

Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon

WARWICK F. VINCENT and CLIVE HOWARD-WILLIAMS Taupo Research Laboratory, Division of Marine and Freshwater Science, DSIR, Taupo, New Zealand

SUMMARY. 1. Several dozen summer meltwater streams are located in the McMurdo Sound region (c. 78°S 165°E) of southern Victoria Land. They are characterized by a highly variable flow regime at diel, seasonal and annual timescales; wide fluctuations in temperature and nutrient content; and a very simple epilithic community of cyanophytes (*Nostoc* spp., Oscillatoriaceae), bacteria, fungi and microherbivores.

2. The epilithon survives the dark Antarctic winter as dry, frozen mats which provide a large inoculum for growth the following summer. This overwintering assemblage retains a high metabolic capacity and responds rapidly to rehydration.

3. In a series of artificial substrate experiments, biomass accumulation rates were generally less than 0.1 ln units d⁻¹. Colonization and growth on the substrates was inversely related to the suspended sediment load of the stream. There was also a visual correspondence between per cent algal cover of the natural streambed and the clarity of the streamwater. Sloughing losses may limit community biomass, particularly in the turbid flowing waters.

4. During running water conditions the mature communities had very low gross photosynthetic rates per unit chlorophyll (<0.1 μg chl a.h)⁻¹ and per unit carbon (<0.2 μg C (mg biomass C.h)⁻¹). Respiration was generally a high percentage (up to 92%) of gross photosynthesis, which probably reflected the high population densities of microheterotrophs in the community.

5. The floristically simple epilithic mats slowly accumulate to extreme biomass levels (>20 μg chl a cm⁻², >20 mg C cm⁻²). Production rates per unit biomass are low, probably in response to the cold temperatures of the Antarctic stream environment, and the accumulated biomass represents several seasons of growth.

Introduction

Meltwater streams are widely distributed around the margins of Antarctica (e.g. 64°S,

Correspondence: Dr W. F. Vincent, Taupo Research Laboratory, Division of Marine and Freshwater Science, DSIR, P.O. Box 415, Taupo, New Zealand.

64°W, Wodehouse & Parker, 1981; 68°S 78°E, Hand & Burton, 1981; 77°S 163°E, Allnut *et al.*, 1981) but their ecosystem properties remain little explored. Several dozen of these streams are located in the McMurdo Sound region of southern Victoria Land (c. 78°S 163°E) where they flow for several weeks each

summer. Many of these waters contain a biomass-rich but floristically simple epilithon which coats the rocks, gravels and sands of the streambed. Their communities are commonly dominated by cyanophytes—thick black continuous mats of *Nostoc* and variously coloured mats and films of Oscillatoriaceae (Broady, 1982).

Relative to the epilithon of temperate latitudes these algae and their associated microflora must withstand a highly ephemeral flow regime and extremely low temperatures. For most of the year the algae remain dry and deep frozen, and must rapidly take advantage of the brief summer period of flowing water conditions. Continuous radiation and low grazing pressure (there are no insects or other large herbivores) remove these variables as controls on epilithic biomass and productivity. The community properties of primary importance in this environment would therefore seem to be the ability of the overwintering algae to re-establish growth and metabolism during first flows, their capacity to colonize and grow on new substrates each season, and their photosynthetic and respiratory characteristics during the main period of flow at near-freezing temperatures.

In this report we first describe the basic environmental and community properties of a range of southern Victoria Land streams. We then examine three fundamental aspects of ecophysiology in this cyanophyte epilithon: the metabolic responses of the overwintering community to rehydration, the ability of the algae to colonize and grow on artificial substrates,

and the CO₂-exchange properties (photosynthesis and respiration) of the mature epilithon. From this array of environmental and physiological measurements we attempt to distinguish the primary controls on microbial growth in these southernmost flowing water ecosystems.

Study sites

We sampled twenty-four of the streams in the McMurdo Sound region during the Antarctic summers (November–January) of 1983/84 and 1984/85, but focussed our experimental work on five contrasting waters (Table 1). These ranged from a short discharge to the sea from the Cape Bird Ice Sheet (Northern Rookery Stream, Cape Bird) to the longer (several km) streams of the Dry Valleys. They included the Onyx River, the largest stream in Antarctica, which receives summer meltwater from the Lower Wright Glacier and flows 30 km inland to Lake Vanda. Two of the selected streams (Adams and Fryxell) were clear waters with a low sediment load. Northern Rookery Stream contained extremely high levels of both suspended sediment and dissolved nutrients (Table 1).

Materials and Methods

Environmental measurements

Stream temperatures were measured with a

TABLE 1. General characteristics of five Antarctic streams

	Stream				
	Onyx	Adams	Northern Rookery	Whangamata	Fryxell
Source glacier:	Lower Wright	Adams	Bird Ice Sheet	Commonwealth	Canada
Physical characteristics					
Altitude (m ASL)	270–94	360–238	100–1	150–18	100–16
Width (m)	5	3.5	2.5	3	3
Length (km)	3.0	2.7	1.0	5.6	2.2
Discharge (m ³ s ⁻¹)*	14.7	0.15	0.16	0.09	0.1
Suspended sediment* (g m ⁻³)	201	17	749	185	4.1
Stream nutrients*					
NH ₄ -N (mg m ⁻³)	5	35	3801	13	1
NO ₃ -N (mg m ⁻³)	20	47	943	75	18
SRP (mg m ⁻³)	2	28	453	42	6

* Measured maximum during midsummer flow in 1984/85 (Fryxell) or 1983/84 (others).

Yellow Springs Instrument Co. combined oxygen/thermistor probe. Air temperatures were measured by the New Zealand Meteorological Service using max.-min. thermometers and thermohydrographs placed in Stevenson screens approximately 1.5 m above the ground. Discharge in the Onyx River was gauged with a V-notch weir operated by the New Zealand Ministry of Works and Development (see Chinn, 1981). In the other streams, velocity profiles were obtained with a Tele-dyne Gurley meter, or with surface drogues. These values and detailed cross-sectional area measurements were used to calculate discharge (John, 1978).

Water for nutrient analysis was immediately membrane filtered (filters pre-rinsed with sample), stored frozen and later analysed by Technicon AutoAnalyzer using the methods in Howard-Williams, Pickmere & Davies (1983). Water samples for suspended sediment analyses were filtered through precombusted pre-weighed Whatman GF/C glass fibre filters. These were immediately frozen, and later dried at 70°C for 24 h and reweighed.

