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Sulfate-reducing bacteria in temporarily oxic sediments with bivalves

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ABSTRACT: Under seasonally fluctuating redox conditions in sediment of Kiel Bay (eastern Baltic Sea), viable counts (MPN) of sulfate-reducing bacteria (SRB) ranged between 4×10^2 and 7×10^4 cm^{-3}. These MPN appeared fairly independent of ambient redox potentials and followed peaks of phytoplankton productivity in the water column with a time lag of 2 to 3 wk. The relative proportions of SRB using acetate, lactate or succinate as their electron donors fluctuated widely. Shells of the clam *Arctica islandica*, which can survive anoxia, were, even in oxic sediments, colonized by epizoic SRB. Significant differences between the abundance of epizoic SRB and SRB from ambient sediment were not detected. In terms of enrichment kinetics, however, epizoic SRB, and particularly those depending on succinate as electron donor, showed quicker responses. It is hypothesized that SRB associated with benthic infauna represent the biogeochemically more reactive group.

INTRODUCTION

Anoxic surface sediments, which cover not more than 10 % of the sea floor, are mainly bound to the shallow, most productive areas of the world ocean (Henrichs & Reeburgh 1987). In these, decomposition of organic matter is channeled through fermentative, methanogenic, or respiratory pathways involving reduced nitrate, ferric iron, manganese or sulfate as terminal electron acceptors. Dissimilatory sulfate reduction accounts for the bulk of carbon mineralization in marine anoxic sediments (Crill & Martens 1987). Up to 50 % of the respiratory electron flow in coastal anoxic sediments is mediated by sulfate reduction (Jørgensen & Sørensen 1985).

Rates of sulfate reduction depend on the available concentrations of electron donors and acceptors as well as on population densities of the obligately anaerobic sulfate-reducing bacteria (SRB) as the catalytic agents. Earlier attempts to assess population densities of SRB in the marine environment were based on enrichment media containing lactate as sole carbon source for SRB of the *Desulfovibrio desulfuricans* type (e.g. Jørgensen 1978, Gunnarsson & Rönnow 1982, Hines & Buck 1982). The discovery of further metabolic types of SRB with different substrate requirements (Widdel 1980) made it necessary to extend the range of enrichment substrates in order to update estimates for the standing crop of cultivable populations of SRB (Laanbroek & Pfennig 1981, Battersby et al. 1985).

Many of the potential niches for SRB in marine sediments are only seasonally anoxic depending on bulk input of organic matter via sedimentation of phytoplankton. Thus it appeared desirable to know how SRB populations are affected by seasonal changes of temperature, nutrient input and oxygen depletion (Graf et al. 1982).

According to Hines et al. (1982), sulfate reduction rates can be enhanced in bioturbated sediments. Yet the role of benthic macrofauna as a potential stimulant of sulfate reduction and SRB is far from clear. Low-chain fatty acids as preferred growth substrates for SRB are produced as fermentation products during anoxic survival of clams (Kluytmans et al. 1975). Growth of epizoic SRB among other heterotrophs on clams has been noted only once (Bussmann & Reichardt 1990). In the temporarily anoxic sediments of Kiel Bay, survival of both starvation and exposure to oxygen should become a crucial steering factor for the distribution of obligately anaerobic heterotrophs such as SRB. To search for clues to the influence of predominant benthic macroinvertebrates on the standing crop of SRB, the latter were enumerated in both sediment samples and scrapings from shell surfaces of the

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clam *Arctica islandica*. Distribution patterns of SRB were compared with fluctuations of pertinent environmental variables in Kiel Bay sediment. Furthermore, it was attempted to describe the diversity of marine SRB with respect to substrate preferences and enrichment kinetics.

MATERIALS AND METHODS

Sediment cores and bivalves (*Arctica islandica*) from Kiel Bay (western Baltic; 54° 36' N, 10° 27' E) at 18 m water depth were obtained from March to December 1989 using a Reineck box core sampler aboard RV 'Littorina'. Redox potentials were recorded in sediment profiles down to a depth of 10 cm using a Pt-Ag/AgCl electrode.

In the laboratory, single specimens of *Arctica islandica* were incubated in gas-tight, dark PVC tubes (22 × 10 cm) with sediment from the sampling station, leaving the top 4 cm for a sea water overlay. These tubes were incubated in a water bath at 10 °C and were gassed with N_2/CO_2 (90:10) for 2 min to create anaerobic conditions. To exclude other macrofauna, sediment was sieved through a 1 mm sieve. Experiments were run in triplicate with and without clams.

