Antarctic Science 1 (2): 125–131 (1989)

Microbial biomass, photosynthesis and chlorophyll *a* related pigments in the ponds of the McMurdo Ice Shelf, Antarctica

C. HOWARD-WILLIAMS[1], R. PRIDMORE[2], M.T. DOWNES[1] and W.F. VINCENT[1]

[1] *Taupo Research Laboratory, DSIR, P.O. Box 415, Taupo, New Zealand*
[2] *Water Quality Centre, DSIR, P.O. Box 11–115, Hamilton, New Zealand*

Abstract: The extensive ablation zone on the McMurdo Ice Shelf (78°S, 165°30'E) contains numerous ponds that are lined with benthic mats of cyanobacteria and associated micro-organisms. The photoautotrophic biomass content of these mats was examined in six contrasting ponds. Particulate carbon contributed only 3.2% of the mat dry weight, with C:N ratios generally less than 20:1. The chlorophyll *a* content was low relative to carbon (chlorophyll *a* : C<0.01). Analysis of the mats by high performance liquid chromatography [HPLC] showed that the pigment fraction assayed spectrophotometrically as chlorophyll *a* contained large quantities (up to 70%) of the degradation product chlorophyllide *a* and the epimer chlorophyll *a*'. Photosynthetic rates per unit chlorophyll *a* [HPLC] were extremely slow: <0.1 mg C (mg Chl*a*)$^{-1}$ h^{-1}, less than one tenth the rates recorded in the overlying phytoplankton community. These analyses indicate that in the ice pond benthic mats most of the dry weight is inorganic, most of the organic carbon is non-chlorophyll-containing material, and much of the chlorophyll *a* is not photosynthetically active. Cold temperatures and the associated low activity of herbivores and detritivores may contribute towards this preservation of inactive chlorophyll *a* on the McMurdo Ice Shelf, and perhaps in similar benthic mats in the lakes and streams of southern Victoria Land.

Received 3 January 1989, accepted 20 March 1989

Key words: benthic mats, carbon, cyanobacteria, high performance liquid chromatography, nitrogen, phosphorus.

Introduction

Benthic algal mats comprised largely of cyanobacteria and diatoms are ubiquitous in the summer melt-waters of the McMurdo Sound region of southern Victoria Land. Mats of varying species composition, thickness and colour coat the base of the ponds on Ross Island (Broady 1989), the glacier melt streams of the dry valley region (Vincent & Howard-Williams 1986*a*, Howard-Williams *et al.* 1986), the sediments of the dry valley lakes (Wharton *et al.* 1983), and the cryoconite environments on glacier surfaces (Wharton *et al.* 1985).

The mats themselves are a matrix of mucilage in which cyanobacterial trichomes are embedded together with individual cells and sand grains. In stream benthic mat communities of the area the sand grains and other fine inorganic particles constitute a large percentage of the total dry weight of the mat, with organic carbon typically less than 6% of dry weight (Vincent & Howard-Williams 1986*b*). Much of the carbon in benthic mats may be undecomposed accumulations from previous years of growth, or come from allochthonous sources which are trapped in the mat mucilage. Thus carbon and ash free dry weight may not be adequate indicators of living microbial mat biomass. For this reason we have used chlorophyll *a* as the autotrophic biomass indicator in studies on the mats of the streams, and both chlorophyll *a* and ATP have been used as biomass estimates in the benthic mats of the dry valley lakes in southern Victoria Land (Simmons *et al.* 1983, Palmisano *et al.*, in press). However, even the use of chlorophyll *a* as a biomass indicator in cold Antarctic conditions has been questioned (Vincent & Howard-Williams 1986*b*, Vincent 1988, Hawes 1989). Estimates of chlorophyll *a* determined spectrophotometrically and corrected for phaeopigment by acidification may still be influenced by other degradation products such as the chlorophyllides which absorb at similar wavelengths and are reported as an equivalent weight of chlorophyll *a* (Strickland & Parsons 1968, Wright & Shearer 1984). Thus it is possible that in the cold Antarctic environment with slow decomposition rates, spectrophotometrically determined chlorophyll *a* may not accurately reflect live autotrophic biomass.