Epilithic biomass

The abundance of epilithic mats and films was initially estimated by point transect analysis of *c.* 300 points at 5 cm intervals over several traverses across the stream at each site. Confidence limits were calculated assuming a binomial distribution (Greig-Smith, 1974).

Cyanophyte biomass was estimated by chlorophyll *a* and organic carbon. Cores of the epilithon were obtained for these analyses using 18 mm diameter plastic tubes or 10 mm-diameter cut-off syringes. The cores were later extracted for chlorophyll *a* (chl *a*) using 30 ml of dimethylsulphoxide at room temperature (15–20°C) for 24 h. The extracts were then diluted with 90% acetone/10% water and assayed by spectrophotometry (modification of Shoaf & Lium, 1976).

Additional cores were later dried for 24 h at 70°C for organic-carbon analysis. They were subsampled by weight using a Kahn micro-balance and combusted at 900°C in a Heraeus furnace flushed continuously with pure oxygen. The gas flow outlet was connected to a Beckman Model 865 infrared gas analyser and CO₂ peaks were recorded on a Hewlett-

Packard 3390A integrator. The system was initially calibrated with pure CO₂ and then during each sample run with urea granules.

Rehydration experiments

Discs (1 cm²) of algal crust were sampled from a dry streambed of the Whangamata Stream (unofficial name) on 20 November, at least 2 weeks prior to first flows. These were immediately immersed in 15 ml of freshly melted glacier ice and incubated at 2–4°C under reduced photon flux densities (50–150 $\mu\text{E m}^{-2} \text{s}^{-1}$). At various time intervals triplicate discs were removed, immediately blotted dry and frozen. These were later extracted with cold dimethylsulphoxide and analysed for chl *a* by spectrophotometry (method as above).

Additional discs were removed at each rehydration time interval for photosynthetic assays. They were washed, placed in 15 ml of fresh glacial meltwater and incubated for 20 min under the same conditions with ¹⁴C-HCO₃⁻ (final activity of 0.96 $\mu\text{Ci ml}^{-1}$). The containers were shaken every 5 min. At the end of each 20 min assay the discs were washed twice with meltwater, poisoned for 10 min with mercuric chloride (0.05% final concentration), blotted dry and then stored frozen. They were later macerated in NCS tissue solubilizer; this homogenate was subsampled into scintillation cocktail and the ¹⁴C counted by liquid scintillation spectrometry. Triplicate light and a single dark incubation were performed at each time interval. Dissolved inorganic carbon was measured in a series of subsamples taken through the experiment and stored in sealed Hypovials with glutaraldehyde (2% final concentration). These samples were later acidified and the headspace CO₂ concentration measured by gas chromatography.

Nutrient uptake

Epilithon samples were removed from the *Nostoc*-dominated Fryxell Stream community and the *Phormidium*-dominated Whangamata Stream community as crusts from the dry stream bed (21 November) or hydrated cohesive mats from the flowing stream (4 January). This material was cut into 50 cm² discs and

placed in containers with 500 ml of fresh glacial meltwater enriched with NH_4Cl and Na_2HPO_4 . 50 ml water samples were removed from each container immediately, and at various time intervals thereafter. These were membrane filtered, stored frozen and subsequently analysed for NH_4 , NO_3 and PO_4 (as SRP) by Technicon AutoAnalyzer II using the methods described in Howard-Williams *et al.* (1983). The containers were incubated under reduced photon flux density ($50\text{--}150 \mu\text{E m}^{-2} \text{s}^{-1}$) at $2\text{--}5^\circ\text{C}$ and were well-stirred every 30 min. An additional set of triplicate containers was incubated with enriched meltwater but no algae as a control in each experiment. These were subsampled at each time interval; nutrient concentration in these containers did not vary by more than 10% relative to the beginning of the experiment. The starting concentration of nutrients was approximately $460 \text{ mg NH}_4\text{-N m}^{-3}$, 75 mg SRP m^{-3} and $64 \text{ mg NO}_3\text{-N m}^{-3}$ on 21 November, and $299 \text{ mg NH}_4\text{-N m}^{-3}$, 38 mg SRP m^{-3} and $9 \text{ mg NO}_3\text{-N m}^{-3}$ on 4 January. Chlorophyll *a* levels in each of the mat communities estimated by DMSO extraction and spectrophotometry, did not vary greatly between the two sampling dates: for *Nostoc* mats $15.1 \mu\text{g chl } a$

cm^{-2} on 21 November, $11.8 \mu\text{g chl } a \text{ cm}^{-2}$ on 4 January; for *Phormidium* mats, $25.2 \mu\text{g chl } a \text{ cm}^{-2}$ on 21 November, $20.3 \mu\text{g chl } a \text{ cm}^{-2}$ on 4 January.

Artificial substrates

Roughened 5 cm sections of non-toxic silicone tubing (Silastic) were threaded on to 1 m long fibreglass rods which were anchored in each streambed early in the season prior to, or during, first flows. Three to four sites were assayed in each stream. In the 1983/84 season four substrates near the stream edge and four substrates from midstream were removed at each site after 3–4 weeks of immersion. These were extracted for chlorophyll *a* analysis as above. Additional substrates were retained for microscopic examination. In 1984/85 the substrate rods were anchored in Fryxell Stream during first flows and replicate substrates were removed for analysis after 1 week and 6 weeks of immersion.

Carbon dioxide exchange

Cores were removed from the Adams or Fryxell Stream 2–3 weeks after first flows during November–December 1984. Two or three 18 mm diameter discs were placed into a 30 ml Universal vial, covered with 2–3 ml of streamwater and sealed with a rubber septum held down by a screw-cap. The vial was laid horizontally in the stream and connected by plastic hose to a Binos portable infra-red gas analyser (IRGA) located on the streambank. The IRGA was set up in a differential, closed circuit continuous flow configuration as shown in Fig. 1. The output of the IRGA was connected to an LCD display and readings were noted at 1 min intervals during each incubation. The incubations were continued until linear rates of CO_2 uptake or production were maintained over at least 4 min (generally within 7–15 min of setup). Dark respiration was measured in the same material by covering the vials with aluminium foil. The IRGA was calibrated in the field using two CO_2 air standards prepared by the laboratory of New Zealand Industrial Gases and fine-calibrated at the Plant Physiology Division campus, DSIR, New Zealand, by gas dilution and IRGA.

