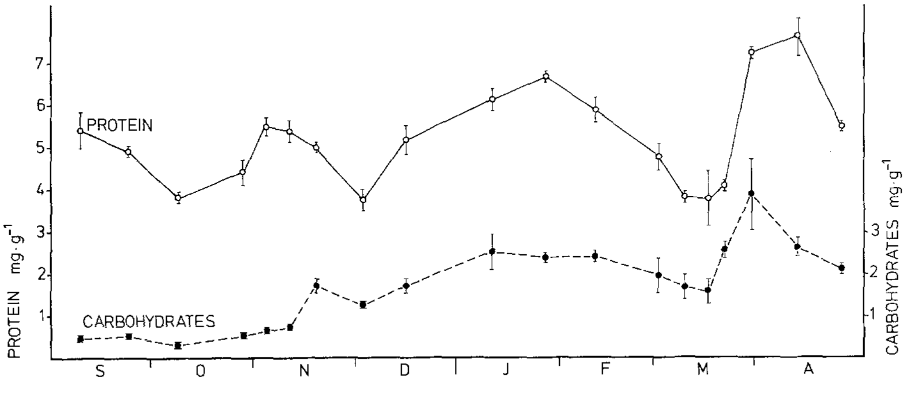

Fig. 4. Protein and carbohydrate concentration in the top centimeter of the sediment (according to Meyer-Reil, 1983, modified)

a equivalents collected by the trap suggest that there was a considerable loss of cells already during early to mid March, when the bloom was still growing vigorously. However, for technical reasons the trap covered the period from March 5 to 17. Compared to the increase of protein in the sediment (Fig. 4), it is most likely that the bulk of the trapped matter settled during the last days of this period. C:chlorophyll *a* ratios in the water column were also < 100:1. The carbon input of both blooms to the sediment, as determined by sediment traps, was in the range of 10–15 g C m^{-2}.

Earlier calculations for an annual budget of the year 1980 at the same station suggest that the vertical input of phytoplankton cells via sedimentation as determined by sediment traps only explains 15 to 25% of the observed activity (Graf *et al.*, 1982). The analysis of organic matter 1981/1982 (Meyer-Reil, 1983) enables a comparison of the results of the sediment trap with the measured net input to the sediment. From November 4 to 19 the organic matter content of the top centimeter of the sediment increased by 15.9 g C m^{-2}, assuming that the carbon content of organic matter is 50%. The carbon consumption during this period, as estimated by direct calorimetry (taken from Fig. 5), was 2.6 g C m^{-2}. During this period the trap only collected 4.8 g C m^{-2}, i.e. the sediment of our station collected four times as much as the trap in the top of the sediment. The ratio between the rate of organic matter accumulating in the top sediment layer plus the rate of organic matter which has been consumed by organisms and the rate of organic matter which sedimented in the sediment trap will be called the "advection factor".

The type of sediment trap used gives rather realistic values when used for budgetary calculations of the pelagic system (Peinert *et al.*, 1982). Thus, the observed discrepancy cannot, at least not exclusively, be explained by the sediment trap methodology. According to the topography of the investigation area, it is more likely that the organic matter was accumulated at our station by horizontal near-bottom transport down the slope. A corresponding calculation for the period March 10–30 revealed an advection factor of 7 to 8. The increase of freshly produced organic matter from the autumn bloom as well as from the spring bloom in the top centimeter of the sediment is also documented by increased protein and carbohydrate contents (Fig. 4).

These figures, however, also document some unexpected events which partly represent other sources of food supply. (1) The protein level still present at the end of the anoxic period is in the same range as found after the input from a plankton bloom; it decreases rapidly after the first breakup of anoxic conditions. Contrary to this, carbohydrates were found to be at a very low level. (2) According to Smetacek and Henrikson (1979), a bloom of armoured dinoflagellates increases carbohydrates in relation to protein in the water column because of their cellulose armour. During October, in terms of concentration of carbohydrates, no such record is to be seen in the sediment. However, as described by Meyer-Reil (1983),