In this study we examine the magnitude and variability of benthic microbial biomass in a contrasting series of ponds on the McMurdo Ice Shelf. We also assess the photoautotrophically active portion of this biomass by the relationship between photosynthetic rates and chlorophyll *a* determined both by spectrophotometer and by high performance liquid chromatography and compare these with analyses of the pond planktonic community.

The study site

The McMurdo Ice Shelf is the largest single area of non-marine biomass in southern Victoria Land (see Kellogg & Kellogg 1987, Vincent 1988, Howard-Williams, *et al.*, in press). The ice shelf is an ablation region of 1500–2000 km^2 with a variable covering of moraine and marine sediment (Debenham 1920, Brady 1980) over which extensive areas of melt-water occur each summer. These take the form of ponds, streams and small lakes up to 30 000 m^2, almost all of which are colonized by benthic algae and cyanobacterial mats. Lenses of mirabilite ($Na_2SO_4 \cdot 10H_2O$), sea-water intrusions and different pond ages provide a widely varied series of water chemistries in the ponds. Although the ice shelf is moving slowly and the surface relief is changing, some of the ponds may have a life span of decades.

We studied six ponds within a few hundred metres of each other of similar morphometry but widely differing water chemistry and microbial mat biomass. They were located 200–400 m south of Bratina Island (78°00'S, 165°35'E). The surfaces of all the ponds were frozen over in mid-November, but the ice had melted by mid-December in all but one (Fresh Pond) which had a surface ice-cover until mid-January. We do not know when the ponds re-freeze, but based on meteorological data and observations on land-based ponds of similar appearance on Ross Island we estimate freezing to be in the period February–March.

All six ponds (designated here by local unofficial names) were colonized by dense mats of cyanobacteria with associated diatoms and coccoid chlorophytes (Howard-Williams *et al.* 1988). Oscillatoriaceae accounted for 70% or more of the total cell counts in all the ponds. The dominant species were *Phormidium autumnale* (Agardh) Gomont, *P. fragile* Gomont, *P. frigidum* Fritsch and *P. laminosum* (Agardh) Gomont. *Oscillatoria deflexa* West & West, and *O. limosa* Agardh were also common. Of the diatoms, the most abundant were *Pinnularia cymatopleura* West & West and *Nitzschia antarctica* (West & West) Fukushima. The very saline ponds also contained *Tropodineis laevissima* West & West and the cyanobacterium *Oscillatoria priestleyi* West & West which were not found in the fresher waters.

Methods

This study was carried out in January 1988. Water samples were collected in acid-washed polyethylene bottles. All samples were filtered either on site or within a few hours of collection using Whatman glass-fibre filters (grade GF/C) pre-rinsed with 100 ml of the sample water. Samples were packed in ice and stored in dark boxes in the ice for periods of up to one week before being returned to base where they were deep frozen for transport to New Zealand.

All water analyses were carried out on a Technicon II auto-analyser system. Methods are given in Downes (1988) and Howard-Williams *et al.* (1986). For saline waters (conductivity >3000 μS cm^{-1}) a modification of Solorzano's (1979) NH_4-N method was used and nitrate was reduced to nitrite by cadmium reduction. Urea-N was estimated by the diacetyl monoxime colorimetric technique of Demanche *et al.* (1973). Detection limits with these analytical procedures were as follows: 0.2 mg dissolved reactive phosphorus m^{-3}, 0.4 mg NO_3-N m^{-3}, 0.5 mg NH_4-N m^{-3}, 1.0 mg total dissolved phosphorus m^{-3}, 1.0 mg total dissolved nitrogen m^{-3}.

Benthic algal samples were collected with a 2.5-cm^2 corer from the 0–0.40-m depth zone. Analyses for nitrogen and phosphorus in the samples were conducted by auto-analyser following acid digestions. Carbon analyses were carried out on dry (oven-dried at 100°C) subsamples combusted at 650°C in a stream of pure oxygen. The combustion gases then passed over a cobaltic oxide catalyst at 900°C to ensure complete conversion of organic carbon to CO_2. The gas flow outlet was connected to a BINOS II differential mode infra-red gas analyser. Calibrations were run with pure CO_2 and with nicotinamide.

