The Chemical Stratification and Microbial Communities of Ace Lake, Antarctica: A Review of the Characteristics of a Marine-Derived Meromictic Lake

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Abstract: This article reviews the history, chemical stratification, biology and biogeochemistry of Ace Lake, which is one of the many marine-derived meromictic (permanently stratified) lakes in the Vestfold Hills, Eastern Antarctica. The lake has an area of 18 ha, a maximum depth of 25 m, and a salinity range from 7 to 43 g l^{-1}. The lake mixes to a depth of 7 m in late winter as a result of brine freeze out during ice formation. Deeper mixing is precluded by a sharp halocline. The water beneath 12 m is permanently anoxic. The lake was formed approximately 10,800 yr BP as the polar ice cap melted. Sea level rise 7,800 yr BP resulted in invasion of seawater into the initially freshwater lake. Subsequently, sea level dropped, and the now saline lake became isolated from the ocean. The biota of the lake was derived from species trapped when the connection between the lake and the ocean was cut off. The oxic zone above 12 m supports a relatively simple community which includes microbial mats, four major species of phytoplankton (including a picocyanobacterium), two copepod species, and a variety of heterotrophic flagellates and ciliates. The anoxic zone contains populations of photosynthetic sulfur, sulfate reducing, fermentative and methanogenic bacteria, which combine to remineralise organic carbon which sediments from the upper waters. Research on the physics, biology and chemistry of Ace Lake has contributed significantly to knowledge of Antarctic meromictic lakes.

Zusammenfassung: Dieser Artikel gibt einen Überblick über die Geschichte, die chemische Schichtung, Biologie und Biogeochemie des Ace Lake, einem der vielen meromiktischen (ständig geschichteten) Seen im Gebiet der Vestfold Hills, östliche Antarktis. Der See hat eine Oberflächenausdehnung von 18 ha, eine maximale Tiefe von 25 m und einen Salzgehalt zwischen 7 und 43 g l^{-1}. Die Freisetzung von Salzen während der Herausbildung der Eisdecke erlaubt gegen Ende des Winters eine Durchmischung der Wasserschichten bis zu einer Tiefe von 7 m. Eine tiefere Durchmischung wird durch eine stark ausgebildete chemische Sprungschicht verhindert. Die Wasserschichten unterhalb einer Tiefe von 12 m sind permanent anoxisch. Der See ist etwa 10.800 J.v.h. im Laufe des Rückzugs der Polareiskappen entstanden. Der Anstieg des Meeresspiegels 7.800 J.v.h. führte zu marinem Einfluß in dem bis dahin reinen Süßwassersee. Infolge der späteren Meeresspiegelsenkung wurde der Kontakt zwischen dem heutzutage salzhaltigen See und dem Meer wieder unterbrochen. Die Lebewesen des Sees stammen von Arten ab, die im Laufe der Abtrennung vom Meereseinfluß im See eingefangen wurden. In der sauerstoffgesättigten Zone oberhalb von 12 m Wassertiefe befindet sich eine relativ einfache Lebensgemeinschaft bestehend aus Bakterienrasen, vier wichtigen Phytoplanktonarten (einschließlich einer Picocyanobakterie), zwei Ruderfußkrebsen, und einer Anzahl von heterotrophen Geißeltierchen und Wimpertierchen. In der anoxischen Tiefenzone leben Organismengesellschaften von photosynthetisch aktiven Schwefelbakterien und Methanbakterien, die gemeinsam die aus den oberen Wasserschichten sedimentierten organischen Kohlenstoffverbindungen verwerten. Forschungsarbeiten über die physikalischen, biologischen und chemischen Eigenschaften von Ace Lake haben entscheidend zu einer besseren Kenntnis der meromiktischen Seen der Antarktis beigetragen.

1. INTRODUCTION

Lakes occur in most, if not all, low level ice-free areas of more than a few square kilometres in area on the Antarctic continent. A wide variety of lake types is represented, ranging from extremely fresh supraglacial and proglacial lakes to some of the most saline lakes in the world. Of particular interest are epishelf lakes, which are dammed by ice shelves (e.g. Beaver Lake): these freshwater bodies rise and fall with the tides as they have contact with the open ocean under the shelf, but are biologically and chemically quite distinct from the marine waters (BAYLY & BURTON 1993). Other freshwater lakes occur where summer runoff from glaciers and the polar ice cap accumulates in rocky depressions. Some of these lakes are large, deep and ultraoligotrophic (LAYBOURN-PARRY et al. 1995). Saline lakes are widespread in coastal regions of Antarctica, and range in salinity from slightly brackish to 10 times seawater (BURTON 1981, WRIGHT & BURTON 1981). The salt in most of these lakes was derived from seawater that was cut off from the ocean as a result of isostatic rebound at the end of the last glacial period (ZWARTZ et al. 1998).

Study of Antarctic lakes over the last 35 years has considered a number of themes. The sediments of the lakes have been much studied, as they record the past history of the area surrounding the lake and give clear insights into climate changes that have occurred in Antarctica since their formation (MCGINNIS 1981, BIRD et al. 1991, MELLES et al. 1997, ZWARTZ et al. 1998). Most of the lakes retain liquid water throughout winter, and thus provide a far less rigorous environment for biota than the frigid land. The lakes are generally far more productive than their catchment areas, and there have been many studies of the biota of the lakes and the adaptations they have made to live in the difficult conditions (e.g. low temperatures, low light levels) (VINCENT 1988). Organisms isolated from Antarctic lake ecosystems may have important biotechnological applications in wastewater treatment, and in medicine (ASHBOLT 1990, MCMEEKIN et al. 1993, TANG et al. 1997).

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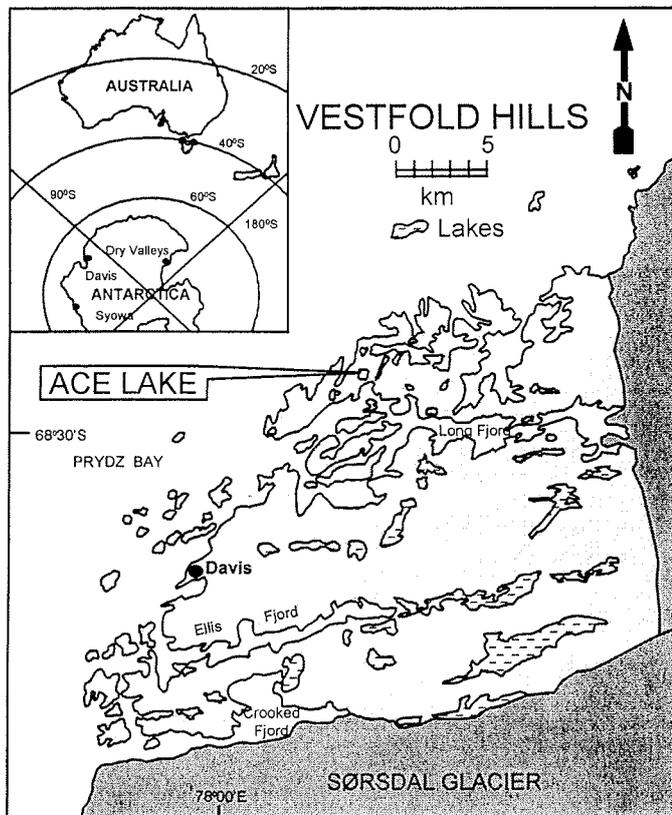
Fig. 1: Map of the Vestfold Hills showing the position of Ace Lake. The inset shows the location of the Davis Station, and the positions of a number of other Antarctic oases mentioned in the text.

Abb. 1: Lage des Ace Lake in den Vestfold Hills. Die Einsatzkarte zeigt eine Großübersicht über die Lage der Vestfold Hills nahe der Station Davis und über die im Text erwähnten Oasen der Dry Valleys.

chemistry and biology, has been the subject of many studies since first visited in 1974. This article is divided into sections that discuss the setting, the history, the physical structure, the chemical stratification, the biology, and finally the carbon cycle of the lake.

2. ACE LAKE AND ITS SETTING

Ace Lake (68° 24' S, 78° 11' E) is located on Long Peninsula in the Vestfold Hills, East Antarctica (Fig. 1). It has an area (1997) of 18.0 ha, a maximum depth of 25 m, and a salinity range from approximately 7 to 43 g l^{-1}. Other morphometric parameters are given in Tab. 1. The bathymetry of the lake (Fig. 2) indicates that it is regularly shaped, with the exception of a small sub-basin, which possibly contains water isolated from the rest of the lake, to the north-west, and a shallow arm to the north-east. The surface of the lake is within 1-2 metres of the lowest sill separating the lake from the nearest marine water, Long Fjord, which is about 150 m distant. The surface level of the lake has risen by approximately 2 m in the last 20 years (GIBSON & BURTON 1996), indicating that it is possible that the level could rise sufficiently for outflow from the basin to occur. There is no observational or geomorphologic evidence, however, of water flowing from the lake in recent times.

Ace Lake lies in an area of low, ice-free hills which reach a maximum elevation of 50 m. It has a small catchment, which has an area approximately three times that of the lake. The catchment consists largely of exposed Archaean gneisses cut by younger dolerite dykes (COLLERSON & SHERATON 1986). There has been little soil development within the drainage area, and the soil pre-

Many of the saline lakes, especially in the Dry Valleys, the Vestfold Hills and the Syowa Oasis (for locations of these areas, see the inset in Fig. 1) are meromictic, a condition in which part of the lake remains unmixed with the surface waters throughout the year. The stagnant lower waters in these lakes become anoxic, leading to interesting biological, physical and chemical characteristics (e.g. BURTON & BARKER 1979, VINCENT et al. 1981, WHARTON et al. 1987, VINCENT 1988, GIBSON et al. 1991, PERRISS et al. 1995). There are approximately 40 meromictic lakes in Antarctica, which represents an important percentage of the world-wide total (WALKER & LIKENS 1975). These lakes were generally formed as a result of the isostatic rebound of the continental margins as the ice sheet retreated at the end of the last ice age (ZWARTZ et al. 1998). The meromictic lakes of the Dry Valleys, however, are much older than these young lakes, and have had more involved histories (GREEN & FRIEDMANN 1993, PRISCU 1998).

To date, there has been no review published discussing the characteristics of marine-derived meromictic lakes from Antarctica. In this article we summarise current knowledge of Ace Lake in the Vestfold Hills, the most intensively studied of this class of lakes. The lake is located close to Australia's Davis Scientific Research Station, and, as a result of its interesting physics,

Surface Level (1997)	8.73 m above sea level
Maximum depth (Z_{max})	25 m
Depth of cryptodepression	16 m
Length	760 m
Breadth	235 m
Volume	1.5×10^6 m^3
Surface Area	18.0 ha
Lake catchment	35.5 ha
Mean depth (Z_{mean})	8.1 m
Z_{mean}/Z_{max}	0.32
Shoreline (SL)	2.44 km
Development of SL	1.6
Total salt	3.05×10^4 tonnes
Maximum salinity	43 g l^{-1}
Average salinity	21 g l^{-1}
Center of mass	8.7 m
Maximum recorded temperature	11.42° C 24 February 1992

Tab. 1: Selected morphometric parameters for Ace Lake.

