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Photosynthetic bacteria in meromictic lakes and stratified fjords of the Vestfold Hills, Antarctica

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Abstract

Thirteen meromictic lakes and two permanently stratified fjords in the Vestfold Hills, Antarctica, were surveyed in 1983 for photosynthetic bacteria. Burton Lake and Ellis Fjord were sampled throughout the year to determine seasonal variations. Physical and chemical parameters were recorded and related to the species present. The dominant species in waters with salinities of ≤ 100.7 g kg ^{1} were *Chlorobium vibrioforme* and *Chlorobium limicola* with populations at the O_2-H_2S interface in the range 0.3 to 6.7 $\times$ 10^6 ml^{-1}. Neither of these species was found at higher salinities. *Thiocapsa roseopersicina* and a *Chromatium* sp. were found in low numbers ($<10^5$ ml^{-1}) in most of the same waters as the *Chlorobium* spp. These bacterial phototrophs developed in a narrow band below the O_2-H_2S interface where both light and H_2S were available. Very low numbers ($<10^2$ ml^{-1}) of *Rhodopseudomonas palustris* were found in both oxic and anoxic waters having salinity ≤ 148 g kg^{-1}. The dominance of the *Chlorobium* spp. is ascribed to their more efficient maintenance metabolism during the darkness, their faster growth at low light intensities (<1 μE m^{-2} s^{-1}) and the lack of selective filtering of incident light. The *Chlorobium* spp. grew well at -2 °C, but not -5 °C in hypersaline waters. The concentration of H_2S had no apparent effect on the development of the bacterial flora. Viable cells were found to depths of 100 m in Ellis Fjord indicating that viability in total darkness could have been maintained for periods of the order of 1700 days.

Introduction

The Vestfold Hills, (68°30′S, 78°E), contain 13 meromictic lakes which originated as relict sea water trapped in valleys by ice-sheet retreat (Adamson & Pickard, 1983). The lakes and fjords are ectogenically stratified with fresh meltwater in summer (Burton, 1981); and stability of this stratification has been aided by the short duration of ice-free periods, usually only four to six weeks each year, if at all. Over the past 8000 years they have had varying water budgets so that current salinities range from 12 g kg^{-1} to 197 g kg^{-1} (Burton, 1981). This study was initiated to identify the photosynthetic bacterial species in these lakes and fjords and to determine, where possible, the environmental parameters which limit their growth and distribution.

Study area

Figure 1 shows the Vestfold Hills and the location of the meromictic lakes (Abraxas, Ace, Anderson, Burton, Clear, Ekho, Farrell, Fletcher, McCallum, Organic, Oval, Pendant and Shield) and the two stratified fjords, Ellis (basins 1 and 2) and Taynaya Bay (basins 1, 2, 3). Burton Lake, including its western lobe, is seasonally tidal and is described in more de-

