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Microbial communities in southern Victoria Land streams (Antarctica) II. The effects of low temperature

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Abstract

Water temperatures in southern Victoria Land streams fluctuated over the range 0 to 10 °C but generally lay close to freezing. In a series of controlled assays at Fryxell Stream, Taylor Valley, the benthic microbial mats showed strongly positive metabolic responses to increases in temperature well above ambient. Rates of polysaccharide and lipid biosynthesis increased with temperature over the range 0 to 25 °C. Between 0 and 10 °C, Q_{10} values for the cyanobacterial mats were 1.7 to 3.2 for gross photosynthesis, 2.5 to 5.7 for respiration, 2.2 to 2.5 for acetate incorporation into lipid, 1.9 to 3.8 for glucose catabolism, and 1.9 to 2.8 for thymidine incorporation. Respiration accounted for a high percentage of gross photosynthesis, and a net respiratory loss of carbon from three communities was either induced or worsened by an increase in temperature from 0 to 10 °C. The chlorophyll *a* content of *Nostoc* discs incubated for one month in darkness decreased by 27% at 5 °C, but by 99% at 25 °C. This set of assays suggests that the cyanobacterial mats contained large amounts of chlorophyll *a* and carbon associated with inactive or senescing cells. This unusual standing stock could probably not persist under warmer conditions, which would promote both increased respiratory losses and faster rates of bacterial decomposition.

Introduction

The cyanobacterial mat and film communities of southern Victoria Land streams inhabit an unusual environment of highly variable discharge, near-zero water temperatures and periodic freezing and desiccation. Large aquatic invertebrates are absent from this region of Antarctica and without the influence of grazing arthropods, the epilithic communities have been able to accumulate to a high biomass that persists from year to year. Despite these large standing stocks, however, the photosynthetic rates per unit chlorophyll *a* or organic carbon are low (Vincent & Howard-Williams, 1986, 1987). These normalised rates do not appear to respond to nutrient enrichment, nor do they seem to be a photoinhibitory response to high photon flux densities during the 24 hour irradiance cycle (Howard-Williams & Vincent, 1988).

These southern high latitude streams are fed by glacier meltwater and flow for only a few weeks each summer. Even at this time of year, however, the air temperatures lie close to zero and streamwater temperatures are correspondingly low. Cold temperatures are an obvious feature of most polar environments and are known to have a restrictive effect on various microbial processes in Antarctica including pelagic photosynthesis and bacterial heterotrophy in the Southern Ocean

(Tilzer *et al.*, 1986; Morita *et al.*, 1977), sea ice algal production in McMurdo Sound (Palmisano *et al.*, 1986), and CO_2 exchange by cryptoendolithic lichens that live beneath rock surfaces in the Dry Valleys (Kappen & Friedmann, 1983). In this paper we examine the influence of water temperatures on the epilithon of Fryxell Stream in the McMurdo Dry Valley region. We measured the temperature responsiveness of community metabolism over the ambient range 0 to 10 °C and compared the influence of temperature on production processes (photosynthesis, synthesis of protein and other photosynthate fractions) and on metabolic loss processes (respiration, bacterial decomposition). Our experiments suggest that the low normalised photosynthetic rates are not simply an inhibitory response to low temperature, but rather that the thick epilithic mats contain a large proportion of non-active organic material (including chlorophyll *a*) that under warmer conditions would rapidly decompose.

Methods

Water temperatures at each of the stream sites were measured either with a Yellow Springs Instrument combined oxygen and temperature probe calibrated against a mercury thermometer, or directly with an unshielded mercury thermometer. Irradiance was measured either with a Li-Cor pyranometer (Vanda Station) or a Li-Cor photosynthetically available radiation sensor (all other measurements).

With the exception of the decomposition experiment (see below) all of the microbial assays were conducted at Fryxell Stream during January 1986. Four types of streambed communities were recognised on the basis of their biomass dominants: thick mucilaginous mats of cyanobacteria dominated by Oscillatoriaceae ('*Phormidium* mat') or *Nostoc commune* with a much smaller population of Oscillatoriaceae ('*Nostoc* mat'); tufts and streamers dominated by *Binuclearia tectorum*, and straps of *Prasiola calophylla*. Further details of these communities are given in Broady (1982).

