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Limnology of Organic Lake, Antarctica, a Meromictic Lake that Contains High Concentrations of Dimethyl Sulfide

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Abstract

Organic Lake in the Vestfold Hills, Antarctica, is a shallow (7·5 m), meromictic, hypersaline lake that contains a microflora of low species diversity. The lake monimolimnion is anoxic but contains no H_2S. Organic Lake has the highest concentrations of dimethyl sulfide (DMS) as yet recorded in a natural aquatic ecosystem. The greatest concentration of DMS in the lake, 97 $\mu g\ l^{-1}$, occurs just above the oxic–anoxic interface. Its presence coincides with maximal numbers of the alga *Dunaliella* sp. and maximal numbers of bacteria. Analysis of head space samples from axenic cultures indicates that *Dunaliella* sp. is not directly involved in DMS production. A bacterial strain that was isolated from Organic Lake and that produced DMS from sulfur-containing amino acids was presumptively identified as a *Halomonas* sp.

Introduction

Organic Lake (68°27·2′S.,78°12·3′E.) is a meromictic lake in the Vestfold Hills, Antarctica. Waters drawn from the chemocline and monimolimnion of this lake possessed a strong odour of reduced sulfur compounds. Hydrogen sulfide has not been detected in these lower waters although oxygen was absent in the monimolimnion (Burton 1981). The approximate salinity of its monimolimnetic waters is 197 g kg^{-1} (Burton 1981). Hypersaline environments often contain a restricted microflora (Post 1977), and this has been recorded for Antarctic hypersaline lakes (Wright and Burton 1981).

The emission of dimethyl sulfide (DMS) from surface waters represents a major flux of biogenically reduced sulfur into the atmosphere (Lovelock *et al.* 1972; Andreae *et al.* 1983). As Organic Lake is well isolated from anthropogenic sources of sulfur and was expected to contain a microflora of limited species diversity, it was considered a most appropriate site in which to study the relationships between a lake's physicochemical limnology, its biota, and the presence of reduced sulfur compounds.

Methods

Chemical and Physical Parameters

In situ water temperatures were measured with a submersible temperature probe (±0·1°C) (Polatherm). Water samples were collected at 1-m intervals with a 2-litre Kammerer bottle, through a hole drilled in the ice when ice was present. The chloride and sulfate concentrations were determined using a Dionex Ion Chromatograph model 10. Water density at 20°C was determined using a PAAR DMA 55 precision calculating density meter (Anton Paar, Graz, Austria). The concentrations of major cations were determined by flame atomic absorption (Varian, model 775 AA). The E_h, pH and ammonium concentrations were measured with electrodes. Acetate, lactate and formate concentrations in water samples were determined by high performance liquid chromatography (Franzmann *et al.* 1987). Winkler titration was used for the determination of oxygen (Strickland and Parsons 1972).

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Determination of Dimethyl Sulfide

Sample collection and gas chromatographic procedures for the determination of volatile reduced sulfur compounds (VRSC) are described in detail elsewhere (Deprez *et al.* 1986).

Lake Biology

A 100-μm mesh net was hauled through the mixolimnion of the lake from a boat when it was ice-free in January 1979. Samples were collected on 7 January 1985 for direct counts of microorganisms and were fixed at the sample site with formalin, which was added to reach a final concentration of 1·0%. Eucaryotic cells were concentrated by centrifugation (at 3000 *g* for 10 min) and counted in a counting chamber (Weber Scientific International Ltd) using a Leitz Laborlux 12 microscope and a ×40 phase-contrast objective. Bacterial cells were concentrated onto Nuclepore polycarbonate filters of pore size 0·2 μm, stained with acridine orange (Zimmermann 1977) and counted by fluorescent microscopy (Leitz Laborlux 12).

