

META-ANALYSIS OF GRAZER CONTROL OF PERIPHYTON BIOMASS ACROSS AQUATIC ECOSYSTEMS¹

*Helmut Hillebrand*²

Institute for Chemistry and Biology of the Marine Environment (ICBM-Terramare), Carl-von-Ossietzky University Oldenburg, Schleusenstraße 1, D-26382 Wilhelmshaven, Germany

Grazer control of periphyton biomass has been addressed in numerous experimental studies in all kinds of aquatic habitats. In this meta-analysis, the results of 865 experiments are quantitatively synthesized in order to address the following questions: (i) Do lotic, lentic, and marine ecosystems differ in their degree of grazer control of periphyton biomass? (ii) Which environmental variables affect the degree of grazer control? (iii) How much does the result of these experiments depend on facets of experimental design? Across all ecosystems, the grazers removed on average 59% of the periphyton biomass, with grazing being significantly stronger for laboratory (65%) than for field (56%) experiments. Neither field nor lab experiments showed a significant difference among lotic, lentic, and coastal habitats. Among different taxonomic consumer groups, crustaceans (amphipods and isopods) and trichopteran larvae removed the highest proportion of periphyton biomass. Grazer effects increased with increasing algal biomass, with decreasing resource availability and with increasing temperature, especially in field experiments. Grazer effects also increased with increasing total grazer biomass in field experiments but showed the opposite trend in lab experiments, indicating a tendency toward overcrowded lab experiments. Other aspects of experimental design, such as cage type, size, and duration of the study, strongly affected the outcome of the experiments, suggesting that much care has to be placed on the choice of experimental design.

Key index words: benthic algae; experimental design; grazer biomass; grazing; meta-analysis; temperature

Abbreviations: CI, confidence interval; LR, log response ratio

Periphyton is a general term used to describe benthic communities colonizing different kinds of substrata in all types of aquatic habitats (Stevenson 1996a, Wetzel 2001). Periphyton comprises primary producers (from unicellular microalgae to filamen-

tous algae), heterotrophic bacteria and consumers (protists and meiofauna) as well as organic material. The autotrophic part of periphyton represents a major source of primary production fueling benthic food webs (Lamberti 1996) and—via important consumer links between benthic invertebrates and fish (Vanni 1996, Vadeboncoeur et al. 2001, Vander Zanden and Vadeboncoeur 2002)—also pelagic food webs. Given the ubiquity of periphyton and its importance for aquatic ecosystem functioning, a strong body of literature has been established on factors controlling periphyton biomass and productivity. The response of periphyton biomass to nutrient concentrations and nutrient ratios (Fairchild and Lowe 1984, Borchardt 1996, Blumenshine et al. 1997), light availability (Hill et al. 1995, Hill 1996, Mosisch et al. 2001), water chemistry (pH, conductivity) (Planas 1996, Pan et al. 1999), substratum heterogeneity (Burkholder 1996, Alvarez and Pardo 2007), flow regime (Stevenson 1996b, Bourassa and Cattaneo 1998), and temperature (DeNicola 1996) has been used to explain both spatial variation and temporal fluctuations in biomass.

Among the factors regulating periphyton biomass, special attention has been paid to grazing (i.e., the removal of periphyton biomass by benthic invertebrate or vertebrate consumers). Steinman (1996) used a vote-counting procedure to identify the number of studies finding positive or negative effects of grazers on algal biomass, algal primary production, or diversity. Feminella and Hawkins (1995) employed an unweighted meta-analysis to summarize effects of grazers in streams. A similar within-system analysis on grazing has been conducted on seagrass epiphytes (Hughes et al. 2004). In previous analyses, I summarized the interactions between grazing and resource availability, focusing on the interaction between grazing and nutrient supply (Hillebrand 2002) or grazing and light availability (Hillebrand 2005). Effects of grazers on periphyton biomass were contrasted to effects on productivity, diversity, and C:N:P ratios using an earlier version of the database used here (Liess and Hillebrand 2004). As informative as these analyses have been, they all have limited generality since they focus on certain habitat types or—when conducted across habitats—use only a small

¹Received 2 July 2008. Accepted 16 March 2009.

²Author for correspondence: e-mail hillebrand@icbm.de.

amount of the available information to test specific hypotheses.

Here, I conduct a weighted meta-analysis of 865 experiments spread across all aquatic habitat types and across large parts of the globe. This analysis comprises an unprecedented number of studies from all major kinds of aquatic habitats and explicitly analyzes potential drivers of grazing intensity across ecosystem boundaries. The intent of this analysis is (i) to provide average effect sizes for grazing in order to test whether there are significant differences in grazing in different ecosystems and (ii) to analyze how ecological and environmental drivers and different experimental approaches affect the estimates of grazing. Finally, by summarizing the existing information, gaps in our knowledge of grazing control of periphyton biomass can be identified.

