Top-down versus bottom-up control of autotrophic biomass— a meta-analysis on experiments with periphyton

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Abstract.   Nutrient supply and herbivore presence can regulate plant biomass. The relative impact of both of these factors, and their interactions, on periphyton biomass were examined in a quantitative meta-analysis. A literature survey revealed 85 experiments with factorial and replicated manipulation of grazer access and nutrient supply. Two measures of effect sizes were calculated for each experiment, one based on final biomass yields (Hedges' d) and the other on rates (Δr). Grazers significantly reduced periphyton biomass across all experiments, whereas nutrient addition significantly increased periphyton biomass. Effect sizes were very large for both factors. Thus, periphyton can be viewed as highly controlled by top-down and bottom-up mechanisms. Grazer effects were greater than nutrient effects. This result would be expected because nutrient enrichment represents a relative relief from nutrient limitation, whereas grazer exclusion represents a categorical removal of grazing pressure. Moreover, nutrient uptake and growth response are time-lagged, whereas grazer effects are more immediate. The assembled data set was used to test for significant impacts of the habitat and of the experimental design on the importance of grazers and nutrients. Both factors had consistent effects in streams, lakes, and coastal environments, although some variation in effect strength was found. Background productivity levels also did not affect the main effects, but increases in periphyton biomass led to increasing grazer effects and decreasing nutrient effects. The interaction between grazing and nutrients differed between habitats from different aquatic realms and with different productivity. The interaction metric for Hedges' d was significantly positive for lakes and coasts, indicating a greater impact of nutrients in the absence of herbivores than in their presence. No such interaction was found for streams or for mesotrophic habitats. Similar trends were evident for Δr. The experimental design profoundly affected the effects of grazers and nutrients on periphyton biomass, with regard to type of grazer manipulation, type of nutrient enrichment, and duration of the experiment. This outcome indicated the crucial role of a careful experimental design.

Key words: grazing, nutrient enrichment, periphyton, interaction, competition, meta-analysis, top-down, bottom-up.

Within the context of bottom-up versus top-down control in ecosystems, the interplay between herbivores, autotrophs, and nutrients has received special attention (McQueen et al. 1989, Power 1992, Lamberti 1996, Leibold et al. 1997). The biomass and composition of plant communities is affected both by the supply of resources and by consumption from herbivores. It is broadly accepted that the 2 factors are not mutually exclusive and that a strict separation of communities in top-down and bottom-up controlled entities is unrealistic (Stewart 1987, Leibold et al. 1997). Still, there is little consensus about the relative importance of the 2 factors under varying environmental conditions (Power 1992). Furthermore, the degree of interaction between herbivory and nutrient supply has rarely

been assessed (Hillebrand and Kahlert 2001). This situation leads to questions such as how grazing counteracts nutrient enrichment and mediates nutrient supply via excretion (McCormick and Stevenson 1991).

The importance of the opposing influences of grazing and nutrients on plants has become especially clear in benthic communities (Lamberti 1996). Periphyton covers most substrates in aquatic habitats and dominates primary production in many littoral habitats. Grazers can be very efficient in removing periphyton biomass and shaping community structure (Feminella and Hawkins 1995, Steinman 1996). However, manipulations of light and nutrient supply can also profoundly affect algal biomass, nutrient content, productivity, and species composition (Hill et al. 1992, Rosemond 1993, Hillebrand and Sommer 1997, Francoeur 2001). Still, there

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is much left to learn about the interactions of grazers and nutrient supply on periphyton (Rosemond et al. 1993, Lamberti 1996). Lamberti (1996) reviewed freshwater experiments on benthic food webs and concluded that these 2 factors can simultaneously affect periphyton. Similar results were found at the plant–herbivore interface in pelagic environments (McQueen et al. 1989). Rosemond et al. (1993) found strongest treatment effects on periphytic biomass when both nutrients and grazers were manipulated.

Most information on this topic has been obtained from experimental manipulations, which often have been conducted at single locations and seasons and might thus depend on local habitat characteristics. Although single studies only allow a limited ability to reach general conclusions (Lawton 1999, Gurevitch et al. 2000), meta-analysis techniques can be used to develop a quantitative synthesis of experimental results (Gurevitch and Hedges 1993, Arnqvist and Wooster 1995, Brett and Goldman 1996). The strength of a meta-analysis is the possibility of testing for significant effects beyond the variability of single experiments. Moreover, meta-analyses allow the detection of small but biologically significant effects, which remain unobserved in single experiments because of low statistical power (Francoeur 2001). This quantitative summary is preferable over verbal or vote-counting reviews (Gurevitch and Hedges 1993). Feminella and Hawkins (1995) conducted a meta-analysis on stream grazing experiments and Francoeur (2001) on stream nutrient-enrichment studies. I extend the approach to all aquatic realms (streams, lakes, and coasts), and investigate the interaction between grazers and nutrients with studies involving factorial manipulation of these 2 factors. This approach allows the investigation of the relative role of herbivory and enrichment in different habitats and the interaction between these 2 factors. My analysis is based on 85 experiments, testing the following hypotheses: 1) grazer presence and nutrient enrichment both significantly affect autotrophic biomass; 2) nutrient enrichment reduces grazing effects and grazer presence reduces nutrient effects, resulting in significant interactions; 3) the effects depend on habitat characteristics, that is, aquatic realms, productivity of the system, and periphyton biomass; and 4) the effects depend on experimental design.

Methods

Data

For the literature survey, 2 abstracting services were checked (Biological Abstracts and Aquatic Science and Fisheries Abstracts, covering 1978–2001), as were recent reviews on either grazing or nutrient manipulations in fresh water (Feminella and Hawkins 1995, Steinman 1996, Francoeur 2001). Older literature (prior to 1978) was obtained by searching the references cited in the abstracted contributions. Only studies dealing with epilithic or epiphytic periphyton were used, excluding sediments as well as studies dealing with macrophytes. Unreplicated or pseudoreplicated studies were also not included in the analyses. Furthermore, studies indirectly manipulating grazer access (e.g., by removing or adding predators) were not included because the efficiency of the manipulation of grazer density differed between studies. Last, 2 other studies were excluded because grazer density was not significantly reduced (Fairchild et al. 1989, Brock et al. 1995). To increase the data set for marine experiments, 1 unpublished study with seasonally replicated experiments from the Canadian Atlantic coast was included (see Appendix). In total, 21 studies were available that directly and factorially manipulated nutrient availability and grazer access to periphyton. These studies reported a total of 85 experiments (Table 1).

The studies were categorized with respect to habitat characteristics and to experimental design. The experiments were conducted in all kinds of aquatic habitats: coasts ($n = 27$), lakes ($n = 21$), and streams ($n = 37$). Most experiments involved either natural grazer assemblages ($n = 32$) or gastropods ($n = 48$), whereas relatively few involved trichopteran larvae ($n = 3$) or vertebrates ($n = 1$ each for amphibians or fish). Grazer removal or access was manipulated by exclosures (e.g., cages) in the field ($n = 34$), by enclosures adding grazers to separate areas in the field ($n = 9$), or by the use of artificial stream channels ($n = 15$) or laboratory aquaria ($n = 27$). Nutrients were added by a long-term diffusing NPK fertilizer ($n = 28$), by agar-filled clay pots ($n = 27$), or from stock solutions ($n = 29$). Almost all experiments enriched both N and P ($n = 68$), compared to 12 experiments with only P enrichment and another 5 with only N enrichment. The experiments were conducted

TABLE 1. Studies used in the meta-analysis of grazer and nutrient effects on periphyton. The variables characterizing the studies are aquatic realm (lotic, lentic, or coastal), the grazer type, the experimental unit used (**chan**nels, **excl**osures, **encl**osures, and **lab**oratory aquaria), the **nut**rients added (NP, N, or P), the type of the nutrient addition (**sol**uble, **fert**ilizer, **red**uction, or **clay** pots), the duration of the experiment (d), the **prod**uctivity of the system (**oligo**trophic, **meso**trophic, or **eu**trophic), and the number of experiments (*n*) taken from each study. na = not available.

