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Fine-scale distribution of hydrolytic activity associated with foraminiferans and bacteria in deep-sea sediments of the Norwegian-Greenland Sea

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Abstract

Pronounced fine-scale gradients of enzymatic degradation of organic material were observed in the uppermost horizons of deep-sea sediments of the Norwegian-Greenland Sea. Since these gradients coincided with the occurrence of dense populations of epibenthic agglutinated foraminiferans, it was hypothesized that the foraminiferans were the main contributors to the large pool of hydrolytic enzymes observed. Parallel analyses of the enzymatic activity associated with individual foraminiferans selected from the sediments confirmed this hypothesis. Measurements of bacterial biomass (by epifluorescence microscopy) and production (incorporation of tritiated leucine) suggest that in the specific ecological situation analysed, bacteria benefit from the metabolism of foraminiferans rather than being the main decomposers. The immediate degradation at the sediment surface without incorporation of the sedimented particles into the sediment may have an impact on the early diagenesis of organic material and its sedimentary record in these deep-sea sediments.

Introduction

It seems to be generally accepted that the sedimentation of detrital material from euphotic waters represents the most important contribution to the nutrient supply of benthic communities in pelagic sediments (e.g. LOCHTE and TURLEY 1988, GRAF 1989). Very little is known, however, about the decomposition processes at the seafloor as well as about the organisms involved (JAHNKE and JACKSON 1987, GRAF 1989). Among these, a key role in the turnover of organic carbon is attributed to bacteria (ROWE and DEMING 1985) although foraminifera may be involved in carbon decomposition processes as well (GOODAY 1988, GOODAY and LAMBSHEAD 1989). Most of the organic material entering the sea floor is oxidized in surface sediment horizons by oxygen and eventually secondary oxidants (e.g. BENDER and HEGGIE 1984) at rates much more rapidly than it was previously thought (REIMERS and SMITH 1986, COLE et al. 1987).

We report here on observations of pronounced fine-scale gradients of enzymatic degradation of organic matter at the surface of deep-sea sediments of the Norwegian-Greenland Sea. These gradients coincided with the occurrence of dense

populations of agglutinated epibenthic foraminiferans. Parallel analyses of bacterial biomass and production suggest that bacteria benefit from the metabolism of foraminiferans.

Material and methods

Sediment cores were withdrawn using a multiple corer during an expedition with RV METEOR (cruise 7/5) from the following stations located in the Jan Mayen Fracture Zone (Norwegian-Greenland Sea): station no. 549 (9/9/88; water depth 1735 m; 70°57.4' N; 5°32.4' W); station no. 579 (9/19/88; water depth 1735 m; 70°57.4' N; 5°32.9' W); station no. 576 (9/18/88; water depth 1745 m; 70°20.1' N; 10°37.8' W); station no. 554 (9/11/88; water depth 2409 m; 72°12.7' N; 12°58.5' W). After retrieval sediments were dissected and the individual horizons were analysed for the activity of hydrolytic enzymes. For one representative station (no. 579), additional biotic parameters (ATP, bacterial number, biomass and production) were determined.

For the analysis of hydrolytic enzymes, 500 µl aliquots of dissected and diluted sediment (1:5 with filter-sterilized bottom water) were supplemented with 10 µl of a solution of fluoresceindiacetate (4.8 mM in acetone), a fluorogenic model substrate which is decomposed nonspecifically by intra- and extracellular esterases mainly responsible for the initial breakdown of organic material in aquatic environments (MEYER-REIL 1991). The enzyme assays were run in time-course experiments (usually 4 incubation periods; duplicate samples) at close to *in situ* temperature (0-2 °C). After centrifugation the release of the fluorescent dye was read in a spectrofluorometer (Kontron SFM 25; excitation 470 nm, emission 510 nm) against a standard of fluorescein. Enzymatic hydrolysis rates (µmol fluorescein released cm^{-3} of wet sediment h^{-1}) were extrapolated from the slope of the activity curve calculated by linear regression. Correlation coefficients were significant at least on the 95 % confidence level. For general remarks of the use of fluoresceindiacetate as a measure of esterase activity and its use in ecological studies compare KÖSTER et al. (1991).

ATP was extracted from dissected sediments by Tris buffer and measured as described by PAMATMAT et al. (1981). Total bacterial number, biomass and biomass spectrum were analysed by epifluorescence microscopy as described by MEYER-REIL (1983). For the assessment of bacterial biomass production, 500 µl aliquots of the dissected and diluted sediment (compare above) were incubated with 10 µl of tritiated leucine (0.5 µCi; specific activity 950 mCi mg^{-1}) in time-course experiments (generally 4 incubation times) at close to *in situ* temperature (0-2 °C). At the appropriate time (usually between 1 and 6 h), the reaction was stopped by deep-freezing. Samples were processed by the extraction of organic material from the thawed sediments with an extraction mixture of NaOH (0.3 M), EDTA (12 mM), and SDS (0.05 %; final concentrations). Following two centrifugation steps, the supernatants were combined, neutralized, and the macromolecules were precipitated by TCA (5 %) at 0 °C. Samples were filtered onto 0.2 µm Nuclepore polycarbonate membranes, washed with TCA (5 %) and ethanol (80 %), dried and counted in a liquid scintillation counter. Bacterial biomass production rates (expressed as nmol tritiated leucine incorporated cm^{-3} of wet sediment h^{-1}) were extrapolated from the slope of the linear part of the activity curve calculated by linear regression. The sample treatment represents modifications of the procedures published by THORN and VENTULLO (1988) and by WICKS and ROBARTS (1988).