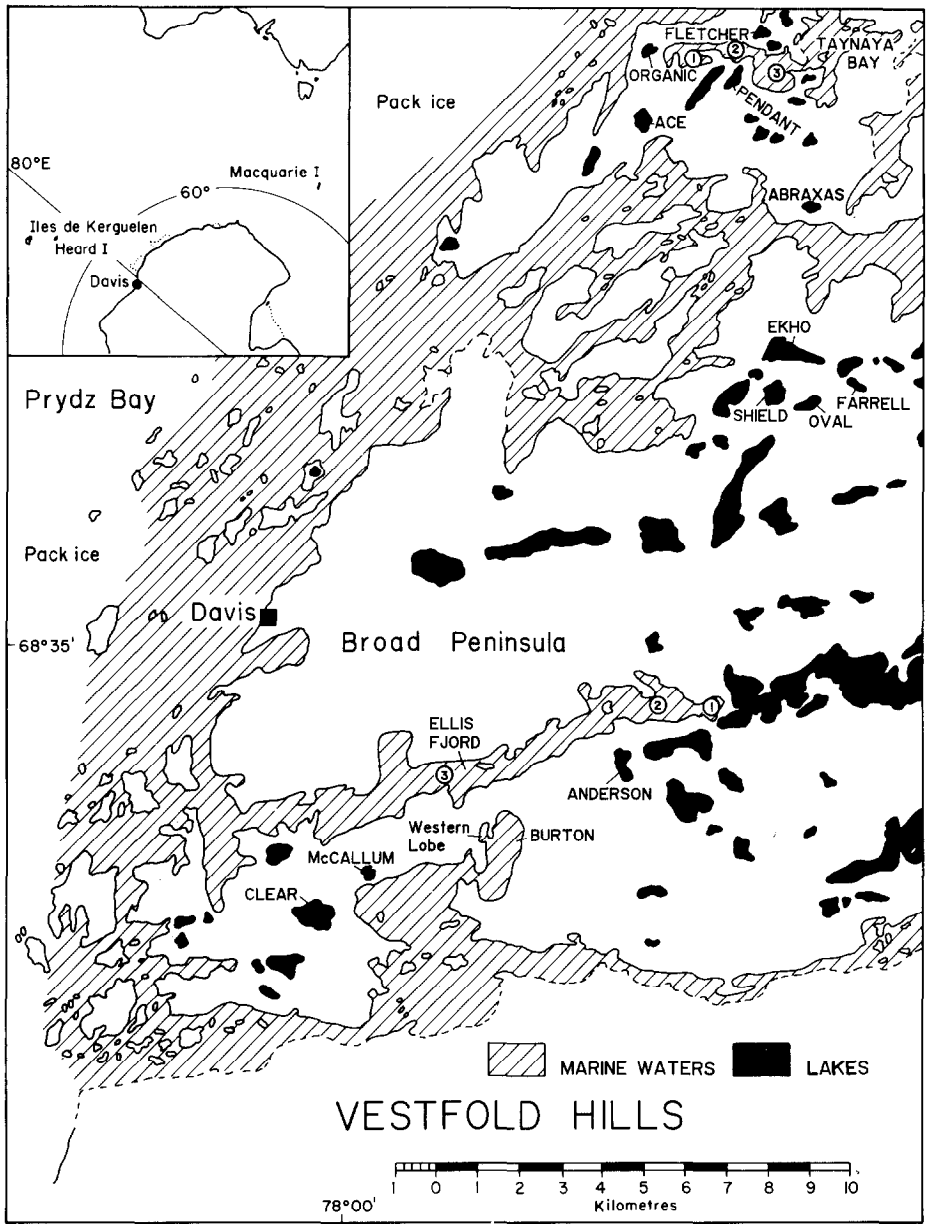

Fig. 1. Map of the Vestfold Hills showing the meromictic lakes and the permanently stratified fjords.

tail in Burke & Burton (this volume). The remaining lakes are all land-locked and some features of each are listed in Table 1. Ellis Fjord is approximately 10 km long and is over 100 m deep at several points in this length. It has a very restricted opening to the sea, less than 4 m deep, and a number of basins (1, 2 & 3 in Fig. 1) of which basins 1 and 2 are stratified. Basin 1, about 12 m deep, was stratified at 6–7 m during winter, 1983. It is separated from basin 2 by a sill less than 1 m deep. Basins 2 and 3 are separated by a sill 23–30 m deep which is adjacent to the innermost island of the fjord. Basin 2 had a chemocline at a depth of 36–43 m at different dates in 1983 and below this the water was anoxic. There was a very substantial flow of fresh water via Ellis Rapids into the head of the fjord during the summer melt. As a result, Ellis Fjord had three distinct layers of water in the stratified basins. In summer there was

a surface layer 2–3 m deep of fresh water lying above approximately 36 m of tidal, oxic sea water (≃31‰) and then at least 60 m of slightly denser, anoxic bottom water. In winter the fresh water was replaced by up to 1.7 m of ice.

Taynaya Bay is more complex in morphology and has six basins, three of which were stratified (see Fig. 1). It is mostly shallower than Ellis Fjord, being less than 30 m deep; however basin 2 is greater than 65 m. Stratification occurred at 10, 15 and 20 m in basins 1, 2 and 3 respectively. As in Ellis Fjord, the bottom water was anoxic while the upper water was tidal and oxygenated. Taynaya Bay maintains a large amount of ice cover throughout most summers and this reduces wind mixing. This may also partially explain the shallower chemocline depths compared with Ellis Fjord.

Materials and methods

A Kemmerer bottle was used to sample the water column of Ellis Fjord from May to December 1983 and in January 1984 at one site in Basin 1, two sites in Basin 2, two sites in Basin 3 and one marine site just outside the fjord entrance. In basin 2, samples were taken at intervals of 10 m from the surface to the interface of the oxic and anoxic waters (O_2-H_2S interface). Five samples were taken in this region at intervals of 1 m and then two or three deep water samples were taken. In the other basins, surface and bottom samples were collected. Sampling of the surface water and O_2-H_2S interface of the lakes and Taynaya Bay was done irregularly in 1983. Field and chemical analyses, enrichment culturings and isolation of bacteria and bacterial counts were carried out as described in Burke & Burton (this volume). Salinity was calculated from density at 20 °C by an equation, Salinity = 1315.7895 × density (20 °C) − 1313.4211 derived from Appendix 1 of Whitfield & Jagner (1981). We recognize the potential weakness of using a linear regression well beyond the bounds of the data from which it was derived (e.g. to infer the salinity of hypersaline Organic Lake) and have given the equation so that measured density (at 20 °C) can be recovered, if desired. Some data collected in 1978 are also used.

Results

Table 1 lists some physical and chemical parameters of the lakes and fjords sampled. The sites are listed in increasing order of salinity of the water at the O_2-H_2S interface. A range in values indicates the extent of annual variation. There was a wide variation in salinity of the interface water samples from a minimum of 12.9 g kg^{-1} in Clear Lake to a maximum of 199.4 g kg^{-1} in Organic Lake. In some of the sites there was only a slight salinity difference between the upper and lower waters but, nonetheless, stratification was still permanent.