Dissolved inorganic carbon in the pond waters was also measured in the field by infra-red gas analysis after acidification of the water samples with excess 0.5 N H_2SO_4.

Samples for biomass (chlorophyll *a*) were analysed at our field laboratory, usually within a few hours of collection. Extraction of chlorophyll *a* was carried out in boiling 90% ethanol for 10 min. Absorbance was read on the GF/F-filtered pigment extract at 750 and 665 nm using a Shimadzu UV/120/02 spectrophotometer. Corrections for phaeophytin were made following acidification of the sample to 7.5 mM HCl. Chlorophyll *a* extracted in this way was checked in New Zealand using a frozen duplicate subset of samples and extracting with cold dimethyl sulfoxide (Shoaf & Lium 1976). The methods yielded similar results. The detection limit in the field was 0.1 μg Chl*a* cm^{-2}. Chlorophyll determined spectrophotometrically in this way is referred to as Chl*a* [SPEC] in the following text.

The pigment composition of the benthic algal mats was further examined by high performance liquid chromatography (HPLC). Samples were extracted in boiling 90% ethanol for 5 min and then filtered through a Whatman glass-fibre filter (grade GF/F). The HPLC system used consisted of a Shimadzu system of two LC-6A solvent pumps, a gradient controller and a SPD-6AV UV-VIS variable wavelength detector and a Hewlett-Packard 1046A programmable fluorescence detector. An Alltech C18 Econosil cartridge column (250 mm × 4.6 mm) with a 10-mm guard column was used with an initial solvent of 90% acetonitrile, 10% deionized water and a linear gradient of 100% acetone at 6% min^{-1} over the first 6 min. Chlorophyll determined by HPLC (436 nm absorbance) is referred to as Chl*a* [HPLC] in the following text.

Photosynthesis of the benthic mats was measured by CO_2 exchange using a portable BINOS II infra-red gas analyser. This was set up on differential closed circuit continuous flow

Table I. Conductivity (μS cm^{-1}) and dissolved N and P concentrations (mg m^{-3}) in the six study ponds, 6–7 January 1988. * = saline interference with analysis. ND = not detectable.

Pond	Conductivity	DRP	DOP	NH_4-N	NO_3-N	DON	Ratio DIN:DRP
Fresh	163	24.3	8.5	4.1	4.9	201	0.37
Skua	818	53.2	20.0	10.6	2.8	521	0.25
Ice Ridge	1415	153.0	9.7	18.4	94.8	215	0.74
P-70	2800	0.7	13.1	5.2	4.0	1294	13.14
Brack	10560	14.1	*	12.8	1.0	3994	0.98
Salt	56200	56.0	*	139.0	ND	21084	2.48

configuration as described in Vincent & Howard-Williams (1986*b*). Analyses were carried out on 5 cm^2 cores of mat material at light intensities of 600–800 μmol m^{-2} s^{-1} (PAR). We assumed that these would be saturating intensities for the communities (cf. Howard-Williams & Vincent 1989).

Photosynthetic assays were conducted on the water column community of each pond using the 14C-bicarbonate assay in light and dark bottles. Following isotope injection (0.28 μCi ml^{-1} final conc.) the bottles were placed at 0.4 m depth in the ponds and incubation times varied from 2.5 to 3.0 h around noon. Labelled organisms were harvested by filtration of the entire sample on to Whatman GF/C filters. GF/C grade was used because the finer grade GF/F filters used for chlorophyll samples clogged after the passage of only a few ml of most of the pond waters. The filters were rinsed with 10 ml deionized water, packed and stored frozen for later analysis by liquid scintillation spectrometry.

Results

Two orders of magnitude variation occurred in conductivity and dissolved nitrogen and phosphorus species in the pond waters (Table I). The highest dissolved reactive phosphorus (DRP) and NO_3-N concentrations occurred in tidally influenced Ice Ridge Pond. Salt Pond, the most saline, had the highest NH_4-N and dissolved organic nitrogen concentrations. The dissolved inorganic N:P ratios were extremely low in all except Pond P-70, and this pond was the only one with low phosphorus values.