MATERIALS AND METHODS

Database creation. The data were derived from a database containing experiments manipulating grazer presence and reporting the mean and standard deviation of periphyton biomass in replicated grazed and ungrazed treatments. This database is continuously updated by searching literature databases such as Web of Science and Aquatic Science and Fisheries Abstracts with the search string “(graz* OR herbivor*) AND (periphyt* OR epiphyt* OR microphytob*).” Additionally, the bibliography of entered studies was searched for additional experiments. Experiments were included when they contained replicated grazed and ungrazed treatments and provided estimates of periphyton abundance or biomass. Different effect sizes could be calculated from the same study if different experiments with corresponding controls were conducted (e.g., in different sites or seasons) or if there were different levels of the grazer treatment (different grazer densities, species composition). This resulted in a database consisting of 865 effect sizes stemming from 178 publications (listed in Appendix S1 in the supplementary material).

From each experiment, I derived the effect size of grazer presence on periphyton biomass using the log response ratio (LR), which is the natural log-transformed ratio of grazed to ungrazed biomass. LR is a measure of relative effect size; that is, it reflects the proportion of biomass change, not the absolute removal (Hedges et al. 1999). The focus on relative biomass removal reflects the efficiency of grazing, whereas a measure of absolute removal would mainly reflect the available amount of biomass. Negative LR indicates biomass reduction by grazer presence (i.e., a 50% reduction in biomass will yield a LR of -0.69). For each LR, I also calculated the sampling variance as a measure of uncertainty (Hedges et al. 1999, Rosenberg et al. 2000).

In addition to the effect size, I obtained information about environmental variables and the experimental design from the publications. For the latter, the experiments were characterized as field (605) and laboratory (260) experiments, where field experiments also included all outdoor components, such as mesocosms or streamside channels. The type of experimental unit was further categorized as lab aquaria (180), lab channels (80), field channels (90), enclosures (266), exclosures (225), and removal experiments (19). A few studies (5) used a natural difference in grazer presence/absence. For each of these experiments, the area of a single unit (replicate) was recorded as experiment size ($\log \text{cm}^2$) as well as the duration of the experiment ($\log \text{days}$). Different measures of periphyton biomass were used in the

studies. Most common were chl *a* (416), AFDM (120) or another measure of dry or wet weight (74), biovolume (121), and microscopic counts (=abundance, 78). Less frequently used measures included direct measurement of optical absorption reflecting algal biomass (12), percent cover (7), organic carbon (12), algal height (7), and a relative measure of biomass (6). The spatiotemporal setting of the study was measured by the absolute latitude ($^{\circ}\text{N}$ or S), the year and the season of the study. The seasons were categorized in four 3-month periods (spring = March to May, summer = June to August, etc., for Northern Hemisphere studies, and spring = September to November, etc., for the Southern Hemisphere).

Habitat type was categorized as lotic (384), lentic (201), or coastal (280), and the substratum was categorized as hard (epilithon, 695), plants (epiphyton, 104), or sediment (epipsammon and epipelon, 66). I recorded the in situ temperature for the experiment ($^{\circ}\text{C}$) and used a rank-based system to evaluate the habitat productivity for each study. This derived measure was necessary as the experiments strongly differed in which kind of nutrient (total or dissolved nitrogen or phosphorus) and light variables they reported. Therefore, I ordered the studies according to their resource availability from high to low concentrations and/or light availability. If a study reported only N availability, I ranked the study within all reporting N and used that rank. If a study reported both N and P, I averaged the two ranks. Thereby, I obtained for each experiment its rank in overall nutrient availability averaged across all reported nutrient and light variables. Thus, high ranks reflect low nutrient or light availability. With respect to the biological components of the experiments, I derived the total grazer biomass ($\log \text{mg dry weight} \cdot \text{m}^{-2}$) and categorized the grazer group as gastropods (322), decapods (46), isopods (15), amphipods (35), trichopterans (104), ephemeropterans (69), echinoderms (6), amphibians (71), and fish (16). There were 171 experiments that employed a mixture of macroinvertebrates. The algal biomass needed to be categorized in a relative measure for two reasons: first to integrate over the different measures and units used, and second to avoid spurious autocorrelation with the effect sizes, which were based on biomass. Therefore, algal biomass was transformed into proportions by expressing the biomass of study *i* using a biomass measure *j* as proportion of the mean observed biomass of all studies using that biomass measure *j*. This relative measure of algal biomass was $\log(x+1)$ -transformed (Hillebrand 2005).