For several of the assays (end products of photosynthesis, lipid biosynthesis, nucleoprotein synthesis, glucose catabolism) the cyanobacterial communities were sampled with a 3 ml plastic syringe that instead of a needle had its tip sharpened into a 2 mm diameter cutting edge. The mats were cut and then expressed from the tip by gently applying pressure with the syringe plunger. For each assay three of these 2 mm diameter 'microcores' from different samples of the same community were expressed into 30 ml Universal vials filled with freshly collected water from Fryxell Stream. This method was not possible for the *Binuclearia* and *Prasiola* communities, and therefore samples of these algae from a known area were suspended in streamwater, and then subsamples were transferred to the Universal vials.

All of the temperature experiments were conducted in water bath incubators under ambient light conditions near the stream. The incubators consisted of 5 litre polystyrene boxes that were filled to their brim with water and further insulated with clear bubble plastic. The water temperatures were frequently checked and adjusted manually. The assay samples were also gently agitated at these time intervals. The large mass of water gave a good level of control and the temperatures varied over less than a $\pm$ 1.5 °C range throughout the experiments.

For the end products of photosynthesis assay the microcore vials were injected with ^{14}C-HCO_3 (final activity of 0.6 μCi per ml). The cores were then filtered either immediately (control) or after 2 h in the controlled temperature incubators onto 25 mm diameter GF/C filters. The filters were washed with streamwater, injected with 0.2 ml of 5% glutaraldehyde and stored frozen until analysis. The filters were later ground in 2 ml of methanol (1.4 ml), and water (0.6 ml) with a Teflon tissue grinder. Four major classes of photosynthate (low molecular weight compounds, lipids, protein and polysaccharide) were then coarsely separated using the method of Li *et al.* (1980), and the ^{14}C-label in each fraction was counted by liquid scintillation spectrometry. Dissolved inorganic carbon levels in the incubation

streamwater (with ^{14}C added) were measured by infra-red gas analysis.

For the glucose catabolism assays the microcore vials were injected with (U-^{14}C)D-glucose, final activity and concentration of 0.1 μCi per ml, 0.4 μM. At t_o and after 4 h incubation the samples were filtered through 25 mm GF/F filters and the filtrate was preserved with NaOH to pH 10. These filtrates were stored cool and unfrozen and later acidified and bubbled with a stream of oxygen through a CO_2 trapping solution (β-phenethylamine). A subsample of this solution was then counted by liquid scintillation.

The microbial lipid assay was a modification of the method described by White *et al.* (1977). Microcore vials were injected with 2-^{14}C-acetate (final activity and concentration of 0.1 μCi, 2.2 μM). The samples were incubated for 90 mins and then uptake terminated by filtration and glutaraldehyde as above. The filters were ground in a single phase mixture of methanol (2.6 ml), chloroform (1.3 ml), water (1.0 ml) and concentrated HCl (0.02 ml) and then sonicated for 5 mins. The phases were then broken by shaking the extract with 5 ml of chloroform plus 5 ml of water. A subsample of the chloroform phase was transferred to a vial, evaporated to dryness at 55 °C and counted by liquid scintillation.

The incorporation of thymidine into DNA was measured using a modified version of the Fuhrman & Azam (1980) assay. Microcore vials were injected with methyl-^3H-thymidine at a final concentration of 6 nM. At t_o and after 2 h of incubation the microcores were filtered on to 25 mm GF/F filters, washed with ice-cold 10% trichloracetic acid (TCA) and stored frozen. The filters were later ground in 3 ml of ice-cold TCA with a Teflon tissue grinder. A subsample of this material was then filtered onto another GF/F filter, washed again with TCA, transferred to a vial containing Brays cocktail, and then counted by liquid scintillation. Overnight dialysis of the TCA extracts in running water produced no major shifts in counts. The efficiency of nucleic acid recovery with this assay (70%) was established using ^{14}C-labelled DNA. The TCA-precipitated material was not washed with a lipid solvent as recently recommended by Robarts *et al.* (1986), and therefore the measurements may be biased towards uptake rather than incorporation.

