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The Biogeochemistry of Hydrogen Sulfide: Phytoplankton Production in the Surface Ocean

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The biogeochemistry of hydrogen sulfide: Phytoplankton production in the surface ocean

Abstract—Hydrogen sulfide can exist in oxic waters in the form of a dissolved gas, dissociated ions, dissolved metal sulfide complexes, and particulate metal sulfides. The sum of the dissolved species is termed total dissolved sulfide (TDS). In addition to the hydrolysis of carbonyl sulfide, it has been speculated that phytoplankton may produce TDS. We present results from preliminary culture studies which demonstrate that phytoplankton produce TDS and particulate acid-volatile sulfide (pAVS). The phylogenetic order of TDS + pAVS production (per unit cell volume) for the oceanic species examined is *Synechococcus* sp. > *Emiliania huxleyi* ≈ *Pyramimonas obovata* > *Thalassiosira oceanica*. Moreover, TDS and pAVS production increases when the concentrations of uncomplexed trace metals in culture media are also increased, suggesting metal detoxification via the formation of metal sulfide complexes.

Aqueous hydrogen sulfide exists in seawater as the dissolved gas, its dissociated bisulfide (SH⁻), and sulfide (S²⁻) ions and is also associated with dissolved metals in metal sulfide complexes. Here the term "total dissolved sulfide" (TDS) refers to the sum of these species. TDS was previously considered too unstable with respect to oxidation by oxygen in surface waters to play any significant role in the biogeochemistry of sulfur (Östlund and Alexander 1963). Nevertheless, the presence of picomolar concentrations of TDS in the upper ocean has been reported (Cutter and Krahorst 1988; Luther and Tsamakis 1989; Andreae et al. 1991). Luther and Tsamakis (1989) reported that sulfide can persist in seawater for months, even in the presence of the oxidants O₂, H₂O₂, and IO₃⁻. They concluded that this stability arises from the formation of metal sulfide complexes. These results have focused interest on the contribution of TDS to the atmospheric sulfur budget (Andreae et al. 1991) and on the possible role of TDS in trace metal complexation (Dyrssen and Wedborg 1989).

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However, the mechanisms responsible for the production of TDS in surface waters are not well understood.

One likely source of TDS in oxic seawater is carbonyl sulfide (OCS) hydrolysis, which proceeds at a rate sufficient to support the observed surface concentrations of TDS (Elliott et al. 1987, 1989). In depth profiles from the western North Atlantic, however, subsurface maxima in TDS occasionally correspond to those of chlorophyll *a* (Cutter and Krahorst 1988; Luther and Tsamakis 1989), implying the involvement of phytoplankton in TDS production. Indeed, the possibility that marine phytoplankton might produce TDS has been suggested by Andreae (1990). Biotic production of TDS under oxic conditions is not unprecedented; H₂S_(g) emission by terrestrial plants is well documented (e.g. Rennenberg 1984), although very little is known about production by marine plants. In studies of resistance to Hg poisoning, Davies (1976) measured up to 1 μmol liter⁻¹ TDS in cultures of the neritic phytoplankton *Dunaliella tertiolecta*. The remarkable tolerance of *D. tertiolecta* to Hg was largely attributed to the detoxification of the metal within the cell, possibly by the precipitation of highly insoluble mercuric sulfide (Davies 1976).

We examine the production of TDS using results from laboratory cultures of four oceanic phytoplankton species and two neritic species. We had two objectives. The first was to ascertain whether oceanic phytoplankton species are capable of TDS production. Our goal here was to determine whether TDS production is a general feature of marine phytoplankton populations. Our second objective was to identify factors that affect TDS production. With respect to this second objective, we investigated two factors that could control the production of TDS: nutrient and trace metal concentrations. Under low nutrient conditions, TDS production could be a part of the assimilatory sulfate uptake pathway. In this scenario, which was first proposed by Rennenberg (1984) to account for H₂S_(g) emission by terrestrial plants,

Table 1. Total dissolved sulfide (TDS), particulate acid-volatile sulfide (pAVS), and total sulfide (TS = TDS + pAVS) produced by phytoplankton during log phase growth in f/20 medium.

