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The Seasonal Dynamics of *Spirogyra* in a Shallow, Maritime Antarctic Lake

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Summary. The filamentous chlorophyte *Spirogyra* forms a mat covering extensive areas of Spirogyra Lake, a small, shallow, Antarctic lake. It has an annual growth pattern, with a maximum standing crop of 400 μg chlorophyll-*a* m^{-2} during the ice-free summer period. Nutrient concentrations were low and there was evidence for P-limitation. The attainment of such a high standing crop was probably dependent on the lake's high specific dilution rate. Radiation flux was very low under winter ice cover and *Spirogyra* died back almost completely. The lake water became hypoxic and inorganic nutrients accumulated in both the water column and overwintering algal filaments. Spore formation was not observed, but changes in the composition of filaments indicated that polysaccharides, which had accumulated in summer, were depleted over the long, ice-covered winter period.

Introduction

Signy Island (60°43′S 45°38′W) lies at the northern limit of the Weddell Sea and forms part of the northern maritime Antarctic climatic zone (Smith 1984). There are 17 freshwater lakes on the island, all of which are small and shallow. They are typically clear and oligotrophic, with a poorly developed phytoplankton, but support extensive benthic populations of algae and/or aquatic mosses (Priddle 1980a). Ice cover, which persists for 8–12 months each year and attains a thickness of 1–2 m, has a profound influence on the environment within these lakes, by compounding the already high annual variation in incident radiation flux and sealing the lake water from inflows, outflows and atmospheric gas exchange.

Different components of the benthic flora have different responses to the constraints that ice cover imposes. Aquatic mosses and cyanophyte-based felts are perennial and undergo little change in biomass over the annual cycle. They are extremely shade-adapted and able to maintain net photosynthesis through most of the winter period, but their rate of photosynthesis is consequently light saturated at very low levels and they are unable to exploit the relatively high radiation fluxes prevalent during open water (Priddle 1980a, b). Conversely, filamentous chlorophytes, notably species of *Spirogyra*, adopt an annual growth strategy, dying back during winter and growing rapidly during spring and summer (Heywood et al. 1980; Priddle 1980a).

This paper investigates the changes occurring in a population of the annual filamentous alga *Spirogyra* (Chlorophyta) in Spirogyra Lake, Signy Island, over an annual cycle. It investigates the inter-relationships between physical and chemical features of the lake and changes in algal standing crop, composition and physiology. The predominance of this alga in Spirogyra Lake, where it occurs as a dense, unialgal mat, devoid of epiphytes, makes it particularly suitable for this type of autecological study.

Study Site

Spirogyra Lake is situated on the west coast of Signy Island at a height of 25 m above sea level (Fig. 1). It is small and shallow with a mean depth of only 0.85 m. It has a surface area of ca. 3500 m^2 and a volume of ca. 3000 m^3 (Fig. 1). The lake comprises a shallow, rocky shelf zone which extends around most of the shoreline and has a patchy covering of an algal mat based on the cyanophyte genus *Phormidium*. Much of this shelf, which represents approximately 65% of lake area, freezes during winter, when ice attains a thickness of approximately 1 m. The shelf falls steeply to a flat, sediment-covered trough area, sufficiently deep (2–3 m) to avoid winter freezing. *Spirogyra* occurs as dense clumps overlying much of the sediment in this trough region. Where it is found on the shelf slope it overlies patches of sediment and is not attached to rocks. It is not found in areas of the lake which freeze during winter and does not form

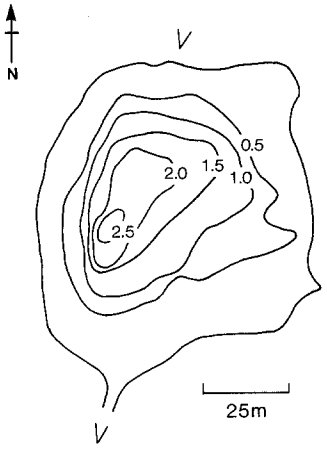

Fig. 1. Bathymetric map of Spirogyra Lake. The countour interval is 0.5 m and *arrows* mark the main inflow and outflow

floating scums. There is no perennial vegetation in the trough and, as in other Signy Island lakes, there is no floating or emergent vegetation, fish, molluscs or insects.

The catchment has an area of 21.6 ha and comprises permanent snowfields and extensive areas of scree and unconsolidated glacial till. It is poorly vegetated with isolated clumps of moss and lichen. The only sources of biotic enrichment are a few giant petrels (*Macronectes giganteus*) and terns (*Sterna vittata*) which nest in the area. The main inflow is wide, shallow and slow flowing and has deposited a well defined alluvial fan where it enters the northern end of the lake. Clumps of a species of *Zygnema*, washed in from the inflow, grow on this fan. The outflow at the southern end is rocky and follows a well defined channel. *Spirogyra* is not found in the inflow or outflow.