Results and discussion

Fine-scale analyses of sediment profiles revealed pronounced gradients in enzymatic activity comprising almost two orders of magnitude within the top centimeter (Fig. 1). The enzymatic response measured was unexpectedly high for these permanent cold and generally nutrient-limited sediments. Even in coastal, nutrient-rich sediments, gradients in hydrolytic activity at the sediment surface were generally much less pronounced (own unpublished data).

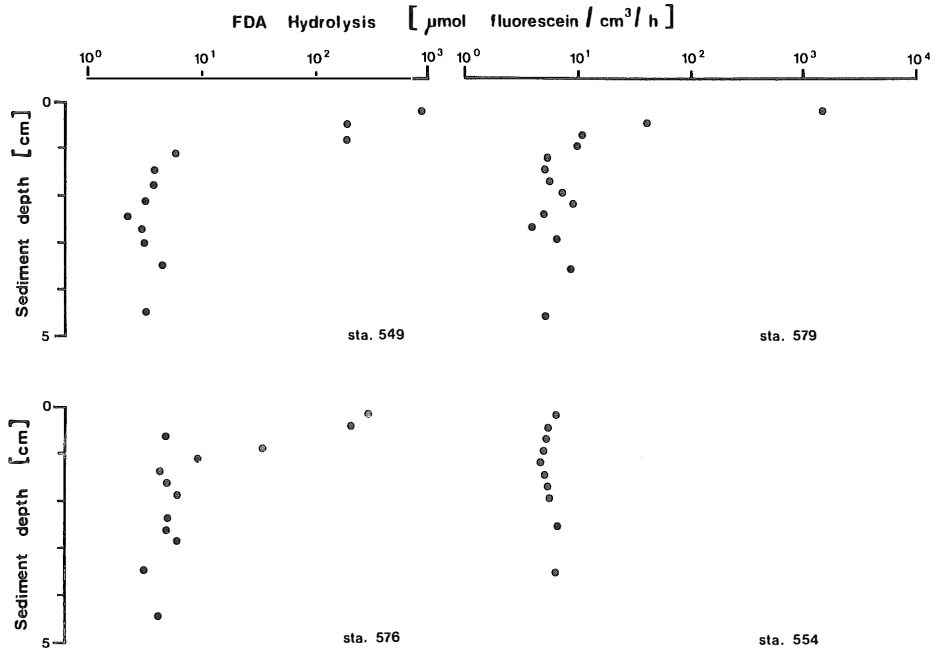

Fig. 1. Fine-scale variations of enzymatic degradation of organic material (measured by hydrolysis of fluoresceindiacetate) in sediment profiles of four stations located in the Jan Mayen Fracture Zone (Norwegian-Greenland Sea).

Sediments from stations no. 549, 576 and 579 were characterized by high abundances of epibenthic agglutinated foraminiferans (according to A. THIES identified as genera *Hyperammina* and *Reophax*; dimensions between 1 and 3 cm in length and approximately 0.5 cm in width) which densely colonized the uppermost sediment layer. Since at these stations, the enzymatic activity revealed strong gradients, we hypothesized that the foraminiferans were the main contributors to the large pool of hydrolytic enzymes observed. Parallel analyses of the enzymatic activity associated with individual foraminiferans selected from the sediments confirmed this hypothesis. The hydrolytic activity of one living organism generally could already account for the activity measured in one cubic centimeter of material from the uppermost sediment horizon (foraminiferans embedded in sediment). However, as indicated by the reduction of plasma strings, most of the foraminiferans were inactive (dead?; THIES pers. commu-

nic.). If analysed for hydrolytic enzymes, these inactive organisms revealed indeed very low enzymatic activity comparable to the activity measured in the surrounding sediment (KÖSTER et al. 1991). It can be expected that the dynamics of the foraminiferal population are governed by the supply with organic material. This supports indirectly the observations of GOODAY (1988) and GOODAY and LAMBSHEAD (1989) suggesting that some deep-sea benthic foraminiferans bloom opportunistically when appropriate nutrients become available.

