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Studies on the role of benthic animals of the Western Baltic in the flow of energy and organic material*

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Abstract

Some of the benthos studies carried out by working groups of the Institut für Meereskunde and the Joint Research Programme „Interaction Sea – Sea Bottom“ of Kiel University are briefly reviewed. As an introduction, main structural features of the large-scale pattern of macrozoobenthos of the Western Baltic are discussed in connection with the governing environmental factors (sediment type, temperature, salinity, discontinuity layer, seasonal O₂-deficiency and H₂S). Sedimentation of primary production and its fluctuations considerably affect benthic activity. In addition, locally reduced competition leads to high production rates, established from observations on population dynamics of single species. Trophic relations of important macroinvertebrates throw light on the position of the macrobenthos within the whole system. Experimental studies *in situ* and in the laboratory contribute to the analysis of processes involved in the functioning of the ecosystem and its subunits.

Introduction

Research on marine benthos has a long tradition in the Western Baltic. For literature consult: GRIMPE and WAGLER (1928–1960), SEGERSTRÅLE (1957), REMANE (1958). A short introduction was presented by THEEDE (1974). As predecessors for the present zoological benthology the faunistic work of MEYER and MÖBIUS (1865–72), MÖBIUS (1871), and BRANDT (1897) in the last century as well as the establishment of bottom communities by PETERSEN (1914, 1918) may be mentioned. In the twenties and thirties HAGMEIER (1930) and HERTLING (1928) studied benthos mainly under the aspect of its value as fish food, as PETERSEN (1914) had done already. REMANE (1933, 1940) and some of his famous pupils introduced an era of meiobenthos research (see REMANE 1958, AX 1960, GERLACH 1971, NOODT 1974). SCHLIEPER was a pioneer in the study of ecophysiological adaptations to the environmental conditions of the Baltic (SCHLIEPER 1958, 1972, SCHLIEPER and THEEDE 1975, THEEDE 1978).

In the last decade benthos research mainly developed as an interdisciplinary science, performed within working teams, taking into account both the different traditional biological disciplines and hydrographic, chemical and geological aspects (HEMPEL 1975, LUTZE 1974, ZEITZSCHEL and DAVIES 1978; collection of literature: MÖLLER 1980). Preliminary rough ecosystem models, which were advanced earlier for the pelagic system, gave a type of frame to channel the different activities in benthos research (cf. JANSSON 1972, ELMGREN 1978).

The rough picture of the features of zoobenthos of the Western Baltic I want to draw results mainly from work carried out by teams of the Institut für Meereskunde and the „Joint Research Programme SFB 95“ including scientists from different institutes.

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General aspects of macrozoobenthos in Kiel Bight

A characteristic of Kiel Bight is its instability in comparison with the Baltic proper or the depths of the Kattegat/Skagerrak (see SCHWENKE 1974). This is mainly because of its transitory position between these seas. It concerns both hydrographic conditions and the composition of the fauna.

The relatively shallow area of about 10–25 m in depth is cut across by trenches down to about 35 m. The grain size of sediment decreases from the shallow to the deeper parts, where at the bottom mud prevails, often containing H_2S . Above the discontinuity layer the low salinity shows considerable irregular changes, the temperature pronounced seasonal fluctuations. Below the thermohaline stratification layer both these factors are more stable. Mainly in summer and autumn the stratification layer, which may have stabilizid in a depth of about 15 – 20 m, inhibits vertical exchange of water, as a consequence of which oxygen deficiency and formation of H_2S will occur.

The large-scale pattern of macrozoobenthos distribution in Kiel Bight is relatively well known (KÜHLMORGEN-HILLE 1963, ARNTZ 1971, 1978a, 1978b). Altogether the number of species is reduced because of the lower salinity. More than 150 macrofauna species may be found; most of them belong to polychaetes, crustacea and molluscs.