Tab. 1: Verschiedene Kenndaten für Ace Lake.
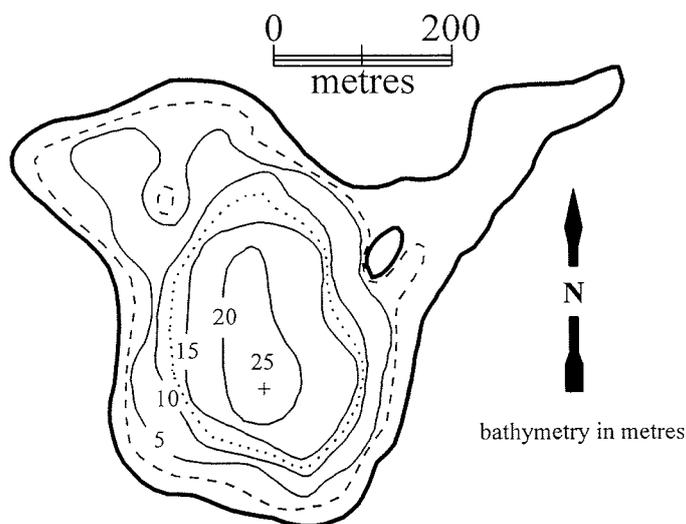
Fig. 2: Bathymetric map of Ace Lake determined in 1991 (DARTNALL, in press). The point where the majority of sampling was undertaken is marked. Also shown are the position of the shoreline in 1978 (dashed line) and the depth of the oxic-anoxic interface (dotted line).

Abb. 2: Tiefenkarte des Ace Lake nach Aufnahmen von 1991 (DARTNALL, im Druck). Markiert ist der Punkt, an dem die meisten Proben genommen wurden. Die gestrichelte Linie beschreibt den Uferverlauf von 1978, die gepunktete Linie die Tiefenlage des oxisch-anoxischen Überganges.

Mean Annual Temperature	-7.5 °C
Mean January Maximum	3.1 °C
Absolute Recorded Maximum	13.0 °C
Mean July Minimum	-20.7 °C
Absolute Recorded Minimum	-40.1 °C
Mean Wind Speed	17.8 km h^{-1}
Maximum Recorded Wind Speed	206 km h^{-1}
Mean Daily Sunlight Hours, January	8.9 h day^{-1}
Mean Daily Sunlight Hours, July	0.2 h day^{-1}
Global Radiation	3527 MJ m-2 yr^{-1}
Estimated Precipitation	69 mm yr^{-1}

Tab. 2: Summary of weather conditions at Davis Station, located approximately 15 km from Ace Lake (data from COMMONWEALTH BUREAU OF METEOROLOGY 1961, STRETEN 1986, KLOKOV 1997).

Tab. 2: Zusammenstellung von Wetterdaten der Davis-Station, ca. 15 km entfernt vom Ace Lake (nach COMMONWEALTH BUREAU OF METEOROLOGY 1961, STRETEN 1986, KLOKOV 1997).

sent is mineralogenic rather than organic in nature. During winter snow banks develop in the lee of the hills, which, when they melt in summer, provide the major water input to the lake. The catchment is devoid of plant growth except for small areas of algal- and cyanobacterial mats that develop in seasonally damp areas downslope from snow banks and in meltstreams. Each summer two or three pairs of Snow Petrel (*Pagodroma nivea*) and Wilson's Storm-petrel (*Oceanites oceanicus*) nest near the lake. The nearest Adélie Penguin (*Pygoscelis adéliae*) rookery is approximately 2 km distant, and on occasions birds from this or other rookeries pass through the catchment.

The climatic conditions recorded at Davis Station, located approximately 15 km from Ace Lake (Fig. 1), are summarised in Tab. 2. No data are available from the lake itself. Compared to other areas of coastal Eastern Antarctica, the weather in the Vestfold Hills is relatively mild and calm (BURTON & CAMPBELL 1980, STRETEN 1986, KLOKOV 1997). This is a result of the moderating influence of the ice-free rock of the hills, which serves to dissipate the strong katabatic winds experienced at the edge of the polar ice plateau, and to absorb, and then reradiate, solar radiation (STRETEN 1986). The location of the Vestfold Hills to the south of the Antarctic Circle results in the area experiencing a period of 6 weeks in June and July during which the sun does not rise above the horizon, and a similar period in December and January when the sun does not set.

The below freezing temperatures experienced for most of the year in the Vestfold Hills result in Ace Lake having an ice cover for approximately eleven months of the year. The ice generally melts out completely in January, and begins to reform in late February or early March. In some summers, however, the ice does not melt completely, and an ice cover remains (BURTON 1980). Ice growth in autumn is initially rapid, but slows as conductive heat loss is reduced as the ice thickens. Maximum ice thickness occurs in spring or early summer, when a thickness of 1.6 to 1.8 m is reached.

The water balance for the lake is quite simple, as there is no outlet and the rocky basin appears to preclude any groundwater flow. Water input is limited to summer meltstreams and direct capture of precipitation when the lake is ice free, and loss to ablation of the ice and evaporation. The loss terms account for approximately 0.25-0.3 m of water per year from the surface of the lake (J. Roberts, personal communication), equivalent to a volume of 4.5-5.4 10^4 m^3. Variations in water level are a response to the balance between these terms: during periods of water level increase, direct and indirect meteoric input is greater than ablation and evaporation, and vice versa.

3. ISOLATION AND EVOLUTION OF ACE LAKE

The Holocene history of Ace Lake has been the subject of a series of studies involving a number of techniques, including the distribution of stable and radioactive isotopes (^{13}C, ^{14}C, ^{18}O, ^{34}S), pigments and microfossils in the sediments and in the water column (BURTON & BARKER 1979, MATSUBAYA et al. 1979, VOLKMAN et al. 1986, 1988, VAN DEN HOFF et al. 1989, BIRD et al. 1991, FULFORD-SMITH & SIKES 1996, ROBERTS 1997, ZWARTZ et al. 1998). However, the history of the lake is still not entirely clear.

Ace Lake has undoubtedly experienced a marine phase which has played a major role in determining its current chemical and biological characteristics. Evidence for the oceanic influence includes the similarity of the ratios of major ions in the water of the lake to those in seawater (Tab. 3) (MASUDA et al. 1988), the relict marine terraces which ring the lake (PETERSON et al.

	5 m	10 m	18 m	23 m	Sea-water	Ratio (10m)
Specific gravity (g cm⁻³ at 20°C)	1.0139	1.0204	1.0234	1.0286		
Cl (mM)	348	383	563	652	563	1.00
Sulfate (mM)	17.0	17.9	4.59	0.85	28.6	0.92
Na (mM)	271	324	498	538	481	0.99
K (mM)	6.22	7.78	10.1	11.7	10.4	1.09
Mg (mM)	35.9	40.1	60.1	85.9	54.2	1.08
Ca (mM)	3.04	3.54	5.31	7.34	10.5	0.49
Al (µM)	2.8	3.4	4.8	3.3	0.03	170
Cr (nM)	11	<5	74	226	4.1	~1.8
Mn (nM)	39	76	1460	78	5.1	22
Fe (µM)	0.69	0.96	1.51	2.69	1.0	1.4
Co (nM)	3	3	10	29	0.03	150
Ni (nM)	ND⁺	ND	110	310	8.2	–
Cu (nM)	120	140	<8	<8	4.1	50
Zn (nM)	230	290	76	390	6.1	70
Se (nM)	14	91	420	75	1.7	80
Sr (µM)	17	16	21	28	89	0.27
Sb (nM)	0.75	0.25	2.6	2.1	1.23	0.30

Tab. 3: Concentrations of selected chemical species at various depths in Ace Lake (MASUDA et al. 1988). Samples were collected using a polyvinylchloride Van Dorn water sampler and preserved for analysis; chloride was analysed by the Mohr titration (STRICKLAND & PARSONS 1972); specific gravity was measured in an Anton Paar DMA 55 density meter; sulfate was measured gravimetrically after precipitation with barium; Na, K, Mg and Ca were measured by atomic absorption spectrometry; trace metal elements were measured using neutron activation methods. Given for comparison are the concentrations in seawater (BROECKER & PENG 1982), and the ratio between the concentrations in the lake water at 10 m (normalised to the concentration of chloride in seawater) and seawater. Note that the concentrations given for the trace elements in the lake are the sum of dissolved and particulate fractions. ND = not detected

Tab. 3: Konzentration ausgewählter chemischer Spezies in verschiedenen Wassertiefen im Ace Lake (MASUDA et al. 1988). Die Proben wurden mit einem PVC-Van-Doorn-Wasserschöpfer genommen. Chlorid wurde analysiert mittels Mohr-Titration (STRICKLAND & PARSONS 1972). Die spezifische Dichte wurde in einem Anton Paar DMA 55 Dichtemesser, Sulfat gravimetrisch nach der Fällung mit Barium, Na, K, Mg und Ca mittels AAS und die Spurenelemente mittels Neutronenaaktivierung bestimmt.Zum Vergleich sind die Meerwasser-Konzentration (BROECKER & PENG 1982) und das Verhältnis zwischen Seewasser bei 10 m Tiefe (normiert auf die Chlorid-Konzentration von Meerwasser) und Meerwasser angegeben. Die Angaben für die Konzentration der Spurenelemente im Ace Lake umfassen die gelöste und partikuläre Fraktion. ND = nicht bestimmt.

1988), and the suite of marine organisms, including phytoplankton and zooplankton, which inhabit the lake (BAYLY 1978, BURCH 1988, PERRISS et al. 1995). ROBERTS (1997) presented the most recent, diatom-based chronology, which can be summarised as follows (dating of sediment samples has been carried out using ¹⁴C and ²¹⁰Pb methods (BIRD et al. 1991, ROBERTS 1997). All ¹⁴C dates have been adjusted for an estimated Antarctic reservoir effect of 1000 years):

1. 10400 - 7800 yr BP: The lake basin was exposed as the polar ice cap retreated at the end of the last glacial period, and was initially filled with freshwater, presumably from the melting ice cap. The date for the formation of the lake given by ROBERTS (1997), 10400 yr BP, is significantly older than the 9000 yr BP indicated by FULFORD-SMITH & SIKES (1996) and the 7000 - 8000 yr BP suggested by ADAMSON & PICKARD (1986). According to ROBERTS (1997), the diatom assemblage in sediments formed in this period was dominated solely by freshwater species. No evidence of an initial marine phase postulated by FULFORD-SMITH & SIKES (1996) was observed. Carbon isotopic data indicated that a productive microbial mat community occurred in the lake at this time (BIRD et al. 1991).

2. 7800 - 1600 yr BP: Relative sea level rise in the area (ZWARTZ et al. 1998) led to a connection forming between the lake basin and the ocean, which resulted in the basin becoming saline and an abrupt change in the suite of diatom species present. Initially, the now marine basin was mixed, presumably by tidal action, but approximately 5000 yr BP anoxic conditions and microbial mats became re-established (BIRD et al. 1991). At the same time resting spores of the diatoms *Navicula glacei* and *Chaetoceros* sp. disappeared from the newly-forming sediments (ROBERTS 1997) and the scale type produced by the prasinophyte *Pyramimonas gelidicola* changed (VAN DEN HOFF et al. 1989). ZWARTZ et al. (1998) interpreted this interface as indicating a change from marine to lacustrine conditions, but ROBERTS (1997) found that the diatoms present continued to be of marine origin, and argued for a continued connection to the ocean. The status of the lake during the period 5000 yr BP to 1600 yr BP remains uncertain, but possibly involved isolation of the basin from the ocean by ice during the winter, a situation which still occurs in at least six stratified basins in the Vestfold Hills (BURKE & BURTON 1988b).

3. 1600 yr BP - present: The lake was unambiguously isolated from the sea and initially became more saline as evaporation occurred. That the average salinity is at present lower than that of marine water indicates that some flushing with meltwater must have occurred since isolation. This would occur during periods of high water level when the lake overflowed to the ocean. Water salinity has varied considerably during this period, with the maximum occurring approximately 700 years BP (ROBERTS 1997).

Many other lakes in the Vestfold Hills have had a similar history (ZWARTZ et al. 1998). Clear Lake (ADAMSON & PICKARD 1986) and Anderson Lake (ROBERTS & MCMINN 1997, 1998) had an initial freshwater stage followed by a marine phase and, eventually, isolation. Pre-lacustrine marine phases have also been identified in Organic and Highway lakes (BIRD et al. 1991). These last two lakes have lower ocean-lake sills than Ace Lake, and possibly did not have an initial freshwater stage.

