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Big Soda Lake (Nevada). 2. Pelagic sulfate reduction

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Abstract

The epilimnion of hypersaline, alkaline, rneromictic Rig Soda Lake contains an average 58 mmol sulfate liter-' and 0.4 pmol dissolved iron liter^{-1}. The monimolimnion, which is permanently anoxic, has a sulfide concentration ranging seasonally from 4 to 7 mmol liter^{-1}. Depth profiles of sulfate reduction in the monimolirnnion; assayed with a ^{35}S tracer technique and in situ incubations, demonstrated that sulfate reduction occurs within the water column of this extreme environment. The average rate of reduction in the monimolimnion was 3 pmol sulfate liter^{-1} d^{-1} in May compared to 0.9 in October. These values are comparable to rates of sulfate reduction reported for anoxic waters of more moderate environments. Sulfate reduction also occurred in the anoxic zone of the mixolimnion. though at significantly lower rates (0.025–0.090 μmol liter^{-1} d^{-1} at 25 m). Additions of FeS (1.0 mmol liter-') doubled the endogenous rate of sulfate reduction in the monimolimnion. while MnS and kaolinitc had no effect. These results suggest that sulfate reduction in Big Soda Lake is iron limited and controlled by seasonal variables other than temperature. Estimates of the organic carbon mineralized by sulfate reduction exceed measured fluxes of particulate organic carbon sinking from the mixolimnion. Thus, additional sources of electron donors (other than those derived from the sinking of pelagic autotrophs) may also fuel monimolimnetic sulfate reduction in the lake.

Lakes that contain zones of permanently anoxic water offer a good opportunity to study geochemical processes mediated by anaerobic microorganisms. Many of the processes that occur in anoxic sediments, such as denitrification, sulfate reduction, and methane production, also occur in anoxic waters. However, these processes have been studied much less extensively in anoxic waters than they have in sediments. This lack of information is especially acute in habitats that represent environmental extremes of temperature, salinity. or pH. Indeed, it has not been fully established whether patterns of bacterial mineralization in the water column of extreme environments are comparable to those occurring under more moderate conditions.

Sulfate reduction is an example of a bacterial process that can occur in anoxic water columns of both moderate and extreme environments. Sorokin (1970) demonstrated sulfate-reducing activity in waters of two meromictic lakes (Lake Belovod and Lake Gek Gel). In both cases, depth profiles of sulfate reduction exhibited two maxima: an upper maximum associated with a zone of bacterial photosynthetic and chemosynthetic activity and a deeper maximum near the sediment--water interface. Similar situations have been reported by others. For example, the highest rates of sulfate reduction were found just beneath the oxic--anoxic interface of a permanently stratified estuary (Indrebø et al. 1979) and in meromictic Knaack Lake (Parkin and Brock 1981). Sulfate reduction also was reported immediately above the sediment water interface in freshwater Rotsee in Switzerland, although this activity may have been due to resuspended sediment rather than plankton (Kohler et al. 1984). With respect to extreme environments, Jørgensen et al. (1979) conducted a detailed study of the sulfur cycle in the hot brines of Solar Lake. In that lake, rates of sulfate reduction increased with depth from the chemocline to a maximum rate near the sediments and were adapted to the in situ temperature (48°C). Interestingly, the rates of this thermophilic sulfate reduction were comparable in magnitude to those measured in Lake Belovod (Sorokin 1970)—a more moderate environment in terms of temperature and salinity.

Apart from these studies, however, little work has been done on planktonic sulfate

reduction. To our knowledge. rates of this process in a highly alkaline, saline environment have not been reported. Therefore, we chose to examine sulfate reduction in the water column of Big Soda Lake, Nevada. The lake is moderately hypersaline, alkaline (pH 9.7), and meromictic (see Zehr et al. 1987). Since the monimolimnion is permanently anoxic and the lower mixolimnion is seasonally anoxic, the lake is an unusual habitat in which to study anaerobic microbial processes. Our goals were to determine whether sulfate reduction occurs in these hypersaline, alkaline waters, the extent and distribution of the activity, some of the factors controlling the process, and the contribution of sulfate reduction to organic carbon mineralization within the lake. We now report that rates of planktonic sulfate reduction in Big Soda Lake are comparable with rates reported for less extreme environments. The activity was evenly distributed throughout the rnonimolimnion and appears to be iron limited.