Clone*	Single cell vol.† (μm^3)	TS per cell‡ (pmol S cell^{-1})	TDS	pAVS	TS	
			per cell vol. (nmol S cm^{-3})			
<i>Synechococcus</i> sp.	DC2 (o)	2.78	$1.74 \times 10^{-6} (\pm 9\%)$	580±52	45.3±4	625±56
<i>Emiliania huxleyi</i>	BT6 (o)	61.0(±6%)	$1.57 \times 10^{-5} (\pm 20\%)$	184±48	72.7±19	257±67
<i>Pyramimonas</i> <i>obovata</i>	13-10PYR (o)	147(±9%)	$2.80 \times 10^{-5} (\pm 14\%)$	134±31	56.5±13	191±44
<i>Thalassiosira</i> <i>oceanica</i>	13-1 (o)	162(±11%)	$6.51 \times 10^{-6} (\pm 12\%)$	26.5±6	13.7±3	40.2±9
<i>Dunaliella</i> <i>tertiolecta</i>	DUN (n)	223(±8%)	$1.24 \times 10^{-4} (\pm 16\%)$	529±127	28.2±7	557±134
<i>Amphidinium</i> <i>carterae</i>	AMPHI (n)	1183(±8%)	$2.68 \times 10^{-4} (\pm 19\%)$	205±55	22.0±6	227±61

* Oceanic—o; neritic—n.

† Cell volume calculations were based on the average dimensions of 20 phytoplankton cells sampled during log phase growth (Strathmann 1967).

‡ Error in the amount of sulfide per cell was estimated as the standard error of the mean in TS during log phase growth. This includes the results from replicate cultures ($n = 6-8$).

sulfide ion production serves a regulatory function for the electron transport chain (e.g. controls the concentration of NADPH produced by photosynthesis but not used in the production of organic matter because of nutrient limitation). Since large regions of the ocean are nutrient limiting for phytoplankton and since sulfur is abundant in the form of sulfate, we considered that such a process might also occur in phytoplankton. TDS could also be produced as a response to metal ion stress. Because trace metals interact strongly with sulfur, the formation of metal-sulfur complexes can lower biologically available trace metal concentrations (i.e. lower the concentration of free metal ions; Bruland et al. 1991).

To examine the relationship between total sulfide [total sulfide (TS) = TDS + particulate acid-volatile sulfide (pAVS)] and phytoplankton growth, we investigated TS production by six species of phytoplankton (obtained from the CCMP; Bigelow Laboratory for Ocean Sciences). Four of the species were isolated from the Sargasso Sea and two from neritic environments (Table 1). The phytoplankton species were cultured over periods of 5–15 d at two nutrient concentrations to examine the production of TS as a function of growth phase and the concentrations of nutrients and trace metals. The low nutrient experiments were run for a shorter time than the high nutrient experiments. These shorter times were used because it is difficult to maintain a batch culture of phytoplankton at low nutrient concentrations.

Growth media were prepared in 0.4- μm filtered Sargasso Sea water collected from 15-m depth with trace metal clean procedures and stored in the dark. We used the "f" medium devised by Guillard and Ryther (1962). The cultures were prepared by autoclaving 100-ml portions of medium in acid-cleaned Erlenmeyer flasks and cooling them. Next, 2–5 ml of inoculum were added, and the flasks were sealed with silicone rubber stoppers (unlike many stopper materials, silicone does not release contaminating sulfur compounds such as OCS). Species intended for low nutrient experiments were initially transferred from stock solution to f/10 medium to reduce culture shock. Near the end of the log phase in f/10, an aliquot was transferred to f/20, and the time recorded as day 0. The temperature was held at 20°C and light delivered at 194 $\mu\text{Einst m}^{-2} \text{s}^{-1}$ in a 12:12 L/D cycle.