The CO_2 exchange characteristics of the microbial mat communities were measured by infra-red gas analysis (IRGA). The assays were run with 18 mm diameter cores of the epilithon (details in Howard-Williams & Vincent, 1988).

A decomposition experiment was run on *Nostoc* mats incubated in darkness or under 350 $\mu E\, m^{-2}\, s^{-1}$ cool white fluorescent lighting. Dry frozen *Nostoc* was collected from the lower reaches of the Fryxell Stream bed in early November prior to streamflow. These mats were then stored in the dark and frozen (−20 °C) in sterile plastic containers for 8 months prior to the experiment. The dry frozen mat was then cut into 4 mm diameter cores with a cork borer and these sections were each transferred to 15 ml of inorganic nutrient media sterilised in 25 ml scintillation vials. The only inoculum of heterotrophic bacteria was therefore the natural assemblage of cells that survived in the dry *Nostoc* mat. The cores were allowed to hydrate for 2 days under the various treatments and then the first set of samples was removed for chlorophyll and phaeophytin analysis. The remaining cores were incubated for 1 month (31 days) and then harvested for pigment analysis.

Two methods were adopted for chlorophyll *a* determinations depending on the size of the mat community sample. The large discs used for the IRGA measurements were stored frozen and then extracted in dimethyl sulfoxide overnight. This extract was diluted 1 : 1 with 90% acetone and the pigment content then assayed spectrophotometrically (Strickland & Parsons, 1968). In the microcore and decomposition experiments the microbial cells were initially filtered on to 25 mm diameter glass fibre filters (Whatman grade GF/C) which were stored frozen and then later cut up and transferred to 90% acetone. This material was then ground with a Teflon tissue grinder and the extracts cleared by centrifugation and assayed by spectrofluorometry (Strickland & Parsons, 1968).

Results

Temperature

Throughout our 3 year study of the streams in the McMurdo Sound region water temperatures rarely exceeded 8 °C and were typically in the range 0 to 5 °C (Table 1). For example, for 40 measurements in the mid afternoon (the warmest time of day) at a downstream site on the Onyx River (Vanda Weir) the mean temperature over the December–January season of streamflow was 4.4 °C with 95% of the measurements ($\bar{x} \pm 2SD$) within the range 0.2 to 8.6 °C. Stream water temperatures were generally close to freezing for several hours over each 24 h cycle or during days of persistent cloud cover or high wind velocities. The warmest water temperature measured was 13 °C in a shallow portion of the *Phormidium* mat area in the Onyx River 3 km upstream from Vanda Weir.

In almost all of the streams there were large diel fluctuations in water temperature that more or less followed the diel radiation cycle at a lag (Fig. 1). The amplitude of these 24 h variations was typically about 5 °C (Table 1). An exception to these observations was the Alph River where temperatures and also discharge remained constant, probably reflecting the influence of water storage in Trough Lake which feeds this system (Howard-Williams *et al.*, 1986). In most of the streams the 24 h radiation cycle also generated large variations in discharge (Fig. 2), and as a result the algal communities at the edge of the stream were periodically exposed to sub-zero temperatures.

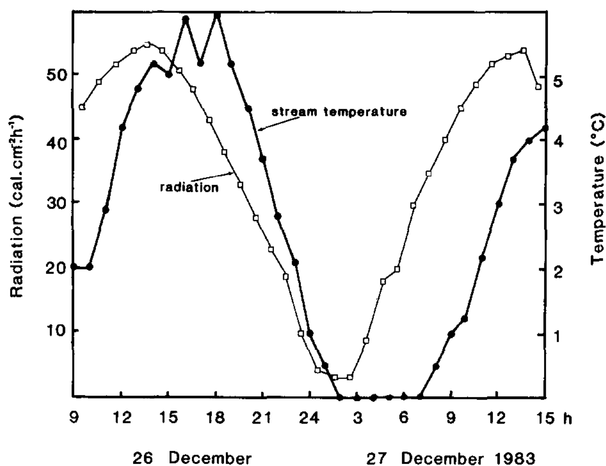

Fig. 1. Diel variations in water temperature and incoming radiation for the Onyx River at Vanda Weir, Wright Valley.