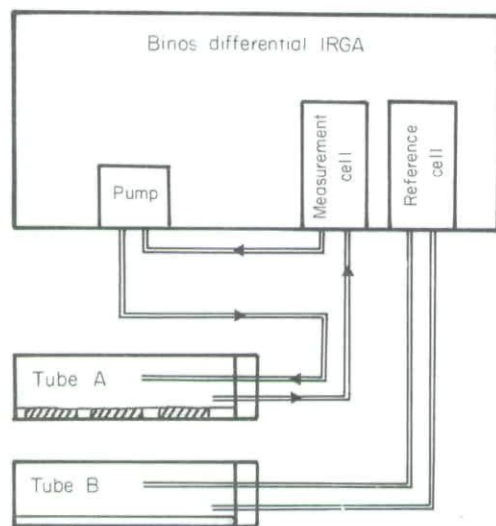


FIG. 1. Infra red gas analyser (IRGA) configuration for photosynthesis and respiration measurements of the epilithon. Universal tubes A and B were immersed in the flowing stream. Tube A contained two or three discs of cyanophyte epilithon plus streamwater. Tube B contained streamwater only.

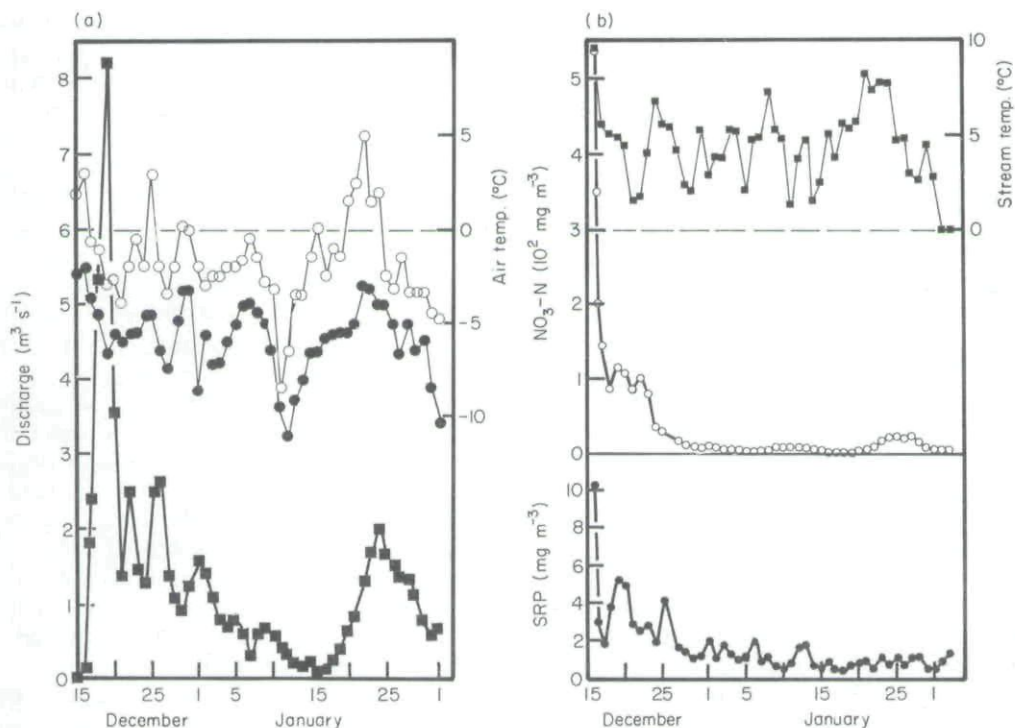


FIG. 2. Physical and chemical characteristics of the Onyx River, Antarctica, over its 1983/84 flow cycle. (a) Daily air temperature minima (closed circles) and maxima (open circles) at a stream site within 2 km of the Wilson Piedmont Glacier (data from NZ Meteorological Service); squares: discharge at 14.00 hours at Vanda Weir, 200 m above Lake Vanda (data from NZ Ministry of Works and Development). (b) Stream temperatures (squares), nitrate (open circles) and soluble reactive phosphorus (SRP) concentrations (closed circles) at Vanda Weir c. 14.00 hours each day.

Results

General environmental properties

The discharge of each stream was highly variable with time. Stream flow began in mid November–early December and persisted through January. Earlier data from the Onyx (Chinn, 1981) show that the duration of flow varies irregularly between years, but that the river typically freezes solid by late January–early February. Over the 1983/84 summer early afternoon flow in the Onyx fluctuated by two orders of magnitude with a 14.00 hours maximum of $8 \text{ m}^3 \text{ s}^{-1}$ (Fig. 2a). Similar day-to-day variations were seen in the smaller streams of the region, but in these waters variability was equally great at diel timescales. For example, in the Whangamata Stream, which flows from the western face of the Commonwealth Glacier into Lake Fryxell, discharge changed almost 200-fold over the day; on 8 January it

rose from $0.006 \text{ m}^3 \text{ s}^{-1}$ at noon when the west-oriented glacier face was in shadow, to approximately $0.1 \text{ m}^3 \text{ s}^{-1}$ when exposed to direct sunshine at 20.00 hours. At each of the stream sites near the source glacier, air temperatures lay close to the freezing point of water (Fig. 2a), and throughout the period of flow radiation was continuous during the day and night (e.g. daily range from 65 W m^{-2} at 24.00 hours to 400 W m^{-2} at 12.00 hours, Taylor Valley, 8 January). Under these relatively warm conditions, small changes in the radiation balance at each glacier face and surface could account for significant changes in discharge.

This irregular hydrology was accompanied by large shifts in other physical and chemical variables. Stream temperatures were always low but varied from day to day (Fig. 2b) and diurnally (e.g. from 0°C at 02.00 hours to 6°C at 18.00 hours in the Onyx River at Vanda

Weir, 26 December). Suspended silt load was considerable at certain times of day in some of the streams. In the Northern Rookery Stream it rose from 1 g m^{-3} (dry weight) at 09.00 hours to 749 g m^{-3} at 15.00 hours when discharge was maximal.

Nutrient concentrations were highest at first flows and declined markedly over the course of the season. In the Onyx River nitrate levels dropped by three orders of magnitude, and soluble reactive phosphorus (SRP) by a factor of 20 between the first date of discharge at Vanda Weir (16 December) and mid-January (Fig. 2b). Analysis of the melthead of the river as it flooded the dry streambed confirmed that the water contained elevated nutrient concentrations well before it reached Lake Vanda (e.g. $15.8 \text{ mg SRP m}^{-3}$ and $99.8 \text{ mg NO}_3\text{-N m}^{-3}$ in the melthead 25 km up valley from Vanda, 11 December). Water samples from the dripping ice face of each glacier early in the season had a much higher nutrient content than the underlying ice (e.g. $351 \text{ mg NO}_3\text{-N}$ and 59 mg SRP m^{-3} in meltwater down the face of the Commonwealth Glacier, 16 November, but $12 \text{ mg NO}_3\text{-N m}^{-3}$ and 4 mg SRP m^{-3} in the blue ice beneath). These data suggest that the glacier surface accumulates wind-blown materials over the course of winter, and that these compounds are largely released in the first melt of the following summer.