Two sets of controls were also cultured to evaluate total sulfide production by bacteria: the first being the sterile medium only, and the other containing the medium plus inoculum filtrate that was passed through a 0.8- μm pore-size filter. Eucaryotic cultures were treated with antibiotics to minimize bacterial growth. All phytoplankton and control culture experiments were run in duplicate.

Two additional experiments were performed in duplicate whereby the effect of varying only the concentration of one metal (copper or zinc) was investigated with *Synechococcus*. The total concentrations added to the most concentrated cultures were 160 nmol

Zn liter⁻¹ and 79.0 nmol Cu liter⁻¹. Subsequent dilutions of 2, 10, 20, 50, and 100 times these total concentrations provided a range of Cu and Zn concentrations. The total concentrations of the medium constituents added other than Cu or Zn were: EDTA, 11.7 μ mol liter⁻¹; Fe³⁺, 11.7 μ mol liter⁻¹; NaNO₃, 88.3 μ mol liter⁻¹; NaH₂PO₃·H₂O, 3.63 μ mol liter⁻¹; thiamin·HCl, 0.01 mg liter⁻¹; biotin, 0.05 μ g liter⁻¹; B₁₂, 0.05 μ g liter⁻¹.

Previous work has demonstrated that only the uncomplexed (free) and kinetically labile portions of medium constituents are available for biological uptake (Sunda and Guillard 1976; Hudson and Morel 1990; Bruland et al. 1991). Therefore, the free ion concentrations of Cu²⁺ and Zn²⁺ were estimated with a PC version of the MINEQL thermodynamic multiple equilibria program (Westall et al. 1976). In these calculations it was assumed that EDTA dominates Cu²⁺ and Zn²⁺ complexation. Without adding Zn or Cu, the total Zn concentration already present in the seawater was estimated to be 0.06 nmol liter⁻¹, and the total Cu concentration to be 1.2 nmol liter⁻¹ (based on Sargasso Sea data from Bruland and Franks 1983). The concentrations of TDS and pAVS were determined after 5 d, when the cultures were near the end of log phase growth.

On sampling days, duplicate whole flask contents were sacrificed and pAVS and TDS, in vivo fluorescence, cell number, and cell size were determined. Cell numbers were determined by a cell hemacytometer (levy chamber, 0.004 mm² × 0.1 mm deep). Subsamples of culture solutions were passed through a 0.4- μ m polycarbonate membrane; TDS was determined in the filtrate, while pAVS was determined in the cells retained on the filter. The methods used to determine TDS and pAVS have been described elsewhere (Radford-Knoery and Cutter 1993). The TDS procedure determines H₂S_(aq) and its uncomplexed conjugate bases SH⁻ and S²⁻, as well as sulfide associated with most metals except Cu or Hg (Radford-Knoery and Cutter 1993). The pAVS procedure only determines the sulfide fraction bound in labile metal sulfides; it does not determine elemental sulfur, sulfur in pyrite, or S-containing amino acids (Radford-Knoery and Cutter 1993).

Because of the high concentrations of trace metals in the medium, almost all the TDS

should be complexed. Only uncomplexed sulfide is available for oxidation by iodate, oxygen, and hydrogen peroxide (Luther and Tsamakis 1989), so we expect the TDS and pAVS in the cultures to be stable over the duration of the experiments. Oxidative losses may occur, but the results shown below consistently demonstrate net production. Nevertheless, the potential for oxidation means that the calculated production of TS is conservatively underestimated. The overall precision for the experiments (including analytical and biological reproducibility) was 15% (relative SD) at the observed concentrations.

