

ORIGINAL PAPER

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Sulfonates: novel electron acceptors in anaerobic respiration

Received: 2 May 1996 / Accepted: 8 June 1996

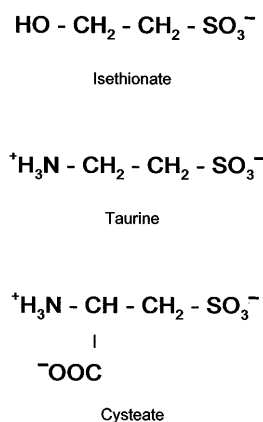
Abstract The enrichment and isolation in pure culture of a bacterium, identified as a strain of *Desulfovibrio*, able to release and reduce the sulfur of isethionate (2-hydroxyethanesulfonate) and other sulfonates to support anaerobic respiratory growth, is described. The sulfonate moiety was the source of sulfur that served as the terminal electron acceptor, while the carbon skeleton of isethionate functioned as an accessory electron donor for the reduction of sulfite. Cysteate (alanine-3-sulfonate) and sulfoacetaldehyde (acetaldehyde-2-sulfonate) could also be used for anaerobic respiration, but many other sulfonates could not. A survey of known sulfate-reducing bacteria revealed that some, but not all, strains tested could utilize the sulfur of some sulfonates as terminal electron acceptor. Isethionate-grown cells of *Desulfovibrio* strain IC1 reduced sulfonate-sulfur in preference to that of sulfate; however, sulfate-grown cells reduced sulfate-sulfur in preference to that of sulfonate.

Key words Sulfonate metabolism · Sulfate-reducing bacteria · Dissimilatory reduction of sulfonate-sulfur · *Desulfovibrio*

Introduction

Sulfonates are organosulfur compounds (Fig. 1) in which the sulfur atom is covalently bound to a carbon atom and

Fig. 1 Structures and trivial names of some aliphatic sulfonates. Sulfur oxidation state: +5



in which the sulfur is at an oxidation state of +5 (Vairavamurthy et al. 1993). Examples of sulfonates produced by diverse biota include sulfonolipids of bacteria, coenzyme M of methanogenic Archaea, sulfoquinovosyl diglyceride of phototrophs, isethionate of the squid axon, and taurine of vertebrate heart muscle and of several algae [for a short review, see Seitz and Leadbetter (1995)]. Taurine is also included in several „health“ drinks. Many sulfonate detergents, chemical dyes, and biological buffers (e.g., Hepes and Mopso) are products of industrial processes and have been introduced into natural habitats. Sulfonate-sulfur has been detected in forest soils (Fitzgerald 1976; Watwood et al. 1988) and in marine sediments (Vairavamurthy et al. 1994); the precise chemical structures of these organosulfur compounds remain unknown.

For some time it has been known that sulfonates can be metabolized as sole sources of carbon, energy, and (often) sulfur for aerobic bacterial growth (Stapley and Starkey 1970; Hashim et al. 1992; Thompson et al. 1995). More recent studies demonstrate that sulfonate-sulfur can be assimilated for both aerobic and anaerobic growth (Seitz et al. 1993; Uria-Nickelsen et al. 1993; Chien et al. 1995) by bacteria unable to utilize the entire molecule(s) as sole nutrient.

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Although Postgate (1951) and others (Ishimoto et al. 1954) have examined the ability of sulfate-reducing bacteria and their cell extracts to substitute sulfonate-sulfur for that of sulfate as electron acceptor, no evidence for this reduction, or for growth, was obtained. Because of the widespread use of isethionate in detergents, we enriched for and isolated a bacterium able to utilize isethionate for anaerobic respiration. Isethionate sulfur was reduced to form sulfide, while the remainder of the isethionate molecule served as an accessory electron donor and was oxidized to acetate.

Materials and methods

Enrichment and isolation

Samples of mud from the freshwater portion of School Street Marsh, Woods Hole, Mass., USA were added to anoxic medium (see below) containing ethanol (20 mM) as electron donor and isethionate (20 mM) as electron acceptor. The primary and secondary enrichment cultures were monitored for growth (OD_{650}) and sulfide production. A pure culture was obtained by anoxic "agar-shake" (dilution) series and streak-plating in an anaerobic chamber. Culture purity was monitored regularly by microscopic examination and lack of growth in samples placed in complex medium (AC broth, BBL). Cultures were incubated at 28°C.

