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Ecological stoichiometry in benthic food webs: Effect of light and nutrients on periphyton food quantity and quality in lakes

Abstract—To quantify the effect of light and nutrients on periphyton food quantity and quality, a series of experiments, consisting of full light and shade treatments, was conducted in 2003 in 11 lakes differing in nutrient status and turbidity. Periphyton chlorophyll *a*, C:P, and benthic macroinvertebrate biomass were measured on rocks or artificial substrates (glass slides) or both. Periphyton biomass increased and periphyton C:P decreased as total phosphorus increased. Periphyton biomass and C:P were higher in light than in shade. Benthic macroinvertebrate biomass was higher with high periphyton biomass and low periphyton C:P. Both turbidity and nutrient concentrations in natural water bodies are altered by human-driven and natural processes; therefore we expect periphyton biomass and C:P to increase in lakes as clarity increases and nutrient content decreases, resulting in high-quantity but low-quality benthic food.

Light and nutrient availability strongly affect the ratio of elements in primary producers (Reynolds 1984; Sterner and Elser 2002). However, relatively little is known about how the stoichiometry of primary producers from different habitats responds to environmental change. Specifically, algae in benthic habitats are likely to be adapted to low

light conditions and may show little alteration in their ratio of carbon (C) to other elements in response to changes in light level. Until we understand how benthic primary producer stoichiometry responds to environmental changes in light and nutrient availability, we cannot predict whole-lake responses to ongoing environmental changes, such as eutrophication, oligotrophication (reversal of eutrophication), and water clearing by introduced grazers such as *Dreissena* (*Dreissena polymorpha* and *Dreissena bugensis*).

In lakes, a fundamental habitat difference exists between bottom-associated and water column habitats; similar differences occur in terrestrial ecosystems where there is a shaded understory. In lake ecosystems, periphyton differ physically and structurally from phytoplankton because they attach to substrate, are sessile, and create a mat. Periphyton production is more likely to be light- than nutrient-limited in turbid lakes or in deep zones of lakes because benthic algae are fixed in space and experience changes in light level when environmental conditions change (Vadeboncoeur et al. 2003). In addition, epipelton (periphyton growing on soft sediment) absorb most of their nutrients from nutrient-rich sediment pore water and groundwater (Pringle 1987; Hagerthey and Kerfoot 1998). Therefore, it is not clear if the response of periphyton

Table 1. General limnological parameters in the experimental lakes, including TP and light level under full or shade treatment. TP ranged from 4 $\mu\text{g L}^{-1}$ to 350 $\mu\text{g L}^{-1}$ in the experimental lakes. The light level under shade is about 6% to 12% of full light across the lakes besides hypereutrophic Lake Neatahwanta.

Lakes	Surface area (km ²)	Depth (m)	Latitude	Longitude	Temperature (°C)	pH	Conductivity ($\mu\text{siemens cm}^{-1}$)	TP ($\mu\text{g L}^{-1}$)	Light ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Shade ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Shade:Light (%)
Little York	0.41	21.34	42°42'N	76°10'W	23.36	7.86	97	4.27	316.05	19.30	6.11
Jamesville	0.91	10.67	42°58'N	76°06'W	24.70	8.08	206	6.06	303.93	30.63	11.37
Owasco	27.49	51.83	42°54'N	76°33'W	25.12	8.05	99	7.26	434.94	31.70	7.24
Otisco	9.05	21.34	42°54'N	76°18'W	23.60	7.88	122	21.57	308.36	30.21	11.18
Seneca	175.44	243.90	42°52'N	76°59'W	25.09	8.59	227	22.59	384.22	29.72	7.57
Sodus Bay	3.04	10.67	43°23'N	76°53'W	24.19	8.23	101	26.10	270.56	17.20	7.25
Oneida	205.97	15.24	43°11'N	76°56'W	26.41	8.74	111	35.15	393.55	27.98	6.85
Mud	0.96	9.15	42°11'N	76°25'W	25.62	8.17	108	40.17	357.50	21.02	5.89
Onondaga	12.06	18.90	43°06'N	76°13'W	24.78	8.03	610	76.98	338.63	25.24	6.43
Barry	0.06	0.61	43°02'N	76°07'W	26.37	8.50	351	102.93	366.21	35.70	9.88
Neatahwanta	2.89	3.66	43°19'N	76°26'W	26.89	9.97	119	343.05	13.25	3.15	34.53

nutrient stoichiometry to changing environmental conditions will be the same as that of phytoplankton (Havens et al. 1999). Consequently, the goal of this study is to determine the stoichiometric response of periphyton to light and nutrient changes and compare it with what is known about primary producers from other habitats.