Of four extensively studied meromictic lakes in the Dry Valleys - Joyce, Hoare, Vanda and Fryxell - only Lake Joyce has an ionic composition similar to that of seawater (GREEN et al. 1988). It is thought that other meromictic lakes in this region were formed after glacial retreat in the Miocene, and that the salinity of the lakes has increased during periods when evaporation was greater than freshwater input into the lakes (GREEN et al. 1988, 1989). Addition of ions from erosion of rock surfaces in the Dry

Valleys is also thought to be an important contributor to the ionic content of the lakes (GREEN et al. 1988). MATSUMOTO et al. (1989) argued, however, that the salt composition in Lake Fryxell was also similar to the ocean, even though it has a maximum salinity only a tenth of seawater. Lake Fryxell may therefore also have had a marine origin and gone through a flushing process similar to the lower salinity meromictic lakes in the Vestfold Hills. The lakes of the Dry Valleys are much older than those in the Vestfold Hills, and therefore have had a longer period to undergo chemical and structural evolution.

Numerous marine-derived lakes also occur near the coast and on islands in the Syowa Oasis (TOMINAGA & FUKUI 1981). These lakes appear to be very similar to those in the Vestfold Hills, and are likely to have had a near identical origin and history.

4. PHYSICAL STRATIFICATION AND MAINTENANCE OF MEROMIXIS

Ace Lake has been continually stratified since first visited in mid-1970s, with the sharp halocline evident in salinity profiles and currently at a depth of 7 m (Fig. 3) being a permanent feature. The halocline has remained at the same position with respect to the bottom of the lake over this period, even though the surface level of the lake has risen markedly (GIBSON & BURTON 1996). No significant variations in the salinity structure beneath 7 m have been recorded, though the salinity above the halocline has generally decreased (GIBSON & BURTON 1996). The physical stratification plays an important role in structuring the biological communities in the lake, as well as providing some insight into the history of the lake.

4.1. Salinity

Two salinity profiles are shown in Fig. 3. The only observed intra-annual changes in salinity occur in the top 7 m. A lens of fresher water forms during summer at the surface due to the melting of the ice. This fresh water undergoes some wind mixing when the lake is open, but this does not extend to any great depth (BURCH 1988). When ice begins to form at the end of summer, the salinity of the water under the ice increases again as brine is excluded from the new forming ice (the bulk salinity of the ice is only 1-2 g l⁻¹ (SWADLING 1998)). A layer of isohaline water forms which becomes more saline and penetrates to greater depths as winter progresses and the ice thickens (GIBSON & BURTON 1996). This layer is mixed by convection. No measurements of the strength of the resulting currents have been made in Ace Lake, though a convective current of 1 cm s⁻¹ has been recorded in the mixed layer of Lake Vanda (RAGOTZKIE & LIKENS 1964). The depth to which mixing occurs eventually reaches the halocline at 7 m, and, even though salinity increases throughout winter, further penetration of mixing into the lake is precluded by the halocline. The mixed layer had not reached 7 m by the time the June 1994 profile was recorded, but had clearly done so by November in 1992.

Beneath the winter mixed layer salinity increases sharply, resulting in the halocline between 7 and 8 m as well as a number of less distinct steps deeper in the water column. The origin of these steps is discussed further below. The lake is less saline than seawater from the surface to 18 m, and more saline below.

4.2 Temperature

Temperature profiles of Ace Lake also exhibit strong stratification (Fig. 3). Water temperature in the lake is a balance between
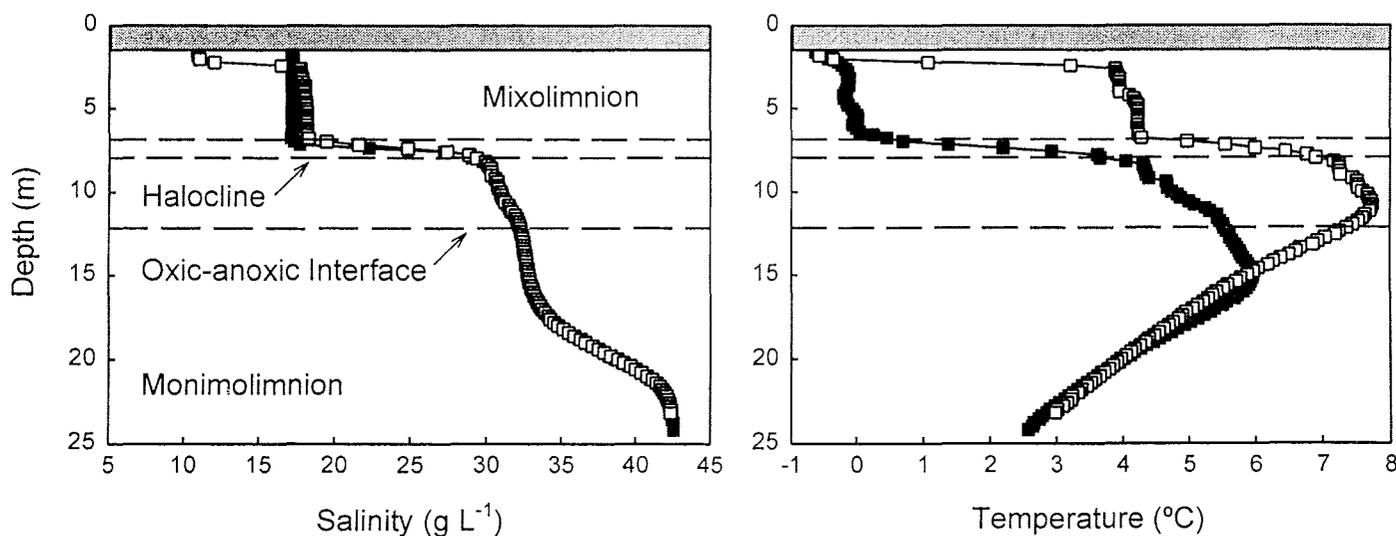
Fig. 3: Physicochemical stratification of Ace Lake: (a) salinity profiles from November 1992 (filled squares) and June 1994 (open squares) calculated from conductivity data; (b) temperature profiles recorded on the same dates. The conductivity and temperature profiles were collected with Platypus submersible data logger.

Abb. 3: Physico-chemische Schichtung im Ace Lake: (a) Salinitätsprofile vom November 1992 (fette Quadrate) und Juni 1994 (offene Quadrate) berechnet aus Leifähigkeitsmessungen. (b) Temperatur-Profile von den gleichen Terminen.

heat transfer into the lake from solar heating and from the surrounding rock, and loss of heat by conduction through the ice to the atmosphere and to the sediment, and evaporative cooling when ice free (WETZEL 1983). Annual temperature cycles for Ace Lake have been presented by HAND & BURTON (1981) and BURCH (1988). During winter, the isohaline layer under the ice is at its freezing point (GIBSON & BURTON 1996). As the ice cover thickens and the water increases in salinity this layer becomes colder, reaching a minimum of about -1 °C. In spring and summer, when ice formation ceases and solar radiation increases, this layer warms, reaching temperatures of approximately 5 °C. (Evidence of this warming is still clear in the June 1994 profile in Fig. 3.) Beneath the halocline temperature increases sharply (Fig. 3). At these depths, temperature is a balance between radiative input and conductive losses to the cooler water both at the surface and at the base of the water column. The seasonality of the input results in the highest temperatures occurring at about 10 m late in summer, and water at this depth being warmer in winter than in early summer. The maximum temperature decreases slowly in winter, and the depth of the maximum increases. Below 14 m the temperature decreases steadily to the sediment, and shows little intra-annual variation. Heat flow from the upper water, however, has increased temperature at the bottom of the lake by approximately 1.5 °C over the past 20 years.

4.3 Physical Stratification

Physical stratification of Ace Lake is maintained by the strong salinity gradient. The effect of the apparently destabilizing temperature increase below the surface winter mixed layer is insufficient to overcome this salinity gradient, and thus large-scale vertical mixing of the water is prevented beneath the halocline.

The lake can be divided into a number of zones (Fig. 3). At the top of the lake is the oxic mixolimnion, which by definition mixes at least once during the year and extends to 7 m. As mentioned above, convective mixing occurs in the mixolimnion during winter due to exclusion of brine from the forming ice, rather than by wind mixing when the lake is ice-free. The mixolimnion is separated from the monimolimnion by the sharp halocline at 7 m. Due to the strong salinity gradient beneath this depth, vertical movement of salt in the monimolimnion occurs largely by diffusive processes (CANFIELD & GREEN 1985), though the possibility of hypersaline brine flows during periods of extreme cold cannot be excluded (FERRIS et al. 1991). Similarly, heat is transported by conduction, a less efficient process than convection or radiative input. This explains the observed mid-water temperature maximum.

Between 7 m and 12.2 m the monimolimnion is oxygenated. The retention of dissolved oxygen in this zone indicates that there is generally a balance between photosynthesis and respiration at these depths. If this zone were to become anoxic no mechanism would currently be available to re-oxygenate the water. Below 12.2 m the monimolimnion is anoxic, with no evidence of vertical mixing. Although not investigated explicitly, it is probable that horizontal advection occurs quite freely at all depths, as has been observed for other meromictic Antarctic lakes (SHIRTCLIFFE 1964, GIBSON et al. 1989).

The volume of the mixolimnion is *circa* 8.6 x 10^5 m^3. Considering that the annual water input is about 4.5-5.4 10^4 m^3, the mean residence time of water in this layer is only 16-19 years. As a result of the lack of mixing between the mixo- and monimolimnion, the residence time of water in the lower section of the lake is much longer, perhaps on a time scale of many hundreds or thousands of years. ^{18}O data, however, indicates that all water present in the lake is of meteoric origin and there is no trapped seawater (BURTON & BARKER 1979, MATSUBAYA 1979). This observation suggests that the lake has been mixed for considerable periods since isolation from the ocean, during which all the lake water became equilibrated with the atmosphere.

The stratification in the saline meromictic lakes of the Vestfold Hills is thought to be produced and destroyed by increasing and decreasing water levels (GIBSON & BURTON 1996). As water level decreases surface salinity increases, the mixolimnion penetrates deeper into the water column, and lake stability is reduced. When the water level rises again and surface salinity decreases, mixing occurs to a shallower depth, leaving a marked step in the salinity profile (this process has not been observed in Ace Lake, but has been seen in other lakes in the Vestfold Hills (J. Gibson, unpublished data)). GIBSON & BURTON (1996) suggested that the steps in the salinity profile of Ace Lake (Fig. 3) reflect depths to which mixolimnetic mixing occurred at some time in the past when the water level of the lake was lower. A small salinity step occurs just below 12 m that is coincident with the depth of the current interface between oxic and anoxic waters (Fig. 3). It appears that mixing of oxygenated water has occurred to this depth at some time in the past when water level was lower and the salinity of the mixolimnion was greater (about 31 g l^{-1}).

If the water level of a lake decreases sufficiently, the density of the surface waters will increase to equal those at the bottom of the water column, and the lake will turn over. The current salinity profile of Ace Lake suggests that at some stage the lake level dropped to such a degree that the lake mixed completely and had a salinity of at least 43 g l^{-1} (GIBSON & BURTON 1996). These authors calculated that this represented a drop in water level of approximately 6 m compared to that at present. ROBERTS (1997) found that the maximum lake salinity occurred approximately 700 yr BP, but that since this time it is likely that the lake has been meromictic. The distribution and isotopic abundance of sulfur (in the forms of sulfate and sulfide) indicate that at least one mixing episode in the lake has occurred since isolation, during which approximately 76 % of the sulfur was lost by an unknown mechanism (BURTON & BARKER 1979).