Other cultures examined

Desulfobacter postgatei DSM 2034, *Desulfobacterium autotrophicans* DSM 3382, *Desulfobulbus propionicus* DSM 2032, *Desulfomicrobium baculatus* DSM 1741, *Desulfovibrio desulfuricans* ATCC 29577, *Desulfovibrio sulfodismutans* DSM 3696, and *Desulfuromonas acetoxidans* DSM 684 were kindly provided by Dr. Derek Lovley, then of the U.S. Geological Survey, Reston, Va.

Chemicals

All chemicals used were of the highest purity available from Aldrich, Eastman, Fisher Scientific, Fluka or Sigma. ^{35}S -sulfate was from ICN Radiochemicals. Sulfoacetaldehyde was synthesized by preparing the bisulfite adduct (Kondo et al. 1971). The adduct was converted to free sulfoacetaldehyde by mixing in solution with an equimolar amount of BaCl_2 , removing the precipitate, and forming the free acid by column chromatography (Dowex 50X8, hydrogen form); the effluent was concentrated under a stream of N_2 , and the product was neutralized with NaOH .

The bicarbonate-buffered and sulfide-reduced (final concentration measured to be 0.5–1 mM) mineral medium employed and the procedures for its preparation and use were essentially those of Widdel and Bak (1992), except that sodium sulfate was omitted. The different carbon and energy sources (electron donors) and terminal electron acceptors were as indicated in the text. Unless otherwise stated, the gas phase employed for growth was $\text{N}_2\text{-CO}_2$ (80:20, v/v).

Analytical procedures

Growth was monitored spectrophotometrically at 650 nm using a Spectronic 20 colorimeter. An OD of 0.2 was equivalent to 78 mg dry weight cells per liter. Positive growth was scored when cultures attained OD values at least 20–30 times greater than that of uninoculated media or of media lacking an electron donor or acceptor.

Dissolved sulfide was measured colorimetrically (Cline 1969); cysteate, isethionate, and taurine did not react with the reagents to give false positive reactions. Acetate, formate, and lactate were identified and quantified (by reference to the behavior of the authentic chemicals) by HPLC using refractometric methods following chromatography on an ion-exclusion and partition/adsorption column (Shodex Ionpak KC-811) used in conjunction with a Shodex KC-810P pre-column; the mobile phase was 0.1% (w/v) phosphoric acid. Samples were prepared by centrifugation of cultures, after which the supernatant fluid was collected and mixed with phosphoric acid (final concentration: 0.1% w/v). The solution was filtered again, and 20 μl of the filtrate was injected for analysis. The detection of desulfovirdin was as described by Postgate (1984).

Stoichiometric relationship of electron donors utilized and end products formed

Minimal medium was prepared (as described above) in 500-ml bottles fitted with screw caps containing butyl rubber septa to allow additions or withdrawals. Electron donors and acceptors were added to the bottles. The medium was then transferred to anaerobic culture tubes (Bellco, Vineland, N.J., USA) via syringes in 10-ml aliquots. Each growth experiment was done at least in duplicate. Growth was monitored until cultures reached the stationary phase. Acetate, formate, lactate, and sulfide assays were carried out before and after growth.

Preferential utilization of terminal electron acceptor

Cultures were inoculated into media with growth-limiting amounts of terminal electron acceptor (2.5 mM SO_4^{2-} or 2.5 mM isethionate). When growth ceased, equimolar amounts (10 mM final concentration) of ^{35}S -sulfate and isethionate were added via syringes. Both growth (OD_{650}) and the disappearance of radioactivity were then monitored. To measure changes in content of ^{35}S -sulfate, 0.5-ml samples were removed via syringes, and duplicate 0.2-ml portions were transferred into microcentrifuge tubes containing 0.3 ml zinc acetate (0.1 M). After agitation, the samples were centrifuged for 5 min to sediment the zinc sulfide formed; ^{35}S remaining in the supernatant phase was assumed to be that of sulfate and was measured by adding 0.3 ml of the supernatant to 5 ml scintillation fluid (Opti-fluor, Packard), and radioactivity was determined.