Since the differentiation between active and inactive foraminiferans by microscopic examination (after staining with Rose Bengal; e.g. BERNHARD 1988) is problematic, the measurement of enzymatic activity associated with individual foraminiferans may offer an alternative, more reliable basis for rather quick dif-

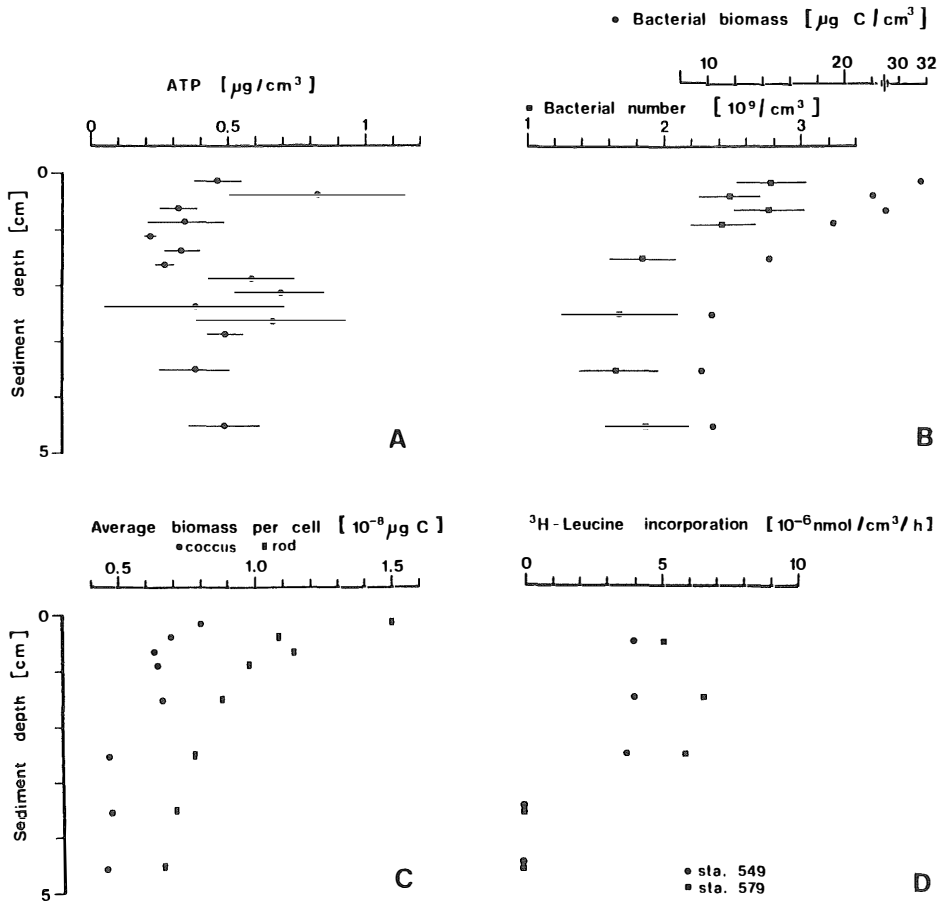

Fig. 2. Fine-scale variations in concentrations of ATP (A), total bacterial number and biomass (B), average biomass of rods and cocci (C), and bacterial production (D) measured in sediment profiles of station no. 579 (in Fig. 2 D additional data from station no. 549 are included; for station specification cf. text).

ferentiation. For one representative station (no. 579) colonized by foraminiferans, additional biotic parameters were determined. Fine-scale analysis of the concentration of ATP gave no indication of increased biomass in the uppermost sediment horizon (Fig. 2B, C). This supports the conclusion derived from microscopic observation and enzymatic measurements that most of the foraminiferans were indeed inactive.

Total bacterial number and biomass determined by epifluorescence microscopy revealed higher values in the top centimeter of the sediment as compared to horizons below. A size fractionation of the bacterial population showed that the accumulation of bacterial biomass at the surface was mainly due to an increase in biomass of rod-shaped cells; the increase in biomass of cocci was much less pronounced (Fig. 2B, C). It is hard to believe that the enrichment of bacteria by less than a factor of 2 in the uppermost sediment horizon could be responsible for the almost two orders of magnitude higher enzymatic activity. Measurements of the incorporation of tritiated leucine into TCA-insoluble macromolecules showed that bacterial biomass production was almost homogeneously distributed within the top 3 cm of the sediment. Instead of an enrichment at the surface, the measurements rather suggest higher bacterial biomass production rates below the sediment surface (Fig. 2 D).

Because of the distance from terrestrial influence and the rather episodical supply with organic material, the sediments investigated in the Jan Mayen Ridge can be characterized as deep-sea sediments. In these sediments, specific locations exist which allow the occurrence of dense populations of foraminiferans. These sites characterized by specific sediment properties must be favoured with regard to the supply with organic material. Epibenthic foraminiferans extend their plasma nets above the sediment surface. Through their feeding strategy, the organisms capture the settled detritus prior to reaching the sediment surface and prior to benthic bacterial attack. The digestion of the organic material in the foraminiferans is mediated by hydrolytic enzymes which are thought to be secreted into digestion vacuoles. The pool of these enzymes is obviously mainly responsible for the high hydrolytic activity measured at the sediment surface (dominated by foraminiferans) and associated with selected organisms. From the observations it can be derived that in the specific ecological situation prevailing at the time of sampling, the main decomposition potential was associated with epibenthic foraminiferans. Bacteria may take advantage of the metabolism of foraminiferans. This could be through the uptake of metabolic products released by the foraminiferans or by the degradation of decaying organisms below the sediment surface. The immediate degradation at the surface without incorporation of the sedimented particles into the sediment may have an impact on the early diagenesis of organic material and its sedimentary record in deep-sea sediments.

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