Considering the trenches, e.g. Vejsnäs Rinne, a trench which penetrates into the Bight of Eckernförde, the following features may be observed with increasing depth (Fig. 1): As already mentioned, the sediment becomes more soft. In the area without phytal, there is an increase in number of species, abundance, biomass and diversity of macrofauna from the shallow to the deeper parts of about 20 m. These highest values at a depth of about 20 m are found in an area of highest probability of occurrence of the thermohaline stratification layer (ARNTZ 1978b). There a great impact of food by sedimentation from the upper parts of the water column is found.

Fig. 2 demonstrates the situation schematically: The region with the optimal settlement in about 15–20 m depth is an area with convenient sediment, relatively high and stable salinity, stable temperature, good oxygen conditions and good food

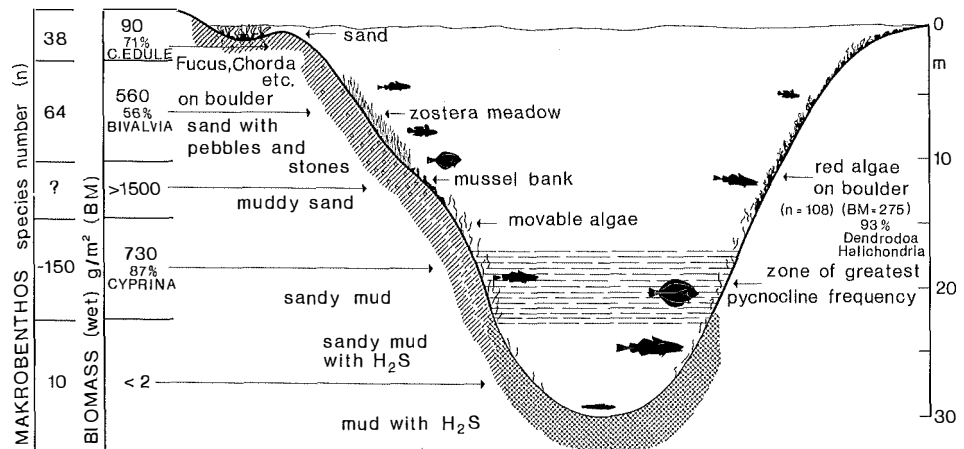


Figure 1

Number of species, biomass and zonation of macrozoobenthos in trenches of Kiel Bight. (After ARNTZ 1978 b)

conditions. Above that region, low salinity as well as temperature and salinity fluctuations reduce settlement, whereas on the bottom of the trenches O_2 -deficiency and H_2S limit distribution.

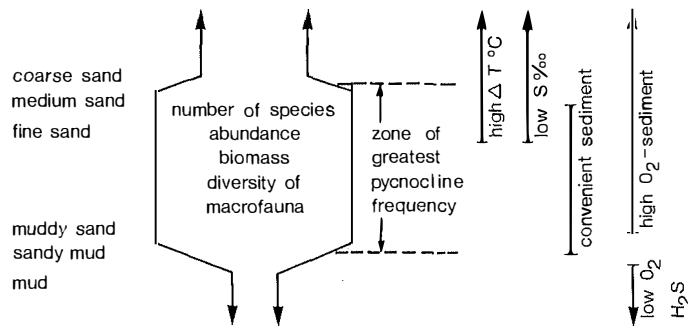


Figure 2

Diagram of the most significant environmental factors and the zonation of benthos in Kiel Bight (After ARNTZ 1978 b, modified)

Altogether the shallow area is inhabited by more euryhaline and eurythermal species of a *Macoma balthica* community; below the thermohaline stratification layer more stenohaline and stenothermal organisms occur, which are typical for an *Abra alba* community (ARNTZ 1978a, b).

Considering the long-term dynamics of the main species ARNTZ found different types:

1. species with long lifespan and relative long-term stability (*Cyprina*, *Astarte*, *Nephtys*),
2. species with regular seasonal fluctuations (*Diastylis*),
3. species with irregular seasonal fluctuations (*Abra*, *Terebellides*).