TDS and pAVS were produced by all the phytoplankton species cultured (Table 1). Both types of control cultures showed no detectable increase of either TDS or pAVS over time, suggesting minimal contributions by bacteria. Two trends connected with the growth phase of the organisms are apparent (illustrated in Figs. 1 and 2 with results from *Thalassiosira oceanica* and *Emiliana huxleyi* cultures). First, in the low nutrient experiments, TDS concentrations increased during log phase growth as cell numbers also increased (Figs. 1a and 2a, days 0–6). Second, in cultures where log phase growth was followed by a stationary phase (only observed in high nutrient cultures; e.g. Fig. 2b, days 5–15, cell numbers were nearly constant), the TDS and pAVS concentrations increased slightly during the stationary phase, and the relative proportion of TDS to pAVS was constant. In contrast, cultures of *T. oceanica* followed their log phase growth with senescence (cell counts decreased; Fig. 1b, days 5–15). In this case, total sulfide was conserved, but nearly all the pAVS appeared to be converted to TDS during senescence. A potential explanation for this conversion is that the pAVS is dissolved in intracellular fluids (the 0.4- μ m filter retains the cells and their contents) and that this fraction is released to the medium during senescence when cell walls lyse.

In general, pAVS concentrations in cultures grown in the low nutrient medium were lower than pAVS in the more concentrated medium (Figs. 1, 2, and 3). Because of this, total sulfide concentrations (TS = TDS + pAVS) after 5 d in the low nutrient cultures were generally lower than those of the high nutrient cultures. An exception was *E. huxleyi*, which displayed high TS concentrations during the last 2 d in the

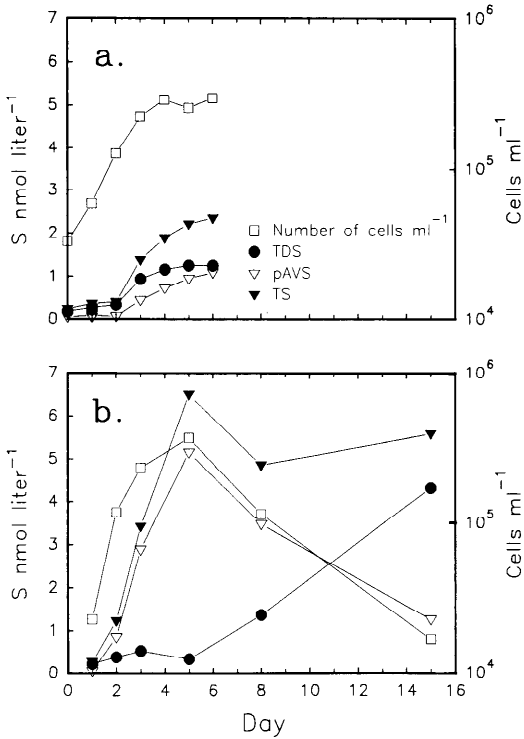


Fig. 1. Temporal variations in the concentrations of total dissolved sulfide (TDS), particulate acid-volatile sulfide (pAVS), total sulfide (TS = TDS + pAVS), and number of cells per milliliter in cultures of the diatom *Thalassiosira oceanica* in (a) low (f/20) and (b) high (f/2) nutrient concentration media. Results presented are averages of duplicate flasks. Overall precision is 15% RSD.

low nutrient medium (4–5 nmol S liter⁻¹ TS, compared to 1 nmol liter⁻¹ TS in the high nutrient culture; see Fig. 2).

In comparison to the eucaryotic cultures shown in Figs. 1 and 2, the results from cultures of the cyanobacterium *Synechococcus* (Fig. 3) generally followed the same trends as described above; TDS dominated in the low nutrient cultures (>90%), while pAVS accounted for a significantly larger proportion of TS (50%) in the high nutrient experiment (Fig. 3). Additionally, very high TDS concentrations were noted after 15 d in the high nutrient medium (25 nmol S liter⁻¹, Fig. 3b). These high TDS concentrations cannot be ascribed to pAVS-TDS conversion, as is suggested for *T. oceanica* because TS was not constant over this period.

