Periphyton biomass and community composition in rivers of different nutrient status

J. Chételat, F.R. Pick, A. Morin, and P.B. Hamilton

Abstract: Epilithic periphyton was investigated in riffle zones of 13 rivers in southern Ontario and western Quebec to describe how algal biomass and community composition vary with nutrient concentration and water velocity during summer. Algal biomass (milligrams chlorophyll *a* (Chl *a*) per square metre) was strongly correlated with total phosphorus concentration (r^2 = 0.56, $p < 0.001$) and conductivity (r^2 = 0.71, $p < 0.001$) of the overlying water but unrelated to water velocity over the range of 10–107 $cm \cdot s^{-1}$. Differences in periphyton Chl *a* were associated with changes in biomass of Chlorophyta (r^2 = 0.51, p = 0.001) and Bacillariophyta (r^2 = 0.64, $p < 0.001$) and were not related to Rhodophyta and Cyanophyta biomass ($p > 0.10$). The relative proportions of taxonomic divisions varied with total standing stock. Percent Chlorophyta biomass increased with periphyton Chl *a* and was the largest fraction at moderately eutrophic sites. Rhodophyta contributed the most biomass at sites with the lowest Chl *a*. *Cladophora*, *Melosira*, and *Audouinella* biomasses were positively correlated with total phosphorus concentration over the range of 6–82 $\mu g \cdot L^{-1}$ (r^2 = 0.39–0.64, $p < 0.005$), and these genera were dominant at sites with the highest nutrient concentrations.

Résumé : On a étudié la végétation épilithique dans des radiers de 13 rivières du sud de l'Ontario et de l'ouest du Québec pour établir comment la biomasse algale et la composition des communautés varient selon la concentration de nutriants et la vitesse du courant durant l'été. La biomasse algale (milligrammes de chlorophylle *a* (Chl *a*) par mètre carré) était fortement corrélée avec la concentration de phosphore total (r^2 = 0,56, $p < 0,001$) et la conductivité (r^2 = 0,71, $p < 0,001$) de l'eau, mais pas avec la vitesse du courant dans la fourchette 10–107 $cm \cdot s^{-1}$. Les différences dans la Chl *a* de la végétation périlithique étaient associées aux changements dans la biomasse des chlorophytes (r^2 = 0,51, p = 0,001) et des bacillariophytes (r^2 = 0,64, $p < 0,001$) et n'étaient pas liées à la biomasse des rhodophytes et des cyanophytes ($p > 0,10$). Les proportions relatives des taxons variaient en fonction du stock total. La biomasse de chlorophytes augmentait en pourcentage avec la Chl *a* de la végétation et constituait la fraction la plus importante dans les sites modérément eutrophes. Les rhodophytes constituaient la biomasse la plus importante dans les sites les plus pauvres en Chl *a*. Les biomasses de *Cladophora*, *Melosira* et *Audouinella* étaient positivement corrélées avec la concentration de phosphore total dans la fourchette 6–82 $\mu g \cdot L^{-1}$ (r^2 = 0,39–0,64, $p < 0,005$), et ces genres étaient dominants aux sites présentant les plus fortes concentrations de nutriants.

[Traduit par la Rédaction]

Introduction

Epilithic periphyton biomass is highly variable in rivers and can span 6 orders of magnitude (from 0.01 to 10 000 mg chlorophyll *a* (Chl *a*)$\cdot m^{-2}$; Morin and Cattaneo 1992). In recent years, periphyton proliferations have become more of a concern in urban and rural rivers because they signal problems of eutrophication and can result in the aesthetic degradation of recreational areas. Biggs (1995) suggested that periphyton biomass accrual in rivers is controlled by a combination of resource and disturbance factors. Resource availability (i.e., nutrients, light) determines biomass gain by regulating growth rates, while disturbance factors (i.e., floods, invertebrate grazing) lead to biomass loss through physical removal. There is considerable inconsistency in the literature over the importance of nutrient control, and some studies have found no association between nutrient concentrations and algal standing crop in streams (Jones et al. 1984; Welch et al. 1988; Kjeldsen 1994), while others have indicated strong relationships with phosphorus and nitrogen concentrations (Biggs and Close 1989; Lohman et al. 1992). In the two latter studies, the hydrological regime was also implicated as an important determinant of periphyton biomass. Causal relationships between nutrients and biomass may be complicated by hydrological disturbance events, in which case, nutrient effects should be more apparent during periods of summer low flow.

Most previous studies of periphyton have focused on biomass accrual. Relatively little effort has been placed on determining relationships between trophy and periphyton community structure. And yet, excessive periphyton biomass has been associated not only with nutrient enrichment but also with the growth of particular filamentous taxa such as *Cladophora* (Biggs and Price 1987; Dodds 1991; Welch et

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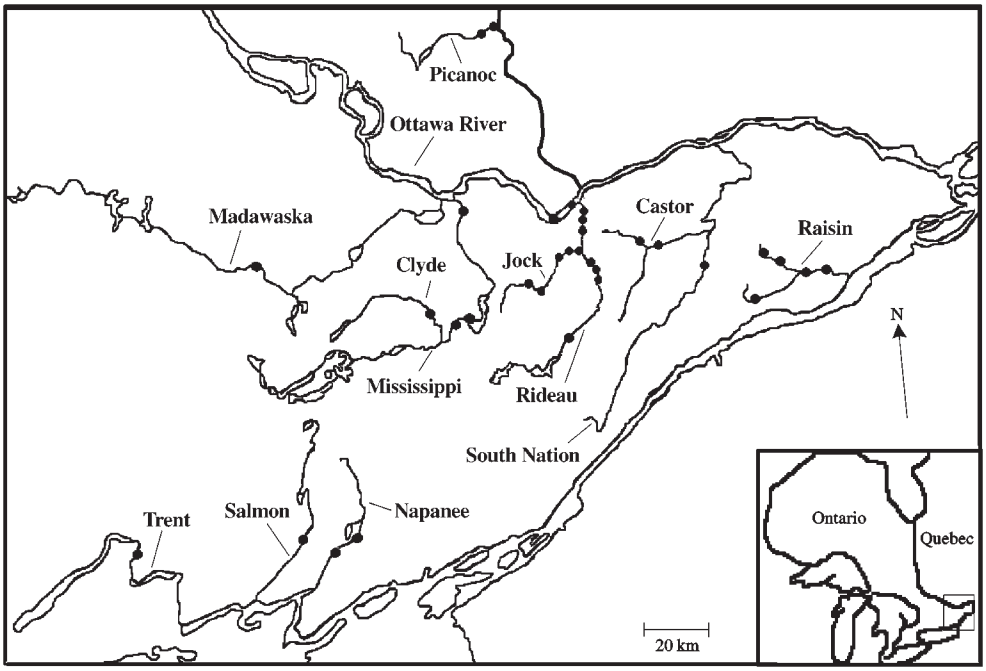
Fig. 1. Location of the 33 sites sampled on 13 rivers in southern Ontario and western Quebec during the summers of 1993, 1995, and 1996.