These types of fluctuations are observed in the northern part of Kiel Bight.

In the southern part of Kiel Bight rather stronger variations in the abundance and biomass of all species are observed. Often breakdowns of the fauna occur as a consequence of O_2 -deficiency and H_2S (mostly at the end of summer). All species, both those with a long lifespan (such as *Cyprina*) and those with more regular seasonal and irregular seasonal variations show stronger fluctuations. After a period of severe oxygen deficiency, a preliminary settlement by opportunistic species like *Capitella capitata* takes place (KÖLMEL, 1979, ARNTZ 1978a). Later crustacea, polychaetes and molluscs follow, in most cases in this order. This has been clearly demonstrated by observations in containers with artificial sediments (ARNTZ, pers. comm.).

Depending on strength and duration of O_2 -deficiency and H_2S -influence, a different age- and size-structure of the bottom fauna is found in different years.

Some trophic relations

From the primary producers, which stand at the beginning of the food cycle, the matter is passed on in food chains of varying lengths. Under the aspect of the same end consumer, e.g. cod, the food chain may vary from 2 to 5 steps (ARNTZ 1978a). The two most important macrobenthos feeders in the deeper parts of Kiel Bight, cod (*Gadus morhua*) and dab (*Limanda limanda*), provide more than 90 % of the commercial fish in

this area. In addition, whiting, plaice and flounder make up over 2% of the fish biomass. These demersal fish up to a size of 35 cm take up over 80 % of their food from macrobenthos. The Van Veen grabs at the locality Millionenviertel in the Western Baltic Sea contain primarily molluscs and polychaetes. The fish select relatively more crustacea (*Diastylis*) and polychaetes (*Harmothoe*, *Nephtys*) (ARNTZ 1978a).

A similarly important role to that of cod on the bottom is played by herring and sprat in the pelagic zone, the last two as important consumers of zooplankton.

Concerning quantitative relations I will restrict myself to some basic remarks (Fig. 3) because many details dealing with the lower part of the benthic food web have been presented in the present symposium volume. It was suggested by planktologists (e.g. v. BRÖCKEL, 1978) that roughly 60 % of the relatively high primary production of phytoplankton may reach the sea floor at the deeper parts of Kiel Bight. By this sedimentation the benthic food web in this area may have between $100 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (v. BRÖCKEL 1978) and $50\text{--}65 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (SMETACEK 1980) at its disposal. In addition it receives unknown amounts of particulate matter from other sources (benthic primary production, terrigenous input, influx from other areas).

One part of the material deposited is taken up directly by macrobenthos, another relatively great share is processed by bacteria and other microorganisms. The daily microbial biomass production in summer in shallow areas of Kiel Fjord ranged in the order of magnitude of meiofauna C-content (RHEINHEIMER 1981). Thus microbial production seems high enough to potentially feed a great part of meiofauna. There were estimations that about 70 % of the food of meiofauna might be delivered by microbial production (MEYER-REIL et al. 1980). However, the various groups of meiofauna participate quite differently in the use of this organic material. Oligochaetes and turbellarians seem to take up more of this microbial organic matter than do nematodes, harpacticoids and ostracods (FAUBEL and MEYER-REIL 1980). However, in the deeper parts particularly nematodes form the main portion of meiofauna biomass, with individual numbers of some 100 000 specimen per m^2 (SCHEIBEL 1976).