Measurements of the stream water temperature next to the mats has never revealed any streambed warming relative to the flowing water above. However, a 10–15 °C warming of the black *Nostoc* thalli in a shallow-water flush area draining into Fryxell Stream has previously been recorded (K. Thompson, University of Waikato Antarctic Research Unit, unpublished data).

Photosynthesis

Photosynthesis as measured by ^{14}C-CO_2 incorporation was strongly responsive to temperature over the range 0 to 10 °C for all of the commu-

Table 1. Stream water temperatures over the 24 h cycle during mid to late summer in the McMurdo Sound region. The mean values are from measurements or interpolated estimates for each hour over the 24 h cycle.

Stream	Date	Stream temperature (°C)		
		mean	minimum	maximum
Onyx River	26/27 Dec 1983	2.6	0	6.0
Onyx River	2/3 Jan 1986	3.3	0	10.5
Onyx River	17/18 Dec 1983	3.4	0	6.2
Alph River	17/18 Jan 1986	0.7	0.5	1.0
Bird Stream	18/19 Jan 1984	1.4	0	3.8
Fryxell Stream	14/15 Jan 1985	6.1	2.5	9.0
Adams Stream	12/13 Jan 1984	2.1	0	5.2

nities tested (Table 2). Q_{10} values varied from 1.8 to 2.7, but there were no major differences in the pattern of labelling of photosynthate fractions between the two temperatures (Table 2). Polysaccharide was the dominant end product of photosynthesis for the *Phormidium*, *Nostoc* and *Binuclearia* communities at both 0 °C and 10 °C, but in the *Prasiola* incubation the low molecular weight fraction (LMW) was more heavily labelled than polysaccharide or protein. The lipid fraction contained the lowest percentage (1–6%) of total label in all of the assays.

The effect of temperature on the end products of photosynthesis was further examined in a series of incubations of *Phormidium* micro-cores over the wider range 0 °C to 25 °C. The biosynthesis of all four photosynthate fractions responded to increasing temperatures, but with the exception of the lipid component the temperature response was much greater over the range 0 to 15 °C than from 15 to 25 °C (Fig. 3). For example, the labelling of polysaccharide (the dominant fraction) had a Q_{10} value of 2.7 between 5 and 15 °C, but dropped to 1.3 between 15 °C and 25 °C. The Q_{10} for protein biosynthesis similarly dropped from 3.1 (5–15 °C) to 1.6 (15–25 °C).

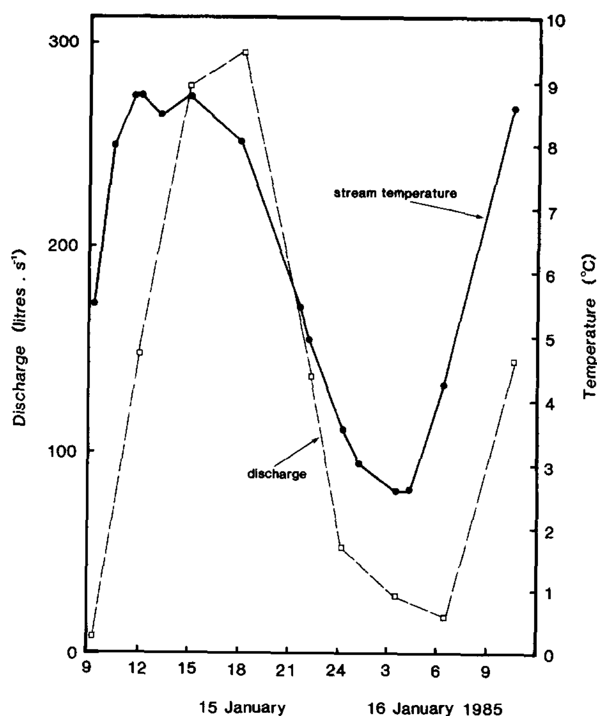

Fig. 2. Diel variation in water temperature and discharge in Fryxell Stream, Taylor Valley.

Table 2. Photosynthesis and the percent labelling of photosynthate fractions at two temperatures for the various mat communities in Fryxell Stream.