Reference	Realm	Grazer	Unit	Nut	Type	d	Prod	*n*
Hill et al. 1992	Lotic	Gastropods	Chan	NP	Sol	21	Oligo	1
Hillebrand and Kahlert 2001	Lentic/coastal	Natural	Excl	NP	Fert	28–38	Meso/eu	11
Hillebrand et al. 2000	Coastal	Natural	Excl	NP	Fert	23	Eu	3
Jones et al. 2000	Lentic	Gastropods	Lab	NP	Sol	56	Meso	8
Kiffney and Richardson 2001	Lentic	Amphibians	Chan	NP	Fert	38	Oligo	1
Marks and Lowe 1989	Lentic	Gastropods	Excl	NP	Clay	28	na	1
McCormick and Stevenson 1991	Lotic	Gastropods	Encl	P/NP	Clay	21	Meso	9
McCormick 1994	Lotic	Gastropods	Lab	P/N/NP	Clay	21	Meso	12
Mulholland et al. 1991	Lotic	Gastropods	Chan	NP	Red	110	Oligo	1
Neckles et al. 1993	Coastal	Natural	Lab	NP	Sol	32–63	Meso/eu	4
Pan and Lowe 1994	Lotic	Trichoptera	Chan	P	Clay	6	Meso	1
Peterson et al. 1993	Lotic	Natural	Excl	NP	Sol	21	Oligo	2
Rosemond 1993	Lotic	Gastropods	Chan	NP	Sol	49	Oligo	2
Rosemond et al. 1993	Lotic	Gastropods	Chan	P/NP	Sol	49	Oligo	3
Rosemond et al. 2000	Lotic	Gastropods	Chan	NP	Sol	48–50	Oligo	4
Steinman et al. 1991			(See Mulholland et al. 1991)					
Stendera 2000	Lentic	Gastropods	Lb	NP	Sol	7	Eu	3
Stewart 1987	Lentic	Fish	Excl	NP	Fert	11	na	1
Walton et al. 1995	Lotic	Trichoptera	Chan	NP	Sol	21	Oligo	2
Wootton et al. 1996	Coastal	Gastropods	Excl	NP	Clay	51–123	na	4
Worm et al. (see Appendix)	Coastal	Natural	Excl	NP	Fert	21	Oligo	12

from late March to December, with summer experiments dominating (*n* = 44) over autumn (*n* = 21) and spring (*n* = 18). These studies covered a broad range of background productivity and nutrient availability, which was reported differently in different studies (e.g., as dissolved or total concentrations of nutrients). For this reason, the studied systems were categorized into 3 productivity groups: 1) lowest productivity was designated oligotrophic (dissolved inorganic N [DIN] <40 µg/L, dissolved inorganic P [DIP] <5 µg/L, total N [TN] <70 µg/L, total P [TP] <10 µg/L); 2) highest productivity was defined as eutrophic (DIN >200 µg/L, DIP >10 µg/L, TN >350 µg/L, TP >25 µg/L); and 3) medium productivity was designated mesotrophic (values in between). There were 28 experiments in oligotrophic habitats, 35 in mesotrophic, and 18 in eutrophic habitats, respectively.

Four numerical variables were used to characterize the habitats and experiments: 1) duration of the experiments, 2) enrichment factor, 3) grazer abundance, and 4) mean algal biomass in the controls. The duration of experimental manipulations ranged from 6 to 123 d (Table 1), with a median of 28 d. If >1 sampling date was reported for a single experiment, only the last date was used. For those experiments reporting the success of nutrient manipulation, the enrichment factor was calculated as the ratio between enriched and ambient nutrient levels. If both N and P were enriched, the mean of the 2 enrichment factors was used. The enrichment factors ranged from 1.25 to 28 (median = 5.1). Most grazer treatments compared the presence of the target species or community against its absence, resulting in a 100% difference between grazed and ungrazed treatments. Grazer treatment factors were obtained from the ratio of the abundance (or biomass) in grazed treatments against

the grazer abundance (or biomass) in the habitat outside the experiments. The grazer ratio ranged from 0.3 to 4 (median = 1) but for most studies the range was 0.8 to 1.3. The mean periphyton biomass in the control treatments (no grazers, no nutrient enrichment) was used as an estimate of available prey biomass (B_{CON}). Because different measures of biomass were reported in different studies, chlorophyll a (Chl a) was used as the basis for the comparison. Ash-free dry mass (AFDM) and biovolume (VOL) were converted by using log-log regression. These equations were obtained from studies measuring >1 biomass variable, resulting in significant empirical relations ($p < 0.01$) for AFDM (log Chl a = 0.84 + 0.86 log AFDM; $n = 9$) and VOL (log Chl a = 0.97 + 1.23 log VOL; $n = 13$).

To conduct the meta-analysis, measures of periphyton biomass were obtained for each experiment and each of 4 different treatment combinations: 1) CONtrol (no grazing, ambient nutrients), 2) GRaZed (grazing, ambient nutrients), 3) ENRiched (no grazing, nutrients enriched), and 4) ComBiNation (grazing, nutrients enriched). CON, GRZ, ENR, and CBN are used as abbreviations throughout the text. If >1 grazer density or enrichment level was applied, these were analyzed separately. Most studies increased nutrient availability, but some (Mulholland et al. 1991, Steinman et al. 1991) reduced nutrients by recirculating water. In these cases, the calculation was done with inverted signs, i.e., reduced nutrient levels were assigned to CON and GRZ, and ambient levels to ENR and CBN. This procedure assured that increases in biomass as a result of greater nutrient supply always were associated with positive effect sizes. Data were obtained from tables and figures in the original contribution. If >1 biomass parameter was reported, Chl a and biovolume were preferred over AFDM or cell counts.

Choice of effect metric

Choice of a meaningful effect metric is of central importance in meta-analyses (Gurevitch and Hedges 1993, 1999, Osenberg et al. 1997, 1999, Downing et al. 1999, Hedges et al. 1999, Gurevitch et al. 2000). Gurevitch et al. (2000) reviewed the importance of predation and competition in plant and animal communities and proposed a factorial meta-analysis technique allowing an investigator to test for significant interactions between 2 manipulations. As a measure of effects, Gurevitch et al. (2000) calculated standardized mean differences (Hedges' d), which are commonly used as metrics in weighted meta-analysis (Gurevitch and Hedges 1993). This metric uses final biomass yields as basis of the calculations. However, Hedges' d is standardized by the SD and may reflect differences in variability as well as treatment effects; that is, it can confound effects of sampling with effects of treatments (Osenberg et al. 1997). For this reason, Osenberg et al. (1997, 1999) proposed that metrics used in meta-analyses should be based on the biological processes underlying the experimental results. These metrics are often based on rates instead of yields, but for these rates no sampling variances are available and, therefore, the possibility of conducting a more powerful weighted meta-analysis is precluded (Gurevitch and Hedges 1993). The discussion on this matter is still in a state of flux, so the following 2 approaches were used to validate the results of my analysis:

Factorial meta-analysis on biomass yields.—In this analysis, Hedges' d was used as the effect measure, representing the standardized difference between treatment and control means divided by the combined SD of both treatments (Gurevitch and Hedges 1993). The effect sizes (d) were calculated for each experiment according to the factorial design proposed by Gurevitch et al. (2000):

Overall nutrient effect:

$$d_N = \frac{(B_{ENR} + B_{CBN}) - (B_{CON} + B_{GRZ})}{2S} \times J$$

Overall grazer effect:

$$d_G = \frac{(B_{CON} + B_{ENR}) - (B_{GRZ} + B_{CBN})}{2S} \times J$$

Grazer vs nutrient interaction:

$$d_I = \frac{(B_{ENR} - B_{CON}) - (B_{CBN} - B_{GRZ})}{S} \times J$$

where B denotes the biomass in the respective treatment, J denotes a correction factor for small sample bias ranging from 0 to 1 (Gurevitch and Hedges 1993, Gurevitch et al. 2000), and S represents the pooled SD, which is calculated as

$$S = \{[(n_{ENR} - 1)(SD_{ENR})^2 + (n_{CBN} - 1)(SD_{CBN})^2$$

$$+ (n_{GRZ} - 1)(SD_{GRZ})^2 + (n_{CON} - 1)(SD_{CON})^2]$$

$$\div (n_{ENR} + n_{CBN} + n_{GRZ} + n_{CON} - 4)\}^{1/2}$$

where n is the number of replicates and SD is the standard deviation of the respective treatment.

Positive values of d_N indicate an increase in biomass with nutrient enrichment, positive values of d_G indicate an increase in biomass in grazer exclusion treatments, and positive values of d_I indicate a greater effect of nutrient supply when herbivores were absent. To conduct a weighted meta-analysis, the sampling variance was also calculated for each of the 3 effect sizes. The method for these calculations is outlined in detail by Gurevitch et al. (2000). For the yield-based effect size, d^{++} denotes grand mean effect sizes and d^+ category-specific effect sizes (see below).

Biological model meta-analysis on rates.—To integrate biological processes into the effect size, the difference of net growth rates between treatment and controls was used as a metric. The experiments summarized here report the biomass of periphyton following exposure to nutrient and grazer treatments for a specified time period t. Two processes, growth and loss of biomass caused by herbivores, generate the outcome of these manipulations (Sommer 1997). The observed (net) rate of change (r) can be expressed as

$$r = \mu - g = \frac{\ln B_t - \ln B_0}{t}$$

where μ = gross growth rate, g = gross grazing rate, t = time, and B = periphyton biomass.