al. 1992) and *Rhizoclonium* (Biggs and Price 1987). In a study of New Zealand rivers, Biggs (1990) found that conductivity was the variable most strongly related to periphyton communities identified using cluster analysis. Biggs (1990) proposed that conductivity was an indicator of nutrient enrichment in the studied rivers because it was also positively correlated with the area of Tertiary siltstone in the watersheds, a sediment rich in cations and inorganic phosphorus. These observations suggest that nutrient enrichment may affect periphyton standing crop and also cause a shift in community composition towards particular algal taxa that form undesired benthic algal mats.

The purpose of the present study was to investigate the relationship of nutrients to periphyton biomass and community composition during summer low flows. We tested a model incorporating both nutrient concentration and water velocity to determine if water velocity effects could account for more variation in periphyton biomass. Periphyton taxonomy was examined to determine whether community composition changes in relation to trophy and to identify dominant algal taxa.

Materials and methods

Study areas

A total of 33 sites were sampled on 13 temperate lowland rivers in southern Ontario and western Quebec during periods of low flow (Fig. 1). Samples were collected on one occassion at a site between June and August in 1993, 1995, or 1996 (Table 1). The rivers ranged widely in size, with drainage basin areas from 404 km^2 (Raisin River) to 90 900 km^2 (Ottawa River) and summer low flows typically ranging from <1 $m^3 \cdot s^{-1}$ to nearly 700 $m^3 \cdot s^{-1}$ (Water Survey of Canada 1990). Watershed land use also varied among rivers from undisturbed forest to agricultural and urban development.

Epilithic periphyton was sampled in the main channel of shallow riffle zones. Fast-water areas were sufficiently wide (>10 m, except some sites on the Raisin River) and shallow (<0.5 m) to assume that light was not limiting for periphyton growth. Riverbeds were primarily composed of rock substrate.

Field sampling

Rocks were collected randomly from each site by walking across the shallow riffle zone along a transect perpendicular to the shoreline. The number of replicate rocks collected from a site depended on the sampling year (1993, $n = 20$; 1995, $n = 8$; June 1996, $n = 2$; August 1996, $n = 3$). Rocks were roughly fist size and ranged in surface area from 70 to 360 cm^2. Water velocities (centimetres per second) were measured above each rock at a height of 0.4 times the depth (mean current velocity) and just above the substrate (proximal velocity) using a Gurley No. 625 Pygmy current meter. Water conductivity was measured with a Hydrolab in 1995 and YSI model 33 S-C-T probe in 1996. Samples were placed in Ziplock bags, stored in a cooler in the field, kept in a refrigerator in the laboratory, and processed within 24 h of collection.

Periphyton biomass

Periphyton biomass was estimated on each rock from Chl *a* standing stock. First, rocks were scraped with a nylon-bristled nailbrush. The scraped material was washed off the brush and rock with 250–500 mL of filtered river water and then homogenized in a blender. A sample of 5–30 mL of homogenate was filtered through a Whatman HA-195 for Chl *a* analysis. Pigments were extracted with a 10-mL mixture of dimethyl sulfoxide – acetone solvent heated at 65°C for 10 min (Burnison 1980). Spectrophotometer readings were used to calculate Chl *a* with a trichromatic equation (Jeffrey and Humphrey 1975). A 50-mL subsample of periphyton homogenate was also preserved in Lugol's solution for taxonomic identification of the algal community. Rock surface area was estimated by wrapping the rock in aluminum foil and multiplying the mass of the foil by an area/mass conversion factor. Chl *a* (milligrams per square metre) is reported in units of rock surface area

Table 1. Ranges in mean Chl *a*, TP, and TN concentrations, water conductivity, and current velocity measured at 33 sites on 13 rivers during the summers of 1993, 1995, and 1996.

River	Drainage area (km^2)	Year	No. of sites	Chl *a* ($mg \cdot m^{-2}$)	TP ($\mu g \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	Conductivity ($\mu S \cdot cm^{-1}$)	Current velocity ($cm \cdot s^{-1}$)
Castor	433	1996	2	311–470	52–82	795–2433	685–723	34–58
Clyde	614	1996	1	14	14	476	264	19
Jock	559	1995	5	38–172	44–130	765–1618	441–495	32–45
Madawaska	8 310	1993	1	27	8	323	na	na
Mississippi	3 780	1996	3	32–59	12–25	383–566	184–225	34–107
Napanee	777	1996	2	40–78	21	560–583	175–191	46–59
Ottawa	90 900	1995	2	17–26	9–10	na	65	10–40
Picanoc	1 290	1996	2	9–12	6–11	200–206	74–101	63–83
Raisin	404	1996	5	42–148	40–76	179–1579	379–547	39–53
Rideau	3 830	1993, 1995	7	85–153	27–42	673–799	362–401	25–41
Salmon	891	1996	1	32	15	429	238	33
South Nation	3 810	1996	1	238	70	2873	560	84
Trent	12 000	1993	1	114	27	577	na	na
Total range and sample size				9–470 (n = 33)	6–130 (n = 33)	179–2873 (n = 30)	65–723 (n = 25)	10–107 (n = 25)

Note: Estimates represent means from one sampling date and do not include temporal variability. TN concentration, conductivity, and current velocity were not measured at all sites (na, not available). Total ranges and sample sizes for each parameter are listed at the bottom of the table. Watershed drainage area for each river was obtained from the Water Survey of Canada (1990).

assuming that periphyton occupied 60% of the stone surface (Biggs and Close 1989).