	Total photosynthesis (μg C·cm^{-2}·h^{-1})	% Photosynthate labelling			
		LMW	Lipid	Protein	Polysaccharide
Phormidum					
0 °C	1.2	9	2	36	50
10 °C	3.1	11	1	39	49
Q_{10}	2.6				
Nostoc					
0 °C	9.7	13	3	22	62
10 °C	23.7	7	3	23	66
Q_{10}	2.4				
Binuclearia					
0 °C	7.6	6	6	17	71
10 °C	14.0	4	5	24	68
Q_{10}	1.8				
Prasiola					
0 °C	2.0	43	2	27	27
10 °C	5.4	36	4	29	32
Q_{10}	2.7				

Community CO_2 exchange

Gross photosynthetic rates were measured by IRGA for each of the stream communities as the light minus dark CO_2 exchange (final 3 columns in Table 3). These rates were low per unit chlorophyll *a*, less than 1 μg C (μg chl *a*)$^{-1}$ h^{-1} at 0 °C, but were stimulated by a factor ranging between 1.6 and 3.2 by a 10 °C rise in temperature. The

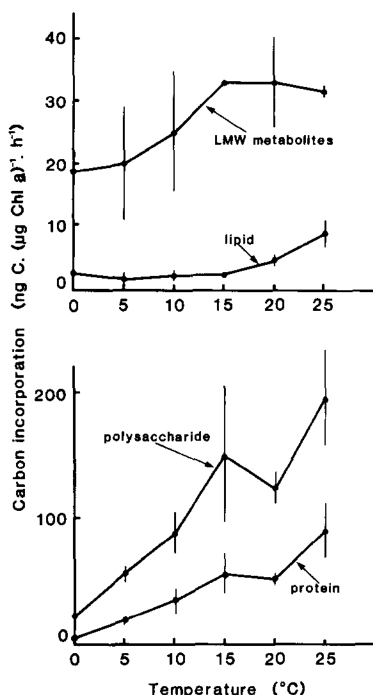

Fig. 3. The influence of temperature on the incorporation of ^{14}C-CO_2 into end products of photosynthesis, for *Phormidium* mats at Fryxell Stream.

Q_{10} values for respiration (dark CO_2 production, Table 3) were comparable or higher. Respiration as a percentage of gross photosynthesis varied greatly between stream communities; e.g. at 0 °C from 23% for *Binuclearia* to 171% for the thick *Nostoc* mat. This percentage respiratory loss increased for all of the communities tested except the *Nostoc* mats with the 10 °C increase in temperature.

The combined effect of temperature on photosynthesis and respiration is expressed by the CO_2 exchange rate in the light (first two columns in Table 3) which may be considered the community net productivity. The *Binuclearia* community showed a simple, almost twofold increase in net photosynthesis between 0 and 10 °C. The *Prasiola* community showed no significant response to temperature because the increase in gross photosynthesis was offset by a greater increase in respiration. For the cyanobacterial mats the net community photosynthesis at 0 °C was below zero (i.e. more CO_2 was respired than was fixed by photosynthesis) or only slightly above zero. The net carbon loss from the community was either induced (*Phormidium* b) or further stimulated (*Phormidium* a, *Nostoc*) by the 10 °C rise in temperature.

Heterotrophic activity

Three measures of microbial heterotrophy suggested that the stream mat communities, particularly the thick *Nostoc* and *Phormidium* mats,

Table 3. CO_2 exchange by the Fryxell Stream mat communities, January 23/24, 1986. + = CO_2 production; − = CO_2 uptake. The production or uptake values are expressed as μg C per μg chlorophyll *a* per hour. Incubations were under full ambient sunlight (320–900 μE m^{-2} s^{-1}).

Community dominant	Light		Dark			Light minus dark		
	0 °C	10 °C	0 °C	10 °C	Q_{10}	0 °C	10 °C	Q_{10}
Phormidium a*	+0.22	+1.01	+0.75	+1.92	2.6	−0.53	−0.91	1.7
Phormidium b**	−0.14	+2.06	+0.80	+4.56	5.7	−0.94	−2.5	2.7
Nostoc	+0.12	+0.16	+0.29	+0.71	2.5	−0.17	−0.55	3.2
Binuclearia	−0.61	−1.18	+0.18	+0.69	3.9	−0.79	−1.87	2.4
Prasiola	−0.45	−0.42	+0.08	+0.42	5.2	−0.53	−0.84	1.6