Methods

1 Collection and Analysis of Water Samples

Water samples were collected in acid-washed, opaque, 500 ml polypropylene bottles. During summer open water they were collected from immediately beneath the surface after wading out as far as possible. Under winter ice cover, samples were pumped through a hole in the ice from the required depth using a "Whale Gusher" diaphragm pump. Bottles were rinsed three times and filled to exclude air. A separate sample was taken in a 125 ml polythene bottle for pH and alkalinity determination. Samples were returned to the laboratory in an insulated box.

The sample for pH measurement was equilibrated to 5 °C in a cooled water bath and pH determined to 0.01 units with a Pye Unicam PW9409 pH meter. The alkalinity of the same sample was then determined by Gran titration (Talling 1973). The sample for chemical analysis was passed through a GF/C filter and analysed for nitrate, ammonia, filtrable reactive phosphate (FRP) and total filtrable phosphorus (TFP). Nitrate was determined according to Morries (1971) and ammonia according to Chaney and Marbach (1962). FRP and TFP were determined using methods described in Eisenreich et al. (1975).

2 Oxygen, Temperature and Light

Oxygen concentrations and temperatures were measured in situ using a Y. S. I. model 57 oxygen meter equipped with a polarographic probe and stirrer. Penetration of light through ice cover was measured using a selenium photocell (Dawson 1981) with a wavelength response corrected with filters to approximate to PAR (photosynthetically available radiation). The corrected cell was calibrated against a PAR quantum sensor (Llambda Instruments). During winter, a 2 m cantilever arm (after Light et al. 1981) was used to position this sensor away from the abnormal radiation climate close to the sampling hole. Incident radiation was measured using a Kipp and Zonen solarimeter recording onto a Grant Instruments CR50 data logger. Readings from these two types of sensor are not directly comparable but approximate interconversions can be made using the relationship 1 W m^{-2} = 4.66 µmol photons m^{-2} s^{-1} (Richardson et al. 1983).

3 Water Turnover

The large area of catchment in proportion to lake volume suggested that water turnover within the lake could be rapid. To assess this, dilution gauging of the outflow was undertaken at intervals through the summer, using methods described by Church (1975).

4 Standing Crop Estimates

A sampling grid was laid out on the floor of the trough using two, 20 m lines marked at 1 m intervals and positioned 3 m apart. On each sampling occasion, the cover of filamentous algae within the delimited zone was estimated by SCUBA divers.

Quantitive estimates of the standing crop of filamentous algae, as chlorophyll-*a*, were made on cores taken from randomly selected 1 m squares within the grid. The corers comprised sharpened aluminium tubes, of open area 53.1 cm, which could be sealed at both ends with plastic caps after insertion into the sediment. One cap had a pinprick hole to permit pressure equilibration. On return to the laboratory, the filamentous algae were removed from the top of the core, blotted dry and frozen to −20 °C overnight. They were subsequently extracted into 95% methanol for chlorophyll-*a* estimation. Prior freezing of cells has been found to increase chlorophyll-*a* extraction efficiency (Marker 1980). Phaeopigments in the extract were estimated by acidification with dilute hydrochloric acid for 2 min followed by neutralisation with ethanolamine (Marker et al. 1980). The equations given by Marker et al. (1980) were used throughout.

5 Collection and Analysis of Algal Samples

Algal samples were collected by SCUBA divers. Filaments were sucked into a wide bore 60 ml catheter syringe and injected into a 1 litre glass jar. The lid of the jar was drilled to fit the syringe tip, while an additional series of small holes permitted water to exit but retained filaments. On return to the laboratory, filaments were rinsed three times with filtrable lake water. Subsamples were taken for direct observation, analysis of C N and P content and lipid/carbohydrate analysis.

Subsamples for C, N, P analysis were dried at 105 °C in acid washed, snap-cap vials then frozen for −40 °C for transport to the U. K. In the U. K., C and N were estimated using a Carlo-Erba 1106 CHN analyser. P was estimated as FRP (Bartlett 1959) following digestion for 30 min at 180 °C with 800 µl 72% perchloric acid of a weighed subsample containing approximately 0.1 µmol P.

Samples for lipid/carbohydrate analysis were frozen fresh to −70 °C and returned to the U. K. There they were divided into three weighed subsamples and treated as follows:

a) Storage carbohydrates. Dried at 105 °C to establish a wet weight: dry weight conversion then extracted in 5 ml 10% trichloroacetic acid (TCA) at 100 °C for 30 min. This converted storage carbohydrates to soluble sugars which were then estimated using the Phenol-sulphuric acid technique of Dubois et al. (1956).

b) Sugars. Extracted into cold (4 °C) 70% ethanol for 12 h following ultrasonication in an MSE Soniprep 150 ultrasonic disintegrator for 5 min at 75% power. Triplicate subsamples of the extract were analysed for sugars using the Dubois et al. (1956) technique.

c) Lipids. Extracted into 24 ml 2:1 (by volume) methanol:chloroform mixture, using 5 min of ultrasonication, filtered (GF/A) and washed through with a further 8 ml chloroform. Water was then added to give