Nutrient analyses

In 1993 and 1996, three replicate water samples were collected per site at the time of periphyton sampling. In 1995, water chemistry data were obtained from the Regional Municipality of Ottawa–Carleton, Surface Water Quality Branch, who measured nutrient concentrations at corresponding sites within 24–72 h of our periphyton sampling. Chemical analyses were performed by the Regional Municipality of Ottawa–Carleton for all three years. Total phosphorus (TP) was determined by acid digestion to orthophosphorus followed by reaction with ammonium molybdate and ascorbic acid, and total Kjeldahl nitrogen (TKN) was determined by converting organic nitrogen to ammonium sulfate through acid digestion (Regional Municipality of Ottawa–Carleton 1993). Nitrate–nitrite (NO_3–NO_2) was determined by reducing nitrate to nitrite. Nitrite was then diazotized with sulfanilimide and coupled with ethylenediamine dihydrochloride (Regional Municipality of Ottawa–Carleton 1993). Total nitrogen (TN) was calculated as the sum of TKN (unfiltered) and NO_3-NO_2.

Periphyton taxonomy

Seventeen of the 33 sites sampled for periphyton biomass were also examined for algal community composition. We chose a particular subset of samples that were collected over a 7-day period (August 7–14, 1996, 14 sites) in order to avoid the effects of seasonality on periphyton composition. To further broaden the range in trophy, taxonomic samples from three other sites collected between July 22 and 25, 1995, were also included. Three replicate samples were analyzed per site. Each of these samples was a 50-mL subsample from the scraped homogenate used for Chl *a* analysis (see Periphyton biomass above) and was preserved with Lugol's solution.

Identifications were made from aliquots of 0.2–0.5 mL settled in a modified Utermöhl counting chamber and counted using an upright Leitz diaplan or Olympus BH-2 compound microscope with phase and differential interference contrast optics. Benthic algae were identified to genus using Prescott (1973) for non-diatom taxa and Krammer and Lange-Bertalot (1986–1991) for diatoms. Collected algae were assigned to four algal taxonomic divisions: Chlorophyta (green algae), Rhodophyta (red algae), Bacillariophyta (diatoms), and Cyanophyta (cyanobacteria). Small pennate diatoms (i.e., *Achananthes* spp., *Navicula* spp.) were not identified but were counted together in the category "pennate diatoms". Transects were counted at 250 and 500× magnifications. The average number of filament fragments and single-celled algae counted per sample was 368 (n = 51). The number of cells per filament fragment ranged from two to >30. Fragment and cell densities and biomass were calculated for each recorded taxon. Cell dimensions were measured in each sample and cell volumes were estimated by approximation to geometric shapes of known volume. Algal biomass was measured by converting calculated cell volumes to biomass assuming a specific density of 1 $g \cdot cm^{-3}$. Algal biomass (micrograms per square centimetre) was calculated in units of rock surface area assuming that periphyton occupied 60% of the stone surface and was averaged over three replicates to determine mean biomass levels for each site.

Data analysis

Estimates of Chl *a*, nutrient concentrations, conductivity, water velocity, and taxonomic biomass represent site means from one sampling date and do not include temporal variability. TN concentration, conductivity, and water velocity were not measured at all sites.

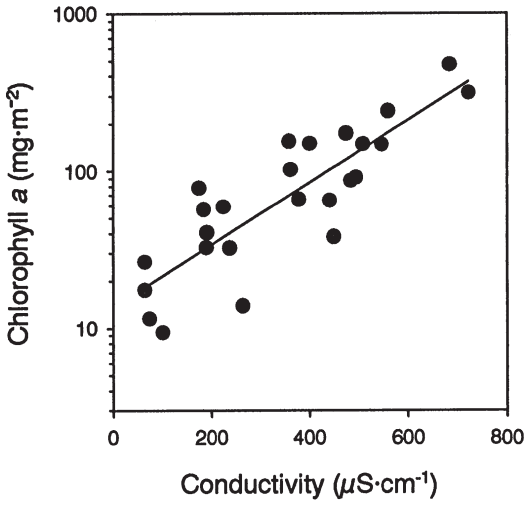
Relationships between trophy and periphyton biomass and community composition were examined by linear regression analysis. Periphyton Chl *a* (milligrams per square metre) was regressed against TN (micrograms per litre), TP (micrograms per litre), and conductivity (microsiemens per centimetre). Each regression was performed separately due to high multicollinearity of the predictor variables. Division and genus biomass (micrograms per square centimetre) were regressed against Chl *a* (milligrams per square metre) and TP (micrograms per litre). Mean current velocity and proximal velocity (centimetres per second) were tested as predictors of the residual variation in each regression model. Trends of percent division biomass in relation to periphyton standing crop

Table 2. Summary of regression models relating periphyton Chl *a* ($mg \cdot m^{-2}$) to water conductivity ($\mu S \cdot cm^{-1}$) and TP and TN concentration ($\mu g \cdot L^{-1}$).

Equation	r^2	*F*	RMS	*p*	*n*
log Chl *a* = 0.002 conductivity + 1.134	0.71	59.5	0.058	<0.001	25
log Chl *a* = 0.905 log TP + 0.490	0.56	41.6	0.071	<0.001	33
log Chl *a* = 0.984 log TN – 0.935	0.50	30.2	0.079	<0.001	30

Note: All variables required log transformation except conductivity. The coefficient of determination (r^2), *F* value, residual mean square (RMS), *p* value, and number of observations (*n*) are presented for each model.

Fig. 2. Regressions of periphyton Chl *a* as a function of water conductivity (r^2 = 0.71, $p < 0.001$, n = 25) and TP concentration (r^2 = 0.56, $p < 0.001$, n = 33). All variables are log transformed except conductivity.