Results

Characteristics of the isolate

Strain IC1 was a strictly anaerobic, gram-negative, motile spirillum, $0.5\text{--}0.6 \times 2.7\text{--}2.9 \mu\text{m}$; endospores were not observed; a polar flagellum was revealed on negatively stained cells using transmission electron microscopy. We regard the isolate as a *Desulfovibrio* sp. because it was desulfovirdin-positive and because of the following characteristics. With sulfate as the terminal electron acceptor, the isolate could grow using ethanol, H_2 or formate (with 1 mM acetate present as additional carbon source), lactate, malate, or pyruvate, while acetate, *n*-butyrate, and *n*-propionate did not support growth. With lactate as the electron donor, fumarate, nitrate, sulfate, sulfite, or thio-sulfate (and, as demonstrated below, some sulfonates) could serve as electron acceptors for anaerobic respiratory growth. Pyruvate supported growth when present as sole oxidant

Table 1 Stoichiometric relationship between electron donors utilized to end products formed

Electron donor and acceptor (mM)	OD ₆₅₀	Donor utilized (mM)	Acetate		Sulfide	
			Produced (mM)	Percent of theoretical ^a	Produced (mM)	Percent of theoretical ^b
40 Lactate + 5 isethionate	0.17	7.1	11	91	5	100
40 Lactate + 7.5 isethionate	0.26	9.4	17	101	7.2	96
40 Lactate + 10 isethionate	0.34	12	21	95	10	100
40 Formate + 10 isethionate	0.18	23	11	110	11	110
40 Lactate + 10 sulfate	0.32	22	22	100	10	100

^aPercentages calculated assuming formation of one acetate from each lactate or isethionate consumed

^bPercentages calculated assuming formation of one sulfide from one electron acceptor (either isethionate or sulfate) when electron

donor is in excess. Values have been corrected for the initial sulfide concentration

and reductant. The strain did not grow when either lactate or isethionate was present alone (as sole electron donor/acceptor); no growth ensued when isethionate was tested as electron donor with sulfate as electron acceptor. The generation time of strain IC1 with lactate as electron donor and isethionate as electron acceptor (ca. 8.5 h) was similar to that with sulfate as terminal electron acceptor (ca. 9.5 h).

SSU rRNA sequence analysis

A partial sequence (J.R. Leadbetter, unpublished data) of strain IC1 (GenBank U60095; corresponding to *Escherichia coli* SSU rRNA nucleotide positions 108–519) was inferred from the sequence of the corresponding rDNA; this indicated that strain IC1 clusters with, and is most closely related to, *Desulfovibrio desulfuricans* ATCC 27774 (GenBank M34113), *D. desulfuricans* strain KRS1 (GenBank X93146), *Desulfomonas pigra* ATCC 29098 (GenBank M34404), and *Bilophila wadsworthia* ATCC 49260 (GenBank L35148) with 97.7%, 97.7%, 92.0%, and 90.9% sequence similarity, respectively. The partial sequence of the SSU rRNA of strain IC1 was significantly less similar to the other sequences currently available from major databases. Although the corresponding and complete sequence information from the type strain of *D. desulfuricans* (strain Essex 6; ATCC 29577, GenBank M37313) seems not to be available, based upon both phylogenetic and phenotypic arguments, Devereux et al. (1990) have concluded that both ATCC 27774 and the type strain of the genus are essentially identical. These authors have also noted that, of the *Desulfovibrio* strains examined, the ability to utilize nitrate as an electron acceptor for anaerobic respiration was restricted to these two strains.

Thus, given the observations that both strain IC1 and strain ATCC 29577 utilize isethionate and nitrate in anaerobic respiration, we conclude, on phenotypic and phylogenetic considerations, that the isolate studied here is most similar to *D. desulfuricans*.

Comparative growth with sulfate or isethionate as terminal electron acceptor

Growth of strain IC1 with lactate as electron donor and sulfate as terminal electron acceptor was in accord with the classic expectation (Traore et al. 1982) of two lactate needed to reduce one sulfate, which leads to the production of two acetate and one sulfide (Table 1). When the relationship between lactate consumption and isethionate reduction was examined with increasing concentrations of isethionate, a consumption ratio of approximately one lactate to one isethionate, giving rise to essentially two acetate and one sulfide, was noted. Of significance was the observation that increases in acetate and sulfide production were proportional to the increases in isethionate availability (Table 1). Growth with formate as electron donor and isethionate as electron acceptor also resulted in acetate accumulation (Table 1).

