

Filamentous green algae in freshwater streams on Signy Island, Antarctica

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Abstract

The streams of Signy Island are varied and extremely seasonal environments. Water flows from November/December to March/April; streams are frozen for the rest of the year. Streams usually flow through small, barren catchments and are nutrient poor, though they may be enriched by dense summer populations of seabirds and seals. Temperatures are consistently low. Stream depth is maximal during the spring melt period, declining over the course of the summer. Vegetation is exclusively algal, and filamentous chlorophytes form a particularly conspicuous component. Small numbers of vegetative cells survive the long frozen period in situ. A steady increase in standing crop results in a maximum 2 to 3 months after flow begins. Sloughing is the major loss mechanism and grazers are effectively absent. Three taxa of filamentous algae are common in Signy streams, species of *Zygnema*, *Mougeotia* and *Klebsormidium*. The distributions of these algae are described and related to physical and chemical features of their environment.

Introduction

There is a wide variety of freshwater habitats on the Antarctic continent and its off-lying islands, ranging from small meltwater streams to large permanently ice-covered lakes. Recent reviews of Antarctic freshwater biology have not presented the full extent of this range and instead have concentrated on the relatively well understood lake ecosystems with scant, if any, reference to streams (Heywood, 1977a, 1984; Priddle, 1985). This omission reflects more the lack of information on Antarctic streams than their abundance and probable significance as centres of biological activity (Heywood, 1977b; Broady, 1982; Howard-Williams *et al.*, 1986). It is only in the

last few years that these ephemeral ecosystems have begun to be studied.

Antarctica has been divided into 2 climatic zones, the continental and the maritime Antarctica (Holdgate, 1964). The latter comprises the western side of the Antarctic Peninsula and its off-lying islands and is characterised by mean monthly winter temperatures which rarely fall below -20°C but where at least one month each summer has a mean temperature above freezing. The former has mean monthly temperatures which do not rise above freezing in summer and regularly fall below -20°C in winter.

Antarctic stream studies have until now been confined to continental Antarctica (Hirano, 1979; Broady, 1982; Howard-Williams *et al.*, 1986).

Here, streams are often dominated by perennial, slow growing cyanobacteria, though filamentous chlorophytes and xanthophyceae have also been recorded. There is little information available on maritime Antarctic streams despite their widespread occurrence. Heywood (1977b) and Priddle and Belcher (1982) reported Zygnematales (which have not been noted from continental Antarctica – Hirano, 1965) as the dominant stream vegetation at Alexander Island (at the southern limit of the maritime Antarctic) and Signy Island (towards the northern limit of the maritime Antarctic) respectively. The purpose of this study was to investigate the distribution and seasonality of filamentous chlorophytes in streams at Signy Island in relation to environmental variables.

Study sites

Signy Island (Fig. 1) is a small (8×5 km), roughly triangular island forming part of the South Orkney Islands. It comprises a mostly ice-capped central system of ridges which isolates areas of relatively flat, low-lying coastal plain. The ice cap covers a third of the island and descends to the sea on the south and east coasts as the McLeod and Orwell Glaciers respectively. Geologically, the island comprises heavily folded metamorphic rocks of pre-Cambrian age. Garnetiferous quartz-mica-schists predominate (Mathews & Maling, 1967). Most deglaciated areas comprise frost-shattered rock or scree or are covered in a heterogenous layer of unconsolidated glacial till.

The island accumulates a considerable depth of snow (largely as drifts) during winter, most of which melts during summer. Mean monthly temperatures typically rise above zero for two months each year, and large numbers of meltstreams are found during this period.

The length and discharge of streams at Signy Island is limited by the size of the island. The maximum observed length was 535 m and the maximum drainage basin area 99.2 ha. All samples described in this paper were collected

from shallow, freshwater streams. Only streams which were flowing for most or all of the summer period were sampled. Sites within these streams were delimited in the field by clear differences in substratum, current velocity, nature of the terrain through which they flowed or after the confluence of two smaller streams. Samples were taken from locations considered to be typical of each site. A total of 36 sites were chosen. All of these sites were sampled at least twice (mid January and mid February 1985) and some on more frequent occasions.

In general, the streams fell into three categories,

- i. Meltwater runnels
- ii. Larger streams and lake outflows
- iii. Glacial streams

Meltwater runnels were found mainly at the heads of catchments and were fed by melting snow-banks. They were shallow and diffuse, apparently lacking sufficient volume or duration of flow to excavate clearly defined channels. Substrata were often unstable, comprising sand and silt as well as gravel and small stones. Meltwater runnels fed into larger streams or more usually drained into one of the island's sixteen lakes. The larger streams, which formed lower down catchments after the confluence of a number of meltwater runnels, and outflows from the lakes could have substantial discharges. They frequently occupied well-defined channels which had been swept clear of sedimentary material to leave a substratum of stable rocks and boulders. Glacial streams drained the island's glaciers, which are in retreat. Substrates comprised well-rounded boulders and stones in the faster flowing regions, interspersed with unstable areas of gravel and silt. They were fast flowing streams, with a high load of suspended silt giving a milky appearance.

Stream vegetation also fell into three categories. First, a sparse flora of epilithic diatoms was the only vegetation in the most torrential streams, mostly *Achnanthes austriaca* and *Synedra rumpens*. Secondly, a patchy covering of epilithic, epiphytic and epipsammic diatoms and cyanophytes – mostly *A. austriaca*, *S. rumpens*, *Gomphonema angustatum*, *Cymbella* spp., *Phormidium fragile*, *P. antarcticum* and *P. frigidum* – was found in the

