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Source: *Journal of the North American Benthological Society*, Vol. 17, No. 4 (Dec., 1998), pp. 420-429
Published by: The North American Benthological Society
Stable URL: http://www.jstor.org/stable/1468363
Accessed: 14/03/2009 17:30

Control of periphyton biomass in Laurentian streams (Québec)[1]

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Abstract. Hypotheses concerning the factors controlling periphyton biomass are mostly based on experimental evidence. To examine their application under natural conditions, we sampled periphyton and invertebrate biomass in 12 Laurentian streams (Québec) covering a range of total phosphorus from 5 to 60 μg/L. We sampled at open and shaded sites to explore light limitation by canopy cover. Periphyton biomass measured as chlorophyll *a* or ash-free dry mass was not related to nutrient concentration or canopy cover. Only current velocity and depth explained a significant but relatively small fraction (10% and 20% respectively) of periphyton variation among sites. Grazer biomass and mean grazer size were positively correlated with phosphorus concentration, which explained 48% and 45% of their variation respectively; canopy cover was not significant. These results indicate that, at least in summer under stable flow, grazer biomass rather than periphyton biomass would increase along a nutrient gradient typical in Laurentian streams. The results suggest top-down control of periphyton biomass.

Key words: periphyton, invertebrates, herbivory, nutrients, canopy, streams.

Agriculture, deforestation, and urbanization have resulted in increasing eutrophication of streams and rivers. These activities increase nutrients and light levels in streams and may lead to obnoxious algal proliferations and/or increases in higher trophic levels. The response would ultimately depend on which factor controlled the biomass of primary producers, a long-time central question of ecology (Hairston et al. 1960). According to contemporary theories (Fretwell 1977, Oksanen et al. 1981, Power 1992), resource augmentation would result in algal (bottom-up control) or grazer increase (top-down control) depending on the resource range (i.e., nutrients and light) under observation and the number of trophic levels in the community. Bottom-up control of periphyton would be observed where herbivores are reduced by insufficient resources, or by predation. In contrast, top-down control would predominate under intermediate resources in even-numbered trophic chains.

The biomass of algae and invertebrates generally increases as a result of experimental fertilization of artificial channels or of a stream reach (Hart and Robinson 1990, Mundie et al. 1991, Hill et al. 1992, Peterson et al. 1993, Rosemond et al. 1993). Periphyton response to nutri-

ents is less clear in comparisons of natural streams along trophic gradients (Jones et al. 1984, Aizaki and Sakamoto 1988, Welch et al. 1988, Biggs and Close 1989, Lohman et al. 1992) because such responses can be altered by other abiotic (light, substratum, disturbance) and biotic (grazing) variables.

Light is a resource that, besides nutrients, can control algal biomass in streams shaded by riparian vegetation (Hill and Knight 1988, Feminella et al. 1989, Steinman 1992). The prediction of algal control in streams is further complicated by the importance of hydraulic disturbance. Flood intensity and frequency are often correlated with periphyton accumulation (Lohman et al. 1992, Biggs 1996). Poff and Ward (1989) hypothesized that stream communities depend on flow regime: abiotic controls should prevail in streams prone to flood, whereas those characterized by a more stable flow would be controlled by biotic factors.

These different hypotheses concerning periphyton control in streams have been tested mostly in experiments that lasted a few weeks and where one or more of the controlling variables were manipulated. The objective of this study was to provide a natural test that avoided the possible artefacts of variable manipulation and of insufficient time for a community to attain equilibrium. The results so obtained should be realistic and therefore readily applicable to stream management. To this end, we sampled

several streams in the Laurentian mountains of Québec along a trophic gradient, selecting a shaded and an open section for each stream. We could not test the effect of severe hydraulic disturbance because the study covered an inter-flood period.

We hypothesized that 1) if algae were controlled by nutrients, periphyton would be positively correlated to nutrient concentrations; 2) if canopy cover were limiting, periphyton would have higher biomass in open than in shaded sections; and 3) if grazers controlled periphyton, grazers rather than algal biomass would be related to nutrients and/or canopy cover.