Community biomass

An epilithic community dominated by filamentous algae, but also containing bacteria, fungi, protozoans, nematodes and rotifers, reached a high areal biomass in many of the streams. For the twenty-four streams surveyed, the dominant algal genera were *Nostoc*, *Phormidium*, *Oscillatoria*, *Gloeocapsa*, *Microcoleus*, *Prasiola* and *Tribonema* (further details in Broady, 1981, 1982). The three cyanophytes *Nostoc*, *Phormidium* and *Oscillatoria* formed thick (up to 8 mm) cohesive mats and films with chlorophyll *a* levels up to $30 \mu \text{ cm}^{-2}$, comparable with the highest values in temperate latitude streams (cf. Lock, 1981). In the field experiments reported below we visually distinguished 'Nostoc mats', containing almost exclusively *Nostoc commune*, from 'Phormidium mats' containing several species of *Phor-*

midium, *Oscillatoria* and occasionally *Microcoleus*. In general, clear streamwaters supported an abundant epilithon (e.g. Fryxell, Adams, Walcott, upper Garwood) while turbid streams contained sparse communities with epilithic mats confined to shallow, slow-moving side-arms or tributaries (e.g. Whangamata, Commonwealth, Bird, lower Salmon, Lacroix).

A large proportion of stream epilithon appeared to survive the dark winter months dry and deep frozen (winter temperatures drop below -55°C , New Zealand Meteorological Service, 1984) until the next season of streamflow. We estimated the percentage cover of this epilithic crust by point transect analysis when the streambeds were still dry (early November) and later towards the end of the season after 3–4 weeks of flow. In the silt-laden Northern Rookery Stream there was no visible algal material or extractable chl *a* either before or during discharge. In the main region of *Phormidium* growth in the Onyx River a 500 m-wide, 750 m-long region of pools and multiple channels 5 km upstream from Vanda Weir, percentage cover varied over the course of the season depending on local conditions: from an overall average of 42% (95% confidence limits of $\pm 6.5\%$) in November to 79.7 ($\pm 6.0\%$) in early January in a slow flowing reach, and 17.0 ($\pm 5.7\%$) at a site inundated by flood-derived sediment. At downstream sites on three other flowing waters the percentage cover consistently increased after flow, but by at most a factor of 2: from 25 ($\pm 6\%$) to 46 ($\pm 7\%$) in the Adams Stream, Miers Valley; from 61 ($\pm 19\%$) to 84 ($\pm 5\%$), in Fryxell Stream, Taylor Valley, and from 1.2 ($\pm 1.7\%$) to 2.7 ($\pm 2.5\%$) in the Whangamata Stream. The dry overwintering epilithon therefore represents an important fraction of attainable streambed cover.

Metabolic response to rehydration

(a) *Photosynthesis*. A series of experiments conducted early in the season showed that the dry, frozen epilithon was viable, and capable of quickly resuming metabolic activities upon rewetting. The overwintering mats and films contained high chl *a* levels which did not significantly change over 40 h of rehydration (Fig. 3). When dry *Phormidium*-dominated

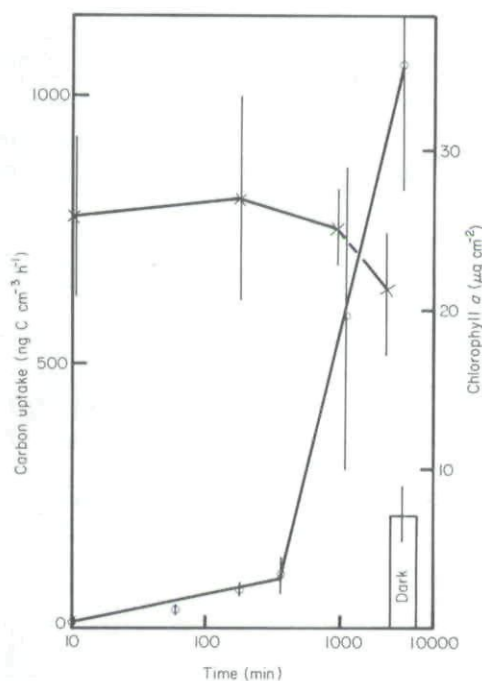


FIG. 3. Photosynthetic recovery by the *Phormidium* epilithon as a log function of hydration time. Crosses: Chlorophyll *a* content; open circles: photosynthesis. Each point is the mean of triplicate samples ± 2 SE.

samples from the Commonwealth Stream were immersed in glacial meltwater light-dependent CO_2 -fixation was detected within the initial 20 min of hydration (plotted at t10 min in Fig. 3). In this first photosynthetic assay dark ^{14}C - CO_2 uptake was 38% of uptake in the light; this percentage dropped with increasing time of prehydration, to 11% at t2880 min. Photosynthetic capacity rose as a log function of time over the first 6 h, and then at a faster rate over the subsequent 2 days (Fig. 3). A set of mat samples incubated with water but in darkness for 48 h and then assayed for photosynthesis showed enhanced, light-dependent, CO_2 -fixation relative to the first 20 min, but a low photosynthetic capacity relative to the 48 h light treatment (histogram, Fig. 3). Simple rehydration permitted immediate photosynthesis but full recovery was more protracted and light dependent.

(b) *Nutrient uptake.* In a related set of experiments, dry algal mats were immersed in glacial meltwater containing NO_3 and enriched levels of NH_4 and PO_4 . Two Taylor Valley

communities were tested for their nutrient uptake characteristics, first in early November, 2–3 weeks prior to flow and again in January after they had experienced 4–6 weeks of immersion in the stream. The mats took up NH_4 immediately upon re-wetting (Figs. 4a, 4b). Uptake followed first order rate kinetics with respect to NH_4 concentration, but was slow by comparison with uptake velocities later in the season: in November dry *Nostoc* mats removed NH_4 from solution at $39.6 \mu\text{g N mg chl } a^{-1} \text{ h}^{-1}$ over the first 3 h of hydration, but rates were more than 2-fold faster in January ($90.4 \mu\text{g N mg chl } a^{-1} \text{ h}^{-1}$). Unlike NH_4 , PO_4 uptake was delayed for several hours after wetting (Figs. 4c, 4d) and then proceeded at rates about 10% of late season uptake, e.g. $0.9 \mu\text{g P mg chl } a^{-1} \text{ h}^{-1}$ for *Phormidium* mats hydrated for 6 h as opposed to $8.0 \mu\text{g P mg chl } a^{-1} \text{ h}^{-1}$ for the same community of January. The two types of epilithon responded differently to nitrate (Figs. 4e, 4f). Samples from the *Phormidium*-dominated epilithon took up NO_3 immediately upon hydration while for *Nostoc* mats, significant nitrate uptake was delayed by 6–12 h after immersion. Nitrate uptake was apparently much faster later in the season, although initial concentrations of NO_3 were low and preclude any rigorous comparisons. For all three nutrient species, however, these experiments consistently show a recovery of substantial uptake capacity within the first few hours of rewetting.