In grazer-exclusion treatments, r mainly reflects μ, although small grazers (ciliates, nematodes) were normally not removed by the manipulations, so that some level of grazing pressure was still present. In grazer-inclusion treatments, mainly g is changed, but so also is μ because of indirect effects of grazing such as nutrient regeneration or an increase in light or nutrient availability (McCormick and Stevenson 1991, Steinman 1996, Sommer 1997). Similarly, both rates (μ and g) can be affected in nutrient-addition treatments. Thus, the difference between any treatment (*treat*) and its corresponding control (*con*) can be written as a difference in net rate of change, Δr:

$$\Delta r = (\mu_{treat} - g_{treat}) - (\mu_{con} - g_{con}) = r_{treat} - r_{con}.$$

This difference in rates, in turn, can be used as a biologically meaningful effect metric in meta-analysis involving time-dependent processes such as grazing or growth (Osenberg et al. 1997, 1999). The general equation for Δr is

$$\Delta r = \frac{\ln B_t^{treat} - \ln B_0^{treat}}{t} - \frac{\ln B_t^{con} - \ln B_0^{con}}{t},$$

which simplifies in cases where the starting biovolume (B_0) is equal for treatments and control. In many cases, the equality of B_0 for treatments and controls is assumed (more or less explicitly); thus, Δr can be calculated as

$$\Delta r = \frac{\ln\left(\frac{B_{treat}}{B_{con}}\right)}{t}.$$

To compare the effects of nutrients and grazing, Δr was calculated for nutrients (N) in the absence of grazers (ABS):

$$\Delta r_{N-ABS} = \frac{\ln\left(\frac{B_{ENR}}{B_{CON}}\right)}{t}$$

and for grazing (G) in the absence of nutrient enrichment (AMB for ambient nutrients):

$$\Delta r_{G-AMB} = \frac{\ln\left(\frac{B_{GRZ}}{B_{CON}}\right)}{t}.$$

I also tested for an interaction by comparing the main effects with nutrient effects in the presence of grazing (PRS):

$$\Delta r_{N-PRS} = \frac{\ln\left(\frac{B_{CBN}}{B_{GRZ}}\right)}{t}$$

and for grazing under nutrient enrichment (ENR)

$$\Delta r_{G-ENR} = \frac{\ln\left(\frac{B_{CBN}}{B_{ENR}}\right)}{t}.$$

For Δr_N, positive values indicate an increase in biomass with enrichment, whereas for Δr_G,

negative values indicate a decrease in biomass with grazer presence. The loss of periphyton biomass as a result of grazing results in negative Δr_G and positive d_G; thus, positive d_G and negative Δr_G have different signs only because of calculation differences.

Testing of hypotheses

Grand mean effects were calculated to quantify overall effects of nutrients and grazers (hypothesis 1) and their interaction (hypothesis 2) on periphyton biomass. MetaWin 2.0 (Rosenberg et al. 2000) was used to calculate the grand mean effect size for d (weighted) and Δr (unweighted). The weighting procedures are outlined in detail elsewhere (Gurevitch and Hedges 1993). Confidence intervals (CI, 95%) were calculated for each effect size using bootstrapping with 9999 recalculations (Rosenberg et al. 2000). Significant deviation of the CI from 0 was taken as evidence for significant overall effects, and non-overlapping CI were taken as evidence for significant differences between effects.

The impact of habitat (hypothesis 3) or the experimental design (hypothesis 4) on the importance of grazer and nutrients were tested by doing separate correlations on continuous variables (Spearman rank correlation, r_s) and analyses of heterogeneity with categorical variables. Similar to an ANOVA, the analysis of heterogeneity allocates the total heterogeneity to *between-group* and *within-group* heterogeneity, then tests for a significant influence of the grouping on the effect sizes (Rosenberg et al. 2000). Differences in effect sizes as a result of habitat characteristics were tested by analyses of heterogeneity using the classification of studies into aquatic realms, seasons, and background productivity. Ambient periphyton biomass (B_{CON}) was used as a continuous predictor also representing the productivity of the habitat. Concerning the impact of experimental design, the type of grazer treatment and the type of nutrient manipulation were used as categorical variables, whereas the duration of the experiment and the nutrient-enrichment factor were used as continuous variables. No tests were conducted on grazer type, grazer treatment ratio, or enriched nutrients (NP, N, or P), because there was little contrast between studies (Table 1).

Results

Factorial meta-analysis on biomass yields

The effects of nutrient addition and grazer removal were both positive and significantly different from 0 (Fig. 1A). Nutrient enrichment and removal of grazers resulted in greater periphyton biomass across all experiments. However, the absence of grazers had stronger effects than nutrients on periphyton biomass ($d^{++}_G \gg d^{++}_N$). The interaction between grazers and nutrients was also significantly >0 (Fig. 1A). Thus, the effect of nutrients on periphyton biomass was more pronounced in nongrazed assemblages compared to grazed assemblages.

The effects of grazers and nutrients differed significantly between the major aquatic realms, but the general pattern of positive effects of grazer removal and positive effects of nutrient addition remained unchanged (Table 2, Fig. 2A). However, experiments conducted in coastal habitats seemed to respond less to nutrients compared to the freshwater habitats. For the effect size on interactions, the differences were more profound between habitats than for the main effects (Table 2). Greater nutrient effects were observed in the absence of grazers (i.e., positive interaction effects) in lakes and at coastal sites; however, in streams, this interaction did not differ significantly from 0 (Fig. 2A).

Habitat productivity did not affect d, except for d^+_I, which was significantly positive only for oligo- and eutrophic habitats (Table 2, Fig. 3A). However, grazer and nutrient effects showed a marginal decrease from oligotrophic to eutrophic habitats (Fig. 3A). Seasonal setting did not the affect the effect sizes ($p > 0.2$).

The ambient periphyton biomass (B_{CON}) had a significant positive impact on the effects of grazer exclusion ($r_s = 0.35$, $p = 0.002$, $n = 73$); that is, grazers tended to remove more biomass when more biomass was available (Fig. 4A). For nutrient effects, the correlation was significantly negative ($r_s = -0.31$, $p = 0.009$, $n = 73$), indicating less nutrient impact in high-biomass environments (Fig. 4B). In contrast, the interaction effects were not correlated to periphytic biomass ($r_s = 0.10$, $p = 0.389$, $n = 73$) (Fig. 4C).

The experimental design significantly affected all 3 effect sizes (Table 2). The type of grazer exclusion slightly changed grazer and nutrient effects, without changing the general pattern
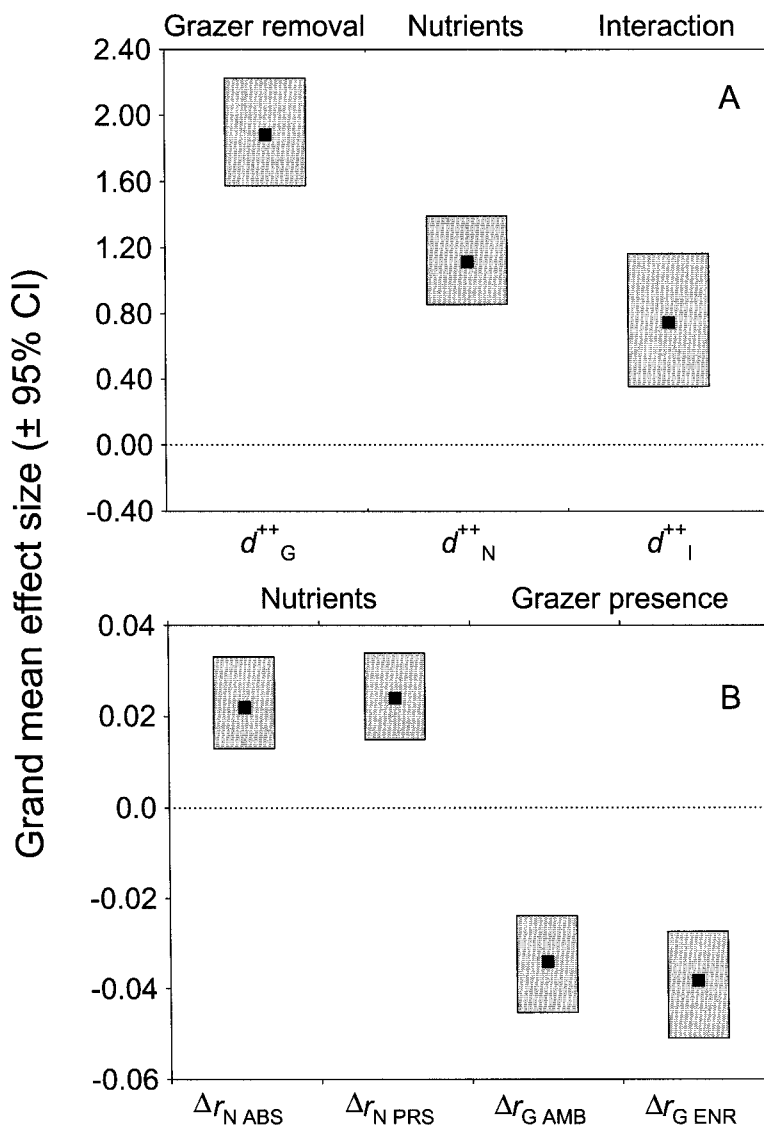
FIG. 1.   Grand mean effect sizes for experiments on grazing and nutrient addition on periphyton biomass. A.—Grand mean effects, measured as Hedges' d, of grazer removal (d^{++}_G), nutrient addition (d^{++}_N), and the interaction (d^{++}_I) between both factors on algal biomass. Grand mean effects and their confidence intervals (CI) were calculated from weighted meta-analysis. B.—Grand mean effects, measured as Δr, of nutrients in the absence ($\Delta r_{N\ ABS}$) and presence ($\Delta r_{N\ PRS}$) of grazing and effects of grazers under ambient ($\Delta r_{G\ AMB}$) or enriched ($\Delta r_{G\ ENR}$) nutrient levels. Grand mean effects and their CI were calculated from unweighted meta-analysis.