Cell Cultivation

All media were sterilized at 121°C for 15 min. For Organic Lake water broth (OLWB), water collected from Organic Lake at a depth of 2 m was filtered through a 0·2-μm Sartorius membrane filter and sterilized. For Organic Lake water agar (OLWA), OLWB was solidified with 1·5% (w/v) Noble Agar (Difco) before sterilization. Sea-water agar (SWA) was prepared with the same ingredients as OLWA but sea-water was substituted for Organic Lake water. Organic Lake water yeast broth (OLWYB) consisted of: OLWB, 1·0 litre; yeast extract (Difco), 0·1 g. For antibiotic selective medium (ASM), 1·0 ml of each of penicillin stock solution and streptomycin stock solution (Buckley 1971) was sterilized by filtration through a sterile 0·2-μm membrane filter and added to 100·0 ml of sterile OLWYB. For cystine Organic Lake water agar (COLWA), 0·5 g of L-cystine was added to 1·0 litre of OLWA before sterilization. Volatile sulfur gas production medium (VSGM) contained L-methionine, 0·01 g; L-cysteine, 0·01 g; yeast extract (Sigma), 0·01 g; Organic Lake water, 1·0 litre.

Isolation of Bacteria

Single drops of water samples were allowed to flow across the surface of SWA, OLWA or COLWA plates which were incubated aerobically and anaerobically (GasPak, BBL) at 10°C. After 14 days, plates were examined using a Leitz microscope and a ×32 phase-contrast objective. No bacteria grew on plates incubated anaerobically. From the plates incubated aerobically, cells were isolated by micromanipulation, used as described by Skerman (1968). The resultant axenic cultures were maintained on OLWYA or SWA.

Isolation of Algae

A single drop of each water sample was inoculated into OLWB and incubated in the light at 0°C. Of the algae present in the lake, only *Dunaliella* sp. developed in these enrichments. An axenic culture of *Dunaliella* was obtained by passage twice through ASM.

VRSC Production by Organisms in Culture

In each case, VRSC production by Organic Lake microorganisms was tested after growth of the organism in 10·0 ml of broth culture in 28 by 70 mm open-top, screw-capped vials with Teflon septa (Pierce) by injection of 1·0 ml of headspace gas directly onto the gas chromatographic column.

Production of VRSC by *Dunaliella* sp. from Organic Lake was tested after growth of the organism in OLWYB in the light at 4°C for 1 month. Production of VRSC by axenic strains of bacteria from Organic Lake was tested after growth of each strain in VSCM for 7 days at 10°C, and after growth with heat-killed cells of *Dunaliella* sp. from Organic Lake. The latter was performed as follows; cells of *Dunaliella* sp. were grown in OLWYB at 4°C in the light for 1 month, reaching *c.* $3{\cdot}4 \times 10^5$ cells ml^{-1}. These cells were heated at 60°C for 30 min. Each of the bacterial strains isolated from Organic Lake was inoculated into a separate broth, which contained the heat-killed cells of *Dunaliella* sp. These cultures were incubated at 10°C for 4 days, after which each culture headspace was tested for VRSC.

Results

Organic Lake is a shallow lake with a maximum depth of 7·5 m and an elevation of 2 m above sea level. A bathymetric map (Fig. 1) was produced from data obtained on