Colonization and growth

The artificial substrates measurably accumulated chlorophyll *a* at most stream sites (Tables 2 and 3). Microscopic analysis of this material showed that the dominant colonizers were filamentous blue-greens of the Oscillatoriaceae group. However, although the species assemblage resembled the *Phormidium* mat community the final accumulated biomass differed considerably. In virtually all of the sites on the streams assayed in 1983/84 the chlorophyll *a* levels on the substrates were 1% or less of values typical of the streambed mats. A single exception was at a downstream site on the Adams (Site 3, Table 2) where the substrate rods had dammed and trapped bed-load material. A thick algal layer had accumulated on these sands and gravels upstream of the rod and extended over the substrates. This epi-

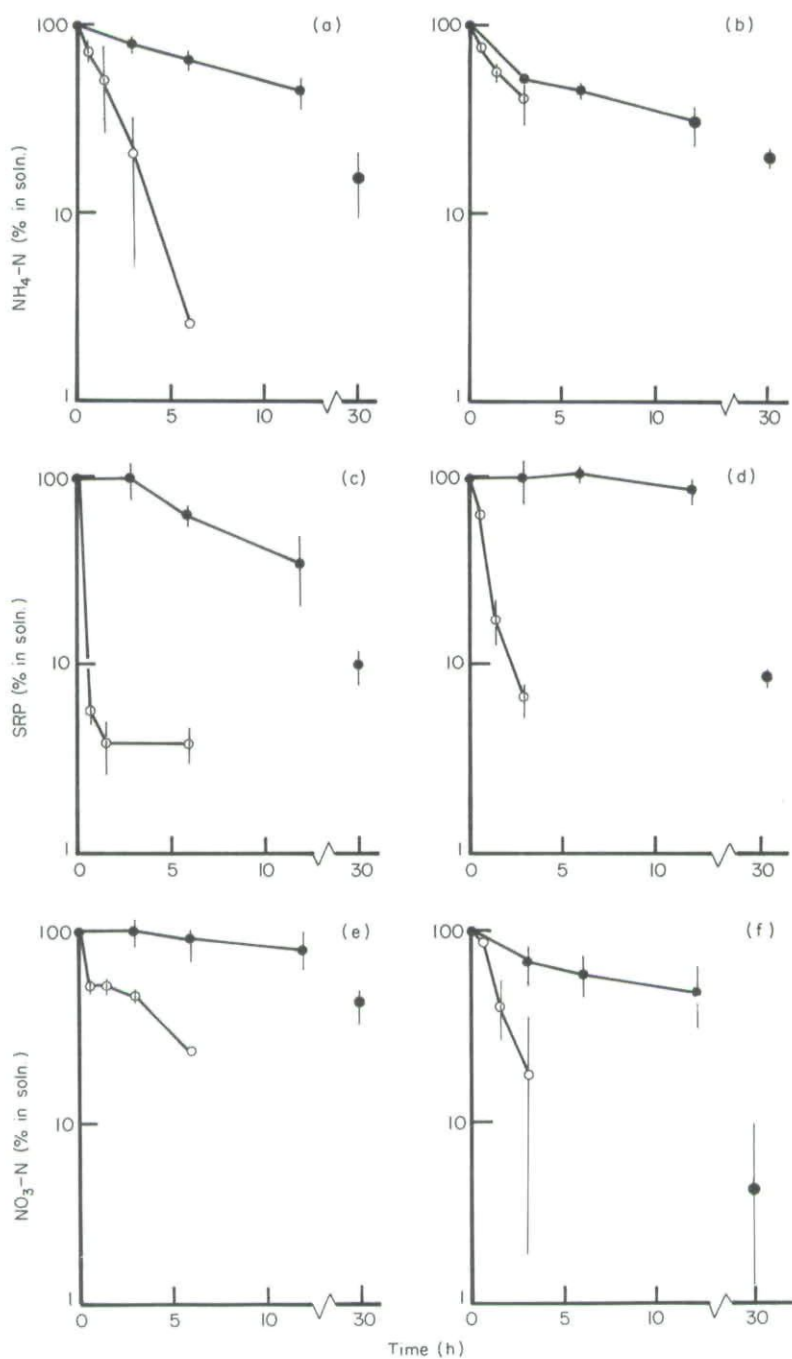


FIG. 4. Nutrient uptake by Antarctic stream epilithon. Closed circles: early season before flow; open circles: late season after 3-4 weeks of flow. (a), (c) and (e) *Nostoc* mats; (b), (d) and (f) *Phormidium* mats. Each point the mean for triplicate incubations ± 2 SE. Note the break in scale between 12 and 30 h.

TABLE 2. Algal growth, measured by chlorophyll *a* (chl *a*) accumulation, on artificial substrates placed in four streams of southern Victoria Land. Each value is the mean (± 2 SE) for four replicates. ns, no significant change in fluorescence of the extract after acidification.

River	Site	Chl <i>a</i> (ng chl <i>a</i> cm ⁻²)	
		Edge	Mid
Onyx	1	ns	ns
	2	1.3 (± 0.8) $\times 10^2$	0.9 (± 0.06) $\times 10^2$
	3	ns	ns
Adams	1	4.6 (± 0.8)	2.4 (± 0.2)
	2	2.1 (± 1.1) $\times 10$	1.4 (± 0.5) $\times 10$
	3	1.6 (± 0.2) $\times 10^4$	1.1 (± 0.3) $\times 10^4$
	4	1.9 (± 1.0) $\times 10^2$	0.8 (± 0.8) $\times 10^2$
Whangamata	1	3.3 (± 0.4)	ns
	2	3.6 (± 0.6)	3.4 (± 0.5)
	3	0.8 (± 0.4) $\times 10$	1.5 (± 1.2) $\times 10$
Bird	1	3.4 (± 1.3)	3.5 (± 1.1)
	2	4.3 (± 1.3)	2.0 (± 0.5)
	3	ns	ns

TABLE 3. Algal growth measured by chlorophyll *a* accumulation (ng cm⁻²) on artificial substrates incubated in Fryxell Stream for 8 days and 44 days. Each chlorophyll *a* value is the mean (± 2 SE) for four substrates (8 day incubation) or eight substrates (44 day incubation) at each site. μ values are the net accumulation rates assuming exponential kinetics between day 8 and 44.