(Fig. 5A). The most important difference was a significant negative interaction effect in enclosures (Fig. 5A). All other experimental units revealed a positive interaction; thus, only in enclosures was nutrient enrichment more effective if grazers were present.

The type of nutrient enrichment affected the nutrient effect size d^{+}_N, which was highest if soluble nutrients were added (d^{+}_N = 1.96, CI = 1.38–2.62), compared to experiments conducted with clay pots (d^{+}_N = 1.23, CI = 0.70–1.76) and NPK fertilizers (d^{+}_N = 0.69, CI = 0.18–1.10). Still, all nutrient effects were significantly positive. However, the differences were more pro-

TABLE 2. Results of tests of homogeneity on effect sizes of grazer removal (d^+_G), nutrient addition (d^+_N), and of the interaction between both factors (d^+_I) on algal biomass. The table lists the degrees of freedom (df), the heterogeneity (Q) between (B) and within (W) groups, respectively, and the significance level (p) of the heterogeneity explained by the groups. Different analyses were conducted comprising the impacts of aquatic realm (A), productivity (B), experimental unit (C), and nutrient manipulation (D) on the effect sizes.

	d^+_G			d^+_N			d^+_I		
	df	Q	p	df	Q	p	df	Q	p
A: Aquatic realm									
B	2	7.70	0.042	2	18.28	<0.001	2	6.08	0.072
W	82	101.08		82	99.11		82	111.55	
B: Productivity									
B	2	5.56	0.101	2	1.92	0.434	2	11.45	0.009
W	75	90.59		75	89.15		75	96.00	
C: Experimental unit									
B	3	14.53	0.010	3	15.18	0.006	3	20.08	<0.001
W	81	97.93		81	100.88		81	103.35	
D: Nutrient manipulation									
B	Not applicable			2	13.28	0.004	2	38.62	<0.001
W				81	99.80		81	101.90	

nounced for the interaction effect because positive interactions were confined to soluble nutrient addition (d^+_I = 2.51, CI = 1.61–3.55) and NPK fertilizers (d^+_I = 1.02, CI = 0.43–1.67). In contrast, the interaction was significantly negative for clay pots (d^+_I = −0.84, CI = −1.44 to −0.23). The factor by which ambient nutrient concentrations were experimentally enriched significantly increased the nutrient effects (r_s = 0.42, p < 0.001, n = 77), but not the interaction effects (r_s = 0.06, p = 0.584, n = 77). Thus, increasing the nutrient enrichment clearly gave greater nutrient treatment effects.

Nutrient effects slightly decreased with the duration of the experiments (r_s = −0.18, p = 0.105, n = 85), but grazer effects (r_s = 0.13, p = 0.228, n = 85) and interaction effects (r_s = 0.20, p = 0.066, n = 85) slightly increased with the duration. None of these correlations, however, was significant.

Meta-analysis on rates

The analysis of net rates of change (Δr) revealed overall positive nutrient effects on periphyton biomass and negative effects of grazer presence (Fig. 1B). The grazing effects were greater than those caused by nutrients, but the difference was not significant (Fig. 1B). In contrast to the positive interaction found in the pre-

vious analysis, the analysis of rates did not reveal differences in overall nutrient effects with or without grazing. In addition, it did not detect differences in the overall effects of grazing with or without nutrient enrichment (Fig. 1B).

The difference in either grazing or nutrient effects between the aquatic realms seemed to be minor (Table 3, Fig. 2B). There was a significantly lower impact for coastal sites compared to the freshwater habitats only for $\Delta r_{N\ PRS}$ (Fig. 2B). In addition, there were no significant differences in effect sizes with productivity, except for a somewhat smaller effect of grazing at enriched nutrient levels in mesotrophic environments (Table 3, Fig. 3B). None of the rate-based effect sizes was affected by the seasonal setting of the experiments (p > 0.2).

Ambient periphyton biomass correlated significantly to the effects of nutrients and grazing. Increasing biomass resulted in decreasing nutrient effects, both in the absence (r_s = −0.36, p = 0.004, n = 65) and in the presence (r_s = −0.32, p = 0.005, n = 73) of grazers (Fig. 4E). Nutrient effects thus became less important as biomass increased. For grazing effects (Fig. 4D), the correlation suggested greater removal of biomass when more biomass was available. However, the correlation was only significant for enriched treatments (r_s = −0.26, p = 0.029, n = 73), whereas the effect was nonsignificant at am-
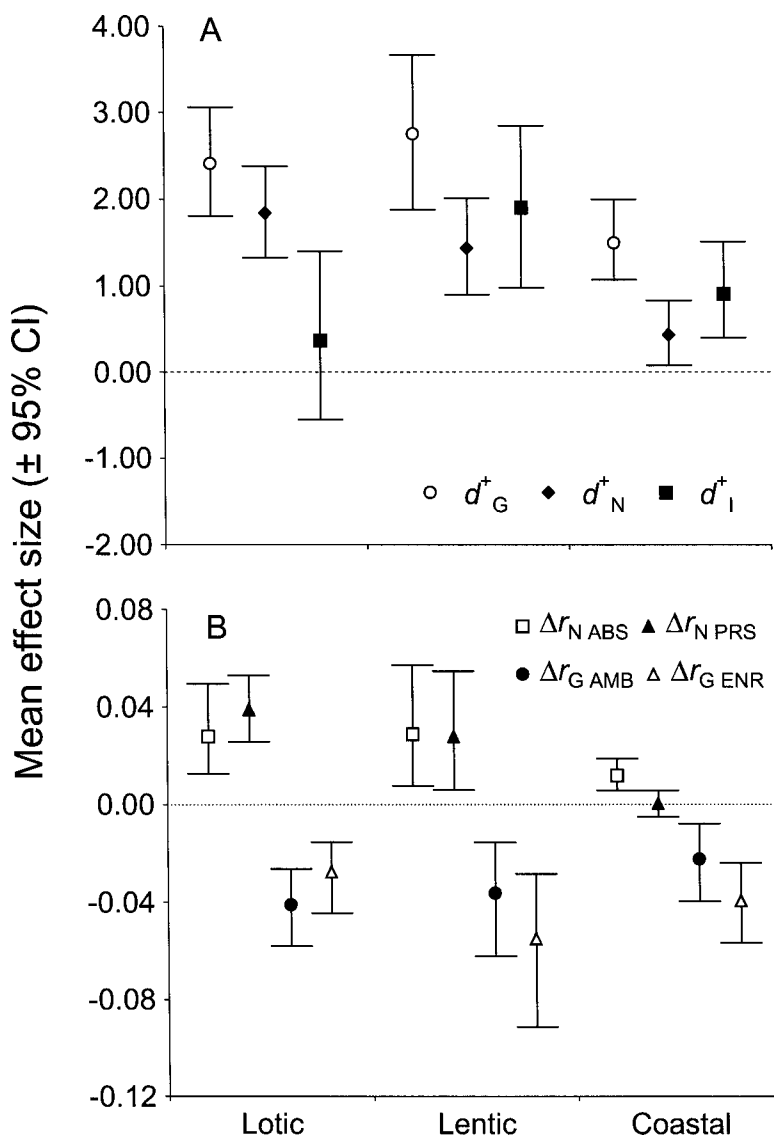
FIG. 2. Mean effect sizes for experiments on grazing and nutrient addition on periphyton biomass for stream (lotic), lakes (lentic), and coastal environments. The figure gives group mean effect sizes measured as Hedges' d (A) or as Δr (B). Abbreviations as in Fig. 1 except that d^+ denotes group-wise mean effect sizes instead of the grand means d^{++}.

bient nutrient levels ($r_s = 0.10$, $p = 0.509$, $n = 50$).