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Materials and methods

Sulfate reduction– Water samples were collected at depth from Big Soda Lake with a 7-liter Niskin bottle and transferred directly to sterile 10-ml Glaspak syringes (Becton-Dickinson, Inc.) for field experiments. The syringes were flushed with several volumes of lake water to ensure removal of residual air, filled to volume, and capped. Care was taken to remove bubbles trapped within the container before closure. The syringes were capped with injection hubs, which were made from plastic disposable syringe needles by removing the stainless steel needle and placing a small piece of butyl rubber inside the Luer hub. When placed on a syringe. the butyl rubber served as a septum. Water samples were stored in an ice bath before beginning an experiment (1–3 h). We determined rates of in situ sulfate reduction in sets of duplicate or triplicate syringes with the ^{35}S tracer technique (Jørgensen 1978). An N_2-sparged solution of carrier-free $Na_2{}^{35}SO_4$ (50 or 100 μCi, 0.1 ml, New England Nuclear Corp.) was added to each sample with a syringe and needle. The syringes were placed in nylon-mesh bags and incubated in the lake at the depths from which the water samples were collected. At the end of the incubation (2 d, unless otherwise indicated), samples were removed from the lake and transported to shore in an ice bath for analysis. The contents of each syringe were transferred to a 30-ml serum bottle. which was sealed with a Teflon-coated septum and a crimp. The bottles were connected to a flushing train (Smith and Klug 1981a). 10 ml of 3 N HCl added, and the H_2S in the saniple was stripped and flushed into two traps, each containing 10 ml of a solution of zinc acetate (20 g liter^{-1}) + Antifoam B (Dow Corning Corp.; 10 drops liter^{-1}). Samples were sparged for 30 min. We then added 10 ml of Aquasol (New England Nuclear) to the contents of each trap and determined the radioactivity with a Packard Tri-Carb liquid scintillation counter. Results were corrected for counting efficiency, as determined with [^{14}C]toluene as internal standard, and for recovery efficiency of $H_2{}^{35}S$ in the flushing train (85%).

The effect of various amendments on sulfate reduction was examined with in situ incubations. We collected water samples in 10-ml syringes as previously described and amended quadruplicate sets with 0.2 ml of an O_2-free stock of one of the following (concentrations are indicated in text): distilled water, FeS, MnS, kaolinite, sodium tungstate, methanol, sodium lactate, sodium acetate, 2-bromoethanesulfonic acid (BES), or H_2. The FeS and MnS stocks were prepared by combining equimolar solutions of $FeCl_2 \cdot 4H_2O$ or $MnCl_2 \cdot 4H_2O$ and $Na_2S \cdot 9H_2O$. In addition, another set of syringes was filled with a water sample from which the dissolved CH_4 had been purged with N_2 for an hour. as described by Iversen et al. (1987). Sulfate reduction rates then were assayed with ^{35}S as previously described.

Analytical techniques---Sulfide was analyzed by the methylene blue method (Cline 1969). Because of high pH and high sulfide content in the monimolimnion, the method was modified. To avoid exposure to air,