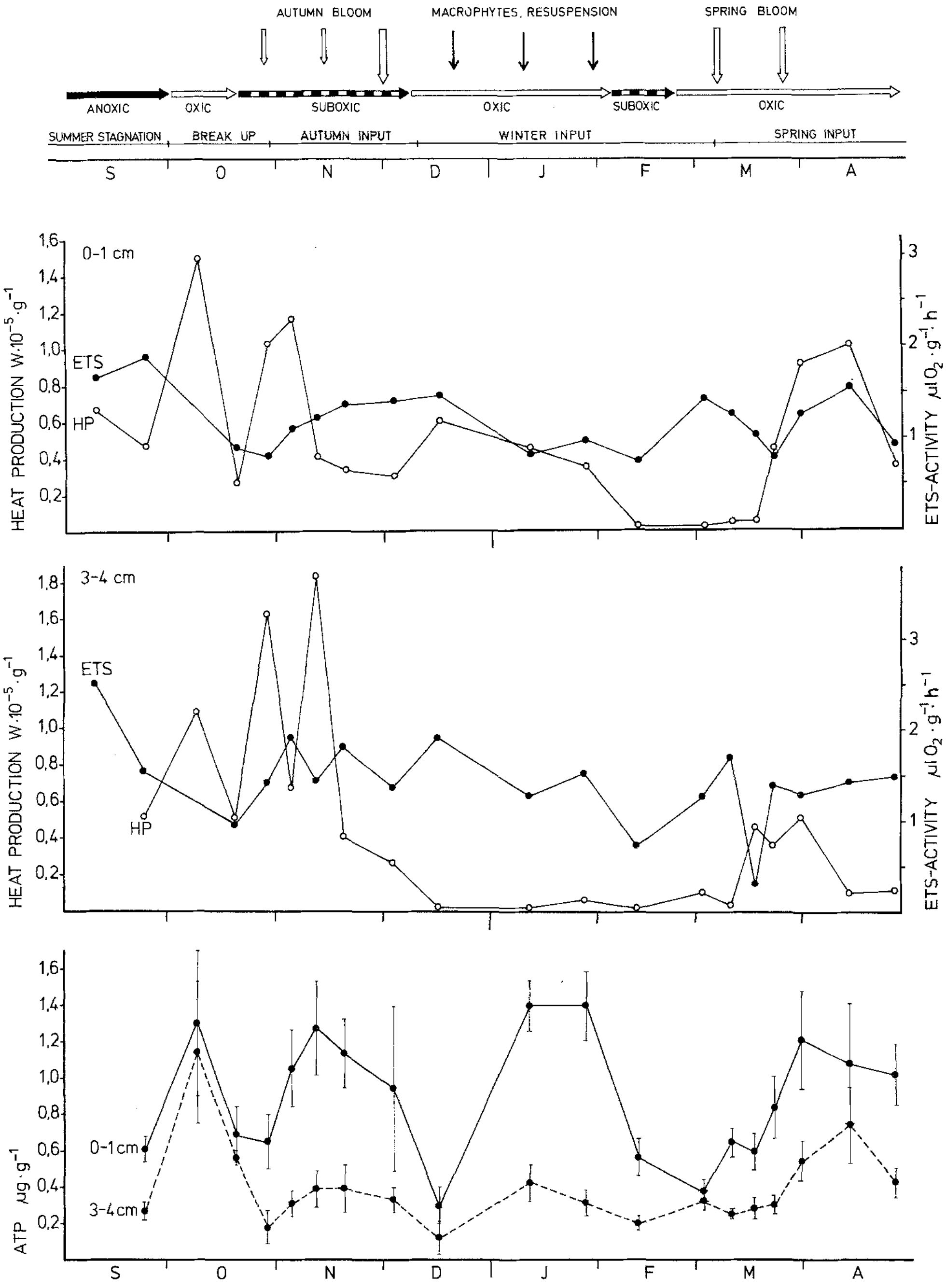

Fig. 5. The scheme at the top of the figure demonstrates the periods as defined according to physical conditions and the sedimentation events. The curves below give activity of the sediment in terms of heat production (HP) and the activity of the electron transport system (ETS) and ATP-biomass in two different strata of the sediment