Statistical analysis. A major advantage of meta-analysis is the ability to weight effect sizes by the inverse of their sampling variance, thus giving higher impact to experiments with less variation in results and/or higher replication (Hedges et al. 1999, Gurevitch et al. 2000, Rosenberg et al. 2000, Hillebrand 2002). I used weighted mixed-model meta-analysis to calculate the grand mean effect size (i.e., the average effect size across the entire data set) and group-wise mean effect sizes (i.e., the average effect size for each of the groups in the categorical variables) with their respective 95% confidence intervals (CI). If these 95% CI include zero, an average effect is considered not to be significantly different from zero. In the results, I display these means and their CI for each categorical factor. For continuous factors, I display bivariate relationships between single effect sizes (each representing one experiment) and the explanatory variable. The variance in these plots appears higher than it is in the statistical analysis, as the effect sizes are not weighted in the graphical display.

Significant differences between groups were tested by a weighted analysis of heterogeneity (Rosenberg et al. 2000), which separates the total heterogeneity (Q_{total}) into heterogeneity between groups (Q_{model}) and within groups

(Q_{residual}). These analyses test whether the grouping was able to explain significant variation in the effect sizes (analogous to analyses of variance). For continuous variables, I used a weighted continuous meta-analysis to test for significant associations between predictor variables and grazer effect sizes (analogous to a weighted regression analysis). All calculations were performed with MetaWin 2.0 (Rosenberg et al. 2000). As not all explanatory variables could be obtained from all studies, the degrees of freedom vary among different analyses. These analyses were performed on the entire data set and then also separately for field and laboratory experiments.

RESULTS

Across all studies, the grand mean effect size was $LR = -0.9$, which corresponds to a 59% reduction in periphyton biomass by grazer presence. In laboratory experiments, this estimate was significantly larger (mean $LR = -1.09$ equals 65% reduction) than in field experiments ($-0.82 = 56\%$ reduction) (Table 1, Fig. 1A). There was no significant difference in grazing effect sizes among habitat types, either for the entire data set or for field and lab experiments separately (Table 1). In all habitat types, the effects were significantly negative, and group-wise averages corresponded to 57%–62% removal of periphyton biomass through grazer presence (Fig. 1B). Among the three systems, lotic experiments exhibited the strongest divide between lab and field experiments (Fig. 1B). Substratum type affected grazing effect sizes, as the grazing effect on sediment-dwelling microalgae was significantly lower than for either epilithic or epiphytic algal assemblages (Table 1, Fig. 1C). This effect was also significant for field studies alone, whereas lab studies showed the same (but nonsignificant) trend.

Different consumer groups exerted significantly different effects on periphyton biomass, which was true for all experiments as well as for the split analyses on field and lab experiments (Table 1). Strong grazer effects were especially exerted by two crustacean groups (isopods and amphipods) and trichopteran larvae (Fig. 1D). Weak group-wise average effects were determined for dipteran larvae, echinoderms, and amphibians. Still, the group-wise means were all significantly separated from zero with the sole exception of dipterans. Thus, all grazer groups except Diptera exert a significant negative impact on periphyton biomass (Fig. 1D). Total grazer biomass strongly affected periphyton biomass removal, but interestingly with different signs for field and lab experiments (resulting in a nonsignificant relationship across the entire database) (Table 1). In field experiments, increasing grazer biomass led to increased biomass removal, whereas in lab experiments, the effect size became smaller with increasing grazer biomass (Fig. 2A). These contrasting relationships may be the two sides of a unimodal trend. Lab experiments were stocked with higher grazer biomasses than field experiments. The average

TABLE 1. Statistical results of weighted meta-analysis on grazing effect sizes on periphyton biomass.