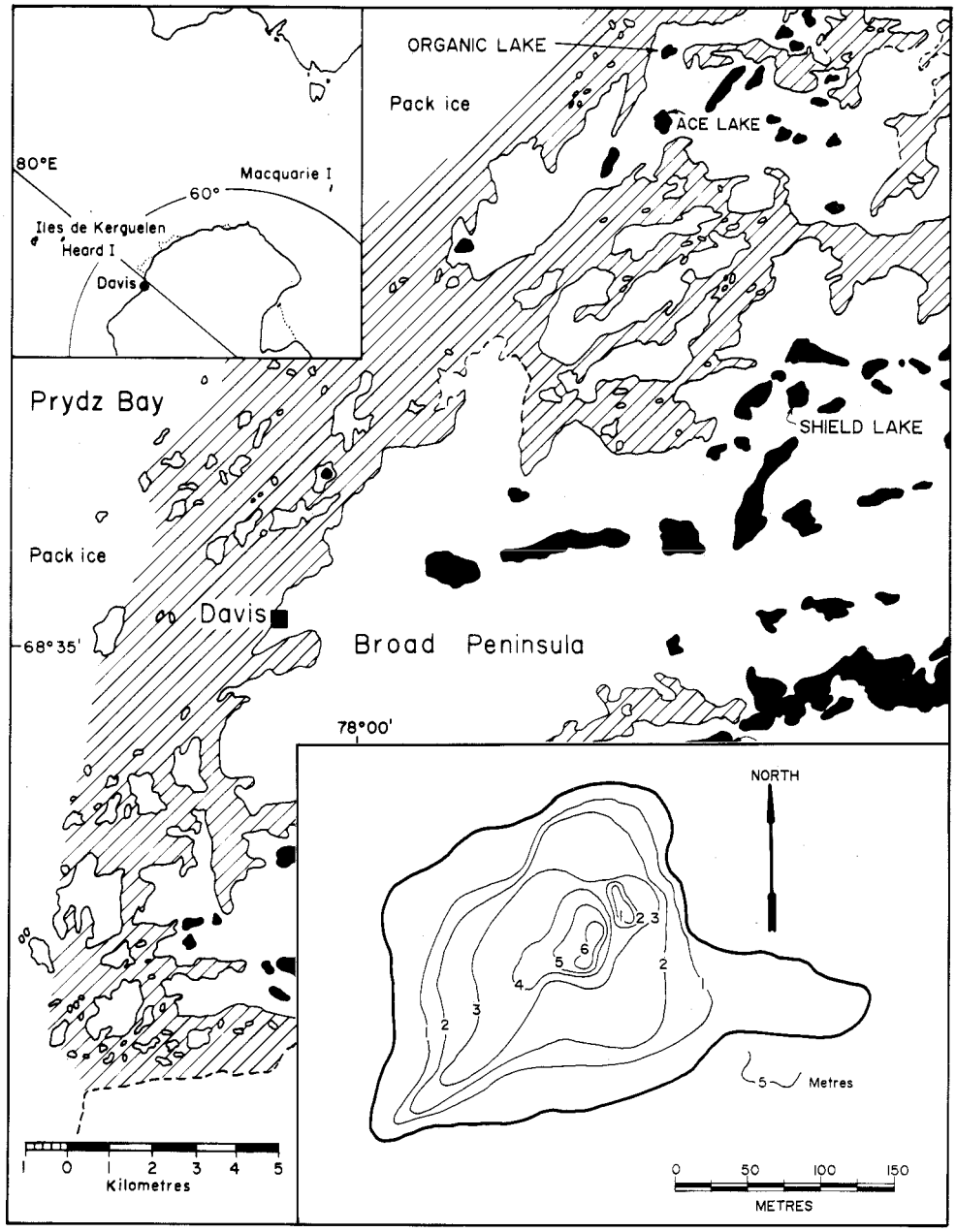

Fig. 1. Map of the Vestfold Hills with a bathymetric map of Organic Lake (insert lower right).

22 February 1978 but since that time the lake level has risen 1 m, as have many of the lakes of the Vestfold Hills (H. R. Burton, unpublished data). Ice cover persists for approximately 9 months of the year (April to December). A partial cover of unstable ice was present in

January 1985 when samples were collected for analysis of their reduced sulfur compound content. The region of the lake safely accessible at that time permitted sample collection only to a depth of 5 m.

Table 1. Temperature profiles (°C) of the water from Organic Lake on six occasions

Depth (m)	22.ii.78	22.viii.78	31.i.79	24.x.84	15.xii.84	7.i.85
0	+0·3	n.d.[A]	+3·1	n.d.	n.d.	+3·6
1	+0·3	−14·1	+3·2	−10·0	−3·9	+8·9
2	+11·0	−13·8	+15·0	−7·3	−4·9	+2·6
3	+9·1	−10·8	+6·1	−6·8	−6·1	−3·7
4	−0·4	−6·8	−2·5	−6·2	−6·5	−6·3
5	−5·1	−5·8	−5·0	−5·3	−5·9	−6·3
6	−6·6	−6·1	n.d.	−5·6	−5·8	n.d.

[A] n.d., not determined.