Succinate concentrations in pore water were determined after centrifugation of sediment samples at 14 000 × *g* (20 min) under N_2/CO_2. An enzymatic assay based on the production of NADH in a coupled reaction of succinate thiokinase and pyruvate kinase was employed according to Michal et al. (1976) using reagents from Boehringer.

MPN (most probable number) determinations of SRB were made using (1) ambient sediment subsamples from cores with *Arctica islandica* from below 5 cm depth and at a distance of at least 10 cm from the clam, and (2) epizoic samples from the periostracum of this clam. In the latter case, material scraped from up to 10 individuals had to be combined. Using cut off 5 ml syringes, 2.5 cm^3 aliquots were suspended in Erlenmeyer flasks containing 50 ml of anoxic artificial seawater ('Tropic Marin', S = 15 ‰). These suspensions were sonicated 4 times for 10 s at 50 W (field samples) or magnetically stirred for 1 h (laboratory experiments). Serial dilutions (10-fold) were prepared in screw-capped tubes (150 × 16 mm) with rubber-coated aluminum caps containing brackish water enrichment medium No. 2 (Widdel 1980).

This enrichment medium was reduced with either 50 mM of sodium dithionite (crystals) for field samples or 3 mM of sodium disulfide for laboratory experiments. The medium contained the following vitamins (µg l^{-1}): biotin 10, nicotinic acid 20, thiamine 10, *p*-aminobenzoic acid 10, pantothenic acid 5, pyridoxamine 50, cobalamine 5 (Laanbroek & Pfennig 1981, modified) and was gassed with N_2/CO_2 (90:10). Organic substrates serving as sole carbon sources and electron donors were added from sterile-filtered solutions at the following final concentrations: 15 mM sodium acetate, 7.5 mM sodium lactate, and 5 mM disodium succinate. To enrich spore-forming SRB, the samples were pasteurized and incubated with 10 mM of ethanol. Resazurin (1 µm) served as redox indicator.

MPN determinations comprized 5 dilution steps with 5 parallels each. The tubes were incubated for 8 wk at 20 °C in the dark. Turbidity and hydrogen sulfide concentrations (Cord-Ruwisch 1985) were checked at 2 wk intervals.

RESULTS

Distribution patterns

From March to December 1989, MPNs of SRB obtained with acetate, succinate and lactate as electron donors ranged between 4 × 10^2 and 7 × 10^4 per cm^3 of sediment. These viable counts roughly matched primary production rates in the water column, allowing a time lag of 2 to 3 wk (Fig. 1). Decreasing redox potentials in the sediments coincided with increasing densities of SRB. However, even under the most oxidized conditions (+280 mV), population densities as high as 2.9 × 10^4 cm^{-3} were obtained (Fig. 1). Further-

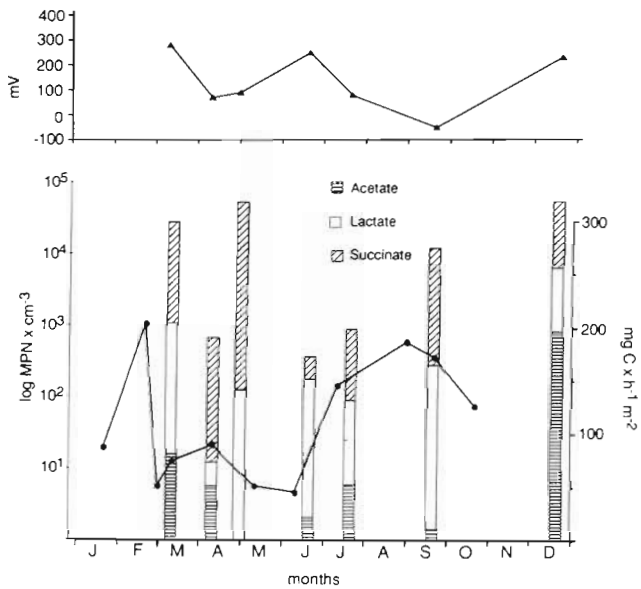

Fig. 1. Top: Fluctuations of redox potential (mV) at 5 cm sediment depth at Kiel Bay sampling station in 1989. Bottom: Seasonal changes of primary production (•——•) in the water column and MPNs of SRB in sediment obtained with acetate, lactate and succinate as carbon sources in 1989