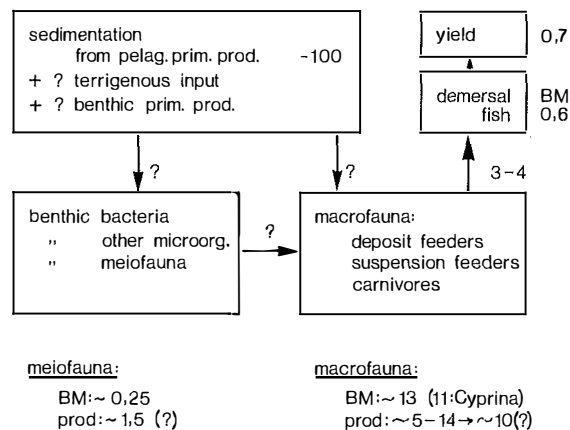


Figure 3

Simplified diagram of the role of benthic macrobenthos of the Kiel Bight in the flow of organic matter. Production figures are presented as annual mean $\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, biomass figures in $\text{g C} \cdot \text{m}^{-2}$. (After ARNTZ 1978 a, modified)

Biomass values of meiofauna are in the magnitude of about $0.25 \text{ g C} \cdot \text{m}^{-2}$ in the deeper parts of Kiel Bight. In comparison, macrobenthos biomass is about $13 \text{ g C} \cdot \text{m}^{-2}$, 11 g of which (according to ARNTZ) are formed by *Cyprina*, 2 g by molluscs, polychaetes and crustacea. Locally higher biomass values may be found.

If we consider relations between meiofauna and macrofauna, we find that details on the extent to which macrofauna feeds on meiobenthos are not available. There is a great lack of information regarding the exact connection between macrobenthos and the lower links in the food web. The production of meiobenthos was estimated by ARNTZ (1978a) to be in the magnitude of $1.5 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, that of the macrofauna between $5 - 14 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, simplified: about 10 g C . About $3 - 4 \text{ g C}$ are estimated to be consumed by demersal fish. The fish yield of demersal fish is found to be about 0.7 g C . In relation to food intake the yield of demersal fish was estimated to be about 20 %.

Among the sublittoral phytal areas of the Western Baltic the *Fucus* belt is poorest in epibenthic species whereas the red algae zone shows the greatest variety (LÜTHJE 1978). Here 109 species were found, 68 of them genuine inhabitants of the phytal zone. Greatest individual numbers were found of the tunicate *Dendrodoa grossularia*. Its share in biomass represented about three quarters. Sponges represent about 15 % of epifauna biomass. Among the endofauna, bivalves (e.g. *Astarte* species) represent more than 90 % of biomass. Most species belong to molluscs, crustaceans and polychaetes. Altogether diversities of macrobenthos are higher in shallow phytal areas than in the depths or in the middle of the Baltic. Biomass values are not higher. A minimum production of utilizable food of $71 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ was estimated. This is within the order of magnitude calculated for the deeper areas of Kiel Bight too. The carnivores of the red algal phytal are represented mainly by *Asterias* (NAUEN 1978). It is suggested that a strong predation from outside the system, presumably by fish, takes place. Analyses of cod and whiting stomachs have indicated that in the red algal zone crustaceans (particularly amphipods and isopods) are preferred to polychaetes and molluscs (ZARKESCHWARI 1978).

Analysis of processes within the ecosystem

Experimental studies have sought to contribute to the analysis of processes involved in the function of ecosystems. The procedure for this was to study such processes at the sea bottom (e.g. gas exchange; transport, uptake and release of inorganic nutrients or dissolved organic compounds) *in situ* within isolated enclosures, e.g. in flexible polyethylene bags. These devices are installed by divers in the study area (SCHRAMM and MARTENS 1976, ZEITZSCHEL and DAVIES 1978). In order to analyse the functional relations between different components, such as macrophytes, epifauna, endofauna, sediment, bacteria etc., these may be studied separately *in situ* or also in the laboratory (ASMUS et al. 1980). Sometimes a combination of different methods is tried.

Within different enclosures the oxygen budget of isolated small communities of e.g. *Fucus*, eelgrass, red algae and sediment has been studied. The results were used for the establishment of partial models of the oxygen (or energy) budget in such ecosystems (e.g. GUTERSTAM 1979).