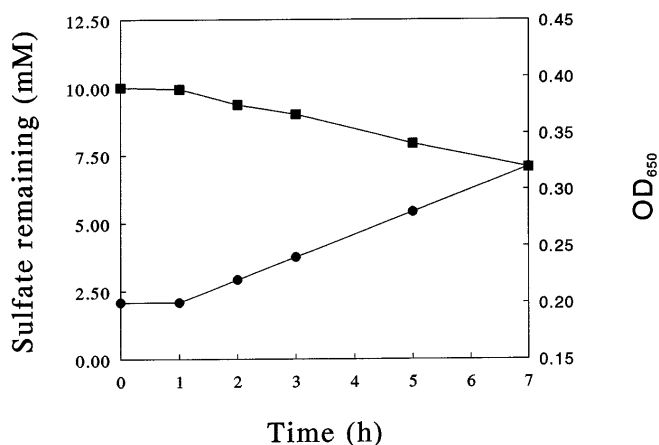


Fig. 2 Time course utilization of sulfate-sulfur [disappearance of ³⁵S-sulfate (■)] by a culture of strain IC1 grown with lactate (40 mM) + sulfate (2.5 mM, a growth-limiting amount) following addition, at time 0, of equimolar (10 mM final concentration) amounts of isethionate and ³⁵S-sulfate. Growth was monitored as increase in OD (●)

Specificity of sulfonate use for anaerobic respiration

Of the several aliphatic and aromatic sulfonates tested as electron acceptors (5 mM) with lactate (20 mM) as carbon and energy source, the strain was able to grow only with isethionate, cysteate, and sulfoacetaldehyde; compounds that did not function as electron acceptors included methane-, ethane-, *n*-propane-, 2-aminoethane- (taurine), 2-bromoethane-, 2-mercaptoethane- (Coenzyme M), *p*-analine-, *p*-toluene-, *m*-nitrobenzene-, and 3-aminobenzene-sulfonates, the „sulfonate“ buffers Hepes and Mopso, and sulfoacetate (technical grade).

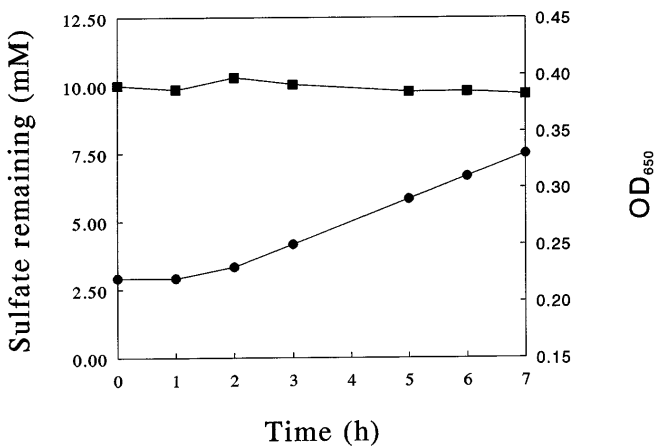


Fig. 3 Time course utilization of sulfate-sulfur [disappearance of ^{35}S -sulfate (■)] by a culture of strain IC1 grown with lactate (40 mM) + isethionate (2.5 mM, a growth-limiting amount) following addition, at time 0, of equimolar (10 mM final concentration) amounts of isethionate and ^{35}S -sulfate. Growth was monitored as increase in OD (●)

