Periphyton community structure and dynamics in a subarctic lake

Marie-Josée Maltais and Warwick F. Vincent

Abstract: Periphyton species composition was analysed at 20 stations around an island in a large (1239 km^2) oligotrophic lake in subarctic Quebec (Lac à l'Eau Claire; latitude 56°10′N, longitude 74°30′W) to describe the mature communities colonizing the upper littoral region and to evaluate periphyton abundance and distribution relative to the physical environment. Four major communities could be clearly distinguished in the field by their macroscopic features, specifically colour (black, brown, and green) and growth form (filamentous or encrusted), as well as by their standing stock (cover and areal Chl a concentration) and photosynthetic characteristics. (1) *Black crust*—This community was dominated by the cyanobacterium *Gloeocapsa*, with highest percent cover in shallow waters ($\leq$0.25 m) protected from wave action by offshore boulder barriers. Photosynthesis under full sunlight was low per unit biomass (0.7 μg C $\cdot$ (μg Chl a)$^{-1}$ $\cdot$ h^{-1}). (2) *Brown film*—This community was dominated by *Calothrix*, with *Gloeocapsa* and *Phormidium* as subdominants. Maximum abundance was at 0.5 m, with photosynthetic rates that were similar to the black community. (3) *Green crust*—This community was dominated by the mucilaginous chlorophyte *Gloeocystis*, with *Oscillatoria* as subdominant, and colonized shallow depths ($\leq$0.25 m) in the shaded underlayer of rocks. It had slow, light-limited photosynthetic rates (0.1 μg C $\cdot$ (μg Chl a)$^{-1}$ $\cdot$ h^{-1}). (4) *Green filaments*—This community was dominated by *Ulothrix zonata*, with associated chlorophytes and diatoms, and was a rapidly growing assemblage characterized by the highest diversity, species richness, and productivity per unit biomass (3.5 μg C $\cdot$ (μg Chl a)$^{-1}$ $\cdot$ h^{-1}). It occurred on gravel beds at depths $\leq$0.5 m and was restricted to the well-illuminated south-facing shores of the island. Communities 1, 2, and 3 had similar maximum standing stocks throughout the period of sampling (mean of 1.3 μg Chl $a \cdot$ cm^{-2}), whereas the *Ulothrix* community rose from 1.9 μg Chl $a \cdot$ cm^{-2} in late July to 5.5 μg Chl $a \cdot$ cm^{-2} by mid-August. The overall rich biodiversity of the Lac à l'Eau Claire periphyton (>200 taxa recorded) may reflect the diversity of microenvironments and intermediate disturbance in the upper littoral zone.

Key words: cyanobacteria, chlorophytes, diatoms, epilithon, periphyton, photosynthesis.

Résumé : Les auteurs ont analysé la composition en espèces dans 20 stations autour d'une île située dans un grand lac (1239 km^2) oligotrophe du Québec sub-arctique (Lac à l'Eau Claire; 56°10′N, 74°30′O), afin d'en décrire les communautés matures colonisant la région du littoral supérieur et d'évaluer l'abondance et la distribution du périphyton en relation avec le milieu physique. Sur le terrain, on peut clairement distinguer quatre communautés majeures d'après leurs caractéristiques macroscopiques, spécifiquement la couleur (noir, brun, et vert) et la forme biologique (filamenteuse ou incrustée), aussi bien que par la biomasse mesurable (couverture et teneur en Chl a en surface) et leurs caractéristiques photosynthétiques. (1) *Croûte noire*. Cette communauté est dominée par les cyanobactéries *Gloeocapsa*, avec les plus forts pourcentages de couverture en eaux peu profondes ($\geq$0,25 m), protégées de l'action des vagues par des barrières de roches au large. La photosynthèse en pleine lumière solaire est faible par unité de biomasse (0,7 μg C $\cdot$ (μg Chl a)$^{-1}$ $\cdot$ h^{-1}). (2) *Film brun*. Celle-ci est dominée par des *Calothrix*, avec des *Gloeocapsa* et des *Phormidium* comme sous-dominants. L'abondance maximum se retrouve à 0,5 m, avec des taux photosynthétiques qui sont semblables à ceux de la communauté noire. (3) *Croûte verte*. Dominée par les chlorophytes mucilagineuses *Gloeocystis* avec des *Oscillatoria* comme sous-dominants, cette communauté colonise des eaux peu profondes (0,25 m) à l'ombre des rochers. Elle possède des taux photosynthétiques faibles, limités par la lumière (0,1 μg C $\cdot$ (μg Chl a)$^{-1}$ $\cdot$ h^{-1}). (4) *Filaments verts*. Cette communauté est dominée par l'*Ulothrix zonata*, associé à des chlorophytes et des diatomées, et constitue un ensemble à croissance rapide caractérisée par la diversité, la richesse en espèces et la productivité par unité de biomasse (3,5 μg C $\cdot$ (μg Chl a)$^{-1}$ $\cdot$ h^{-1}) les plus élevées. On la retrouve sur des lits de graviers à des profondeurs de $\leq$0,5 m et est restreinte aux rives exposées au sud et bien illuminées de l'île. Les communautés 1, 2 et 3 ont montré des biomasses mesurables maximales semblables tout au long de la période d'échantillonnage (moyenne de 1,3 μg Chl a cm^{-2}), alors que la communauté à *Ulothrix* passe de 1,9 μg Chl a cm^{-2} en fin de juillet, à 5,5 μg Chl a cm^{-2} vers la mi-août. La riche biodiversité globale du périphyton du lac à l'Eau Claire (>200 taxons enregistrés) pourrait refléter la diversité des micro-milieux et la perturbation intermédiaire de la zone littorale supérieure.

Mots clés : cyanobactéries, chlorophytes, diatomées, épilithon, périphyton, photosynthèse.
[Traduit par la rédaction]

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Introduction

Oligotrophic lakes are a major ecosystem component of the subarctic region (e.g., Shortreed and Stockner 1986; Pienitz et al. 1997). The high transparency of such lakes is likely to favour extensive development of periphyton throughout their littoral zones; however, very little is known about northern waters in this regard. Most of the relevant studies to date have been on benthic algal communities at higher polar latitudes such as the north of Alaska (e.g., Stanley 1976a, 1976b) and northern Northwest Territories (e.g., Moore 1977; Sheath and Cole 1992; Douglas and Smol 1995). Approximately 40% of Quebec lies within the subarctic zone but the phycology of this lake-rich region has been virtually unexplored. The potential sensitivity of this region to climate change (Laurion et al. 1997; Vincent and Pienitz 1996), and the increased exploitation of freshwater resources in the Canadian subarctic (Verdon et al. 1991) highlights the need for an improved understanding of these ecosystems at all trophic levels.

A broad range of environmental factors are likely to influence periphyton distribution, abundance, and community structure. Many of these effects, however, may be indirect, or may operate via a combination of positive and negative controls. For example, the mechanical effects of wind and wave action tend to maintain the periphyton at low standing crop in some systems (Duthie and Jones 1990, Hawes and Smith 1993); however, turbulence can also stimulate periphyton growth and biomass by increasing nutrient supply (Tanimizu et al. 1981, Cattaneo 1990). Periphyton community development reflects the capacity of different algal taxa to colonize, grow, compete, tolerate stress, and resist loss processes; the net result is the production of different community structures in different habitats (Cox 1990). This complex ensemble of controlling variables is illustrated by the relatively low amount of variance in periphyton species composition which can be explained by traditional limnological descriptors. For example, in a detailed study of periphytic diatoms in ponds of the Canadian High Arctic, Douglas and Smol (1995) found that only 26% of the total variance in diatom species composition could be accounted for by the measured environmental and habitat variables such as major ions, pH, and substrate type.