The densities (kg l^{-1}) at 20°C of waters collected on four separate occasions (22 February 1978; 22 August 1978; 24 October 1984; 12 December 1984) from depths of 3 m and >4 m, respectively, were 1·140, 1·150; 1·142, 1·148; 1·120, 1·149; 1·119, 1·149. In each case,

Table 2. Physical and chemical data for Organic Lake

n.d., Not determined because of ice cover; Tr, present in trace amounts which could not be quantified

Depth (m)	Cl^{-}[A] (g l^{-1})	Cl^{-}[C] (g l^{-1})	E_h[A] (mV)	O_2[A] (mg l^{-1})	O_2[C] (mg l^{-1})	NH_4[B] (mg l^{-1})	pH[A]	DMS[A] (μg l^{-1})	Acetate[C] (mmol l^{-1})	Formate[C] (mmol l^{-1})	Lactate[C] (mmol l^{-1})
0	4·16	n.d.	+378	12·8	n.d.	0·02	7·7	0·21	n.d.	n.d.	n.d.
1	19·28	99·54	+363	9·8	7·6	0·03	7·0	0·22	Tr	Tr	Tr
2	107·74	106·64	+370	6·2	2·9	0·03	7·0	0·58	Tr	Tr	Tr
3	104·75	107·16	+367	3·2	0·4	0·19	7·0	19·29	Tr	Tr	Tr
4	144·79	110·04	+208	1·1	0·0	0·64	7·0	97·65	0·22	0·09	0·04
5	132·52	129·19	+120	0·0	0·0	0·82	6·9	51·77	0·32	0·17	0·07

[A] Samples collected 7.i.1985. [B] Samples collected 26.i.1985. [C] Samples collected 24.x.1984.

water from a depth >4 m was more dense than water from a depth of 3 m. Water from a 3-m depth was less dense in 1984 than in 1978, most likely as a result of dilution of the salts due to a rise in lake level (maximum depth 6·5 m 1978; 7·5 m 1984). Temperature

Table 3. Concentrations (mol l^{-1}) of major cations and anions in Organic Lake and in sea-water

Samples collected on 12 December 1984

Depth (m)	Na^{+}	K^{+}	Mg^{2+}	Ca^{2+}	Cl^{-}	SO_4^{2-}
1	2·05	0·047	0·267	0·041	2·82	0·032
2	2·31	0·053	0·304	0·047	3·12	0·036
4	2·44	0·058	0·317	0·048	3·31	0·049
6	2·87	0·072	0·371	0·051	4·19	0·078
Sea-water[A]	0·48	0·011	0·054	0·011	0·56	0·029

[A] Values for sea-water of salinity 34·9 g/l (Walton Smith 1974).

profiles for the water column on six separate occasions are given in Table 1. The temperature of the water at a depth of 5 m was relatively stable (−5·0°C to −6·3°C) compared with that of the overlaying waters (Table 1). Further physical and chemical parameters determined for Organic Lake are listed in Tables 2 and 3. The concentrations of chloride ions at the

surface and in water at 1-m depth on 7 January 1985 were low compared with concentrations in the under-ice water (ice thickness 1·03 m) measured on 24 October 1984 (Table 2). The water of the upper mixolimnion on 7 January 1985 originated from the melted ice, or from water derived from the ice mixed with water from beneath the ice.

The concentrations of the major cations and anions in Organic Lake water samples and in sea-water are given in Table 3. The ratio of each cation's concentration to chloride concentration in Organic Lake is very similar to the corresponding ratio in sea-water, although the concentrations of the ions in Organic Lake are about six times their concentration in sea-water. The $[SO_4^{2-}]:[Cl^-]$ and $[Na^+]:[Cl^-]$ ratios differ most from the corresponding ratios in seawater.

Oxygen was present in the upper 4 m but was not detected below that depth (Table 2). DMS was the only volatile reduced sulfur compound VRSC detected in the water column with the chromatography system which had a detection limit of *c.* 10 ng l^{-1} for H_2S, SO_2, methyl mercaptan, ethyl mercaptan, DMS and dimethyl disulfide (DMDS). The absence of H_2S in the anoxic water is consistent with E_h measurements which remained positive throughout the water column. Acetate, lactate and formate, the products of bacterial fermentation, were present in greater than trace amounts in the monimolimnion (Table 2). Ammonium concentration increased with depth, probably partly because of the use of nitrate as a terminal electron acceptor as discussed by Hamilton (1984).

