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SEASONAL DEVELOPMENT OF BACTERIAL COMMUNITIES IN A COASTAL MARINE SEDIMENT AS RELATED TO THE INPUT OF ORGANIC MATERIAL

L.-A. MEYER REIL and G. GRAF

Institut für Meereskunde an der Universität Kiel, Düsternbrooker Weg 20, 2300 KIEL (FRG)

ABSTRACT - The seasonal development of benthic communities was followed in a coastal marine sediment of the Kiel Bight (Baltic Sea ; FRG). Total benthic biomass (ATP), bacterial biomass, overall benthic activity (heat production), and enzymatic decomposition rates of carbohydrate (d-amylase activity) followed a seasonal cycle strongly related to certain events in the sediment. Among these, the input of the phytoplankton blooms in autumn and spring, the accumulation of organic material during winter, and changes in the physical characteristics of the sediment turned out to be most important for the development of benthic biomass and activity. Processes within the benthic community occurred in very short time scales (within days).

Key words: bacterial biomass, heat production, enzymatic decomposition, seasonal cycle, sediment, sedimentation.

RÉSUMÉ - Le développement saisonnier des communautés benthiques a été suivi dans les sédiments marins côtiers de la baie de Kiel (Mer Baltique, RFA). La biomasse totale benthique (ATP) la biomasse bactérienne, l'activité benthique globale (production de chaleur), et taux de décomposition enzymatique des carbohydrates (activité de l'amylase) suivent un cycle saisonnier fortement lié à certains événements dans le sédiment. Parmi ceux-ci, l'apport des blooms phytoplanctoniques en automne et au printemps, l'accumulation de matière organique en hiver et les changements dans les caractéristiques physiques du sédiment sont considérés comme les plus importants pour le développement de la biomasse et de l'activité benthique. Ces processus dans les communautés benthiques ont lieu à une échelle de temps très courte (de l'ordre de quelques jours).

Mots clés : biomasse bactérienne, production de chaleur, décomposition enzymatique, cycle saisonnier, sédiment, sédimentation.

INTRODUCTION

The supply of organic material is the dominating factor determining structure and activity of benthic communities. Whereas the benthos in shallow waters may be directly supplied with benthic primary production, the benthos in deeper waters is greatly dependent upon the sedimentation of organic material from the water column.
Based upon data published in recent publications (Graf *et al.* 1983, Meyer-Reil 1983), this paper summarizes information on the seasonal development of benthic communities in coastal sediments of the brackish water Kiel Bight (Baltic Sea ; FRG) as related to the input of organic material.

THE EXPERIMENTAL APPROACH

Various parameters related to benthic biomass as well as to metabolic activities were applied and examined for their ability to characterize the seasonal development of benthic communities in a sandy-mud sediment of the brackish water Kiel Bight (Baltic Sea; FRG) between September 1981 and June 1982. From these parameters, the following will be discussed in this paper. ATP-measurements were used to describe overall benthic biomass. Bacterial number and biomass were extrapolated from epifluorescence microscopy preparations. Direct calorimetry (heat production) served as an indicator for overall benthic metabolism. Decomposition of particulate organic material was derived from exoenzymatic activity measurements. Details of the methods used as well as a characterization of the sediments sampled are described in two recent papers and literature cited therein (Graf *et al.* 1983, Meyer-Reil 1983).

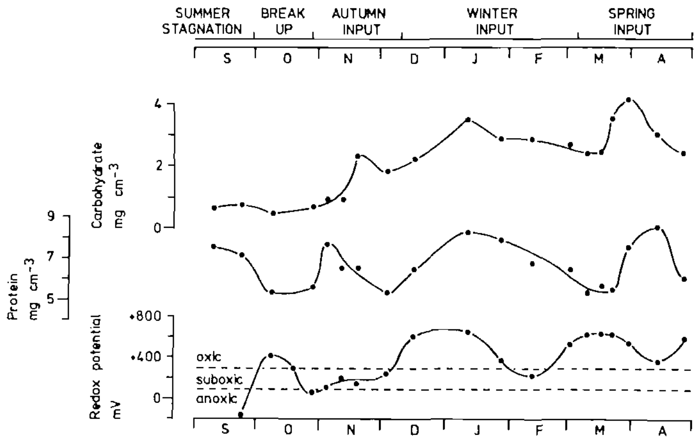

Figure 1 : Seasonal variations in redox potential, protein, and carbohydrate in the top centimeter of a sandy-mud sediment of the Kiel Bight (Baltic Sea; FRG) sampled between September 1981 and April 1982.