an increase of α-amylase activity could be observed. (3) The most surprising finding, however, is the continuous increase of protein and carbohydrates during December and January. The processes leading to this accumulation have been summarized by Graf *et al.* (1983): the resuspension of organic particles in the deeper parts of the channel system and their redeposition in the shallower areas, and the near bottom transport of macrophytes that are torn off and macerated during these months (Schomann, 1977), documented by the high chlorophyll *a* concentrations in the sediment during late January (up to 4.7 μg cm^{-3}), a range that is only found after an input of freshly produced phytoplankton (Schulz, 1983). The input of macrophyte debris would also explain the high concentration of carbohydrates that is present in spring. This is most likely due to resistant, structural carbohydrates. The protein level, however, during early March is as low as during early October and early December.

Defining the relevant periods

For a further presentation of the results and discussion it seems useful to define certain periods within the entire 8-month period observed, based on the changing physical environment and the food supply of the benthos. We do not know for how long the anoxic conditions had prevailed before the program was started. Thus, for the first period, called "summer stagnation" only the end between September 23 and October 8 was recorded. For budgetary calculations, we will assume October 1 as the end of the anoxic period (Fig. 5). The second period, the "breakup", was terminated by the commencement of sedimentation of the autumn bloom on October 28. This date takes into consideration the fact that the suboxic conditions from October 19 to 28 were not a result of the settling bloom. The third period "autumn input" is characterized by the input of the autumn bloom onto a suboxic sediment. The same storm event terminated phytoplankton growth in the water column and with a delay in time the suboxic conditions in the sediment by a lateral inflow of colder water. This exchange of water masses caused strong resuspension and as demonstrated by Meyer-Reil (1983) changed the composition of the benthic community. For the calculations, the end of "autumn input" was fixed as December 10.

The following two periods are characterized by the type of food supply. The "winter input" period was fixed until March 6, followed by the "spring input" period. Both periods represent a food input at low water temperature. These five periods will be used to describe benthic energy flow, the concomitant biomass production, and the consumption of organic matter by the sediment community.

Benthic response

The characteristics of the periods defined above suggest that very different types of metabolism are involved and they are of varying importance during the successive periods. While "summer stagnation" might have been dominated by sulfate respiration and fermentation processes, the "breakup" may have aerobic metabolism and the "autumn input" a mixture of both types of metabolism in addition to nitrate respiration. Under these conditions, direct calorimetry is the most reliable method to estimate total benthic community metabolism, because it is a direct measure of energy flow through the system (Pamatmat, 1982).

The benthic response in terms of heat production in the top sediment layer is given in Fig. 5. In the top centimeter, there is a strong response to the "breakup", increasing heat production by a factor of 3. During this period there is a significant loss of protein (folin positive matter) in the sediment (Fig. 4), suggesting that it was consumed. From a microbiological point of view, there is no reason why bacteria should not be able to decompose protein under anoxic conditions (Fenchel and Blackburn, 1979). The high concentrations found, however, suggest that it was not available to them. Meyer-Reil (1983) reported a strong decrease of the activity of proteolytic enzymes in anoxic sediments. Thus, the stored protein food became available during the "breakup" when the anoxic situation terminated. The fast decomposition of large amounts of protein probably significantly contributed to the following buildup of suboxic conditions by oxygen consumption.

A second response is caused by the sedimentation of the autumn bloom. However, although there was a steady sedimentation of fresh, undecomposed matter throughout November, heat production already decreased on November 11 and stayed at this low level thereafter until mid December.

A less obvious response is found during "winter input". However, considering that a part of benthic metabolism is dependent on temperature, there is still a considerable and long lasting heat production during this period, and this even caused a decrease of the redox potential (Fig. 1). Such high levels of benthic activity during winter were also found by Hargrave (1973) in Saint Margaretes Bay, where macrophytes represent a major part of the food supply (Webster *et al.*, 1975).

During early March, heat production was at the lower detection limit, but increased drastically after March 17, indicating that the bulk of the settling spring bloom arrived during the second half of March. In contrast to spring 1980, when activity lasted at least until mid May (Graf *et al.*, 1982), benthic activity following the 1982 sedimentation event decreased as early as late April.