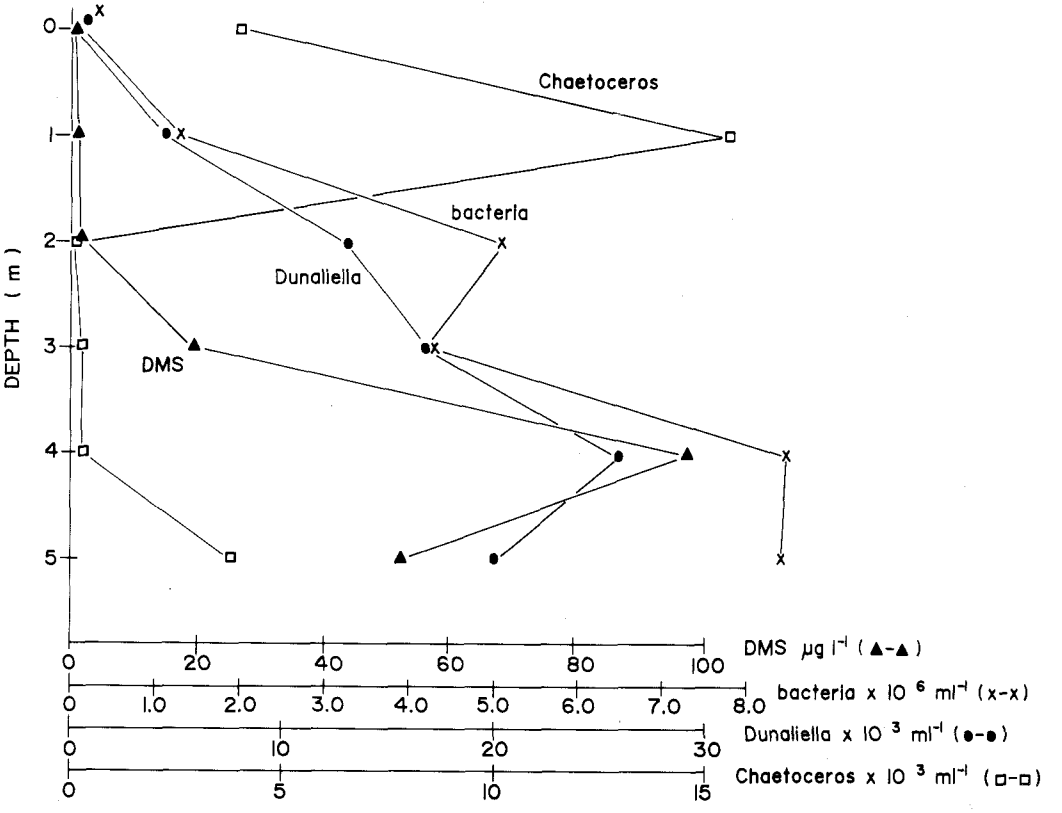

Fig. 2. Profiles of dimethyl sulfide concentration and different components of the microflora in Organic Lake (7 January 1985).

A summary of the dominant microflora of the lake is given in Fig. 2. Maximal numbers of a diflagellated green alga, *Dunaliella* sp., and of bacteria were correlated with the peak of DMS concentration. On 7 January 1985, a diatom, *Chaetoceros* sp., occurred in maximal numbers at a depth of 1 m where Cl^- concentration was low (19·28 g l^{-1}). Ice thickness 23 days before this was 0·95 m. No invertebrate animals were collected in the 100-μm mesh

net when it was hauled through the lake. Only single-celled organisms were found in the lake. Besides the eucaryotes listed in Fig. 2, a further three eucaryotic species were present in the lake's mixolimnion but their abundance never exceeded 500 cells ml^{-1}. These species were a diatom, *Navicula* sp., a flagellated green alga, *Pyramimonas* sp., and a choanoflagellate, *Acanthoecopsis unguiculata*.