The experimental units used did not affect the direct effects of nutrients or grazing, but they did change the effects when both factors were manipulated (Table 3, Fig. 5B). In enclosures, nutrients caused greater effects when grazers were present ($\Delta r_{N\ PRS}$) compared to nongrazed enclosures or to any other type of experimental unit. Grazers had smallest effects in enriched enclosures ($\Delta r_{G\ ENR}$), but the difference was not significant. The type of nutrient addition only affected $\Delta r_{N\ PRS}$ significantly: stronger effects were observed with clay pots ($\Delta r_{N\ PRS} = 0.044$, CI = 0.028–0.062) compared to soluble nutrient addition ($\Delta r_{N\ PRS} = 0.027$, CI = 0.011–0.046), and NPK fertilizer ($\Delta r_{N\ PRS} = 0.003$, CI = −0.004–0.010).
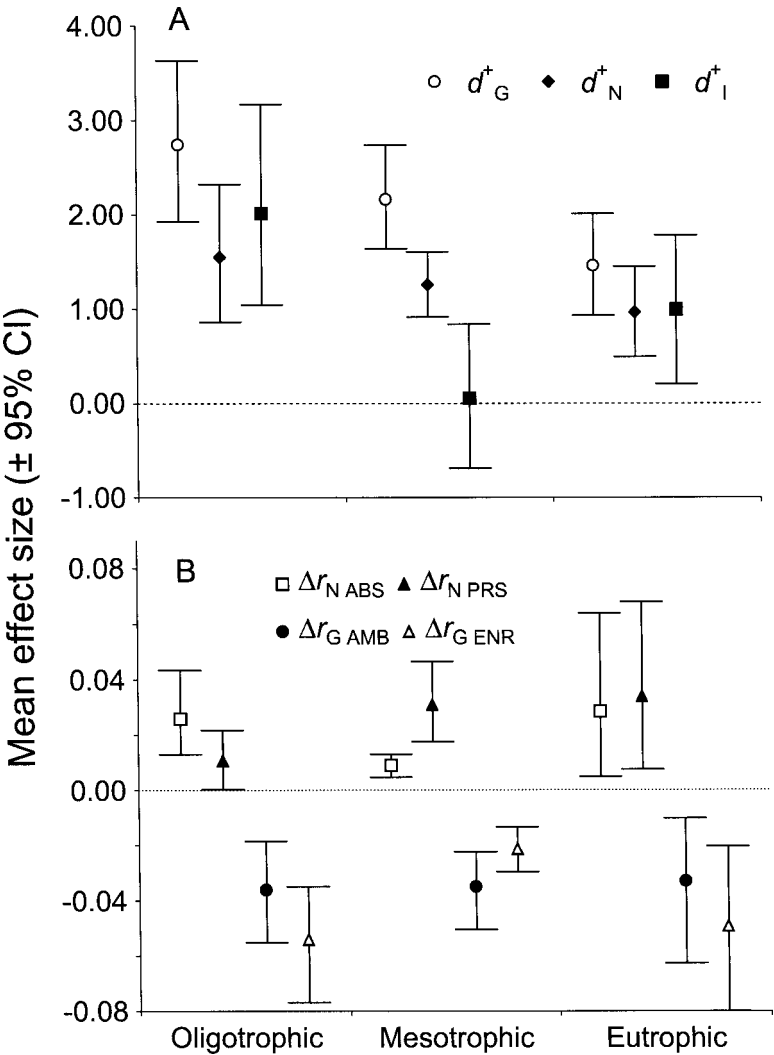
FIG. 3. Mean effect sizes for experiments on grazing and nutrient addition on periphyton biomass for oligotrophic, mesotrophic, and eutrophic habitats. The figure gives group mean effect sizes measured as Hedges' d (A) or as Δr (B). Abbreviations as in Fig. 1.

In contrast to the yield-based effect sizes, all Δr correlated significantly to the duration of the experiments, with both effects (grazer and nutrient) decreasing with experiment duration; that is, duration was negatively correlated to nutrient effects ($\Delta r_{\text{N ABS}}$: $r_S = -0.31$, $p = 0.011$, $n = 68$; $\Delta r_{\text{N PRS}}$: $r_S = -0.48$, $p < 0.001$, $n = 85$) and positively correlated to grazer effects ($\Delta r_{\text{G AMB}}$: $r_S = 0.48$, $p < 0.001$, $n = 54$; $\Delta r_{\text{G ENR}}$: $r_S = 0.20$, $p = 0.061$, $n = 85$). The nutrient-enrichment factor did not correlate to any rate-based measure, except for $\Delta r_{\text{N ABS}}$, where there was a trend of in-

creasing effects with increasing enrichment ($p = 0.102$).

Discussion

The meta-analysis of 85 experiments revealed that periphyton biomass is strongly influenced by nutrient supply and grazer presence. The effects of grazers were generally stronger than the effects of nutrients. The overall findings were consistent for periphyton in lakes, streams, and coastal environments, reflecting a similar im-
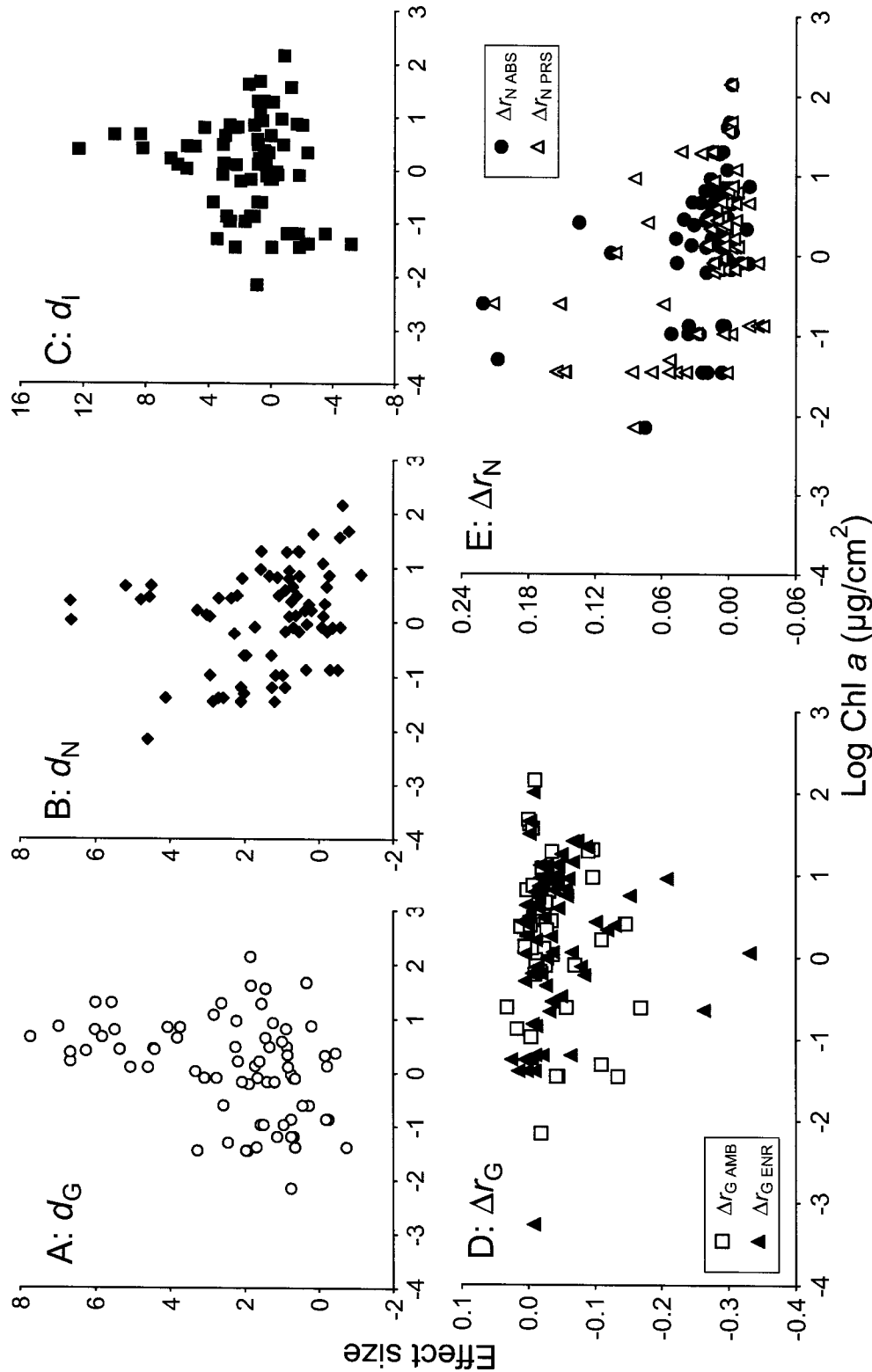
FIG. 4. Correlation between log-transformed algal biomass and 2 different metrics of effect size, Hedges' *d* (A–C) and Δr (D–E). For *d*, the effects of grazer removal (d_G, A), nutrient addition (d_N, B) and the effect of their interaction (d_I, C) are shown. For Δr, the effects of grazing ($\Delta r_{G\ AMB}$ and $\Delta r_{G\ ENR}$, D) and nutrients ($\Delta r_{N\ ABS}$ and $\Delta r_{N\ PRS}$, E) are shown.
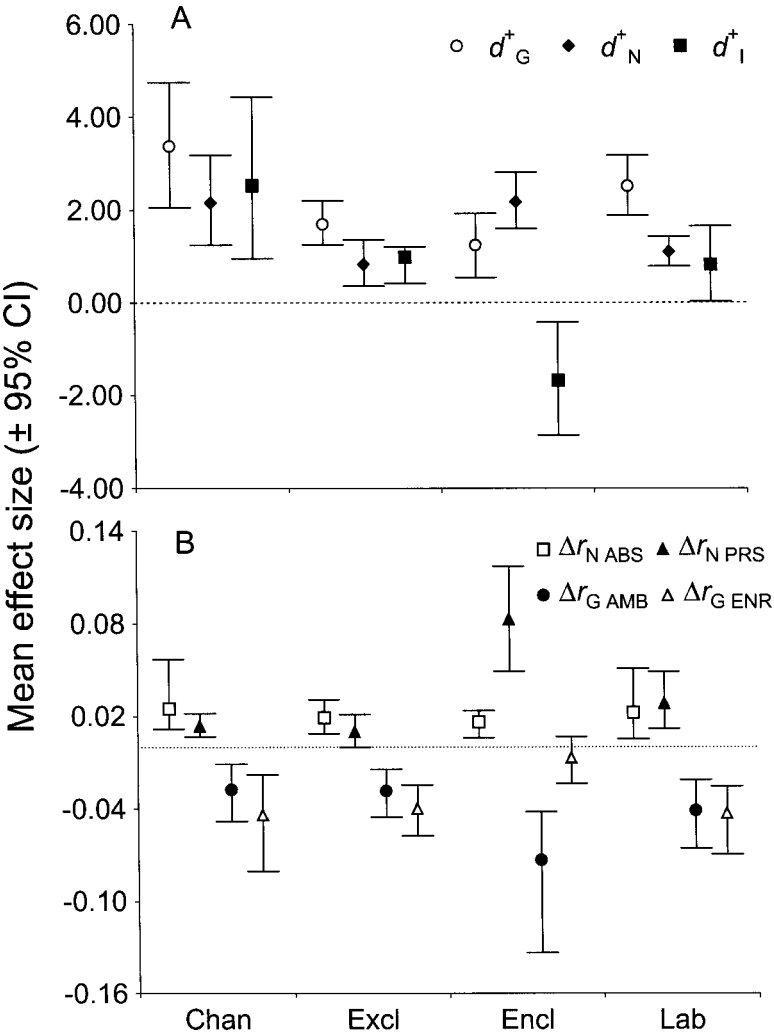
FIG. 5. Mean effect sizes for experiments on grazing and nutrient addition on periphyton biomass for different experimental designs: channels (Chan), exclosures (Excl), enclosures (Encl), and laboratory (Lab) experiments. The figure gives group mean effect sizes measured as Hedges' d (A) or as Δr (B). Abbreviations as in Fig. 1.