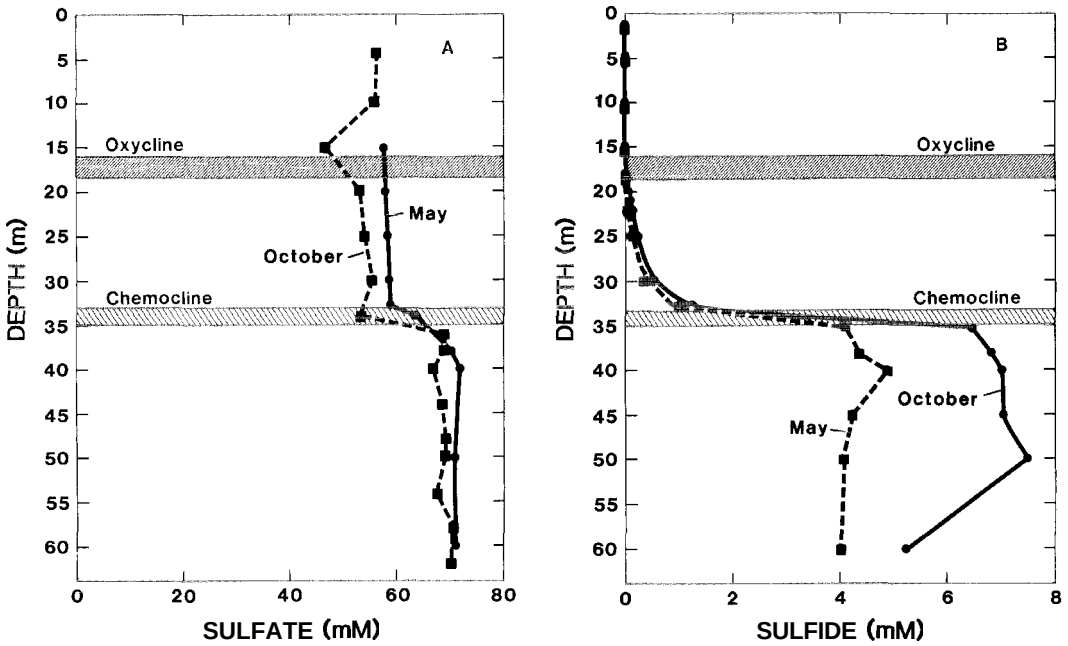

Fig. 1. Depth profiles of sulfate and sulfide in Big Soda Lake in May and October 1983. The oxycline denotes the region of oxygen depletion.

water samples were transferred with a syringe directly from the Niskin sampler into tubes containing the appropriate reagent. Sample volume was 20 ml; reagent volume was 0.8 ml for samples containing 0–0.03 mM sulfide or 1.6 ml for those with 0.03–0.3 or 0.3–1.6 mM sulfide. For samples taken below the chemocline (which contained >3 mM sulfide), 1 ml of sample was added to 1.6 ml of reagent prepared for the 0.3–1.6 mM sulfide standard curve. I-ollowing color development, all samples were diluted as necessary to obtain an absorbance reading that conformed with Beer's law at 670 nm. Water samples were assayed for sulfate content by gravimetric analysis (Am. Public Health Assoc. 1971).

Results

Chemical profiles—Depth profiles of sulfate concentration in Big Soda Lake showed little variation between spring and fall 1983 (Fig. 1A). The average sulfate concentration in the mixolimnion was 55 mmol liter^{-1}, while the average sulfate concentration in the monimolimnion was somewhat higher at 69 mmol liter-'. In both May and October the water column was oxygenated from the surface down to 16–18 m; sulfide was first detectable at 20 m (Fig. 1B). The sulfide concentration at this depth was 0.03 and 0.05 mmol liter ^{1} in May and October. In general, the sulfide concentration increased with depth in the anoxic mixolimnion, increasing dramatically across the chemocline, but was relatively constant throughout the monimolimnion. Sulfide values in the monimolimnion did differ between the two sampling periods. May values were 4 mM, as compared to a range of 5–7 mM in October of both 1982 and 1983 (data not shown for 1982).

Sulfate reduction—Water samples taken from 40 m produced $H_2{}^{35}S$ when amended with $^{35}SO_4{}^{2-}$ and incubated at depth in the lake (Fig. 2). The time-course of sulfate reduction was linear for at least 60 h, with no apparent initial time lag. Consequently, a standard incubation time of 48 h was used for subsequent assays. In this case (Fig. 2), the rate of sulfate reduction was 0.74 μmol $SO_4{}^{2-}$ liter-' d^{-1}.