The aim of the present study was to describe the community structure, abundance, and distribution of the periphyton in the upper littoral zone of a subarctic lake. We performed this study at Lac l'Eau Claire, a large (1269 km²) oligotrophic lake (phytoplankton concentrations of 0.2–2.0 μg Chl $a \cdot L^{-1}$, Milot-Roy and Vincent 1994) that potentially offered a broad range of benthic habitats for algal colonization and growth. We obtained detailed measurements at 20 stations around an island that differed in wind and wave exposure, light availability, microtopography, and substrate type. These measurements allowed us to identify discrete communities that differed in their floristic and other biological characteristics, and to associate these communities with specific habitats.

Methods

Study area

Lac à l'Eau Claire is located at latitude 56°10'N, longitude 74°30'W, 150 km northeast of Poste-de-la-Baleine (Fig. 1). The lake is composed of two main basins, the eastern basin of 20 km diameter, and the western basin of 30 km diameter. Lac l'Eau Claire is believed to originate from a double meteoritic impact during the Pennsylvanian (Reimold et al. 1981). We chose 20 sampling stations around an island located in the western basin (Île des Foreurs). This selection of stations encompassed a broad range of orientations, bathymetric profiles, and wind and wave exposure, and could be grouped in four geographic quadrants as shown in Fig. 2. The sampling was undertaken during the open-water period of 1992, beginning immediately after ice-out, which was not until the fourth week of July. There was little change in lake level (<10 cm) over this midsummer to late summer period of study.

Physical and chemical environment

A meteorological station was installed on an island in the centre of the western basin. This station recorded wind orientation and velocities with a Young model 05103 anemometer. These measurements were recorded automatically at 15-min intervals with a Campbell Datalogger model CR-10 throughout the sampling period. For all stations, wind exposure was estimated by maximum effective length (L_{max}; Håkanson 1981) using a 1 : 50 000 scale map of the lake. Bathymetric profiles were made for each station from the shoreline to 54 m perpendicular to the shore. The depth and substratum were noted at every metre.

Nutrients, temperature, and pH were measured at each station on four sampling dates during the open-water period. Water for nutrient analysis was sampled from 0.5 m, stored frozen, and later analysed on a Alpkem model RFA-300 autoanalyser. Nitrate was measured by diazotization after cadmium reduction to nitrite (American Public Health Association 1976), dissolved reactive phosphorus (DRP) by the method of Whitledge et al. (1981), and silicate, after repolymerization at room temperature, by the method of Truesdale and Smith (1975). The limits of detection were 1 μg $P \cdot L^{-1}$, 3 μg $Si \cdot L^{-1}$, and 0.6 μg $N \cdot L^{-1}$. Water temperatures and pH were measured at 0.2 m with a Corning micro-electrode system (precision of 0.01 pH units and 0.1°C).

Periphyton sampling

Periphyton at 20 stations was sampled on July 29 and again on August 16 to determine biomass and species composition of communities which could be distinguished in the field by their macroscopic properties, specifically colour (black, brown, green) and growth form (crustose, surface film, filamentous). We selected rocks at each station that had a macroscopically visible, well-developed algal coating. One rock (per community) at 0.25 m depth and another at 0.5 m were sampled by scraping with a scalpel blade 5.3 cm² from the part of the rock where the algal film was best developed. This intentional sampling bias towards well-developed communities provided an upper estimate of periphyton biomass around the island at each sampling date and is referred to below as maximum biomass.

Community structure

Subsamples of material scraped from the rocks were preserved in 1% gluteraldehyde plus 0.1% paraformaldehyde final concentrations (Lovejoy et al. 1993) for microscopic analysis. The aggregates of epilithon (rock-surface) samples were subsequently disrupted by brief agitation in a loose-fitting Teflon tissue grinder. These disaggregated samples were then transferred to Utermöhl sedimentation chambers, allowed to settle, and then examined directly with a Zeiss Axiovert 10 inverted microscope at 400× and 1000× magnification. For the identification of diatoms, separate subsamples were removed and cleaned with hydrogen peroxide, concentrated, and examined by light microscopy.

A total of at least 400 cells (all species) or 100 cells of the dominant species were counted in each sample (without peroxide pre-

Fig. 1. Location of the study site in northern Quebec. The arrow indicates Île des Foreurs.
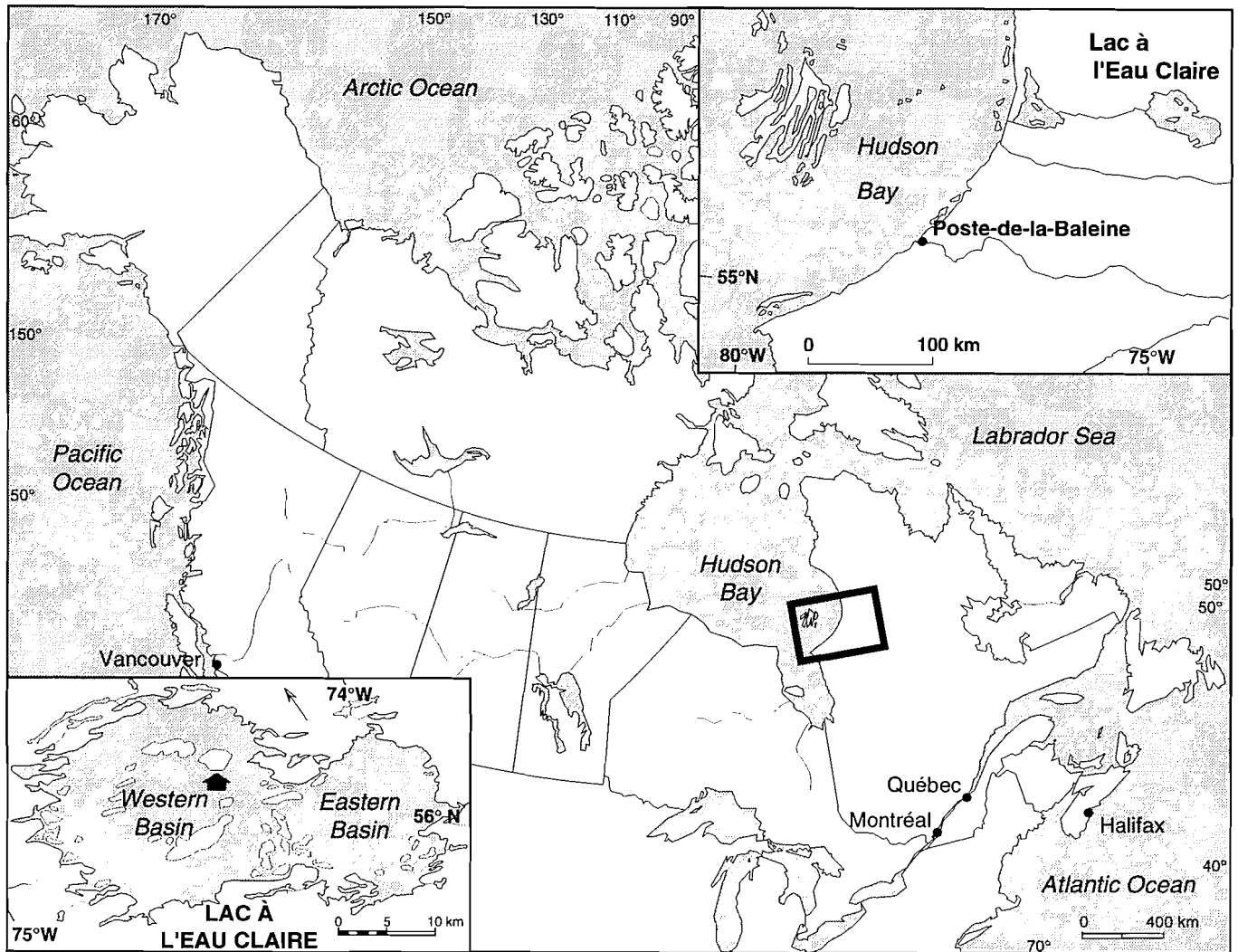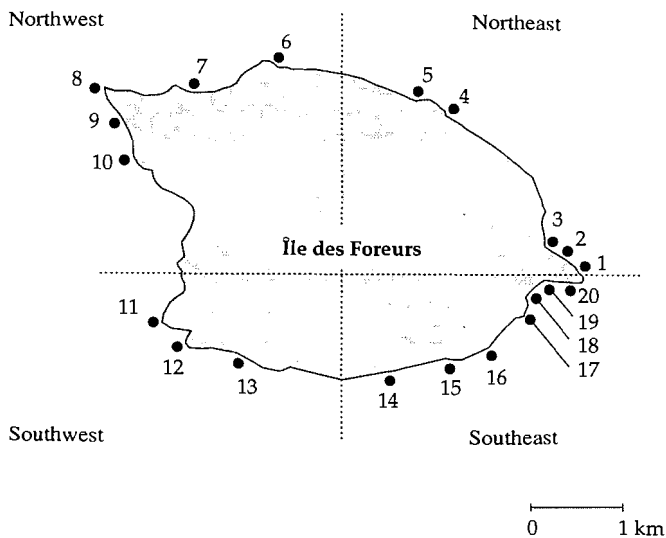