Factor	All experiments					Field experiments					Lab experiments				
	df	Q_m	Q_{res}	b	P	df	Q_m	Q_{res}	b	P	df	Q_m	Q_{res}	b	P
Lab/field	1;863	17.48	1300.08	na	0.00003	na	na	na	na	na	na	na	na	na	na
Habitat	2;862	3.03	1292.55	na	0.21936	2;602	3.96	952.50	na	0.13783	2;257	1.34	304.60	na	0.51223
Substratum	2;862	36.87	1305.83	na	<0.00001	2;602	36.89	959.90	na	<0.00001	2;257	3.67	303.59	na	0.15999
Consumer	10;853	38.55	1100.98	na	0.00003	10;593	26.85	823.63	na	0.00275	6;252	17.70	291.80	na	0.00704
Grazer biom.	1;802	2.78	1220.61	-0.059	0.09554	1;542	19.28	916.13	-0.180	0.00001	1;258	12.97	317.87	0.263	0.00032
Algal biomass	1;628	18.00	912.16	-0.620	0.00002	1;450	4.34	714.19	-0.314	0.03715	1;176	15.64	173.07	-1.542	0.00008
Productivity	1;483	0.00	622.73	0.000	0.98558	1;307	7.37	386.89	-0.001	0.00665	1;174	3.63	217.19	0.002	0.05684
Temperature	1;469	14.46	622.45	-0.025	0.00014	1;251	6.68	296.54	-0.019	0.00975	1;216	1.35	258.61	-0.017	0.24520
Year	1;749	9.69	1115.27	0.012	0.00185	1;546	9.80	880.19	0.012	0.00174	1;201	41.52	211.93	0.028	0.03360
Season	3;756	2.92	1137.00	na	0.40374	3;563	1.26	905.22	na	0.73970	3;189	10.39	226.81	na	0.01536
Latitude	na	na	na	na	na	1;603	1.41	859.51	-0.003	0.23530	na	na	na	na	na
Exp. units	6;858	40.69	1221.40	na	<0.00001	4;600	23.60	924.60	na	0.00010	1;258	2.20	308.25	na	0.13834
Exp. size	1;769	6.47	1164.88	-0.057	0.01100	1;537	12.46	860.61	-0.082	0.00042	1;230	0.21	275.04	-0.027	0.64440
Exp. duration	1;851	0.14	1293.25	-0.024	0.71168	1;595	0.98	958.37	0.078	0.32130	1;254	11.66	298.32	-0.466	0.00064
Measure	9;855	62.66	1158.51	na	<0.00001	8;596	31.30	877.65	na	0.00012	6;253	60.26	286.52	na	<0.00001

na, not applicable.

For each factor, three tests were performed comprising all experiments and then field and lab experiments separately. For each test, the degrees of freedom (df), the heterogeneity explained by the factor (Q_m), the residual heterogeneity (Q_{res}) and the significance value (P) are given. Bold P -values indicate significance levels $P < 0.01$; italics indicate significance levels $P < 0.05$. For continuous variables, the estimate of the regression slope b is also given.