Light and nutrients can each affect growth and stoichiometry of periphyton separately (Larned and Santos 2000; Stelzer and Lamberti 2001), but changes in light and nutrients usually interact in lakes because light decreases with shading from increasing phytoplankton biomass (caused by high nutrients) (Kirk 1983). There is strong evidence that phytoplankton C:nutrient is regulated by the ratio of mixed-layer light to water column nutrients (Sterner et al. 1997). However, we predict that periphyton will respond differently from phytoplankton to the light:nutrient ratio depending on whether they are attached to hard or soft substrate. Specifically, we expect epipelton production and elemental composition to be relatively insensitive to changes in water column nutrient concentrations because these algae are in contact with nutrient-rich sediments. On the other hand, epilithon (periphyton growing on rock) are similar to phytoplankton in that they absorb most nutrients from water. Therefore, epilithon P content should respond positively to P enrichment, but the growth response of epilithon in lakes will depend on the balance of the positive effects of greater P availability and the negative effects of reduced light from shading by phytoplankton.

Recent work has found that P enrichment increased periphyton biomass and decreased periphyton C:P (Frost et al. 2002); however, few studies consider light as another primary factor affecting periphyton (but see Frost and Elser 2002a; they found that shading did not affect periphyton C:P in oligotrophic lakes). The overall objective of our study is to quantify light and nutrient effects on periphyton quantity and quality (C:P) in lakes. We conducted in situ experiments where we manipulated light and took advantage of a natural gradient of nutrient concentration existing in 11 lakes. We expect that: (1) increasing light will increase periphyton biomass; (2)

increasing P concentrations in water will increase periphyton (especially epilithon) growth if light is not limiting; (3) increasing light will increase C:P ratios of periphyton; and (4) decreasing phosphorus will increase periphyton (especially epilithon) C:P ratio.

Methods—Experimental design and sampling methods: We selected 11 lakes in the area of Syracuse, NY (42°–43°N, 76°–77°W; Table 1). The lakes had a wide range of total phosphorus (TP) (range from 4 to 350 $\mu\text{g L}^{-1}$) due to natural and anthropogenic activities (Table 1). Periphyton was grown in shade or full sun conditions in these 11 lakes for 3 weeks in summer 2003 (end of July to early August). Sixteen artificial substrates (glass slides) were placed in metal cages (30 cm \times 20 cm \times 8 cm) and attached to the lake sediment at 0.3–0.5 m depth. The cages were covered with 2-mm mesh that excluded some large invertebrate grazers, especially snails, which do not have compressible bodies. However, most macroinvertebrates, including amphipods, isopods, chironomids, oligochaetes, and small snails, were able to enter the cages. A preliminary experiment conducted in one lake showed that the mesh cages had no significant effect on grazer densities ($F_{1,8} = 0.69$, $p = 0.43$); most macroinvertebrates, including amphipods, isopods, chironomids, oligochaetes, and small snails, were able to enter the cages. The cages did exclude fish and ducks and protected the slides from being dislodged by waves. The slides were placed vertically to avoid shading of one slide by another. The slides either received full light or shade conditions created by covering half of each cage with neutral density shade cloth. Light levels in the shade treatment were decreased to 6–12% of full light (Table 1). After 3 weeks the slides were brought back to the lab, gently scraped with a razor, and filtered on precombusted (500°C for 1 h) and preweighed Whatman GF/F filters to measure chlorophyll *a* (Chl *a*), C, N, and P content of periphyton (see lab analysis methods for details). In the field, slides from both light and shade treatments from each cage were also preserved with 2.5% glutaraldehyde for later invertebrate and benthic algae identification and enumeration. When present, large macroinvertebrates

such as snails and amphipods were removed before scraping to reduce the animal contribution to the periphyton C, N, and P signature.