* Thick pink mat

** Orange tufted mat

contained active populations of heterotrophic bacteria. The cyanobacterial as well as *Binuclearia* communities incorporated ^{14}C-acetate into lipid, and these rates were stimulated more than two-fold by a 10 °C rise in temperature (Table 4). Comparable or higher Q_{10} values were recorded for the catabolism of ^{14}C-glucose to CO_2 by the cyanobacterial mats (Table 5). No incorporation of thymidine into microbial nucleoprotein was detected with *Binuclearia* samples, but the three other communities showed significant uptake and incorporation (Table 6) suggesting bacterial DNA synthesis and growth within the mats. The thymidine incorporation responded positively to the temperature increase from 0 to 10 °C, consistent with the acetate and glucose assays.

As a further measure of the effects of temperature on bacterial metabolism and growth, microcores of *Nostoc* mat were incubated for 48 h at 0 °C or 10 °C, and then assayed with ^3H-thymidine for 2 h at the two temperatures. In all of the assays the rate of thymidine incorporation was stimulated by the 10 °C increase in temperature, but the greatest effect was seen in response to the 48 h pre-incubation (Table 7). If the incorporation values can be considered a rough measure of the population size of the heterotrophically active bacteria then their growth rates over 48 hours may be approximated as 0.5 ln [(48 h at T_1)/(0 h at T_1)] where T_1 is the temperature. This gives growth estimates of 0.13 and 0.21 d^{-1} at 0 °C, but 0.51 and 0.55 d^{-1} at 10 °C.

Table 4. Incorporation of 2-^{14}C-acetate into lipid in the stream mat communities. Each value is the mean ± 2SE for triplicates.

	Lipid biosynthesis (ng ^{14}C $cm^{-2} \cdot h^{-1}$)		
	0 °C	10 °C	Q_{10}
Nostoc	2.6 ± 0.8	5.7 ± 0.7	2.2
Phormidium	3.3 ± 0.8	8.2 ± 2.6	2.5
Binuclearia	2.0 ± 0.3	5.1 ± 1.4	2.5

Table 5. Catabolism of U-^{14}C-glucose by Fryxell Stream mat communities at two temperatures. Each value is the mean ± range for duplicates.

Community dominant	CO_2 production (ng ^{14}C $cm^{-2} \cdot h^{-1}$)		
	0 °C	10 °C	Q_{10}
Phormidium a*	0.29 ± 0.11	0.85 ± 0.21	2.9
Phormidium b**	0.38 ± 0.04	0.73 ± 0.05	1.9
Nostoc	0.23 ± 0.03	0.88	3.8

* Thick pink mat
** Orange tufted mat

Decomposition

The dark incubations of *Nostoc* mat showed a strong response to temperature (Table 8). The samples incubated at 5 °C averaged a relatively small loss in chlorophyll *a* indicating that large quantities of chlorophyll can persist inactive but undecomposed in the algal mats at low stream temperatures. At 25 °C, however, the chlorophyll *a* was almost completely decomposed. In both dark treatments the amount of phaeophytin increased as a percentage of total pigment, but at 25 °C even the phaeophytin concentrations were reduced to almost zero after the month long period of decomposition.

Table 6. Incorporation of ^3H-thymidine by the Fryxell Stream mat communities. Each value is the mean ± 2SE for triplicates.

Community dominant	Thymidine incorporation ($pmol \cdot cm^{-2} \cdot h^{-1}$)		
	0 °C	10 °C	Q_{10}
Phormidium	0.18 ± 0.04	0.53 ± 0.19	2.8
Nostoc	0.45 ± 0.22	0.85 ± 0.23	1.9
Prasiola	0.31 ± 0.11	0.45 ± 0.11	1.5

Table 7. Effect of preincubation temperature on the incorporation of ^3H-thymidine by *Nostoc* dominated mats from Fryxell Stream. Each value is the mean ± 2SE for triplicates.