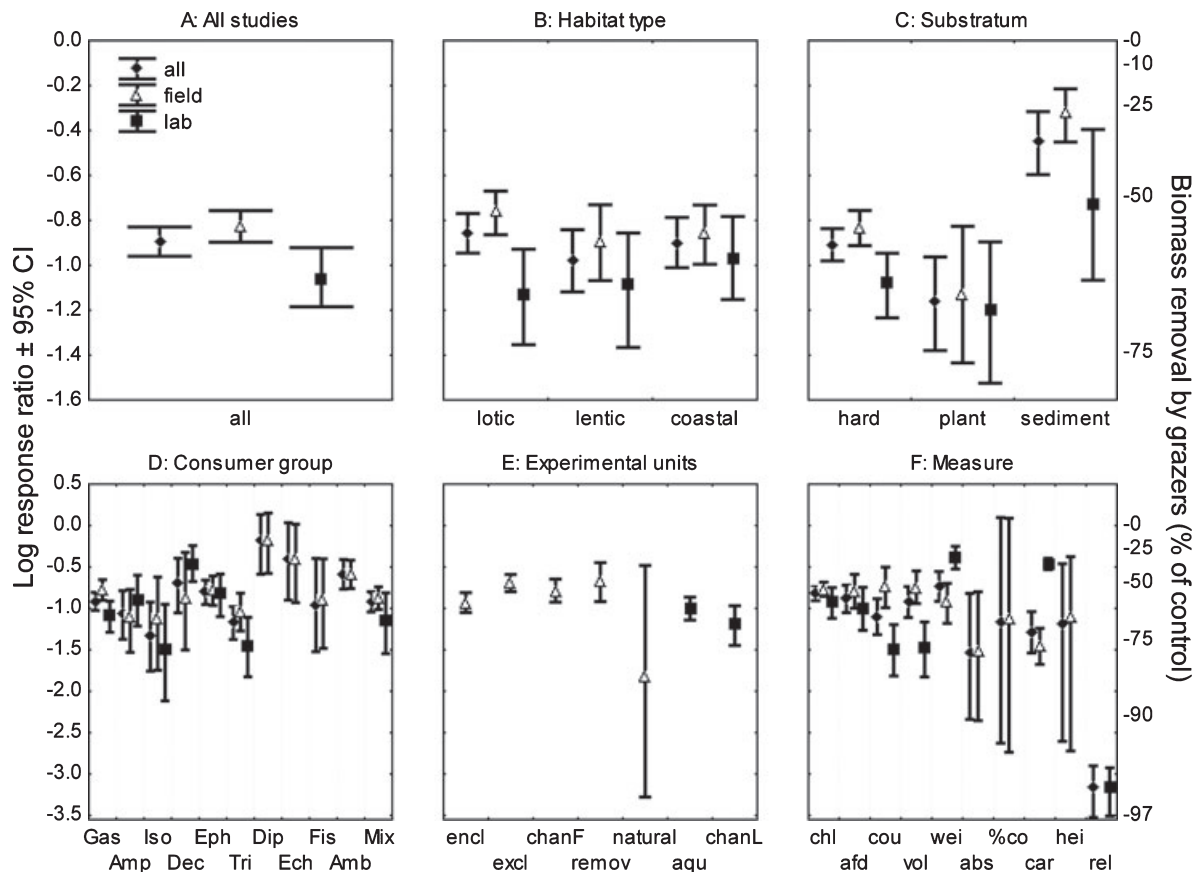


FIG. 1. Average effect sizes of grazers on periphyton biomass (log response ratio \pm 95% confidence interval) in all field or lab experiments for all studies (A), different habitat types (B), substratum types (C), consumer groups (D), experimental units (E), and biomass measures (F). Missing symbols reflect the absence of data for a certain category. (D) Gas, Gastropoda; Amp, Amphipoda; Iso, Isopoda; Dec, Decapoda; Eph, Ephemeroptera; Tri, Trichoptera; Dip, Diptera; Ech, Echinodermata; Fis, Fish; Amb, Amphibia; Mix, mixed grazer assemblages. (E) encl, enclosures; excl, exclosures; chanF, field channels; remov, removal experiments; natural, natural grazer gradient; aqu, aquaria; chanL, laboratory channels. (F) chl, chlorophyll; afd, ash-free dry mass; cou, count; vol, biovolume; wei, weight; abs, absorption; %co, percent cover; car, carbon; hei, height; rel, relative measure.

grazer biomass across all field experiments was only about one-third of the biomass in the lab experiments (i.e., 1,776 vs. 4,995 mg dry weight \cdot m⁻²). At higher biomass (and densities), grazers either spend more time searching for limited food or engage in interference interactions (both within and between species), which reduces the relative effect size on algal biomass.

With increasing algal biomass, grazers remove significantly more periphyton biomass across all experiments, in lab experiments and—although only marginally significant—also in field experiments (Table 1, Fig. 2B). Since LR measures the proportional removal, it can be concluded that as more algal biomass is available, grazers are able to remove larger proportions of the periphyton. By contrast, the increased availability of nutrients and/or light did not lead to more grazing; that is, environments with low resource supply yielded strong grazing effects (Table 1, Fig. 2C). Increasing temperature triggered stronger grazer effects (Fig. 2D), which

was significant across all experiments and for field experiments, but not for lab experiments (Table 1). However, the latter experiment type showed a similar trend.

A significant difference in grazer effect sizes was found between different types of experimental units (Table 1). In the first place, this difference reflected the stronger effects of grazing in lab experiments, as both lab categories (aquaria and lab channels) revealed stronger group-wise effect sizes than most of the field experimental units (Fig. 1E). There was no significant difference between the two lab categories (Table 1). However, within the field experiments, enclosures yielded significantly stronger grazing effects than exclosures (Table 1, Fig. 1E). The few experiments using natural differences between grazer absence and presence were highly variable in their outcome, which reflects both the incoherence in experimental setup and the low number of studies in this analysis. The scale of the experiment also affected grazer effects: in field