Methods

We sampled 12 streams in the lower Laurentian mountains of Québec chosen to cover the gradient of productivity found in the area. The streams, some in pristine forests and some in urban areas, were located in a 50-km radius from the Station de Biologie des Laurentides (lat 45°59′N, long 74°01′W ; 80 km north of Montréal). They were 2nd and 3rd order, varied in width from 5 to 12 m, and their substratum was dominated by boulders and cobbles. Flood disturbance is generally limited to spring in these snowmelt streams. We sampled all the streams twice, in July and August 1994, at least 10 wk after the spring flood. Prior to sampling at each stream, three 4-L bottles were filled with subsurface water for chemical analyses. Total seston concentration was measured from the dry mass retained on a Gelman glass fiber filter (Type A/E, pore size = 1 μm) (Morin and Nadon 1991). Water color was determined by measuring the absorbance at 440 nm (ABS_{440}) in a cuvette of 10-cm path length containing filtered water (Gelman A/E glass fiber filters). Unfiltered aliquots were used to determine total phosphorus (TP) and total nitrogen (TN), whereas total dissolved phosphorus (TDP) was measured on filtered samples (Millipore filters, pore size = 0.45 μm). TP and TDP were analyzed with the ascorbic acid modification of the molybdenum blue technique (Strickland and Parsons 1972) preceded by potassium persulphate digestion under pressure (Menzel and Corwin 1965). TN was measured by the method of Raimbault and Slawik (1991). Sample loss and analytical problems precluded a consistent measurement of total dissolved nitrogen, so this variable was omitted.

For each stream, we selected 2 sections differ-ently shaded by riparian vegetation (mainly deciduous trees and some conifers). Open sections were mostly unshaded with an average canopy cover of 10%; closed sections were shaded by a more developed riparian canopy (80% cover, on average). The distance between the 2 sections was ≤100 m to minimize chemical variations. No shaded site was available for St-André, so only the open canopy section was sampled. Canopy cover was estimated with a canopy analyzer (LAI 2000, Li-Cor, Nebraska), an instrument with fisheye lens optics that can be used for obtaining indices of shade (Davies-Colley and Payne 1998), or visually upon occasional failure of the canopy analyzer (7 measurements out of 47). Visual estimates were comparable to those obtained with the canopy analyzer (r = 0.85, n = 40). Three estimates were averaged at each site and at each date.

We randomly collected 6 rocks (diameter 6–10 cm) from each stream section. For each rock, we recorded depth and current velocity (measured with a Pygmy current meter).The rocks were gently lifted and placed in a bowl with a known volume of stream water and brushed, at the sampling site, with a nylon nailbrush to remove loosely attached algae and invertebrates. This method may have underestimated the biomass of very mobile invertebrates able to escape from the rocks during sampling.

Two aliquots of the suspension obtained by brushing were filtered (Whatman GF/C glass fiber filters, pore size = 1.2 μm) for measurement of chlorophyll (Chl) a and ash-free dry mass (AFDM). These filters were kept frozen until analysis, as were the rocks on which remained tightly attached algae. For analyses of Chl a (uncorrected for phaeopigments) of loosely and tightly attached algae, filters and rocks, respectively, were immersed for 24 h in 95% ethanol and the extracts were read in a spectrophotometer (Ostrofsky and Rigler 1987). Total Chl a was obtained by adding the loose and tight fractions. We calculated the proportion of loose algae by dividing the loose fraction by the total Chl a to describe the physiognomy of the algal assemblages. AFDM was measured as the difference in weight between filters dried at 60°C for 24 h and combusted at 550°C for 4 h. The autotrophic index (AI), which is an indicator of the relative importance of autotrophs vs heterotrophs and detritus in the community, was calculated as the ratio between AFDM and

TABLE 1. Physical and chemical variables observed in 12 Laurentian streams (Québec). The values of canopy cover, total nitrogen (TN), total dissolved phosphorus (TDP), color, conductivity, alkalinity, seston, and pH are the average of 3 replicates for 2 sampling dates. Total phosphorus (TP) values are the average of 3 replicates collected at least 3 times in the summer of 1994. Canopy cover is the average of 6 estimates (3 replicates × 2 dates) of the % of sky covered by trees, (O = open sites, C = shaded sites). Current velocity (V) and depth (Z) are the average of 24 measures (6 rocks × 2 sections × 2 sampling dates). na = not available (see methods).