Fig. 2. Location of the 20 sampling stations around Île des Foreurs.

treatment), and these data were used to calculate the community diversity index (H') as in Shannon and Weaver (1963), and the species richness index (R) as in Menhinick (1964). Only living cells were considered for the enumeration by Utermöhl (empty frustules were not counted). To summarize the characteristics of each community, we distinguished four categories of abundance: dominant (most abundant taxon), subdominant (>50 individuals per 100 of the dominant), abundant (10−50 individuals per 100 of the dominant), and rare (<10 individuals per 100 of the dominant).

Periphyton biomass

At each date and station, additional samples were taken for measurements of total periphyton biomass as estimated by chlorophyll a (Chl a). Samples of the scraping from rocks at 0.25 and 0.5 m depth were transferred into 120-mL bottles with 5 mL of 95% ethanol. Epilithon samples were then extracted at 60°C in a water bath for 5 min (Nusch 1980). The Chl a content of the extracts was estimated by fluorometry with a Sequoia−Turner fluorometer model 450, before and after acidification.

Periphyton photosynthesis

Photosynthetic rates were measured by the ¹⁴C method modified from Strickland and Parsons (1972). Individual rocks of 10 cm

Table 1. Physical and chemical characteristics measured at four geographic orientations around Île des Foreurs.

| | Island quadrants | | | |
Parameter	Northeast	Southeast	Southwest	Northwest
Stations	1−5	14−20	11−13	6−10
L_{max} (km)	13.3 (1.1)	21.3 (1.3)	24.9 (0.4)	24.9 (1.2)
Wind frequency (%)	22.2	16.6	39.9	21.3
Max. velocity (km · h^{-1})	46.8	31.0	37.1	36.2
Mean velocity (km · h^{-1})	13.7	8.7	14.7	12.7
Water temperature (°C)	6.6 (0.7)	7.4 (1.1)	6.8 (0.7)	6.7 (1.2)
pH	6.2 (0.2)	6.7 (0.3)	7.4[a]	6.6 (0.2)
SiO_2 (μg Si · L^{-1})	61.9 (5.3)	73.1 (14.5)	84.0 (29.6)	58.9 (4.0)
NO_3^- (μg N · L^{-1})	39.9 (12.3)	33.7 (7.2)	27.3 (0.6)	41.1 (15.4)

Note: Seasonal (July−August) mean values are given for water temperature, pH, and nutrients.
Standard errors are given in parentheses.
[a]Only one value from three stations on July 20.

diameter were placed in sterile polyethylene Whirlpacks© with 300 mL of water from the sampled station (southeast sector), and then 20 μCi of $NaH^{14}CO_3$ was injected. Each rock was incubated in its original orientation, on a shallow gravel substrate within the lake (0.25 m water depth), under morning, clear sky irradiance conditions (ca. 1400 μmol photons · m^{-2} · s^{-1}). For each community tested, 5−10 replicate rocks were incubated in separate bags exposed to the light; an additional 2−4 rocks with each community type were incubated in black bags to correct for dark uptake. At the end of 1 h incubation, the rocks were rinsed and a 5.3-cm^2 area of the epilithon was scraped off with a scalpel blade. These samples were filtered onto GF/C filters and stored frozen until further analysis. The filters were subsequently cut into four equal pieces. One quarter was use for the estimation of productivity, and another quarter for the estimation of Chl a biomass by spectrophotometry (Strickland and Parsons 1972). The productivity sample was acidified for 10 min in an atmosphere of HCl and was subsequently ground in 3 mL of Cytoscint with a Teflon tissue grinder. We added 0.5 mL of Scintigest tissue solubiliser and then left the solution to digest for 24 h. A subsample (0.5 mL) of this solution was transferred to a vial containing 9.5 mL of Cytoscint, and the ^{14}C activity was measured in an LKB 1219 RackBeta liquid scintillation counter. Dissolved inorganic carbon was estimated by Gran titrations of subsamples of the lake water used for the incubations, as in Milot-Roy and Vincent (1994).

Community distribution

The percent cover of each of the three epilithic communities that colonized the upper surface of rocks was determined by visual observations at points along transects. The 5-m transects were laid out parallel to the shore at 0.25 m and also at 0.5 m mean depth, at 16 locations northwest (8) and southeast (8) of Île des Foreurs. At each 0.05-m interval along the transect, the exact depth as well as substrate type and community type were recorded, and the results were then analysed by binomial statistics.

The effect of local topography was studied by estimating maximum algal biomass (Chl a sampled and quantified as above) inside and outside boulder barriers (reefs), which occurred at many stations around the island, 10−20 m offshore. At each of nine stations, we sampled one rock at 0.5 m depth inside and one at 0.5 m depth outside the boulder barrier.

Results

The littoral environment

Bathymetric profiles differed greatly between stations; however, there were two types of littoral topography. For the majority of stations the depth of water increased sharply with distance offshore. However, at 30% of the stations (1, 6, 8, 9, 10, and 20), a barrier of large boulders formed a reef 10−20 m offshore that protected the inshore waters from direct wave action (see the insert in Fig. 6).

A comparison of maximum effective length values (L_{max}) and the wind record during the study indicates that the western side of Île des Foreurs is likely to receive greater wave action than the eastern side (Table 1). High mean wind velocities were recorded from the northeast, northwest, and southwest sectors. Winds from the southeast were relatively rare and had low mean velocities. The strongest wind was from the northeast; however, this sector had an L_{max} well below values elsewhere around the island, and was therefore likely to be less affected by wind action.

Water temperatures were low (range = 3−15°C) during the sampling period, with a seasonal mean of 6.9°C (SD for the four quadrants of ±0.2), with no significant differences between stations (Table 1). The pH averaged 6.7 (±0.2) for all orientations, with an overall range for the study of 6.0−7.6. Silicate averaged 69.5 μg Si · L^{-1} (±5.7), and nitrate averaged 35.5 μg N · L^{-1} (±3.2), with no consistent differences between sectors. Dissolved reactive phosphorus concentrations were always below detection.

Periphyton community structure

More than 200 algal taxa were identified in the periphyton community of Lac à l'Eau Claire during the study period. All taxa identified to genus or species are listed in the Appendix, and the most commonly encountered genera are given in Table 2, excluding coccoid cyanobacteria of the order Chroococcales which were abundant in every community. Four distinct periphyton communities could be distin-

Table 2. Taxonomic structure of the four distinct periphyton communities found around Île des Foreurs.