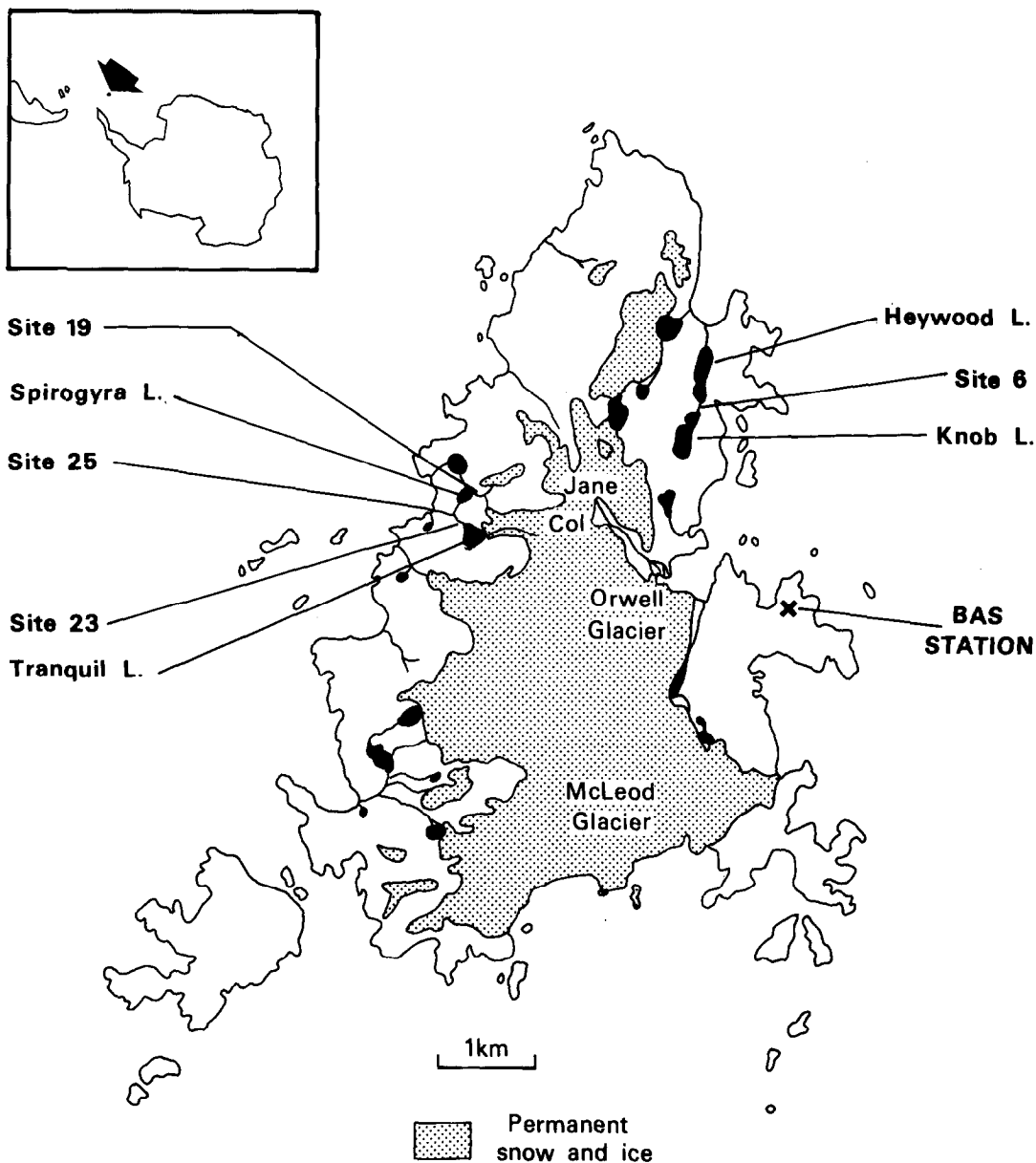


Fig. 1. Map of Signy Island, showing lakes and major streams (black) and areas of permanent ice cover. Inset shows the location of Signy Island.

slower flowing streams, particularly those enriched with nutrients. This community was poorly developed in streams with unstable substrata and/or relatively high current velocities. Splash zones often had encrusting colonies of *Gloeocapsa magma* growing on them. Filamentous chlorophytes were the third major component of stream

vegetation and were found in conspicuous amounts in 31 of the 36 sites examined. Three genera were found to predominate, *Mougeotia*, *Zygnema* and *Klebsormidium*. The last of these, *Klebsormidium* was identified as such on the basis of chloroplast morphology. This is a variable feature and this alga may have belonged to the

Table 1. Physical characteristics of main study streams at Signy Island.

Stream Number	Max Obs Depth ⁽¹⁾ (cm)	Min Max Depth ⁽²⁾ (cm)	Width ⁽³⁾ (m)	Length (m)	Gradient	Catchment area (ha)	% Snow/ice in catchment
6	11.0	3.0	3.5	115	1 : 30	31.5	7
19	3.5	1.0	7.0	140	1 : 12	12.5	39
23	21.0	7.5	6.0	55	1.10	74.0	58
25	7.5	1.5	7.0	100	1.5	99.2	48

¹ Maximum depth at sites used for estimating cover over the entire sampling period.

² Maximum depth at sampling site at time of minimum water level.

³ Width of transect site at maximum water level.

similar genus *Ulothrix*. Filaments were epilithic in the larger and glacial streams and formed loosely attached mats on softer substrata.

Four stream sites were selected for more detailed study of the seasonal dynamics of filamentous algae. These were sites 6, 19, 23 and 25. Physical characteristics of these sites are given in Table 1.

Site 6. The outflow from Knob Lake. A braided, moderately fast flowing stream draining a lake which is surrounded by moss banks heavily populated by fur seals during summer. The stream bed comprises stones and rock which are mostly swept clear but there are occasional patches of sand and gravel. *Klebsormidium* formed a dense cover particularly early in the summer.

Site 19. A broad, shallow meltwater runnel indirectly draining part of the ice-cap and forming the main inflow to Spirogyra Lake. It flows slowly through an extensive area of glacial till with little or no terrestrial vegetation. The stream is poorly defined with no confining channel, the substrate mostly comprising small stones and silt. *Zygnema* forms a near complete cover.

Site 23. Situated on the Tranquil Lake outflow approximately 50 m downstream of the lake. The stream is approximately 5 m wide and 5–15 cm deep at this point and current velocity is moderate to high. The stream bed again comprises boulders and large stones but is swept free of sand and

gravel. *Mougeotia* is the most abundant filament forming long (up to 90 cm) trailing strands in the braided channel.

Site 25. A high velocity, braided stream flowing over a steep, raised beach of large, rounded stones and boulders with patches of soft substrata in the more sheltered areas. This stream is formed after the confluence of the outflows from Tranquil and Spirogyra Lakes and in addition, receives substantial quantities of meltwater direct from snowfields. It discharges directly into the sea. Both *Mougeotia* and *Zygnema* are found in this stream, though rarely together.

Methods

Collection and preparation of water samples

Water samples for chemical analysis were collected in acid-washed, opaque, 500 ml polypropylene bottles. Each bottle was rinsed three times and filled, expelling all air. Separate samples were taken in 125 ml polyethylene bottles for determination of pH and alkalinity. Sample bottles were returned to the laboratory in an insulated box to prevent freezing. The pH and alkalinity samples were then equilibrated to 5 °C in a cooled water bath. Water for other analyses was filtered through a GF/C filter and then used for analysis of ammonia, nitrate, DRP (dissolved reactive phosphorus), TDP (total dissolved phosphorus) and DRSi (dissolved reactive silicate). At

each collection site, the water depth and temperature were measured and current velocity was estimated on a scale of 1–5 where:

- 1 = no flow
- 2 = slight
- 3 = moderate
- 4 = fast
- 5 = very fast

Analysis of water samples

pH was measured using a Phillips PW9409 pH meter, and alkalinity of the same sample by Gran titration (Talling, 1973). Nitrate was determined according to Morris (1971). DRP was determined using the method of Murphy and Riley (1962 – as given by Mackereth *et al.*, 1978). Preparation of samples for TDP involved digestion with acid persulphate followed by determination of DRP (Mackereth *et al.*, 1978). Ammonia was determined according to Chaney & Marbach (1962) and DRSi according to Mullin & Riley (1955).

Preparation and analysis of algal samples

Algal samples were removed from streams with forceps and placed in acid washed polythene bottles or 'whirl-pack' bags with a small volume of water; these were returned to the laboratory in an insulated box. Samples were rinsed three times in filtered stream water and sub-samples set aside for identification. Further sub-samples were dried at 105 °C for 24 h then frozen at –40 °C for return to the UK. There they were analysed for C, N, P and ash content. C and N were estimated using a Carlo-Erba 1106 elemental analyser. P was estimated as FRP (Bartlett, 1959) after digestion of a weighed sample containing approx 0.1 µmol P with 800 µl of 72% perchloric acid at 180 °C for 30 min. Ash content was taken as that remaining after combustion at 500 °C for 12 h.

Standing crop estimation

Two measures of algal standing crop were made. The cover of filamentous green algae was estimated using a point quadrat system. A line marked at 5 cm intervals was stretched between 2 stakes permanently fixed at each side of the

stream. The presence or absence of filamentous algae was noted at each mark (marks were approximately 3 mm wide). Three traverses were made at each site and cover expressed as a % of the number of sites occupied at the time of maximum observed cover. This method enabled a rapid assessment of the development of algal communities.