Stream	Canopy cover (%)		TP (μg/L)	TDP (μg/L)	TN (μg/L)	Conductivity (μmhos/cm)	Alkalinity (mg CaCO$_3$/L)	Color ABS$_{440}$	Seston (mg/L)	pH	V (cm/s)	Z (cm)
	O	C										
Brière	5	95	54	20	884	137	28	0.407	6.4	7.5	36	23
Caron	0	90	8	9	303	30	5	0.034	3.0	6.4	11	8
Connely	25	75	15	6	553	61	20	0.257	2.4	7.2	46	14
Dupuis	20	80	45	34	732	19	8	0.626	1.1	6.4	26	17
Jourdain	0	90	22	9	697	200	40	0.214	2.6	7.5	15	12
Millette	10	90	16	5	524	350	28	0.154	1.6	7.4	35	11
Mulets	0	75	10	6	627	625	77	0.128	1.4	7.9	22	13
Pauzé	0	88	5	2	384	269	37	0.138	4.9	7.6	16	15
Quatre	0	75	14	3	464	19	5	0.212	1.2	5.9	27	20
St-Amour	25	75	7	1	387	300	42	0.043	1.3	7.9	17	12
St-André	0	na	48	25	996	760	135	0.138	2.2	7.9	16	20
Violon	25	50	5	2	231	42	14	0.041	1.4	6.9	12	11

Chl *a*. It was impossible to weigh the algae that remained attached to the rock, so AFDM and AI could only be measured for the loosely attached algae.

Invertebrates were only analyzed in the August samples. Once the aliquots for the periphyton analysis were collected, the remaining suspension was concentrated through a 63-μm sieve and fixed with 95% ethanol. Samples were sorted under a dissecting microscope at 25×. Samples containing >200 individuals were separated into 2 fractions (63 μm-1 mm, >1 mm) by sieving. Animals in the coarse fraction were all sorted, whereas those in the fine fraction were subsampled with a Folsom plankton splitter to yield 50–200 individuals. Invertebrates were identified to order or family, and then classified into different functional groups (scrapers, collector-gatherers, filterers, predators) following Merritt and Cummins (1996). The invertebrates were measured to the nearest 0.01 mm using an image analysis system connected to a dissecting microscope. Individual dry mass was estimated using published length–mass relations (Smock 1980, Meyer 1989).

Periphyton and invertebrate biomass were expressed per unit of colonized rock surface. Total surface area of the rock was measured by the weight of aluminum foil necessary to enclose it;

we considered that only 2/3 of the total surface was colonized by algae (Biggs and Close 1989). Average individual body weight for the invertebrates was obtained by dividing total biomass (mg/m²) by total density (no. of individuals/m²).

Data for periphyton, invertebrates, current velocity, and depth were averaged over the 6 rocks collected at each site and date. Single and multiple regressions were calculated using a statistical package (Statistix, version 4.1, Analytical Software, St Paul, Minnesota). Prior to analysis, several variables were log transformed to stabilize the variance and linearize the relations. Arcsin transformation was used for variables expressed as %.

Results

Physical and chemical variables

The streams showed a wide range of P concentrations (TP: 5 to 54 μg/L; TDP: 1 to 34 μg/L; Table 1). N concentrations spanned a less broad range (TN: 231 to 996 μg/L) but were closely correlated to P concentrations (r = 0.89, p = 0.0001 with TP; r = 0.75, p = 0.0047 with TDP; n = 12 in both relationships). Four of the 12 streams were slightly acid whereas the other 8

TABLE 2.   Values observed for periphyton biomass expressed as total chlorophyll *a* (Chl *a* T = sum of loosely and tightly attached fractions in mg/m²), ash-free dry mass (AFDM, loosely attached fraction only in g/m²), proportion of loosely attached algae (PL = Chl *a* in loosely attached/Chl *a* T), and autotrophic index (AI = AFDM/Chl *a* loosely attached) in 12 Laurentian streams in summer 1996. The numbers represent the average of 12 rocks collected in open and shaded sections of the streams.