The depths of the O_2-H_2S interfaces in the permanently stratified water bodies varied from 3.5–43 m; but only four were deeper than 20 m. The principal effect of the deeper interfaces was a further reduction in the light intensity available to photosynthetic bacteria. For example, on 23 December 1983 the light incident at the surface of Burton Lake was 171 microeinsteins m^{-2} s^{-1} (μE m^{-2} s^{-1}) and the light intensity at the O_2-H_2S interface (11 m) was 4.9 μE m^{-2} s^{-1}. In contrast, on 5 January 1984 the light incident on Ellis Fjord basin 2 was 1316 μE m^{-2} s^{-1} but the intensity at the chemocline (41 m) was 0.14 μE m^{-2} s^{-1}.

The temperatures at the O_2-H_2S interfaces were generally above 0 °C throughout the year, the highest temperature recorded being 13.2 °C in Ekho Lake. However, Burton Lake (see also Burke & Burton, this volume: Fig. 1) and Ellis Fjord both had temperatures below zero (−0.5 to −2.2 °C) throughout the year. They were also tidal for at least five to six months of the year. A temperature of −0.7 °C was recorded in the anoxic water of Taynaya Bay (which is also intermittently tidal) in 1978, but no seasonal data are available. The coldest sites were the western lobe of Burton Lake (minimum temperature −5.2 °C) and Organic Lake (minimum temperature −6 °C); however both warmed to above 0 °C in summer. These sites were much shallower than the other lakes and fjords investigated. Organic Lake was the most saline.

Hydrogen sulphide (H_2S) was present in all the meromictic lakes except Organic lake. The western lobe of Burton Lake was not meromictic, but it did have H_2S throughout the water column by late

Table 1. Salinity, depth, temperature and H_2S and bacteriochlorophyll *c* concentration at the O_2-H_2S interfaces in stratified lakes and fjords of the Vestfold Hills.

Site	Salinity (g kg^{-1})	Depth (m)	Temp (°C)	H_2S (mg l^{-1})	Bacteriochlorophyll *c* (mg l^{-1})
Clear Lake	12.9	29	+4.8	+	0.08
McCallum Lake	17.9	19.5	+5.6	+	0.31
Abraxas Lake	18.1	18	+2.7	2.5	0
Pendant Lake	19.9	10	+5.4	2	0.086
Ace Lake	29.3	11	+7.7	2	0.11
Ellis Fjord 2	34.9	36 to 43	−1 to −2	20	0.01 to 0.06
Taynaya Bay 3	36.0	21	−0.7	2	0
Ellis Fjord 1	40.2	7	−1 to −2.2	2	0.1 to 0.23
Taynaya Bay 1	40.6	10.5	−0.7	797	4.6
Burton Lake	30.7 to 40.5	8 to 12	−0.5 to −2	1 to 268	0.1 to 0.11
western lobe[a]	40.0 to 89.5	0 to 2.75	−1.7 to −5.2	0 to 37	0
Fletcher Lake	100.7	6.5	+2.9	481	0.49
Anderson Lake	131.3	3.5	+2.3	+	0
Ekho Lake	139.0	23	+13.2	2	0
Shield Lake	148.0	18	+6.3	1	0
Farrell Lake	168.8	8	+5.5	2	0
Oval Lake	193.3	8	+5.5	2	0
Organic Lake	199.4	4	−6	0	0

[a] The western lobe is a part of Burton Lake which is isolated by ice formation from the main body of the lake in winter.

winter. In Lakes Farrell and Oval, H_2S was restricted to the very bottom of the water column and on some occasions was not detected (e.g. Farrell Lake on 28 February 1983). H_2S concentration just below the O_2-H_2S interface was usually <20 mg l^{-1}; but rose rapidly so that the photosynthetic bacteria were growing, at times, in several hundred mg l^{-1} of H_2S. For example, the concentration of H_2S in Burton Lake on 23 November 1983 at 11.96 m was zero while at 12.31 m it was 121.8 mg l^{-1} (see Burke & Burton this volume: Fig. 6). Sulphate-reducing bacteria

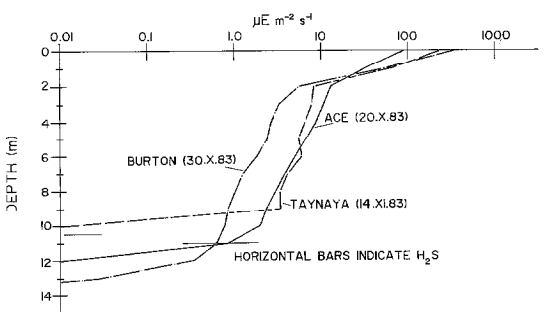

Fig. 2. Light penetration (microeinsteins m^{-2} s^{-1}) in Ace Lake, Burton Lake and Taynaya Bay. NB: H_2S was first detected at 11 m in both Ace and Burton lakes on these dates.

were enriched from the water column of all lakes containing H_2S.