Developments in the sediment horizon 3 to 4 cm were very different. This deeper layer was anoxic until December 3 (Fig. 1). Thus, we do not know which mechanism caused the heat production response to the "breakup" (Fig. 5) and which reasons may explain the fluctuations during "autumn input". The possible role of bioturbation was of minor importance as will be discussed later. The final break of suboxic conditions in early December caused a drastic decrease of heat production, which remained at a low level throughout the winter. The response of the deeper sediment layer to the spring bloom sedimentation is less distinct than in the top centimeter. Surprisingly, however, the response seems to start 5 d earlier than at the sediment surface and this cannot be explained. The low ETS-activity simultaneously observed on March 17 indicates that fermentation was of importance as will be discussed later. The measurement of ETS-activity based on INT reduction comprises several types of respiration chains (cf. Tabor and Neihof, 1982). Besides O_2-respiration, the method positively responds to nitrate respiration (Packard *et al.*, 1983) and most likely to sulphate respiration (Bengtsson, 1982). During this program, however, the method turned out not to be very informative. Two factors strongly influencing *in-situ* activity, namely food limitation and low temperature, are optimised or kept constant in the enzyme reaction. Thus, only potential activity is given. The high ETS-activity found during "summer stagnation" obviously indicates the importance of sulfate respiration (Fig. 5). In the top centimeter of the sediment (Fig. 5), there is only a slight response in ETS-activity to "autumn input" and to the preceding changes in the physical environment and to "spring input". No response is to be seen of "winter input" and the low activity during the end of this period.

Benthic biomass excluding macrofauna was determined by ATP-measurements. The ATP-concentration comprises the biomass of bacteria, protozoa (especially ciliates, flagellates, and foraminifera), meiofauna, and temporary meiofauna. As shown in Fig. 5, there is a good agreement between the development of the ATP-biomass with the defined periods given. The consumption of stored food during the "breakup", as well as the three following external supplies of organic matter, elicit immediate response by an increase in ATP-biomass.

Changes in the physical environment as indicated by redox potential was one factor explaining the decrease of ATP-biomass at the end of the periods "breakup", "autumn input", and "winter input". The concomitant minima of protein concentration in the sediment, however, also suggest that food limitation might have been of importance and that organic matter, including attached organisms, were resuspended.

The deeper sediment horizon (3 to 4 cm) showed a corresponding biomass pattern (Fig. 5). The effects, however, are found to be less pronounced, especially during "autumn input" and "winter input".

The ratio of heat production:ATP reflects ATP-turnover. Pamatmat *et al.* (1981) demonstrated that the heat loss and ATP-turnover of a bacteria culture is most pronounced during exponential growth, but can be significantly reduced during steady state conditions. A corresponding explanation may be given for the shape of the curve in Fig. 6. In the top centimeter of the sediment, every increase in ATP-biomass (Fig. 5) is accompanied or preceded by an increase in ATP-turnover. Thus, it is likely that the high ratio of 11.0×10^3 W mol^{-1} found on December 16 indicates that the population responsible for the high ATP-biomass during January had already started to grow, although biomass itself is still rather low. For this type of process, periods between sampling were too long.

The high ratios of heat production:ATP found in the deeper sediment horizon during the anoxic period indicate a faster turnover of ATP under these conditions. Especially such extreme ratios of 43.6×10^3 and 26.0×10^3 W mol^{-1} as found in October and November have otherwise only been reported from the exponential growth phase of an obligate anaerobic bacteria culture (Pamatmat *et al.*, 1981).

Type of metabolism

As already discussed, direct calorimetry measures all types of metabolism, but it also includes the activity of exoenzymes and the heat release of chemical oxidation. The latter two components, however, are thought to be of minor importance for the heat loss of the sediments (Pamatmat, 1982; Bengtsson, 1982).