The standing crop was also estimated in terms of chlorophyll *a*. At 2–3 weekly intervals 5 stones with maximum linear dimensions between 5 and 15 cm were taken from the stream bed. Algal cover was removed by first scraping and then scrubbing with a stiff nylon brush. The algal material was collected by centrifugation, then resuspended in 95% methanol and stored at 4 °C for 24 h for extraction of pigments. Absorbance of the extracts at 665 and 750 nm was measured with a Pye Unicam SP6-550 spectrophotometer. Absorbance measurements were repeated after acidification with dilute hydrochloric acid and neutralisation with ethanolamine to permit estimation of phaeopigments (Marker *et al.*, 1980). The equations given in Marker *et al.* (1980) were used for calculations of pigment concentrations in extracts. Chlorophyll *a* was then expressed on an areal basis after estimating the surface area of each stone by dividing its shape into component triangles and measuring each side with calipers. The tendency of the quartz-mica-schist bedrock to split along the flat planes of schistosity facilitated this approach.

Taxonomy

Filamentous green algae could be classified to genus level only. All samples examined were sterile, with no species specific morphological characteristics.

Results

Distribution of filamentous algae

Three genera were found to predominate in Signy Island streams, *Mougeotia*, *Zygnema* and *Klebsoridium*. There was no indication from cell morphology that more than one species of each genus

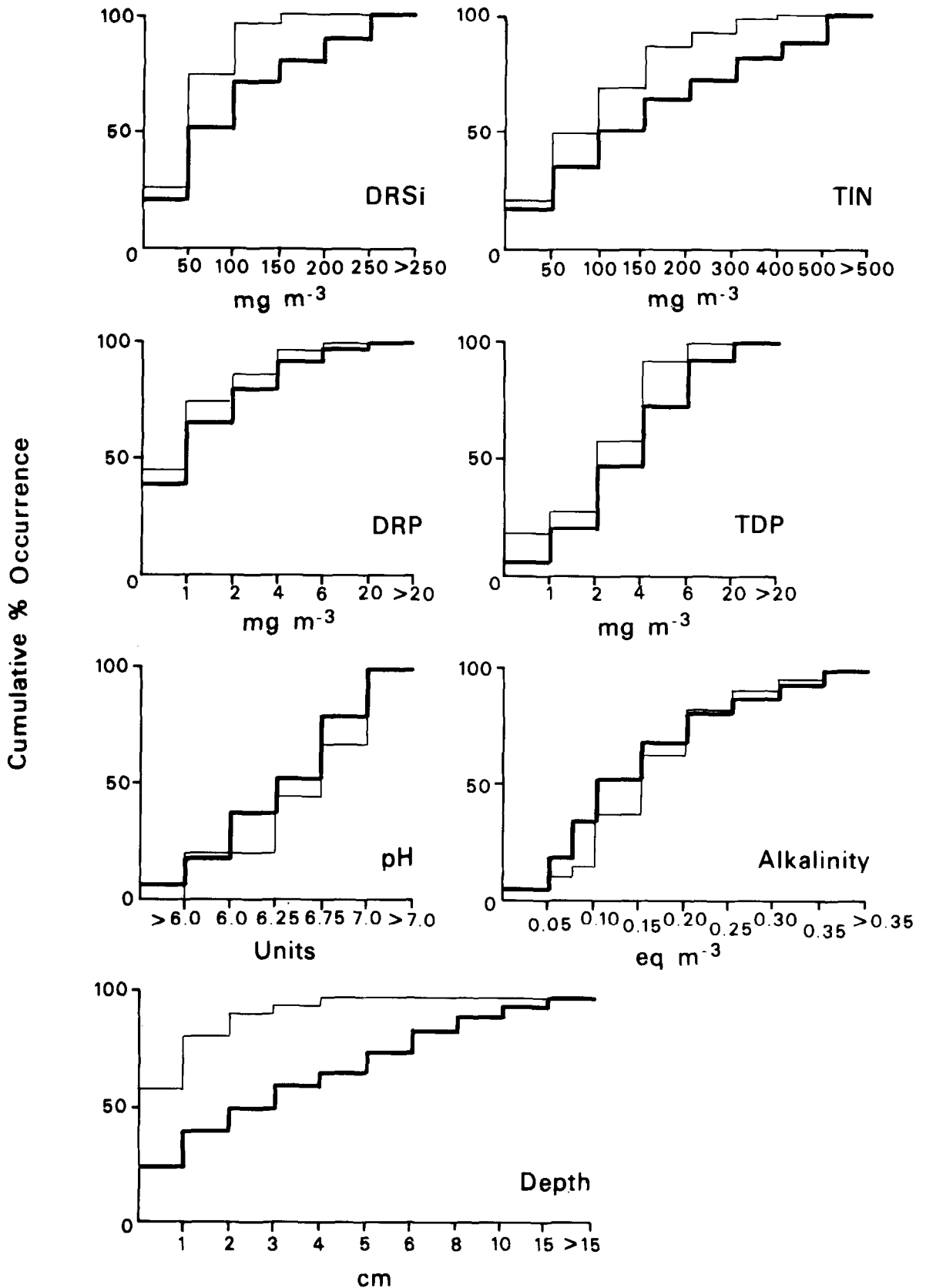


Fig. 2. Kolmogorov curves for *Zygnuma* (see text). The cumulative distribution of a given variable at all streams sampled is shown by the bold line (the reference curve), that of the streams where *Zygnuma* occurred is shown by the narrower line.