Particulate carbon comprised less than 32 mg g^{-1} of the dry weight of mat samples except in Salt Pond where values were almost four times higher at 119 mg g^{-1} (Table II). Particulate nitrogen concentrations were also low in all except Salt Pond (Table II). Between pond variability in concentrations was one order of magnitude for C and N and there was little variability in particulate P. The carbon:nitrogen ratios were highest in Ice Ridge Pond (25.5), but none were extreme values. In contrast the nitrogen:phosphorus ratios of the mat material were very low in all except Salt Pond (Table II). The values of less than 1.0 reflect the low dissolved N:P ratios of the pond waters (Table I). The ratio of carbon to Chl*a* [SPEC] was high (Table II). For a predominantly autotrophic mat community values of less than 100 may be expected (see e.g. APHA 1985, Biggs & Close, in press) and values from 20–60 are commonly used to estimate carbon from chlorophyll *a* (Clark *et al.* 1979). Most of the carbon in Skua, Ice Ridge, P-70 and Brack Ponds would not be associated with chlorophyll *a*, and even in the Fresh and Salt Pond mats the ratios indicate a major heterotrophic or detrital component.

Pond biomass (as Chl*a* [SPEC]) was dominated by the benthic mats where, on an area basis two orders of magnitude greater values were recorded than in the water column (Table III). Even in relatively plankton-rich Salt Pond (15.7 mg m^{-3} Chl*a*) the area based value was only 11 mg m^{-2}. Estimates of variability in benthic biomass (unit area basis) between and within ponds were made from 18 cores collected from the mats at approximately equal spacing around each pond for Chl*a* [SPEC]. Biomass per unit area was highest in the two most saline ponds with almost an order of magnitude difference between the mean biomass in Ice Ridge Pond (81 mg m^{-2}) and Salt Pond (705 mg m^{-2}) (Table III). A one-way analysis of variance showed that variance in Chl*a* [SPEC] between ponds was significantly ($P < 0.001$) greater than within pond variability. However, within pond variability was high, being maximal in Brack Pond where the coefficient of variation was 79%. The unusual extreme shown by Brack Pond was due to a progressive increase in biomass from less than 20 μg cm^{-2} in the west end of the pond to more than 110 μg cm^{-2} at the east end (Fig. 1). The mat at the east end

Table II. Concentrations of carbon, nitrogen, phosphorus and chlorophyll *a* [SPEC] in core samples taken from mats in the six study ponds on 19 January 1988, and the ratios of C:N, N:P and C:Chl*a* [SPEC]. Results are expressed per unit of dry weight.

Pond	Carbon mg g^{-1}	Particulate nitrogen mg g^{-1}	Particulate phosphorus mg g^{-1}	Chl*a* [SPEC] mg g^{-1}	Carbon: nitrogen	Nitrogen: phosphorus	Carbon: Chl*a* [SPEC]
Fresh	12	1.64	2.34	0.093	7.3	0.70	129
Skua	32	1.73	3.07	0.085	18.5	0.56	376
Ice Ridge	24	0.94	2.50	0.067	25.5	0.38	358
P-70	32	2.31	2.32	0.065	13.8	0.99	492
Brack	31	3.58	2.23	0.137	8.7	1.61	226
Salt	119	9.78	2.32	0.734	12.2	4.23	162

https://doi.org/10.1017/S0954102089000192 Published online by Cambridge University Press

Table III. Mean planktonic biomass and mean benthic biomass with coefficient of variation (CV) in the six study ponds (6, 7 January 1988). *n = 18 for all except Pond P-70 (n = 23) and Brack Pond (n = 32).

Pond	Benthic biomass * mg Chl*a* [SPEC] m^{-2} $\bar{x}$	CV%	Planktonic biomass (n = 3) mg Chl*a* m^{-2}	mg Chl*a* m^{-3}
Fresh	91	40	<4.0	<1.4
Skua	256	48	4.0	4.0
Ice Ridge	81	38	4.2	1.4
P-70	227	48	1.4	1.4
Brack	418	79	4.8	4.8
Salt	705	56	10.9	15.7

was similar to that in adjacent Salt Pond. It was very thick with a dark green gelatinous layer below the typical orange coloured cyanobacterial mat. This layer smelled strongly of H_2S and oxygen microelectrobe measurements showed this was anaerobic. The top mat layer contained 312 mg m^{-2} Chl*a* [SPEC] and the lower gelatinous layer had 27.2 mg m^{-2} Chl*a* [SPEC]. We assumed that the marked horizontal gradient in biomass in Brack Pond was due to a gradient in sediment characteristics as the pond water was similar in conductivity and pH at both east and west ends. Pond P-70 (Fig. 1) illustrates a more typical type pond with biomass varying in no consistent pattern.