The average TDS, pAVS, and TS produced per cell during log phase growth was calculated

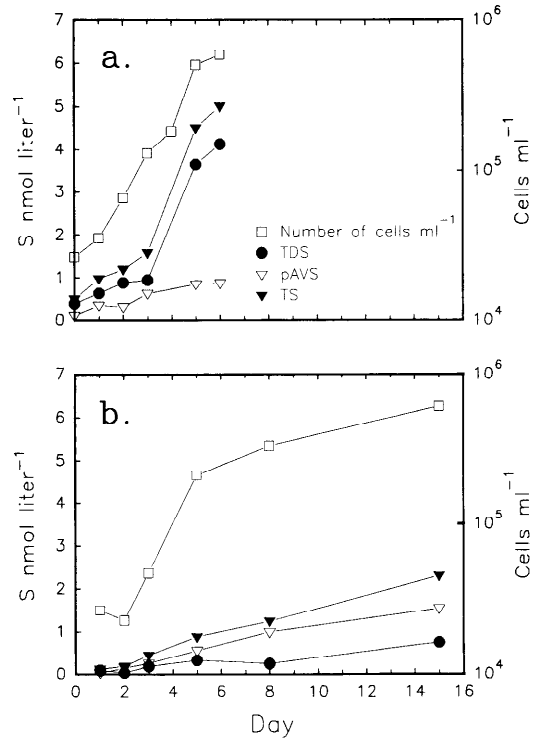


Fig. 2. As Fig. 1, but of the coccolithophore *Emiliania huxleyi*.

for each species using cell counts and concentrations of TDS and pAVS (Table 1). Only results from low nutrient cultures are presented because this medium more closely resembles nutrient conditions in ocean waters (the low nutrient medium contains 3.62 $\mu\text{mol liter}^{-1}$ phosphate and 88.3 $\mu\text{mol liter}^{-1}$ nitrate, compared to maximum surface concentrations measured during the GEOSECS program of 1.7 $\mu\text{mol liter}^{-1}$ phosphate and 26 $\mu\text{mol liter}^{-1}$ nitrate). Direct comparisons made on a per cell basis can be misleading since cell volumes vary over four orders of magnitude among the species. Therefore, TDS and pAVS concentrations per unit cell volume were also calculated (Table 1). The order of TS production per unit cell volume for the oceanic species is *Synechococcus* sp. (cyanobacterium, 625 nmol cm⁻³) > *E. huxleyi* (coccolithophore, 257 nmol cm⁻³) \approx *Pyramimonas obovata* (prasinophyte, 191 nmol cm⁻³) > *T. oceanica* (diatom, 40.2 nmol cm⁻³; Table 1).

As noted above, cultures in high nutrient media produced a relatively higher proportion

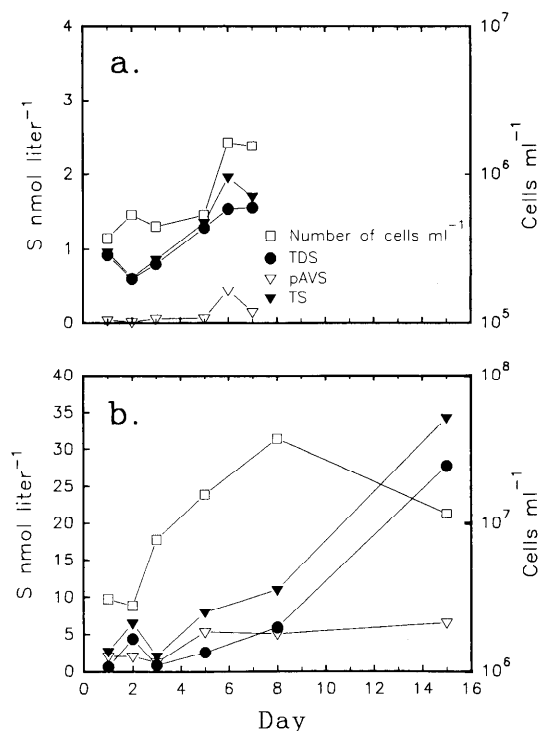


Fig. 3. As Fig. 1, but of the cyanobacterium *Synechococcus* sp. Note that in panels a and b the y-scales differ.

of pAVS than those in low nutrient media. For example, at the end of log phase growth of *T. oceanica*, pAVS was 86% of TS when cultured in the high nutrient medium, compared to only 41% in the low nutrient medium (Fig. 1). Similar trends were noted for all the species cultured, suggesting that some of the constituents in the medium (which contains nutrients, vitamins, and trace metals) may account for this behavior. We speculate that both the increase of TS and the switch from dissolved to particulate acid-volatile phases may be responses to increased concentrations of trace metals in the media. Since trace metals strongly interact with sulfur and can affect phytoplankton growth (Brand et al. 1983, 1986), they are potential candidates for influencing TS production and sulfide partitioning.