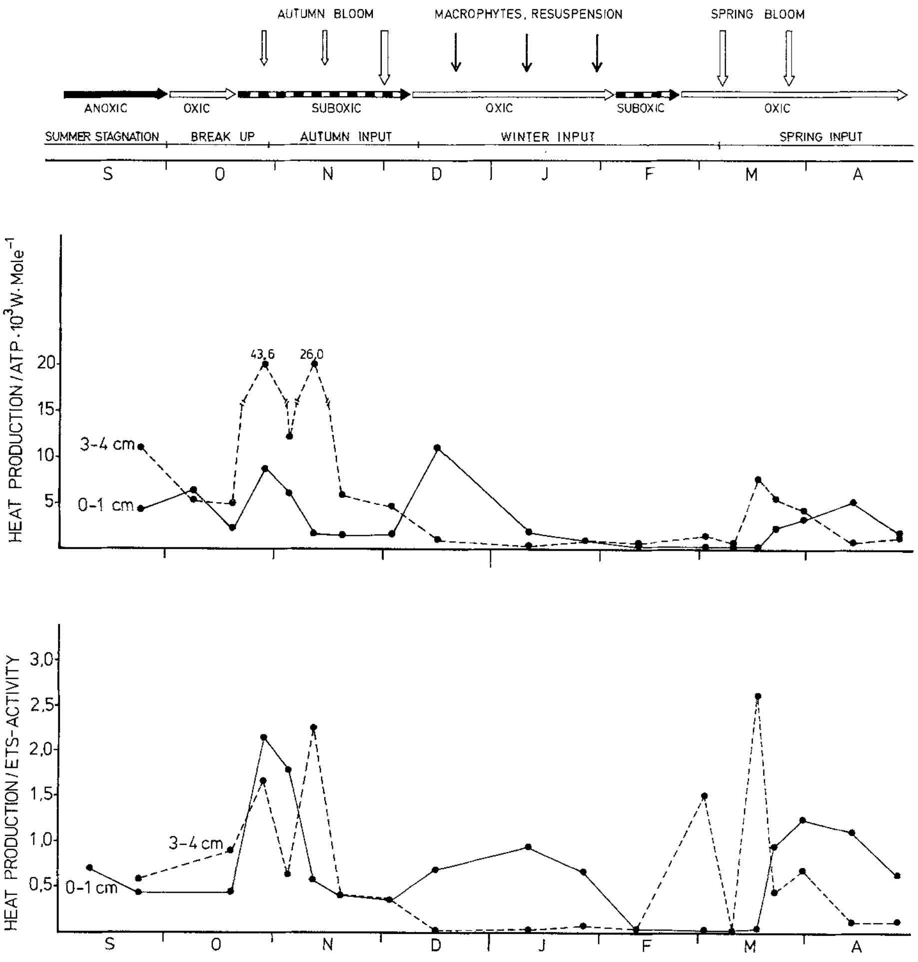

Fig. 6. The ratio heat production:ATP, reflecting ATP-turnover and the ratio heat production:ETS-activity, describing the type of metabolism calculated for the two sediment strata. An increase in the latter indicates an increasing importance of anaerobic metabolism, especially of the fermentation processes

The difference between the activity as determined by direct calorimetry and ETS-activity, which describes the activity of respiration chains, should thus mainly indicate substrate phosphorilation, i.e. fermentation processes. ETS-activity, however, is only a potential measure and it is not possible to calculate an absolute amount of fermentation. Therefore, it was preferred to establish the quotient heat production:ETS-activity as a qualitative indicator for changes in the type of metabolism (Pamatmat *et al.*, 1981). This calculation employs a conversion of ETS-activity into heat using the Ivlev coefficient (Ivlev, 1934).

In the top centimeter of the sediment, the three "external" food supplies during "autumn input", "winter input", and "spring input" were accompanied by a shift in the type of metabolism towards fermentation (Fig. 6). This change is especially pronounced during the suboxic period of the "autumn input". Unfortunately, ETS-activity was not measured on October 8 and it is unknown whether such a shift also occurred when the "internal" food store was used during "breakup".

For the deeper sediment horizon (3 to 4 cm), no values for the organic content are available. Therefore, it is not known whether the food supply influenced changes in the type of metabolism, as evident from Fig. 6, for the periods "autumn input" and "spring input". During "winter input" there was no response to the food supply of the sediment surface and it is not clear which process influenced the shift to fermentation on March 2 and 17. From the results obtained by the sediment traps and the protein content of the sediment surface, it is very unlikely that there was any connection with the spring bloom.