HPLC analyses of chlorophyll pigments from the benthic mats of the ponds showed some unusual characteristics. The chromatograms all demonstrated a significant peak on the shoulder of the chlorophyll *a*. This was positioned immediately after the main chlorophyll *a* peak, and its otherwise similarity to chlorophyll *a* suggested that it was chlorophyll *a*', an epimer of chlorophyll *a* (Hynninen 1979). It showed up more strongly in the absorption chromatograms than in the fluorescence chromatograms. We have not recorded this peak as a significant component in our HPLC chromatograms of plankton material from temperate latitudes, or in chlorophyll/phaeophytin mixed standards. The amount of this epimer and its value expressed as a proportion of chlorophyll *a* [HPLC] increased in the salinity series from Fresh to Salt Pond (Table IV). On average, chlorophyll *a*' amounted to 11–46% of the chlorophyll *a* [HPLC] value, and chlorophyllide

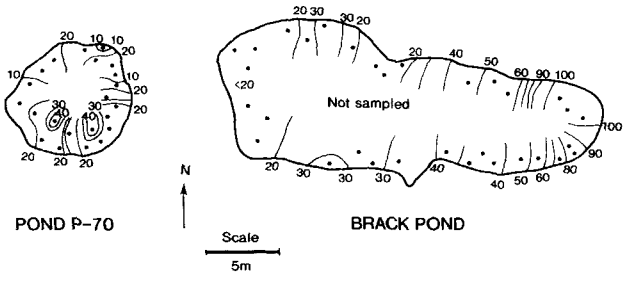

Fig. 1. Horizontal distribution of Chl*a* [SPEC] in Pond P-70 and Brack Pond. Isopleths in μg Chl*a* cm^{-2}. Dots = sampling points.

Table IV. HPLC analysis of chlorophyll pigments from benthic mats in the six ponds. Data as μg cm^{-2}.

Pond	Chlorophyll *a*	Chlorophyll *a*'	Chlorophyllide	Σ Chl
Fresh	16.09	1.83	2.52	20.5
Skua	20.48	4.26	6.28	31.0
Ice Ridge	21.82	2.58	6.84	31.2
P-70	14.68	4.84	1.88	21.4
Brack	17.58	6.78	7.62	32.0
Salt	20.22	9.30	2.05	31.6

varied from 13–43% of chlorophyll *a* [HPLC]. The sum of the three chlorophyll related pigments chlorophyll *a* [HPLC], chlorophyll *a*' and chlorophyllide is designated as ΣChl (Table IV). In duplicate samples where we compared Chl*a* [SPEC] with Chl*a* [HPLC] (Table V) it can be seen that the latter was only 60–70% of the former in four of the ponds and only *c.* 30% in Brack and Salt Ponds.

ΣChl closely approximated Chl*a* [SPEC] in Fresh, Skua, Ice Ridge and P-70 Ponds, indicating that the spectrophotometric determination of chlorophyll *a* includes both the degradation product and the allomer (Table IV). The large discrepancy between ΣChl and Chl*a* (SPEC) in Brack and Salt Ponds may be due to bacteriochlorophyll *a* associated with the anaerobic green gelatinous layer beneath the cyanobacterial mat. We did not attempt to separate bacteriochlorophyll *a*.

The degradation product phaeophytin *a* determined by HPLC was always very small compared with chlorophyll *a* [HPLC], varying from 1.4 to 5.7% (Table VI). Much higher values of phaeophytin were found from the spectrophotometric determination where values were typically 7.9%. In order to examine the persistence of chlorophyll *a* in this ice shelf environment we sampled a series of benthic mats at Skua Pond which had been subjected to varying degrees of desiccation as pond levels changed (Table VII). Samples were taken from mats still submerged (wet), those which had been exposed by low water levels for seven days (moist), for 14 days (dry) and from very old mats several metres above the pond. The HPLC analyses (Table VII) showed that desiccation resulted in an increase in chlorophyll *a* and related pigments per unit area of mat. This is because the

Table V. Comparison of spectrophotometric determination of chlorophyll *a* (Chl*a* [SPEC]) with HPLC analysis of chlorophyll *a* (Chl*a* [HPLC]) in six study ponds. Data as μg cm^{-2}.