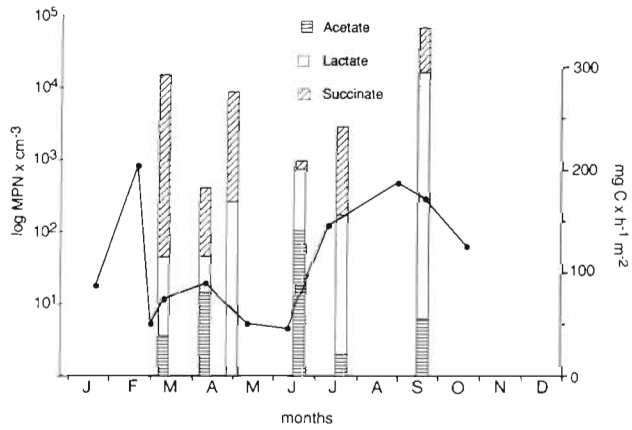

Fig. 2. Seasonal changes of primary production (•——•) in water column above sampling station (18 m water depth) and MPNs of epizoic SRB on *Arctica islandica* obtained with acetate, lactate and succinate as carbon sources in 1989

more, no overriding impact of temperature (ranging between 4 and 15 °C) on viable counts of SRB was detected.

Viable counts of epizoic SRB on shells of *Arctica islandica* (Fig. 2) were insignificantly higher than those in the ambient sediment (Fig. 1). In the latter, the percentage of lactate-, acetate- and succinate-oxidizing SRB fluctuated widely from 11 to 85 %, <0.1 to 26 % and 10 to 62 %, respectively. In epizoic samples, the relative incidence of acetate-oxidizing SRB (0.1 to 67 %) tended to be greater than in the ambient sediment (<0.1 to 26 %) (Table 1).

Table 1 Relative abundance of SRB (%) with respect to different electron donors (carbon sources) and tentative classification of the predominant taxa of SRB

Electron donor	Predominating genera	Sediment	Periostracum
Lactate	*Desulfovibrio*	11.0–85	20.0–71
Acetate	*Desulfobacter* and *Desulfotomaculum*	<0.1–27	<0.1–67
Succinate	*Desulfobacterium* and *Desulfococcus*	10.0–62	4.0–61
Ethanol[a]	*Desulfotomaculum*	<0.1–3	<0.1–1

[a] Pasteurized samples only

Laboratory experiments

In jar experiments carried out to induce anaerobic survival of the clams, no significant differences between epizoic SRB and SRB in ambient sediment were found. However, the kinetics of enrichment in the MPN tubes revealed differences between epizoic SRB and SRB from the ambient sediment. To describe these enrichment characteristics, a value ($t_{MPN/2}$) was defined as the time (in days) to reach 50 % of the final MPN value obtained after 8 wk. Enrichment was slower in the ambient sediment samples than in the epizoic samples. In epizoic samples, $t_{MPN/2}$ values of succinate-utilizing SRB were only half as high as in samples from the ambient sediment (Table 2).

In a second experiment, overall differences of paired $t_{MPN/2}$ values for ambient sediment SRB and epizoic SRB indicated that succinate-utilizing epizoic SRB responded significantly more quickly ($p = 0.05$, $n = 6$) (Fig. 3).

Succinate concentrations in the pore water of sediment with *Arctica islandica* were below the detection limit of 4 µmol l^{-1}. This contrasted to the higher concentrations measured in the surrounding sediment.

DISCUSSION

The assessment of bacterial densities in sediments suffers from difficulties in separating and identifying individual cells. In addition, indirect techniques based on cultural enrichment, such as the determination of 'most probable numbers' (MPN), are affected by the selectivity of the growth conditions chosen and by the physiological state of the cells *in situ*. Even recovery of cultured SRB added to previously sterilized sediment is only about 50 % (Gibson et al. 1987). Comparisons with measurements of sulfate reduction *in situ* and yield data obtained with cultured SRB have indicated that the standing crop of viable SRB in marine sedi-

Table 2. Final MPN values (after 8 wk), and $t_{MPN/2}$ values describing the velocity of enrichment of SRB using different electron donors in sediment tubes with *Arctica islandica* after 14 d of anaerobic survival. n = 3, standard error of the mean SE = s $\sqrt{n}$