To test our speculation that TS production by phytoplankton and the TDS:pAVS ratio may respond to changes in trace metal concentrations, we determined TDS and pAVS in *Synechococcus* sp. batch cultures in which the concentration of only one constituent (free-

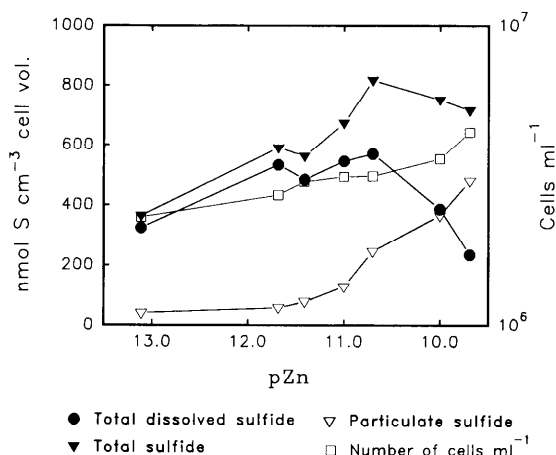


Fig. 4. Effect of varying free $[Zn^{2+}]$ on the production of TDS, pAVS, and TS by *Synechococcus* sp. after 5 d of culturing. $pZn = -\log$ free $[Zn^{2+}]$. Results presented are averages from duplicate flasks. Overall precision is 15% RSD.

Zn^{2+} or free- Cu^{2+}) was altered. *Synechococcus* was chosen because it is very sensitive to the concentration of trace metals in the medium (Brand et al. 1986). The free concentrations of Zn and Cu were calculated because only this fraction is available for biological uptake. The effect of free- $[Zn^{2+}]$ on TS production by *Synechococcus* is shown in Fig. 4. The sulfide results are normalized to cell volume since the Zn or Cu concentrations affect cell growth as well as the production of TDS and pAVS. No toxic effects were apparent for free Zn^{2+} concentrations ranging from $10^{-13.0}$ to $10^{-9.5}$ mol liter $^{-1}$; cell numbers increased as free $[Zn^{2+}]$ also increased (Fig. 4). This observation agrees with previous results that show Zn^{2+} is not toxic to *Synechococcus* in this concentration range (Brand et al. 1983). TS concentrations normalized to cell volume also increased with increasing free $[Zn^{2+}]$ (Fig. 4). Thus, increases in TDS and pAVS are not merely due to an increase of the number of cells. However, when free $[Zn^{2+}]$ was $>10^{-11.0}$ mol liter $^{-1}$, the proportion of pAVS increased while that of TDS decreased (Fig. 4).

When the experiment was repeated with Cu, cell growth increased with increasing free $[Cu^{2+}]$ up to $10^{-13.5}$ mol liter $^{-1}$. The number of cells then decreased at higher free- Cu^{2+} concentrations (Fig. 5). In a study by Brand et al. (1986), *Synechococcus* exhibited reduced

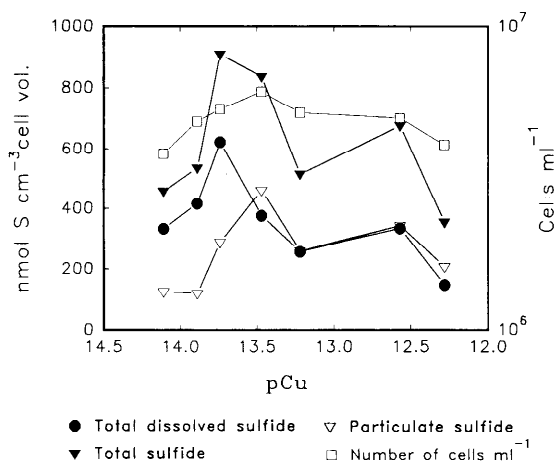


Fig. 5. As Fig. 4, but of varying free $[Cu^{2+}]$. $pCu = -\log \text{ free } [Cu^{2+}]$.