| Stream	Chl *a* T		AFDM		PL		AI	
	July	August	July	August	July	August	July	August
Brière	9.9	9.5	6.2	5.4	0.50	0.53	1863	1268
Caron	12.7	17.0	9.1	10.2	0.53	0.64	1474	1222
Connely	4.8	8.3	2.3	2.4	0.24	0.28	2448	2308
Dupuis	21.4	21.5	13.3	14.4	0.67	0.70	1017	1025
Jourdain	10.9	9.8	5.2	6.1	0.48	0.60	1172	1371
Millette	8.2	6.6	3.8	2.5	0.49	0.40	1320	1568
Mulets	8.7	9.1	10.0	8.6	0.44	0.46	3292	3030
Pauzé	17.0	19.1	7.9	8.2	0.63	0.69	1559	933
Quatre	27.7	39.9	18.2	22.6	0.77	0.74	946	866
St-Amour	35.5	45.3	20.0	19.0	0.67	0.66	1008	826
St-André	34.2	54.6	14.1	15.2	0.70	0.76	2870	2151
Violon	10.6	5.1	4.6	4.8	0.65	0.60	795	1707
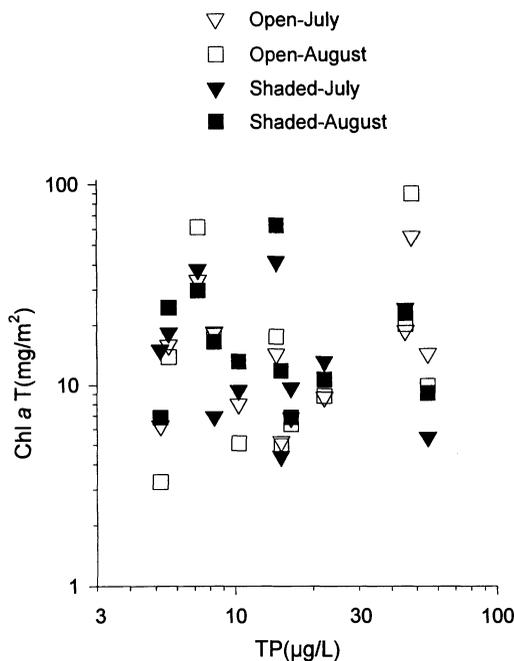
FIG. 1.   Correlation between total periphyton biomass expressed as chlorophyll *a* (Chl *a* T) and total phosphorus (TP) concentration for cobbles collected in 12 streams along a trophic gradient. Each data point represents the average of 6 replicates.

had pH >7. Most of the streams had colored waters, which is typical for the Laurentian mountains. Because we sampled in runs, all sites were relatively shallow with moderate current (Table 1).

Periphyton biomass

Periphyton biomass varied considerably among sites (Table 2) but was not significantly different between the 2 sampling dates (paired *t*-test, $p > 0.5$); therefore, we combined the data for further analysis. None of the variables indicative of trophy, (TP [Fig. 1], TDP, TN), nor canopy cover could explain a significant fraction of the Chl variation among sites ($p > 0.05$ for all variables). When all the physical and chemical variables measured in the streams were tested with stepwise multiple regression (Table 3), periphyton Chl was negatively correlated with current velocity (V) and positively with depth (Z) (Fig. 2). Similar results were obtained when periphyton biomass was described as AFDM instead of as Chl (Table 3). V and Z also explained a significant fraction of the variation in AI (Table 3). The proportion of loosely attached algae (PL) varied widely among sites, but was never >80% and could be as low as 24% (Table 2). This variation was partly explained by V and pH; both were negatively correlated with PL (Table 3).