The only bacteriochlorophyll detected was bacteriochlorophyll *c* and while the waters were sometimes bright green at the O_2-H_2S interface, the concentrations were generally <0.2 mg l^{-1}. In basin 1 of Taynaya Bay, 4.6 mg l^{-1} of bacteriochlorophyll *c* was observed at 10.5 m; and though light was extinguished between 9 and 10 m (Fig. 2) it indicates that a considerable population of Chlorobiaceae was present in the photic zone of the anoxic water.

Table 2 shows from which lakes and fjords photosynthetic bacteria of the families Chlorobiaceae, Chromatiaceae and Rhodospirillaceae were enriched. Species of Chlorobiaceae (*Chlorobium vibrioforme* Pelsh and *Chlorobium limicola* Nadson) were the most commonly enriched bacterial phototrophs and were found in those sites with salinity ≤ 100.7 g kg^{-1} at the O_2-H_2S interface. *Thiocapsa roseopersicina* Winogradsky, *Chromatium* sp. Perty (Chromatiaceae) were enriched sporadically from sites with salinities ≤ 89.5 g kg^{-1}. They were only enriched in media exposed to light of wavelengths greater than 780 nm which selectively inhib-

Table 2. Photosynthetic bacteria found in stratified lakes and fjords of the Vestfold Hills.

Site	Chl.[a]	Chr[b]	R[c]
Clear Lake	+	+	−
McCallum Lake	+	+	−
Abraxas Lake	+	+	+
Pendant Lake	+	−	+
Ace Lake	+	+	−
Ellis Fjord 2	+	+	+
Taynaya Bay 3	+	−	−
Ellis Fjord 1	+	−	−
Taynaya Bay 1	+	−	−
Burton Lake	+	+	+
western lobe	+	+	+
Fletcher Lake	+	−	−
Anderson Lake	−	−	−
Ekho Lake	−	−	+
Shield Lake	−	−	+
Farrell Lake	−	−	−
Oval Lake	−	−	−
Organic Lake	−	−	−

[a] Chlorobiaceae; [b] Chromatiaceae; [c] Rhodospirillaceae.

ited the Chlorobiaceae. Both *T. roseopersicina* and *Chlorobium* spp. were enriched from samples taken at 100 m in Ellis Fjord where they were in permanent darkness. The only species of Rhodospirillaceae isolated, *Rhodopseudomonas palustris* Molisch, was present in both oxic and anoxic waters with salinities ≤ 148 g kg^{-1}. They numbered <100 ml^{-1}.

Total bacterial counts from Burton Lake and Ellis Fjord (basin 2) typically showed lowest counts in the mixolimnion with approximately an order of magnitude increase across the O_2-H_2S interface. In Burton Lake, the lowest count at the interface (0.5×10^6 ml^{-1} in July) was recorded in mid-winter and the highest in summer (5.4×10^6 ml^{-1} in December). In Ellis Fjord, the seasonal range was from 1.01×10^6 ml^{-1} in May to 6.7×10^6 ml^{-1} in December: but a much lower count of 0.3×10^6 ml^{-1} was observed in September. This was associated with a destratifying mixing process which increased the depth of the O_2-H_2S interface from 37 m in August to 43 m in September. The majority of the phototrophic cells were members of *Chlorobium* spp. as *T. roseopersicina* and *Chromatium* sp. totalled $<10^5$ cells ml^{-1} and *R. palustris* <100 cells ml^{-1}.

Figure 2 shows the penetration of light through

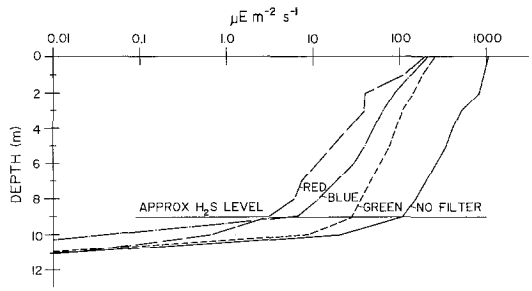

Fig. 3. Penetration of different wavelengths of light (microeinsteins m^{-2} s^{-1}) in Ace Lake on 8 February 1977.