Naturally occurring epilithon was also sampled in each lake when the artificial slides were collected. We randomly picked three natural rocks with flat surfaces, close to the cages in each lake, except at one site, Barry Park, which lacked natural rock. We measured the length and width or height of the rocks to estimate their area. In the field, rocks were scraped using a razor, and periphyton were transferred to a bottle with filtered lake water. All samples were returned to the laboratory on dry ice. Samples were adjusted to 100 mL using filtered lake water. After mixing, 10-mL subsamples were filtered on GF/F filters for chlorophyll analysis. The remaining samples were dried at 60°C for at least 48 h. Subsamples of this dried periphyton were used to measure particulate C, N, and P.

Phytoplankton biomass and nutrient content were also measured at the same time that artificial glass slides were collected. Five hundred milliliters of lake water were collected at 0.5 m depth in each lake. One hundred milliliters of water were filtered on GF/F filters for Chl *a* analysis. Additional 100-mL water samples were filtered on precombusted GF/F filters to measure particulate C, N, and P (see methods below).

Limnological parameters: At the beginning and end of the experiment, temperature, conductivity, and pH were measured using a YSI water probe (650 MDS, YSI Incorporated). Water samples were collected close to each cage at 0.5 m depth for TP and soluble reactive phosphorus (SRP). At the same time, light intensity was measured using a light meter (LI-1400, LI-COR) with a spherical quantum sensor (LI-1935A) in air, below the water's surface, and inside each cage in both open and shaded areas.

Lab analysis: Large and easily visible invertebrates were removed from the periphyton before other analyses were conducted. Chlorophyll was measured by placing glass slides and filters in 90% buffered acetone and extracting for 24 h at 4°C in the dark, then measured with a spectrophotometer (Beckman DU640) according to standard methods (APHA 1992). Chl *a*, Chl *c*, and Chl *c*:Chl *a* ratio were calculated (APHA 1992).

Phosphorus content of periphyton was determined using the persulfate digestion method, followed by measurement of SRP according to the standard molybdate blue method (Langner and Hendrix 1982; APHA 1992). C and N contents of periphyton were determined using a CHN analyzer (Finnigan MAT Delta Plus XL MAT 252) according to standard dry combustion methods (APHA 1992). Benthic invertebrates on glass slides were identified to Family (except oligochaetes kept at Class level), enumerated, and weighed to micrograms (Mettler Toledo MT/UMT balance) after drying 48 h at 60°C (Thorp and Covich 1991). Because we could not get C:P from the preserved invertebrate samples, live invertebrates were collected from Oneida Lake and Lake Neatahwanta and C:P of each invertebrate taxon was measured using the same methods as for periphyton.

Periphyton is a complex matrix and small animals such as oligochaetes and chironomids are difficult to separate from the algae. Consequently we measured C:P of invertebrates from separate collections, and numbers and weights of invertebrates from this study to estimate total animal contributions to biomass and C:P in our experimental system. Nutrient content (C and P) and dry weight of benthic algae were estimated by subtracting that parameter (dry weight, C, or P) of benthic invertebrates from the respective value for total periphyton. For example, benthic algal C or P content was calculated by using the total C or P of the periphyton community minus that of benthic invertebrate C and P and dividing by benthic algal dry weight. Note that our periphyton samples did include detritus, minerals, and bacteria as well as algae, similar to seston from pelagic ecosystems. We removed large and easily visible macroinvertebrates from the periphyton before analysis, so only small benthic microinvertebrates remained on the GF/F filters.

Data analysis: Original data were not normally distributed ($p < 0.001$, Shapiro–Wilk test). Therefore, all the data were log transformed to increase evenness of variance and the transformed data became normally distributed ($p > 0.1$, Shapiro–Wilk test). Periphyton biomass on glass slides was analyzed using ANCOVA (analysis of covariance), with light treatments (shade vs. light) as a categorical variable and water column TP as a covariate. This analysis provides the following comparisons: (1) differences in light treatment are tested by differences in the intercepts of the biomass–TP regressions; (2) the effect of TP is tested by the significance of the relation of biomass to TP, with data from both treatments included; (3) the slopes of the biomass–TP relations were compared between treatments via the treatment–covariate interaction term. A parallel ANCOVA analysis was conducted for C:P, with the same independent variables. Additionally, ANCOVA was used to compare biomass and C:P on glass slides under full light and on natural rock also under full light with substrate as a categorical variable, and TP as a covariate. We tested for differences on the basis of treatment (slides and rock) and covariate (TP), and for differences in the slopes of the biomass (or C:P)–TP relation using ANCOVA as described above. This additionally allowed us to determine if our slides provided a reasonable approximation of natural conditions and to control for any differences in periphyton due to differences in natural rock substrate between the lakes.