Depth profiles of sulfate reduction in the water column of Big Soda Lake (Fig. 3) were

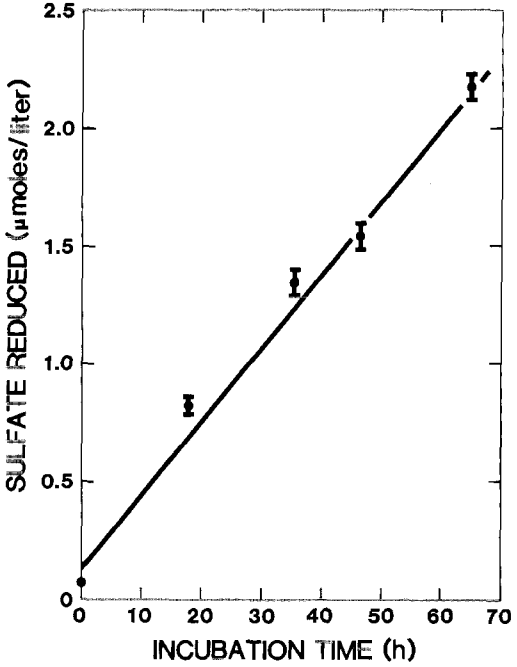

Fig. 2. Time-course of sulfate reduction for a water sample from 40 m amended with $^{35}SO_4^{2-}$ and incubated in the lake at the depth of origin. Error bars represent ±1 SD.

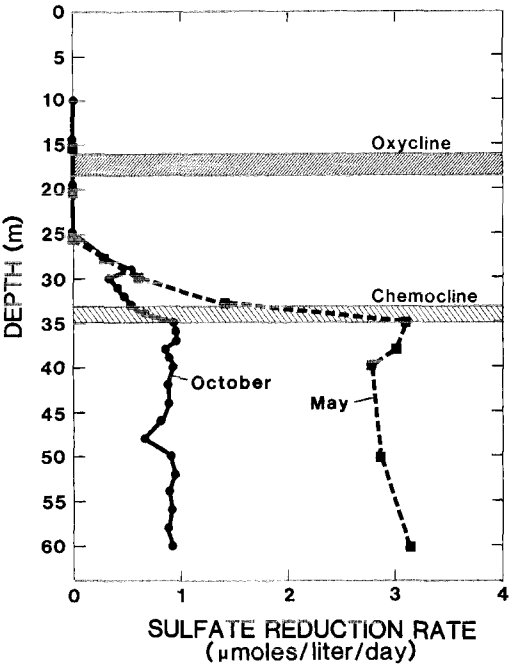

Fig. 3. Depth profiles of sulfate-reducing activity for water samples collected in May and October 1983, when amended with $^{35}SO_4^{2-}$ and incubated in the lake at the depth of origin. The oxycline denotes the region of oxygen depletion.

similar in nature to the sulfide depth profiles (Fig. 1B). The rate of sulfate reduction in the monimolimnion in May was about 3 μmol SO_4^{2-} reduced liter^{-1} d^{-1}, and in October the rate was about threefold lower (0.9 μmol liter^{-1} d^{-1}). In both cases, the rate was relatively constant with depth beneath the chemocline. Sulfate reduction also occurred in the anoxic mixolimnion, though at significantly lower rates. Although not evident from the scale in Fig. 3, measurable rates of sulfate reduction did occur at 25 m, but not at 20 m. The rates at 25 m ranged from 0.025 to 0.090 μmol SO_4^{2-} reduced liter^{-1} d^{-1}. In October 1983 a photosynthetic bacterial layer was located at 20–21 m (R. W. Harvey pers. comm.), but no measurable sulfate-reducing activity was evident in samples taken from this depth, either when they were incubated in the dark or under the natural light regime.

Amendment experiments—The effect of iron and other inorganic compounds on sulfate reduction in the monimolimnion was studied in October 1983 under in situ conditions (Table 1). Iron was added as FeS to prevent a significant change in the dissolved sulfide pool. The FeS addition doubled the rate of sulfate reduction over that of the control. On the other hand, the addition of MnS slightly inhibited sulfate reduction, while kaolinite had no significant effect. The kaolinite added was 20 times greater (by weight) than the FeS or MnS added. Sodium tungstate, which inhibits sulfate-reducing bacteria (Taylor and Oremland 1979) inhibited sulfate reduction in Big Soda Lake, but the inhibition was incomplete (about 64%) at the concentration of Na_2WO_4 tested.

In a similar set of experiments, the effect of adding potential electron donors for sulfate-reducing bacteria was tested (Table 2). The addition of methanol had no effect on sulfate reduction, whereas lactate and acetate were slightly stimulatory. Hydrogen, on the other hand, increased the rate of sulfate reduction twofold over that of the control.