portance of top-down and bottom-up regulation of periphyton biomass in different aquatic realms. The available periphyton biomass correlated positively to grazer effects and negatively to nutrient effects. In contrast, habitat productivity and season had only a minor influence on grazer and nutrient effects. In addition, the importance of grazers and nutrients were clearly related to the experimental design, with respect to manipulation type and duration of the experiment. These results were similar overall for both effect sizes, the yield-based d and the

rate-based Δr, although they deviated in some details.

Meta-analysis approach

The potential to detect central tendencies in data sets from different investigations is the major advantage of meta-analyses (Gurevitch and Hedges 1993, Arnqvist and Wooster 1995), and makes quantitative meta-analyses a powerful tool in ecology. However, the results of the meta-analysis can be influenced by the type of

TABLE 3. Tests of homogeneity on effect sizes of grazer presence (Δr_G) and nutrient addition (Δr_N) on algal biomass. The different analyses (A–D, see Table 2) were conducted on the 4 different effect sizes calculated for Δr, which are nutrient effects at grazer absence (ABS) and grazer presence (PRS), and grazer effects at ambient (AMB) and enriched (ENR) nutrients. The table lists the degrees of freedom (df), the heterogeneity (Q) between (B) and within (W) groups, respectively, and the significance level (p) of the heterogeneity explained by the groups.

	$\Delta r_{N\,ABS}$			$\Delta r_{N\,PRS}$			$\Delta r_{G\,AMB}$			$\Delta r_{G\,ENR}$		
	df	Q	p	df	Q	p	df	Q	p	df	Q	p
A: Aquatic realm												
B	2	0.004	0.299	2	0.024	0.002	2	0.004	0.374	2	0.010	0.182
W	65	0.112		82	0.141		54	0.094		82	0.249	
B: Productivity												
B	2	0.004	0.276	2	0.008	0.123	2	<0.001	0.977	2	0.019	0.032
W	58	0.095		75	0.147		47	0.080		75	0.205	
C: Experimental units												
B	3	0.001	0.874	3	0.040	<0.001	3	0.007	0.267	3	0.010	0.348
W	64	0.115		81	0.125		53	0.091		81	0.249	
D: Nutrient manipulation												
B	2	0.002	0.669	2	0.024	0.001	Not applicable			2	0.012	0.150
W	64	0.114		81	0.140					81	0.247	

effect size selected for use (Osenberg et al. 1997, 1999, Gurevitch and Hedges 1999, Hedges et al. 1999). To increase the reliability of my analysis, I chose to conduct 2 different meta-analyses and to compare the approaches. The main overall results were only marginally affected by the choice of the metric (Table 4). For both d and Δr, the impacts of grazers and nutrients were highly significant and the impact of grazers was higher than the impact of nutrients. The weighted meta-analysis (Hedges' d) detected significant differences more often than the unweighted meta-analysis (Δr) (Table 4), but differences in effects that were identified with these 2 methods were analogous (Figs 2–5). With regard to productivity, mesotrophic habitats showed different patterns both for d^+_I and $\Delta r_{G\,ENR}$. The analyses of experimental design showed that

TABLE 4. Summary of meta-analysis results comparing 2 effect sizes (Hedges' d and Δr). The table lists the results for analyses of heterogeneity and correlations, stating significance level (– = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). The sign of the impact is shown for correlation analyses: $\Uparrow$ = increasing effect size, $\Downarrow$ = decreasing effect size, nm = not measured. Abbreviations as in Figs 1 and 2.

	Hedges' d			Δr			
	d^+_G	d^+_N	d^+_I	$\Delta r_{N\,ABS}$	$\Delta r_{N\,PRS}$	$\Delta r_{G\,AMB}$	$\Delta r_{G\,ENR}$
A: Analyses of heterogeneity							
Aquatic realm	*	***	–	–	**	–	–
Productivity	–	–	**	–	–	–	*
Experimental units	*	**	***	–	*	–	–
Nutrient manipulation	nm	**	***	–	*	nm	–
Season	–	–	–	–	–	–	–
B: Correlation analyses							
Enrichment factor	nm	$\Uparrow$***	–	–	–	nm	–
Ambient biomass	$\Uparrow$**	$\Downarrow$**	–	$\Downarrow$**	$\Downarrow$**	–	$\Uparrow$*
Experiment duration	–	–	–	$\Downarrow$*	$\Downarrow$***	$\Downarrow$***	–

enclosures as experimental units and clay pots as nutrient-enrichment devices changed the interaction between grazers and nutrients for d^+_I as well as $\Delta r_{N\ PRS}$. Ambient biomass (B_{CON}) correlated similarly to the effects of grazers and nutrients for both types of effect sizes.

Two major differences between the yield- and the rate-based effect size occurred. First, the significant interaction effect (d^{++}_I) was contrasted by small differences in Δr for either nutrients or grazers, irrespective of whether or not the other factor was manipulated. In general, the main effects were greater than the interaction effects (i.e., $d^{++}_G > d^{++}_N > d^{++}_I$), so interactions would become marginal if grand mean effects with or without manipulation of the 2nd factor are calculated (as for Δr). Second, the duration of the experiment correlated significantly to Δr, but not to d. This result is clearly related to the fact that time was included in the calculation of Δr. Osenberg et al. (1997) described that Δr was invariant over time for up to 100 d, a value great enough to include almost all of the experiments used in my study. However, the assumption of consistent growth and mortality rates is less applicable to long-term experiments, and thus a decrease in effect size with experiment duration is implicit in the rate-based model.