Other meromictic lakes in the Vestfold Hills, the Dry Valleys and the Syowa Oasis are similarly stratified, though each lake has individual physical and chemical characteristics (GIBSON & BURTON 1996, SPIGEL & PRISCU 1998). Lake Fryxell in the Dry Valleys, for example, is 19 m deep, has a salinity range of ap-

proximately 1 g l⁻¹ to 4 g l⁻¹, has a mid-water temperature maximum of 3.6 °C and an anaerobic interface at approximately 10 m (VINCENT 1981). Lake Vanda, also in the Dry Valleys, is 68 m deep and has a temperature maximum of 23.5 °C at the bottom of the lake where the salinity is three times that of seawater (VINCENT & VINCENT 1982). Ekho Lake in the Vestfold Hills is 40 m deep, has an oxic-anoxic interface at 23 m, a salinity range of 31 g l⁻¹ to 165 g l⁻¹ and a temperature maximum of 18 °C at 18 m (RANKIN 1998).

4.4 Light

Like all high-latitude locations, the climate of the Vestfold Hills is dominated by the extreme contrasts in the seasonal inputs of solar radiation (CAMPBELL & AARUP 1989). As mentioned earlier, the sun does not rise above the horizon in the Vestfold Hills for six weeks during winter (June-July), and does not set for six weeks during summer (December-January).

The percentage of the incident light (measured as photosynthetically active radiation (PAR)) reaching the water column of ice covered lakes is altered by the opaqueness, depth and age of the ice (KIRK 1994). Snow cover will also affect total light penetration as well as penetration of certain wavelengths. BURCH (1988) reported that the vertical attenuation coefficient (K_d) of the ice on the lake was between 0.5 and 3.3 m⁻¹, depending on snow cover and the age of the ice. Approximately 21 % of the incident radiation passed through 1.6 m of ice in snow-free conditions, but only 7 % when there was a 30 cm cover of snow (BURCH 1988).

In the water column, light penetrates to a depth of only 2 m in winter due to the ice cover and low levels of incident radiation. In contrast, PAR reaches 11.5 m in summer (Fig. 4) (HAND & BURTON 1981, BURCH 1988, RANKIN 1998). In summer K_d ranges from 0.2 m⁻¹ in the upper 10.5 m to 4.4 m⁻¹ between 10.5 m and 11.5 m (Fig. 4). This increase is due to the strong absorption of light by a dense band of picocyanobacteria and photosynthetic sulfur bacteria at the deep chlorophyll maximum (DCM) located in the lower depth interval. The DCM effectively prevents light penetrating beneath 11.5 m. Red light is attenuated most rapidly by the lake ice, while green light has the greatest penetration (BURCH 1988). The euphotic depth in Ace Lake varies with season and ice thickness and ranges from 2 m over winter to 10 m in summer (HAND & BURTON 1981, BURCH 1988, RANKIN 1998).

Phytoplankton in Antarctic lakes need to be able to respond to dramatic seasonal changes in solar radiation. In the surface waters of ice free lakes phytoplankton may be photoinhibited by intense summer light (WRIGHT & BURTON 1981). During the winter months and also at the bottom of the euphotic zone in ice covered lakes, phytoplankton must be adapted to survive at very low light intensities. Phytoplankton at the DCM in Antarctic lakes often photosynthesise at far less than 1 % of the surface light intensity.
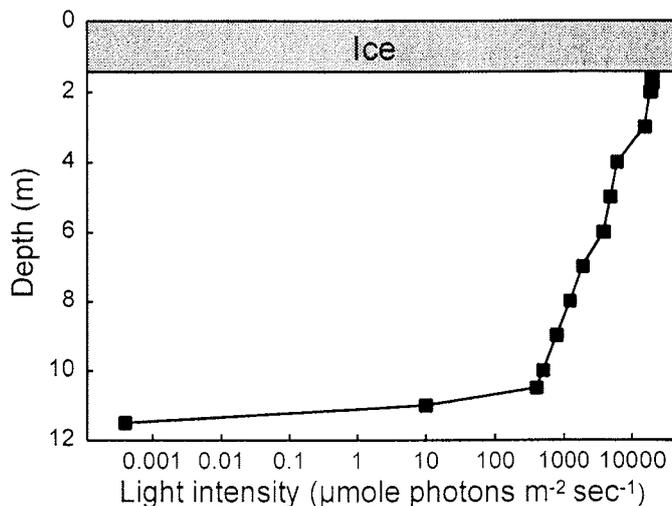
Fig. 4: Light intensity as a function of depth in Ace Lake in December 1992. Photosynthetic available radiation was measured using a Licor underwater quantum sensor.

Abb. 4: Lichtintensität im Ace Lake als Funktion der Tiefe im November 1992. Die photosynthetisch verfügbare Strahlung wurde mit einem unterwasser Licor quantum sensor gemessen.

5. CHEMICAL STRATIFICATION

In addition to salinity, discussed above, the concentrations of many chemical species also show stratification in Ace Lake. The major ions - chloride, sodium, magnesium, potassium - behave essentially conservatively with salinity (Tab. 3), and require no further discussion. Calcium is present at circa 50 % of the expected concentrations, probably as a result of the precipitation of $CaCO_3$ during periods of high productivity or during freeze concentration. Other chemical species, including sulfate, macro- and micronutrients, and dissolved gases, exhibit a variety of behaviours. This section discusses the distribution of a number of these species within the lake.

5.1 Macronutrients

The vertical distributions of the major nutrients (ammonia and amino acids, total phosphorus, soluble reactive phosphate (SRP)) in Ace Lake are shown in Fig. 5. Seasonal variations in total oxidised nitrogen (TON, measured as the sum of nitrate and nitrite) and SRP at two depths are shown in Fig. 6.

TON is present in the oxygenated waters at low concentrations (< 0.4 mM) (HAND & BURTON 1981, BURCH 1988, PERRISS et al. 1995, GIBSON et al. 1997b), often being close to or below the limit of detection of the analytical methods used. The seasonal cycle (Fig. 6) indicates an increase in winter, when regeneration of organic matter occurs, followed by a sharp decrease at the onset of primary productivity in spring. Nitrate has not been detected in the anoxic zone. Reduced nitrogen (NH_4^+ and ami-

Fig. 5: Vertical distribution of: (a) ammonia and amino acids (November 1978) (BURTON 1980); (b) total organic phosphorus (September 1979) (BURCH 1988) and (c) soluble reactive phosphate (November 1978) (BURTON 1980). Ammonia and amino acids were measured by a modification of the total Kjeldahl method (BURTON 1980), total organic phosphate was measured by the ascorbic acid-molybdenum blue method after persulfate oxidation (APHA 1981), and soluble reactive phosphate by the method of STRICKLAND & PARSON (1972).

Abb. 5: Vertikale Verteilung von (a) Ammonium und Aminosäuren im November 1978 (BURTON 1980), (b) des gesamten borganischen Phosphors im September 1979 (BURCH 1988) und (c) des löslichen reaktivien Phosphats im November 1978 (BURTON 1980).
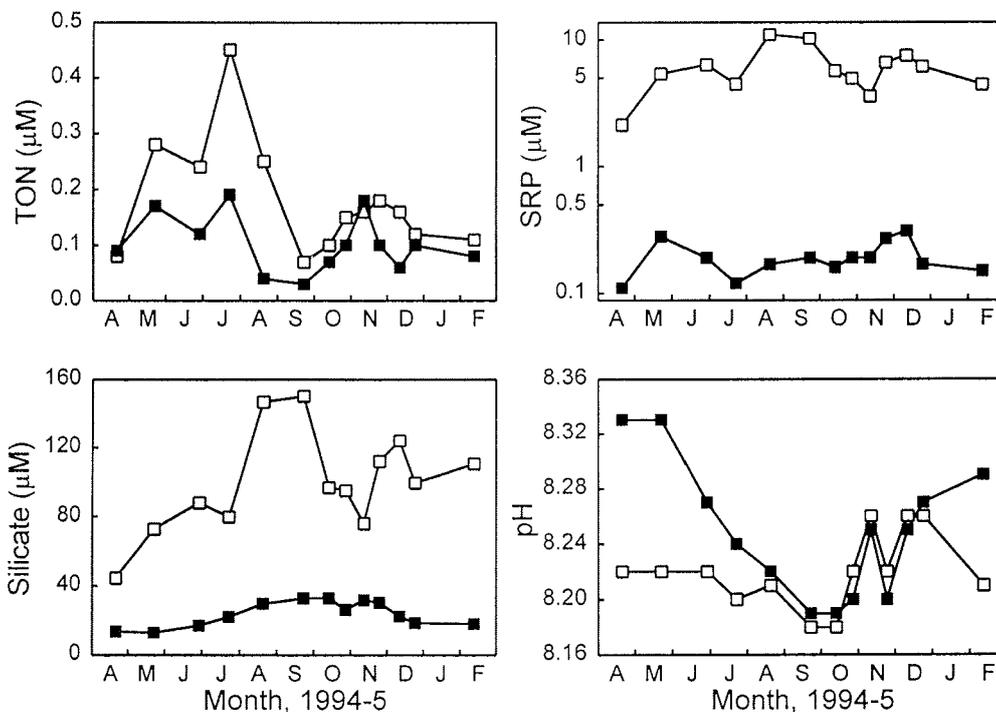
Fig. 6: Seasonal variation of (a) total oxidised nitrogen (nitrate + nitrite); (b) soluble reactive phosphate; (c) dissolved silicate; and (d) pH in Ace Lake at 2 m (filled squares) and 10 m (open squares) (GIBSON et al. 1997b; Gibson, unpublished data). Nutrients were measured by the methods of PARSONS et al. (1984) and pH by the spectrophotometric method of BYRNE & BRELAND (1989).

Abb. 6: Jahreszeitliche Änderungen des (a) gesamten oxidierten Stickstoffs (Nitrat + Nitrit), (b) des löslichen reaktiven Phosphats, (c) des gelösten Silikats und (d) des pH im Ace Lake in 2 m (fette Quadrate) und 10 m Tiefe (offene Quadrate), (GIBSON et al. 1997b; Gibson, unveröffentlichte Daten). Nährstoffe wurden nach der Methode von PARSONS et al. (1984) gemessen. Die pH-Bestimmung erfolgte spektroskopisch nach BYRNE & BRELAND (1989).

no acids) is also low above the halocline, but becomes more abundant in the monimolimnion, reaching a maximum concentration (in 1979) of 55 mM at 15 m (BURTON 1980). The increase of NH_4^+ and amino acid concentrations is probably due to the deamination of proteins which accumulate due to the slow rates of organic matter mineralisation. These reduced forms of nitrogen also diffuse up from the top of the anaerobic zone, where they will play an important role in the nutrition of phytoplankton. VINCENT et al. (1981) observed a band of nitrifying bacteria above the DCM in Lake Vanda where the same diffusion process occurs, and such bacteria are also likely to be present in Ace Lake. Total nitrogen continues to increase through the monimolimnion, reaching a maximum at the base of the water column.

Sources of nitrogen to the lake include organic and inorganic forms in summer melt water, nitrogen fixation by cyanobacteria in algal mats both in the lake and in melt streams, and direct input in precipitation. The concentration of nitrate in meltwater entering Ace Lake has not been determined, but concentrations between 1.2 and 12.4 µM have been recorded in streams elsewhere in the Vestfold Hills (HAND & BURTON 1981). Similar concentrations in the water entering Ace Lake would result in the addition on between 0.08 and 0.8 µM nitrate to the entire mixolimnion each year. Nitrogen fixation within the algal mats, which has been shown to occur in other Antarctic lakes (VINCENT 1988), could provide an important source of bio-available nitrogen for organisms in the mixolimnion. No measurements of nitrogen fixation have been made in Ace Lake, though heterocysts of nitrogen fixing cyanobacteria have been observed in the mats (J. Gibson, unpublished data). It is clear, however, that bio-available nitrogen is in short supply in this zone and, particularly during spring and summer, rapid uptake of any bio-available nitrogen occurs.