Pond	Spectrophotometric chlorophyll *a*	HPLC chlorophyll *a*	HPLC Σ Chl
Fresh	22.7	16.1	20.45
Skua	29.2	20.5	31.02
Ice Ridge	31.8	21.8	31.24
P-70	25.9	14.7	21.40
Brack	58.3	17.6	31.98
Salt	64.1	20.2	31.57

https://doi.org/10.1017/S0954102089000192 Published online by Cambridge University Press

Table VI. HPLC analyses of phaeophytin *a* in six study ponds.

Pond	Phaeophytin *a* μg cm^{-2}	Phaeophytin *a* % of chlorophyll *a*
Fresh	0.22	1.4
Skua	0.41	1.7
Ice Ridge	0.53	2.4
P-70	0.80	5.4
Brack	0.36	2.0
Salt	1.15	5.7

Table VII. *HPLC analyses of a series of benthic mats of different degrees of dryness at Skua Pond, January 1988. Chl-ide = chlorophyllide, Phaeo*a *= phaeophytin* a*. Data as μg cm^{-2}.*

Mat description	Chl*a*	Chl*a*'	Chl-ide	Phaeo*a*
1. Wet mat (submerged)	12.0	3.4	1.4	0.21
2. Moist mat (desiccated for seven days)	20.5	4.3	6.3	0.41
3. Dry mat (desiccated for 14 days)	34.4	7.2	8.2	4.40
4. Very dry mats (desiccated for more than two years)	53.8	13.6	9.7	7.10

mats shrink on desiccation so a core sample through a dried mat collected a concentrated sample. The degradation products chlorophyllide and phaeophytin *a* also increased on a unit of chlorophyll *a* basis. In wet mats phaeophytin was 2% of the chlorophyll *a* value, while in dry mats this increased to 10–20%. However, even in the very dry mats (>2 years old) chlorophyll *a* rather than degradation products still dominated the mat material.

Photosynthetic rates of the pond phytoplankton which we assumed would be comprised mostly of actively metabolizing cells, showed values ranging from a relatively high 74.4 mg C m^{-3} h^{-1} in Salt Pond to a low 0.7 mg C m^{-3} h^{-1} in Fresh Pond (Table VIII). Assimilation numbers ranged from 4.7 to 14.5 mg C (mg Chl*a* [SPEC])$^{-1}$ h^{-1}. On a unit area basis, planktonic photosynthetic rates varied from 2.1 (Fresh Pond) to 60.9 (Ice Ridge Pond) mg C m^{-2} h^{-1}. The rates of gross photosynthesis (light-dark CO_2 exchange) for the benthic mats ranged from 14.7 (Salt Pond) to over 40 mg C m^{-2} h^{-1} (Skua and Ice Ridge Ponds), values similar to the area based plankton production rates. However, the mat assimilation values were an order of magnitude lower than those of the pond phytoplankton (i.e. less than 0.1 mg C (mg Chl*a* [SPEC])$^{-1}$ h^{-1}) for all the communities. The lowest values were recorded in the three ponds with the highest conductivity. Values for the freshwater ponds were similar to those recorded for dry valley streams (Vincent & Howard-Williams 1986*b*).