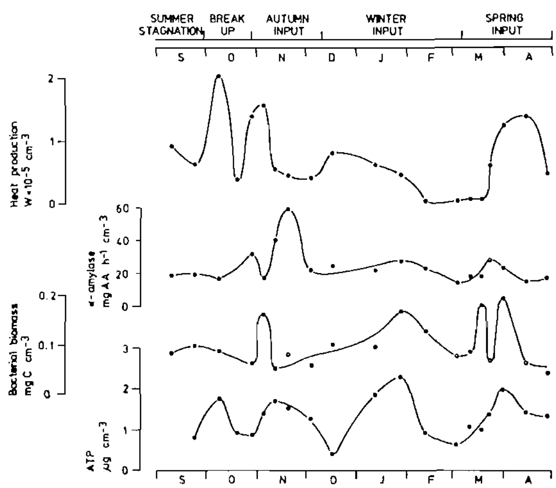

Figure 2 : Seasonal variations in ATP, bacterial biomass, α-amylase activity, and heat production in the top centimeter of a sandy-mud sediment of the Kiel Bight (Baltic Sea, FRG) sampled between September 1981 and April 1982.

PERIODS RELEVANT TO THE DEVELOPMENT OF BENTHIC COMMUNITIES

Seasonal variations in the food supply for the benthos as well as changes in the physical characteristics of the sediment gave rise to the definition of certain periods which turned out to be of high relevance for the development of the benthic communities (legends in fig. 1 and 2).

Physical characteristics of the sediment

Typical for a boreal region, temperature dropped gradually in the near bottom water from autumn to winter (14°C to 2°C) and increased slowly towards spring (4°C in April). The first period of observation coincided with the termination of "summer stagnation", a period in which anoxic conditions (hydrogen sulfide) were prevailing in the sediment (Fig. 1). At that time, the stratification in the water column limited the access of oxygen to the sediment. A storm in the beginning of October temporarily allowed the introduction of oxygen into the sediment surface ("break up" of summer stagnation). During November, suboxic conditions were observed in the sediment. These conditions may have been caused by both a chemical oxygen demand and increased biological activity. Stable oxic conditions, however, were achieved in December and maintained through winter and spring with the exception of a temporary reduction in redox potential in February and April, which again may have been caused by increased biological activity (Hargrave 1980)

Input of organic material into the sediment

Three periods of accumulation of organic material in the sediment surface could be distinguished : in autumn, winter and spring (fig. 1). During November protein, carbohydrate and total organic matter accumulated with distinct separate peaks. This input ("autumn input") could be traced back to the breakdown and sedimentation of the autumn phytoplankton bloom composed of dinoflagellates in the beginning and diatoms at the end of the bloom (Graf *et al.* 1983). During winter, we observed a continuous slow increase of organic material in the sediment surface ("winter input"). Resuspended sediment, material from terrestrial origin as well as macrophyte debris eroded by winter storms represented sources of the organic material. The breakdown of the spring phytoplankton bloom (mainly diatoms ; Peinert *et al.* 1982) led to an enrichment of organic material during late March to mid April ("spring input"). In contrast to autumn, the first peak in organic material was made up by carbohydrates.

RESPONSE OF THE BENTHIC COMMUNITY

In the following , the seasonal development of the benthic community will be discussed as a reflection upon the different ecological situations and events as described above (cf. headlines in fig. 1,2). During the successive periods, quite different types of benthic metabolisms are involved, some of which are microbial-dominated (Fig. 2).

Break up of summer stagnation

During the anoxic period of summer stagnation, protein accumulated in the sediment surface. The concentration of stored protein was even comparable to that measured after the sedimentation of the phytoplankton blooms in autumn and spring, respectively. Following the introduction of oxygen into the sediment ("break up"of summer stagnation), protein concentrations significantly decreased. Parallel peaks in heat production and ATP imply that the stored protein was rapidly consumed and incorporated into benthic biomass(Fig. 2). However, the question still remains open, which of the benthic organisms were responsible for the increase in biomass, since bacterial number and biomass remained almost constant during this period. Consequently, bacterial ATP as percentage of the total ATP strongly decreased from 43 % (anoxic conditions) to 18 % (oxic conditions). With decreasing redox potential towards the beginning of November, however, bacterial ATP again increased (up to 40 % of the total ATP) indicating an increasing importance of bacteria in benthic metabolism under anoxic and suboxic conditions (Meyer-Reil 1983). The inhibition of protein decomposition under anoxic conditions is not easy understandable. Under the same conditions, the decomposition of carbohydrates is much less affected as it could be shown by laboratory experiments (Meyer-Reil, unpublished data).