Sole carbon source	Ambient sediment		Periostracum	
	MPN × 10^4 cm^{-3} ± SE	$t_{MPN/2}$ (d) ± SE	MPN × 10^4 cm^{-3} ± SE	$t_{MPN/2}$ (d) ± SE
Acetate	0.6 ± 0.2	29 ± 8.6	1.1 ± 0.4	38 ± 6.9
Lactate	5.7 ± 0.7	11 ± 1.2	11.1 ± 8.7	12 ± 1.7
Succinate	7.2 ± 3.1	33 ± 8.6	4.2 ± 1.6	18 ± 2.3

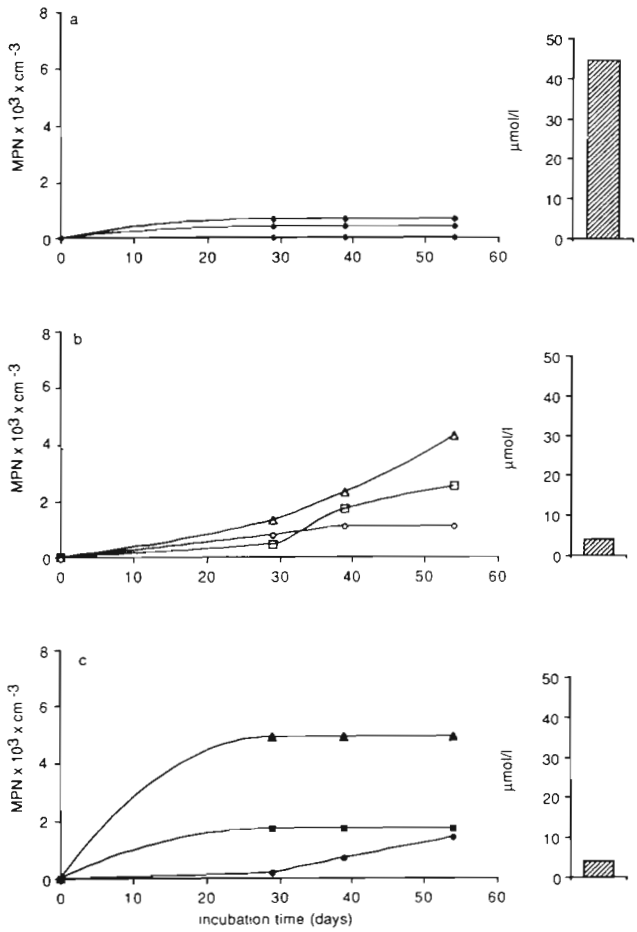

Fig. 3. Impact of anaerobic conditions (5 d) on development of MPN of SRB using succinate as sole carbon source in (a) the clam-free sediment (sieved), (b) sediment (sieved) surrounding *Arctica islandica*, and (c) samples from periostracum of *A. islandica*. Columns show succinate concentrations in the pore water

ments can be underestimated by a factor of 20 (Gibson et al. 1987). Other calculations have led to 1000-fold underestimates (Jørgensen 1978). Alternative techniques based on immunofluorescence do not appear promising due to their pronounced specificity below the level of taxonomic or physiological categories (Widdel 1988). Another alternative, phospholipid fatty acid biomarker analysis (e.g. Taylor & Parkes 1985), depends on often extremely low percentages of fatty acids qualifying as specific biomarkers and has still to prove its superiority over conventional viable count estimates.

The spectrum of SRB as a target for estimates of viable counts has been considerably widened by the detection of new taxa and physiological groups (Pfennig et al. 1981). Our choice of lactate, acetate, and succinate (plus ethanol for spore formers) as single electron donors enabled us to distinguish between the major categories to be expected (Laanbroek & Pfennig 1981, Widdel 1988). Also, if lactate in selective media is replaced by alternate electron donors, maximum abundances are still noted for lactate utilizers (Laanbroek & Pfennig 1981, Battersby et al. 1985). Presumably, many of the *Desulfovibrio* spp. enriched on lactate medium (Table 1) are effective H_2-scavengers *in situ* (Abram & Nedwell 1978, Widdel 1988).

From activity measurements Banat et al. (1981) drew the conclusion that acetate- and H_2-oxidizers coexist as 2 distinct functional groups in marine sediments. The great variations noted for acetate utilizers may be caused by frequent underestimates as a result of clumping as reported by Widdel & Pfennig (1981). Furthermore, these counts may account for only a fraction of acetate oxidation, if, by means of interspecies hydrogen transfer (Phelps et al. 1985), even H_2-utilizing *Desulfovibrio* spp. were able to participate in acetate oxidation (Widdel 1988).