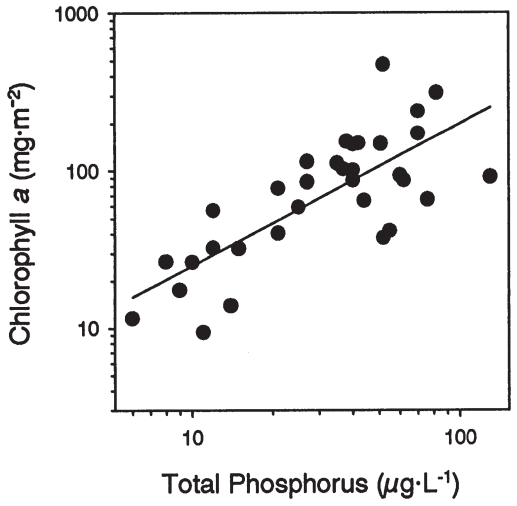
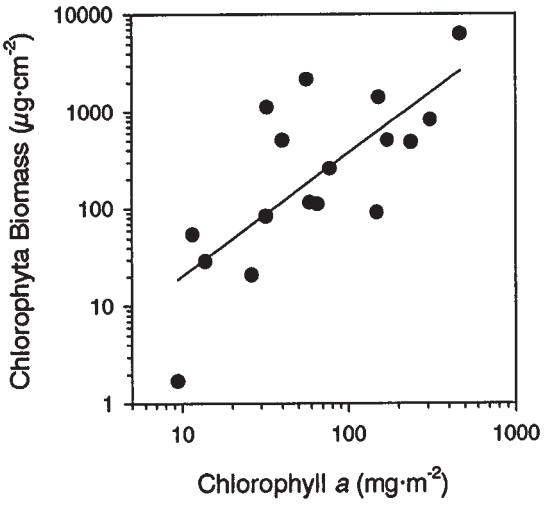
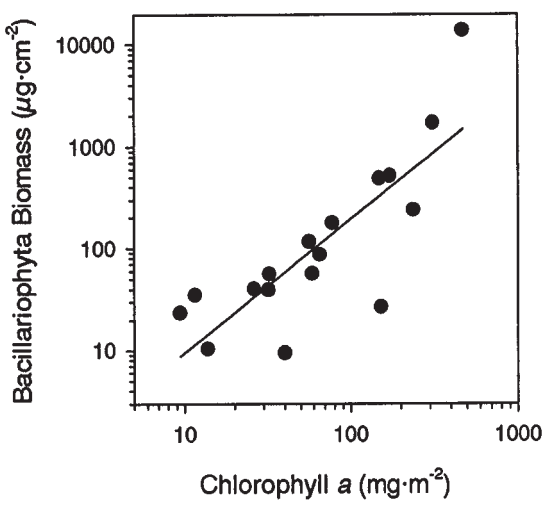


Fig. 3. Regressions of periphyton Chl *a* in relation to Chlorophyta biomass (r^2 = 0.51, p = 0.001, n = 17) and Bacillariophyta biomass (r^2 = 0.64, $p < 0.001$, n = 17). Variables are log transformed.





were nonlinear and were examined with a model-free, locally weighted sequential smoothing technique (LOWESS).

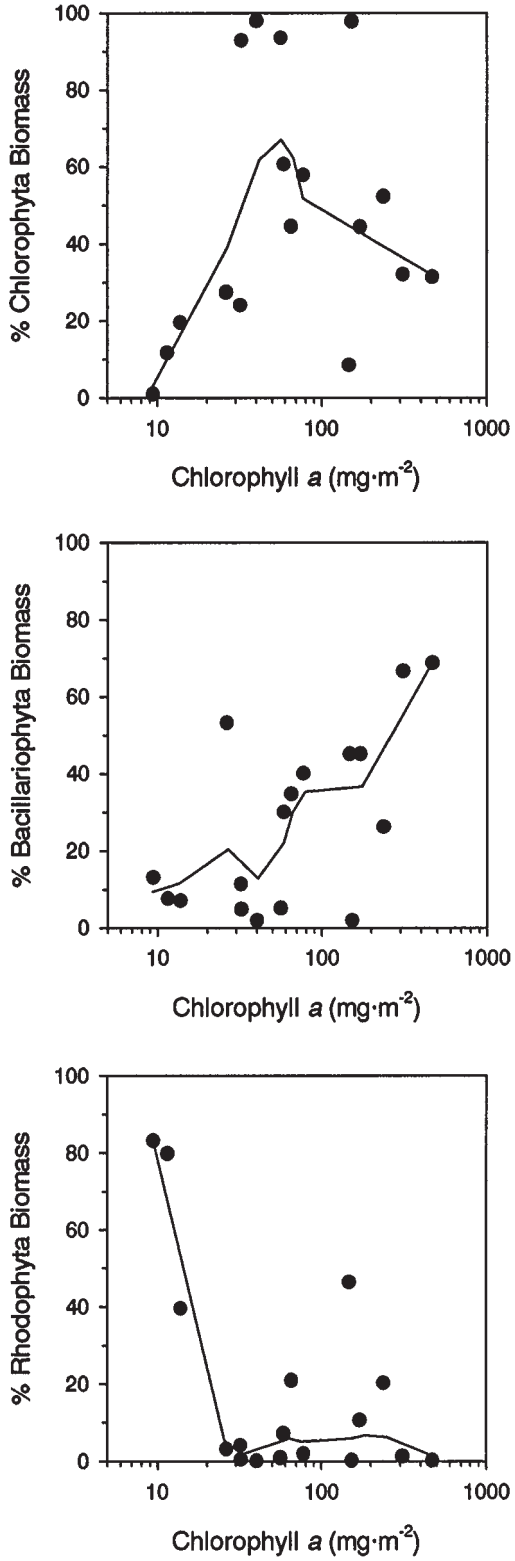
Statistical analyses were performed using Systat (Wilkinson 1996). For multiple regression analyses, a second independent variable was included if it improved the fit of the model. Significance of a term was tested using coefficients of determination from the higher and reduced models to calculate an *F* statistic (Sokal and Rohlf 1995). Variables were log transformed or log(Y + 1) transformed (if the biomass of a genus was zero at a site) to meet the assumptions of the parametric test.