Table 1. Effect of selected inorganic compounds on sulfate reduction in the monimolimnion of Big Soda Lake. Samples were collected from 40 m in October 1983. Standard deviation in parentheses.

Addition	Final concn	Rate of sulfate reduction (μmol liter^{-1} d^{-1})	Fraction of control
None	—	0.81 (0.03)	1.00
FeS	88 mg liter^{-1}	1.61 (0.14)	1.99
MnS	87 mg liter^{-1}	0.69 (0.01)	0.85
Kaolinite	800 mg liter^{-1}	0.88 (0.09)	1.09
Na_2WO_4	40 mM	0.29 (0.06)	0.36

Table 2. Effect of added electron donors on sulfate reduction in the monimolimnion of Big Soda Lake. Samples were collected from 40 m in October 1983. Standard deviation in parentheses.

Addition	Final concn (mM)	Rate of sulfate reduction (μmol liter^{-1} d^{-1})	Fraction of control
None	—	0.81 (0.03)	1.00
Methanol	1	0.84 (0.08)	1.04
Lactate	1	0.94 (0.01)	1.16
Acetate	1	1.04 (0.12)	1.28
H_2	3.8	1.62 (0.08)	2.00

The amount of H_2 added was in excess of its solubility in these saline waters, hence an H_2 gas phase was present in the syringe. This excess ensured that the added H_2 would not be depleted over the course of the incubation. In addition, the effect of altering the dissolved CH_4 pool and the rate of CH_4 production was examined (Table 3). The endogenous rate of sulfate reduction was unaffected by sparging a water sample with N_2 to remove ambient CH_4, or by increasing the ambient CH_4 pool by exogenous additions, or by adding BES—an inhibitor specific for methane production.

Discussion

The monimolimnion of Big Soda Lake is a thermally stable, anoxic environment that contains high concentrations of dissolved organic carbon (60 mg liter^{-1}) and dissolved methane (50–60 μM) (Kharaka et al. 1984; Kimmel et al. 1978; Iversen et al. 1987). It also has a substantial amount of free sulfide (4–7.5 mM; Fig. 1B), which exceeds the range of 0.025–2.5 mM reported for most other meromictic lakes with anoxic bottom waters (Hamner et al. 1982; MacIntyre and Melack 1982; Parkin and Brock 1981) and tropical Solar Lake (Jørgensen et al. 1979). Sulfate concentrations are also high, nearly three times greater than seawater. Both sulfate and sulfide exhibit uniform depth profiles within the monimolimnion, as do methane, dissolved organic carbon, and the major inorganic cations and anions (Oremland and Des Marais 1983; Kharaka et al. 1984). The absence of a sulfide gradient of increasing concentration near the sediment–water interface suggests that either the sulfide is produced primarily within the water column rather than entering the monimolimnion by diffusion from the underlying sediments or that vertical mixing in the monimolimnion prevents the establishment of a gradient.

In situ incubations with ^{35}S-tracer experiments confirmed that sulfate reduction occurs in the water column of this extreme environment. In general, the activity was evenly distributed throughout the monimolimnion for both sampling periods, but the rate was threefold higher in May than in October (Fig. 3). This difference between May and October (which was also evident in 1982, data not shown) may be linked to seasonal changes in phytoplankton populations in the lake. During thermal stratification (May–November) the epilimnion has low concentrations of dissolved inorganic nitrogen and consequently low phytoplankton biomass (Cloern et al. 1983). However, when the epilimnion is isothermal (December–March), phytoplankton biomass increases significantly. This bloom dies off in late winter–early spring and can be detected in seston traps placed beneath the chemocline (Cloern et al. 1987). This increased

Table 3. Effect of altering methane concentrations on sulfate reduction in the monimolimnion of Big Soda Lake. Samples collected from 40 m in October 1983. Standard deviation in parentheses.

Addition	Final CH_4 concn (μM)	Rate of sulfate reduction (μmol liter^{-1} d^{-1})	Fraction of control
None	41	0.81 (0.03)	1.00
BES*	41	0.81 (0.03)	1.00
N_2-sparge	0.4	0.81 (0.02)	1.00
CH_4	64	0.87 (0.02)	1.07

* 2-bromoethanesulfonic acid, an inhibitor of methane production (Gunsalus et al. 1978). Final concentration was 40 mM.

input of particulate organic matter may be responsible for the higher sulfate-reducing activity found in May. Indrebø et al. (1979) reported that sulfate reduction rates in a stratified estuary correlated with primary productivity in the overlying surface water.