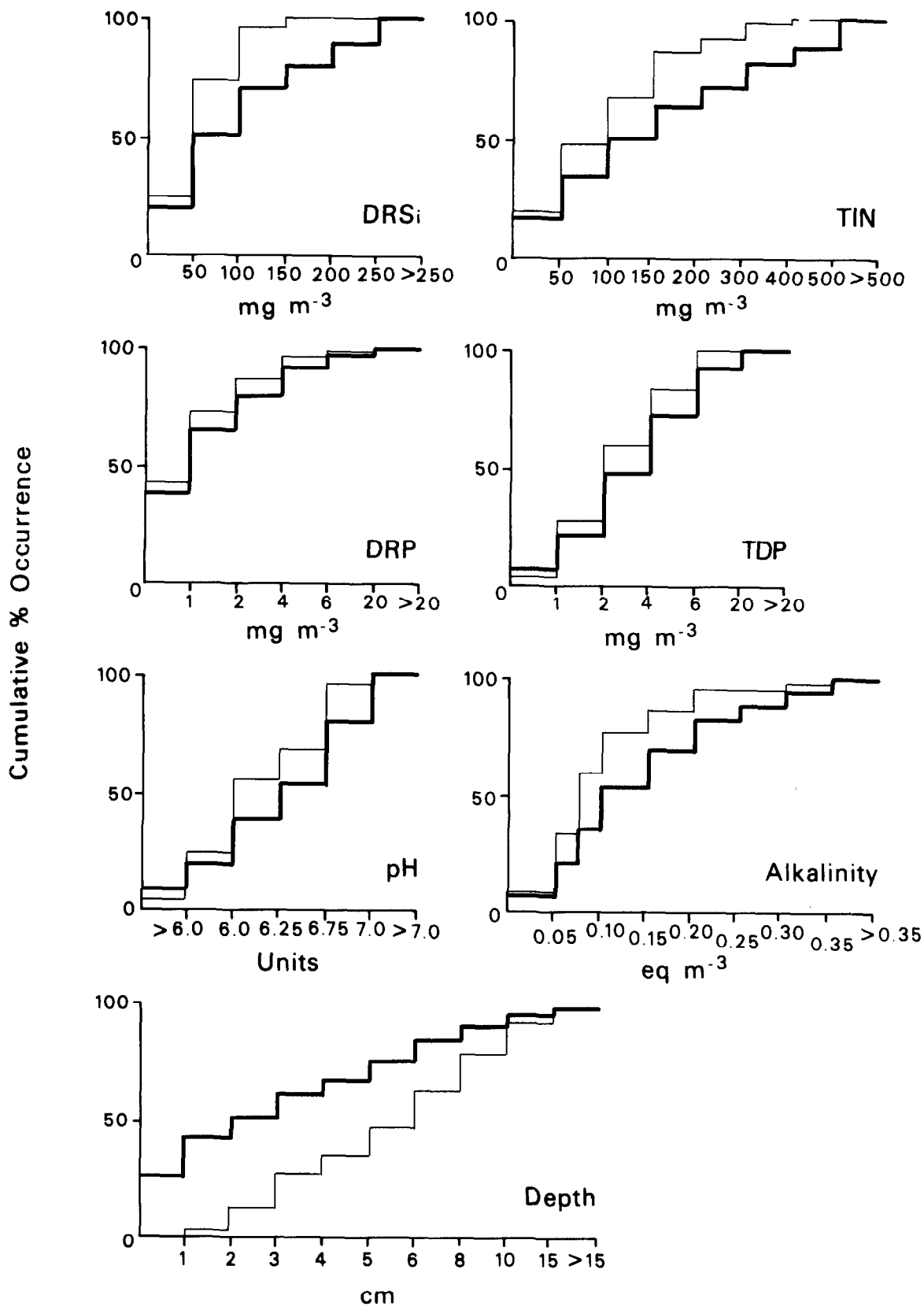


Fig. 3. Kolmogorov curves for *Mougeotia* (see text). The cumulative distribution of a given variable at all streams sampled is shown by the bold line (the reference curve), that of the streams where *Mougeotia* occurred is shown by the narrower line.

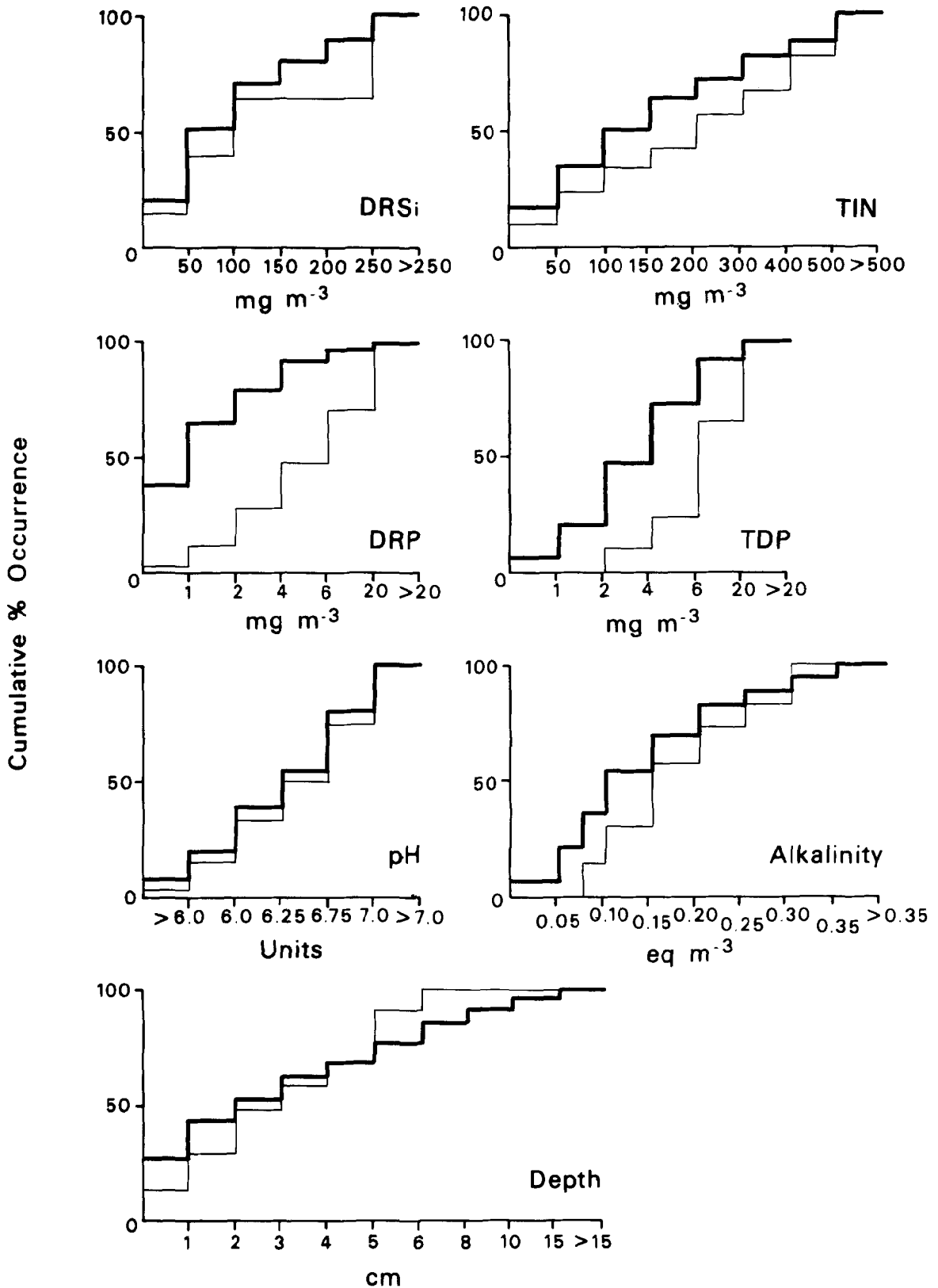


Fig. 4. Kolmogorov curves for *Klebsormidium* (see text). The cumulative distribution of a given variable at all streams sampled is shown by the bold line (the reference curve), that of the streams where *Klebsormidium* occurred is shown by the narrower line.

Table 2. Correlation matrix for determinands included in Kolmogorov analysis. TIN, Total inorganic nitrogen; DRP, Dissolved reactive phosphorus; TDP, Total dissolved phosphorus; SRSi, Dissolved reactive silicon; ALK, Alkalinity. The significance of the correlations and their signs are indicated: + + + or - - - $p < 0.001$; + + or - - $0.001 < p < 0.01$; + or - $0.01 < p < 0.05$; ns $p > 0.05$.

	TIN	DRP	TDP	DRSi	ALK	pH	DEPTH
TIN	X						
DRP	ns	X					
TDP	ns	+ + +	X				
DRSi	+ + +	ns	ns	X			
ALK	+ + +	ns	ns	+ + +	X		
pH	- -	ns	ns	+ +	+ +	X	
DEPTH	- -	ns	ns	-	-	ns	X

was present. A Kolmogorov analysis (Conover, 1971) was used to attempt to relate the distribution of these genera at the 36 sites to measured environmental variables. The Kolmogorov approach is designed to compare the cumulative distribution curves of an environmental variable (e.g. depth) at all sites sampled (the reference curve), with the cumulative distribution of that variable at sites supporting one particular taxon. Cumulative distribution curves for seven variables and the three genera are shown in Figs. 2–4. Confidence intervals (not shown in the figures) were applied after Kolmogorov and used to assess the significance of deviations from the reference curves (Conover, 1971: 299). Care had to be taken in interpreting these data as there were strong correlations between some variables (Table 2).