Preincubation	Thymidine incorporation ($pmol \cdot cm^{-2} \cdot h^{-1}$)		
	0 °C	10 °C	Q_{10}
0 h	0.45 ± 0.22	0.85 ± 0.23	1.9
48 h at 0 °C	0.68 ± 0.08	1.11 ± 0.44	1.6
48 h at 10 °C	1.36 ± 0.08	2.34 ± 0.33	1.7

Table 8. Changes in the chlorophyll *a* content of *Nostoc* discs incubated in nutrient media in darkness or 350 μE m^{-2} s^{-1} at two temperatures. Day 2 values are means for triplicates ± 2SE. Day 33 values are means for duplicates ± range.

Treatment	μg Chl *a* · cm^{-2}		
	Day 2	Day 33	% change
5 °C dark	26 ± 0.6	19 ± 5	−27
25 °C dark	27 ± 3	0.16 ± 0.04	−99
5 °C light	18 ± 3	28 ± 8	+56
25 °C light	27 ± 10	14 ± 0.5	−46

Similar effects are suggested by the light incubation data (Table 8), but the results are not conclusive because of the high variability between certain replicates. The chlorophyll *a* levels increased in the 5 °C treatment (but $t = 1.8$, $p > 0.05$) and decreased in the 25 °C treatment (but $t = 1.2$, $p > 0.05$).

Discussion

All of the microbial processes measured in this study responded positively to an increase in temperature from 0 to 10 °C. However, although Arrhenius-like effects operated over this range there was no abrupt suppression of metabolism at 0 °C, indicating that the communities are able to function reasonably well at the near-zero stream temperatures.

The microbial phototrophs and heterotrophs on the Fryxell streambed appear to be cold-tolerant but they do not seem to be closely adapted to the low temperatures of this environment. Ambient water temperatures typically lay in the range 0 to 5 °C yet the temperature optima for protein, polysaccharide, and lipid biosynthesis from carbon fixed by the *Phormidium* mats lay at or above 25 °C (Fig. 3). These responses contrast with various antarctic marine communities that have optima below 10 °C e.g. 6 °C for sea ice algal photosynthesis (Palmisano *et al.*, 1987), 3–10 °C for growth of phytoplankton isolates from the Southern Ocean (Jacques, 1983), 7 °C for bacterial growth rates in the Scotia Sea (Azam *et al.*, 1981). Much higher optima, however, have been reported from freshwater environments in Antarctica e.g. 14–19 °C for the growth of bacterial isolates from lakes in the maritime zone (Ellis-Evans & Wynn-Williams, 1985); 12.5–18 °C for growth of phytoflagellate isolates from Dry Valley lakes (Seaburg *et al.*, 1981); > 14 °C for benthic algal mats from a pond on Ross Island (Goldman *et al.*, 1963). The Q_{10} values for photosynthesis by the Fryxell epilithon typically lay in the range 2–3, and these also were comparable with other freshwater measurements in the region (e.g. Q_{10} of 2.3 for benthic algal photosynthesis, Goldman *et al.*, 1963) but well below the values derived from various marine studies e.g. 4.6 for phytoplankton photosynthesis in the Scotia Sea, 5.9 for congelation ice algal photosynthesis in McMurdo Sound (Palmisano *et al.*, 1986). These lower temperature optima and the relatively high responsiveness to temperature change by the marine phototrophs is presumably a reflection of the persistently low but highly stable temperature condition in the sea. Micro-algae typically have their temperature optima for photosynthesis several degrees higher than the temperature at which they are growing (Li, 1980). A similar generalisation would seem to apply to heterotrophs as well as phototrophs for a wide range of microbial communities in Antarctica with the temperature optimum for metabolic activity above the upper range of habitat temperatures. This effect is especially pronounced for the epilithic microbiota of Fryxell Stream.

The highly unstable environmental conditions that characterise the Dry Valley streams probably select for broad tolerances to chemical and physical fluctuations, including temperature. Our data are consistent with the observations of Seaburg *et al.* (1981) who measured the temperature minimum and maximum for growth in culture of a wide range of algal isolates (including cyanobacteria) from the Dry Valleys. Most of their meltwater stream isolates grew within the temperature range 5 to 25 °C, although almost one third of them ceased growth at 2 °C. Although there were some differences in the upper and lower temperature limits between strains of the same species

there was no evidence that any of the isolates grew especially fast at low temperature, or had an optimum for growth near 0 °C.