Periphyton Chl *c*:Chl *a* ratio, which is an indicator of diatom relative abundance (Jeffrey 1976), and C content of periphyton on glass slides were analyzed using ANOVA with light treatments as a categorical variable, because these variables were not significantly correlated to TP gradient in lakes ($p > 0.1$). We analyzed the response of grazers to primary producer quantity and quality using multiple regression with log-transformed grazer biomass on glass slides as the dependent variable and log-transformed periphyton biomass and C:P as predictor variables. SAS 9.0 (SAS Institute Inc.) was used for all statistical analyses.

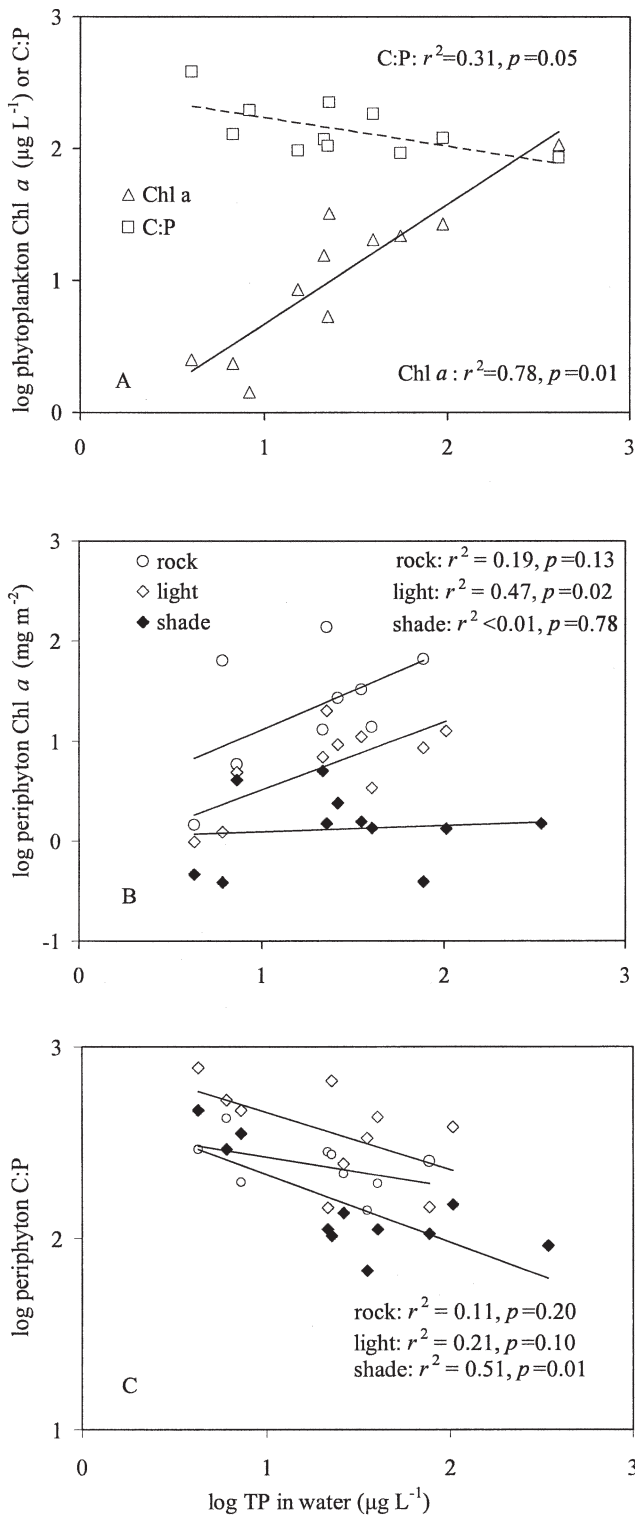


Fig. 1. Relation between TP in sampled lakes and (A) phytoplankton Chl *a* and C:P, (B) periphyton Chl *a*, and (C) periphyton C:P. Phytoplankton biomass increased as TP increased and phytoplankton C:P decreased as TP increased (A). Periphyton biomass increased as TP increased in full light on glass slides and rocks, but not in shade. The slopes of the lines are not significantly different between rock and light treatments (ANCOVA, $p = 0.84$) (B). Periphyton C:P decreased as TP increased