TABLE 3. Regression models of total periphyton chlorophyll (Log$_{10}$ Chl a T = sum of loosely and tightly attached fractions in mg/m^2), ash-free dry mass (Log$_{10}$ AFDM, loosely attached fraction only in g/m^2), proportion of loosely attached algae (Arcsin PL = Chl a in loosely attached algae/Chl a T), and Autotrophic Index (AI = AFDM/Chl a loosely attached) with current velocity (Log$_{10}$ V, cm/s), depth (Z, cm) and pH. Numbers in parentheses = % variation explained by the variable. RMS = residual mean square of the model. * = p < 0.05, ** = p < 0.01, *** = p < 0.001.

	Chl a T	AFDM	PL	AI
Intercept	1.383***	1.201***	1.715***	2.828***
V	−0.523**	−0.487**	−0.279**	0.297*
	(9%)	(11%)	(10%)	(6.6%)
Z	0.028**	0.020*	—	−0.013*
	(20%)	(10%)	—	(8%)
pH	—	—	−0.104*	—
	—	—	(9%)	—
R^2 adjusted	0.290	0.205	0.190	0.146
RMS	0.079	0.072	0.034	0.044
F	10.30	6.81	6.27	4.86
p	0.0002	0.0027	0.0041	0.0125
n	46	46	46	46

Invertebrate biomass

Invertebrate taxonomic and functional-group composition varied among streams (Table 4), and their biomass spanned 3 orders of magnitude (45 to 45,000 mg/m^2). There was no significant difference in invertebrate biomass between open and shaded sites (paired t-test, p = 0.78), so we combined all data in the analyses. Invertebrate biomass was significantly correlated to TP (Fig. 3) if the outlying data from Quatre Stream were excluded from the calculation. In this stream, samples were collected <50 m downstream from a lake, and were dominated by filterers (Hydropsychidae; 96% of the biomass). None of the other variables was correlated with invertebrate biomass.

We tested if the relationship between nutrients and invertebrates could be improved by considering only the potential grazers, i. e., the organisms that feed on periphyton. We included the scrapers and collector-gatherers (Chironomidae, Coleoptera, Copepoda, Ephemeroptera, Gastropoda, Oligochaeta, and Plecoptera) and excluded filterers and predators (Hydropsichydae and other Trichoptera, Unionidae, *Hydra*, *Planaria*, Nematoda, Hirudinea). The relationship with TP became stronger and Quatre Stream was no longer an outlier (Fig. 3). The other nutrient variables, TDP and TN, also had significant but weaker relationships with grazer biomass (r = 0.63 and 0.65, respectively). Average grazer individual body mass was also positively correlated with nutrients; the relationship was stronger with TDP (Fig. 4) than with TP (r = 0.51) or TN (r = 0.48).

Grazer biomass was not significantly correlated with periphyton biomass, either expressed as Chl or AFDM (r = 0.13, p = 0.56 for both relations) the AI (r = −0.13, p = 0.56), or PL (r = 0.10, p = 0.66).

Discussion

Periphyton biomass was not significantly related to nutrient concentration over the range of trophic conditions typical of southern Québec streams. A chlorophyll–nutrient relationship is consistently observed for phytoplankton (reviewed in Peters 1986) but the results are mixed in periphyton. Significant correlations between stream periphyton and nutrients have been reported in some studies (Aizaki and Sakamoto 1988, Biggs and Close 1989, Lohman et al. 1992, Dodds et al. 1997), whereas in others (Jones et al. 1984, Welch et al. 1988) the lack of a significant relationship has been attributed to grazing, sloughing, or inherent periphyton variability. Contradictory results have also been reported for lake periphyton (Cattaneo 1987, Fairchild and Sherman 1993, Marks and Lowe 1993).

In this study, the nutrient gradient was reflected by a significantly higher biomass of in-