the water column of three ice-covered sites in 1983. They show a similar pattern of high absorption through the snow and ice, and steady absorption in the water column culminating in extinction of the remaining light just below the O_2-H_2S interface. For Taynaya Bay, the bar indicating H_2S is shown 0.5 m below the depth of zero light. However, the concentration of H_2S at 10.5 m was 781 mg l^{-1} and of bacteriochlorophyll *c* was 4.6 mg l^{-1}. It is therefore reasonable to assume that H_2S was present in the lower region of the photic zone. The penetration of light into Ellis Fjord on 20 December 1983 is shown in Fig. 4. The intensity measured at the O_2-H_2S interface was always less in the fjord than in Burton Lake (see Burke & Burton, this volume) because of the fjord's greater depths. The measured intensity of light at different O_2-H_2S interfaces varied from 0–4.9 μE m^{-2} s^{-1} in 1983. However, greater intensities have been recorded in ice-free conditions as illustrated by Fig. 3, which shows the penetration of red, blue and green wavelengths in Ace Lake. The three wavelengths were present at the O_2-H_2S interface with green and blue predominating, but each were extinguished rapidly below this level. A profile taken on 15 November 1974, when about 2 m of ice covered the lake, showed a similar relative absorption of wavelengths with 0.2 μE m^{-2} s^{-1}, 7 μE m^{-2} s^{-1} and 22 μ m^{-2} s^{-1} of red, blue and green wavelengths respectively present at the interface.

The limnological characteristics of Burton Lake are described in Burke & Burton (this volume).

Figure 4 shows a typical profile of Ellis Fjord with a slight density stratification between 41 and 43 m. This is coincident with a decrease to zero of both dissolved oxygen and redox potential and the occur-

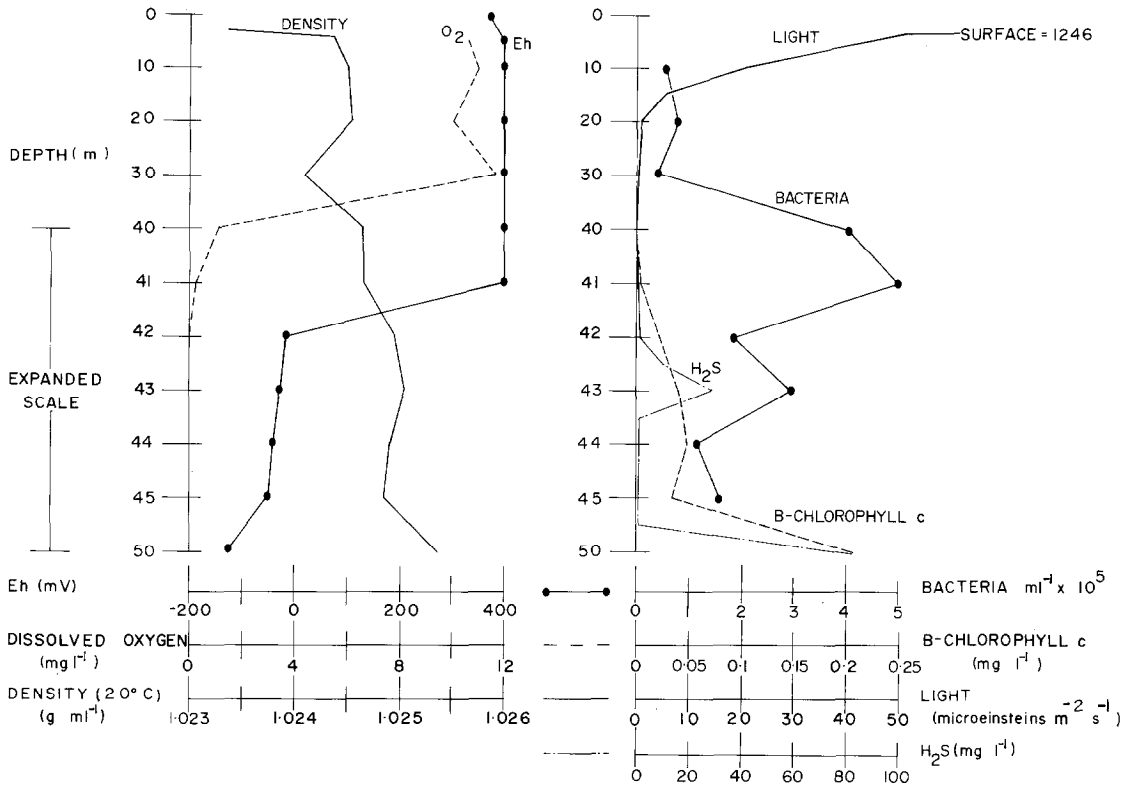

Fig. 4. Selected limnological and biological characteristics of the water column of Ellis Fjord (basin 2) on 20 December 1983.

rence of low concentrations of H_2S (2 mg l^{-1}). It is possible that both O_2 and H_2S are present for about 0.5–1 m because of the instability of the density stratification. There was a small, but measurable quantity of light at the oxycline (0.1 μE m^{-2} s^{-1}. The main peak of bacterial numbers was associated with the oxic zone just above the O_2-H_2S interface and there was a second peak coinciding with a peak in H_2S at 43 m from where *Desulfotomaculum* spp. and *Desulfovibrio* spp. were enriched. The concentration of bacteriochlorophyll *c* increased with depth from the interface. However, at most other times there was a small peak of up to 0.06 mg l^{-1} of bacteriochlorophyll *c* associated with an increased cell count just below the interface. It was difficult to determine when growth first occurred, though new bacteriochlorophyll *c* was noted in November–December when light intensity at the O_2-H_2S interface was less than 0.1 μE m^{-2} s^{-1}. At all times the concentration of pigment (bacteriochlorophyll *c* and/or bacteriophaeophytin *c*) was highest at depths of 60–70 m and below.