SRP is present in the mixolimnion of Ace Lake at a concentration of 0.5-3 mM (BURTON 1980, GIBSON et al. 1997b, RANKIN 1998) (Figs. 5, 6). Quite marked interannual variation has been recorded. SRP concentrations increase below the halocline, reaching a concentration of approximately 10 mM at the bottom of the aerobic zone (Figs. 5, 6). There is an apparent reduction in SRP at the anaerobic interface but the concentration then continues to increase to the bottom of the lake where it reaches 330 mM (BURTON 1980). As in other meromictic lakes in Antarctica, (CANFIELD & GREEN 1985, LAWRENCE & HEDRY 1985), it is probable that diffusion from the nutrient rich anaerobic waters contributes to the increased SRP concentrations below the halocline in Ace Lake. SRP input in melt streams is much lower than for nitrate (HAND & BURTON 1981).

Due to the low concentrations of bio-available nitrogen and SRP in the mixolimnion of Ace Lake it is difficult to calculate accurately an N:P uptake ratio. Nitrogen appears to be the limiting nutrient in the zone, as it is rapidly depleted at the onset of primary productivity whereas SRP remains at measurable levels (Fig. 6). Beneath 7 m SRP rises dramatically, and as nitrate and ammonia remain low, it is clear that bio-available nitrogen will

continue to be the limiting nutrient. This situation is different to those in many other Antarctic lakes, where phosphorus has been found to limit primary production (VINCENT 1981).

During 1994-95, silicate was present at relatively low concentrations in the surface waters, but increased significantly with depth (Fig. 6) (J. Gibson, unpublished data). Concentrations were lowest in summer, when uptake by diatoms in the benthic mats was probably highest, but recover to maxima during winter.

5.2 pH

pH in the mixolimnion and oxic monimolimnion of Ace Lake varied between 8.18 and 8.33 during 1994-95 (Fig. 6) (J. Gibson, unpublished data). Minimum values occurred in winter, when regeneration of organic material would be expected to decrease pH. With the onset in organic productivity in spring pH rose sharply. In the anoxic monimolimnion, pH decreases to 6.8 at the sediment (BURTON 1980).

5.3 Sulfur

Total S (the sum of the concentrations of SO_4^{2-} and H_2S) is present throughout the water column at concentrations far lower than calculated from salinity (Fig. 7, Tab. 3), though the total concentration is conservative with salinity. The isotopic signature of the sulfur is uniform throughout the water column. BURTON & BARKER (1979) concluded that about 76 % of the sulfur had been lost from the lake at a time when the lake was mixed. Since then, the formation of stratification has led to the redistribution of S through the water column. The mechanism by which the S was lost is uncertain.

The reduction in the SO_4^{2-} concentration beneath the oxic-anoxic interface (Fig. 7) is due to the activity of sulfate reducing bacteria (SRB), which produce H_2S. The concentration of SO_4^{2-} has been reduced to near zero at the bottom of the lake (BURTON & BARKER 1979). The highest concentration of hydrogen sulfide recorded in the lake, which was greater than 15 mM (FRANZMANN et al. 1988), is less than the highest recorded for any meromictic lake (60 mM, OVERMANN 1997), but is similar to other anoxic environments in the Vestfold Hills (BURKE & BURTON 1988b). The hydrogen sulfide below 12 m maintains the reducing conditions in the anaerobic monimolimnion.

GIBSON et al. (1991) found extremely high concentrations of the reduced sulfur gas dimethylsulfide in the monimolimnia of many of the saline lakes of the Vestfold Hills. The concentration in Ace Lake, however, was comparatively low, which was attributable to active recycling of this form of sulfur.

5.4 Dissolved gases

Fig. 7 shows vertical profiles of oxygen, methane and nitrogen
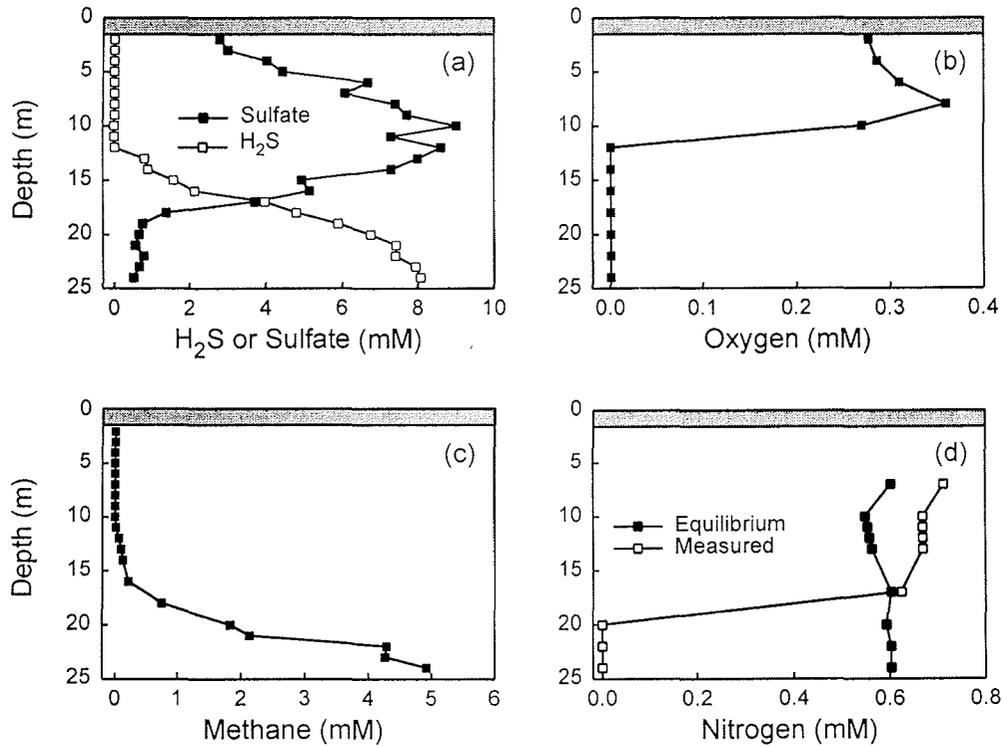
Fig. 7: Vertical distribution of (a) hydrogen sulfide and sulfate in Ace Lake (December 1987) (FRANZMANN et al. 1991b); (b) oxygen (February 1996) (E. Bell and J. Laybourn-Parry, personal communication); (c) methane (December 1987) (FRANZMANN et al. 1991b); and (d) nitrogen (October 1978) (BURTON 1980). Also shown is the calculated saturation concentration for nitrogen. SO_4^{2-} was measured by the method of CULBERTSON et al. (1981); sulfide by colorimetry after reaction with 5,5-dithiobis-2-nitrobenzoic acid (ELLMAN 1959); dissolved oxygen by Winkler titration (PARSONS et al. 1984); methane by GC-TCD using the syringe technique of MARTENS & VAN KLUMP (1980); and nitrogen by gas chromatography (STAINTON et al. 1977).

Abb. 7: Vertikale Verteilung (a) der Sulfide und Sulfate im Ace Lake im Dezember 1987 (FRANZMANN et al. 1991b), des Sauerstoffs im Februar 1996 (E. Bell und J. Laybourn-Parry, persönl. Mitteilung), des Methans im Dezember 1987 (FRANZMANN et al. 1991b) und (d) des Stickstoffs im Oktober 1978 (BURTON 1980) sowie die berechnete Sättigungskonzentration für Stickstoff. SO_4^{2-} wurde gemessen nach der Methode von CULBERTSON et al. (1981), Sulfid durch Colorimetrie nach Reaktion mit with 5,5-dithiobis-2-nitrobenzoic Säure (ELLMAN 1959), gelöster Sauerstoff durch Winkler-Titration (PARSONS et al. 1984), Methan mit GC-TCD mittels Spritztechnik nach MARTENS & VAN KLUMP (1980) und Stickstoff mittels Gaschromatographie (STAINTON et al. 1977).

in Ace Lake. The profiles of methane and nitrogen are consistent with those recorded approximately 10 years earlier (HAND & BURTON 1981). Profiles of oxygen, however, show considerable intra-annual variation, reflecting changes in the balance between photosynthesis and respiration.

Dissolved oxygen is present in the aerobic zone of Ace Lake at between 90 % and 200 % saturation (Fig. 8). In the permanently ice-covered meromictic lakes of the McMurdo Dry Valleys the water directly under the ice is generally supersaturated with oxygen (200-400 %) due in part to the ice cover preventing oxygen and other dissolved gases from reaching equilibrium with the atmosphere (VINCENT et al. 1981, WHARTON et al. 1987). The lower saturations in Ace Lake could in part be due to the absence of ice cover for part of the year. Wind-driven turbulent gas exchange will reduce the concentration of oxygen in the water column, but it must not be sufficient, except perhaps in the wind-mixed surface waters, for equilibrium with the atmosphere to occur. The higher oxygen saturations in the Dry Valley lakes could also be due to the greater input in highly oxygenated meltwater streams, which accounts for approximately 50 % of the dissolved oxygen

in Lake Hoare (VINCENT 1988).

Like oxygen, molecular nitrogen is also supersaturated in the mixolimnion of Ace Lake (Fig. 7), presumably as a result of the actions of denitrifying bacteria. In the monimolimnion below 18 m, however, the concentration falls to undetectable levels. It is probable that the formation and ebullition of methane bubbles has physically stripped the nitrogen from beneath 18 m in the water column (BURTON 1980). Similar supersaturation of nitrogen has been recorded in lakes in the Dry Valleys (WHARTON et al. 1987).

The high concentrations of methane in Ace Lake (Fig. 7) result from the activity of methanogenic bacteria in the monimolimnion and the sediments (HAND & BURTON 1981, FRANZMANN et al. 1988). The maximum concentration of methane is similar to that in the bottom waters of Lake Vanda (VINCENT 1988), reflecting saturation of the gas in both these environments. Methane is lost from the anoxic zone by ebullition of bubbles or by diffusion across the oxic-anoxic interface, where methanotrophic bacteria utilise the gas as a carbon source.
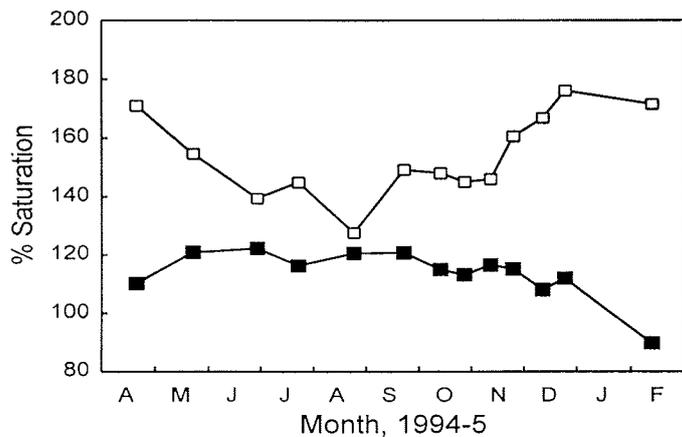
Fig. 8: Oxygen saturation in Ace Lake, 1994-95 at 2 m (filled squares) and 10 m (open squares). The data were calculated using the equation of BENSON & KRAUSE (1984) from the in situ temperature, salinity and oxygen concentrations determined by Winkler titration (PARSONS et al. 1984).

Abb. 8: Sauerstoff-Sättigung im Ace Lake im Sommer 1994/95 in 2 m (fette Quadrate) und 10 m Tiefe (offene Quadrate). Die Werte wurden berechnet nach BENSON & KRAUSE (1984) aus den in-situ-Messungen von Temperatur, Salinität und Sauerstoffkonzentration bestimmt aus Winkler-Titration (PARSONS et al. 1984).