Site	Description	Chlorophyll <i>a</i> accumulation		
		8 days	44 days	μ (d ⁻¹)
1	Upstream near glacier face	2.1 ± 1.2	2.5 (± 1.5) $\times 10$	0.07
2	0.5 km below site 1, gentle stream slope	2.8 ± 0	9.5 (± 7.7) $\times 10^3$	0.23
3	Boulder drop region of fast-flowing water	2.8 ± 0.1	1.3 (± 1.0) $\times 10$	0.04
4	Downstream channel, gentle stream slope	2.9 ± 0.1	1.8 (± 1.7) $\times 10^4$	0.24

lithon had similar areal chlorophyll *a* levels to the cyanophyte mats, but may largely have been material dislodged from the thick mats growing upstream near the glacier face.

The same mechanism (colonization rather than growth) probably gave rise to the high biomass accumulations at two sites in Fryxell Stream over the 1984/85 season (Table 3). Very low but similar chlorophyll *a* levels were recorded on the rod substrates at all sites after 8 days, but 36 days later these had increased at least 5-fold. Extreme accumulations were recorded at sites 2 and 4 where stream velocities were moderate (>0.5 m s⁻¹). These sites were downstream from rich *Phormidium* mats that occurred near and below Site 1 and which could have provided much of this accumulated material. By contrast, relatively low accumula-

tion rates were recorded at the upstream Site 1 where the concentration of drifting mat material would have been much reduced. Site 3 was located in a steep gradient, high velocity, downstream reach. Despite a continuous inoculum of mat material torn away from the upstream epilithon there was a low net accumulation of chlorophyll on substrates at this site (Table 3). The Site 1, 2 and 4 substrates collected mostly Oscillatoriaceae, but at Site 3, green strands of *Binuclearia* also colonized the rods.

There was general correspondence between algal biomass development on the rods and the naturally occurring epilithic biomass of the stream. The Whangamata and Northern Rookery streams had very little epilithon except in side tributaries where flow velocities were

much reduced and the average water depth too shallow (<1 cm) to allow the deployment of substrate rods. A high biomass accumulation on substrate rods in the Onyx occurred at Site 2 located in the wide region of multiple channels (Table 2) where the *Phormidium* community was prolific, 5 km upstream from Vanda Weir. Epilithic algae occurred abundantly throughout the Adams Stream and Fryxell Stream, and in these flowing waters substrate colonization was high at most sites.

There was no relationship between chlorophyll *a* accumulation and the nutrient content of the streams. Northern Rookery Stream had extremely high levels of inorganic N and P (Table 1) but very low levels of biomass grew on the substrate rods (Table 2). Nutrient levels decreased with distance downstream in many of the flowing waters, but algal accumulation was sometimes greatest at the downstream sites.

There was an inverse relationship between accumulated biomass and suspended sediment in the stream (Fig. 5). Highest chlorophyll *a* levels were recorded on the rods in the clearest stream samples, the Adams and Fryxell Streams, while the highly turbid Northern Rookery Stream supported little colonization and growth on the substrates. For geometric

means of the data in Table 2 and Table 3 (44 day incubation) there is a significant negative correlation between log chlorophyll *a* values and log maximum suspended sediment ($r = -0.994$, $df = 3$, $P < 0.01$).

Photosynthesis and respiration

A series of *in situ* CO₂-exchange measurements were conducted by IRGA during November–December 1984 when streamflow was well established. Stream temperatures during these incubations ranged from 0.5 to 3.5°C and ambient photon flux densities varied between 250 and 500 $\mu\text{E m}^{-2} \text{s}^{-1}$.

Gross photosynthetic rates for the two major types of cyanophyte epilithon varied over a relatively small range from 0.39 to 2.15 $\mu\text{g C cm}^{-2} \text{h}^{-1}$ (Table 4). Respiration, however, was a highly variable fraction of total carbon uptake and as a result net photosynthetic rates varied widely. In most of the mats respiration accounted for more than 30% of gross photosynthesis and for both types of community sometimes exceeded 80%. Lowest respiratory losses were recorded in two thin film (<1 mm thick) *Phormidium* communities—a grey-green coloured epilithon found throughout the Adams Stream (sample A4 in Table 4), and a layer of *Phormidium* and *Oscillatoria* which turned bright orange over the first 2 weeks of flow in the upper reaches of Fryxell Stream (Sample F6).

A sample was also taken from an overwintering *Nostoc* crust over an unflooded side arm of the Adams Stream. This epilithon was dry and brittle but the sand beneath it was damp and the epilithon may have been exposed to elevated humidities. When initially assayed without water the mat produced CO₂ at the same rate in the light and dark (Sample A2, Table 4). The cores were then hydrated with 5 ml of Adams streamwater for 1 h and remeasured. Respiration rates increased by almost a factor of 3. Photosynthesis was detectable, but gross rates were less than 50% of respiratory CO₂ production (Sample A3).

At the end of each incubation the core samples were frozen and stored for chlorophyll *a* and carbon analysis. Chlorophyll levels per unit area were similar in both the *Nostoc* and *Phormidium* epilithon (Table 5), but the two communities differed considerably in their car-

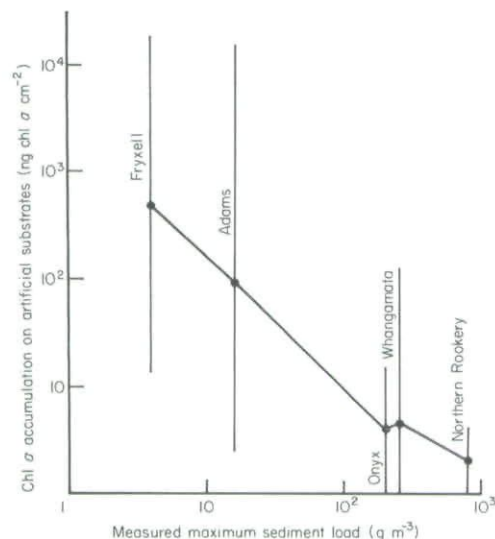


FIG. 5. Relationship between chlorophyll *a* accumulation on the artificial substrates and maximum measured sediment load during the season of growth assay. The data are plotted as geometric means (\pm range) on log scales.