Community	Dominant	Subdominant	Abundant	Rare
Black crust	*Gloeocapsa*[a]		*Ulothrix,*[b] *Gloeocystis,*[c] *Achnanthes*[e]	*Mougeotia,*[b] *Phormidium,*[d] *Calothrix,*[d] *Tabellaria*[e]
Brown film	*Calothrix*[d]	*Gloeocapsa,*[a] *Phormidium*[d]	*Plectonema, Schizothrix,*[d] *Tabellaria,*[e] *Lyngbya*[d]	*Nitzschia,*[e] *Achnanthes,*[e] *Gloeocystis,*[c] *Fragilaria,*[e] *Oscillatoria*[d]
Green crust	*Gloeocystis*[c]	*Oscillatoria*[a]	*Gloeocapsa,*[a] *Plectonema,*[d] *Phormidium,*[d] *Anabaena*[d]	*Stigeoclonium,*[b] *Calothrix,*[d] *Lyngbya,*[d] *Xenococcus,*[a] *Spirogyra,*[b] *Tabellaria*[e]
Green filaments	*Ulothrix*[b]		*Stigeoclonium,*[b] *Gloeocystis,*[c] *Achnanthes,*[e] *Fragilaria,*[e] *Cymbella,*[e] *Ceratoneis*[e]	*Bulbochaete,*[b] *Zygnema,*[b] *Binuclearia,*[b] *Calothrix,*[d] *Mougeotia,*[b] *Gloeocapsa,*[a] *Tabellaria,*[e] *Chroococcus,*[a] *Oedogonium*[b]

[a]Coccoid cyanobacterium.
[b]Filamentous chlorophyceae.
[c]Coccoid chlorophyte.
[d]Filamentous cyanobacterium.
[e]Diatom.

guished in the field according to colour and macroscopic form. The subsequent microscopic analyses revealed that, although most taxa could be found in all communities, their relative abundance varied greatly and each community was dominated by different genera (Table 2). The four communities and their floristic characteristics were as follows.

(1) Black crust: This was a widespread community dominated by the coccoid cyanobacterium *Gloeocapsa* and forming a black crust on shallow rocks. This community contained two abundant genera of Chlorophyceae (*Gloeocystis* and *Ulothrix*) but was generally lacking in species relative to the other communities (Table 2). Diatoms were rare and restricted to *Tabellaria* and *Achnanthes*. The diversity index for this community was the lowest of the four ($H' = 0.71$), and the species richness index was similarly low ($R = 0.02$).

(2) Brown film: This was also widely distributed and occurred at most stations around the island. This community was dominated by the filamentous cyanobacterium *Calothrix*, forming a brown film over deeper rocks. *Gloeocapsa* (same species as in the black crust community) and *Phormidium* were subdominants, along with several other cyanobacterial taxa (Table 2). Diatoms were relatively abundant in comparison to the black encrusted community. *Tabellaria* was the most abundant diatom; *Nitzschia*, a genus not recorded in any of the other three communities, was also present. In contrast to the two other epilithic communities, no filamentous Chlorophyceae could be identified in samples of the brown film. Community diversity was slightly higher than that for the black crust dominated by *Gloeocapsa* ($H' = 0.85$), although richness of species was equivalent ($R = 0.03$).

(3) Green crust: This dark green pigmented community occurred in cracks and on the shaded sides and undersurfaces of rocks. It was dominated by the coccoid mucilaginous chlorophyte *Gloeocystis*, with *Oscillatoria* as subdominant. *Tabellaria* persisted in this community in low numbers. Community diversity was higher (particularly in cyanobacteria) than in the two previous communities ($H' = 0.96$), but species richness was almost identical ($R = 0.02$).

(4) Green filaments: This community was dominated by the filamentous chlorophyte *Ulothrix zonata*. It contained many diatom taxa but unlike the three other communities it had few cyanobacteria (Table 2). Certain taxa were largely restricted to this community (e.g., *Bulbochaete*, *Zygnema*, *Binuclearia*, *Oedogonium*). The diatom *Tabellaria* was also observed, but less commonly than the chlorophytes. Diversity and richness indices were the highest for this community ($H' = 2.10$, $R = 0.06$), reflecting the numerous taxa which composed this community, with all species well represented.

Photosynthesis

There were major differences between communities in terms of primary production rates per unit biomass (Chl a) and per unit area (Fig. 3). For the analysis of the data per unit biomass, all values were square-root transformed before a one-way ANOVA and Bonferroni's multiple comparisons t-test. The ANOVA showed that there were significant differences between the four communities ($F = 19.77$, df $= 3, 26$, $P < 0.001$). The production per unit Chl a in the green filamentous community was at least five times the values measured for the other communities; the brown and black communities did not significantly differ ($P > 0.1$), but the extremely low production rate of the green-encrusted community (incubated in its natural position, i.e., in shade) was significantly below that of the brown film (Fig. 3).

The production data expressed per unit area did not achieve normality before or after the usual transformations, and nonparametric methods were therefore used (Kruskall–Wallis test; Dunn's multiple comparisons tests). There were significant overall differences between communities ($H = 15.54$, df $= 3$, $P = 0.001$) which were due to the 20-fold greater areal production rate of the green filamentous assemblage. The three other communities did not significantly differ from each other ($P > 0.1$; Fig. 3), averaging 0.15 μg $C \cdot cm^{-2} \cdot h^{-1}$ (black crust $= 0.13$, green crust $= 0.15$, and brown filaments $= 0.18$).

Community biomass and cover

Periphyton biomass (as measured by Chl a) was first analysed by a two-way nonparametric ANOVA on the pooled

Fig. 3. Photosynthesis of the four periphyton communities. Number of observations is given in parentheses. Vertical bars represent standard errors, and horizontal bars separate statistically different groups ($p < 0.05$).
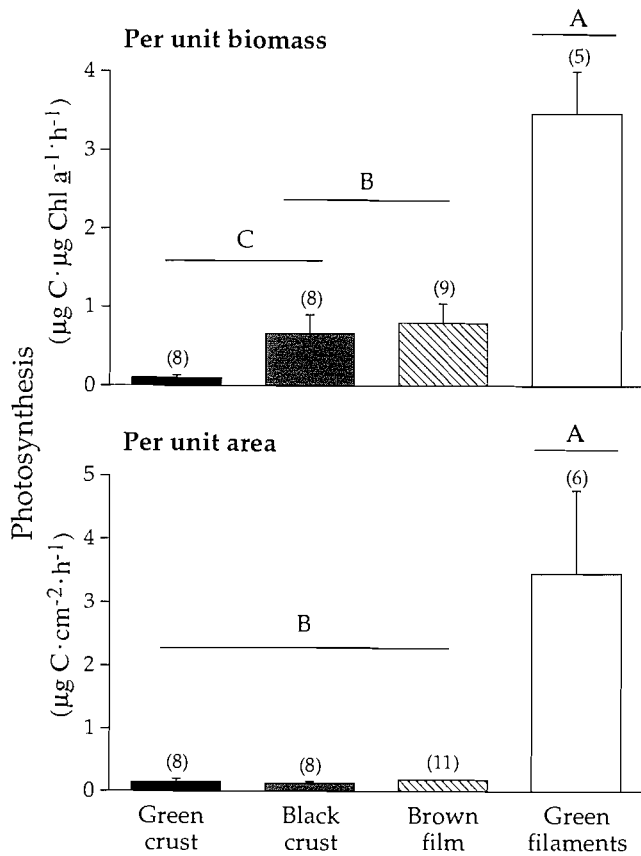