The rates of sulfate reduction in the monimolimnion of Big Soda Lake ranged from 0.7–3.2 pmol sulfate reduced liter^{-1} d^{-1}. They correspond to turnover times for the monimolimnetic sulfate pool of 60–270 yr (with respect to suifate reduction only). These values are similar to the rates of sulfate reduction found in other anoxic waters. In the bottom waters of meromictic Lake Belovod, Sorokin (1970) measured rates up to 3.8 pmol of sulfate reduced liter^{-1} d^{-1}, while the rate below the chemocline in Lake Gek Gel was 0.03–0.3 pmol liter^{-1} d^{-1}. Jørgensen et al. (1979) reported rates of 1–7 pmol of sulfate reduced liter^{-1} d^{-1} in the 45°C bottom waters of Solar Lake, and in a stratified Norwegian estuary sulfate reduction reached a maximum of 1.0 pmol liter^{-1} d^{-1} (Indrebø et al. 1979). Unlike these other habitats, monimolimnetic sulfate reduction in alkaline Big Soda Lake was uniform with depth (Fig. 3). On an areal basis, the total amount of sulfate reduced in the water column in May was 80 mmol m^{-2} d^{-1}. By comparison, in surface sediments collected in July and incubated at 25°C (which is about 15°C above in situ temperature), the rate of sulfate reduction was 140 (SD – 10) μmol SO_4^{2-} reduced (liter sediment)$^{-1}$ d^{-1} (K. L. Smith unpubl. data). The amount of sulfate reduced in the water column, then, was equivalent to a m^2 sediment column at least 60 cm deep. This calculation, however, assumes that the activity was distributed evenly throughout the sediment depth profile, which is usually not the case. For example, in a coastal marine sediment the rate of sulfate reduction at 60 cm is >20-fold lower than the reduction rate in the upper 10 cm (Jorgensen 1977). Obviously, then, sulfate reduction in the water column of Big Soda Lake is a significant fraction of the total (sediment + water) sulfate-reducing activity within the lake on an areal basis.

Meromixis in Big Soda Lake is a relatively recent event (Hutchinson 1937; Oremland and Des Marais 1983; Zehr et al. 1987). On the basis of sulfate and chloride concentrations in the lake in 1882 and 1980 and the assumption that sulfate reduction is the only process that modifies the sulfate concentration in the bottom water, Kharaka et al. (1984) calculated an average sulfate reduction rate of 6.6 pmol liter^{-1} d^{-1} for a 60-yr period from 1920–1980. Although this value represetits a composite rate for the sediments and the water column and does not account for sulfide oxidation, it agrees fairly well with the measured rates of sulfate reduction reported here.

In contrast to the monimolimnion, sulfate reduction rates in the mixolimnion of the lake were much lower (Fig. 3), with no significant difference between sampling dates. In the region of the photosynthetic bacterial layer (in October), sulfate reduction was undetectable in samples incubated in the dark or with in situ light conditions. Both the light and dark sample sets were incubated for 2 d, which would eliminate the potential for rapid reoxidation by photosynthetic bacteria of the [^{35}S]sulfide produced. Therefore, our results indicate that sulfate reduction is not closely coupled with autotrophic processes in the photosynthetic bacterial layer. This finding contrasts with the observations of other workers who reported sulfate reduction maxima in the vicinity of such layers. Sorokin (1970) found a localized maxinium of sulfate reduction just beneath a zone of high bacterial photo- and chemosynthesis and suggested that the sulfate reducers were dependent on freshly fixed organic matter from this biosynthetic zone. On the other hand, Parkin and Brock (1981) concluded that regeneration of sulfate by photosynthetic bacteria was the mechanism responsible in freshwater Knaack Lake. Apparently, neither of these situations applies to mixolimnetic suifate reduction in Big Soda Lake.