Results—General limnology and phytoplankton: Average temperature, pH, and conductivity ranged from 23°C to 27°C , 7 to 10, and $100 \mu\text{siemens cm}^{-1}$ to $600 \mu\text{siemens cm}^{-1}$, respectively (Table 1). TP ranged from $4 \mu\text{g L}^{-1}$ to $350 \mu\text{g L}^{-1}$ in the sampled lakes (Table 1). Phytoplankton biomass, as estimated by Chl *a* (ranged from 1.42 to $106.1 \mu\text{g L}^{-1}$), was higher as TP increased (Fig. 1A). Phytoplankton C:P (ranged from 84.71 to 381.68) was lower as TP increased (Fig. 1A).

Periphyton biomass and taxonomic composition: Light attenuation was very high in hypereutrophic Lake Neatahwanta; therefore the light intensity did not differ significantly between light and shade treatments (Table 1, $13.25 \pm 16.62 \mu\text{mol m}^{-2} \text{s}^{-1}$ for light and $3.15 \pm 3.46 \mu\text{mol m}^{-2} \text{s}^{-1}$ for shade). Consequently, we excluded the light treatment from this lake from the analysis, but included the shade treatment; we did not exclude the shade treatment because this lake represents an end point on our continuum of eutrophication and therefore provides useful information. On glass slides, periphyton biomass (estimated by Chl *a*) increased with increasing TP under full light conditions (Fig. 1B; $p = 0.02$), but not in shade (Fig. 1B; $p = 0.78$). Overall, periphyton biomass was greater under light than under shade (ANCOVA, $F_{1,20} = 15.23, p = 0.001$). Similar to periphyton growth on unshaded glass slides, periphyton biomass on natural rocks showed an increasing trend with increasing TP (Fig. 1B). Overall, periphyton biomass was greater on rocks than on glass slides (ANCOVA, $F_{1,18} = 10.33, p = 0.01$), which is not surprising given that periphyton had already accumulated on the rocks when we put the glass slides in the lakes. The slopes between periphyton biomass and TP were the same on rocks and on glass slides (Fig. 1B; ANCOVA, $F_{1,18} = 0.04, p = 0.84$). Chl *c*:Chl *a* under shade was significantly higher than that under light (mean of light treatment is $13.7\% \pm 1.5\%$; mean of shade is $39.7\% \pm 5.2\%$; $t = 4.70, \text{df} = 18, p = 0.001$), suggesting a higher proportion of diatoms in the shade.

Periphyton C:P: On glass slides, periphyton C:P significantly decreased with increasing TP in lakes (Fig. 1C; ANCOVA, $p = 0.001$). Overall, periphyton C:P was greater under light than under shade (ANCOVA, $F_{1,20} = 15.59, p = 0.001$). The slopes of the regressions between periphyton C:P on slides and TP were the same under light and under shade (Fig. 1C; ANCOVA, $F_{1,20} = 0.09, p = 0.77$). Periphyton C:P on unshaded glass slides was similar to that on natural rocks, with a decreasing trend with increasing TP (Fig. 1C). Overall, periphyton C:P on glass slides under light was greater than that on rocks (ANCOVA, $F_{1,18} = 6.48, p = 0.05$). The regression slopes

←

on glass slides and rocks. The slopes of the lines are the same under light and shade treatments (ANCOVA, $p = 0.77$). The slopes of the lines are not significantly different between rock and light treatments (ANCOVA, $p = 0.22$) (C). Every data point in the figure represents the average of two or three replicates for panels B and C.