▽ **Open-July**

□ **Open-August**

▼ **Shaded-July**
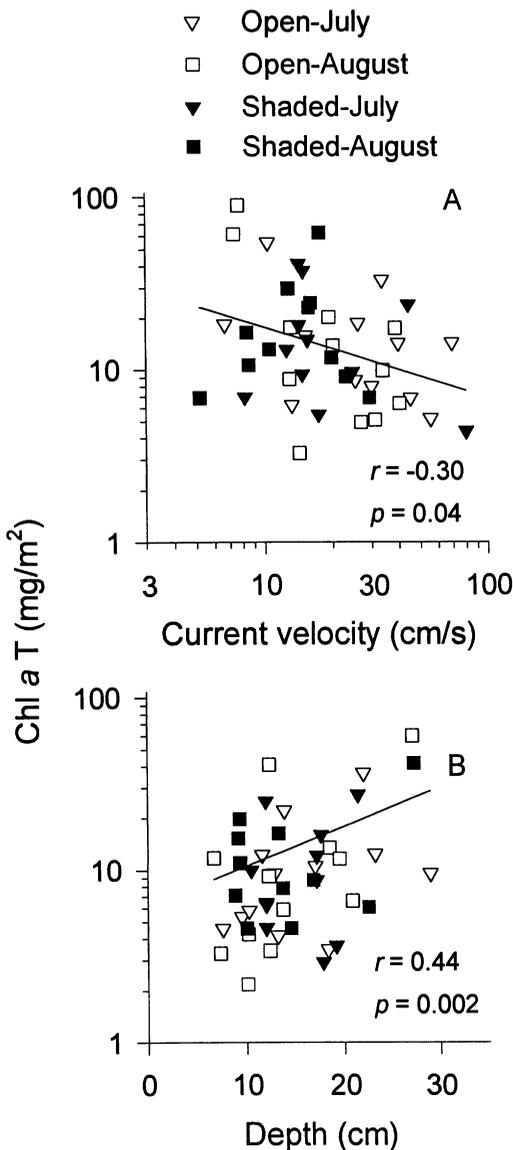
■ **Shaded-August**

FIG. 2. Correlation between total periphyton biomass expressed as chlorophyll *a* (Chl *a* T) and current velocity (A) and depth (B). Each data point represents an average of 6 replicates.

vertebrates in richer sites. The effect of trophy was more evident when we only considered the grazers. The evidence suggests that in these streams the nutrient effect on periphyton was obscured by grazing. Grazers were also larger in rich streams. Increased invertebrate growth has been observed under nutrient enrichment (Dubé et al. 1997) but, in this instance, the size

increase was mostly related to taxonomic differences in the invertebrate communities (i.e., Ancylidae were important at the rich sites, whereas small Oligochaeta and Chironomidae were prevalent at the oligotrophic sites). The capacity of grazers to control periphyton accumulation has been repeatedly demonstrated in experiments where grazer densities were manipulated (reviewed in Feminella and Hawkins 1995). Grazers were also able to counterbalance nutrient addition in natural streams (Stewart 1987, Rosemond et al. 1993). A natural assemblage of grazers increased enough to prevent periphyton buildup in the last 2 y of a 4-y arctic stream enrichment (Peterson et al. 1993). To our knowledge, however, our results are the 1st observation consistent with the prey-dependent (top-down) model in a series of natural streams where neither nutrients nor grazers were manipulated. Comparisons of trophic biomasses across both terrestrial and aquatic ecosystems usually support the alternative ratio-dependent model where all trophic levels are correlated to nutrient inputs (Ginzburg and Akçakaya 1992). It remains to be tested if prey-dependent trophic interactions are generally stronger in benthic stream communities than elsewhere

We could not detect any effect of the extent of canopy cover on algal or grazer biomass. A different light regime was instead reflected in differential invertebrate growth in some experiments where periphyton was heavily grazed (Hill et al. 1995). A significant inverse relation between canopy cover and periphyton biomass has been observed in field studies spanning a range of canopy covers similar to those of this study (Feminella et al. 1989, DeNicola et al. 1992). The deciduous canopy of streams that were >5 m wide was generally >3 m high. In such conditions, sunflecks, pulses of direct sunlight, and radiation received from low sun angles can provide a non-negligible amount of light (Chazdon 1988, Canham et al. 1990). Light reduction may not have been sufficient to result in detectable differences in periphyton biomass. Dodds et al. (1996) found that production could attain maximum rates despite a 75% reduction of full sunlight. Photoinhibition by UV and visible radiation, light saturation, and shade adaptation (Hill 1996) are other possible but untested mechanisms for the lack of canopy effect in our study. Whatever the mechanisms, canopy cover does not seem to control periphyton and

TABLE 4. Total biomass and proportion of dominant invertebrates and their functional groups (C-G = collectors-gatherers, F = filterers, G = grazers) observed on rocks in open- and closed-canopy sections in 12 Laurentian streams during August 1994. Values are the average of 6 replicates.