5.5 Trace metals

MASUDA et al. (1988) measured the concentrations of a suite of trace elements, including many required for algal and bacterial growth, in water from four depths in Ace Lake (Tab. 3). Most of the elements were present at concentrations far higher than in ocean water. MASUDA et al. (1988) suggested that input from aerosol particles and chemical weathering from nearby rocks were probably an important source of these elements. It is unlikely that any of the trace elements are limiting microbial growth in the lake.

Many of the elements were far more concentrated in the anoxic zone, with the highest concentrations occurring at 23 m. Some, however, were distributed in a different manner. Cu was essentially absent from the anoxic water, whereas Al, Se and Mn were present at maximum concentrations, and Zn at a minimum, at 18 m. By comparison to other meromictic Antarctic lakes, it would be expected that maximum Mn and Se concentrations would occur near the oxic-anoxic interface (MASUDA et al. 1988). It is possible that the maximum concentration at 18 m reflects the location of the oxic-anoxic interface being at this depth some time in the past.

5.6 Iodine

BUTLER et al. (1988) noted a close correlation between bacterial numbers and total iodine concentrations. They proposed that the distribution of iodine might be the result of a long term interaction with micro-organisms, where the element is assimilated by phytoplankton, which are in turn grazed by copepods. Iodine then sinks in faecal pellets, and other detritus, to be remineralised by anaerobic heterotrophic bacteria at the top of the anaerobic zone or in near-bottom and sediment pore waters.

Reductive dehalogenation of organic compounds has been observed in cultures of methanogenic Archaea and sulfate-reducing bacteria (TANDOI et al. 1994).

6. THE BIOTA OF ACE LAKE

Community form and function in stratified ecosystems is greatly influenced by the physiochemical gradients. The species composition and the role of the biota in Ace Lake is therefore discussed according to position in the water column.

6.1 Oxic Zone

6.1.1 Benthic communities

Benthic algal and microbial mats occur in the littoral zone of Ace Lake to a depth of approximately 10 m (HAND & BURTON 1981, WRIGHT & BURTON 1981, DARTNALL (in press). At times, portions of the mats detach and drift around the lake (J. Gibson, unpublished observations). These types of mats, known as lift-off mats, have been reported in other lakes in the Vestfold Hills (HEATH 1988) as well as in the meromictic lakes of the Dry Valleys (SIMMONS et al. 1993 and references therein). The pinnacle mats that occur in most of the Dry Valley Lakes (PARKER & WHARTON 1985) have not been reported from Ace Lake.

The benthic mats of Ace Lake have a relatively high species diversity compared to other lakes in the Vestfold Hills (DARTNALL 1997, in press); species reported include the algae *Ectocarpus* sp., *Urospora penicilliformis* and *Rhizoclonium implexium*, as well as many diatom and cyanobacterial species. ROBERTS & MCMINN (1996) found twenty-three species of diatom in the surface sediments of Ace Lake, most of which undoubtedly live in association with the algal mats. Many of these species were also observed in sediment cores (ROBERTS 1997). The fauna associated with the mats also includes the small harpacticoid copepod *Idomene scotti* (R. Hamond, personal communication), many ciliates, a large tube dwelling member of the family Folliculinidae, a platyhelminthe, nematodes and three species of rotifer (DARTNALL 1997, in press).

6.1.2 Zooplankton

Apart from the animals associated with the algal and microbial mats, the calanoid copepod *Paralabidocera antarctica*, which is usually associated with sea ice in the marine environment (TANIMURA et al. 1996), is the only metazoan zooplankter known to inhabit Ace Lake (BAYLY 1978, BAYLY & BURTON 1987, SWADLING 1998). BAYLY (1978) also reported a small number of *Acartia* sp., but this species has not been observed in the lake since that time, and was probably the result of sample contamination (BAYLY & BURTON 1987). A significant difference between Ace Lake and the meromictic lakes of the Dry Valleys is that planktonic crustaceans are not present in the latter (PARKER

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& Simmons 1985), although Vincent & Howard-Williams (1985) reported the presence of rotifers at the oxic/anoxic interface in Lake Fryxell.

Paralabidocera antarctica undergoes a single life cycle per year in Ace Lake. Nauplii appear in autumn and develop to adults by early summer when eggs are produced (Swadling 1998). Two density maxima of *P. antarctica* were observed in a detailed study of the vertical distribution undertaken in January 1982 (Bayly & Burton 1987): one just beneath the ice (27,700 individuals m^{-3}), and another near the bottom of the aerobic zone (3,020 individuals m^{-3}). High abundances of *P. antarctica* just above the oxic-anoxic interface could be sustained by the high abundance of phytoplankton in this region (Burch 1988, Rankin et al. 1997). It is probable that the adult stage of copepods do not feed on picocyanobacteria that occur just above the interface (see below), as these cells are too small for most copepods to feed on (Johnson et al. 1982). *Paralabidocera antarctica* is, however, a small species (Bayly 1978), and the juvenile stages may be able to feed on the picocyanobacteria.

6.1.3 Eukaryotic Plankton

The phytoplankton ecology of Ace Lake has been the subject of three annual (Burch 1988, Gibson et al. 1997b, and T. Pitman, unpublished data) and several summer studies (Wright & Burton 1981, Volkman et al. 1988, Mancuso et al. 1990, Laybourn-Parry & Perriss 1995, Perriss et al. 1995). Water samples were generally collected using a Kemmerer bottle and preserved using Lugol's Iodine, glutaraldehyde or formalin, depending on the method of phytoplankton identification. Samples were analysed using techniques that included microscopy, flow cytometry, lipid and pigment chemistry. The general conclusions from these investigations were that the phytoplankton of Ace Lake show low species diversity, strong vertical zonations, and vertical migration of flagellated forms according to light intensity. Two comprehensive reviews on plankton diversity in Antarctic lakes and streams have recently appeared (Ellis-Evans 1996, Vincent & James 1996) and, although in Ace Lake species diversity is low, throughout Antarctica as a whole each of the major phytoplankton classes is well represented.

In a year-long study chlorophyll *a* levels in Ace Lake were found to average 2 mg m^{-3} to a depth of 10 m in autumn and summer, with lower concentrations (0.5 mg m^{-3}) in winter (Burch 1988). Similar levels were recorded between April 1994 - March 1995 (Swadling 1998), when the range was 0.7-3.2 mg m^{-3}. In this latter study, however, highest chlorophyll *a* concentrations were recorded immediately under the ice in the middle of winter, possibly as a result of the migration of phototrophic organisms to this depth in order to take advantage of what little light was available. Both these studies indicate that significant photosynthetic activity begins in September as the light levels in the lake increase dramatically, which is well before the loss of the ice cover, when highest light levels occur. Significantly lower chlorophyll *a* concentrations - 0.12 to 0.16 mg m^{-3} - were reported in water samples collected in November 1993 (Perriss et al. 1995).

Phytoplankton species that occur in Ace Lake include the prasinophyte *Pyramimonas gelidicola*, an undescribed cryptomonad (pictured in Volkman et al. 1988), and the autotrophic ciliate *Mesodinium rubrum* (Haptorida). *P. gelidicola*, which also occurs in marine waters offshore from the Vestfold Hills (Davidson & Marchant 1992), is present throughout the year, and in one study reached a maximum density (3.5 10^3 cells ml^{-1}) in January just above the oxic-anoxic interface (Burch 1988). It is likely that the nutrient rich conditions in this zone support the growth of this shade adapted species. In the same study, the cryptomonad (which also occurs offshore (Gibson et al. 1997a)) began to bloom in September, when low but sufficient light returned. Initially the species occurred in highest numbers just below the ice, however, it appeared to migrate downwards as light intensity increased. It reached a maximum density (7.0 10^2 cells mL^{-1}) in November at 6 m (Burch 1988, Gibson et al. 1997b). Other studies have recorded slightly different spatial and temporal distributions. For example, total abundance of photosynthetic nanoflagellates (including *P. gelidicola* and the cryptomonad) reached 3 10^2 to 5 10^2 cells ml^{-1} in December 1993 (Laybourn-Parry & Perriss 1995), with the peak at just above the halocline.

Mesodinium rubrum, a ciliate which contains numerous cryptophycean endosymbionts, has only recently been identified in Ace Lake (Perriss et al. 1995). Earlier workers observed *M. rubrum* but did not positively identify the organism nor recognise it as being photosynthetic (H. Burton, unpublished data). *Mesodinium rubrum* is commonly found in marine phytoplankton assemblages, including Antarctic waters, and probably has occurred in Ace Lake since its isolation from the sea (Laybourn-Parry & Perriss 1995). Like other phytoplankton species, *M. rubrum* was found to survive in low numbers over winter but bloomed (maximum abundance: 3 10^2 cells ml^{-1}) in spring and summer (Gibson et al. 1997b). Perriss et al. (1995) indicated that nutrient levels did not appear to be an important factor controlling *M. rubrum* distribution in saline lakes of the Vestfold Hills as no significant relationship was detected between the abundance of *M. rubrum* and phosphate and nitrate levels in a range of meromictic lakes.

Phospholipid fatty acid profiles confirm that microeukaryotes are the major microbial group in the oxic zone of the lake (Mancuso et al. 1990), and pigment and lipid signatures determined by Volkman et al. (1988) confirmed the major planktonic assemblage of Ace Lake. The recent identification of *Mesodinium rubrum* is also confirmed by previous lipid and pigment chemistry in which pigments attributable to its cryptophycean endosymbiont were detected (Volkman et al. 1988).

Heterotrophic and autotrophic dinoflagellates have been observed in low numbers in the mixolimnion (Burch 1988, Laybourn-Parry & Perriss 1995). Laybourn-Parry & Perriss (1995) recorded densities of between less than 1 cell ml^{-1} and 2 10^3 cells ml^{-1} in December 1993. At this time the greatest den-

sities occurred just below the ice and the lowest densities at the bottom of the euphotic zone. In the preceding month, maximum densities were recorded near the bottom of the euphotic zone.

A number of other ciliate species, apart from the autotrophic *Mesodinium rubrum*, occur in the lake (PERRISS & LAYBOURN-PARRY 1997). Total abundance was found to be *circa* 1 10^3 m^{-1} in October 1994. No information regarding vertical stratification in the ciliate population is available.

Heterotrophic nanoflagellates (HNAN) also occur in the lake. During the study by BURCH (1988) the most common eukaryotic species was a small, non-pigmented flagellate (maximum abundance: 9.5 10^3 ml^{-1}). The lack of chlorophyll in this species indicated that it was heterotrophic, and the biochemical analyses of VOLKMAN et al. (1988) suggested that it may be a prymnesiophyte. The identity of this taxon awaits confirmation. LAYBOURN-PARRY & PERRISS (1995) reported HNAN densities of between 1 and 2 10^2 cells ml^{-1}, with a peak at 6 m in samples collected in December 1993. The significance of the HNAN in regulating bacterial cell numbers has yet to be determined, but it is anticipated that they form an important link in the microbial food web in the lake. Nanoflagellate grazing in freshwater lakes of the Vestfold Hills removed only between 0.1 and 9.7 % of bacterial production per day (LAYBOURN-PARRY et al. 1995) and bacterial abundance in these lakes have been predicted to be controlled by bottom up processes. However, as the plankton community structures, and the chemical and physical conditions in the saltwater meromictic lakes are very different, direct comparisons between the two systems are not truly valid.

