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Burrowing macrozoobenthos as major determinant of bacteria in sediments

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Abstract

Deposit-feeding benthic macrofauna withdraw substantial amounts of bacterial biomass from marine sediments. On the other hand, burrowing macro-invertebrates can mediate epizoic and perizoic enrichment of bacteria by tapping or "conditioning" energy carriers (for heterotrophic and chemolithotrophic bacteria) that are stored in the sediment. Selected examples show how this applies particularly to reduced sediments.

Introduction

Idealized concepts of diagenetic processes in marine sediments are based on vertical patterns of deposition of sedimented organic matter. With increasing sediment depth these patterns are progressively affected by depletion of easily degradable organic carbon, dissolved O_2 and alternative electron acceptors. Limited diffusion of dissolved gases and microbial growth factors in the pore water cause relatively stable patterns of stratification with successions of densely populated microhabitats of physiologically most diverse microorganisms.

This model is disturbed by sediment reworking of deposit feeding macrozoobenthos. Even anoxic sediment layers are inhabited by certain infaunal organisms that are able to survive for weeks or even months by fermentative metabolism (THEEDE et al. 1969). Other macro-invertebrates such as the bulk deposit feeder *Arenicola marina* penetrate anoxic sediment layers by means of irrigated and aerated tubes (REICHARDT 1988).

Removal of sediment bacteria by deposit feeders

First of all, deposit feeders impose a constant drain on the biomass of geochemically active microorganisms. In intertidal sediments, the loss of bacterial biomass via digestive removal (gut passage) by the polychaete *Arenicola marina* alone amounts to 3.1×10^{10} cells $h^{-1} cm^{-3}$ (GROSSMANN and REICHARDT, ms. submitted). This removal rate is not balanced by current estimates of bacterial productivity in the order of 10^8 cells $h^{-1} cm^{-3}$ (MORIARTY and POLLARD 1981, FALLON et al. 1983, REICHARDT 1988). Nevertheless, the intestinal tract of

arenicolid polychaetes and other benthic invertebrates contains sites of maximum bacterial growth in which generation times of less than one h can reach the lower limits obtained under optimal laboratory conditions (DEMING and COLWELL 1982, PLANTE et al. 1989).

Macrofauna-mediated enrichment of bacteria in reduced sediments

Apparently, major fractions of bacterial productivity in sediments remain undetected, presumably due to both extremely patchy distribution patterns and systematic underestimates of current methodologies. Attempts to determine the contribution of obligate anaerobes to total bacterial productivity, suffer from severe underestimates of major constituents such as sulfate reducers (PIKER and REICHARDT 1991). On the other hand, sulfate-reducing bacteria are not confined to sediments in which negative redox potentials prevail, but can reach similar high densities in oxidized sediments, too (BUSSMANN and REICHARDT, ms. submitted).

To counterbalance losses of bacterial biomass by deposit feeding, not only the above mentioned gut fermentation is important. "Bioturbation" or restructuring of depositional sediment patterns by burrowing invertebrates play a crucial role in creating secondary microhabitats for sediment bacteria (YINGST and RHODADS 1980, KRANTZBERG 1985, DOBBS and GUCKERT 1988, FINDLAY et al. 1990). In nutrient limited environments, pulses of nutrients for copiotrophic bacteria are made available through macrofaunal digestion and "conditioning" of particulate organic matter. Thus standing crops of TCBS-agar-selected vibrios in the burrow walls of *Arenicola marina* have been found to be one to two orders of magnitude greater than in the ambient sediment (REICHARDT unpubl.).

Enrichment experiments with macroalgal exudates in seawater suggest that during the initial phase of enrichment TCBS-selected vibrios maintain a competitive advantage over the residual populations. This effect was most pronounced under anaerobic conditions (DONNER and REICHARDT 1991). In contrast to competitive growth, survival of starved *Vibrio* cells was better under aerobic conditions. The same applies to the positive influence of particles on starvation (HEISE and REICHARDT, ms. submitted). Hence, vibrios as copiotrophic, facultative anaerobes appear particularly adapted to perizoid biofilms of infaunal burrows and similar bioturbated microenvironments in which bacteria are exposed to extreme changes of redox potential and nutrient availability.

Despite severe limitations of benthic macrofauna in anoxic sediments, even strictly anaerobic bacteria are positively affected by burrowing invertebrates. In addition to previous observations of enhanced sulfate reduction rates in sediments bioturbated by clams (HINES and JONES 1985), we have found that sulfate-reducing bacteria (SRB) attached to the clam *Arctica islandica* are able to enrich more rapidly than SRB from ambient sediment (BUSSMANN and REICHARDT, ms. submitted).

Finally, epizoid bacterial growth can be viewed as an important factor for the dispersal of bacteria in sediments. Primarily triggered by enhanced availability of nutrients on the animal's surface, bacterial enrichment can depend on an array of further parameters. For example, growth on a macro-invertebrate "carrier" which moves frequently between oxidized and reduced sediment layers, may account for the existence of complex benthic microhabitats for most exacting bacteria (v. JUTERZENKA and REICHARDT 1991).