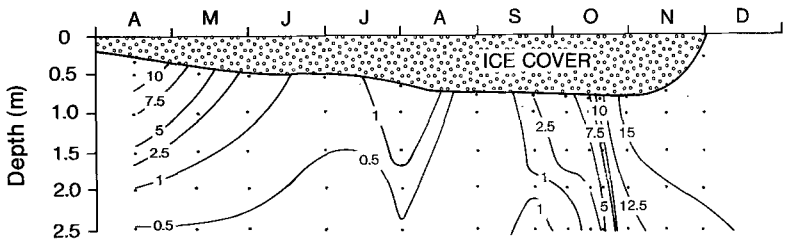

Fig. 2. Concentration of dissolved oxygen (g m^{-3}) under winter ice of Spirogyra Lake during 1984. Ice cover is shown *stippled*

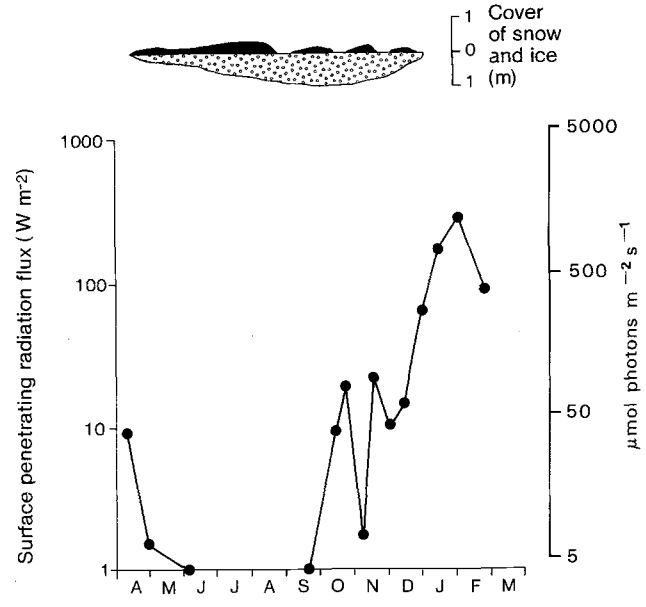

Fig. 3. Seasonal variation of surface penetrating radiation flux (total short-wave radiation – not PAR) in Spirogyra Lake during 1984/1985. Note logarithimic scale. The right-hand vertical scale shows estimated quantum flux using a conversion of 1 W m^{-2} = 4.66 µmol photons m^{-2} s^{-1}. From May to September the flux was below instrumental limit of detection (1 W m^{-2}). Snow (*black*) and ice (*stippled*) are shown above

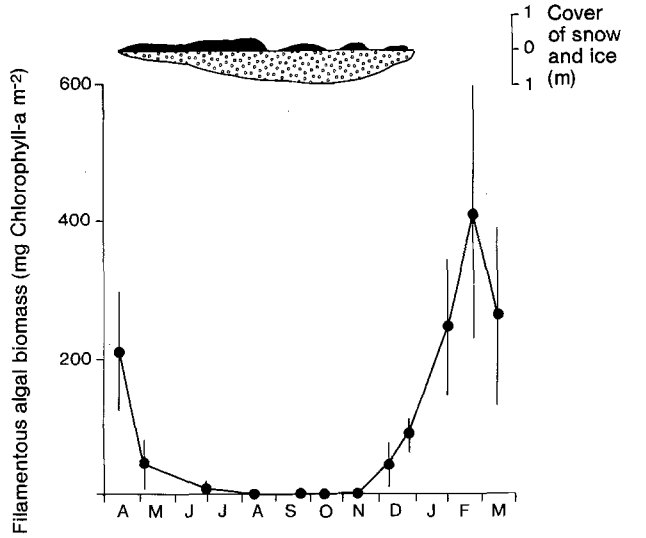

Fig. 4. Seasonal variation of chlorophyll-*a* amount at the trough sampling site. Snow (*black*) and ice (*stippled*) are shown above

a final content of 14.4 ml. After allowing to seperate overnight, the lower layer (chloroform) was removed and evaporated in a rotary evaporator at 45 °C to near dryness. After making up to 1 ml, duplicate aliquots containing approximately 50 µg lipid were evaporated to dryness, in test tubes, under a stream of nitrogen gas and the lipid content estimated by the reduction of dichromate in concentrated sulphuric acid (Amenta 1964). Cod liver oil was used as a lipid standard.