Considerations for a budget

In marine sediments the bulk of available food is consumed by microorganisms and meiofauna, whereas macrofauna is quantitatively less important (Kuipers *et al.*, 1981; Kemp and Boynton, 1981). The role of the macrofauna is a more indirect one. By stimulating activity of smaller organisms, i.e. by grazing and bioturbation, it controls how much organic matter is incorporated into the sediment, and how deep significant decomposition of organic matter occurs (Yingst and Rhoads, 1980).

Our program started during an anoxic period, which considerably diminished the individual number of macrofauna, especially the infauna polychaetes *Pectinaria koreni* and *Nephtys ciliata*, which are mainly responsible for bioturbation in the study site. Only a few individuals of *Astarte* sp. and *Arctica islandica* survived. A quantitative faunistic appraisal will be given elsewhere.

The 18-m station was situated at the upper limit of the anoxic area. By the end of September the cumacean crustacean *Diastylis rathkei* had recolonized the area, indicating that at least the sediment surface was free of hydrogen sulfide. During early November, small individuals of *Pectinaria koreni* (1–2 cm length) were found. In the course of the winter, other species settled at the station, most likely from shallower areas, e.g. *Nephtys ciliata.* During spring, the composition of macrofauna was still very different from that in other years (cf. Arntz, 1978). The low individual numbers, comprised largely of small molluscs, and the smaller size of the individuals present, support the finding of Arntz (1981), who described the development of macrofauna after anoxic periods.

From the results presented thus far, it appears that the low response of the deeper sediment layers during "autumn input" and "winter input" is due to the reduced effect of bioturbation. During "spring input", bioturbation already reached the 3- to 4-cm horizon. Differences in the type of macrofauna also represents one reason for the higher advection factor of particulate organic matter in the sediment from the spring bloom (advection factor 7–8), when compared to the atumn bloom (4).

The strong response of the deeper sediment layer during "breakup" is very surprising and can hardly be explained by bioturbation. One possible explanation is that this horizon had become temporarily oxic during the period September 23 to October 8. As a consequence, for budget calculations, different sediment depths have to be considered for the different periods (Table 1). During the anoxic period, the consumption of organic matter is 0.8 g C m^{-2} d^{-1}, demonstrating that under these conditions a considerable amount of organic matter can also be consumed. However, it is less than half of the value given for August 1980 under oxic conditions in summer (Graf *et al.*, 1982).

During "breakup", a very high daily carbon need of 1.4 g C m^{-2} d^{-1} was found. This is as high as during "spring input". Thus it is likely that the decrease of protein content in the sediment is caused by the consumption of stored organic matter. If the stored food had mainly consisted of protein, the conversion factor of carbon into heat release should have been changed. However, as already discussed, the protein analysis is not very specific (cf. Meyer-Reil, 1983) and we preferred not to change the conversion factor.

As stated previously, the food supply of deeper sediment layers was only influenced by bioturbation to a minor extent. Thus it is difficult to decide, whether the observed response during "breakup" and the high activity at the beginning of "autumn input" in the 3- to 4-cm layer is based on stored organic matter, or if there are any transport mechanisms supplying the deeper layers.

Figure 6 demonstrates the shift towards fermentation processes during periods of external food supply. Thus energy rich end products should enter the interstitial water and may be transported to deeper sediment layers by diffusion and bioturbation effects of meiofauna and the remaining macrofauna. The relevance of short-chained fatty acids and their enhanced turnover in marine sediments has recently been demonstrated by Christensen and Blackburn (1982).