The temperature of all but the top 3 m of the water column was −1.5 °C, varying only in the range −0.8 to −2.0 °C throughout the year. A similar series of profiles to those in Fig. 4 were recorded in 1983 except that the depth of the O_2-H_2S interface varied from 36–43 m.

Discussion

A comparative study of the different habitats of certain photosynthetic bacteria has been made possible by the presence of lakes and fjords in the Vestfold Hills which differ in depth, morphology, dissolved salts and consequently, stratification. Previous studies have identified six factors that influence the development of photosynthetic bacterial populations: light intensity, light quality, temperature, the presence of other phototrophs (bacterial or algal), salinity and the concentration of sulphide (Takahashi & Ichimura, 1970; Cohen *et al.*, 1977; Parkin & Brock, 1980a, b; van Gemerden, 1980; Montesinos

et al., 1983; Pedros-Alio *et al.*, 1983).

Biota

A limited number of species of photosynthetic bacteria were found in the lake samples and further species could possibly be revealed by more extensive sampling. Hand (1980) reported *Rhodospirillum* sp. in Ace Lake. However, the methods used support the conclusion that while *Thiocapsa roseopersicina*, *Chromatium* sp. and *Rhodopseudomonas palustris* were present, the dominant species were *Chlorobium vibrioforme* and *Chlorobium limicola*. In accordance with the observations of Cohen *et al.* (1977), only one plate of photosynthetic bacteria existed in these meromictic lakes. *T. roseopersicina*, *R. palustris* and *Chromatium* sp. did not form a plate distinct from the populations of *Chlorobium* spp.

Light

While it is always the case that the light intensity at the O_2-H_2S interface of a lake will vary seasonally, such fluctuations are extreme in the lakes of the Vestfold Hills. For example, at the O_2-H_2S interface in Burton Lake there were three months of darkness, six months of intermediate intensity and three months of relatively high light intensity (estimated maximum of 10 μE m^{-2} s^{-1}; Burke & Burton, this volume). In Ace Lake, an intensity of 100 μE m^{-2} s^{-1} has been recorded at the O_2-H_2S interface (Fig. 3); but periods of very high light intensity are likely to be brief in Antarctica and occur well after the establishment of the photosynthetic bacterial populations. Conceivably, high light intensities in summer could alter the species composition; but the data of Burke & Burton (this volume) do not appear to support this as *Chlorobium* spp. were dominant in Burton Lake throughout the ice free period in early 1983. The amount of snow and the transparency of the ice varied considerably between the sites sampled in this study, but their location at high latitude and the extended period of ice cover of all the sites produce a lengthy period of zero, or very low light intensity at their O_2-H_2S interfaces.

If all the lakes sampled were to have similar spectral distributions to that shown in Fig. 3 for Ace Lake, then both Chlorobiaceae and Chromatiaceae should grow well. However, Chlorobiaceae were dominant in all lakes in which they occurred. Burke & Burton (this volume) suggested that the more efficient maintenance metabolism of the Chlorobiaceae in darkness (van Gemerden, 1980), together with their faster generation times at low light intensities (Herbert & Tanner, 1977; Biebl & Pfennig, 1978), allowed them to dominate the monimolimnion of Burton Lake. If our assumption that the lakes have similar light regimes at their O_2-H_2S interfaces is valid, then the three months of winter darkness followed by three months of low light intensities become important factors in selecting for Chlorobiaceae.

These bacteria possess a light harvesting system which enables them to grow at lower light intensities than Chromatiaceae (Biebl & Pfennig, 1978). This system includes carotenoids which have absorption maxima in the range 450–515 nm; the wavelengths of light that penetrate water most deeply in the absence of biological filtering (Kirk, 1977; Truper & Pfennig, 1981). This ability is particularly important in Ellis Fjord where the depth of the O_2-H_2S interface varied from 36–43 m during 1983. Montesinos *et al.* (1983) reviewed the species of Chlorobiaceae found in different lakes and concluded that β-isorenieratene-containing species were dominant at depths greater than 9 m. This is not the case in the lakes and fjords of the Vestfold Hills which have deep O_2-H_2S interfaces (e.g. Ellis Fjord, Clear Lake, Abraxas Lake). In Ellis Fjord the dominant species were *Chlorobium vibrioforme* and *Chlorobium limicola* which contain chlorobactene, although some of the spectral scans of enrichment cultures had small peaks suggestive of the presence of β-isorenieratene as well. Biebl & Pfennig(1978) concluded that in the absence of selective filtering of incident light by photosynthetic organisms there would be no advantage for species containing β-isorenieratene. Therefore, it is not simply increased depth below the surface which favours species with β-isorenieratene, rather increased depth together with selective filtering of incident light. In Ellis Fjord the growth of chlorobactene-containing species indicates that there was little or no selective

filtering of incident light by photosynthetic organisms.