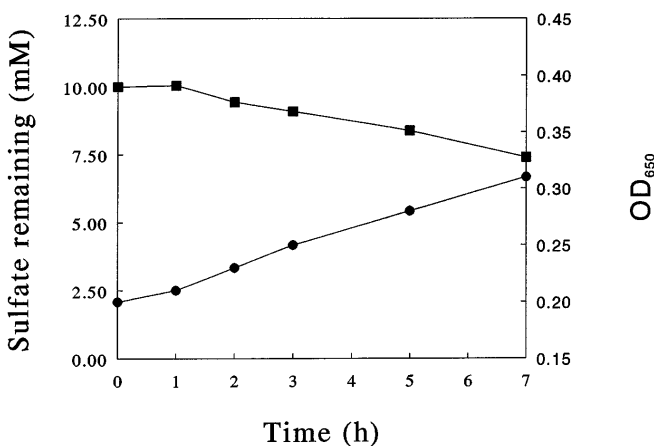


Fig. 4 Time course utilization of sulfate-sulfur [disappearance of ^{35}S -sulfate (■)] by a culture of strain IC1 grown with lactate (40 mM) + sulfate (2.5 mM, a growth-limiting amount) following addition, at time 0, of only ^{35}S -sulfate, (10 mM final concentration). Growth was monitored as increase in OD (●)

Preference in electron acceptor utilization

When the cells had attained maximal growth with sulfate (2.5 mM; a growth-limiting amount), equimolar concentrations of two electron acceptors (^{35}S -sulfate and unlabeled isethionate) were added; the OD of the culture increased after a short lag, and ^{35}S -sulfate disappeared from the growth medium (Fig. 2). However, when cells grew with isethionate (2.5 mM) as electron acceptor, ^{35}S -sulfate did not disappear although growth continued (Fig. 3). Moreover, with fumarate (2.5 mM) as electron acceptor for growth, ^{35}S -sulfate disappeared from the medium following addition of the mixture of ^{35}S -sulfate and non-radioactive isethionate (data not shown). Figure 4 displays the rate of ^{35}S -sulfate disappearance in a control culture growing in the absence of a competing electron acceptor.

Sulfonate utilization by authentic strains of sulfate-reducing bacteria

Several authentic sulfate-reducing bacteria were examined for the ability to utilize cysteate, isethionate, or taurine as electron acceptors for anaerobic respiratory growth. Of the strains examined, only three were able to utilize sulfonate-sulfur: *Desulfovibrio desulfuricans* grew only with isethionate, *Desulfomicrobium baculatus* grew with either cysteate or isethionate, while *Desulfobacterium autotrophicans* was able to grow only with cysteate; none of the strains grew with taurine, as was also the case for enrichment isolate IC1 (data not shown).

Lack of ability to ferment glycols

Strain IC1 was unable to ferment 1,2-propanediol, 1,3-propanediol, or tetraethylene glycol (all 20 mM); neither did the strain oxidize 1,2- or 1,3-propanediol with sulfate as terminal electron acceptor. Ethylene glycol was fermented by neither strain IC1 nor *D. desulfuricans* ATCC 29577.

Discussion

These results establish the ability of certain sulfonates to serve as terminal electron acceptors for anaerobic respiratory growth of various classic sulfate-reducing bacteria. Curiously, in none of the instances examined could any of these organosulfur compounds also act as a source of carbon and energy for growth either by dismutation reactions or with sulfate as terminal electron acceptor. Despite this observation, no evidence for toxicity of the sulfonates was noted when tested at concentrations up to 10 mM.

The strain examined in most detail (IC1) oxidized lactate and reduced sulfate with the expected stoichiometry of two lactate:one sulfate; however, this strain oxidized lactate and reduced isethionate in essentially a 1:1 ratio. The production of two acetate from one molecule each of