Significant deviations from the reference curves were found for all three genera (Table 3). *Klebsor-*

Table 3. Significance of deviations from the reference curve in the Kolmogorov analyses for the three main genera and selected determinands. 109 stream sites were included in the analysis. Abbreviations and symbols as in Table 2.

Variable	<i>Zygnema</i>	<i>Mougeotia</i>	<i>Klebsormidium</i>
TIN	NS	-	NS
DRP	NS	NS	+ + +
TDP	NS	NS	+ + +
DRSi	NS	- -	NS
ALK	NS	NS	+
pH	NS	NS	NS
DEPTH	- - -	+ + +	NS

midium was most frequently encountered in P-rich streams. This was the only genus which may have had a nutrient response. The most significant deviations from the reference curves for both *Mougeotia* and *Zygnema* related to depth; the former being most abundant in deep streams, the latter in shallow ones. Significant relationships between low nitrate ($p < 0.10$) and silicate ($p < 0.05$) concentrations and *Mougeotia* abundance may be due to the negative relationships between these variables. Quantitative measures of current velocity were not made. Visual estimates suggested that the shallow streams which tended to be occupied by *Zygnema* were slow flowing, while in faster streams *Zygnema* was rare and *Mougeotia* or *Klebsormidium* predominated. *Mougeotia* was also found in slow flowing and even static water but *Klebsormidium* was not. Filamentous algae were very rarely encountered in very fast (category 5) streams.

The reference curves are useful indicators of the distribution of variables in the streams. Most streams can be described as shallow (65% less than 5 cm deep), slightly acidic (80% pH less than 7) with low concentrations of DRP (70% less than 2 mg m^{-3}) but relatively high TIN concentrations (50% above 150 mg m^{-3}).

Main study sites

Year-round observations were made at the four main study sites. These were frozen from late April to November. During this winter period, samples were excavated from the streams which,

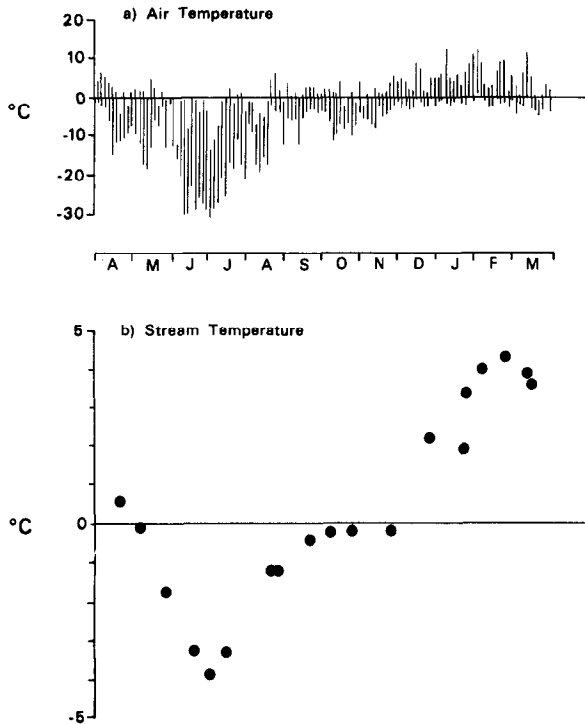


Fig. 5. Seasonal changes in a) air temperature and b) water temperature at stream site 23. Bars in a) represent the range of air temperatures over consecutive three day periods.

on transfer to sterile culture medium, yielded viable filaments of all three genera. A thermistor buried in the thick ice (30–50 cm) at site 23 showed a minimum temperature of only $-4\text{ }^{\circ}\text{C}$ (Fig. 5), while air temperatures fell to $-25\text{ }^{\circ}\text{C}$ or below over the same period. This minimum was reached shortly after stream freezing but by August, when 30 cm of snow had accumulated on the stream surface the temperature at the stream bed had risen to just below freezing point. Accumulation of snow and ice clearly offers very effective insulation.

The opening of the streams coincided with the melting of the winter snow accumulation in their catchments. Maximum stream depths were recorded at this time and flow velocities were high (categorised as 3–5) in all streams. Almost all of the thin, patchy cover of filamentous algae revealed during the melt was rapidly sloughed away by these high discharges. The subsequent pattern of stream depth (which is taken here to reflect discharge) was similar at all sites. Depth

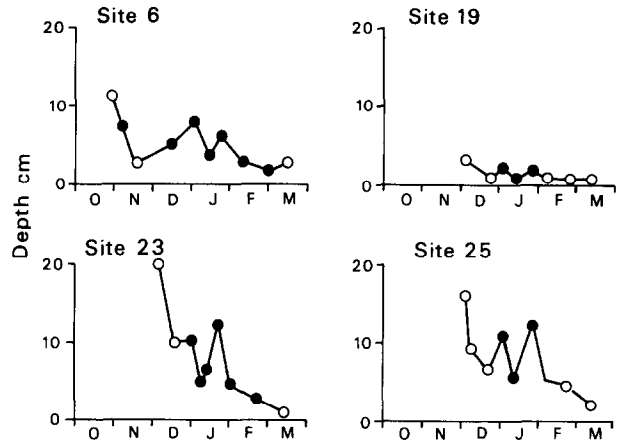


Fig. 6. Changes in stream depth at controlled locations in the four main study sites over the 1984/85 austral summer. Open symbols indicate the presence of surface ice on the transect at the time of sampling, closed symbols indicate no ice present.

tended to decrease gradually over the course of the summer, with peaks in early and late January (Fig. 6) associated with periods of high insolation. Liquid water was found on all sampling occasions, though surface ice was frequently encountered (Fig. 6).

Stream chemistry showed some temporal variation. Streams mainly comprising meltwater (e.g. site 19) were initially very dilute with nutrient concentrations, particularly TIN, tending to increase as the summer progressed (Fig. 7). At site 19, TIN rose from 58 to 616 mg m^{-3} from 3/1/85, to 14/3/85, while TDP rose from 0.5 to 2.5 mg m^{-3} . Streams initially comprising displaced lake water (e.g. sites 6 and 23) had relatively high nutrient concentrations which declined to lower, relatively stable, summer levels. Summer TDP concentrations in unenriched streams were relatively constant at around $1\text{--}2\text{ mg m}^{-3}$, with enriched site 6 considerably higher at 20 mg m^{-3} .