Discussion

The average biomass values found in the six study ponds (80–700 mg Chl*a* [SPEC] m^{-2}) were higher than those reported for benthic mats in other Antarctic inland waters, and indeed, for many temperate waters. As an example from a temperate system the massive benthic algal development in the Lake Tahoe littoral zone which has been attributed to eutrophication shows biomass values to 140 mg Chl*a* m^{-2} (Loeb 1986). The large seasonal changes in the Lake Tahoe biomass indicate that an annual turnover of most of this community occurs. Data from Antarctic lakes and ponds show similar values. In Spirogyra Lake on Signy Island seasonal maximum biomass values of the benthic filamentous community were *c.* 400 mg Chl*a* [SPEC] m^{-2}. This community was entirely autotrophic and died back each winter with the onset of lake ice cover and an associated snow overlayer (Hawes 1988). Hawes pointed out that 400 mg Chl*a* m^{-2} is approaching the theoretical maximum for autotrophic communities predicted by Steeman Nielson (1962) from an analysis of light attenuation due to self shading. The algal-rich streams of the McMurdo area of southern Victoria Land had mean maximum biomass values ranging from less than 10 to 150 mg Chl*a* [SPEC] m^{-2} (Howard-Williams *et al.* 1986) whilst those of the streams in the maritime Antarctic ranged from *c.* 10–400 mg Chl*a* [SPEC] m^{-2} (Hawes 1989).

In spite of the benthic mats of Lake Hoare in the McMurdo dry valleys being several cm thick, the area based chlorophyll *a* values (Parker *et al.* 1981) were much lower (e.g. 20 mg Chl*a* m^{-2}) than those of the McMurdo Ice Shelf ponds (Table III). The Lake Hoare mats were equated with stromatolite systems (Parker *et al.* 1981) and demonstrate a laminar structure with layers of sediment bound between the living material. The major organism was the cyanobacterium *Phormidium frigidum.* In a further analysis of these mats in

Table VIII. Photosynthetic rates of the benthic and planktonic communities of the study ponds, expressed on a unit volume and area (planktonic), unit area (benthic) and unit of chlorophyll *a* [SPEC] (both) basis. — = not determined as Chl*a* value was below field detection limit of 1.4 mg m^{-3} (see Table III).

Pond	Benthic mg C m^{-2} h^{-1}	Benthic mg C (mg Chl*a* [SPEC])$^{-1}$ h^{-1}	Planktonic mg C m^{-3} h^{-1}	Planktonic mg C m^{-2} h^{-1}	Planktonic mg C (mg Chl*a* [SPEC])$^{-1}$ h^{-1}
Fresh	16.3	0.043	0.7	2.1	—
Skua	40.7	0.076	26.0	26.0	6.5
Ice Ridge	42.6	0.078	20.3	60.9	14.5
P-70	25.8	0.010	8.4	8.4	6.0
Brack	25.3	0.006	33.7	33.1	7.0
Salt	14.7	0.003	74.4	52.1	4.7

https://doi.org/10.1017/S0954102089000192 Published online by Cambridge University Press

Lake Hoare, Simmons *et al.* (1983) reported chlorophyll *a* values of 1.9 μg Chl*a* (fluorometric determination) per mg ash-free dry wt. This equates to a carbon: Chl*a* ratio of 263 (assuming C = 50% of ash-free dry wt) which is within the range reported for our McMurdo Ice Shelf ponds (Table II). In several of the Lake Hoare samples there was an abundance of chlorophyll *a* with no detectable ATP, nor any living micro-organisms as viewed by direct light microscopy. On the basis that Chl*a* has not been found in the absence of ATP in temperate lakes Simmons *et al* (1983) suggested that the peculiar set of conditions in Antarctic dry valley lakes of low light, no arthropod herbivores and low temperatures, led to the preservation of Chl*a* there. Recent studies on the Lake Hoare mats (Palmisano *et al.*, in press) using HPLC separations showed that some lipophilic pigments do undergo decay, but a surprising variety of such pigments occurred even under anaerobic conditions.

HPLC analyses of benthic mat pigments from our study show that spectrophotometrically determined Chl*a* can overestimate actual chlorophyll *a* by 20–45%. In some of these communities this was due to the presence of the epimer chlorophyll *a'* and the degradation product chlorophyllide *a* (Table V). In the more saline waters a further interference occurred, possibly bacteriochlorophyll *a*. Furthermore, it is likely that some of the Chl*a* [HPLC] would be in an inactive, preserved state as suggested for the Lake Hoare benthic mats (Simmons *et al.* 1983). The mats in the ponds on the McMurdo Ice Shelf are in a high light environment so here the factors most likely to preserve Chl*a* are the low temperature and lack of arthropod grazers and detritivores. In a series of experiments on *Nostoc* mats from the adjacent dry valley streams, Vincent & Howard-Williams (1989) found that Chl*a* [SPEC] degraded four times more slowly at 5°C than at 25°C. Heterotrophic bacterial activity which may also enhance chlorophyll degradation was shown to be markedly suppressed by low water temperatures in the benthic mats of the dry valley streams. A suite of heterotrophic bacterial assays in the temperature range 1–10°C revealed no special adaptation by the heterotrophs to cold conditions (Vincent & Howard-Williams 1989). A further factor likely to minimize the degradation of chlorophyll *a* in the ponds is the short time during the year when water is in liquid form. We estimate that the mats would be frozen for eight months in the year.