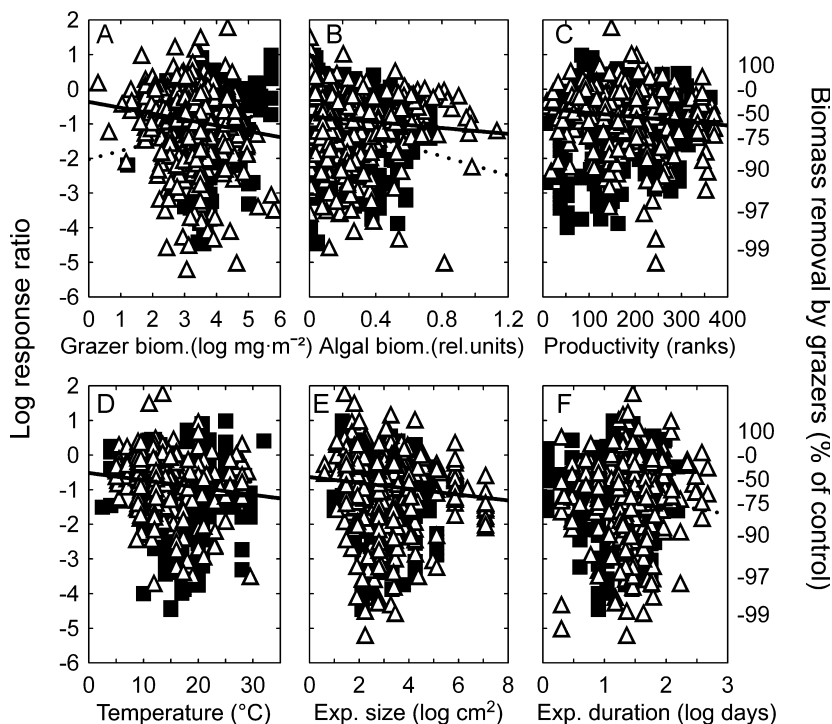


FIG. 2. Single effect sizes of grazers on periphyton biomass (log response ratio) in relation to grazer biomass (A), algal biomass (B), productivity (C), temperature (D), experiment size (E), and duration (F). Please note that productivity is ranked from high to low. Symbols represent field (open triangles, solid lines) and lab (filled squares, dotted lines) experiments, respectively.

experiments, effect sizes became stronger in larger experiments, whereas in lab experiments, it was a longer duration leading to significantly stronger grazer effects (Table 1, Fig. 2, E–F).

Interestingly, an effect of history could be detected in the data set, as more recent studies tend to find lower effect sizes (Table 1). Consistently for

all field and lab experiments, larger grazer effects were observed in older experiments (Fig. 3A). Whereas the year in which the study was performed was important, the season had no significant effect on average effect sizes (Table 1). The effect of latitude was tested only for field experiments and yielded no significant trend (Table 1). However, plotting the effect sizes across latitude clearly shows the dominance of Northern Hemisphere temperate and boreal experiments in the database (Fig. 3B). Even within this large sample size of >800 experiments, the number of effect sizes in tropical latitudes remains extremely low.

The actual measure chosen for periphyton biomass also had an effect on the magnitude of biomass removal, which was significant across the entire data set as well as in the separate analyses for field and lab experiments (Table 1). Microscope-based estimates (counts and biovolume) revealed strong grazer effects, especially in lab experiments (Fig. 1F). Weight as a measure of biomass yielded weak grazer effects in lab-based studies. In field experiments, the deviation was mainly based on some rarely used and derived measures of algal biomass, such as relative measures of biomass, which yielded comparably strong effect sizes (Fig. 1F). However, these measures were often used in only one or two studies, whereas the most commonly used measures (>90% of the experiments used either chl, AFDM, biovolume, counts, or weight) did

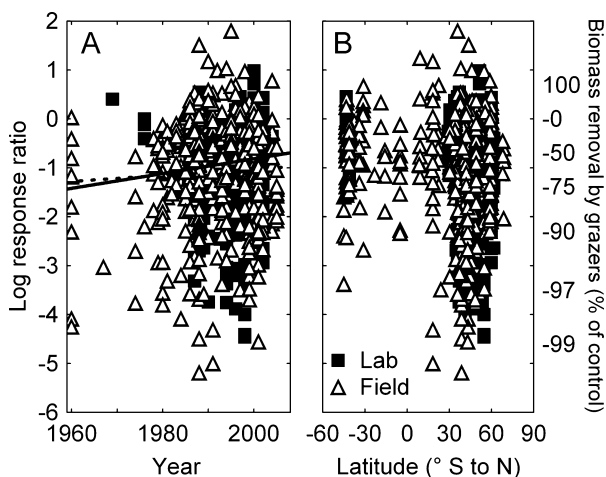


FIG. 3. Single effect sizes of grazers on periphyton biomass (log response ratio) in relation to year of study (A) and latitude (B). Symbols represent field (open triangles, solid lines) and lab (filled squares, dotted lines) experiments, respectively.

not show any significant difference in effect sizes for either the full data set or for field experiments alone.

DISCUSSION

The first major conclusion of this meta-analysis is that grazers have an exceptionally strong impact on periphyton biomass, removing on average 59% of the standing stock, with extremes going up to 99%. System-specific analyses found averages of 56% (sea-grass epiphytes) to 70% (stream periphyton) removal (Feminella and Hawkins 1995, Hughes et al. 2004). Compared to other types of primary producers, periphyton biomass is thus strongly controlled by herbivores. Cebrian (1999) presents data on the percentage of primary production consumed by herbivores for different types of primary producers. He finds a median of 42% removal with the 25% and 75% quartiles being 38% and 75%, respectively (for comparison, in this study the interquartiles are 24% and 76%). Thereby, benthic microalgal beds (Cebrian's category comparable to periphyton) and phytoplankton had the highest grazing effects of all investigated groups of producers (Cebrian 1999). The strong effect of grazing on periphyton can also be seen in a recent comparison of herbivory versus fertilization effects on plant biomass (Gruner et al. 2008). Using data from factorial herbivore and fertilization studies, Gruner et al. (2008) observed strongest herbivory effects across all habitat types in lake and stream benthos, which was strongly dominated by studies on periphyton.