Fig. 4. Community abundance, as measured by Chl a, on two sampling dates around Île des Foreurs. Number of observations is given in parentheses. Maximum biomass refers to the sampling of rocks with the highest standing stocks at each site (assessed visually). Vertical bars represent standard errors, and horizontal bars separate statistically different groups ($p < 0.05$).
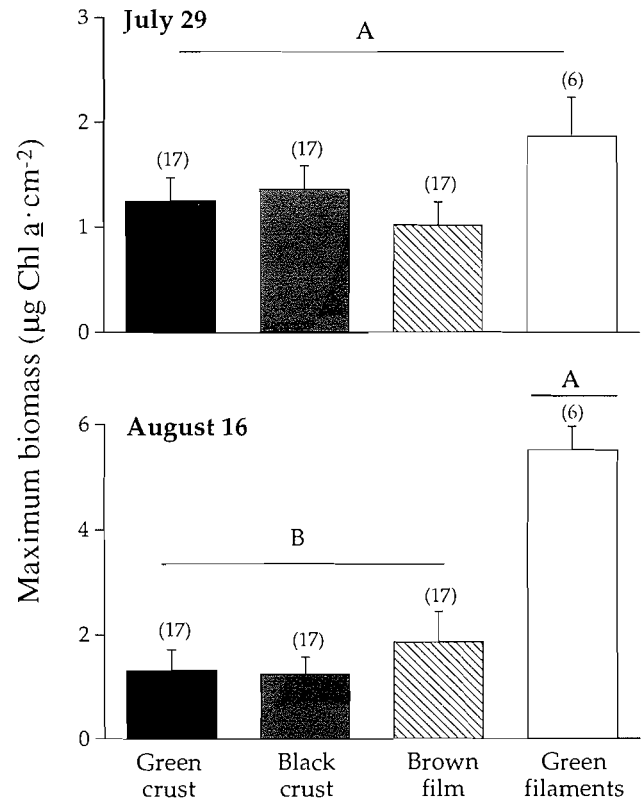
data for all stations and communities. This analysis showed that overall there was no statistically significant effect of depth ($H = 0.51$, df $= 1$, $P = 0.48$), nor an effect of date of sampling ($H = 0.05$, df $= 1$, $P = 0.82$). The data were then partitioned according to community type. There were no significant differences among the community types on the first date of sampling (ANOVA: $F = 1.32$, df $= 3$, $P = 0.28$), but 2.5 weeks later the rapid growth of the green filamentous community resulted in biomass values that were fourfold higher than those for the other three communities (Fig. 4). At this time there were significant differences among communities (nonparametric ANOVA: $H = 13.5$, df $= 3$, $P = 0.004$) which were due to the significantly higher biomass of the green filaments; there were no statistical differences between the other three communities (Fig. 4). A two-way ANOVA of the Chl a data (square-root transformed) for the green filamentous community showed a significant effect of date of sampling ($F = 14.9$, df $= 1$, $P = 0.005$), but no effect of 0.25 m versus 0.5 m depth ($F = 0.5$, df $= 1$, $P = 0.5$). This major increment in this green community biomass was also observed visually with the filaments increasing from a few millimetres in length to about 50 mm between the two sampling times.

The percent cover of each community type varied with substrate, depth, and location of the station. The green filamentous community achieved high standing stocks in the

Table 3. Percent cover of the communities observed at two depths in two opposite orientations around Île des Foreurs on Aug. 1. The green crust community could not be observed from above for cover estimates.
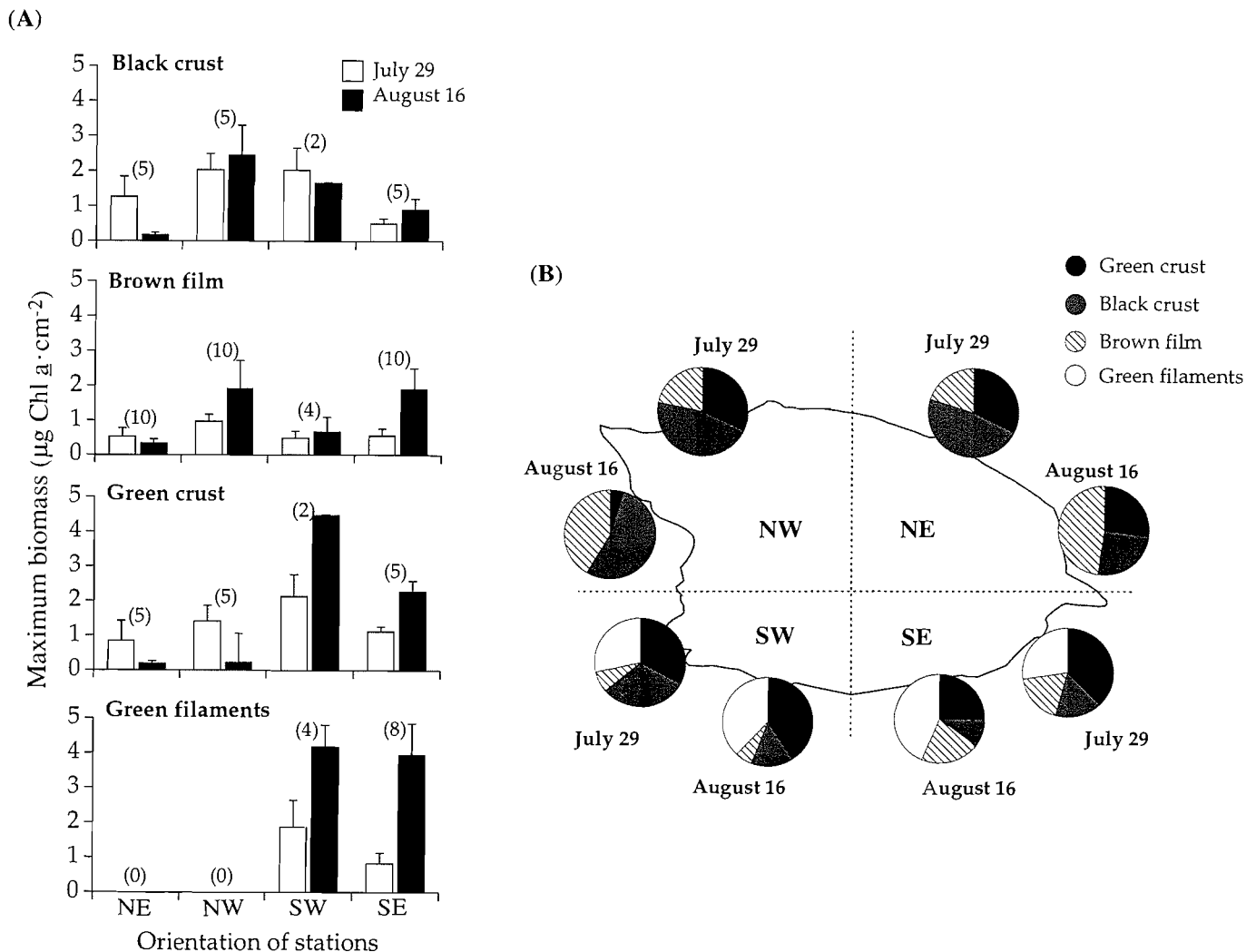
Location	Black crust			Brown film			Green filaments		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
0.25 m									
Northwest	72	6.6	6	22	6.1	6	0	0	6
Southeast	27	4.1	8	29	4.7	8	14	7.2	8
0.5 m									
Northwest	13	3.8	8	68	7.3	8	0	0	8
Southeast	17	3.9	8	51	6.4	8	0.5	0.5	8

Note: The green crust community could not be observed from above for cover estimates. n, number of transects.

southeast and southwest quadrants, but was completely absent from the northern side of the island (Fig. 5; Table 3). The black community was two to six times more abundant (in terms of cover) at 0.25 m than at 0.5 m; conversely the brown community was two to three times (on average) more abundant at 0.5 m irrespective of the geographic orientation of the stations (Table 3).

On 12 August there was a severe storm with winds up to

Fig. 5. Abundance of the four communities in each sector of Île des Foreurs on two sampling dates. (A) Mean Chl a for rocks with maximum biomass. Vertical bars represent standard errors, and number of observations is given in parentheses. (B) Relative maximum biomass of each community type in the four sectors.

(A)

(B)

Maximum biomass (μg Chl $a \cdot$ cm^{-2})

Black crust

☐ July 29
■ August 16

Brown film

Green crust

Green filaments

NE   NW   SW   SE

Orientation of stations

● Green crust
◉ Black crust
◌ Brown film
○ Green filaments

July 29

July 29

August 16

August 16

NW   NE

SW   SE

July 29

July 29

August 16   August 16

50 km · h^{-1} from the northeast. The heavy wave action associated with this event may have contibuted to the significant decline in maximum biomass of the black crust community in the northeast sector between the July 29 and August 16 sampling dates (Fig. 5). There was no significant change in this community within any of the other three sectors around the island.