Results

Periphyton biomass

Periphyton Chl *a* was positively related to water conductivity and ambient nutrient concentrations. Chl *a* ranged from 9 to 470 $mg \cdot m^{-2}$ among sites, while TP and TN ranged from 6 to 130 and from 179 to 2873 $\mu g \cdot L^{-1}$, respectively (Table 1). The study rivers drained watersheds of either granitic Canadian Shield or St. Lawrence Lowland sedimentary bed-

Fig. 4. Relationships between percent contribution of taxonomic groups (Chlorophyta, Bacillariophyta, Rhodophyta) and periphyton Chl *a*. Data are fitted with a locally weighted smoothing technique (LOWESS). Periphyton Chl *a* is log transformed.



rock, and water conductivities reflected these differences in underlying geology with values ranging from 65 to 723 μS·cm^{-1}. Chl *a* was most strongly related to conductivity (r^2 = 0.71), but ambient TP and TN concentrations also explained 56 and 50% of the variation, respectively (Fig. 2; Table 2). TN and TP were positively correlated with water conductivity ($r^2 > 0.70$, $p < 0.001$), suggesting strong relationships between concentrations of nutrients and drainage basin characteristics. Furthermore, TP, TN, and conductivity were negatively correlated with the drainage basin area (square kilometres) of study sites (TP: $r^2 = 0.26$, $p = 0.002$; TN: $r^2 = 0.13$, $p = 0.034$; conductivity: $r^2 = 0.27$, $p = 0.006$), indicating that nutrients tended to be slightly higher in smaller rivers. The collinearity between nutrients, conductivity, and drainage area precluded these factors from being related to Chl *a* in a multiple regression model.

Chl *a* standing stock, once corrected for nutrient concentration or conductivity, was not related to water velocity. Multiple regression analysis was performed to determine if mean current velocity and proximal velocity could explain any of the residual variation in Chl *a* when TP, TN, and conductivity were used as predictor variables. Sample sizes were lower in the multiple regressions (TP, $n = 25$; TN, $n = 23$; conductivity, $n = 25$) because water velocity data were not available for all sites. Neither velocity parameter accounted for more than 2% of Chl *a* variation in the three models ($F \leq 0.9$, $p > 0.05$) despite the wide range in mean current velocities (10–107 cm·s^{-1}, Table 1).

Periphyton community composition

Differences in periphyton standing stock were related to changes in Chlorophyta and Bacillariophyta biomass. Chlorophyta and Bacillariophyta biomasses ranged 4 orders of magnitude among sites from 2 to 6226 and from 9 to 13 647 μg·cm^{-2}, respectively. Rhodophyta and Cyanophyta biomasses tended to be lower but also ranged 4 orders from 0.2 to 495 and from 0.5 to 209 μg·cm^{-2}, respectively. Chlorophyta and Bacillariophyta biomasses were positively correlated with periphyton Chl *a* (Fig. 3), whereas Rhodophyta and Cyanophyta biomasses were not ($p > 0.10$). Biomass of each taxonomic division was not related to mean current velocity or proximal velocity ($F \leq 1.2$, $p > 0.05$).

The relative proportions of taxonomic divisions varied with total standing stock. Overall, Chlorophyta accounted for the highest portion of biomass, averaging 47% among sites. Bacillariophyta, Rhodophyta, and Cyanophyta represented smaller fractions of total biomass, averaging 27, 19, and 7%, respectively. Percent Chlorophyta biomass increased with periphyton Chl *a* and was the largest fraction at moderately eutrophic sites (Fig. 4). At the highest standing crops, the percent biomass of Chlorophyta decreased with an associated increase in the proportion of Bacillariophyta. Rhodophyta contributed the most biomass at sites with the lowest Chl *a* (Fig. 4). Cyanophyta represented <3% of total biomass at 80% of the sites.

Particular algal genera were dominant at nutrient-enriched sites. Genera were ranked by highest percent contributors to site total biomass and were considered dominant if they were among the top ranking taxa that cumulatively accounted for 70% of total biomass. Despite the wide variation in dominant algal genera among rivers, patterns were observed

Table 3. Dominant genera of river periphyton communities.

River and site No.	TP ($\mu g \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	Conductivity ($\mu S \cdot cm^{-1}$)	Dominant genera (%)
Picanoc 1	6	200	74	*Boldia* (76)
Ottawa 3	10	—	65	*Gomphonema* (45), *Coleochaete* (25)
Picanoc 2	11	206	101	*Boldia* (70)
Mississippi 2	12	383	183	*Spirogyra* (90)
Mississippi 3	12	386	190	*Oedogonium* (73)
Clyde 1	14	476	264	*Audouinella* (40), *Lyngbya* (31)
Salmon 1	15	429	238	*Tolypothrix* (60), *Oedogonium* (23)
Napanee 2	21	583	175	*Rhizoclonium* (51), *Cocconeis* (30)
Napanee 1	21	560	191	*Cladophora* (98)
Mississippi 1	25	566	225	*Cladophora* (41), *Coleochaete* (20), pennate diatoms (14)
Rideau 3	38	688	358	*Cladophora* (68), *Hydrodictyon* (17)
Raisin 7	51	1170	509	*Audouinella* (46), *Melosira* (32)
Castor 2	52	795	685	*Melosira* (61), *Cladophora* (30)
Jock 2	70	942	475	*Cladophora* (44), *Melosira* (20), *Audouinella* (11), *Cymbella* (11)
South Nation 1	70	2873	560	*Cladophora* (48), *Audouinella* (20), *Melosira* (10)
Raisin 2	76	1579	379	*Cladophora* (31), *Audouinella* (21), pennate diatoms (14), *Oedogonium* (13)
Castor 1	82	2433	723	*Melosira* (57), *Cladophora* (30)

Note: Taxonomic samples were collected in late July or mid-August, and three replicate samples were analyzed per site. Genera are ranked by highest percent contributors to site total biomass and were considered dominant if they were among the top ranking taxa that cumulatively accounted for 70% of total biomass. River sites are ranked by TP concentration.

along a TP gradient (Table 3). There was a high diversity of periphyton communities among sites with TP concentrations <20 $\mu g \cdot L^{-1}$. In contrast, *Cladophora*, *Audouinella*, and (or) *Melosira* were dominant taxa at sites with TP roughly >20 $\mu g \cdot L^{-1}$ (Table 3).