The problems discussed above complicate a comparison of food supply and consumption during "autumn

Table 1. Budget for the periods defined in Fig. 5 based on direct calorimetry

	Sediment depth cm	Energy flow KJ m^{-2}	Carbon flow gC m^{-2}	Daily energy flow KJ m^{-2} d^{-1}	Daily carbon flow gC m^{-2} d^{-1}
Summer stagnation 9. 9.–1. 10. 81	5	7	16.8	32	0.8
Breakup 2.10.–27. 10. 81	5	1 411	35.3	54	1.4
Autumn input	2	589	14.7	13	0.3
28.10.–10. 12. 81	5	1 700	42.5	38	0.9
Winter input 11.12.–6. 3. 82	2	588	14.7	7	0.2
Spring input 7.3.–26. 4. 82	4	2 817	70.4	55	1.4

The top two centimeters were calculated with the upper sediment layer (0–1 cm) and the deeper sediment layers with the 3- to 4-cm layer. For the conversion of Joule into C it was assumed that 1 g C is equivalent to 40 KJ

input". Therefore, two alternatives were calculated (Table 1). Although the consumption of 42.5 g C m^{-2} estimated for 5-cm sediment depth fits very well with the trapped input of 10–15 g C m^{-2} and an advection factor of 4, it is more likely that this fit occurred merely by chance. The sudden decrease of protein from November 19 to December 3, which is not accompanied by comparable levels of heat production, indicates that the sediment lost a considerable amount of organic matter, possibly by horizontal transport due to resuspension during the stormy period in late November.

Thus, it can be stated that the input of the autumn bloom is not completely consumed rapidly. This was also concluded by Smetacek and Hendrikson (1979) from the analysis of particulate organic matter from the water column during autumn and winter, which, in terms of chemical composition, remained similar to freshly produced phytoplankton.

The increase in protein (folin positive matter) and carbohydrates during December and January can thus also be an effect of resuspended matter still derived from the autumn bloom. However, it is not possible to separate this part of accumulation from the input of macrophytes.

Although there is a small maximum in heat production during winter, total consumption of organic matter is only 14.7 g C m^{-2}. This amount is not sufficient to explain the decrease of organic matter from January 27 to March 10, which was in the range of 54 g C m^{-2} (Meyer-Reil, 1983). Again physical processes such as resuspension and erosion must have been involved. A corresponding loss of organic matter was described by Graf *et al.* (1983) for a 10-m station at the same slope.

During spring, the latter processes are less important and thus the budget for "spring input" fits very well. 70.4 g C m^{-2} corresponds to an input of 10 to 15 g C m^{-2} and an advection factor of 7–8. The spring bloom was consumed within 5–6 wk and the decreasing activity at the end of the period was caused by declining food supply.

General conclusions

The extraordinary position of the 18- to 20-m zone within the channel system of the Kiel Bight was already pinpointed by Arntz (1978), who demonstrated that highest diversity and biomass production of macrofauna is to be found in this zone and who thought that this zone is of utmost importance for the food supply of demersal fish. On artificial substrate raised above the sediment level, macrofauna was able to produce as much as 600 g fresh weight m^{-2} yr^{-1} (Arntz and Rumohr, 1982). Graf *et al.* (1982) estimated the consumption of organic matter at a 20-m station to be 405 g C m^{-2} yr^{-1} under the assumption that no anoxic period occurs and that the macrofauna population is dominated by *Pectinaria koreni.* The peculiarities of the physical environment and the reduced role of macrofauna during the study period explain the lower carbon consumption during the period from September 1981 to April 1982. However, the advection factors observed sufficiently underline the favourable situation of the study site compared to other areas in the Western Kiel Bight. This preference might even be more improved, when an intact macrofauna population, which is able to diminish the loss of sedimentary organic matter by erosion, and resuspension, and by vertical transport into deeper sediment strata, is present.

In spite of the abundant food supply, there are still strong indications that benthic activity is food limited. This is demonstrated by the consistent pattern of food input and activity as determined by direct calorimetry and by the budget for the spring bloom. The similar minima of protein on October 8, December 3, and March 17 suggest that they represent the lower limit of available protein. Because of the unspecific analysis, the bulk of the remaining protein (folin positive matter) is represented by humic acids. Although there is a high level of carbohydrates present during the last protein minimum, benthic activity in terms of heat production is nearly zero. The latter finding would strongly support the hypothesis of Hargrave (1980) and Hanson (1982) that benthic activity and microbial decomposition of detritus is limited by nitrogen supply. However, as already discussed, the remaining carbohydrates are difficult to decompose because of their macrophyte origin. Thus, we can only postulate the limitation of available food as a controlling factor of benthos.