Influence of boulder barriers

There was a strong effect of position in the littoral at those stations characterized by boulder barriers. On average, the concentration of Chl a was twice as high in the protected region between the shore and the barrier by comparison with the same depth (0.5 m) on the open-water side of the barrier (Wilcoxon paired-sample test, $P = 0.01$; Fig. 6). The highest biomass concentrations recorded over the course of this study were for the brown film at stations inside the barrier (7—9 μg Chl $a \cdot$ cm^{-2}).
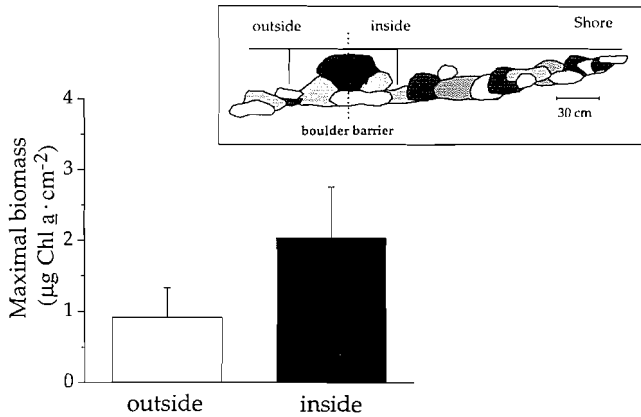
The black and brown communities occurred in all quadrants but with significant effects of depth and (or) substrate (presence or absence of boulders >30 cm in diameter) on the

distribution of each type (Fig. 7). A previous stepwise multiple regression analysis showed that the substrate type was a better predictor of percent cover than variation in depth (estimated as the coefficient of variation in depth at each site). The two-way ANOVA analysis of transformed percent cover data showed a significant depth effect ($F = 18.61$, df = 1, 34, $P = 0.0001$) and a significant positive effect of the presence of boulders on the black community ($F = 13.26$, df = 1, 34, $P = 0.0009$). The black crust had higher percent cover at 0.25 m when inside a boulder barrier (Fig. 7; and shown statistically by the significant interaction term depth x substrate, $F = 4.24$, df = 1, 34, $P = 0.05$), whereas the percent cover of the brown film was only influenced by depth ($F = 23.97$, df = 1, 34, $P < 0.0001$), with a much greater abundance at 0.5 m.

Discussion

This study revealed four inshore periphyton communities that could be distinguished in terms of their growth form and colour, taxonomic composition (species dominants), commu-

Fig. 6. Mean algal concentration at 0.5 m depth inside and outside the boulder barriers. The values are the means for the rocks with maximal biomass accumulation at nine stations. Vertical bars represent standard error.

Fig. 7. Influence of depth and substrate on the percent cover of the two cyanobacteria communities. Vertical bars represent standard errors, and number of observations from two sampling dates is given in parentheses.


nity biomass and cover, and photosynthetic rates. These four communities also differed in their habitat preferences. One of the communities (green crust) was restricted to shade conditions while the other three occupied open exposed habitats.

Cyanobacteria were found at all sites and were the dominant components of two of the communities. Although cyanobacteria are considered to prefer warm environments and have high temperature optima for growth, they are often the most abundant phototrophs in high-latitude lakes and streams (Vézina and Vincent 1997). Their success in these environments appears to result from a tolerance to a broad range of environmental extremes including cold temperature, high solar radiation, and periodic desiccation, rather than an ability to grow fast at low temperatures (Tang et al. 1997). Such attributes are also likely to have favoured their development in Lac à l'Eau Claire. An additional competitive factor that allows these organisms to prosper is their ability to maintain large overwintering populations which then provide the inoculum for the next growing season (Vincent and Howard-Williams 1986). This preemptive dominance of habitat space also occurred in Lac à l'Eau Claire; the cyanobacterial communities had a high concentration of Chl a immediately after ice-out and showed little evidence of increase over the subsequent period of sampling. The nitrogen-fixing capability of some cyanobacteria can favour their development in nitrogen-poor environments, and may be a factor contributing to the success of certain heterocystous species, in particular *Calothrix*, at Lac à l'Eau Claire.

The surface green algal community exhibited a growth strategy which sharply contrasted with that of the cyanobacteria. The *Ulothrix* filaments were initially inconspicuous and then grew rapidly to achieve the highest Chl a standing stocks to be measured during this study. This combination of small inoculum size and rapid growth (in contrast to the strategy of large inoculum and slow growth observed in the cyanobacteria) has also been observed in certain polar freshwater systems, in particular in the Antarctic maritime zone. In these south polar habitats, the filamentous chlorophytes *Klebsormidium*, *Zygnema*, and *Mougeotia* achieve high concentrations (>10 μg Chl $a \cdot$ cm^{-2}) which then die back almost completely in winter (Hawes 1989).
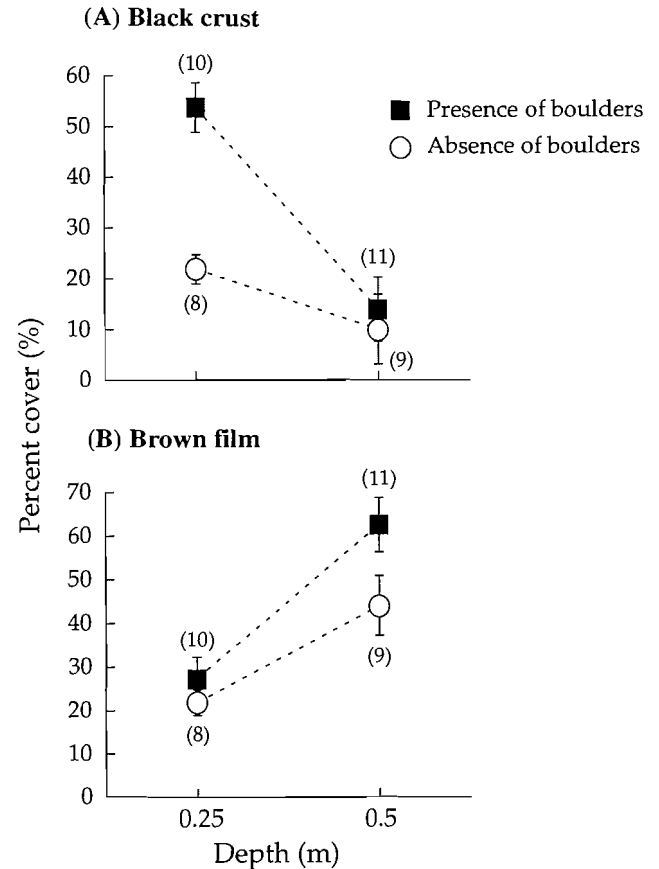
The cyanobacterial and green algal communities described here live within a shallow, clear water habitat that experiences high levels of incident photosynthetically active radiation (PAR) and ultraviolet radiation (UVR). Although there is increasing concern about the effects of stratospheric ozone depletion on subarctic lakes (Laurion et al. 1997), these upper littoral communities are likely to be tolerant of moderate increases in solar UVR. Mat- and film-forming cyanobacteria have a broad range of defenses including the production of UVR-screening compounds such as scytonemin (Vincent and Quesada 1994). The black (or brown) pigmentation of the *Gloeocapsa* and *Calothrix* communities in Lac à l'Eau Claire is likely to be due to this compound. Absorbance by this pigment extends into the PAR range, and the resultant shading may have contributed to the low photosynthetic rates per unit biomass observed in these communities. These low rates may also reflect the slow intrinsic growth rates of mat- and film-forming cyanobacteria relative to other taxonomic groups at low temperature (Tang et al. 1997).

Filamentous green algae are well-known inhabitants of bright irradiance environments. In Lac à l'Eau Claire the *Ulothrix* community appeared to have an obligate requirement for bright light, with its development restricted to the well-illuminated south-facing side of the island. The growth conditions under which we observed the development of the

Ulothrix community (seasonal mean of 7°C, maximum irradiance of about 1500 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}) correspond closely to the optimal growth conditions for *Ulothrix zonata* as measured by Graham et al. (1985), namely 5°C and 1100 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}.