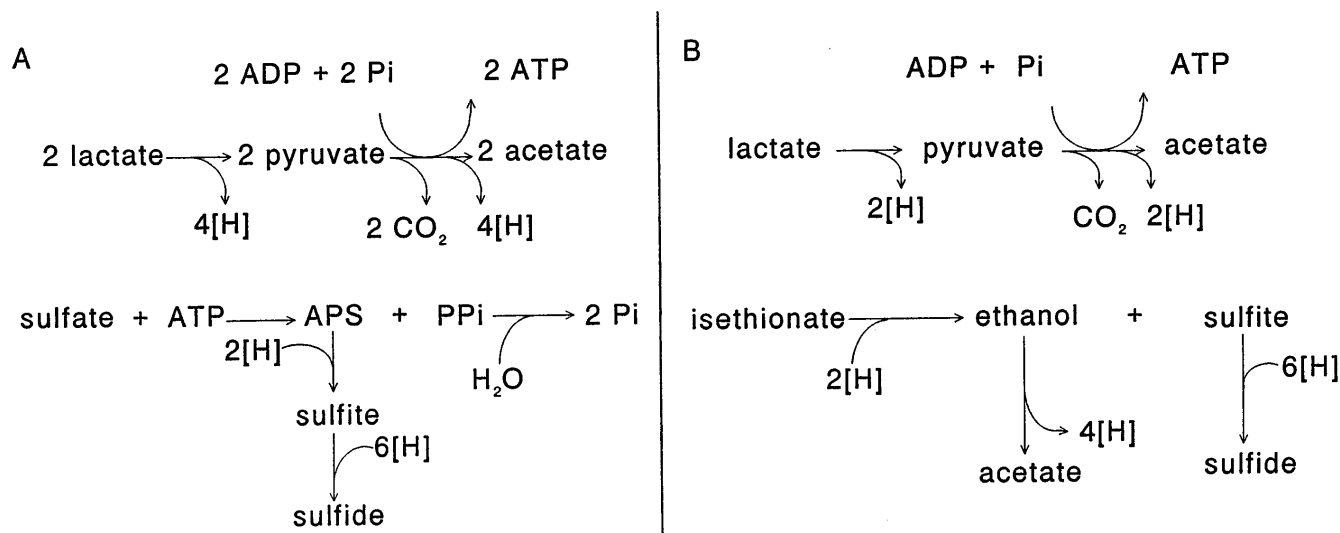
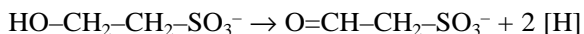


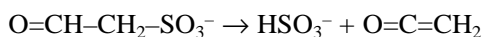
Fig. 5 Schemes, in part hypothetical, for dissimilatory reduction of **A** sulfate and **B** isethionate. The overall reactions are balanced to give no net oxidation or reduction

lactate and isethionate indicated that isethionate carbon was oxidized to give rise to the second acetate molecule formed. This conjecture was supported by studies using different ratios of lactate:isethionate and measuring the amount of acetate formed; even more convincing evidence was supplied by the demonstration of both sulfide and acetate formation resulting from growth on formate and isethionate. Although formate serves as a source of energy for many desulfobivrios, no growth ensues on a formate:sulfate mixture because formate does not serve as a source of carbon for biosynthesis (Hansen 1993). This was shown to be also true for strain IC1. Clearly, then, the only source of acetate for biosynthesis with the formate:isethionate mixture must be carbon from isethionate. A parallel situation may exist in strain IC1 cells growing with formate and cysteate (T. J. Lie, unpublished results) since both sulfide and acetate were produced, presumably reflecting deamination, decarboxylation, and desulfonation of the cysteate.

Two distinct pathways, both with identical overall stoichiometries and products, could account for the metabolism of isethionate to sulfite and acetate. The first of these presumes the oxidation of isethionate to sulfoacetaldehyde:



followed by desulfonation of the sulfoacetaldehyde to bisulfite and ketene by a sulfolyase:



Ketene would then presumably be converted to acetate by the nonenzymic addition of water. Such events have been proposed (Kondo and Ishimoto 1975; Kondo et al. 1977) to account for sulfoacetaldehyde transformation detected in extracts prepared from cells of an unidentified bacterium that were grown aerobically with taurine as a

source of carbon and energy. This explanation is an attractive one especially since we found that sulfoacetaldehyde can serve as terminal electron acceptor for strain IC1. Of the six electrons needed for reduction of sulfite to sulfide, four would be derived from oxidation of lactate and the remaining two from initial oxidation of isethionate.

A second possible pathway proceeds by initial reductive cleavage (Fig. 5) of the C-S bond of isethionate, releasing sulfite and ethanol:



Ethanol could then undergo oxidation to acetaldehyde and acetaldehyde to acetate, giving rise to 4 [H] in the usual manner [an ability shared by many *Desulfovibrio* sp. (Hansen 1993)]. Of the four electrons resulting from lactate oxidation, two would be used in the reductive cleavage and the remaining two, along with four derived from the oxidation of ethanol, would be available for reduction of the sulfite to sulfide. Studies under way should permit determination of which of these, or other, possibilities account for the transformation of isethionate.