Salinity

The Chromatiaceae and Chlorobiaceae were detected only in lakes with salinities ranging from 12.9 g kg^{-1} (Clear Lake) to 100.7 g kg^{-1} (Fletcher Lake). Therefore, the upper limit for these bacteria was between 100.7 and 131.3 g kg^{-1} (the salinity of the monimolimnion of Anderson Lake where neither were found) which is a lower maximum than reported elsewhere (e.g. Cohen *et al.*, 1977). The Rhodospirillaceae had a greater salt tolerance in these lakes, being isolated from Shield Lake which had a salinity of 148 g kg^{-1}. However, their low numbers suggest they were only a minor component of the microbial flora of these lakes.

Cohen *et al.* (1977) reported the occurrence of *Chromatium violescens* and *Prosthecochloris* sp. in Solar Lake in salinities of about 180 g kg^{-1}; but in other respects Solar Lake is very different from the lakes of the Vestfold Hills. It is situated at low latitude and can reach temperatures of 60 °C and is shallow enough for light to penetrate the entire water column during stratification. These factors may allow photosynthetic bacteria to develop at a salinity which inhibits them in areas such as the Vestfold Hills which are much colder and with comparatively very low light intensities.

Apart from direct salinity effects on viability, the position of the photosynthetic bacterial populations in the water column was affected by salinity gradients. Most lakes and fjords studied here had very stable density stratifications due to the morphology of the drainage basins, the lengthy periods of ice cover, and the large density gradients that commonly existed. This implies that the O_2-H_2S interface, and therefore the populations of photosynthetic bacteria, were stable. In Burton Lake and Ellis Fjord however, there was a variation of up to 5 m in the depth of the O_2-H_2S interface in 1983. In Burton Lake this was attributed to salt exclusion during ice formation (Burke & Burton, this volume); but though likely, this was less certain in Ellis Fjord. The end result in both cases was that the initial populations at the O_2-H_2S interfaces, when mixed with oxic waters, were lost, H_2S was chemically oxidized and new populations of photosynthetic bacteria developed at the deeper O_2-H_2S interface.

Temperature

An indirect effect of hypersalinity in cold environments is a reduction in the temperature at which the water freezes. Very low temperatures occur because heat gained during summer is rapidly lost when air temperatures are well below zero and there is no ice cover. Kerry *et al.* (1977), Tominaga & Fukui (1981) and Torii & Yamagata (1981) reported antarctic lakes or ponds that do not freeze over even though surface water temperatures may reach −20 °C. Organic Lake in the Vestfold Hills had a temperature of −6 °C in November 1978 and the western lobe of Burton Lake was −5.5 °C in October 1983. Therefore organisms growing in these environments must be adapted to both extreme cold and extreme salinity. Wright & Burton (1981) concluded that the biochemical adaptations required for either cold or salt tolerance in bacteria seemed to be incompatible and therefore cold, hypersaline lakes were likely to have an impoverished bacterial flora. This may explain why the western lobe of Burton Lake had a much reduced photosynthetic bacterial flora in comparison with Burton Lake. In the main lake bacteriochlorophyll *c* was detectable and Chlorobiaceae in particular were frequently found by enrichment, whereas in the colder, more saline western lobe no bacteriochlorophyll *c* was detectable and enrichments rarely led to growth of any photosynthetic bacterial species. However, most environments sampled had temperatures above −2 °C at the O_2-H_2S interface, which Burke & Burton (this volume) found did not inhibit the growth of *Chlorobium* sp. in Burton Lake. The higher temperatures could be attributed to insulation during the lengthy periods of ice-cover and, in Ekho Lake, to a heliothermal effect (Sonnenfeld & Hudec, 1980) as well.

Hydrogen sulphide concentration

Many authors have reported that the concentration of H_2S is unlikely to affect the development of

either Chlorobiaceae or Chromatiaceae (e.g. Biebl & Pfennig, 1978; Parkin & Brock, 1980b; Pedros-Alio *et al.*, 1983).

Three factors are given to explain this. First, the Chromatiaceae can store elemental sulphur intracellularly; second, the Chlorobiaceae have a pronounced capacity for syntrophic growth with sulphate reducing bacteria; and third, H_2S is often abundant. However, Takahashi & Ichimura (1970) and Steenbergen & Korthals (1982) concluded that sulphide concentration could limit growth particularly if sulphate reduction was insignificant at the O_2-H_2S interface. The concentrations of H_2S at the interfaces of those sites of the Vestfold Hills which possessed photosynthetic bacteria were often high (up to 781 mg l^{-1}) and sulphate reducing bacteria were enriched from the interface waters of all but one of the sites. The exception was Organic Lake in which the anoxic bottom water was both cold and salty during winter and in which no photosynthetic bacteria were found. So, while H_2S together with the available light delineated a zone in which *Chlorobium* spp. and *T. roseopersicina* grew, no evidence was found that they were H_2S-limited within this zone. *R. palustris* was found in both oxic and anoxic water. It is known to use H_2S as a photosynthetic electron donor, but is also able to grow photoorganotrophically or heterotrophically, so even low concentrations of H_2S are not required for growth. Hence H_2S concentration was not significant in determining the photosynthetic bacterial flora of these sites.