The *Dunaliella* sp. was the only eucaryote from the lake which was isolated in culture. An axenic culture was obtained after two passages through ASM. Attempts to grow the *Chaetoceros* sp. in OLWB were unsuccessful, perhaps because of the inappropriate concentration of salts in that medium for that species. Thirty-one axenic cultures of bacteria were obtained from the lake. The Australian Collection of Australian Microorganisms (ACAM) strains which produced DMDS and the depth in the water column from which they were obtained were as follows:

Strain No.	2	3, 4	5–9	10–12	16–18	19, 20, 24	22–26	28–31
Depth (m)	3	7	3	2	3	4	5	6

Strains Nos 25 (depth 5 m) and 2 (3 m) produced DMS and methyl mercaptan respectively but no VRSC were produced by strain Nos 1 (3 m), 13–15 (5 m), 21 (4 m) or 27 (6 m). Neither were VRSC detected in headspace gas from actively growing *Dunaliella*. The only bacterial strain to produce reduced sulfur compounds from heat-killed *Dunaliella* cells was strain ACAM 2, which produced methyl mercaptan and DMS. This bacterium produced these same compounds in media which contained methionine and cysteine.

Discussion

Although Organic Lake is shallow (7·5 m) we consider that it is meromictic. It was stratified with respect to dissolved salts (measured as density). The stability of the water temperature at a depth of 5 m (Table 1) would also suggest that the water column does not overturn. The maintenance of this stratification is aided by the 9 months of ice cover which prevents wind access to the water surface at the time of most frequent cyclone events (Burton and Campbell 1980). When the ice does melt, stratification is enhanced by this production of surface water of lower density. Heat was retained in the mixolimnion throughout summer (Table 1). The temperature gradient then contributed to the stability of the stratification throughout the open-water period.

The ratios of cations to chloride and of calcium to sodium in Organic Lake are very similar to those in sea-water (Table 3), although the concentration of ions in the monimolimnion of Organic Lake is about six times that in sea-water. The ratios of ions would suggest that the lake is composed of relic sea-water, although greatly concentrated. The ratios for sodium to chloride and sulfate to chloride show the greatest contrast of ionic ratios when compared with their ratios in sea-water. This could be due to the precipitation of $Na_2SO_4 . 10\ H_2O$ (mirabilite) which commences in brines at $-8·2°C$ (Thompson and Nelson 1956). On 24 October 1984, a temperature of $-10·0°C$ was recorded from the mixolimnion of Organic Lake. The winter temperature in the lake has been known to fall as low as $-14·1$ (22 August 1978; Table 1). Because sodium ions are in relatively far greater concentrations in brines than the sulfate ions, the precipitation of mirabilite has a less noticeable effect on sodium ion concentration.

Isolation of the monimolimnion, coupled with the metabolic activity of the increased numbers of bacteria in the monimolimnion (Fig. 2), has resulted in depletion of oxygen from the monimolimnion (Table 2). Although the monimolimnion was anoxic below 4–5 m, the redox potential remained positive. This is usual for environments from which oxygen has been removed unless reducing agents such as sulfide are present (Hamilton 1984). The substrates required for sulfate reduction, sulfate and organic acids, are both available in the lake (Tables 2 and 3). The end product of sulfate reduction, sulfide, was not detected, which suggests that dissimilatory sulfate reduction does not occur in the lake.

Sulfide does occur in a number of other meromictic lakes in the Vestfold Hills, e.g. Shield Lake and Ace Lake (Fig. 1; Franzmann *et al.* 1987). It is possible that the high salinity and very low temperature of the anoxic waters of Organic Lake have exceeded the tolerance limits for growth of sulfate-reducing bacteria.

The *Chaetoceros* sp. of Organic Lake occurred mostly in water of low chlorosity at a depth of 1 m (7 January 1985). This depth was approximately the depth of the ice-water boundary 23 days earlier (15 December 1984) and was less than the ice thickness in the spring (24 October 1984). *Chaetoceros dichaeta* can reach $>5 \times 10^5$ cells l^{-1} in congelation ice, the ice which results from the slow removal of heat under an existing ice sheet, in the Weddell Sea (Clarke *et al.* 1984). It is possible that the *Chaetoceros* sp. was essentially part of the ice microflora of Organic Lake. A review which listed the distribution of algae in 53 Antarctic lakes (Wright and Burton, 1981) made no mention of the presence of a *Chaetoceros* sp. *Chaetoceros elmorei* is 'common' (10^5–10^7 μm^3 l^{-1}) in lakes in southern Saskatchewan with salinity of up to 104 g l^{-1} (Hammer *et al.* 1983). The organism is frequently a dominant phytoplankter in hypersaline and mesosaline lakes in Australia and North America (Hammer *et al.* 1983). A *Dunaliella* sp. was reported in three Antarctic lakes: Deep Lake, Vestfold Hills (Cl^- = 141 g l^{-1}); Lake Hunazoko, Skava Nes (Cl^- = 121 g l^{-1}); Lake Stinear, Vestfold Hills (Cl^- = 119 g l^{-1}). The presence of both algae in the anoxic water at 5 m in Organic Lake is probably due to cell sedimentation.