Physical and biological processes in the shallow water ecosystem of the Kiel Bight turned out to proceed on the same time scales. At certain periods of the year, the processes are so quick that they have to be followed within days. Directly coupled to the weather conditions, processes such as sedimentation, accumulation, and inflow of oxygen rich water happen within few days and are immediately responded to by the biological component of the system without any time delay. Especially during autumn and winter, physical processes dominate the system. The food limitation during early December and early March discussed above is due much more to resuspension than to biological activity. One might speculate that there are areas, most likely in the deeper parts of the channel system, where no food limitation exists and where no zero activity occurs during winter.

The benthic response also includes a significant increase of ATP-biomass. This biomass is a storage for essential elements and in combination with fermentation end products it will lead to a delayed nutrient release from the sediment to the water column as was also suggested by Pollehne (1981).

As late as spring 1982, the benthic community was still being influenced by processes that took place in autumn 1981, indicating that the system has a historical aspect. Considering the coupling to weather and regional hydrography, it is easy to imagine how variable these processes may be. The input of the autumn bloom and of the macrophytes during winter will vary within 6 to 8 wk from year to year, whereas the input of the spring bloom is a more regular event and settles during mid March to mid April. Benthic response to the autumn and winter input might also be very different from the one described above. Whether a settling autumn bloom can be completely consumed by a well established benthic community remains to be seen. Under oxic conditions it is most likely. The minimum activity found during the period before the spring bloom input was 0.03×10^{-5} W g^{-1} in 1982, but 0.3×10^{-5} W g^{-1} in 1980 (Graf *et al.,* 1982). In the spring periods analysed thus far, the input of freshly produced phytoplankton cells turned out to be a trigger for benthic activity, however, the starting level each year was very different. This variability will represent one reason for the completely opposite shift in the type of metabolism, from anaerobic to aerobic, found in spring 1980 (Graf *et al.,* 1982). Another reason is obviously given by the different type of macrofauna in 1980, which will have caused a much more extensive bioturbation especially caused by the very abundant polychaete *Pectinaria koreni.* However, as we do not know the history of the benthic community of spring 1980, this is only speculation. The problem encountered is that the benthic community is influenced by several years' cycles and that it is very difficult to set a zero point for an annual cycle in the Western Kiel Bight. This was already stated by Arntz (1981) for macrofauna.

The present investigation started during an anoxic period, which, during 1981, was obviously longer than in other years. It remains a matter of controversy whether this is due to the cumulative effect of increasing eutrophication or has a natural cause in unusual hydrography. This is not the place to enter this discussion. The processes described in this paper, however, are of relevance for further eutrophication studies.

The food supplies during winter, spring and most likely during autumn led in 1981/1982 to a temporary decrease of redox potential, indicating an oxygen debt. This has already been postulated by Pamatmat (1977) and Hargrave (1980). In an oxidized sediment, this debt is resolved rapidly and even an advection factor of 7–8, as found in spring 1982, decreased the redox potential only temporarily.

The critical point of such a system is therefore the time interval between the major sedimentation events. The variability of the processes during autumn and winter discussed here can lead to the following hypothetical pattern of processes. The oxygen debt caused by the winter input of macrophyte debris is not yet compensated when the spring bloom comes in. Thus, the spring bloom is burned less efficiently and when the water column becomes stratified during summer there will still be available food and an uncompensated oxygen debt. Such a pattern would strongly increase the probability of an anoxic period during summer.

An anoxic period that results in an incomplete consumption of the following autumn bloom will increase the probability of an anoxic period in the following year, because it increases the starting level of benthic activity and the amount of available food during the next spring. This effect, however, is partly compensated for by the disturbed macrofauna and the concomitantly reduced activity of the community. In summary it can be stated that it is possible to analyse relevant ecological processes and to estimate energy flow in benthos on a community level. This holistic approach to ecosystem analysis can, however, be significantly strengthened if combined with analyses at more specific levels. This has been demonstrated by the work of Meyer-Reil (1983), who analysed the bacterial component of the community simultaneously with this investigation.

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