between periphyton C:P and TP were the same on rocks and on unshaded glass slides (Fig. 1C; ANCOVA, $F_{1,18} = 0.56$, $p = 0.47$). C content of periphyton ash free dry weight (AFDW) under light and shade treatments was compared by *t*-test. Periphyton in light treatments had significantly higher carbon content (mean of light treatment is $59\% \pm 4\%$; mean of shade is $39\% \pm 4\%$; $t = 3.22$, $df = 18$, $p = 0.01$). The regression between periphyton P content and TP showed that periphyton P content was higher with increasing TP under both light and shade (for light: $y = -0.04 + 0.12 \times \log(\text{TP})$, $n = 10$, $r^2 = 0.24$, $p = 0.07$; for shade: $y = -0.04 + 0.21 \times \log(\text{TP})$, $n = 11$, $r^2 = 0.26$, $p = 0.07$).

Periphyton food quantity and quality effects on benthic invertebrate biomass: Multiple regression of benthic invertebrate biomass on glass slides with periphyton biomass and C:P yielded the relation: $\log(\text{grazer biomass}) = 4.67 + 1.31 \times \log(\text{periphyton Chl } a \text{ biomass}) - 1.42 \times \log(\text{periphyton C:P})$, $n = 21$. All the parameters and the whole model are significant at $p = 0.01$, and the model explains 54% of the variance in benthic invertebrate biomass. This regression analysis suggests that grazer biomass on glass slides increases with increasing periphyton biomass and decreasing periphyton C:P. Although there were fewer benthic invertebrates in shade than in light conditions, the regression indicates that a given amount of food from light conditions would support fewer invertebrates than the same quantity of shade-grown food, presumably because it is lower quality (higher C:P).

Discussion—Light and phosphorus influence on periphyton biomass and community: Several current anthropogenic effects on lake ecosystems make understanding the response of benthic algae to changes in light and P level important. In some North American lakes, P abatement alone (e.g., Nicholls et al. 2001) and invasive *Dreissena* have increased water clarity (e.g., Caraco et al. 2000; Mayer et al. 2002), which tends to favor increased growth of benthic primary producers (Lowe and Pillsbury 1995; Zhu et al. 2006) and greatly extend periphyton growth area into deeper parts of lakes (Mills et al. 2003). Therefore, total periphyton biomass in lakes should increase because of higher water clarity, but, as P levels decline because of P abatement programs, this abundant source of benthic primary production may result in low-quality (low P) food. It has been suggested that the process termed “benthification” (Mills et al. 2003) will increase the importance of benthic contributions to food webs. Consequently, understanding how the quality as well as quantity of benthic production will change is vital to understanding whole-lake energy and nutrient flows.

Our data are in agreement with the common finding in freshwater systems that phytoplankton biomass is tightly related to TP (Fig. 1A and Schindler 1978; Hecky and Kilham 1988). We also show here that without light limitation, TP is similarly related to periphyton biomass on both artificial and natural substrates (Fig. 1B). However, under low light, periphyton biomass was not correlated with TP (Fig. 1B); similarly, in situations where another

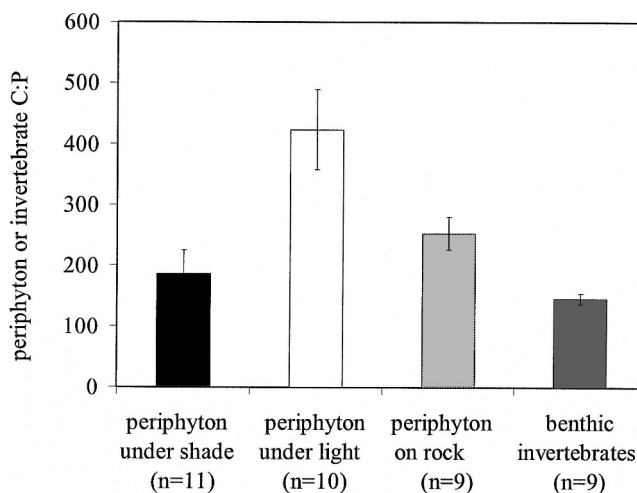


Fig. 2. Possible phosphorus imbalance between periphyton and benthic invertebrates. Bars are means \pm SE.