The low-irradiance community containing *Gloeocystis* is reminiscent of certain shade communities found elsewhere in high-latitude regions. In Antarctic streams the green alga *Prasiola calophylla* achieves high concentrations in the undersurface and cracks of rocks in certain stream beds and is rich in green pigmentation (Chl *a* and Chl *b*) as found in the Lac à l'Eau Claire community (Howard-Williams and Vincent 1989). A green algal community dominated by *Prasiola* appears to occupy a similar shade habitat in High Arctic stream water systems (Hamilton and Edlund 1994). Phycocyanin-rich cyanobacteria are also found in a variety of shade environments elsewhere in the polar regions, including rock undersurfaces and fissures (Vincent 1988).

Diatoms were a subdominant but conspicuous component of all of the communities. Attention has especially focused on this group because of their preservation as microfossils within lake sediments, and the value of this record as a guide to paleoclimatic change in the subarctic (Pienitz et al. 1995) and Arctic (Douglas et al. 1994). In the present study there was little separation of diatom species between the four distinct community types, nor was there a relationship with the measured physical and chemical variables. However, to establish such relationships requires a more quantitative analysis of species distribution (e.g., cluster analyis or ordination) and better measurements of the microenvironment in the immediate vicinity of the growing cells. These microhabitat characteristics may differ considerably from the bulk properties of the surrounding water mass; for example, concentrations of dissolved reactive nutrients within cyanobacterial mats in Antarctica were one to three orders of magnitude higher than in the overlying water column (Vincent et al. 1993). As subdominant organisms the diatom communities may profit from the UVR protection offered by the greater biomass of chlorophyte and cyanobacterial components. The presence of heterocystous cyanobacteria (*Calothrix, Anabaena, Scytonema*) in the communities of Lac à l'Eau Claire also implies that nutrient conditions within the epilithon differed from the P-deficient surrounding lake water. Bioassays on the phytoplankton community at Lac à l'Eau Claire have shown that phosphorus is the primary limiting nutrient for algae as well as other components of the microbial food web (Bergeron and Vincent 1997), but these findings from the pelagic zone cannot be directly extrapolated to the epilithic microenvironment, which is strongly influenced by biogeochemical processes at the rock surface.

The hydrodynamic environment of Lac à l'Eau Claire would appear to exert some influence on the periphyton community of the littoral zone of this lake. Greatest biomass of the cyanobacterial communities occurred in the shallow waters protected by boulder barriers. A major decrease in biomass of one of these communities occurred after a storm event in the sector exposed to greatest wave activity. These observations are consistent with in situ experiments. The colonization and accumulation of biomass on artificial substrates placed in the lake at the 20 sites during this study period showed a negative, statistically significant relation-

ship with fetch (unpublished data). These results contrast with findings from smaller lakes which experience much less wave energy, and in which moderate turbulence may have a stimulatory effect by enhancing recruitment and resource supply. Ice scour is also likely to have an important influence on over-wintering communities, particularly during the period of ice-out in Lac à l'Eau Claire when the ice sheet breaks up into large floes. These blocks of ice are displaced by the wind and are blown up onto the shore, causing shoreline erosion and damage to the supralittoral vegetation. Periphytic communities behind the boulder barriers are likely to be better protected from these abrasive effects of ice rafting.

The chemical variables measured at Lac à l'Eau Claire showed no consistent trends around the island which would be indicative of a controlling effect on periphyton development. Nutrient effects, however, have been identified on periphyton communities in other systems. For example, Hansson (1992) found a positive correlative relationship between periphytic biomass and total phosphorus (sediment pore water) in Antarctic and Swedish (including subarctic) waters, with a decrease in biomass in more enriched waters which he attributed to shading by the overlying phytoplankton. Antarctic periphyton communities, however, represent many seasons of growth and can achieve high standing stocks even in ultraoligotrophic lakes (Vincent 1988). More compelling evidence of a nutrient-related effect is provided by the extensive observations and experimental results of Turner et al. (1994) in lakes of the Experimental Lakes Area (northwestern Ontario). Rates of epilithic photosynthesis in these lakes were unrelated to phosphorus concentrations, but were strongly dependent on the rate of inorganic carbon supply. Similar limitation by carbon is also likely in the low-alkalinity waters of subarctic Quebec.

Although the sampling sites in the present study were restricted to only one island of the lake, the biodiversity of periphytic species was considerable. Intermediate disturbance theory (Connell 1978) predicts that periodic mild disruption of an environment should lead to higher diversity. Such conditions are likely to be found in the upper littoral zone where ice scour and variations in water level would disrupt any prolonged stability that may be required for competitive exclusion to fully operate. The broad range of physical environments around the island (particularly in terms of degree of exposure to sunlight and wave action) contributes a diverse array of potential niches for colonization and growth. Finally, the long convoluted shoreline of Lac à l'Eau Claire with its many side arms may favour the development of different periphyton communities in different parts of the lake and thereby contribute to a diverse bank of inocula for recruitment into the littoral zone at all sites.

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Appendix

Table A1. List of genera and species recorded in the periphyton of Lac à l'Eau Claire during the present study.

Order	Genus	Species
Cyanophyta (cyanobacteria)		
Chroococcales	*Aphanocapsa* Nägeli	2 spp.
	Aphanothece Nägeli	? spp.
	Chroococcus Nägeli	*C. limneticus* Lemmermann
		1 sp.
	Coelosphaerium Nägeli	? spp.
	Gloeocapsa Kützing	2 spp.
	Gomphosphaeria Kützing	*G. lacustris* Chodat
	Merismopedia Meyen	1 sp.
	Pleurocapsa Thuret ex Hauck	1 sp.
	Radiocystis Skuja	1 sp.
Nostocales	*Anabaena* Bory	2 spp.
	Calothrix Agardh	*C. parietina* (Näg.) Thuret ex Born. & Flah.
		? spp.
	Scytonema Agardh	1 sp.
Oscillatoriales	*Lyngbya* Agardh	2 spp.
	cf. *Pseudanabaena* Lauterborn	1 sp.
	Oscillatoria Vaucher	*O. agardhii* Gomont
		O. tenuis Agardh ex Gom.
		O. nigra Vaucher ex Gom.
		O. subbrevis Schmidle
	Phormidium Kützing	*P. corium* (Ag.) Kütz. ex Gom.
		P. laminosum (Ag.) Gom.
		3 spp.
	Plectonema Thuret	*P. nostocorum* Bornet
	Schizothrix Kützing	? spp.
Chlorophyta		
Chlorococcales	*Ankistrodesmus* Corda	*A. falcatus* (Corda) Ralfs
		A. spiralis (Turner) Lemmermann
	Botryococcus Kützing	*B. sudeticus* Lemm. = *Botryosphaerella sudetica* (Lemm.) Silva
	Chlorella Beijerinck	*C. vulgaris* Beijerinck
	Crucigenia Morren	*C. quadrata* Morren
	Dictyosphaerium Nägeli	*D. pulchellum* Wood
	Dimorphococcus Braun	*D. lunatus* Braun
	Elakatothrix Wille	*E. gelatinosa* Wille
	Kirchneriella Schmidle	*K. obesa* (W. West) Schmidle
	Oocystis Nägeli	? spp.
	Palmodictyon Kützing	*P. viride* Kützing or *Oocystidium* Korchikoff
	Planktosphaeria Smith	1 sp.
	Scenedesmus Meyen	*S. armatus* (Chodat) Chodat
		S. javanensis Chodat
		S. obtusus Meyen
	Sphaerocystis Chodat	*S. schroeteri* Chodat
	Sphaerobotrys Butcher or *Gloeococcus* Braun	1 sp.
	Tetraedron Kützing	*T. minimum* (A. Braun) Hansgirg
		T. quadratum (Reinsch) Hansgirg
	Treubaria Bernard	2 spp.
Tetrasporales	*Asterococcus* Scherffel	1 sp.
	Gloeocystis Nägeli	3 spp.
	Tetraspora Link	*T. gelatinosa* (Vaucher) Desvaux

Table A1 (*continued*).