6 Photosynthesis

In situ photosynthesis incubations were not carried out. Instead, a light gradient incubator was constructed using "cool white" fluorescent tubes and neutral density filters. It was maintained at 5 °C and provided a range of five photon flux densities from 3.4 to 500 µmol photon m^{-2} s^{-1}. Photosynthesis was estimated using a 14-C method derived from that of Lewis et al. (1982). Small samples (approximately 10 mg dry weight) of fresh filaments were placed in 25.0 ml filtrable lake water in polycarbonate, screw-cap bottles with 2 µCi of 14-C bicarbonate (Amersham International) for 10–60 min. Three to five replicate incubations were made at each light level. Incubation was terminated by rapid filtration (GF/C - less than 5 s). After rinsing with 25 ml filtrable lake water, the algae were removed and dried at 105 °C, weighed and digested in conc. nitric acid for 3 h at room temperature. 0.5 ml of digest was mixed with 4.5 ml 0.75 M tris buffer. 1.0 ml of this mixture was dissolved in 10 ml Insta-Gel liquid scintillation fluid (Packard) and counted in a Nuclear Enterprises model 6500 scintillation counter. Photosynthetic rate was calculated as carbon fixed per unit dry weight (mg g^{-1} h^{-1}).

Results

The annual cycle in Spirogyra Lake can be divided into three phases, with a short spring period (November through mid-December) marking the transition from winter (April through October) to summer (mid-December through March).

Table 1. Nutrient chemistry of Spirogyra Lake. TIN = total filtrable inorganic nitrogen; FRP = filtrable reactive phosphorus; TFP = total filtrable phosphorus. All values are µg l^{-1}. N:P ratio is calculated from TIN and TFP

Date	Depth	TIN	FRP	TFP	N:P ratio (atoms)
26 April 1984	2.0 m	286	1.9	7.8	81.3
11 Sept. 1984	2.0 m	306	94.5	108.9	6.2
11 Oct. 1984	2.0 m	145	6.2	14.0	23.0
27 Oct. 1984	2.0 m	54	4.6	27.5	4.4
26 Nov. 1984	2.0 m	48	0.8	2.2	48.3
03 Jan. 1985	0.1 m	102	1.2	1.6	141.3
18 Feb. 1985	0.1 m	305	0.6	5.2	130.0
14 March 1985	0.1 m	632	1.2	2.5	560.2

Winter

During winter, the inflow and outflow ceased to flow and ice cover sealed the lake from atmospheric gas exchange. Within three months of the onset of ice cover, the lake had become anoxic (Fig. 2). Up to September, nutrients accumulated within the water column, particularly TFP, which resulted in a low atomic ratio of N:P in the water column (6.2 – Table 1). Very low levels of radiation were present beneath the thick layers of ice and snow (Fig. 3).

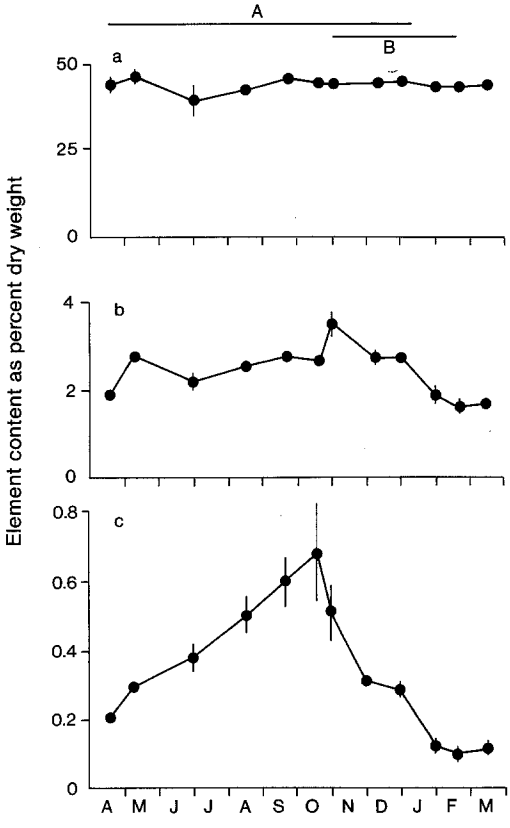

Fig. 5a–c. Elemental composition of *Spirogyra* from Spirogyra Lake during 1984/1985. **a** Carbon, **b** Nitrogen, **c** Phosphorus. Points are the means of 3–5 replicates, *bars* indicate 95% confidence interval. *Horizontal bars A and B* represent duration of ice cover and the period of biomass increase, respectively

Table 2. Photosynthetic characteristics of *Spirogyra* populations from Spirogyra Lake at different times of year. P_{max} is the light saturated rate of photosynthesis, as rate of carbon uptake per unit dry weight and I_k the radiation flux where an extension of the radiation-dependant portion of the photosynthesis/irradiance curve intercepts P_{max}

Date	I_k µmol photons $m^{-2} s^{-1}$	P_{max} µg $mg^{-1} h^{-1}$
20 April 1984	90	3.1
26 July 1984	100	0.8
09 Dec. 1984	100	17.2
31 Jan. 1985	110	13.1
23 Feb. 1985	90	11.6
16 March 1985	95	4.4

Between June and September, radiation fluxes were below the limits of detection (1 W m^{-2}). The temperature was consistently less than 1 °C.