The concentration of DMS in Organic Lake peaked at 97·65 μg l^{-1} at a depth of 4 m. DMS has a mean concentration of 91 ng l^{-1} in surface ocean water; the highest level thus far recorded is in the estuary of the Rio de la Plata, viz. 743 ng l^{-1} (Barnard *et al.* 1982). Prior to this present study, the highest recorded concentration of DMS in a natural aquatic ecosystem, a temperate freshwater pond, was 70 μg l^{-1} (Bechard and Rayburn 1979). DMS is produced by axenic cultures of marine (Andreae *et al.* 1983) and freshwater (Bechard and Rayburn 1979) algae. It has also been recorded as having been produced by a number of bacterial and fungal species from substrates such as dimethyl-β-propiothetin, *S*-methylmethionine, methionine, *S*-methylcysteine (Kadota and Ishida 1972). Soils treated with methionine, methionine sulfoxide, methionine sulfone, *S*-methylcysteine and homocystine evolve DMS and usually methyl mercaptan and DMDS (Banwart and Bremner 1975). Dimethyl sulfoxide can be reduced to DMS by a range of microorganisms (Zinder and Brock 1978; De Bont *et al.* 1981; Scheulderman-Suylen *et al.* 1985).

Although the peak of DMS concentration in the water column correlated with peaks in numbers of both *Dunaliella* sp. and bacterial cells, pure cultures of the Organic Lake *Dunaliella* and bacterial degradation of the heat-killed *Dunaliella* did not yield any DMS; however, they did produce methyl mercaptan and DMDS in one instance. It is therefore most unlikely that DMS was produced by the metabolic activities of the population of *Dunaliella* in the lake. Two species of the genus *Dunaliella* have been examined for dimethyl-β-propiothetin production but it was not found (Ackman *et al.* 1966). The DMS is probably of bacterial origin. In Organic Lake, the peak of DMS concentration occurred just above the oxic-anoxic interface, where numbers of both bacteria and *Dunaliella* peaked (Fig. 2). Only one of the 31 axenic bacterial cultures obtained from Organic Lake produced DMS in VSGM. Although DMDS was the major VRSC detected in culture headspaces it was not detected in the water column of the lake.

Strains ACAM 3 to ACAM 31 are non-pigmented halotolerant bacteria similar to *Halomonas elongata* (Vreeland *et al.* 1980). Like *Halomonas elongata*, the mol% (guanine + cytosine) of the DNA of 10 of these strains was 61 ± 2. Unlike *Halomonas elongata*, these Organic Lake strains possess cytochrome *c* oxidase and are psychrotrophic. A number of the strains are non-motile. Some of the strains could reduce nitrate to nitrite; however, unlike *Halomonas elongata* (Vreeland *et al.* 1980), none could grow anaerobically with nitrate as a terminal electron acceptor. A taxonomic study of these strains is currently being undertaken and will be reported elsewhere. Strains ACAM 1 and ACAM 2 are orange- and yellow-pigmented Gram-negative bacteria respectively. Thus far we have been unable to identify these two strains.

Wakeham *et al.* (1984) noted that two sources of DMS were important in a stratified coastal pond in the United States of America. They observed elevated concentrations of DMS in association with some algal blooms. Most of the DMS was produced and/or preserved in conditions of low oxygen concentration just above the oxic–anoxic interface. They postulated that this peak of DMS production resulted from the decomposition of phytoplankton or other detritus at the interface or from the effect of low oxygen tensions creating a physiological stress on phytoplankton near the interface, or both. In Organic Lake, DMS production would appear to be associated with bacterial degradation of sulfur-containing compounds (e.g. amino acids, dimethyl sulfoxide, dimethyl-β-propiothetin) some of which may have originated from algal cells.

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