Order	Genus	Species
Volvocales	*Carteria* Diesing	*C. klebsii* (Dang.) Dill
	Characium Braun	1 sp.
	Chlamydomonas Ehrenberg	*C. sphagnicola* Fritsch & Takeda
		C. globosa Snow
		C. snowii Printz
		1 sp.
	Scourfieldia West	2 spp.
Ulotrichales	*Binuclearia* Wittrock	*B. tectorum* (Kütz.) Beger ex Wichmann
	Microspora Thuret	*M. wittrocki* Lagerh
	Ulothrix Kützing	*U. zonata* (Weber & Mohr.) Kützing
Chaetophorales	*Microthamnion* Nägeli	*M. strictissimum* Rabenh
	Stigeoclonium Kützing	2 spp.
Oedogoniales	*Bulbochaete* Agardh	1 sp.
	Oedogonium Link	1 sp.
Zygnematales	*Arthrodesmus* Ehrenberg =	
	Staurodesmus Ehrenberg	1 sp.
	Cosmarium Corda	*C. reniforme* (Ralfs) Archer
		C. portianum Archer
	Mougeotia Agardh	1 sp.
	Spirogyra Link	1 sp.
	Staurastrum Meyen	*S. hexacerum* (Ehrenberg) Wittrock
	Xanthidium Ehrenberg	3 spp.
	Zygnema Agardh	1 sp.

Euglenophyta

	Petalomonas Stein	1 sp.
	Trachelomonas Ehrenberg	1 sp.

Dinophyta

	Gymnodinium Stein	? spp.
	Peridinium Ehrenberg	1 sp.

Cryptophyta

	Chilomonas Ehrenberg	1 sp.
	Chroomonas Hansgirg	*C. nordstedtii* Hansgirg
		1 sp.
	Cryptomonas Ehrenberg	>4 spp.

Chrysophyta

Order	Genus	Species
Chromulinales	*Chromulina* Cienkowski	*C. wislouchiana* Bourrelly
	Chrysococcus Klebs	*C. rufescens* var. *compressa* Skuja
	C. diaphanus var. *astigma* Bourrelly	1 sp.
	Kephyrion Pascher or	
	Pseudokephyrion Pascher	14 spp.
Rhizochrysidales	*Bitrichia* Woloszynska	*B. chodatii* (Reverdin) Chodat
Ochromonadales	*Chrysoikos* Willen	*C. angulatus* Willen
	Chrysolykos Mack	*C. planctonicus* Mack
	Dinobryon Ehrenberg	*D. bavaricum* Imhof
		D. divergens Imhof
		D. sertularia Ehrenberg
		D. cylindricum Imhof
		D. sociale Ehrenberg
		D. vanhoeffenii (Krieg.) Bachmann
	Erkenia Skuja	*E. subaequiciliata* Skuja

Table A1 (*continued*).

Order	Genus	Species
	Mallomonas Perty	2 spp.
	Ochromonas Wyssotzki or	
	Spumella Cienkowsky	1 sp.
	Synura Ehrenberg	*S. uvella* Ehrenberg
	Uroglena Ehrenberg	*U. volvox* Ehrenberg
Prymnesiales	*Chrysochromulina* Lackey	1 sp.

Bacillariophyta

Order	Genus	Species
Aulacoseirales	*Aulacoseira* Thwaites	*A. distans* (Ehr.) Simonsen = *Melosira distans* (Ehr.) Kützing
Rhizosoleniales	*Urosolenia* Round & Crawford	*U. eriensis* (H. L. Smith) Round & Crawford = *Rhizosolenia eriensis* Smith
Thalassiosirales	*Cyclotella* Kützing	*C. bodanica* Grun.
		C. comta (Ehr.) Kützing = *C. radiosa* (Grun.) Lemmermann
		C. tripartiti Hakanson
		C. kuetzingiana Thwaites = *C. krammeri* Hakansson
		C. kuetzingiana var. *radiosa* (Thwaites) Fricke
		C. ocellata Pantocsek
		C. stelligera (Cleve & Grunow) Van Heurck
Fragilariales	*Asterionella* Hassall	*A. formosa* Hassall
	Hannaea Patr. = *Ceratoneis* (Ehr.) Grunow	*H. arcus* (Ehr.) Patr.
	Diatoma Bory	*D. elongata* (Lyng.) Agardh or *D. tenuis* Agardh
		D. vulgaris Bory
		D. hiemale (Lyng.) Heiberg
	Fragilaria Lyngbye	*F. crotonensis* Kitton
		F. virescens var. *exigua* (Ralfs) Grunow
		F. capucina var. *austriaca* (Desmazires) Grunow
		1 sp.
	Pseudostaurosira	*P. brevistriata* var. *inflata* (Pant.) Poulin = *Fragilaria inflata* (Heiden) Hustedt or *Staurosira construens* Ehrenberg
	Staurosirella	*S. leptostauron* (Ehr.) Williams & Round = *F. leptostauron* (Ehr.) Hustedt
		S. pinnata (Ehr.) Williams & Round = *F. pinnata* Ehrenberg
	Synedra Ehrenberg	*S. acus* Kützing
Tabellariales	*Tabellaria* Ehrenberg	*T. flocculosa* (Roth) Kützing
		T. fenestrata (Lyng.) Kützing
		T. binalis var. *binalis* (Ehr.) Grunow
Eunotiales	*Eunotia* Ehrenberg	*E. bilunaris* (Ehr.) Mills = *E. lunaris* (Ehr.) Grunow
		E. praerupta Ehrenberg
		1 sp.
Achnanthales	*Achnanthes* Ehrenberg	*A. flexella* var. *flexella* (Kütz.) Brun
		A. oestrupii (Cleve) Hust.
		A. minutissima Kützing
		3 spp.
	Cocconeis Ehrenberg	*C. placentula* Ehrenberg
Bacillariales	*Nitzschia* Hassall	*N. angustata* (Smith) Grunow = *Tryblionella angustata* W. Smith
		N. cf. fonticola Grunow or *N. capitata* Östr.
		N. palea (Kütz.) Smith
		1 sp.
Cymbellales	*Anomoeoneis* Pfitzer	*A. vitrea* (Grun.) Ross = *Brachysira microcephala* (Grun.) Compère
		A. brachysira (Brb.) Grunow
		A. styriaca (Grun.) Hustedt

Table A1 (*concluded*).

Order	Genus	Species
	Cymbella Agardh	*C. minuta* Hilse ex Rabenh. *C. microcephala* Grunow *C. incerta* Grunow or *C. hybrida* Grunow *C. proxima* Reimer *C. cymbiformis* Agardh 1 sp.
	Gomphonema Ehrenberg	*G. truncatum* Ehrenberg *G. olivaceum* var. *minutissimum* Hustedt *G. angustum* (Kütz.) Rabenh. *G. acuminatum* Ehrenberg
Naviculales	*Caloneis* Cleve	*C. backmanii* Cleve-Euler
	Frustulia Rabenhorst	*F. rhomboides* (Ehr.) De Toni
	Navicula Bory	*N. mediocris* Krasske *N. pseudoscutiformis* Hustedt = *Cavinula pseudoscutiformis* (Hust.) Mann. & Stickel *N. lanceolata* (Agardh) Ehrenberg *N. jaernefeltii* Hustedt *N.* cf. *pusio* Cleve or *N. pusioides* in Foged N. (diatoms in Alaska) *N. minima* Grunow *N. rhynchocephala* Kützing var. *elongata* Mayer 1 sp.
	Pinnularia Ehrenberg	*P. dubitabilis* Hustedt *P. viridis* (Nitzsch) Ehrenberg 1 sp.
	Stauroneis Ehrenberg	*S. phoenicenteron* (Nitzsch) Ehrenberg 1 sp.
Thalassiophysales	*Amphora* (Ehr.) Kützing	*A. neglecta* Stoermer & Yang
Surirellales	*Surirella* Turpin	*S. angustata* Kützing *S. linearis* Smith

Note: The number (*n*) of unidentified species within each genus is given as *n* spp. (or 1 sp. for a single unidentified taxon within a genus); the notation ? spp. refers to genera where we observed a large variability in morphotypes with probably more than one species.