Under ice cover, algal biomass declined rapidly (Fig. 4), though isolated clumps of algae, containing viable vegetative cells, could be found year-round. Viable cells were found throughout the unfrozen area of the lake trough but were most frequently found on patches of sediment among the rocks of the shelf slope. No spore formation of any kind was observed.

Over-wintering algae were found to accumulate N and P from the nutrient-rich water (Fig. 5). P content rose from 0.2% at the onset of ice cover to 0.7% by mid October. N content rose only slightly from 2 to 3.5% and C content was constant at 40–45% all winter. Atomic ratios of C:N:P in October were 178:9:1. While the total C content remained constant, the relative proportion of lipid and carbohydrates within the cells varied over winter. Hot TCA-soluble carbohydrate declined from 20 to approximately 5% dry weight (Fig. 6). Lipid, on the other hand showed no similar reduction, remaining constant at around 15% dry weight, slightly higher than the value on ice formation. Cold-soluble sugars also rose slightly after ice formation and remained constant over the winter at around 10% dry weight.

The relationship between radiation flux and photosynthesis (P vs I curve) followed the widely recognised curvilinear pattern (Fig. 7), from which the two parameters I_k and P_{max} can be estimated (Harris 1978). P_{max} is defined as the light-saturated photosynthetic rate (here

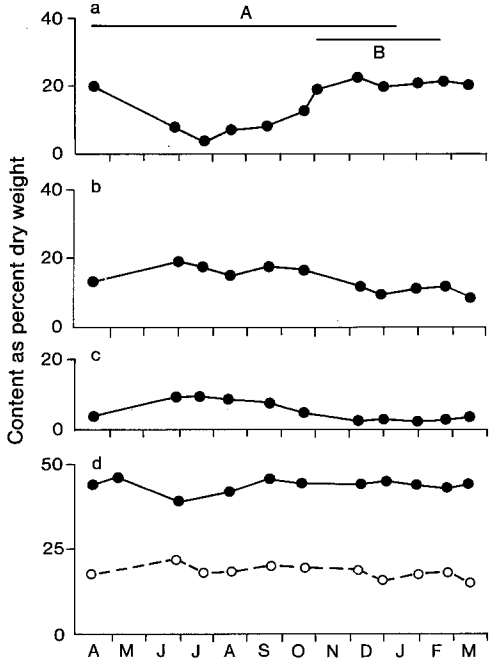

Fig. 6a–d. Carbohydrate and lipid content of *Spirogyra* from Spirogyra Lake during 1984/1985. **a** Polysaccharide, **b** Lipid, **c** Sugars. **d** shows total cell carbon (●———●) and lipid+carbohydrate carbon (○– – –○). *Horizontal bars A and B* represent duration of ice cover and the period of biomass increase, respectively

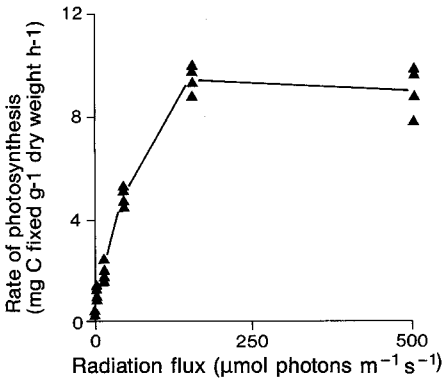

Fig. 7. The relationship between weight-specific photosynthetic rate of *Spirogyra* at 5 °C and radiation flux on 23 Feb. 1985

expressed on a dry weight basis) and I_k, the radiation flux at which an extension of the light dependent portion of the P vs I curve intersects P_{max}. The I_k of the winter sample (July) was high at 100 µmol photons m^{-2} h^{-1} (Table 2). Using a conversion of 1 W m^{-2} to 4.66 µmol photons m^{-2} h^{-1}, this equates to 21 W m^{-2}, greatly in excess of in situ values at this time (Fig. 3). P_{max} was the lowest recorded during the study at 0.8 mg C g^{-1} dry weight h^{-1}.

Spring

Two events marked the end of Winter, the opening of the inflow and outflow and the increase of radiation within the lake. During spring, specific dilution rates were high giving a residence time of only 1.3 days (Table 3). Much of this initial flow was occurring under the melting snowpack and was not accessible for sampling. It is likely that it was as nutrient-poor as later inflowing water (Table 4) and that it was the inflow of dilute meltwater which drastically reduced nutrient concentrations within the lake (Table 1) and reoxygenated the water column (Fig. 3).

Mean daily radiation levels began to increase in late October and remained at 10–20 W m^{-2} (equivalent to 50–100 µmol photons m^{-2} s^{-1}) for most of November and December (Fig. 3). Algal standing crop began to increase shortly afterwards and by the end of November, had reached detectable levels (Fig. 4). As the standing crop increased, so the N and P contents fell (Fig. 5). At the same time, hot TCA-soluble carbohydrates accumulated within the population, while lipids and cold-soluble sugars declined (Fig. 6). P_{max} measured on 9 Dec. 1984 was the highest value recorded in the study, though I_k was similar to the winter value.