Increase in algal standing crop after the initial meltwater pulse was rapid. Both cover of filamentous algae and chlorophyll *a* showed similar patterns of increase, with maxima reached 2–2.5 months later (Figs. 8, 9). This maximum was towards the end of the summer at all but site 6, the outflow from nutrient-enriched Knob Lake, which began to flow in October and attained a

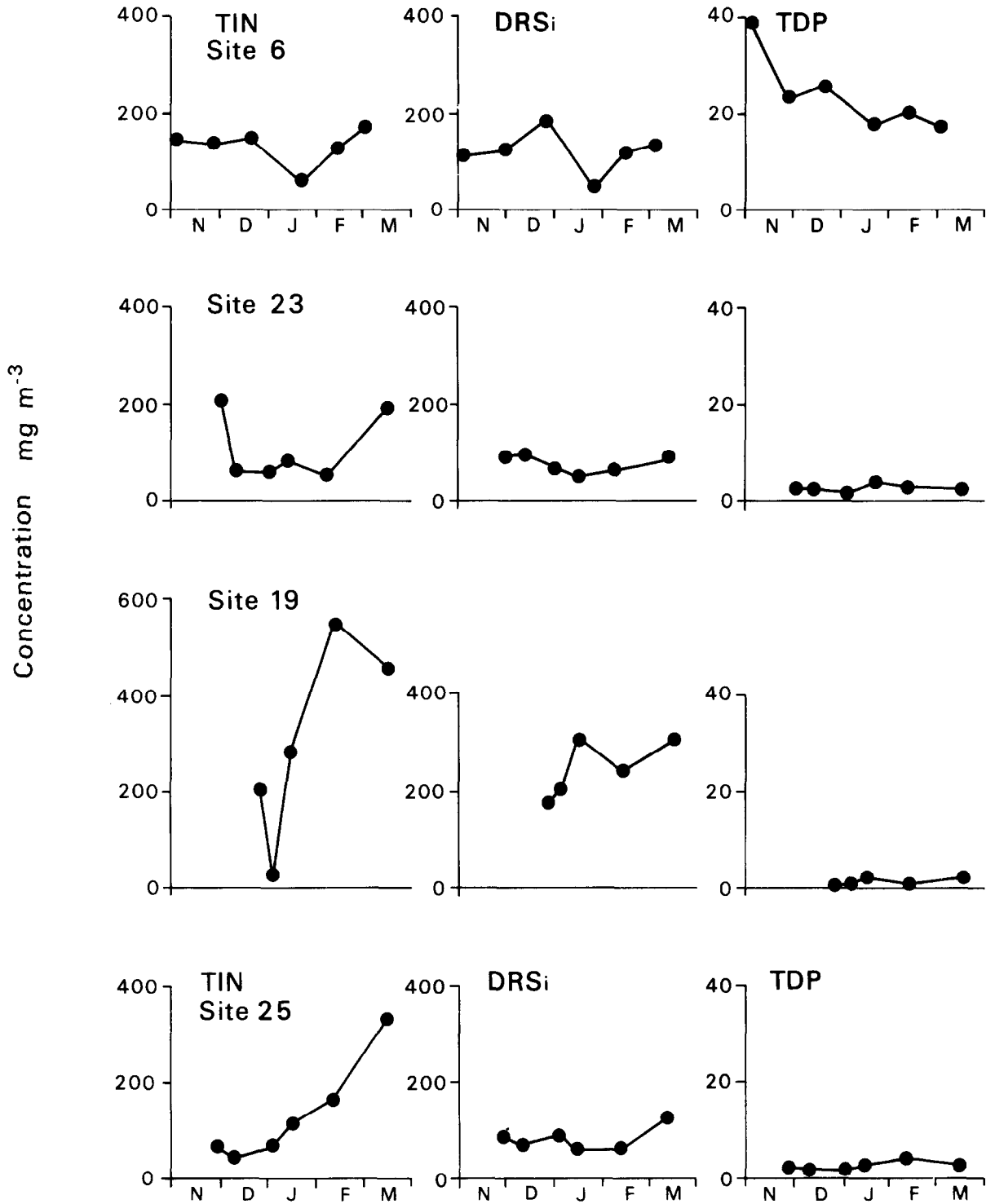


Fig. 7. Concentrations of total inorganic nitrogen (TIN), dissolved reactive silicate (DRSi) and total dissolved phosphorus (TDP) at main study sites during the 1984/85 austral summer. Each point is the mean of three determinations.

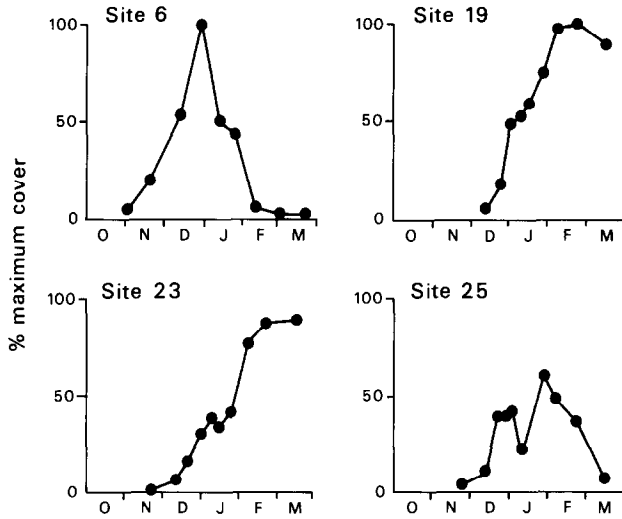


Fig. 8. Cover of filamentous algae at the four main study sites over the 1984/85 austral summer. Results are expressed as a percentage of the maximum observed cover at each site during the study period.

maximum algal standing crop, expressed both as cover of *Klebsormidium* and chlorophyll *a*, by late December. Early growth comprised *Klebsormidium* alone, but later, increasing amounts of *Phormidium* spp. began to overgrow the filamentous cover. By the end of December, long (> 30 cm), thick strands of algae were trailing in

the stream flow. The dramatic decline in algal cover in January (Fig. 8) was due to sloughing. It coincided with the loss of ice cover from the lake itself, and one of the periods of high discharge mentioned above. Wind induced turbulence in shallow Knob Lake (mean depth 1.2 m) resulted in increased suspensoids. This was incorporated into the *Klebsormidium/Phormidium* mat and large areas were seen to slough away. Little new development occurred after this loss.

At sites 19, 23 and 25, cover of filamentous algae increased at similar rates (Fig. 8), until most of the available substrate was occupied (Fig. 10). *Zygnema* was not found in the deeper, faster flowing runnels of site 19, and *Mougeotia* did not occur in areas of site 23 which were periodically exposed to the air (Fig. 10). This is consistent with the depth distributions identified by the Kolmogorov analysis. Chlorophyll *a* cover in the *Mougeotia* and *Zygnema* dominated streams did not attain such high levels as at site 6, but filamentous green algae in these streams were not subject to overgrowth by *Phormidium*. Sloughing losses were nonetheless evident in these streams, with clear checks to the steady increase of cover or declines in existing cover occurring during the two discharge peaks in early and late January (Fig. 6).

C : N and N : P ratios

A considerable range of C : N and N : P ratios was found in the complete set of algal samples from all 36 sites (Table 4). When the three genera were examined separately, *Klebsormidium* was found to show significantly lower ratios of both C : N and N : P than either *Mougeotia* and *Zygnema* (small sample 't-test', $p < 0.001$) while those of *Mougeotia* and *Zygnema* did not differ significantly from each other ($p > 0.05$). No significant correlation could be found between algal N : P and C : N ratios and any of the measured environmental variables. The crude categorisation of the current velocities of streams suggested that there was a tendency for C : N and N : P ratios to be lower in faster-flowing water than in slow (Table 5). This applied both when the complete set of samples was considered together and when the genera were examined separately.