Cladophora represented a large fraction of Chlorophyta biomass at nutrient-enriched sites. Although 16 genera of Chlorophyta were identified, including eight filamentous taxa, *Cladophora* accounted for >65% of green algal biomass at sites with TP concentrations >20 $\mu g \cdot L^{-1}$ (Fig. 5). Other green macroalgae, primarily *Spirogyra*, *Oedogonium*, and *Coleochaete*, represented a large fraction of Chlorophyta biomass at nutrient-poor sites (Fig. 5). *Cladophora* biomass was strongly correlated with ambient TP concentration (Fig. 6) and was unrelated to mean current velocity or proximal velocity ($F \leq 0.2$, $p > 0.05$). Conductivity also had a positive effect on *Cladophora* biomass after controlling for the effect of TP concentration (Fig. 6). *Cladophora* was recorded at all sites except for those with the lowest TP concentrations ($\leq$ 11 $\mu g \cdot L^{-1}$) and conductivities ($\leq$ 101 $\mu S \cdot cm^{-1}$) on the Ottawa and Picanoc rivers.

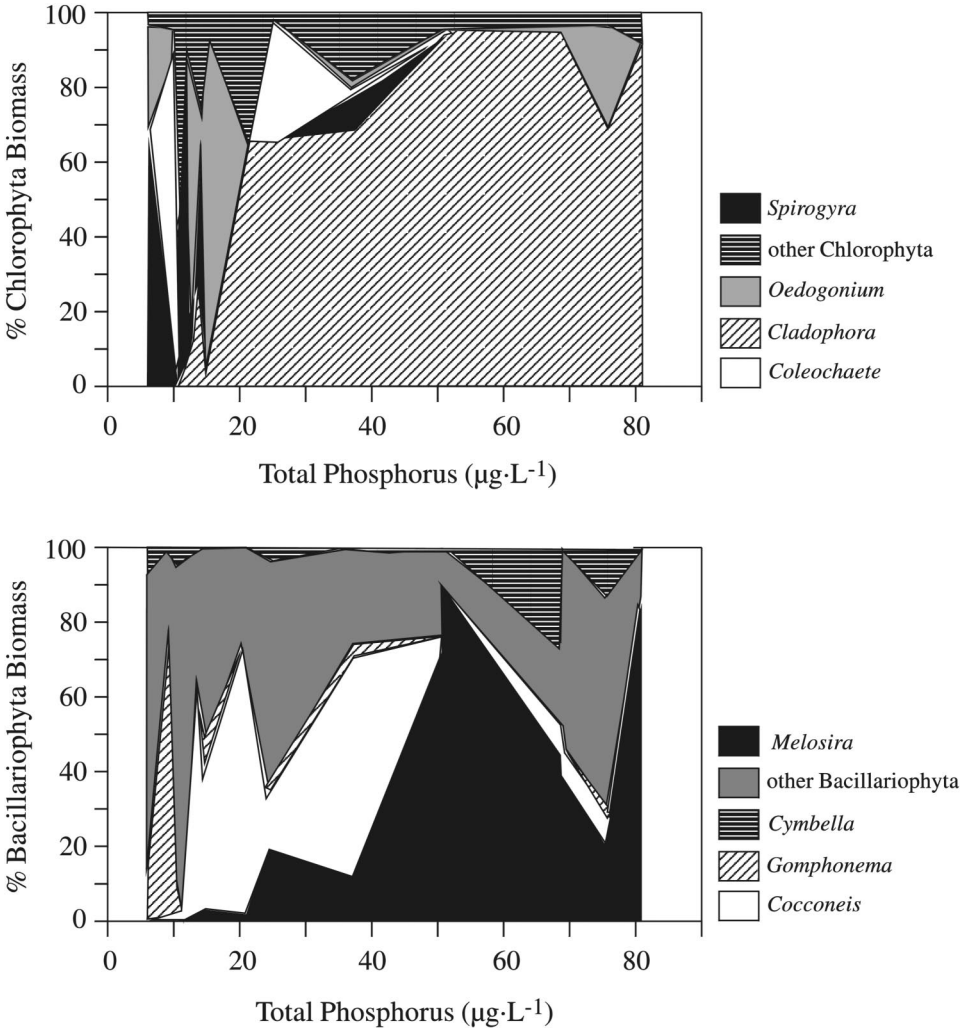
The diatom *Melosira* also responded positively to nutrient enrichment. *Melosira* biomass increased with TP concentration ($r^2 = 0.64$, $p < 0.001$) and was a dominant contributor to both Bacillariophyta biomass (Fig. 5) and total biomass (Table 3) at eutrophic sites. *Gomphonema* represented a significant portion of diatom biomass at some low-TP sites, and there was a shift in dominance from *Cocconeis* to *Melosira* between intermediate to high TP concentrations (Fig. 5). These trends describe only major changes in Bacillariophyta composition, and more than 16 diatom genera were identified, some of which were important taxa at a few sites (i.e., *Achananthes*, *Cymbella*, *Navicula*, *Amphora*). Nutrients may have indirectly affected diatom composition by stimulating the growth of filamentous biomass and thereby increasing the surface area available for colonization by epiphytic taxa. This is suggested by the positive relationship between TP concentration and biomass of the epiphytes *Cocconeis* ($r^2 = 0.32$, $p = 0.010$) and *Rhoicosphenia* ($r^2 = 0.56$, $p < 0.001$).

Audouinella, a red filamentous alga, was a dominant taxon in a few nutrient-enriched rivers (Table 3). Only three Rhodophyta genera were identified, one (*Audouinella*) of which represented 100% of red algal biomass at the majority of sites. The two other genera, *Batrachospermum* and *Boldia*, were only found in the low-nutrient and low-conductivity Picanoc River. *Audouinella* was present at all sites examined for taxonomy, and its biomass was positively correlated with TP concentration ($r^2 = 0.39$, $p = 0.004$) and not related to mean current velocity or proximal velocity ($F \leq 0.8$, $p > 0.05$).