Summer

Ice cover was lost at the beginning of January. This marked the beginning of a period of high radiation fluxes during which maximum standing crop of filamentous algae was attained (Figs. 3 and 4). TFP concentrations were low in both inflow and lake water, while TIN concentrations increased resulting in a dramatic rise in lake water N:P atomic ratios over winter levels, to a maximum of 560. Strong wind mixing ensured that the lake remained isothermal, with the maximum temperature recorded in February at 4 °C. The lake was fully oxygenated.

During the summer period, hot TCA-soluble carbohydrates reached their maximum of 20% dry weight. Cold-soluble sugars and lipids were at their minima of 2 and 10%, respectively. However, if the C content of lipid is taken as 77% and of carbohydrates as 40% by weight, the total lipid+carbohydrate carbon was found to be similar at approximately 20% dry weight throughout the year (Fig. 6). The decline in N and P content which began in spring continued and maximum biomass was associated with minimum algal P and N contents (0.1% and 1.8% dry weight, respectively). C content was constant at 40%–45% dry weight. Atomic C:N:P ratios in February 1985 were 1174:38:1.

Spirogyra growing in open water had a lower chlorophyll-*a* content than that which had developed under spring ice cover. In November, chlorophyll-*a* represented 1.1% dry weight whereas by late February this had fallen to only 0.4%. This fall was associated with changes in the relative sizes of the chloroplasts and could be visualised as tighter coiling of the spiral. The November samples had an average of 3.7 turns per 100 µm and the February sample 2.4 turns per 100 µm.

P_{max} fell from the spring maximum over the course of the summer, but values remained higher than in winter (Table 2). I_k remained similar to spring and winter levels throughout.

Table 3. Specific dilution rate and water residence time of Spirogyra Lake. Calculated from dilution gauging of outflow and lake volume

Date	Specific dilution rate	Residence time (days)
23 Nov. 1984	0.78	1.3
07 Jan. 1985	0.24	4.2
10 Feb. 1985	0.37	2.7
12 March 1985	0.14	7.1

Table 4. Concentrations of nitrogen and phosphorus in the inflow to Spirogyra lake. TIN = total filtrable inorganic nitrogen; FRP = filtrable reactive phosphorus; TFP = total filtrable phosphorus. All values are µg l^{-1}. Atomic N:P ratio is calculated from TIN and TFP

Date	TIN	FRP	TFP	N:P ratio
03 Oct. 1985	59	0.8	1.1	120
15 Jan. 1985	406	0.6	1.6	562
10 Feb. 1985	897	0.4	0.9	2208
14 March 1985	748	1.2	3.2	518

Discussion

Antarctic lakes have been described as simple ecosystems: natural laboratories, readily amenable to study due to low

species diversity, restricted environmental variables and short food chains (Heywood 1977). In many ways, Spirogyra Lake fits this description. The dominant vegetation is a monospecific stand of *Spirogyra*, which is neither grazed by the invertebrate fauna nor colonised by epiphytes. During the summer growth period, nutrient concentrations were consistently low and temperature fluctuated over only 4 °C during the complete annual cycle. Radiation flux was the variable to show most seasonal variation and the growth cycle of *Spirogyra* appeared to closely follow these changes. The unimodal growth pattern which ensued is typical of polar annuals (notably phytoplankton – Kalff and Welch 1974; Priddle et al. 1986). It was only during winter that extreme conditions existed within the lake, when cells had to survive long periods of near darkness and hypoxia.

Standing Crop and Photosynthesis

Using the summer chlorophyll-*a* content of 0.4% dry weight, the maximum standing crop of 400 mg chlorophyll-*a* m^{-2} in Spirogyra Lake equates to approximately 100 g dry weight m^{-2}. This biomass approaches the maximum areal chlorophyll-*a* concentrations attainable under natural conditions pedicted by Steeman Nielsen (1962), of 400 – 800 mg m^{-2} from considerations of light attenuation by self-shading. It is comparable to values reported for similar communities in temperate regions. McCracken et al. (1974) found a maximum standing crop of *Oedogonium* of 45 g m^{-2} in a Wisconsin lake and O'Neal et al. (1985) 200 g m^{-2} of *Pithophora* in Surrey Lake, Indiana. Photosynthetic rates were also comparable between the three studies. If an equimolar carbon : oxygen ratio is assumed for conversion of C-fixation and oxygen evolution data, light-saturated rates of 3 – 17 mg C g^{-1} dry weight h^{-1} from *Spirogyra* compare with maximum in situ rates of 7.4 – 14.8 mg C g^{-1} dry weight h^{-1} reported by O'Neal et al. (1985). Both the present study and that of O'Neal et al. (1985) avoided the problem of self-shading within the filamentous masses by incubating small samples in relatively large containers. As *Spirogyra* in Spirogyra Lake was able to attain comparable photosynthetic rates and standing crops, at ambient temperature, to similar algae in temperate lakes, it is unlikely that low temperature imposed serious contraints on growth, although the temperature-dependence of P_{max} was not examined. The ability to maintain high rates of photosynthesis at low temperatures has been demonstrated for other cold-water filamentous algae (Auer et al. 1983).