6.1.4 Prokaryotic Plankton

A population of picocyanobacteria was identified in Ace Lake in 1992 using flow cytometric techniques (RANKIN et al. 1997). Based on phylogenetic and chemotaxonomic evidence the cyanobacteria was characterised as a member of the *Synechococcus* group (RANKIN 1998). It occurred in relatively low numbers (10^3 to 10^4 cells ml^{-1}) throughout the oxic zone over winter, but increased dramatically over spring and peaked at 11 m in early December (maximum abundance: 8 10^6 cells ml^{-1}). The population began to decline again in January. The occurrence of picocyanobacteria had not been recognised previously in Ace Lake even though during November and December it occurs in high numbers just above the oxic-anoxic interface. In 1974, when the oxic-anoxic interface was at 10 m, it was reported that there was a high concentration of bacterial cells (bacillus and coccoid shaped) between 7m and 10 M (BURTON & BARKER 1979). It is likely that these authors observed coccoid *Synechococcus* species in 1974 without recognising it as a photosynthetic organism. The rod shaped bacteria were likely to have been *Chlorobium* sp. which occur in high numbers at the top of the anoxic zone. Other studies since 1974, including those utilising lipid analysis (VOLKMAN et al. 1986, 1988, MANCUSO et al. 1990) and direct microscopic observations of phytoplankton (BURCH 1988), did not detect these small but abundant cyanobacteria. This may have been due to the time at which samples

were taken (*Synechococcus* might only be detectable by lipid chemistry when it blooms in December), the depths from which samples were taken, filter sizes used for filtration, or the microscopic techniques employed. The other possibility is that *Synechococcus* is a relatively new or newly abundant inhabitant of Ace Lake. Changes in species composition have been reported in other Antarctic meromictic lakes (SPAULDING et al. 1994). *Synechococcus* is not common in the Southern Ocean (MARCHANT et al. 1987, LETELIER & KARL 1989), nor in coastal Antarctic waters (WALKER & MARCHANT 1989) where it has been reported to occur at low abundances (less than 10 cells ml^{-1}).

To date there have been few studies of the heterotrophic bacteria of the oxic zone of Ace Lake. Population density and seasonal variation in cell numbers have been recorded, but little is known about species composition, their role in organic carbon cycling, or the effect of grazing pressure on the bacterial population. HAND & BURTON (1981) presented an isopleth diagram of bacterial population density for the period July 1977 - January 1978. They reported a maximum of 2.5 10^7 cells ml^{-1} at a depth of 10 m in October-November with lower numbers (5 to 10 10^6 cells ml^{-1}) in the surface waters and in winter. Similar results were obtained by RANKIN (1998). The higher abundances in spring were probably a response to increased primary production at this depth, and an increase in photosynthetic sulfur bacteria.

A psychrophilic, group 1 methanotrophic bacteria has recently been characterised from just above the oxic-anoxic interface in Ace Lake (BOWMAN et al. 1997b). *Methylosphaera hansonii* made up only a small proportion of the total microbial population in this region, with higher populations detected in the surface sediments.

6.2 *Anoxic Zone*

6.2.1 Photosynthetic Bacteria

A plate of photosynthetic sulfur bacteria occurs at the top of the anoxic zone, between approximately 12.2 m and 12.8 m (BURKE & BURTON 1988b, RANKIN 1998). (The position of this layer has changed with respect to the lake surface over the last 20 years as a result of changes in water level.) The major species present are the green sulfur bacteria *Chlorobium vibrioforme* and *Chlorobium limicola* (BURKE & BURTON 1988a). These anaerobic bacteria use bacteriochlorophylls for photosynthesis, and reduced sulfur compounds, such as H_2S or simple organic compounds, as electron donors. Species of purple photosynthetic bacteria (Rhodospirillaceae) and *Chromatium* sp. have also been reported from Ace Lake (HAND 1980), but it is thought that the *Chlorobium* spp. dominate because of their faster growth rate at low temperature and light, and their ability to survive long periods of low light levels (BURKE & BURTON 1988b). A flow cytometric study indicated that in 1992-93 the abundance of photosynthetic sulfur bacteria was at its lowest between May and July, but increased from August and reached a maximum of 6 10^7 cells ll^{-1} in December/January (L. Rankin, unpublished data).

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6.2.2 Anaerobic Heterotrophs, Sulfate Reducing Bacteria and Methanogens

HAND & BURTON (1981) reported significant numbers of bacteria in the anoxic zone of Ace lake, with the maximum abundance exceeding 4 10^7 ml^{-1}. It is uncertain, however, what percentage of these cells were viable, and it probable that these abundances were the result of sedimentation of bacteria from higher in the water column.

To date four species of bacteria and two species of archaea have been characterised from the anaerobic waters of Ace Lake. These include two psychrotrophic species belonging to the genus *Carnobacterium* (FRANZMANN et al. 1991a), an anaerobic wall-less spirochete (FRANZMANN & DOBSON 1992), an obligate anaerobic coiled bacterium (FRANZMANN & ROHDE 1991) and two methanogens (FRANZMANN et al. 1992, 1997). It is thought that these bacteria are important for anaerobic organic carbon degradation.

Due to their ability to grow, albeit sub-optimally, in oxic conditions it is thought that *Carnobacterium funditum* and *Carnobacterium alterfunditum* may have played a role in the initial establishment of a reduced environment in the lake and the supply of electron donors for the sulfate-reducing bacteria that co-exist in the monimolimnion (FRANZMANN et al. 1991a). These two species produce lactic acid as an end product of carbon metabolism and have a generation time of between 17 h and 19 h at 1 °C, the temperature of the water column from where they were isolated. They have significantly higher optimal growth temperatures (23 °C).

Unlike the carnobacteria, conclusive statements regarding the taxonomy of the Ace Lake coiled bacterium await phylogenetic analysis (FRANZMANN & ROHDE 1991). It is presumed that this bacterium has an intermediate role in the breakdown of biomass, as it ferments peptides and a limited number of sugars and produces hydrogen, formic, acetic and butyric acids, the precursors for methanogenesis and acetogenesis.

The wall-less spirochete was initially considered a mycoplasma-like organism (FRANZMANN & ROHDE 1992) until phylogenic analysis placed the organism within the Spirochaetales (FRANZMANN & DOBSON 1992). The organism is a psychrophile, with a optimal growth temperature of between 12 °C and 13 °C.

Lipid analysis of water column particulates suggests that large populations of methanogenic Archaea are present in the monimolimnion (MANCUSO et al. 1990). Phospholipid-derived ether lipids (PLEL), cell membrane lipids that are unique to Archaea (TORNABENE & LANGWORTHY 1979, LANGWORTHY et al. 1982), were used to determine the biomass and activity of methanogens in the monimolimnion of Ace Lake. In the water column, methanogenic archaea were present below 17 m at concentrations of 1-7 10^5 cells ml^{-1}. Methanogen biomass was higher in the sediment (MANCUSO et al. 1990).

Two species of methanogens have been characterised from Ace Lake. *Methanococcoides burtonii* was characterised from the bottom waters of Ace Lake (FRANZMANN et al. 1992). The organism utilised methylamines and methanol as precursors to methanogenesis. In contrast, *Methanogenium frigidum* is a $H_2:CO_2$ utilizing methanogen (FRANZMANN et al. 1997). It is not known which methanogen type is predominant in Ace Lake, but given that methanogenesis is largely limited to the region of the lake that is depleted in sulfate, it is probable that the $H_2:CO_2$ methanogen is the major contributor to methanogenesis.

Although limited taxonomic data are available on SRB in Ace Lake, biomass of these species in the water column of Ace Lake has been estimated from lipid analysis to comprise 25 % of the microbial population at 23 m (MANCUSO et al. 1990). Phospholipid-derived fatty acid profiles indicated that bacteria belonging to the genera *Desulfobacter* and *Desulfovibrio* were present in the monimolimnion and in the sediments of Ace Lake.

The characterisation of other bacteria from the monimolimnion continues. Recently, a facultative anaerobic bacteria from the algal mats of Ace Lake was characterised. *Shewanella frigidimarina* is a motile, rod-shaped bacterium which is capable of anaerobic growth either by fermentation of carbohydrates or by anaerobic respiration. It utilized a variety of electron acceptors, including ferric compounds (BOWMAN et al. 1997a). No doubt the metabolic requirements and products of as yet undescribed species from Ace Lake will shed more light on the complex interactions between bacterial species and chemical cycles.

7. THE CARBON CYCLE IN ACE LAKE

The carbon cycle in Ace Lake is shown schematically in Fig. 9. The boxes in the figure represent the various carbon pools, and the arrows the transfer of carbon from one pool to another. Discussion of the carbon cycle is again divided into processes occurring in the oxic and anoxic zones.

7.1 Anaerobic Carbon Production and Consumption

The two possible external sources of carbon for the lake are uptake of atmospheric CO_2 by the surface waters and carbon input in the meltstreams that form during summer. Carbon dioxide uptake from the atmosphere will only occur in the water is undersaturated with respect to the atmosphere. Dissolved inorganic carbon (DIC) in Ace Lake is supersaturated with respect to the atmosphere at all depths (BURTON 1980), precluding uptake of CO_2 and instead resulting in loss of carbon during the period that the lake is ice free. Thus it is probable that the atmosphere at present is a carbon sink for the lake rather than a source.

The input of carbon in the forms of DIC, dissolved organic carbon (DOC) or particulate organic carbon (POC) from the catch-

ment area of the lake has not been measured, but is likely to be minor. Unlike lakes that are close to penguin rookeries, there is no evidence that organic matter from birds has a significant input into the carbon cycle of Ace Lake. The input of organic carbon and nutrients from higher plants is also insignificant (VOLKMAN et al. 1986), as the density of mosses and lichens in the area is low (HAND & BURTON 1981, SEPPELT 1988). It is probable that some organic carbon is leached from the cyanobacterial mats which grow in meltstreams which enter the lake, but, even assuming high concentration of 10 mg C l⁻¹ in the streams, this input would be minor.

Primary production by autotrophs, including phytoplankton in the water column and photosynthetic components of the microbial mats, converts DIC to cell material. Some of the photosynthate is released, even by healthy cells, as DOC (LYNCH & HOBBIE 1988). PARKER et al. (1977) found that in Lake Hoare (in the Dry Valleys), 75 % of the total photosynthetically fixed organic matter appeared as extracellular products. Few measurements of primary productivity have been

reported for Ace Lake. WRIGHT & BURTON (1981) reported that primary productivity rates in February 1979 were 0.16 mg C m⁻³ h⁻¹ at 5 m and 0.47 mg C m⁻³ h⁻¹ at 10 m. In November 1993 primary production rates at 2 m and 8 m were measured at 0.68 mg C m⁻³ h⁻¹ and 0.47 mg C m⁻³ h⁻¹ respectively (LAYBOURN-PARRY & PERRISS 1995). These rates of primary production are similar to rates measured in other Antarctic meromictic lakes (VINCENT 1981, VINCENT & VINCENT 1982, PARKER et al. 1982, HEATH 1988, SPAULDING et al. 1994) and in the Southern Ocean (WEBER & EL-SAYED 1987) but are low in comparison to rates measured in tropical and temperate lakes (WETZEL 1983). There is insufficient data from Ace Lake to comment on the relationship between productivity and depth, except to state that the rates of photosynthesis at the bottom of the aerobic zone, at relatively low PAR irradiances, are significant.