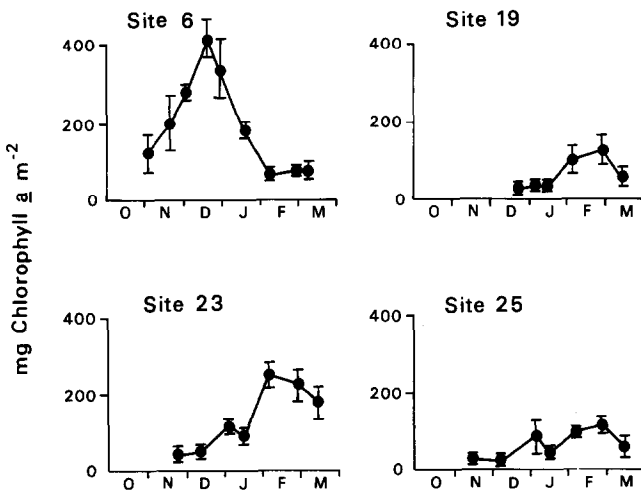


Fig. 9. Areal concentration of chlorophyll-*a* at the four main study sites during the 1984/85 summer. Bars represent means \pm 95% confidence limits ($n = 5$).

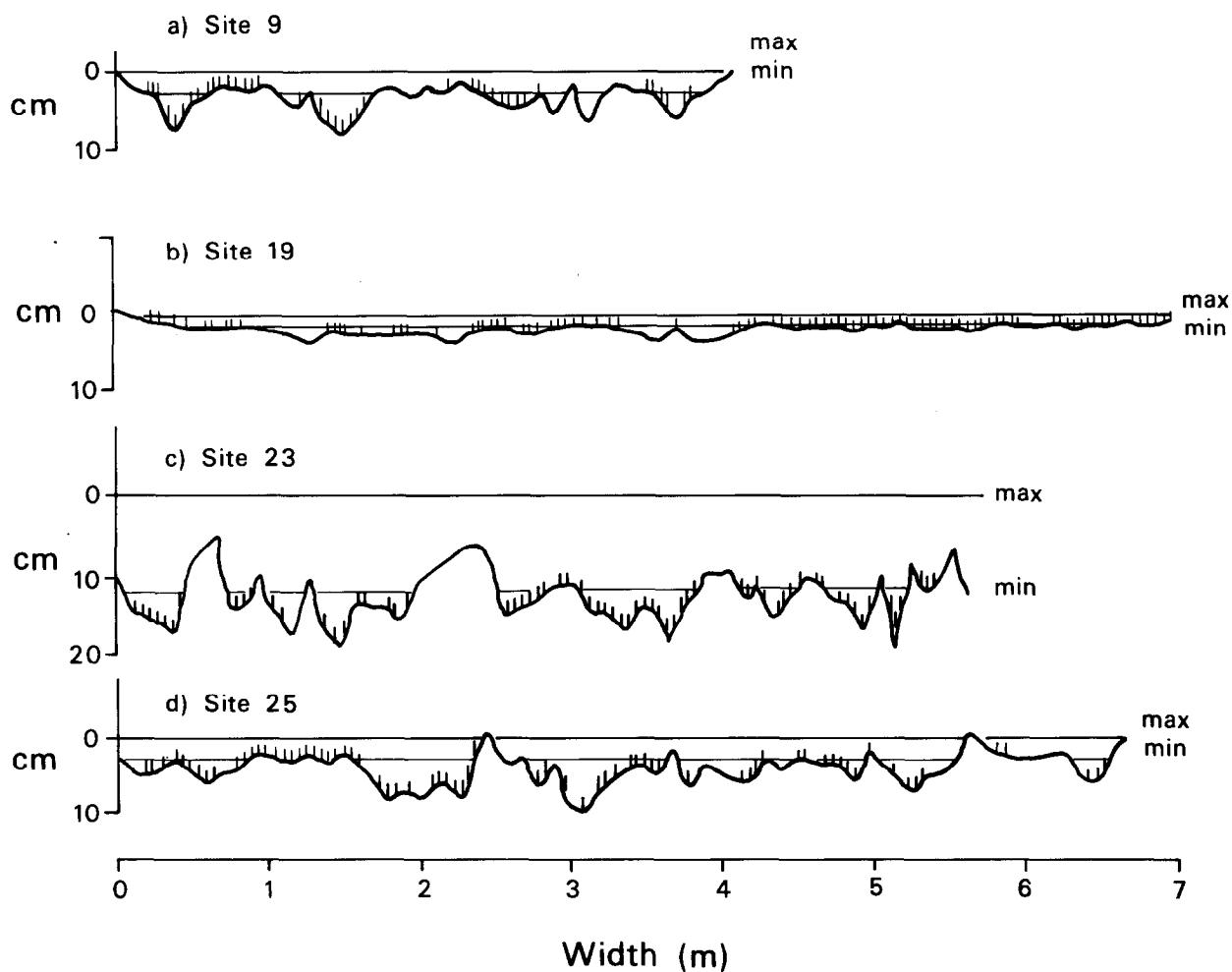


Fig. 10. Transects across the four main study sites to show minimum and maximum water levels. Vertical bars indicate the maximum extent of filamentous algal coverage. Depths were measured at 10 cm intervals and the presence or absence of filaments every 5 cm.

Table 4. C : N and N : P ratios of stream algal samples.

	C : N			N : P		
	Mean	Range	n	Mean	Range	n
All samples	16.3	5.6–20.6	55	12.3	4.4–22.1	42
<i>Zygnema</i>	12.4	8.9–20.6	22	12.7	6.0–22.1	14
<i>Mougeotia</i>	13.3	10.1–19.5	24	14.7	6.6–20.9	19
<i>Klebsormidium</i>	7.6	5.6–11.9	9	6.5	4.4– 8.9	9

Table 5. C : N and N : P ratios in algal samples taken from streams with different current velocities. Velocity was estimated visually on a scale of 1–5.

Current Velocity	C : N			N : P		
	Mean	Range	n	Mean	Range	n
1	20.6	–	1	15.8	–	0
2	13.4	10.1–19.5	21	14.2	7.6–22.1	18
3	11.3	5.6–15.7	23	10.9	5.4–17.9	15
4	8.9	6.5–13.2	10	9.9	5.6–14.7	10
5	–	–	0	–	–	0

Seasonal as well as spatial differences in elemental composition were seen. Those at site 23 are shown in Table 6. C : N and N : P ratios increased in late summer as stream depth and discharge rates declined, despite increasing nutrient concentrations.

Discussion

Freshwater lakes at Signy Island are assumed to be typical of the maritime Antarctic. This assumption is based on considerations of climate and the scant information available on other maritime Antarctic freshwater ecosystems (see review by Heywood, 1978). If Signy Island streams are also typical of the maritime Antarctic climatic zone, it seems there are major physical and biological differences between these and the streams of continental Antarctica for which relatively comprehensive information is now available (Howard-Williams *et al.*, 1986; Vincent & Howard-Williams, 1986).

Table 6. C : N and C : P ratios in samples of *Mougeotia* from site 23 over the course of the 1984/85 austral summer. Each point represents the mean of 3 replicates.

Date	C : N	N : P	C : P
11/12/84	10.7	24.4	261
3/01/85	12.3	15.9	196
16/01/85	15.1	15.3	231
8/02/85	12.5	16.5	206
28/01/85	16.9	19.6	331
2/03/85	17.2	25.0	430

Physical differences are consistent with the climatic differences between the two areas. Higher air temperatures allow maritime Antarctic streams to flow for longer than continental ones, typically 4 to 5 compared to 1 to 2 months, although water temperatures are similar. Relatively high precipitation (Signy Island received 230 mm water equivalent in 1984 – D. Limbert pers. comm.) permits extensive winter snow accumulation in maritime Antarctica, which has two important effects. Firstly, it insulates streams from the low winter air temperatures and secondly, it permits very high discharges of melt-water to accumulate during the first flows of spring (see also Hawes, 1983). This contrasts with continental Antarctica, where there is little snow accumulation and frozen streams often ablate over winter, leaving a freeze-dried periphyton exposed to air temperatures down to -55°C (Howard-Williams *et al.*, 1986).