Phytoplankton in Signy Island lakes have also been shown to have high photosynthetic rates at low ambient temperatures, with assimilation numbers of up to 11 mg C fixed mg^{-1} chlorophyll-*a* h^{-1} attained (Hawes 1983, 1985). In contrast, photosynthesis of the perennial phytobenthos in these same lakes is low. Priddle (1980b) reported oxygen evolution rates of 0.2 – 0.8 mg g^{-1} dry weight h^{-1} (chlorophyll-*a* content not given) for a variety of perennial plant communities. Assuming an equimolar conversion between oxygen evolution and carbon uptake, this equates to approximately 0.1 – 0.3 mg C g^{-1} dry weight h^{-1}. The photosynthetic performance of *Spirogyra* is, as might be expected of a fast growing annual, much more like that of the phytoplankton than the perennial benthos. The maximum rate of photosynthesis was 17 mg C g^{-1} dry weight h^{-1}, and a maximum assimilation number of 2.9 mg C mg^{-1} chlorophyll-*a* h^{-1} could be calculated. Similarly the photosynthesis saturating radiation fluxes of *Spirogyra* were more in line with the phytoplankton than the perennial phytobenthos. Priddle (1980b) found the latter to be adapted to the low radiation fluxes present under ice and were saturated at light levels equivalent to 5 µmol photons m^{-2} s^{-1}. The annual benthos was far more capable of utilising the high open-water radiation fluxes than the perennial benthos. The rapid depletion of oxygen after ice formation suggests that it was not able to maintain an adequate rate of photosynthesis, at the very low winter radiation fluxes, to offset respiration. Direct comparisons of in situ productivity of filamentous assemblage phytoplankton and perennial benthos cannot be made from the current data as it is not possible to describe the light climate within the dense clumps of *Spirogyra*.

Winter Oxygen Depletion

On ice formation, approximately 20 kg (1700 moles) of carbon was present in the standing crop of *Spirogyra*, while only 14 kg (440 moles) of oxygen was in the overlying water column. Ice cover effectively prevents influx of oxygen (Welch 1974) and it is not surprising that respiration and decomposition of this algal material quickly removed all of the oxygen from the water column. The full range of anaerobic decomposition processes are known to occur in Antarctic lakes (Ellis-Evans 1985) and these must be postulated to explain the complete breakdown of algal material.

Very few algal cells survived the winter period. Those which did, overwintered as vegetative cells rather than as spores. This contrasts with the strategy of planktonic algae characteristic of spatially anoxic lakes, where survival in anoxic regions is usually as resting stages (Reynolds 1984). It is not possible from the current data to determine whether the algae survived prolonged anoxia, or whether micro-sites were exploited where local conditions were less extreme, though the tendency for more viable algae to be found in the shallower, unfrozen regions suggests that this may be so. Similarly, the importance of very low light levels, particularly in shallower regions, as opposed to complete darkness, cannot be assessed. Further experimentation is required to investigate these aspects of overwintering.

The absence of a perennial phytobenthos from Spirogyra Lake may be related to seasonal anoxia. The rapid depletion of oxygen from the water column means that any perennial phyto-benthos must either be capable of

surviving prolonged anoxia or maintain a sufficient rate of photosynthesis under ice cover to preserve oxic conditions. The rate of oxygen consumption immediately after ice formation, estimated according to Welch and Bergman (1985), was 240 mg m^{-2} d^{-1}. The maximum areal rates of photosynthetic oxygen evolution for three perennial benthic plant communities, *Tolypothrix/Plectonema* felts, *Phormidium* felts and aquatic mosses calculated from data in Priddle (1980a) were 316, 72 and 270 mg m^{-2} d^{-1}, respectively. Light-limited rates under winter ice were considerably lower and it seems unlikely that any of these communities could maintain oxic conditions in Spirogyra Lake.

Photo-Adaptation

Although maximum biomass was attained under open water conditions, growth began under ice, when radiation fluxes, though higher than in winter, were still low. Seasonal change in the photosynthetic capacity of *Spirogyra* can be interpreted as adaptation to changing light climate. The ability of algae to adapt their photosynthetic apparatus to changing radiation fluxes has been widely demonstrated. Observed increases in chloroplast size, chlorophyll-*a* content and P_{max} with little change in I_k under low light conditions are consistent with photoadaptation in *Spirogyra* involving an increase in the number, rather than size, of photosynthetic units within the cells (Richardson et al. 1983).

The rate of algal photosynthesis is also related to nutritional state, particularly with respect to phosphorus (Senft 1978). The P content of *Spirogyra* declined from the commencement of growth in November up until February and the possibility that lowering of P_{max} during the open water period was a result of nutrient limitation, rather than photoadaptation, cannot be discounted without further experimental evidence.