Autumn and spring input

The input of the phytoplankton blooms in autumn and spring, respectively, represent external food supplies for the benthos which generally reacted with an outburst in activity and subsequent biomass production (Fig. 2). However, the specificity of the benthic response is caused by differences in the food supply, the physical properties of the sediment, and the composition of the benthic community.

During the "autumn input" a peak in protein succeeded a peak in carbohydrate. In spring, however, the first peak in organic material was an enrichment of carbohydrate which was followed by protein. As an immediate response to the availability of organic material, heat production culminated. It is interesting to note that the peaks in heat production coincided with peaks in protein, but not with peaks in carbohydrate (Fig. 1, 2). Decomposition rates of carbohydrate (activity of α-amylase) were closely related to the enrichment of carbohydrate in the sediment. Enzymatic responses turned out to be much higher in autumn as compared to spring. This is obviously a reflection of both the higher temperature and the higher benthic biomass in autumn. Due to an induction of enzymatic activity with increasing substrate concentrations, a stimulation of enzymatic decomposition rates already occurred when concentrations of carbohydrate started to increase in the sediment surface. Since exoenzymatic activities are thought to be a minor component of the overall heat loss in sediments (Pamatmat 1982) both activity parameters showed no correlation (Fig. 2).

Whereas heat production comprises all types of benthic metabolism, electron transport activity (ETS ; for data cf. Graf *et al.* 1983) relates to the activity of respiratory chains (oxygen-, nitrate, and most likely sulfate-respiration). The quotient between heat production and ETS-activity should therefore serve as an indicator for changes in the type of metabolism (Pamatmat 1982). A strong increase of this quotient following the "autumn-" and "spring-input", respectively, demonstrated a shift in the type of benthic metabolism towards fermentation. This coincided with suboxic conditions mainly caused by biological oxygen consumption (Graf *et al.* 1983).

The stimulation of benthic activity resulted in subsequent biomass production. Prior to peaks in total benthic biomass (ATP measurements) however, bacterial biomass accumulated (Fig. 2). Bacteria primarily reacted to the availability of organic material with an immediate and strong increase in cell volume (biomass production). Deviating from the "normal" distribution of bacterial biomass, medium and large size cells dominated. Subsequently, bacteria responded with cell division (increase in cell number), re-establishing the normal biomass distribution : small-size cells (volume $<0,3\ \mu m^3$) again dominated the bacterial biomass followed by medium and large-size cells (volume $0,3$-$0,6 \mu m^3$ and $>0,6\ \mu m^3$, respectively ; Meyer-Reil 1983).

Winter input

Resuspended sediment, terrestrial material and eroded macrophytes represent an additional food supply for the benthic community during winter (Fig. 1). Although heat production continuously decreased, a high level of benthic biomass accumulated. This applies for bacterial biomass as well (Fig. 2). The high bacterial biomass sustained during winter is surprising taking into account the low temperature and the reduced metabolic activity rates. However, limited number of grazers and the relatively long time the bacteria had available for their "undisturbed" development may explain the biomass accumulation. Additionally, the more refractory kind of food source could have been responsible for the slow, continuous increase in bacterial biomass in winter. In this respect, the development of the bacterial population in winter differed basically from its spontaneous development in autumn and spring, respectively.

Fauna development

Additional samples taken in late spring revealed that the further fate of the bacterial community was greatly influenced by the development of the benthic fauna (data not shown ; Meyer-Reil 1983). A mass occurrence of polychaetes in the sediment was accompanied by a high number of almost exclusively small-size bacteria (volume $<0{,}3 \mu m^3$) which actively grew (high number of dividing cells). Most likely preferentially grazing of medium and large-size cells by the polychaetes was the reason for the impoverishment of the bacterial population.There is indeed evidence from the literature that grazing stimulates bacterial activity (Morrison and White, 1980).

CONCLUSION

From the foregoing discussion it becomes obvious that processes like sedimentation and input of organic material into the sediment may occur in very short time scales (within days), causing an immediate response of benthic activities. Whereas the succession of certain processes in the benthic community could be explained by the interactions between individual parameters, other processes still need explanation. This applies especially to the decline of benthic activities and biomass after certain levels were reached. Control mechanisms, such as the growth limiting effect of certain population densities and interactions between the individual components of the benthic communities, have to be considered.

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