What leads to this high efficiency of grazers? First of all, microalgae are on average high-quality food in terms of P and N content. Cebrian and Lartigue (2004) showed that a large percentage of the variance in the importance of herbivory across ecosystems can be explained by food quality, especially the producer content of N and P. Compared to terrestrial vegetation and aquatic macrophytes, periphyton has high nutrient content despite the occasionally high content of detritus (Frost et al. 2005). Second, the growth of periphyton on surfaces can enhance ingestion efficiency in connection to the relative large grazer:periphyton body size ratio. The importance of surface is reflected by the significant differences in grazing pressure with substratum type, where sediment-dwelling microalgae suffered less consumption than hard-bottom or plant-associated microalgae. Thus, rasping or scraping the periphyton off its substratum allows high proportional removal of periphyton biomass, with different taxa of grazers preferentially using different layers of the periphyton (Steinman 1996). For the size ratio, grazers on periphyton are large compared to their prey (Brose et al. 2006) and thus rarely have difficulties removing the majority of the entire biofilm. Moreover, this high grazer:prey size ratio results in highly unselective feeding, where

grazers remove (or dislodge) large patches of the periphyton.

Despite this strong average grazing effect, the variance of effect sizes is considerably large. Ninety-seven out of 865 effect sizes were positive, roughly corresponding to 11% of the experiments in which algal biomass increased in the presence of grazers. Even though these positive effect sizes tended to have small magnitudes, this proportion clearly indicates the potential for indirect effects in grazer-periphyton interactions. Positive effect sizes can be observed under numerous conditions: (i) when grazers are omnivorous and also consume specialist herbivores, which reduces overall consumption (Pringle et al. 1993); (ii) when grazers remove detritus or sediment (James et al. 2000) and enhance growth conditions for the living algae—in fact, grazers quite often tend to enhance the biomass specific productivity of periphyton (Steinman 1996, Liess and Hillebrand 2004)—or (iii) when grazers enhance nutrient recycling to the point that algal growth exceeds the consumptive capacity of the grazers (Lamberti et al. 1989)—however, this is purportedly rare in nature (Steinman 1996, De Mazancourt et al. 1998).

A second general and striking conclusion from this analysis is that the average grazing pressure on periphyton is very consistent across different habitat types. Thus, the trophic transfer to herbivores has similar magnitudes in streams, lake littoral, and coastal zones. This consistency suggests that the efficiency of grazing is defined by general features of the herbivore-periphyton interaction, such as the body size ratio between grazers and microalgae or the similarity of marine, lotic, and lentic periphyton in terms of functional groups, whereas large-scale differences between realms, such as flow regime or salinity, play a minor role. The consistency of grazing across habitats is also highlighted by many factors that affect grazing across ecosystem boundaries. Some of these factors have previously been discussed in system-specific analyses of benthic grazing but are here shown to apply more generally.

Grazing effects increased with increased grazer biomass, but very large grazer biomasses in some laboratory experiments resulted in lowered grazer effect size. Thus, overcrowding can actually lead to reduced grazing pressure, which presumably is linked to intra- or interspecific interference competition (Munoz et al. 2000, Ruesink 2000). The general trend of increasing effect size with increasing grazer biomass and abundance had been described earlier for stream periphyton (Feminella and Hawkins 1995). Almost all grazer groups comprised in the experiments exhibited a significant negative effect on periphyton biomass, the only notable exception being dipteran larvae (mainly chironomids), which in a vote-counting review also were identified as having low biomass impact (Steinman

1996). The differences among different consumer groups partly reflects previous findings in streams (Feminella and Hawkins 1995).

Increasing algal biomass led to a larger proportion of biomass being removed by herbivores; that is, efficiency increases with availability (see also Feminella and Hawkins 1995). This overcompensation of increasing algal standing stock by the grazers indicates either higher accessibility or ingestibility of biomass-rich periphyton or easier dislodging of less firmly attached biomass-rich biofilms. Regarding ingestibility, larger periphyton biomass results in increasing algal height. Three-dimensional periphyton is easier to ingest than two-dimensional biomass-poor assemblages (Steinman et al. 1992, Hillebrand et al. 2000). Low-biomass periphyton assemblages are often dominated by *Cocconeis*-like prostrate algae, which are difficult to abrade from the substrate for most grazer types (Steinman et al. 1992).