Our IRGA analyses of the Fryxell Stream mat communities (Table 3) show that there was a fine dynamic balance between photosynthetic carbon fixation and respiratory carbon loss. Respiration accounted for 90% or more of gross photosynthesis in the cyanobacterial mats at 0 °C, and a 10 °C increase induced or worsened the net loss of carbon from the mats sampled at this time of year. This type of effect has been similarly reported from the cryptoendolithic lichen communities living within the rocks of the Dry Valleys. Under full sunlight net carbon uptake by the community was measured over the range −4 to +8 °C but higher temperatures continued to stimulate respiration and not photosynthesis and the community then experienced a net carbon loss (Kappen & Friedmann, 1983). Like the rock microbial assemblage the cyanobacterial mats from Fryxell Stream would seem to have a temperature compensation point (where net photosynthesis equals zero) at the top of the temperature range typically experienced in the natural habitat. This effect underscores the difficulty of applying optima measured with isolates in culture or from assays of a single metabolic parameter to the performance of a consortium of heterotrophs and phototrophs in a microbial mat community.

In the cryptoendolithic lichen communities assayed by Kappen & Friedmann (1983) the high, temperature-responsive respiratory losses were presumably dictated in part if not dominated by the high biomass of symbiotic fungi and associated bacteria. In the streambed mat communities the primary sources of respiratory carbon are less clearly identifiable. Fungal hyphae were relatively rare in virtually all of the microbial mats we have examined from this region and bacterial rods and cocci, although numerically common, accounted for a small percentage of total biomass. These mat communities are composed mostly of cyanobacterial trichomes and associated mucilage binding together silt particles, and it is probably the *Nostoc* and Oscillatoriacean cells that dominate the respiratory CO_2 production. Light is strongly attenuated within the mat profile by the surface layer of carotenoid-rich cells and the high concentrations of light-scattering silt particles (Howard-Williams & Vincent, 1988). The low saturation irradiance value for the community suggests that at least some of the phototrophs are shade-adapted, and such organisms are known to have a low P_{max} relative to respiration (Raven & Glidewell, 1975). It is also possible that a high percentage of cells in the mat are senescing or have been damaged by the seasonal (or more frequent) freeze-thaw cycle.

Although the heterotrophic bacteria in the cyanobacterial mats were present in a relatively low biomass their metabolic activities were strongly stimulated by a 10 °C rise in temperature with Q_{10} values in the range 2 to 4. The implications of this temperature effect were most clearly illustrated by the *Nostoc* decomposition experiment. The 25 °C treatment resulted in almost the complete decomposition of the thick mat within one month, whereas the 5 °C incubation experienced little change under the same conditions of darkness. This experiment implies that high levels of chlorophyll *a* can remain inactive and undecomposed at low temperatures but not at high temperatures, and these effects were also suggested by the light incubations. Thus the high standing stock of biomass and organic carbon in the Dry Valley streambeds may be a function not only of the absence of large grazing animals, but also due to the cold temperature-depressed growth rates of bacterial decomposers. In this environment slow rates of consumption by secondary producers, both animal and bacterial, as well as slowed respiratory losses may be the main factors allowing large standing stocks of microbial mat to accumulate.

Low temperatures operating directly on photosynthesis do not seem to completely account for the low normalised photosynthetic rates. Photosynthesis was not abruptly suppressed by near-zero stream temperatures and even assuming a Q_{10} of 4 most of the assimilation numbers reported in Howard-Williams & Vincent (1988) would still lie at or below 1 μg C per μg chlorophyll *a* per hour at 10 °C. A more likely explanation is that

a large proportion of organic carbon and chlorophyll *a* persists in the microbial mat associated with metabolically inactive or senescing cells, and that respiratory losses and bacterial degradation of this material are inhibited by the low ambient stream temperatures. It is possible that some of the measured pigment is the degradation product chlorophyllide which would be analysed as apparent chlorophyll *a* in the assay procedure adopted here (T. Jacobsen, personal communication).

Like other aquatic environments in which microbial mats are found (Cohen *et al.*, 1984) the Dry Valley streambeds allow a gradual net accumulation of biologically-derived organic material, but the rate of accumulation and ultimate standing stock is controlled by an unusual combination of slow growth rates, large respiratory losses, slow secondary consumption rates and the influence of low temperatures on all community processes.

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