resource such as C is limiting, P may have no effect, as has been seen in lakes of low alkalinity (Turner et al. 1994; Hecky and Hesslein 1995). Our results support the “benthification” concept and suggest that periphyton biomass may depend on the balance of TP and light changes, since high TP may decrease light penetration by causing phytoplankton shading of benthic algae. Increasing water clarity may also affect periphyton composition. Chl *c*:Chl *a* frequently has been used as an indicator of diatom relative abundance in periphyton communities, since diatoms have Chl *c* and green algae do not (Jeffrey 1976). Microscopic evaluation showed that diatoms and small green algae dominated our glass slides, and we did not find filamentous chrysophytes or xanthophytes. Therefore these possible exceptions to the general idea that increases in Chl *c* to Chl *a* indicate increased diatoms were excluded. The low Chl *c*:Chl *a* ratio under full light indicates that light may decrease diatom relative abundance. Our results support the idea that increasing water clarity because of decreased phytoplankton biomass such as due to *Dreissena* invasion or any increased grazing may shift periphyton communities from domination by diatoms to green algae (Lowe and Pillsbury 1995). We also observed much more nuisance filamentous *Cladophora* under full light than under shade in the eutrophic lakes. In general, we would suspect that the net effect of increasing water clarity and P abatement may increase periphyton production and shift the periphyton communities to domination by green algae.

Light and phosphorus effect on periphyton stoichiometry: The changes in water clarity and nutrient concentration might not only affect periphyton biomass, but also its stoichiometry (specifically C:P). Our data showed that periphyton C:P decreased with increasing TP, as did phytoplankton C:P (Fig. 1A,C). Further, periphyton C:P was higher under full light (Fig. 1C). Thus, as has been shown previously for phytoplankton, epilithon responds to light with increased C content relative to P, because P from

the water column is in fixed supply (Urabe and Sterner 1996; Sterner et al. 1997). For phytoplankton, decreases in available P also reduce the P content (Reynolds 1984), and our results showed similar results for periphyton P content. However, our results do differ from those seen in extremely nutrient-poor lakes where shading had no effect on C:P (Frost and Elser 2002a), suggesting that recent changes in water clarity in meso- and eutrophic waters (e.g., Hudson River, Caraco et al. 2000; Oneida Lake, NY, Mayer et al. 2002; and Lake Ontario, Mills et al. 2003) may favor higher benthic production, but result in relatively low-P food that is of low quality for consumers (Frost and Elser 2002b).

Possible phosphorus imbalance between macroinvertebrates and periphyton: Nutrient imbalance between primary producers and herbivores can decrease herbivore growth (Sterner and Elser 2002). More and more evidence shows that phosphorus can limit zooplankton (mostly *Daphnia*) growth in both lab and field because of an elemental imbalance between this zooplankton and its food (Sterner 1993; Schulz and Sterner 1999; Demott et al. 2001). At the same time, little work has been done on elemental limitation of benthic invertebrates in freshwater (Frost et al. 2002). The nutrient, especially P, imbalance between periphyton and benthic macroinvertebrates is more severe than that between phytoplankton and zooplankton (Frost et al. 2002). Recent work by Frost and Elser (2002b) demonstrated that phosphorus limited mayfly growth in lakes; Stelzer and Lamberti (2002) found that periphyton food quality (high P in periphyton) was important to snail growth in artificial streams. We compared our periphyton C:P to our benthic invertebrate C:P (Fig. 2). This comparison confirms a large elemental imbalance between periphyton and benthic invertebrates in our lakes, supporting the possibility that phosphorus may limit benthic invertebrate growth. Our multiple regression analysis further implies that periphyton C:P may be related to benthic invertebrate growth in lakes, although we cannot exclude that this relation may be due to an increase in another aspect of food quality that was not measured.

Our primary objective was to test how light and nutrients affect periphyton growth and stoichiometry in temperate lakes. Our data showed that periphyton biomass increased with light and increasing TP (when light was not limiting), but periphyton C:P decreased with shading and increasing TP. Many temperate lakes are currently undergoing anthropogenically driven changes in water clarity and nutrient concentrations; our results suggest that periphyton biomass, production, and C:P will increase with increasing water clarity. The increasing periphyton food quantity (biomass) and likely decreasing food quality (high C:P in

our study) may limit the abundance of benthic invertebrates that have high P requirements.

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