The pattern of discharge seen in the four main study streams, where a spring peak declines over the course of summer, is essentially similar to that of Arctic streams (Harper, 1981). These spring flushes can be very abrasive (Stockner & Hynes, 1976) and at Signy Island clear much of the existing benthic flora, particularly the filamentous chlorophytes, from the stream bed. Catastrophic effects of high flow rates on periphyton are frequently recorded (e.g. Wehr, 1981). Filamentous algae appear to be particularly susceptible (McIntire, 1966; Antoine & Benson-Evans, 1982). In the absence of grazers, sloughing would appear to be the only important source of loss of periphyton from Signy Island streams. The

compounding effect of heavy overgrowth with epiphytes was clearly seen in stream 9, which drained Knob Lake. This is consistent with one of the ideas from the river continuum concept (Vannote *et al.*, 1980), which proposes that stream ecosystems are in a continual state of change along temporal and spatial axes, never attaining the sort of climax communities seen in terrestrial ecosystems.

The seasonality of growth of filamentous algae in Signy Island streams stems from this 're-setting' of the environment in spring each year. Such re-setting events favour the dominance of a periphyton which is capable of rapidly attaining high cover at low temperatures, a role which filamentous chlorophytes appear to fill at Signy Island. Similar communities have been found in cold, fast-flowing streams in northern Scandinavia (Round, 1981). Moore (1974a, b) noted a similar seasonality in periphyton growth in a detailed study of three streams in the Canadian Arctic, with maximum standing crop developing towards the end of the period of flow. Although he found diatoms and cyanobacteria to be the dominant groups, he also reported *Zygnema* and *Mougeotia* as locally abundant.

This essentially annual pattern of development contrasts with the situation in continental Antarctic streams where there is extensive overwinter survival and little development of new biomass over the summer period (Howard-Williams *et al.*, 1986). It should be noted that these last authors have assumed, in calculating survival rates, that all chlorophyll *a* extracted from stream bed mats is viable. Such an assumption is not necessarily valid considering the low production:biomass ratios they report, and the near ideal conditions for preservation of dead material which exist in freeze dried continental streams during winter. While lush growths of trailing, filamentous algae can occur in continental streams, the biomass is usually dominated by cyanophytes (Hirano, 1965; Broady, 1982, 1984, 1985; Howard-Williams *et al.*, 1986; Howard-Williams & Vincent, 1987). The persistence of these perennial cyanophyte populations, in contrast to the fast growing annuals of Signy Island, may rest on the

absence of a scouring spring re-setting event. There is little winter snow accumulation in the catchments of continental streams and discharges usually, but not always, build up gradually to a mid-summer peak (Chinn, 1981).

Standing crops of periphyton (as chlorophyll *a*) in Signy Island streams are similar to those in the continental Antarctic streams ($2-40 \mu\text{g cm}^{-2}$; Howard-Williams *et al.*, 1986), with the proviso noted above that all chlorophyll-*a* may not be viable in the latter. Chlorophyll data is not available for the Arctic streams studied by Moore (1974a, b), but, if a dry weight to chlorophyll-*a* conversion factor of 50:1 is assumed (Hawes, unpublished data), similar standing crops were present. These biomasses are similar to those attained in temperate streams (e.g. Wehr, 1981; Round, 1981) so over the course of the summer temperature does not appear to adversely affect the total amount of biomass produced. However, Antarctic algae have been found to be consistently operating below their optimum temperatures (Seaburg *et al.*, 1981; Vincent and Vincent, 1982; Tilzer *et al.*, 1986) and it is likely that temperature will impose an upper limit to the rate at which this biomass is attained.

Nutrients, particularly P, have been implicated in limiting the productivity of the phytoplankton in Signy Island lakes (Hawes, 1983). Nutrient availability may be similarly important to filamentous algae, particularly in the nutrient-poor meltwater streams. Nutrient limitation of periphyton in streams is more difficult to demonstrate as it is complicated by the need to consider discharge as well as nutrient concentration (Whitford & Schumacher, 1964; Lock & John, 1979). Identification of nutrient limitation in lentic algae has usually involved fabricated experimental channels (Wurhman & Eichenberger, 1975; Krewer & Holm, 1982) or extensive perturbations of natural communities (Petersen *et al.*, 1983). In this study, the intracellular concentrations of C, N and P have been used to identify changes in the nutritional status of the algae. This approach was made possible by the tendency of the filamentous algae to occur in dense, mono-generic stands. Significant inter-generic differences were appar-

ent. Increasing ratios of C : N and N : P were taken as evidence of increasing deficiency of N and P respectively with C : N and N : P ratios of around 10–15 frequently thought to indicate balanced nutrient supply (Droop, 1973; Rhee, 1978; Senft, 1978; Goldman *et al.*, 1979; Tett *et al.*, 1985).

Ratios recorded in algae from Signy Island streams suggest that, for the most part, neither N nor P is particularly limiting. The low ratio of N : P in *Klebsormidium*, growing in P-rich streams, suggests that, if any nutrient were to be limiting, it is more likely to be N than P. P enrichment at Signy Island is associated with the activity of seals and sea-birds and is confined to low-lying coastal areas (Hawes, 1983). Low concentrations of TDP in many upland meltwater streams (e.g. site 19) led to relatively high N : P ratios in stream water and would be consistent with potential P limitation as indicated by high N : P ratios in some *Mougeotia* and *Zygnema* samples from such streams. Unlike some recent reports (e.g. Gibson & Whitton, 1987), no statistically significant relationships were found between ambient nutrient concentrations and algal N : P ratios. High current velocity was statistically more important in maintaining a low N : P ratio. It is likely that declining current velocity was responsible for the increase in algal N : P ratio at site 22 as the summer season progressed as dissolved nutrient concentrations did not show any marked decrease.

Care must be taken in interpreting statistical relationships. The techniques used here for sampling and analysis did not permit causative relationships to be established. Samples of algae and water were taken at the same, discrete time, from environments known to be temporally variable. This variation could mask real relationships where they develop over long time scales. Inter-correlation of variables which were not measured with those that were could also lead to erroneous identification of ecologically important variables. This criticism applies both to intra- and inter-stream comparisons. While it appeared that *Klebsormidium* was absent from the streams with lowest TDP concentrations, both this and the apparent relationship between the distribution of

Mougeotia and *Zygnema* and depth potentially represents the effects of a number of other variables. In the latter case, current speed, substrate type, winter temperatures and frequency of summer freezing or drying may be particularly important.

Conclusions

The variables which have been identified as important in determining the spatial and temporal distributions of the three genera of filamentous chlorophytes are essentially the same as those important in streams in any other geographical location. However, maritime Antarctic streams can be characterised by their particular combination of these variables:

1. Barren catchments, giving low concentrations of dissolved nutrients, particularly phosphorus, except where enriched by seal or seabird activity.
2. Consistently low temperatures during the short (3 to 5 month) period of flow.
3. Variable discharge with periodic freezing and drying during the period of flow.
4. Prolonged winter freezing under sometimes thick snow cover.
5. Spring discharge maxima associated with snow-melt.
6. Absence of invertebrate grazers.
7. Highly seasonal vegetation, predominantly algal, with filamentous chlorophytes often abundant, and a single standing crop maximum in mid-summer.

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