Although the 2 meta-analyses revealed results in good general agreement, the data used in both analyses may be biased with respect to geography and season (Feminella and Hawkins 1995). Most experiments were conducted in North America or in northern and central Europe, and >50% of the experiments were conducted in summer. Many of the studies were completed in only 1 season (but see Neckles et al. 1993, Wootton et al. 1996, Hillebrand and Kahlert 2001). Moreover, there will be a tendency towards conducting experiments at the most favorable times, which may be high-light seasons in heavily shaded streams or times without spates in streams where spates regularly occur.

The results of the meta-analysis can also be affected by a publication bias towards preferential submission and publication of significant results of grazing exclusion or nutrient enrichment. Recent publications have warned that a bias against publication of nonsignificant results will have detrimental effects for conclusions drawn from meta-analysis (Blenckner and Hillebrand 2002, Kotiaho and Tomkins 2002, Murtaugh 2002). General caveats of this type apply to all meta-analyses, but also to research in general and to reviews (Gurevitch and Hedges 1999). In my analysis, the database comprised 85 experiments, which were well distributed between aquatic realms and experimental designs (Table 1). The effect sizes for the single experiments (Fig. 4) were highly dispersed and included several studies with weak effects (i.e., close to 0). Thus, there was no evidence for a priori exclusion of experiments with weak effect sizes. Moreover, a correlation between sample size and effect size, which was proposed to indicate a publication bias (Kotiaho and Tomkins 2002), was not detected for any effect measure except for d_I. Adding the consistency of the yield- and rate-based approaches, the general tendency presumably reflects the high importance of combined top-down and bottom-up regulation of periphyton.

General effects of herbivores and nutrients

Periphyton was strongly controlled by both nutrient supply and grazer presence. The importance of grazers and nutrients to periphyton biomass was greater than effects of either factor on other communities. Gurevitch et al. (2000) analyzed effects of competitors and predators on amphibians and plants, and found significant impacts of both factors in their analysis. However, grand mean effect sizes (Hedges' d)—in this case for either biomass or density—were < 0.8 (cf. Fig. 1A for effects on periphyton). In addition, the magnitude of effects of fish presence on zooplankton (measured as d, Brett and Goldman 1996) was slightly lower (-1.39 ± 1.13, effect size $\pm$ 99.9% CI) than the effect of grazer removal on periphyton. Effects of fish on benthic snail density measured as Δr ranged from 0.01 to -0.06 (Osenberg et al. 1997), which is lower than Δr_G on periphyton (Fig. 4D). Only the effect sizes of nutrient enrichment on marine phytoplankton (Downing et al. 1999) had a magnitude similar to the nutrient effect size for periphyton (Fig. 4E).

Grazer removal generally had a greater impact than nutrient enrichment on periphyton biomass. Similar results have also been found for predator exclusion compared to competitor reduction (Gurevitch et al. 2000). This trend may either reflect actual responses to nutrients and grazers, or differences in experimental manipulation. Plants respond to nutrient enrich-

ment via nutrient uptake and growth, whereas the loss of biomass as a result of grazers is nearly immediate. The lag in the response to resources may, in short-term experiments, lead to reduced nutrient effects compared to grazer effects. Moreover, the high importance of nutrient regeneration for periphyton (Wetzel 1996) may reduce the effectiveness of externally provided nutrients. The difference between overall nutrient effects and grazer effects probably depends, however, more on differences in treatment application. Grazer exclusion represents a nearly complete relief from the target organisms. In contrast, nutrient enrichment represents only a relative relief from nutrient limitation. The nutrient treatment varied between studies with respect to the absolute concentrations added and the enrichment over ambient nutrient concentrations. The degree to which added nutrients reduced the observed limitation was rarely investigated (but see Rosemond et al. 1993, Hillebrand and Kahlert 2001). This fundamental difference between treatments may lower the nutrient effect size compared to the effect size related to grazer exclusion. Keeping this in mind, the results should be interpreted with respect to the simultaneous and strong impact of both top-down and bottom-up regulating factors rather than with respect to differences between the factors.

The finding of simultaneous impact is not new (Stewart 1987), but it is not evident if the 2 factors control the periphyton biomass interactively, or if there is a temporal and spatial separation of effects. Hillebrand and Kahlert (2001) suggested that grazers and nutrients might affect different parts of a periphytic assemblage, for example, by different spatial distribution in grazing pressure (Steinman 1996, Sommer 1997, 1999). On the other hand, several studies described a reduction of nutrient effects in the presence of grazers and vice versa (Hill et al. 1992). These kinds of interactions are further corroborated by the significant interaction effect size found in the analysis on yields. This interaction may be based on the opposing direct effects of nutrients and grazing on periphyton biomass or on indirect feedback mechanisms. Thus, grazers may not only reduce periphyton biomass, but may also increase the nutrient content of the periphyton (Mulholland et al. 1991, Rosemond et al. 1993, Hillebrand and Kahlert 2001) or the biomass-specific productivity (Lam-

berti et al. 1987). Other studies have shown propagating nutrient effects from algae to herbivores (Hart and Robinson 1990, Hill et al. 1992).

The contrasting ideas may be the result of patch dynamics and the spatio-temporal scale of sampling. Differential response of grazed and nongrazed parts of periphyton to nutrients may result in interactive or independent effects of nutrients, depending on the sample scale covering this heterogeneity (Hillebrand and Kahlert 2001, see also Kawata et al. 2001). Spatial heterogeneity may thus be a key to understanding the interdependence of top-down and bottom-up control in benthic communities (Poff and Nelson-Baker 1997, Kawata et al. 2001).

Grazer and nutrient effects with regard to habitat

Aquatic realms.—The effects of grazers and nutrients were highly consistent in running and standing freshwater habitats and in coastal environments. My analysis showed, for the first time, that these regulating factors have similar effect-magnitudes for both freshwater and coastal periphyton. The analysis revealed only slightly smaller nutrient effects in coastal habitats compared to fresh water (Fig. 2). The absence of a significant interaction term in streams indicated that stream periphyton does not use nutrients from the flowing water more efficiently if grazers are absent. In general, the difference in the strength of biotic interactions between the aquatic realms is rather minor. Thus, the observed variation in the outcome of the single experiments is not a result of broad distinctions (marine and freshwater or lotic and lentic, respectively) but is a result of factors acting at smaller scales. I will address some of these factors in the following discussion.

Productivity.—Equilibrium foodchain models (Oksanen et al. 1981) predict an increase of trophic levels with productivity and a positive biomass response to enrichment in top- and even-numbered levels, contrasting to top-down control at odd-numbered levels. The propagation of resource enrichment along trophic links has been a central issue in the debate on top-down and bottom-up control (Fretwell 1987, Oksanen et al. 1981, Brett and Goldman 1996, 1997, Leibold et al. 1997). Nisbet et al. (1997) found increasing densities at all trophic levels (plants, herbivores, and predators) with increasing pro-

ductivity when they modelled short-term dynamics in systems similar to the communities investigated here, especially with respect to openness, lack of mixing, and spatial heterogeneity.

In my analysis, there was no significant influence of productivity on grazer or nutrient effects, and only a small difference in their interaction. A trend towards smaller grazer effects with higher nutrient trophy was observed, which is in contradiction to results from pelagic habitats, where zooplankton grazing increased with total P (Sarnelle 1992). However, the definition of the 3 productivity levels in my study may be too coarse to reveal significant trends. Instead, ambient nongrazed periphyton biomass (B_{CON}) could be used as a proximate variable representing potential benthic production. Both grazing and nutrient effects were correlated to B_{CON}; the correlation between B_{CON} and grazer effects was positive. Similar results were reported from stream experiments in a study using simple mean differences (Feminella and Hawkins 1995). The consistent results for both effect measures used here show that the greater grazing of biomass with increasing availability of biomass is not a statistical artifact. These findings are in agreement with the results from zooplankton grazing (Sarnelle 1992, Leibold et al. 1997). However, this correlation cannot be used to test Oksanen's model of top-down and bottom-up control (Oksanen et al. 1981) because the relatively short duration of the experiments included in my analysis did not allow measurement of numerical responses of grazers via reproduction. Instead, the increase in grazer impact with increasing periphyton biomass was based on functional responses or on the ability of the grazers to select and reach high biomass patches. A high probability of food limitation (quantitatively or qualitatively) was proposed for benthic herbivores (Lamberti 1996). Food-limited herbivores may thus increase grazing pressure (functional response) at higher food availability (Hart and Robinson 1990, Sommer 1999). On the other hand, biomass may be positively correlated with other aspects of herbivory (food quality, handling time), which would result in higher removal at high biomass (Sommer 1997). In addition, mobile grazers may actively select high-quality food patches and increase local density, thus showing a numerical response based on dispersion rather than on re-

production (Hill et al. 1992, Nisbet et al. 1997, Cruz-Rivera and Hay 2000). Both of these mechanisms would increase biomass removal by herbivores in high-biomass patches.