Table 1. Impact of macrobenthic infauna on bacteria in bioturbated sediment

Macrofaunal influence:	Effects on bacteria:
1. Sediment feeding (bacterivores)	Removal of bacterial biomass
2. Egestion of "conditioned" microbial nutrients	Enrichment of bacteria, "Gardening"
3. Excretion of dissolved nutrients	Epi-, perizoic biofilms
4. Sloughing of mucus	Perizoic biofilms (burrows)
5. Attachment surfaces	Carrier function, dispersal
6. Formation of internal physicochemical gradients	Chemolithotrophs (E_h), Fermentative Copiotrophs (oxic-anoxic changes)
7. Disturbance, Reworking of sediment	Stimulation of microbial growth and activity

General conclusions

Major impacts of benthic macro-invertebrates on bacteria in sediments are summarized in Table 1. Despite substantial removal of bacterial biomass by bulk deposit feeders, the presence of burrowing macro-invertebrates entails numerous environmental changes which favor the enrichment of bacteria. Perizoic biofilms along burrow walls provide macroscopically visible evidence of this re-structuring of benthic microhabitats (Fig. 1).

Enrichment of microorganisms on bioturbate sediment structures has been likened to positive feed back mechanisms in deposit feeding (YINGST and RHOADS 1980, REICHARDT 1987), and a concept of bacterial "gardening" by macrobenthic infauna has been proposed (HYLLEBERG 1975). Unequivocal evidence for significant contributions of epi- or perizoic bacterial growth to the nutrition of macrozoobenthos, however, is still rather poor (PLANTE et al. 1990).

On principle, macrofauna is able to reinforce benthic energy flows by making two main sources of stored energy available to sediment bacteria. Macrofaunal digestion or other modes of "conditioning" of organic detritus as main sources in benthic energy flows is a prerequisite for effective tapping of this "storage energy" by heterotrophic bacteria. As alternative energy carriers, inorganic electron donors for chemolithotrophs are stored in anoxic sediments. Aerated tubes and burrows mediate tapping of these sources by aerobic chemolithotrophs. Moreover, electron donors such as ammonia are excreted by certain macroinvertebrates, too (REICHARDT 1989, JUMARS et al. 1990).

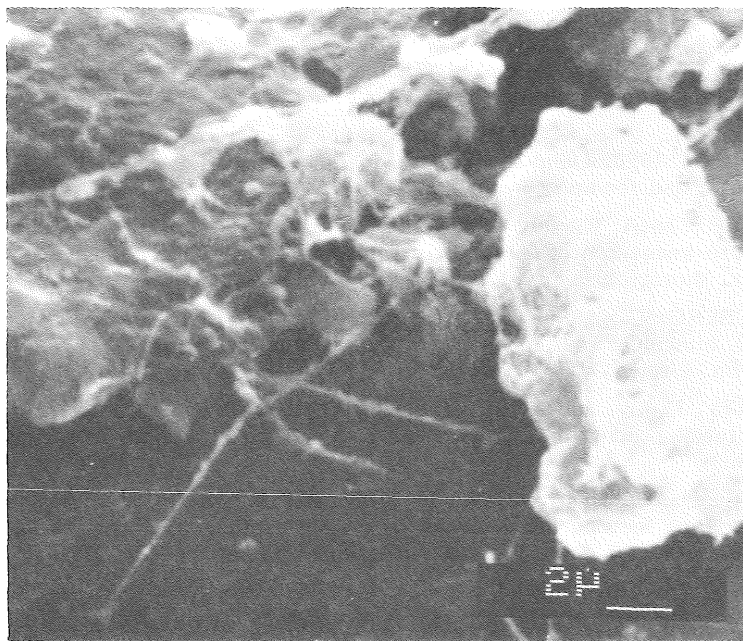
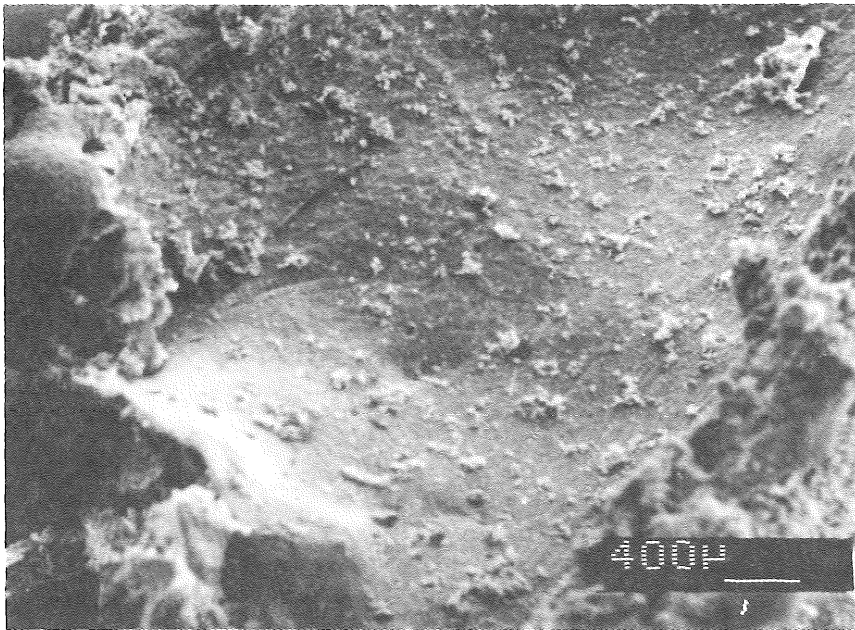


Fig. 1. Scanning electron micrographs of exposed side of burrow of polychaete *Nereis diversicolor* with aggregates of mucus.

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