It remains open to what extent the succinate utilizers, as an important group in this investigation, contained, beside complete oxidizers, also *Desulfovibrio* spp. (Postgate 1984). The consistently low percentage of spore formers (*Desulfotomaculum* spp.) occurring in the partly oxidized environment (Table 1) may indicate that oxygen tolerance of the spores is not the key for competitive advantage under unstable redox conditions.

Survival and activity of SRB in oxidized marine sediments have been explained by anoxic microniches and trapping of oxygen by the end product of sulfate reduction (Jørgensen 1977, Laanbroek & Pfennig 1981, Battersby 1985). Furthermore, *Desulfovibrio* spp. and *Desulfobacter postgatei* show O_2-dependent growth in oxygen-sulfide gradients in which primarily thiosulfate as an autoxidation product of sulfide has been suggested to replace sulfate as electron acceptor (Cypionka et al. 1985). *Desulfovibrio vulgaris* can survive exposure to oxygen for more than 72 h (Hardy & Hamilton 1981).

An upward trend of viable counts between summer and fall coincided with both decreasing redox potentials in the sediment and, with a phase lag, increasing primary productivity in the water column. Enhanced O_2 consumption and decreasing redox potentials in Kiel Bay sediment are characteristic of benthic responses to sedimentation of phytoplankton blooms (e.g Graf et al. 1982). Positive correlations between sedimentation rates and rates of sulfate reduction have already been found in other study areas (Goldhaber & Kaplan 1975, Jørgensen 1982). Our data from Kiel Bay indicate that the standing crop of the obligately anaerobic SRB already increases before negative values of the redox potential are measured.

Irrespective of gross underestimates of true population densities, linear relationships between sulfate reduction rates and SRB occur (Hines & Lyons 1982). Uncoupling of these parameters, however, has been observed in macrofauna-rich sediments in which sulfate reduction rates were enhanced as a result of bioturbation by bivalves and other macro-infauna (Hines & Jones 1985).

Growth of SRB is promoted by fermentation products such as low molecular weight fatty acids and H_2. In oxidized sediments, fermentation is confined to microhabitats with a low redox potential. Such microhabitats occur in the intestinal tracts of marine animals (e.g. Plante et al. 1989). Moreover, under conditions of anaerobic survival, benthic infauna itself is capable of providing certain fermentation products for bacterial growth (Dion 1986, Oeschger 1990).

Manifestations of macroscopic bacterial growth as on *Yoldia* sp. from Antarctic mud samples (Bussmann & Reichardt 1990) may be rare. An apparently similar phenomenon was recently described for a deep-sea mussel (Hook & Golubic 1990). In general, however, bacterial utilization of nutrients released from clams is less spectacular. MPNs of SRB do not even indicate significantly higher densities on the periostracum of *Arctica islandica*. Only qualitative differences related to the velocity of enrichment would suggest a potential influence of the bivalve. Yet underestimates of MPN in samples from the shell surfaces cannot be excluded, because elevated concentrations of Ca, when carried over into the enrichment medium, may cause sulfate-reducing bacteria to form aggregates (Singleton et al. 1988).

Parameters describing the enrichment kinetics ($t_{MPN/2}$ values) support the view that SRB occur in 2 groups with presumably different substrate affinities (Fukui & Fukuhara 1987). By comparing k_M values for SO_4^{2-} uptake by *Desulfovibrio* spp., Ingvorsen & Jørgensen (1984) arrived at the same conclusion. Analogues of $t_{MPN/2}$ values determined for plate counts of cultured lactate-utilizing SRB seem to discriminate between different physiological states of these bacteria (Fukui & Takii 1989a). Prolonged periods of starvation cause steadily declining respiratory activities and slowed-down 'rates of appearance of colonies (f)' (Fukui & Takii 1989b).

Since $t_{MPN/2}$ values were a factor of 2 lower for epizoic compared to ambient sediment succinate-utilizing SRB, succinate availability on the clams ought to be higher than in the surrounding sediment. Since no succinate is detected in the presence of the clam, it appears possible that the turnover of this substrate is strongly enhanced by bacterial populations which have been activated or introduced by the clam. Under anoxic conditions, *Arctica islandica* and other bivalves produce acetate, propionate and succinate, though release of the latter into culture media has still to be verified (Kluytmans et al. 1975, Oeschger 1990). At any rate, as major accumulators of organic compounds and potent bioturbators in coastal sediments, bivalves are likely to exert a positive influence on bacterial sulfate reduction (Hines et al. 1982, Hines & Jones 1985, Oenema 1990).

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