It seems to us that one alternative explanation, namely the reduction of isethionate to 2-mercaptoethanol prior to release of sulfide, is less likely for two reasons. The reduction of sulfonate-sulfur to a thiol would itself require at least seven electrons, none of which would seem to be available from the carbon portion of the sulfonate molecule since the strain neither ferments nor oxidizes isethionate or sulfoacetaldehyde when sulfate is available as terminal electron acceptor. The failure to ferment glycols argues against the involvement of a diol dehydratase or a coenzyme-B₁₂-dependent shift of the terminal hydroxy group (Dwyer and Tiedje 1986), both of which, in this case, would result in the formation of acetaldehyde and sulfite. Also, the inability of our isolate to oxidize glycols [see Ouattara et al. (1992)] in the presence of sulfate as the terminal electron acceptor suggests that the pathway of isethionate oxidation to sulfoacetaldehyde, and then to sulfoacetate, with desulfonation of the latter compound to form acetate and sulfite, was unlikely. As shown above,

strain IC1 could not utilize sulfoacetate as the terminal electron acceptor.

An adaptation by cells to growth on isethionate is apparent. Cells that grew on and depleted available isethionate continued to utilize isethionate when equimolar amounts of isethionate and ^{35}S -sulfate were introduced. Cells growing with isethionate as sole terminal electron acceptor did not consume added ^{35}S -sulfate (T. J. Lie, unpublished results). In contrast, cells grown initially with sulfate continued to consume sulfate even when isethionate was added. The rate of ^{35}S -sulfate depletion and increase in OD was identical to that of the control experiment, in which ^{35}S -sulfate was the only electron acceptor. The arithmetic response(s) seen are not unlike those reported elsewhere (Dalsgaard and Bak 1994). This strongly suggests that isethionate was not used concomitantly with ^{35}S -sulfate during growth of sulfate-grown cells. However, we cannot rule out significant co-utilization of sulfate and isethionate until we have a more direct means of measuring any disappearance of isethionate.

The basis for the preferential utilization of isethionate-sulfur over sulfate-sulfur by cells grown on sulfonate is of continuing interest; future studies should reveal whether this process reflects a transport phenomenon or a down-regulation of enzymes involved in the sulfate-reduction pathway. If one assumes that the ATP used for sulfate activation (Fig. 5A) is not needed for utilization of sulfonate-sulfur and that the resulting pyrophosphate is hydrolyzed in order to drive the reaction (i.e., its bond energy is not otherwise conserved), then there would be no net gain of high-energy phosphate bonds from substrate level phosphorylation during sulfate reduction. In contrast (Fig. 5B), there would be a net gain of one such bond (per isethionate reduced with lactate as electron donor) when isethionate serves as electron acceptor, no matter which of the two pathways for isethionate metabolism were to be employed. This is consistent with the growth yields observed. It seems clear, then, that sulfonate utilization could be advantageous for these bacteria. We believe this to be the first demonstration of utilization of a sulfonate in anaerobic respiration and of the reduction of an organo-sulfur compound by sulfate-reducing bacteria. Whether a greater variety of sulfonates can serve in the dual capacity of oxidant and accessory reductant remains to be studied. Of special interest will be the identification of the sulfonates reported to be present in forest soils and marine sediments, and a determination of their ability to serve as electron acceptors in anaerobic respiration. It is equally tempting to imagine that sulfonate reduction could account, at least in part, for reports that a greater amount of sulfide than what might be expected is produced from the sulfate available (Dunnette et al. 1985) in some habitats.

Acknowledgements This study was begun in the Microbial Diversity course at the Marine Biological Laboratory, Woods Hole, Mass., USA, when J.R.L. was a student supported by a Bernard Davis Fellowship; it was continued by T.P. in the same course the following summer. Funds from the University of Connecticut Research Foundation, the Institute of Water Resources (U.S. Geological Survey Department of the Interior, grant 14-08-0001-G2009),

and Proctor and Gamble made continuation of the study possible. We thank colleagues Jeffrey Dugas and Chih-Ching Chien for their helpful comments.

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Note added in proof We are now aware that another organosulfur compound (dimethylsulfoxide) can serve as terminal electron acceptor for the anaerobic respiration of a *Desulfovibrio* (Jonkers HM, Maarel MJEC van der, Gemerden H van, Hansen TA (1996) Dimethylsulfoxide reduction by marine sulfate-reducing bacteria. *FEMS Microbiol Lett* 136: 283–287).