				Canopy		
		Open			Closed	
Stream	Total biomass (mg/m²)	Taxa	Proportion of total biomass (%)	Total biomass (mg/m²)	Taxa	Proportion of total biomass (%)
Brière	986.8	Ephemeroptera (C-G)	34	1489.0	Ancylidae (G)	56
		Hydropsychidae (F)	29		Chironomidae (C-G)	17
		Ancylidae (G)	24			
Caron	115.3	Chironomidae (C-G)	56	2687.6	Hydropsychidae (F)	93
		Ephemeroptera (C-G)	34			
Connely	758.9	Hydropsychidae (F)	47	172.8	Ephemeroptera (C-G)	44
		Ephemeroptera (C-G)	25		Hydropsychidae (F)	26
Dupuis	431.5	Ancylidae (G)	41	384.7	Ancylidae (G)	42
		Other Trichoptera (F)	33		Ephemeroptera (C-G)	24
Jourdain	884.4	Ancylidae (G)	39	898.3	Hydropsychidae (F)	52
		Hydropsychidae (F)	22		Ephemeroptera (C-G)	18
Millette	514.3	Hydropsychidae (F)	58	1487.3	Simuliidae (F)	46
		Simuliidae (F)	31		Hydropsychidae (F)	43
Mulets	173.6	Ephemeroptera (C-G)	29	167.1	Other Trichoptera (F)	42
		Chironomidae (C-G)	29		Ephemeroptera (C-G)	31
Pauzé	161.9	Chironomidae (C-G)	60	86.9	Chironomidae (C-G)	47
		Ephemeroptera (C-G)	32		Ephemeroptera (C-G)	30
Quatre	43,964.0	Hydropsychidae (F)	96	5089.0	Hydropsychidae (F)	52
St-Amour	683.7	Hydropsychidae (F)	67	652.4	Hydropsychidae (F)	94
		Other Trichoptera (F)	26			
St-André	1082.9	Ancylidae (G)	49			
		Chironomidae (C-G)	48			
Violon	46.3	Chironomidae (C-G)	88	62.7	Other Trichoptera (F)	64
					Chironomidae (C-G)	35

invertebrate biomass in 2nd- and 3rd-order Laurentian streams.

The dramatic effect of floods could not be tested in our study, which covered a period of stable flow typical of this region in summer. However, we could show the effects of subtle differences in flow velocity among sites. Periphyton biomass tended to be higher under slow than fast current. A negative relationship between periphyton biomass and current velocity is usually observed when periphyton biomass is reduced under low nutrient concentrations (Horner and Welch 1981). In thin communities, the advantages of improved water exchange offered by fast current are offset by decreased immigration and increased sloughing (Stevenson 1996). In this study, periphyton was apparently kept thin by grazing even when nu-