Discussion

Periphyton biomass was strongly related to ambient TP concentration. Biggs and Close (1989) and Lohman et al. (1992) also found strong correlations in which TP explained 47–60% of the variation in periphyton Chl *a* (compared with 56% in this study). For the purpose of comparison with our model, their TP and Chl *a* data were log transformed and regressed (Table 4). The slope of our model was similar to that of Biggs and Close (1989) who sampled New Zealand rivers of comparable size with drainage areas from <164 to 2626 km^2 (Table 4). However, the slope of our model was three or four times greater than those of Lohman et al. (1992) who sampled streams mostly smaller than fourth order (Table 4). The difference in slopes may reflect a reduced effect of nutrients on periphyton biomass in stream versus river systems (Lamberti and Steinman 1997). Other stream studies have found no association between nutrients and periphyton Chl *a* (Jones et al. 1984; Welch et al. 1988). Flood events can strongly regulate periphyton biomass in streams (Lohman et al. 1992), but larger rivers tend to have more stable flow

Fig. 5. Area plots of percent contribution of dominant genera to Chlorophyta biomass or Bacillariophyta biomass in relation to TP concentration.

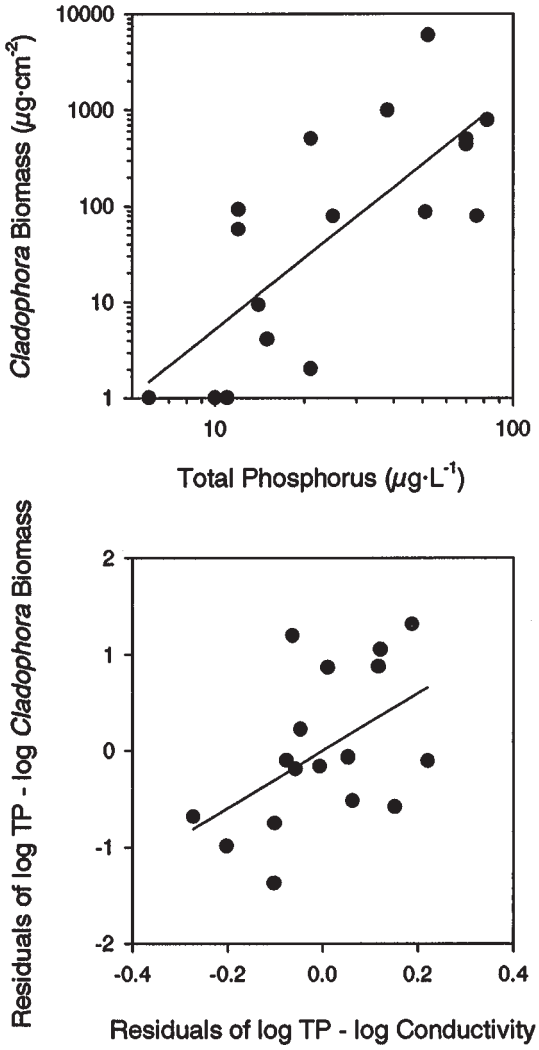


regimes (Poff and Ward 1989; Jowett and Duncan 1990). Thus, riffle zones in larger rivers may represent environments where hydraulic disturbance is less important in periphyton dynamics simply because flood events are less frequent. In the study by Biggs and Close (1989), three lowland rivers exhibited particularly low hydrological disturbance regimes, and they positively influenced the slope of the model. However, the importance of stream size is speculative, and differences in the log TP – log Chl *a* models may simply reflect regional differences in the ecosystem processes that regulate biomass accrual.

Current velocity and proximal velocity were not related to periphyton biomass. There have been conflicting results reported in the literature with respect to water velocity effects (Stevenson 1996). Current can stimulate biomass accrual by increasing nutrient transport to cells and can also reduce biomass through drag (Stevenson 1996). The particular velocity effect depends on the nutrient regime (Horner and Welch 1981) and the morphology of the periphyton community (Biggs et al. 1998). Biggs et al. (1998) found that within-site patchiness in periphyton biomass was strongly related to current velocity but the effect differed for various community growth forms (mucilaginous diatoms, stalked/short filamentous diatoms, long green filamentous algae). Because this study's survey data set was composed of sites with varying community morphologies and nutrient regimes, it is perhaps not surprising that no relationship between water velocity and biomass was observed. Water velocity should better predict periphyton biomass at smaller scales of observation (i.e., within-site patchiness) where more homogeneous nutrient regimes and community types are found.

Composition of the periphyton communities changed in relation to trophy. Higher periphyton standing stocks were primarily associated with increases in green algae and diatom biomass. Filamentous green algae represented the largest fraction of community biomass at moderately eutrophic sites. Proliferations of benthic filamentous Chlorophyta have been commonly associated with nutrient enrichment in both lotic (Perrin et al. 1987; Biggs 1990) and lentic environments (Cattaneo 1987; Jacoby et al. 1991). There was a shift in the dominance among green algal taxa from *Spirogyra*, *Oedogonium*, and *Coleochaete* at low TP concentrations to *Cladophora* above 20 µg TP·L^{-1}. Changes in the diatom community were also observed with the appearance of *Melo-*

Fig. 6. Regressions of *Cladophora* biomass in relation to TP concentration (log *Cladophora* biomass = 2.500 log TP – 1.820; $r^2 = 0.53$, $p = 0.001$, $n = 17$) and water conductivity ($r^2 = 0.20$, $p = 0.041$, $n = 17$) after controlling for the effect of TP. Conductivity and TP are log transformed and *Cladophora* biomass is log(Y + 1) transformed.



sira at nutrient-enriched sites. *Melosira* and *Cladophora* were similarly reported as dominant taxa for higher biomass sites in New Zealand rivers (Biggs and Price 1987).