growth rates when free Cu^{2+} exceeded 10^{-12} mol liter⁻¹. In the range where free $[Cu^{2+}]$ was growth limiting ($<10^{-13.5}$ mol liter⁻¹), TDS and pAVS per cell volume increased as the free $[Cu^{2+}]$ increased (Fig. 5). Above $10^{-13.5}$ mol liter⁻¹ free $[Cu^{2+}]$, TDS and pAVS decreased as free $[Cu^{2+}]$ increased. Because our analytical technique does not detect sulfide ions bound in copper complexes (Radford-Knoery and Cutter 1993), decreases of TDS and pAVS at values of free $[Cu^{2+}] > 10^{-13.5}$ mol liter⁻¹ may have resulted from the formation of copper-sulfide complexes (i.e. TS may have been increasing, but the increase was undetectable by our analytical method). In support of this interpretation, equilibrium calculations using MINEQL (Westall et al. 1976) show that the TDS associated with Cu complexes increases from $<10\%$ to $>90\%$ when free $[Cu^{2+}]$ increases from $10^{-14.5}$ to $10^{-12.3}$ mol liter⁻¹.

Although the number of phytoplankton species examined in this study is small, they span a relatively diverse phylogenetic range. Moreover, four of the species are oceanic isolates and two are from neritic environments. All the species investigated produce TS, and it seems likely on the basis of their phylogenetic diversity that sulfide production is a general phenomenon among phytoplankton populations.

With respect to mechanisms for sulfide production, there was no evidence to support the hypothesis that TS production results from electron transport regulation at low nutrient concentrations since TS was produced at both

high and low nutrient concentrations. However, the results are inconclusive because even the low nutrient concentrations were well above those in oligotrophic waters. In addition, the results appear to have been influenced by the trace metal concentrations in the media. The phylogenetic order of TS production is very similar to the order of phytoplankton sensitivity to the free cupric ion concentration, in which cyanobacteria are the most sensitive and diatoms the least (Brand et al. 1986). Brand et al. (1986) proposed that phytoplankton sensitivity to Cu^{2+} is related to the redox conditions that predominated during the period they evolved their biochemical systems. Because the cyanobacteria evolved under anoxic conditions, the free ion concentrations of elements forming strong complexes with sulfide (e.g. Cu, Hg, Cd, Pb) would have been very low (Österberg 1974; Brand et al. 1986). In contrast, eucaryotes may tolerate higher Cu concentrations than cyanobacteria because they evolved when the ocean was oxic and the free Cu^{2+} concentrations were higher. Metal complexation by sulfide ions both inside and outside the cell may thus be a means of regulating free metal ion concentrations. Such a metal stasis mechanism has many parallels with proposed schemes of metal complexation by organic ligands (e.g. Moffett et al. 1990).

The results of the Cu and Zn experiments confirm that higher trace metal concentrations affect the production of TS. In addition, a switch from the dissolved to particulate sulfide phases occurs. Possible explanations for this switch are that TDS is precipitated in the culture as metal sulfides or that sulfide ions are increasingly retained within the cell. Calculations made with MINEQL using the total added metal concentrations and the maximum TDS concentration attained over the course of the experiments show that the solubility of metal sulfides is not exceeded, thus suggesting that sulfide retention within the cell is the most likely explanation. It is therefore likely that the increased proportion of pAVS with increasing Zn or Cu concentrations is an intracellular phenomenon that could arise from, for example, association of sulfide with metal-complexing biomolecules such as phytochelatins.