trient concentrations were high. Interactions between current and grazing are likely to be complex, and warrant further exploration (Poff and Ward 1995). Current velocity was also negatively related to PL in the community. A similar relationship has been described for other streams in the Montréal region (Cattaneo and Roberge 1991), and probably reflects the tendency of algae to grow prostrate in fast current to avoid scouring (Keithan and Lowe 1985). More surprising was the positive relationship between the AI and current, suggesting that autotrophs were more negatively affected by increased current than heterotrophs. Periphyton biomass was positively related to depth. Depth affects light level mainly in large rivers, but depth in shallow streams probably prevents sloughing. A negative relationship between cur-
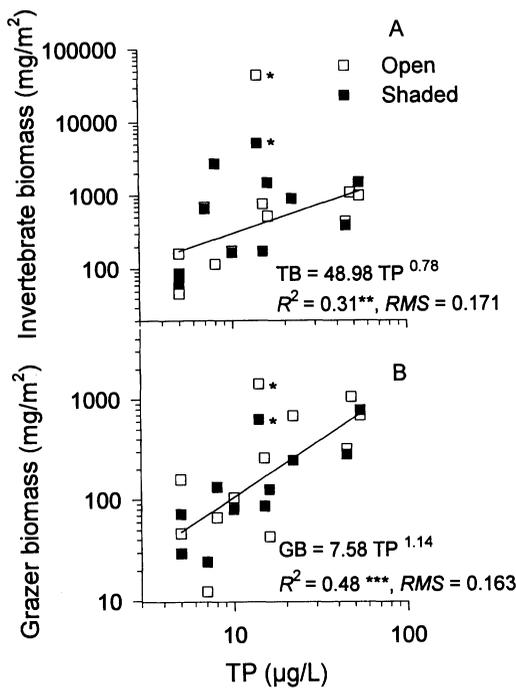
FIG. 3. Relationship of (A) total invertebrate biomass (TB) and (B) grazer biomass (GB) versus total phosphorus concentration (TP, summer average) observed in 12 Laurentian streams in August 1994. Each data point represents the average of 6 replicates. The equation for TB was calculated omitting the outliers (*): $n = 21$. All sites were included in the equation for GB: $n = 23$. * $= p < 0.05$, ** $= p < 0.01$, *** $= p < 0.001$. RMS = residual mean square.
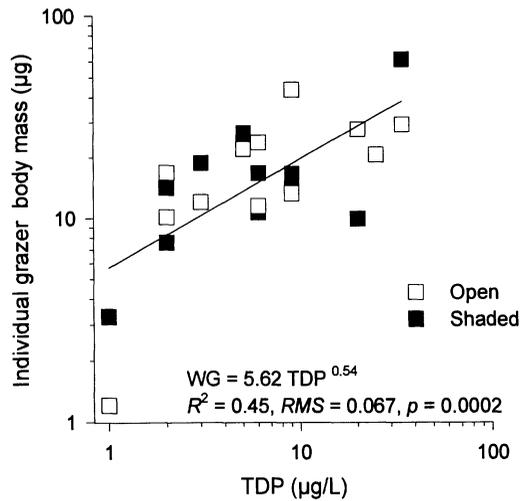

FIG. 4. Relationship between total dissolved phosphorus (TDP) concentration (summer average) and individual grazer body mass (WG) in 12 streams of the Laurentians region in August 1994. Each data point represents the mean of 6 replicates. $n = 23$. RMS = residual mean square.

rent and depth is generally postulated (Petts and Foster 1985) but was not evident in our data ($r = 0.09$, $p = 0.10$, $n = 288$) probably because of rather crude current measurements. Moreover, deep communities are less exposed to water-level fluctuations and consequent occasional drying.

In conclusion, our study supports the hypothesis of biotic control in streams with stable permanent flow (Poff and Ward 1989). Our results also support hypotheses (Fretwell 1977, Oksanen et al. 1981, Power 1992) that predict grazer control of algal biomass in ecosystems with intermediate levels of resources. An increase in nutrients would translate to an increased biomass of herbivores rather than plants in a 2-level trophic chain. We occasionally observed some small fish and invertebrate predators in our

streams, but they did not appear to have a significant impact on herbivores.

Our results suggest that in Laurentian streams in summer, eutrophication results in increased invertebrates rather than algal proliferation. In fact, periphyton chlorophyll did not exceed 100–150 mg/m² considered the nuisance level threshold (Welch et al. 1988) in streams. However, grazers may no longer be able to control algal production if this range of nutrients is surpassed. Moreover, periphyton biomass may better reflect nutrient or hydraulic gradients at other times of the year when grazing is low or flow disturbance is high.

In this study, the hypotheses and results are formulated and expressed in terms of biomass. However, it should be kept in mind that the response to light and nutrient could have been different, and probably stronger, if measured as production. Substratum saturation, self-shading, sloughing, drift, emergence, and predation are some of the mechanisms that may uncouple production and biomass in benthic communities. If our correlative analysis provides a description of benthic biomass patterns across light and nutrient gradients in Laurentian streams, the underlying mechanisms should be tested in controlled experiments.

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