In Fig. 4 examples of continuous recordings of the oxygen content in an enclosed whole *Fucus* community are given, the separately enclosed sediment, the *Fucus* plants with epifauna and *Fucus* plants separately. Not only are great changes evident in the O_2 -budget between day and night, but in addition smaller fluctuations occur, which are not well understood up to the present.

From such recordings one can deduce models of the oxygen or energy budget for single days. The *Fucus* community shows a positive O_2 -budget during the longest part of the year, mainly in summer. However, in winter and during days with poor light conditions, the budget may become negative. Then the consumption of O_2 (or energy) in the *Fucus*-community dominates (see GUTERSTAM 1979).

Studies on the metabolic activity of the different types of organisms *in situ* and in the laboratory allow us to calculate their participation in total energy use. Thus the share of macrofauna ranges from a few percent to more than 40 % of the O_2 -demand of small benthos communities. The % proportion of macrofauna in the total community respiration of phytobenthos communities is greater in summer than in winter (GUTERSTAM 1979).

In the *Zostera* community near Olpenitz (Kiel Bight) proportions of 5–6 % of the total community respiration were found for the epibenthic macrofauna. Among these crustacea, due to their high biomass and activity, consumed most of the oxygen, more than mussels and echinoderms (ASMUS et al. 1980).

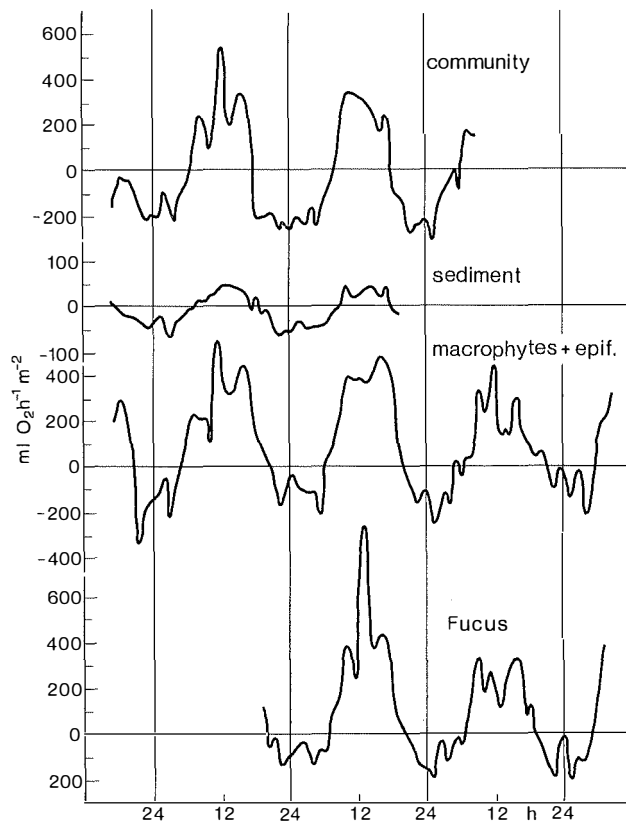


Figure 4

Diurnal fluctuations in the oxygen budget of a *Fucus* community and its partial systems (sediment, *Fucus* plant + epifauna) and components (e.g. *Fucus*, epifauna). Kämpinge (South Sweden), June 1976, depth 1.3 m (After SCHRAMM, pers. comm.)

However, epibenthic macrofauna respiration may represent only about one fourth or one fifth of the total macrofauna respiration, as a recent study of a red algae community in the Bight of Eckernförde suggests (Fig. 5). Taking this into account, macrofauna respiration represents approximately 20–30% of the oxygen consumption in this *Zostera* community. Similar proportions have been found in other Baltic communities. The differences found in the relations of activities of the different groups of organisms depend on type of community, depth, season and environmental conditions.