Phytochelatins are intracellular metal-binding peptides induced by heavy metals in higher plants, algae, and fungi (Reddy and Prasad

1990). Sulfide ions associated with phytochelatin enhance their metal-binding capacity but are easily removed by acidification (Reddy and Prasad 1990). Because our technique for the analysis of the filters involves acidification, increased pAVS concentrations could reflect higher concentrations of phytochelatin. There is evidence that *Synechococcus* produces phytochelatin (Reddy and Prasad 1990), but it is also possible that metal sulfides are simply precipitated within cells. Because it is difficult to estimate the concentrations of TDS and dissolved metals within cells, we are unable to resolve whether the increasing ratio of particulate to dissolved sulfide found in high nutrient cultures is a result of inorganic precipitation within cells or association with phytochelatin.

These culture experiments reveal a new aspect of the biogeochemical behavior of sulfur. All the phytoplankton species cultured produce TS, but some species, especially the oceanic cyanobacterium *Synechococcus* (clone DC2), produce more than others. Thus, we would not expect a simple relationship between TDS or pAVS and bulk phytoplankton parameters such as Chl *a*. Indeed, recent data from the equatorial Pacific (Radford-Knoery and Cutter in prep.) showed little correspondence between TDS and Chl *a*. However, at several sampling stations TDS profiles were strikingly similar to profiles of *Synechococcus* abundance. In a similar manner, dimethyl sulfide, which is also produced by phytoplankton, does not show a simple relationship with Chl *a* (Keller et al. 1989; Andreae 1990). Overall, the results presented in Table 1 and Figs. 1–3 show that phytoplankton have the potential to strongly affect the biogeochemical cycling of TS in the ocean.

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Photosynthesis of *Phaeocystis* in the Greenland Sea

Abstract—During the spring bloom in the northern Greenland Sea in 1989, *Phaeocystis* displayed photosynthetic rates and efficiencies, absorption in the red, and quantum yields approaching predicted theoretical maxima. Average values of these photosynthetic parameters for *Phaeocystis* were about an order of magnitude higher than those typically observed for natural assemblages of diatoms which often dominate the phytoplankton in polar waters. *Phaeocystis* populations were exceptionally well acclimated to temperatures near 0°C and all light conditions encountered. With such high photosynthetic rates and quantum yields, *Phaeocystis* may outcompete other species and play a dominant role in elemental cycles where major blooms are recurrent features. During *Phaeocystis* blooms, primary productivity in polar regions would be seriously underestimated by models using previously reported averages.

Phaeocystis sp. is a remarkable phytoplanktoner because of the magnitude of its blooms, its cosmopolitan distribution, complex life history, and peculiar physiology. Massive blooms of *Phaeocystis* are regular features in coastal and oceanic waters of many temperate and polar regions, often accounting for one-third to two-thirds of annual production (Joiris et al.

1982; Cadée and Hegeman 1986; Smith et al. 1991). These blooms usually occur in spring and frequently deplete most of the available nitrate and phosphate. *Phaeocystis* sp. is a stenohaline, eurythermal alga which is very widespread, with one or possibly two species ranging from subtropical to polar latitudes (Veldhuis et al. 1986). *Phaeocystis* is a prymnesiophyte and, compared with most other phytoplankton, it has a complex life history which involves very small solitary forms that are motile by means of flagella and large colonies with hundreds to thousands of cells embedded in a gelatinous matrix. Its effective size varies as a function of life cycle stage by more than 3 orders of magnitude, from ~3 µm in single cells to >10 mm for large colonies. The colonial structure consists of a gelatinous mucilage, and up to a third of its total photosynthate can be allocated to the colonial matrix (Veldhuis and Admiraal 1985).

The regional and global ecological significance of *Phaeocystis* may be great. In addition to its role in the carbon cycle (Smith et al. 1991), production of dimethylsulfide by *Phaeocystis* in polar waters has been found to be a widespread and globally significant phenomenon (Barnard et al. 1984; Gibson et al. 1990). Furthermore, *Phaeocystis* produces acrylic acid via dimethylsulphonioacetate breakdown, which acts as an antibiotic, and actively growing populations are rarely colonized by bacteria (Sieburth 1960). Binding of trace elements to *Phaeocystis*'s mucilage may

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