In general, sulfate reduction would be controlled by availability of an essential nutrient(s), availability of electron acceptor(s), availability of electron donor(s), or physical or chemical conditions that might restrict growth. In Rig Soda Lake, which has high sulfate concentrations, the supply of electron acceptor is not a limiting factor. However, each of the other three factors might

be. Since the lake is a unique habitat and very little was previously known about sulfate reduction in such environments, amendment experiments were conducted to identify some of the potential controls on sulfate reduction in the monimolimnion of the lake.

Sulfate-reducing bacteria have an absolute requirenient for relatively high concentrations of iron (Postgate 1979), which is incorporated into electron-transferring proteins and hydrogenases (Odum and Peck 1984). Ironically, however, sulfide production by these organisms lowers soluble iron concentrations via FeS precipitation. Unlike in sediments, where sulfate reducers remain associated with the particulate iron, in planktonic environments, such as Big Soda Lake, this process could readily diminish iron availability. In general, the dissolved iron concentration in the lake is low, 0.04 μM in the mixolimnion and 1.2 in the monimolimnion (Axler et al. 1978; Kharaka et al. 1984). When added to water samples collected from 40 m, FeS stimulated sulfate reduction (Table 1). Laanbroek and Geerligs (1983) reported that iron-saturated illite stimulated pure cultures of *Desulfobacter*. However, the effect appeared to be due to the presence of particulate surfaces as it was independent of the cation used to saturate the illite. Such independence was not the case in Big Soda Lake because neither MnS nor kaolinite additions stimulated sulfate reduction. It appears more likely that sulfate reduction in the lake was enhanced either by insoluble FeS or by Fe^{2+} kept in solution via chelation. Chelation could be achieved with siderophores or the abundant dissolved organic carbon present in bottom water. The mechanism that sulfate-rcducing bacteria use to sequester iron is unknown, and further study is needed to interpret the response of these organisms to iron-limiting conditions in natural environments. It is interesting to speculate that the higher sulfate-reducing activity found in the monimolimnion in May could have been due in part to particulate iron associated with the senescing phytoplankton bloom.

In typical marine and freshwater sediments the predominant electron donors utilized by sulfate-reducing bacteria are hydrogen and acetate (Lovley and Klug 1983; Sørensen et al. 1981; Smith and Klug 1981b; Winfrey and Ward 1983). Lactate is often used for culturing sulfate-reducing bacteria (Postgate 1979), while methanol stimulates methane production in Big Soda Lake sediments (Oremland et al. 1982) and also can be utilized by natural populations of sulfate reducers in marine sediments (King 1984; Braun and Stolp 1985). When added to Big Soda Lake bottom water, only hydrogen stimulated the rate of sulfate reduction more than 30% over thc rate of the control (Table 2). This result does not mean that acetate, methanol, and lactate are not natural substrates, but it does imply that if they are natural substrates, then the concentrations are not rate-limiting factors. The hydrogen result indicates that electron donor supply might be limiting.

Another potential electron donor for sulfate reduction is methane. Iversen et al. (1987) demonstrated that anaerobic methane oxidation occurs in the water column of Big Soda Lake and has a depth profile very similar to that of sulfate reduction. However, no evidence linking these two processes was found (Table 3: Iversen et al. 1987). Neither an increase in the ambient methane concentration, nor the removal of the ambient methane, nor the inhibition of methane production had any effect on the rate of sulfate reduction. The addition of 40 mM Na_2WO_4 (a competitive inhibitor of sulfate reduction in sediments and pure cultures: Banat and Nedwell 1984; Taylor and Oremland 1979) to bottom water from Big Soda Lake decreased the rate of sulfate reduction by 64% (Table 1), but had no effect on anaerobic methane oxidation (Iversen et al. 1987). Even if methane is an electron donor for sulfate reduction in the lake, methane oxidation could account for only 2% of the sulfate-reducing activity in the monimolimnion (Iversen et al. 1987).

The quantity of carbon mineralized via sulfate reduction in the moniiiiolimnion (the zone of >95% of the activity) can be estiniated by assuming an overall pattern of carbohydrate (e.g. glucose) intermediary metabolism as follows:

Table 4. Integrated monimolimnetic sulfate reduction and equivalent carbon mineralization compared with estimates of mixolimnetic productivity in Big Soda Lake.