While assimilation numbers (photosynthetic rates per unit of chlorophyll *a*) for the pond phytoplankton (Table VIII) fell within the expected range 1–15 mg C (mg Chl*a*)$^{-1}$ h^{-1}, those of the mat communities were anomalously low for all ponds (Table VIII). Similarly low values were reported by Vincent & Howard-Williams (1986*b*) for the cyanobacteria dominated mats of Antarctic stream communities (typically <0.1 mg C (mg Chl*a* [SPEC])$^{-1}$ h^{-1}). A correction for Chl*a* [SPEC] to Chl*a* [HPLC] would increase the mat assimilation numbers by 21–45%. The very low values for Brack and Salt Ponds may be further increased if other pigments (e.g. bacteriochlorophyll *a*) are corrected for. However, pigment analytical corrections cannot account for the order of magnitude lower assimilation numbers recorded. These provide the strongest evidence supporting the hypothesis that much of the Chl*a* [HPLC] in these communities is in an inactive preserved state. A high concentration of preserved inactive Chl*a* probably also accounts for the low assimilation numbers and is indicative of long biomass turnover times which characterize the mats of the southern Victoria Land streams (Vincent & Howard-Williams 1986*b*).

An extreme example of chlorophyll *a* persistence may be seen in the preserved dry mats around the ponds on the McMurdo Ice Shelf (Table VII). Mats uplifted by ice movement from previous ponds, which had been exposed and desiccated for at least two years, had an abundance of Chl*a* [HPLC] (Table VII). Direct microscopic examination of these revealed only a few trichomes of oscillatoriaceae and some coccoid chlorophytes (Howard-Williams *et al.*, in press) but clearly these would not contribute much to the high Chl*a* [HPLC] values found in the dry mats.

The very low ratios of dissolved inorganic N:P in pond waters (Table I) are characteristic of the McMurdo Ice Shelf in general (Howard-Williams *et al.*, in press) and of ponds on adjacent Ross Island (Vincent & Vincent 1981). Such low N:P ratios were not recorded in flowing waters on Signy Island (Hawes 1989). The low inorganic N:P ratios in the waters account for low biomass N:P ratios in the pond mats (Table II). While such ratios may indicate a shortage of N relative to P for a balanced nutrient supply for growth (e.g. Tett *et al.* 1985) the C:N ratios are not particularly anomalous except perhaps for Pond P-70 (Table II). A deficiency of N relative to C would result in ratios in excess of 20:1. Thus N would not, on the basis of the biomass C:N ratios be in short supply in most of the ponds. It is of interest why, if adequate concentrations of N and P exist, the biomass ratios are so low. An N-fixing ability of the pond mats has been demonstrated (Howard-Williams & Pridmore, unpublished data) which would also tend to alleviate the extreme N:P ratios. At this stage we can only hypothesize that the N:P ratios in the metabolically active portions of the mat may be quite different from those of the whole mat, and that further studies on the nutritional physiology and the carbon metabolism of these systems may depend on some further separation of mat components.

Acknowledgements

We thank DSIR Antarctic Division, particularly Malcolm McFarlane, Jim Barker and Eric Saxby for logistic support. Squadron VXE-6, US Navy provided the valuable helicopter operations. Our field colleagues Paul Broady, Steve de Mora, Rob Whitehead, Alastair Suren and John Roberts are

thanked for assistance and discussions. Max Gibbs, Stuart Pickmere, Lynell May and Virginia Reid provided analytical and laboratory services in New Zealand. The manuscript was typed by Janet Simmiss and we thank Drs J.C. Ellis-Evans, A.B. Viner, R.A. Wharton and E. White for review.

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