TABLE 4. CO₂ uptake and release by *Nostoc* and *Phormidium* dominated epilithic communities. Values in parentheses are respiration rates expressed as a percentage of gross photosynthesis. A series—Adams Stream. F series—Fryxell Stream. Sign convention: -, CO₂ uptake; +, CO₂ production.

	CO ₂ exchange ($\mu\text{g C cm}^{-2} \text{ h}^{-1}$)		
	Light (net photo- synthesis)	Dark (respiration)	Light-dark (gross photosynthesis)
<i>Nostoc</i>			
A1	-0.51	+0.97 (65)	-1.48
A2	+0.24	+0.24 (—)	-0.00
A3	+0.37	+0.68 (219)	-0.31
F1	-0.11	+1.22 (92)	-1.33
F2	-0.93	+1.22 (57)	-2.15
F3	-1.08	+0.57 (34)	-1.65
<i>Phormidium</i>			
A4	-0.80	+0.11 (12)	-0.91
F4	-0.07	+0.54 (88)	-0.61
F5	-0.18	+1.23 (87)	-1.41
F6	-0.81	+0.07 (8)	-0.88
F7	-0.29	+0.10 (26)	-0.39

TABLE 5. Carbon, chlorophyll and normalized photosynthetic values for Antarctic stream epilithon

Sample	$\mu\text{g chl } a \text{ cm}^{-2}$	mg C cm^{-2} (%)	$\mu\text{g chl } a \text{ (mg C)}^{-1}$	Gross photosynthesis	
				ng C ($\mu\text{g chl } a \cdot \text{h})^{-1}$	ng C (mg C.h) ⁻¹
<i>Nostoc</i>					
A1	15.7	16.9 (16.2)	0.9	94	88
A2	11.8	18.8 (22.9)	0.6	0	0
A3	11.8	18.8 (22.9)	0.6	26	16
F1	18.5	43.4 (28.4)	0.4	72	31
F2	26.0	24.7 (22.9)	1.1	83	87
F3	21.4	46.2 (29.8)	0.5	99	46
<i>Phormidium</i>					
A4	23.6	5.2 (2.6)	4.5	38	175
F4	9.5	13.5 (12.1)	0.7	64	45
F5	27.9	6.9 (3.0)	4.0	50	204
F6	21.3	7.1 (6.0)	3.0	41	124
F7	30.1	6.8 (3.1)	4.4	13	57

bon content. Areal organic carbon levels were much higher, and chlorophyll *a* per unit carbon much lower, in the thick *Nostoc* mats. Organic carbon was a very small (<5%) fraction of the total dry mass of *Phormidium* films indicating the high proportion of abiotic sediment material trapped and bound by the fine algal trichomes. Organic carbon was typically a 10-fold higher percentage of total mass in the *Nostoc* epilithon.

Photosynthetic rates per unit biomass were very low (Table 5). Both types of community had assimilation numbers less than 0.1 $\mu\text{g C}$

($\mu\text{g chl } a$) h^{-1} . Rates per unit organic carbon give theoretical C-turnover times of approximately 800 days for the *Nostoc* epilithon and approximately 200 days for the *Phormidium* community.

Discussion

Many of the flowing water ecosystems of southern Victoria Land contain a rich epilithon yet primary production rates per unit biomass (P/B) are extremely low. Several unique fea-

tures of the Antarctic stream environment could account for this apparent inconsistency.

Two environmental properties, nutrient supply and light, seem unlikely constraints on stream productivity. There was no positive relationship between chlorophyll development on the artificial substrate rods and measured nutrient concentrations in the water either between streams or stream sites. Similarly the epilithic biomass in each stream could not be related to soluble reactive phosphorus (SRP) or dissolved inorganic nitrogen (DIN). The streams experience elevated nutrient levels during first flow, and the overwintering epilithon seemed capable of a rapid response to this early SRP and DIN supply. Light is also an unlikely explanation of the reduced P/B ratio. Radiation is continuous throughout the day and 'night' during the season of stream-flow. With the exception of floods and hours of peak discharge each day, the streams are shallow (<25 cm water) and light cannot be significantly attenuated by the flowing water above the epilithon. In this regime of continuous PAR, photosynthesis is unlikely to be light-limited for extended periods of time.

Stream temperature is a more probable overall control on P/B. Water temperatures rarely rise above 5°C and often lie in the range 0–2°C. Seaburg *et al.* (1981) found that nineteen algal isolates from southern Victoria Land streams grew from 2 to 18°C with optimal temperatures for growth likely to be towards the high end of this range, well above ambient. These algae appear to have no unusually rapid growth characteristics at low temperature (Seaburg *et al.*, 1981) and will therefore metabolize slowly in the cold stream environment.

Despite the low P/B ratio of the blue-green algal epilithon we measured chlorophyll *a* up to 30 $\mu\text{g cm}^{-2}$ and organic carbon up to almost 50 mg cm^{-2} . Theoretical turnover times for the epilithon, calculated from gross production and biomass carbon estimates, were of the order of several hundred days. These findings are consistent with the artificial substrate assays. Colonization rates were extremely slow (Table 3) with a final accumulated biomass generally well below the levels measured in the natural epilithon. The streambed biomass could not therefore be formed in a single season (typically 30–90 days) and is probably the accumulation of several years' growth. This

material may include chlorophyll and organic carbon associated with old, damaged and incompletely active cells which would further depress the apparent P/B. However, the overwintering community retains a high metabolic capacity and responds rapidly to hydration at the beginning of summer.

The inhibiting effects of low temperature on growth are well known for many blue-green algal species. For example, Foy, Gibson & Smith (1976) report a sharp decline in the mean daily division rate of *Anabaena flos-aquae*, *Aphanizomenon flos-aquae* and *Oscillatoria agardhii* at temperatures below 10°C. In laboratory enrichment assays of mixed phytoplankton assemblages from Lake Superior, blue green algae become increasingly dominant at higher temperatures (Tilman & Kiesling, 1984). Cyanophytes that are morphologically very similar or even identical to the Antarctic stream species grow extremely rapidly in the epilithic mat communities of hot springs—for example *Oscillatoria amphigranulata* from high sulphide springwaters has a growth rate of 3.5 doublings per day at 45°C (Castenholz & Utkilen, 1984). This temperature responsiveness may not simply be a cyanophyte feature however. The four Antarctic algal isolates (all chlorophytes) studied in detail by Seaburg *et al.* (1981) in unialgal clonal culture all had strongly depressed growth rates near 0°C and growth optima about 10°C. Near-zero stream temperatures must strictly limit the *in situ* growth rates of the Antarctic epilithon.