Interactions

By definition, phototrophic species will be in competition for the available light. While their respective light-harvesting pigments reduce this competition by using different wavelengths (Stanier *et al.*, 1981), the species composition of photosynthetic bacterial flora is known to be influenced by both algal and bacterial filtration (absorption) of light (Pedros-Alio *et al.*, 1983; Montesinos *et al.*, 1983). However, in the lakes and fjords of the Vestfold Hills the species composition of photosynthetic bacteria did not appear to be affected by selective light filtration brought about by populations of either algae or bacteria closer to the surface. In Ace Lake, where there was a plate of flagellate algae just above the O_2-H_2S interface (Burch, this volume) there were still wavelengths of light available for the growth of all photosynthetic bacteria (see Fig. 3). The species of Chlorobiaceae that might be expected to grow beneath an algal plate (those containing β-isorenieratene as the major carotenoid (Montesinos *et al.*, 1983) were absent and chlorobactene-containing species were dominant instead. The absence of any vertical separation of photosynthetic bacteria into distinct plates implies that there was no selection for a particular species by the selective filtration of light by another species.

Because the dominant photosynthetic bacteria, *Chlorobium* spp., produced high *in situ* concentrations of pigments, light was rapidly extinguished within 2–3 m of the O_2-H_2S interfaces in these lakes and fjords, Bacteriochlorophyll *c* concentrations in Table 1 are average to high when compared with values from the literature (e.g. Lawrence *et al.*, 1978; Tominaga & Fukui, 1981; Parker *et al.*, 1983; Croome, 1984; Lindholm *et al.*, 1985). The concentration of 4.6 mg l^{-1} in Taynaya Bay basin 1 is exceeded only by a concentration of bacteriochlorophyll *d* of 6.6 mg l^{-1} reported by Tominaga & Fukui (1981) in Lake Nurume in the Syowa Oasis, Antarctica. Other workers (e.g. Takahashi & Ichimura, 1968; Caldwell & Tiedje, 1975; Parkin & Brock, 1980a; Steenbergen & Korthals, 1982) have reported concentrations of different bacteriochlorophylls in the range 0.015–0.8 mg l^{-1}. The high concentrations of bacteriochlorophyll were very likely to be a response to low light intensities (van Gemerden, 1980) and in turn cause self-shading with the result that only a narrow growth zone was found just below the O_2-H_2S interface.

The highest concentrations of bacteriochlorophyll and/or bacteriophaeophytin occurred at great depth below the photic zone in Ellis Fjord, indicating very slow degradative processes. This is supported by the finding of viable cells of *Chlorobium* spp. and *T. roseopersicina* at 100 m in Ellis Fjord. They had maintained viability in total darkness for the time it took the sediment approximately 60 m from the growth zone at the O_2-H_2S interface. If

there was no turbulent mixing in the monimolimnion, then this time could be of the order of 1700 days, using the fastest sinking rate of 3.54 cm day^{-1} determined by Clark & Walsby (1978) for cells of *Lamprocystis roseopersicina* with collapsed gas vesicles. Pfennig & Truper (1981) reported similar occurrences in the depths of the Black Sea, but weren't able to say how photosynthetic bacteria survived in total darkness, nor whether they were autochthonous or allochthonous. In Ellis Fjord, at least, they are autochthonous, but the mechanism of survival in total darknes is still unknown.

Conclusions

Of the sites examined in the Vestfold Hills, *Chlorobium* spp. were found in large populations ($>10^6$ ml^{-1}) in waters with salinities ≤ 100.7 g kg^{-1}. Low numbers ($<10^5$ ml^{-1}) of *T. roseopersicina* and *Chromatium* sp. were also found in most of these waters with the *Chlorobium* spp. These bacterial phototrophs developed in a narrow band below the O_2-H_2S interface where light and H_2S were available. H_2S concentration did not limit growth. Low numbers of *R. palustris* (<100 ml^{-1}) were also found in both oxic and anoxic waters of salinity ≤ 148 g kg^{-1}. The dominance of species of Chlorobiaceae over species of Chromatiaceae was considered to be a result of the greater efficiency of their maintenance metabolism in total darkness during winter, of their faster growth in the low light intensities prevailing in spring, and of the lack of selective filtering of the incident light. Growth was observed in temperatures as low as -2 °C, but -5 °C appeared unsuitable. Very low light intensities (<1 μE m^{-2} s^{-1}) sustained the growth of photosynthetic bacteria. Sedimentation of inactive, but viable cells continually occurred and these cells maintained viability for extended periods of total darkness possibly of the order of 1700 days.

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