Nutrient Limitation

The molar ratio of N:P in the water column of Spirogyra Lake, during the open water period, varied from 135:580 but was always above the critical values of 7–20 generally accepted as marking the changeover from N to P limitation (Rhee 1978; Forsberg et al. 1978). While no direct assays of nutrient limitation were made, the intracellular N:P ratio supported this view. During open water, intracellular molar ratios were consistently close to 50, considerably in excess of the average optimum ratio of 17 determined by Rhee and Gotham (1980). The absolute P content of 0.1% dry weight is also lower than most of the minimum values for freshwater phytoplankton assembled by Reynolds (1984), while C and N contents were closer to their respective optima.

In contrast, over winter and during the early stages of spring growth, ambient P concentrations were relatively high while low, sub-saturating radiation fluxes suggested that light was more likely to be growth-limiting than P. The cellular N:P ratio at this time was 9, much closer to the optimum, and confirming that nutrients were in plentiful supply relative to growth rate.

Despite the apparent nutrient limitation, the areal chlorophyll concentration attained by *Spirogyra* was considerably higher than that of phytoplankton in even the most nutrient-rich lakes at Signy Island (Hawes 1983). Cattaneo (1987) found that filamentous algae, including *Spirogyra*, were favoured by high TFP concentrations, but although the TFP concentration in Spirogyra Lake was lower than any lake included in this author's study, the chlorophyll-*a* amount was considerably higher.

There are two possible explanations for the anomalously high algal biomass in Spirogyra Lake. Firstly, otherwise limiting phosphorus may have been obtained from the sediments, though this may be unlikely under aerobic conditions (Larsen et al. 1981). Secondly, the absence of grazing losses and washout meant that *Spirogyra* could accumulate over a considerable time period. Over this extended time scale, the rapid turnover of water in Spirogyra Lake permitted the carpet of algae to accumulate phosphorus from the oligotrophic lake water. It can be calculated that, at its maximum, the *Spirogyra* population contained 45 g P, while at the same time the water column contained only 4 g. In Surrey Lake, Indiana, a concentration of 350 mg TFP m^{-3} – seventy times the summer Spirogyra Lake concentration – was necessary to permit a similar standing crop of filamentous algae to develop (O'Neal et al. 1985).

Cell Composition

Chlorophytes are known to store fixed carbon as lipids and carbohydrates. It was hypothesised that accumulation of such intracellular reserves during summer, and their subsequent depletion might provide carbon and energy during the winter. Resting spores are known to accumulate and utilise lipids and polysaccharides in this manner (Erben 1962). In vegetative cells, the accumulation of storage products occurs when the rate of photosynthesis exceeds that necessary for cell growth and division (see review by Morris 1981). There are a variety of circumstances when this may occur, the most frequently encountered being prolonged nutrient limitation (Collyer and Fogg 1955; Mykelstad 1974), high radiation fluxes (Myers 1949; Cook 1963; Morris et al. 1974) and low temperatures (Morgan and Kalff 1975). All three of these situations which enhance storage product formation prevailed in Spirogyra Lake during summer, where temperatures were low, nutrients limiting and radiation fluxes high. These combined to give a high carbohydrate plus lipid content (30–40% dry weight, approx. 50% cell carbon – though some cell wall components may have been included in the assay procedures) but there was no evidence of an accumulation immediately prior to ice formation or of spore formation.

The decrease in polysaccharide levels after ice formation was consistent with the cessation of photosynthesis and the utilisation of reserves. Palmisano and Sullivan

(1982) found a similar decrease in Antarctic sea-ice diatoms subjected to a simulated summer-winter transition. However, in contrast to the last quoted work, lipid levels in *Spirogyra* were higher over winter than in summer, as were the levels of alcohol-soluble sugars (preliminary, unpublished results show the sugars to be mostly sucrose). Smith and Morris (1980) found that at low radiation fluxes and temperatures, Antarctic phytoplankton incorporated as much as 80% of fixed carbon into lipid. Whether the increase in lipid content seen in *Spirogyra* is due to photosynthesis at extremely low radiation fluxes and temperatures or to other factors such as hypoxia and cell decomposition cannot be determined without further experimental investigation.

This paper is a preliminary description of the dominant vegetation of a type of Antarctic lake not previously investigated. Morphometry was found to have strong influences on the characteristics of the lake and its flora. Small size and low volume facilitated a rapid turnover of water during summer, which in turn permitted a high standing crop of the annual filamentous chlorophyte *Spirogyra* to develop, despite low ambient nutrient concentrations. The low volume also meant that little oxygen was available to sustain aerobic metabolism under winter ice cover, and the lake quickly became almost totally anoxic, with the decomposition of almost all of the resident vegetation. Seasonal cycles of biomass and physiological characteristics of the *Spirogyra* population reflected the extreme seasonality of the lake environment.

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