At the highest standing crops, the relative contribution of Chlorophyta decreased with an associated increase in Bacillariophyta. This proportional decrease in Chlorophyta biomass does not necessarily indicate a reduction in the competitive success of green algae. Rather, the percent increase in diatom biomass may reflect the ability of these taxa to successfully colonize microhabitat created by thick filamentous mats (i.e., increased surface area for colonization). Diatoms are highly successful colonizers and can contribute 30–60% to total biomass of *Cladophora* mats in nutrient-rich waters (Stevenson and Stoermer 1982). However, at a few eutrophic sites, the red algal filament *Audouinella* was a dominant taxon, suggesting that this genus can successfully compete for substrate space in the presence of filamentous greens, primarily *Cladophora*. The species of *Audouinella* observed in the study rivers, *Audouinella hermannii*, is widespread throughout North America and is most common in temperate regions (Sheath and Cole 1992). Despite its prevalence, little is known of the effect of nutrients on its distribution, and these findings indicate that this species is able to thrive in nutrient-enriched waters.

Nutrient kinetic theory provides a framework for our field observations that periphyton biomass and community composition are related to nutrients. During summer, when periphyton is exposed to high water temperatures (≥ 20°C) and abundant light in shallow unshaded riffle zones, nutrient availability is likely the primary determinant for benthic algal growth rates. Periphyton biomass measured in this study was not related to summer water temperatures. Nutrients also regulate peak standing crops because biomass accrual reduces nutrient diffusion within benthic mats and causes a shift from cellular to whole-mat growth kinetics (Bothwell 1989). Molecular diffusion of nutrients across the boundary layer of periphyton is a key process affecting the metabolism of the community (Riber and Wetzel 1987), and higher ambient nutrient concentrations continue to stimulate biomass accrual because larger nutrient gradients increase diffusion into thick deficient mats. Bothwell (1989) demonstrated that peak biomass of periphytic diatom communities increased over 100 mg Chl $a \cdot m^{-2}$ with additions of phosphorus concentrations greater than those required to achieve maximum growth rates in thin diatom films. Field observations by Lohman et al. (1992) also indicated that following a catastrophic flood, both the rate of biomass accrual and the peak recovery standing crops of periphyton were higher at more nutrient-enriched sites.

The distribution and abundance of benthic algae may also be in part related to taxa-specific nutrient kinetics. Periphytic algae have wide-ranging nutrient requirements for maximum growth rates from 0.5–1 µg $P \cdot L^{-1}$ for diatoms (Bothwell 1989) to 25–40 µg $P \cdot L^{-1}$ for filamentous greens such as *Stigeoclonium* or *Cladophora* (Rosemarin 1983) or even 60 µg $TP \cdot L^{-1}$ for *Cladophora* (Wong and Clark 1976). Borchardt et al. (1994) examined phosphorus uptake kinetics in *Spirogyra fluviatilis*, and they concluded that this species would best thrive under low steady supplies of phosphorus. In contrast, *Cladophora* has relatively high phosphorus requirements for optimal growth (Wong and Clark 1976; Rosemarin 1983). Our observation that *Spirogyra* was an important green algal filament at low TP concentrations whereas *Cladophora* dominated at higher TP coincides with predictions based on nutrient kinetic experiments.

Ecological information on *Cladophora* growth is of particular interest because nuisance proliferations of this filamentous genus are widespread (Wong and Clark 1976; Biggs and Price 1987; Dodds 1991). In the present study, *Cladophora* biomass increased with TP concentration, and a similar relationship was also observed with total inorganic phosphate in British rivers (Pitcairn and Hawkes 1973). Wong and Clark (1976) observed a positive correlation between ambient phosphorus concentration in the water and phosphorus content of *Cladophora* tissue in southern Ontario rivers. No correlation was found with tissue nitrogen, suggesting that *Cladophora* growth was phosphorus limited. Water hardness may be another chemical determinant of *Cladophora* biomass in rivers. *Cladophora* has long been

Table 4. Regression of periphyton Chl *a* ($mg \cdot m^{-2}$) as a function of TP concentration ($\mu g \cdot L^{-1}$) from the present study in comparison with other models obtained from the literature.

Coefficients						
Intercept (±SE)	log TP (±SE)	r^2	RMS	*p*	*n*	Source
0.490±0.213	0.905±0.140	0.56	0.071	<0.001	33	Present study
0.338±0.310	0.722±0.246	0.49	0.089	0.022	9	Biggs and Close 1989
1.207±0.115	0.247±0.056	0.46	0.038	<0.001	22	(*i*) Lohman et al. 1992
1.383±0.095	0.228±0.047	0.52	0.025	<0.001	22	(*ii*) Lohman et al. 1992

Note: Data sources: Biggs and Close (1989) (data are geometric annual means from nine New Zealand rivers) and Lohman et al. (1992) (data are annual means from 22 sites on 12 Northern Ozark streams for (*i*) 1985 and (*ii*) 1986). Data are log transformed. The coefficient of determination (r^2), residual mean square (RMS), *p* value, and number of observations (*n*) are presented for each model.

suspected to favor hard waters for growth (Whitton 1970), and the positive relationship between conductivity and *Cladophora* biomass after controlling for the effect of TP lends support to the idea that Ca^{2+} concentration is important (Sikes 1978). Sikes (1978) reported a high affinity for calcium by *Cladophora glomerata* which was associated with the thickening of its cell walls.

Neither temporal variability in nutrients and water velocity or invertebrate grazing was explored in this study and may account for unexplained variation. Water samples collected at the time of periphyton sampling may not have been an accurate reflection of nutrient loading due to temporal variability in water chemistry, and estimates of biomass on one sampling date represented growth accumulation over time. Furthermore, water velocities measured at the time of sampling were only coarse estimates of the average hydraulic conditions encountered by periphyton and may have been inadequate to estimate water velocity effects. Invertebrate grazing is believed to affect periphyton and has been demonstrated to remove large amounts of periphyton Chl *a* and alter algal assemblages in experimental studies (Feminella and Hawkins 1995).

In summary, biomass and taxonomic composition of river periphyton from riffle zones were strongly related to ambient nutrient concentrations but unrelated to water velocity. Nutrient-rich sites were associated with high periphyton standing crop and were dominated by particular filamentous taxa. TP concentration was strongly correlated with periphyton Chl *a* and *Cladophora* biomass during summer low flows, but these relationships may not hold during other seasons and periods of high flow.

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