Regarding nutrients, the effect sizes decreased with increasing periphyton biomass. Greater levels of biomass may decrease the nutrient uptake by increases in boundary layer thickness and decreases in nutrient uptake (Wetzel 1996). There is also a tendency towards self-shading and lowered C supply with increasing biomass, decreasing the probability of nutrient limitation. In addition, the presence of larger amounts of periphyton biomass may itself be an indicator of sufficient nutrient supply, thus reflecting the lack of strong nutrient limitation.

Seasons.—The present analysis revealed no significant differences in effect sizes between seasons. In contrast, studies with seasonally replicated experiments at a single site reported strong variation in nutrient and grazer effects between seasons (Neckles et al. 1993, Hillebrand and Kahlert 2001). The absence of such variation in my meta-analysis shows that there is no general trend with seasons, i.e., no one season generally showed great or small effects of grazers or nutrients. Instead, local seasonal changes will modify the outcome of the experimental manipulations.

Other factors.—A variety of other factors not covered in this analysis possibly affect the importance of nutrients and grazers. Among these factors is light availability, including incoming light, shading by trees or phytoplankton, or self-shading of periphyton, which can change herbivore activity and the relative limitation by nutrients. It should be noted, though, that light as a limiting resource would also represent bottom-up control (Rosemond et al. 2000). Currents and disturbances will also affect the importance of grazers and nutrients (Poff and Ward 1995, Steinman 1996). Grazer density and activity (related, e.g., to temperature, light, life-cycle stage) are other important variables for the outcome of the grazer manipulations (Cattaneo and Mousseau 1995, Steinman 1996). Predators are able to reduce grazing activity by removing herbivores or by changing herbivore behavior towards a reduction of predation risk (McCollum et al. 1998, Diehl et al. 2000). Grazer effects may also be reduced if unmanipulated grazer groups can compensate for the absence of the target grazer

(Cattaneo and Kalff 1996, Kiffney and Richardson 2001). Some of these interfering factors were explicitly tested in different studies used in my meta-analysis, e.g., the impact of light (Rosemond 1993, Rosemond et al. 2000), the impact of grazer density (McCormick and Stevenson 1991), or of large-scale disturbances such as El-Niño events (Wootton et al. 1996).

Although other variables could not be included in my meta-analysis, it should be noted that the conclusions derived are robust with respect to variations within single experiments. It is the strength of meta-analyses to detect central tendencies in a variety of experiments that cover a broad range of abiotic and biotic conditions and vary in timing, measurement accuracy, and statistical power.

Experimental design

Several aspects of experimental design affected the results of the analysis, including the duration of the manipulation, the level of nutrient enrichment, the type of experimental units (representing also the means by which grazers were excluded), and the technique used to enrich nutrients. The duration of an experiment clearly affects the calculation for rate-based effect sizes. Several other processes will change the outcome of experimental manipulations over time (Feminella and Hawkins 1995): the response to nutrient enrichment may decrease if periphyton biomass increases (see above), and grazer effects may decrease if less edible species become dominant or the low remaining periphyton biomass requires increased searching and handling time (Sommer 1999).

Both yield- and rate-based meta-analyses showed that enclosure treatments resulted in different grazer and nutrient interactions compared to other experimental units. Only for enclosures was the nutrient effect greater in grazer presence. A possible explanation is that water movements may be low in enclosures and thus diffusion into the biofilm slow, unless grazing breaks up the periphyton assemblage and thus increases the availability of nutrients.

Nutrient-enrichment level was clearly related to the effect of nutrients on periphyton. Most studies used reasonable estimates of biologically relevant increases in nutrient supply, but there were also studies resulting in a very strong increase (up to a factor of 28) in dissolved nutrient concentrations. It is noteworthy that, although all kinds of nutrient enrichment (clay pots, fertilizer, or addition of solutions) resulted in significant positive effects on periphyton biomass, the interactions between grazers and nutrients were affected by nutrient-enrichment type. This result was evident both for yield-based and rate-based effect sizes, both showing an increase in nutrient effects if grazers were present for clay pots, whereas the general trend was a decrease in nutrient effects if grazers were present. Although clay pots have some disadvantages for the assessment of nutrient enrichment (Brown et al. 2001), it is not clear what may have caused the difference in interactions between nutrients and grazing.

The importance of experimental design for the outcome of grazing versus nutrient interactions highlighted the importance of careful analysis of artifacts in experimental manipulations (see also Feminella and Hawkins 1995). Relatively few studies analyzed the possible role of treatment artifacts in separate control experiments (Hillebrand et al. 2000). A thorough analysis of implications related to different means of manipulation should clearly be conducted at the start of experimental tests of top-down and bottom-up effects.

In conclusion, my analysis clearly showed strong control of periphytic biomass by nutrient supply as well as herbivory (hypothesis 1). These simultaneous effects were interactive, mostly by increased nutrient effects with grazer absence (hypothesis 2), but the strength and direction of the interaction was modified by habitat trophy and experimental design (hypotheses 3 and 4). The effects of nutrients and grazers were highly similar in coastal and freshwater habitats (hypothesis 3). Grazing and nutrient effect sizes correlated to the available periphyton biomass (hypothesis 3) and depended on the experimental design (4).

comments of Walter Hill, David Rosenberg, and 2 anonymous reviewers.

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Appendix

Details of seasonally replicated experiments from the Canadian Atlantic using factorial manipulation of grazer presence and nutrient supply.

The experiments in Canada were conducted and analyzed by Boris Worm and Heike Lotze (both Dalhousie University, Halifax, Nova Scotia) as well as Helmut Hillebrand. The experimental setup, the efficiency of the treatments and the results for filaments are described and discussed elsewhere (Lotze et al. 2001). The same methods have previously been used for experiments in the Baltic Sea

APPENDIX TABLE. Results of experiments from Bald Rock. Mean algal biovolume is based on 4 replicates.

| | | Algal biovolume (mm^3/cm^2) | | | |
| | | Grazer exclusion | | Grazer access | |
Experiment	Nutrients	Mean	SE	Mean	SE
Early spring	No	0.12	0.03	0.08	0.02
	Low	0.11	0.03	0.07	0.02
	Medium	0.16	0.03	0.09	0.01
	High	0.13	0.04	0.10	0.01
Late spring	No	0.14	0.04	0.03	0.03
	Low	0.13	0.11	0.03	0.004
	Medium	0.11	0.04	0.02	0.003
	High	0.36	0.12	0.04	0.03
Summer	No	0.24	0.09	0.02	0.01
	Low	0.30	0.28	0.02	0.01
	Medium	0.34	0.21	0.02	0.01
	High	0.65	0.08	0.03	0.003
Autumn	No	0.03	0.02	0.05	0.02
	Low	0.04	0.01	0.03	0.01
	Medium	0.03	0.01	0.03	0.01
	High	0.07	0.02	0.02	0.01

(Hillebrand et al. 2000). In short, the experiments were conducted in Bald Rock, Nova Scotia, using a factorial combination of nutrient enrichment and grazer exclusion. Nutrient enrichment was by NPK-fertilizer in 4 different concentrations (no, low, medium, high). Grazer exclusion was by cages. The experiments were conducted in 4 different seasons during 1999 and analyzed for the effects of the treatments on macrophytes, filamentous epiphytes, and microalgae.

The results on the microflora were used for this meta-analysis. Unglazed ceramic tiles (5 × 5 cm) were used as standard substrates for the benthic microalgae. Experiment duration was 21 d in all seasons. At the end of each experiment (March–April, May–June, July–August, September–October), the periphyton was scraped off and suspended in 15 mL of filtered seawater and fixed with 2 mL Lugol's Iodine. An aliquot was then transferred to standard Utermöhl counting chambers and counted with an inverted microscope at 400× magnification. Biovolume was calculated for each species by measuring linear dimensions in

the microscope and applying geometric models (Hillebrand et al. 1999).

The biomass of benthic microalgae was highly reduced by the presence of grazers (Appendix Table). Grazing impact was high and significant from spring to summer (ANOVA, $p < 0.001$), when grazing reduced algal biovolume by up to 90% compared to the ungrazed treatments. In autumn, the grazer impact was marginally nonsignificant (ANOVA, $p = 0.060$). The impact of nutrients was significant only in the late spring experiment (ANOVA, $p = 0.005$). In autumn, a significant nutrient $\times$ grazer interaction was observed (ANOVA, $p = 0.007$). For unenriched treatments, this interaction resulted in a higher biomass in grazed compared to ungrazed treatments, whereas at highest nutrient-enrichment levels, higher biovolume was found in ungrazed treatments.

The relative contribution of species was only slightly changed by nutrient and grazer treatments, and was always dominated by diatoms. Total biovolume and species composition showed a strong seasonal sequence, total biovolume decreasing from spring to autumn.