With the exception of *Mesodinium rubrum*, the contribution of individual species to primary production in the aerobic zone of the lake is not known, and even for *M. rubrum*, the contribu-
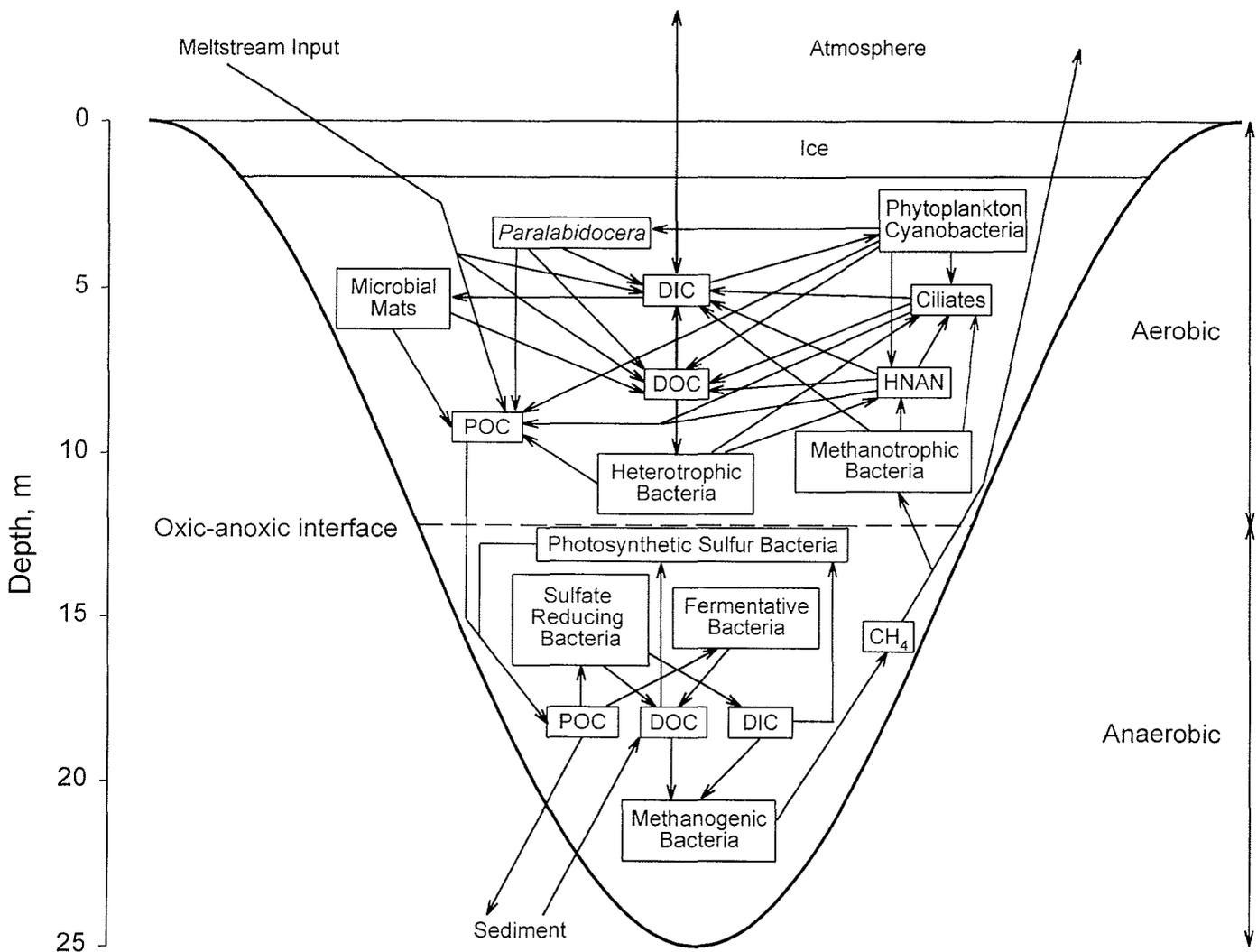
Fig. 9: The carbon cycle in Ace Lake.

Abb. 9: Der Kohlenstoffkreislauf am Ace Lake.

tion is only a rough estimate. Primary productivity measurements indicate that *M. rubrum* may contribute between 15 % and 40 % of carbon fixation in the phytoplankton during the bloom period (LAYBOURN-PARRY & PERRISS 1995). Due to its high abundance, *Synechococcus* also probably contributes significantly to primary productivity (RANKIN 1998). All phytoplankton species bloom at different depths and times over summer and hence the contribution of each species to primary productivity will vary both temporarily and spatially.

The organic carbon produced by the photosynthetic cells is eventually transferred to various other pools. Respiration by the autotrophs returns carbon to the DIC pool, and grazing by ciliates, HNAN and metazoa result in inclusion of some of the carbon in these pools. During grazing some carbon is also released as DOC, a process generally termed "sloppy feeding". Death of the cells results in transferal of the carbon to the POC and DOC pools.

DOC concentrations in the oxygenated waters of Ace Lake range from approximately 6 mg C l^{-1} in the mixolimnion to 11.5 mg C l^{-1} at the bottom of the oxic zone (L. Rankin and J. Gibson, unpublished results). Due to the vertical stability of much of the water column in the lake, DOC produced by primary productivity in the aerobic zone will be primarily cycled within this region. Heterotrophic bacteria play a major role in this procedure, in the process returning carbon to the DIC pool. These bacteria, in turn, are food sources for HNAN and ciliates. It is also possible that some of the nominally autotrophic species in the lake are capable of mixotrophy (i.e. exhibit both heterotrophic and autotrophic modes of nutrition), and are thus able to ingest bacteria and other small particles.

The role of the copepod *Paralabidocera antarctica* in the food web of Ace Lake has not been determined. The copepod undoubtedly feeds on the larger algae and possibly *Mesodinium rubrum* (GIBSON et al. 1997b), but its role in controlling the populations of smaller species is uncertain.

The POC pool consists of faecal pellets and cast carapaces of *Paralabidocera antarctica* and dead bacteria, heterotrophic and phototrophic plankton. Sedimenting POC provides the major link between the carbon cycles of the aerobic and anaerobic zones, though it is also possible that live cells also sediment to the anoxic zone (HAND 1980). The concentration of POC in the oxic waters has been found to be in the range 0.22-0.73 mg l^{-1} (average: 0.40 mg l^{-1}) over a four month period in spring and summer, 1994-95 (J. Gibson, unpublished data).

7.2 *Anaerobic Carbon Production and Consumption*

Between the oxic-anoxic interface and the bottom the lake POC originally produced in the aerobic zone is decomposed anaerobically by SRB (BURTON & BARKER 1979, FRANZMANN et al. 1988, MANCUSO et al. 1990), fermentative heterotrophic bacteria (FRANZMANN & DOBSON 1992), and methanogens (BURTON

1980, FRANZMANN et al. 1991b). The action of these bacteria initially breaks down the POC into smaller, dissolved molecules, and, ultimately, CO_2 and CH_4. Organic carbon will also diffuse into the lake from the sediments, and POC will be lost from the water column by inclusion into the sediment. The total organic carbon concentration increases with depth, reaching a maximum of over 50 mg C l^{-1} at the bottom of the water column (HAND & BURTON 1981).

The PSB that occur at the top of the anaerobic zone use H_2S as an electron donor for anaerobic bacterial photosynthesis (BURKE & BURTON 1988b), which fixes CO_2 and small organic molecules released by SRB and other heterotrophs occurring in their immediate vicinity (OVERMANN 1997). HAND & BURTON (1981) estimated that anaerobic photosynthetic bacteria could account for 45 % of total photosynthetic activity in Ace Lake. As OVERMANN (1997) pointed out, however, this production is not new production, but rather is fueled and limited by the POC flux from the aerobic zone. Atmospheric CO_2 would not contribute directly to this process as molecular diffusion would be too slow to replenish CO_2 fixed by the PSB. As is the case for aerobic photosynthetic bacteria and algae, the contribution of *Chlorobium* spp. to carbon productivity will vary throughout the year.

Below 19 m sulfate reduction is limited by low sulfate concentrations (Fig. 7) and hence methanogenesis becomes the major terminal mineralisation process. At depths at which sulfate is not limiting, SRB out-compete the methanogens for substrates (FRANZMANN et al. 1991b). It is presumed that SRB and other anaerobic heterotrophic bacteria such as the C-shaped bacteria (FRANZMANN & DOBSON 1992) break down particulate and high molecular weight dissolved forms of carbon to low molecular weight forms for methanogenesis (HAND & BURTON 1981). Concentration of dissolved amino acids and short chain fatty acids increase sharply beneath the oxic-anoxic interface in nearby Organic Lake (GIBSON et al. 1994), and butyric acid in Ace Lake decrease at depths where methane producers are active (BURTON & XU 1988).

There appears, therefore, to be a strong interaction between photosynthetic sulfur bacteria, sulfate reducing bacteria, anaerobic heterotrophic bacteria and methanogenic archaea in the anaerobic zone that eventually reduce complex organic compounds to methane. BRYANT et al. (1977) indicated that normally methanogens are not known to utilize lactic acid but a symbiotic consortia of sulfate reducing bacteria and methanogens can co-metabolise lactic acid in the absence of sulfate through hydrogen transfer (FRANZMANN et al. 1991b). A number of organic intermediates have been detected in Ace Lake that would be formed as part of this interaction (ROBERTS & BURTON 1994).

Methanogenesis occurs in the water column and sediments of Ace lake at very slow rates. In the water column, maximum rates of methanogenesis of 2.6 mmol l^{-1} day^{-1} from NaH^{14}CO$_3$ were measured at 20 m (FRANZMANN et al. 1991b). The recorded rates were at the limit of detection for the experimental method used. As substrate (short chain organic acids) was not limiting (FRANZMANN et al. 1991b), the low rates of methanogenisis were

probably a result of the low temperatures at these depths. Methanogenic bacteria usually have an optimal growth temperature between 30 °C and 40 °C (Franzmann et al. 1991b). Further to this evidence, estimates of methanogen biomass (Mancuso et al. 1990) suggested that current microbial degradation of organic carbon in Ace Lake may be occurring at very slow rates.

Methane is lost either by bubble formation and rapid transfer to the surface and the atmosphere, though some is oxidised by methanotrophic bacteria which occur immediately above the oxic-anoxic interface (Bowman et al. 1997b). The high concentrations of H_2S in the bottom waters of Ace Lake does not appear to inhibit methanogenesis at this depth. However, the exact controls of growth of the methanogens in the bottom waters of Ace Lake have yet to be determined.

Methanogenesis has not been reported to occur in any other meromictic lakes in the Vestfold Hills (Franzmann et al. 1991b). Methane has been detected at the bottom of Lake Vanda in the Dry Valleys (Vincent 1988) and in Lake Untersee, central Dronning Maud Land, East Antarctica (Wand et al. 1997) but no production rates have been reported. Rates of methanogenesis have been reported for some lakes on Signy Island in maritime Antarctica (Ellis-Evans 1984).

8. CONCLUSIONS

Ace Lake remains the most studied marine-derived meromictic lake in Antarctica. Its relatively simple trophic structure, its interesting chemistry and the suite of bacteria, ranging from autotrophic photosynthetic sulfur to methanogenic, has made it an attractive study site. However, there is much still to be learned about this lake. For example, the benthic community is poorly known both in terms of structure and function, and there is little information about the rates at which chemical and biological processes as basic as photosynthesis occur. It is thus likely that Ace Lake will continue to be studied for many years to come.

Like other meromictic lakes in the Vestfold Hills, Ace Lake has a dynamic physical and chemical stratification which is dependent on the water budget and local climatic conditions. Within the last few years the water level of Ace Lake has begun to fall. If this trend continues the mixolimnion will become more saline and therefore less stable. The lake may start mixing to a greater depth and the aerobic section of the monimolimnion may eventually be incorporated into the mixolimnion. It remains to be seen how the microbial communities will adapt to these changes in lake structure, or whether future physico-chemical conditions will result in their extinction.

All meromictic lakes in Antarctic differ in structure and microbial composition because each has undergone a unique set of processes which have resulted in the modern lake. There are many other limnologically diverse meromictic lakes in the Vestfold Hills and in other areas of Antarctica, most of which have not been studied in any detail. Like Ace Lake these lakes have interesting geochemical cycles and support a wide diversity of bacterial and algal species. The continued study of Ace Lake, as well as other meromictic lakes in the Vestfold Hills and throughout the continent, will provide more information about the biota and biogeochemical mechanisms of extreme environments, and provide an insight into ancient climatic conditions.

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