	Sulfate reduced (mmol m^{-2} d^{-1})	Carbon mineralized by sulfate reduction* (g m^{-2} d^{-1})	Carbon fixed in mixolimnion† (g m^{-2} d^{-1})	Mineralized by sulfate reduction (%)
May	80	1.94	0.95	204
Oct	24	0.59	0.70	84
Annual	(mol m^{-2} yr^{-1})	(g m^{-2} yr^{-1})	(g m^{-2} yr^{-1})	
	8.76–29.2	210–700	500	42–140

* Assumes that 1 mol of sulfate mineralizes 24 g of carbohydrate (Indrebø et al. 1979).
† From Cloern et al. 1987.

$$C_6H_{12}O_6 + H_2O \rightarrow 2CH_3COOH + 2CO_2 + 4H_2. \quad (1)$$

Since metabolism of acetate and hydrogen by sulfate respirers proceeds as follows:

$$CH_3COOH + SO_4^{2-} \rightarrow 2CO_2 + S^{2-} + 2H_2O, \quad (2)$$

and

$$4H_2 + SO_4^{2-} \rightarrow S^{2-} + 4H_2O, \quad (3)$$

then 1 mol of glucose (72 g C) can potentially reduce 3 mol of sulfate (discounting assimilatory processes); 1 mol of sulfate, therefore, can mineralize 24 g of carbon. Integrated monimolimnetic sulfate reduction in Big Soda Lake consumes 24–80 mmol SO_4^{2-} m^{-2} d^{-1}, which is equivalent to 210–700 g C mineralized m^{-2} yr^{-1} (Table 4). When compared with annual productivity of the mixolimnion, sulfate reduction in the monimolimnion can consume 42–140% of the carbon fixed in the upper waters. However, results of sediment trap experiments indicate that about 90% of this fixed carbon is mineralized above the chemocline and therefore does not enter the monimolimnion (Cloern et al. 1987). Thus, only about 50 g C m^{-2} yr^{-1} enters the monimolimnion from the sinking of biogenic seston. The surface area of the chemocline is only 25% of the surface area of the lake (Kimmel et al. 1978). Since the morphometry of the lake is cone-shaped, the additional carbon fixed in the remaining 75% of the mixolimnion could be funneled into the monimolimnion. This effect could potentially increase the downward flux of organic carbon by as much as a factor of 4, to approximately 200 g C m^{-2} yr^{-1}. On the basis of the rates we measured in October, this quantity of carbon would satisfy 95% of the sulfate reduction in the water column. However, it does not account for sediment sulfate reduction, other respiratory processes, or that water column sulfate reduction rates were 3.3-fold greater in May than in October. Therefore, it appears that downward flux of plankton-derived electron donors entering the monimolimnion cannot fuel the quantity of sulfate reduction occurring therein, suggesting that additional sources of electron donors must be available in the monimolimnion.

The source of these electron donors is not readily apparent. The possibilities include inputs derived from H_2 in geothermal springs, organic carbon entering via groundwater, abundant dissolved organic carbon available in the water column, and benthic productivity in the mixolimnion. The most plausible explanation seems to be the latter. The littoral zone of the lake contains seasonally abundant stands of macrophytes (*Ruppia* sp.: Oremland 1983), while extensive cyanobacterial-*Beggiatoa* mats occur beyond the littoral zone. However, the answer to this question must await future studies that quantify the extent of mixolimnetic benthic productivity and its flux into the monimolimnion.

In summary, sulfate reduction occurs in the water column of an alkaline, hypersaline, meromictic lake, both in the monimolimnion and in the anoxic portions of the mixolimnion. The rate of reduction is similar to rates found in other less extreme environments, but depth profiles lack the maxima and minima reported for other planktonic habitats. Sulfate reduction in Big Soda Lake appears to be iron limited, which

may be an important factor controlling the process within this habitat. Although this study examined sulfate reduction as a process and not the organisms per se, the pH of the lake (9.7) is above the upper limit reported by Postgate (1979) for sulfate-reducing bacteria. Rig Soda Lake may represent a habitat in which these organisms are stressed to the limit of pH tolerance. or, it is possible that populations of unique sulfate-reducing bacteria are present in the lake. The isolation and identification of such organisms is a goal worthy of future effort.

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