The response of the overwinter epilithon to rewetting resembles the behaviour of desert plants at warmer latitudes. *Selaginella lepidophylla*, a so-called 'resurrection' or drought tolerating plant, can survive desiccation for several years, begins CO₂ production immediately upon hydration and resumes net photosynthesis within 3 h (Eickmeier, 1979). This species conserves an operational respiratory system but full recovery takes several hours of *de novo* protein synthesis (Eickmeier, 1982). The kinetics of recovery by the *Phormidium* and *Nostoc* epilithon would be consistent with a similar two-step response: hydration permits immediate but impaired metabolism and full recovery requires longer term biosynthesis and repair. The stream flora of the Antarctic desert also inhabit an arid regime

of seasonal water supply, but must additionally sustain continuous winter darkness and an extreme freeze-thaw cycle. Physiological resilience to freezing is known for at least one *Nostoc* species from temperate latitudes (Dubois & Kapustka, 1983) and must be an essential attribute of the Antarctic cyanophytes.

Arthropod herbivores (insects, crustaceans) are an important control on stream algal biomass at temperate latitudes (e.g. Fisher *et al.*, 1982) but they are completely absent from the epilithic environment in this part of Antarctica. Three species of collembola and three mite species have been found on the mosses which sometimes occur on the banks of southern Victoria Land streams, but these animals do not appear to associate with the algal mats (unpub. data, Dr W. Block, British Antarctic Survey). The cyanophyte mats contain various small animals (ciliates, flagellates, nematodes, rotifers and tardigrades) embedded within the epilithic matrix, but the effects of microherbivory remain untested. Although this microfauna may be locally important for nutrient and carbon recycling the low stream temperatures and brief growing season must restrict population development and their overall impact on the primary producers and associated microflora.

A more important loss process in this streamwater environment may be sloughing either by high water velocities, the abrasive effects of a high sediment load or a combination of both. There was a visual correspondence between algal epilithon and the clarity of the streamwater. The epilithic mats grew most profusely in regions of reduced water velocity where scouring effects must be reduced—near stream edges (e.g. Fryxell Stream), in wide wash regions (e.g. Site 2 on the Onyx) and in slow-moving side arms (e.g. Whangamata near the glacier face). In the substrate rod experiments chlorophyll accumulation was often highest on the substrates located nearest the stream edge (Onyx, Site 2, Adams, all sites; Whangamata, Site 1; Bird, Site 2), and there was an overall inverse correlation between substrate chlorophyll and the maximum suspended sediment load measured in the stream. Lowest chlorophyll accumulation in Fryxell Stream was at Site 3 where water velocities were maximal. In total, these observations

suggest that physical scouring is an important control on stream biomass development.

In the cold environment of Antarctic streams we might expect respiratory rates to be substantially depressed, yet CO₂ production was often a very high percentage of total inorganic carbon uptake. These respiration rates seem too high to be entirely algal. Epilithic communities at all latitudes contain heterotrophic bacteria embedded in the polymeric matrix, and there appears to be a close functional relationship between these organisms and their associated algae (Lock *et al.*, 1984). Microscopic examination of the Antarctic cyanophyte mats revealed very high densities of bacterial rods, filaments and cocci, as well as filamentous fungi. The net organic accumulation each year in these communities must be further reduced by microbial catabolism of photosynthetically fixed carbon.

The flowing waters of the McMurdo Sound region are short (typically <5 km), low discharge (typically <0.2 m³ s⁻¹) streams that flow for several weeks each year. There is no Antarctic equivalent of the large rivers (e.g. MacKenzie River, 10⁴ m³ s⁻¹; Todd, 1970) which flow into the Arctic Ocean. These rise in the temperate or boreal zone and many of their properties are more closely related to their lower latitude origins rather than the Arctic environment (Harper, 1981).

Antarctic stream ecosystems compare in several respects with the smaller flowing waters of the high Arctic. In both systems flow regime may be variable, although Arctic streams do not seem to experience the same intense flood events which characterize the Dry Valleys (Fig. 2a of Meier, 1964). The streams of both regions receive continuous radiation throughout the polar summer. Water temperatures are typically low in both environments and might be expected to similarly depress microbial growth in the Arctic and Antarctic. Glacial streams often contain a high suspended sediment load (Meier, 1964) and physical scouring effects might therefore be important in the high latitude zones of both hemispheres. Similarly, ice cover and ice-scouring may be common to early season and late season flow in both parts of the world.

Although the small streams of the two polar zones share certain physical attributes their biology contrasts sharply. The stream epilithon

in the McMurdo Sound region is dominated by a large overwintering cyanophyte biomass which does not change markedly in either species composition or abundance during summer. A physically similar but biologically contrasting set of ecosystems is described in Moore's (1974a, b) detailed study of three Baffin Island streams in the Canadian Arctic. These flowing waters contained a highly diverse epilithon (240 algal taxa) which developed to maximum biomass in late July and then decreased until freezing. Unlike the Antarctic streams there was a pronounced seasonal succession from diatoms in June to chlorophytes and chrysophytes in August, although cyanophytes were numerically important at all times. Growth rates seemed comparable to temperate latitude streams, but no P/B data are available to compare with our southern Victoria Land measurements. Moore (1974b) speculated that grazing was a relatively unimportant control on stream algal biomass. However, large benthic invertebrates are common in streambeds throughout the Arctic, and although the species diversity is sometimes low (Harper, 1981), the grazing impact could be considerable in some north-latitude waters. Invertebrate grazing is probably of much lesser importance throughout southern Victoria Land where stream insect and crustacean herbivores are completely absent.

Although running waters have been recorded from many sites around Antarctica we know of no previous attempt outside the McMurdo Sound region to examine their microbial ecology. Southern Victoria Land streams share a number of unusual ecosystem properties. Periods of flow are infrequent events confined to a few weeks in summer. In years of unusual weather conditions flow may not occur at all (e.g. 1977/78 in the Onyx River; Chinn, 1981). P/B ratios are low and the net biomass gains during these brief periods of hydration must be small and highly dependent upon the size, viability and metabolic responsiveness of the overwintering inoculum. Biomass accumulation may be further reduced by sloughing losses which appear to control the distribution of epilithic communities within and between streams. The epilithon is floristically simple, but community respiration is high and microheterotrophs may be unusually abundant. It remains to be seen

whether these features of the southern Victoria Land streams are common to flowing water ecosystems throughout the Antarctic region.

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