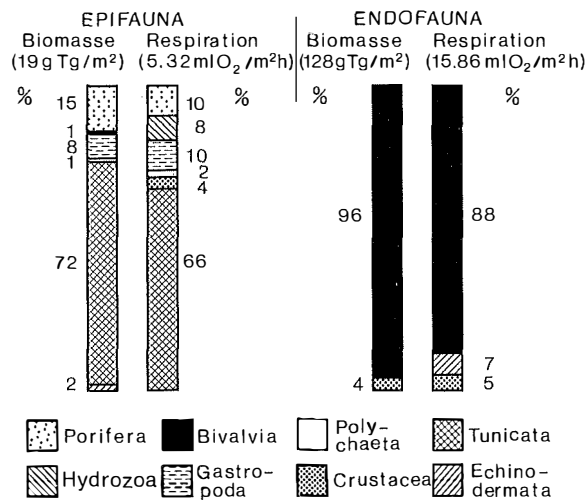


Figure 5

Proportion of different groups of macrofauna in biomass and oxygen demand in a red algae community ("Hausgarten of SFB 95" in Eckernförde Bight; depth 10 m; observation in September 1978, mean values of 4 samples of 0,25 m² each.) (After ASMUS and THEEDE, unpublished)

Such studies give an idea of how much the different groups are involved in different processes. However, continuous recordings or measurements at short intervals reveal that many biotic and abiotic parameters fluctuate strikingly at the interface sea-sea bottom.

In many phytal communities not only O₂ but also inorganic nutrients and dissolved organic compounds show pronounced fluctuations indicating that liberation as well as utilization of these compounds follow certain rhythms or patterns (Fig. 6). An important path for many released organic compounds is the incorporation by microorganisms (MEYER-REIL et al. 1980). Many saprophytes or other specialized microorganisms adapt rather quickly to the availability of certain substrates. By their high specificity to substrate and reproductive rate such microorganisms are able to influence the dynamics of organic turnover within short intervals of time (in the order of hours). Both meiofauna species and filter feeders of bigger size feed on them.

It has been shown that low water temperature, which reduces the speed of development of many bacteria, at the same time improves the conditions for direct uptake e.g. of dissolved amino acids by invertebrates (ALLENDORFF 1981). Many animals are able to take up dissolved amino acids if they are available in concentrations from nanomoles onward.

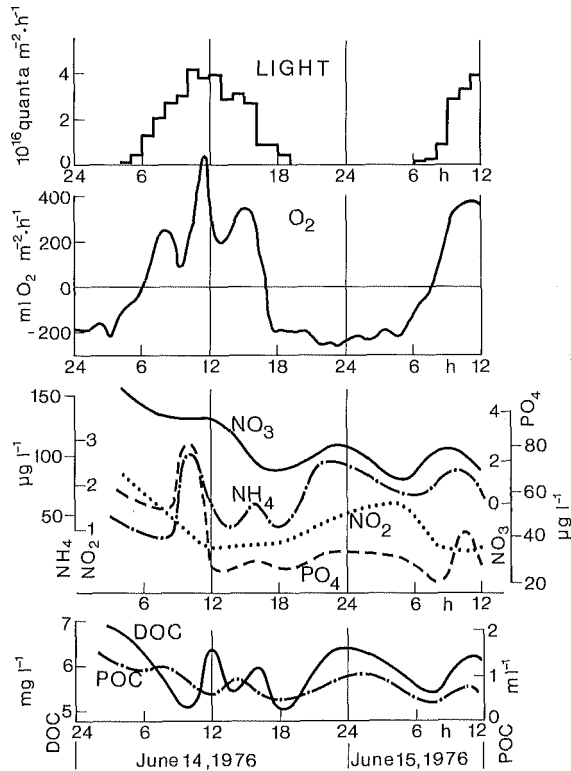


Figure 6

Diurnal fluctuations in the budget of oxygen and inorganic nutrients. Kämpinge (South Sweden), June 1976, depth 1.3 m. (After SCHRAMM 1978, modified)

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