In contrast to the trend with algal biomass, there was a negative correlation between grazer effect size and ecosystem productivity. Possible reasons for this include compensation of low food quality at low nutrient supply by increased ingestion (Cruz-Rivera and Hay 2000) and increased control of herbivores by predators at high productivity (Oksanen et al. 1981, but see Borer et al. 2005 for a meta-analysis showing a lack of increasing top-down control with increasing productivity). Increasing temperatures also lead to higher grazing effects, which most probably reflects a metabolic response of the ectothermic herbivores to increased temperature (Verity 1985). By contrast, seasonal differences were nonsignificant, and there was also no consistent trend in grazing effects with latitude. The lack of a seasonal pattern in effect size is an interesting contrast to the presence of a temperature effect. On one hand, seasonal cycles obviously are more than changes in temperature alone (resource availability, grazer life cycle); on the other hand, the categorization of seasons in this analysis has been coarse, reducing the probability to detect significant differences. In addition, latitude is correlated with average temperatures, but this did not lead to generally higher effect sizes at low latitudes. Instead, the distribution of effect sizes across latitude strongly indicated how little is known about grazing in tropical latitudes. Given the significant temperature effects observed here, we might expect stronger grazing pressure under global warming.

The weighted meta-analysis yielded a number of important relationships with variables describing the experimental design. Stronger grazing effects were observed in lab experiments because they confine grazers and their food without allowing consumer emigration or prey emigration. The same is true for enclosure experiments in the field, which consequently yielded stronger effects

than exclosures. In exclosures, grazers can choose different patches outside the experimental arena for feeding, and algae can reimmigrate into a grazed patch. Both processes reduce grazer effect sizes. Additionally, lab experiments were on average stocked with higher grazer biomass and ran at higher temperatures, which both increased grazer effect sizes. The strongest deviation between lab- and field-based effect sizes was found in lotic systems, which suggests that lotic environments are more difficult to reproduce in lab settings compared to field experiments.

The scale of the experiment also affected its outcome, as larger field experiments and longer-lasting lab experiments increased grazing effect sizes. The size effect was seen only in field experiments, indicating that small experiments might underestimate grazer effect sizes. An analysis of trophic cascade strength did not find any significant impact of experiment size but did find a positive correlation with experiment duration (Borer et al. 2005). The same effect of duration was found in stream periphyton experiments (Feminella and Hawkins 1995). If experiments run longer (especially if they are spatially confined not allowing immigration or emigration), the removal of biomass becomes more complete, which increases grazer effect size. However, there might be a nonlinear relationship of effect size with experiment duration, which could not be tested in this analysis (but see Fig. 2F). In very long-lasting experiments, grazing may be reduced by periphyton communities shifting to less edible forms or grazing insects emerging as adults.

The effect of biomass measures on the estimate of grazer effect size reflects how well these measures reflect algal biomass within the periphyton—microscopic counts and biovolume measures address only the algae, whereas weight- or carbon-based measures comprise algae, heterotrophs, and dead organic matter. Measures reflecting mainly the algal component of periphyton gave on average a higher estimate of grazing pressure compared to measures comprising also heterotrophic organism groups and detritus. Grazing on heterotrophs has been proposed to be less effective than on algae. A series of field experiments indicated that some heterotrophic groups were even able to increase biomass in the presence of grazers (Hillebrand et al. 2002). Potential pathways for this positive effect were increased bacterial production on regenerated nutrients and facilitation by altered community structure in grazed periphyton. Using chl as a measure is also not free of artifacts, as algae regulate their chl content physiologically in response to light and nutrient availability (Hillebrand et al. 2004).

On average, older studies tended to find larger effect sizes than more recent studies. This astonishing trend, which most probably is not an indication of reduced herbivory over the past 50 years, may

reflect that earlier studies focused on habitats with obvious impacts of grazers, whereas more recent papers might comprise habitats with less obvious grazing importance. Alternatively, newer studies may use more conservative treatment levels than the pioneering studies.

In summary, grazing on periphyton is an extraordinarily strong trophic interaction, which has similar magnitudes in very different types of aquatic habitats. Higher grazer biomass, higher algal biomass, higher temperature, and the presence of hard substrata all strongly increase grazer effect sizes across aquatic realms. Researchers should be aware that their choice of experimental design (lab vs. field, enclosure vs. exclosure, size, and duration) strongly affects the estimate of grazing obtained. In this study, average effects are presented for different conditions, which can be used as a baseline to which new experimental results can be compared. This analysis indicated major gaps in the geographic and seasonal coverage of grazing, which should be filled by additional experiments.

I want to sincerely thank all authors of the primary papers building the database of this analysis, especially to those offering unpublished data or additional information on their study. The work on this manuscript has been fueled by tremendous amounts of coffee supplied during a number of long train rides and during stopover at diverse airports (special thanks to Copenhagen-Kastrup airport). Financial support for building this database came from the basic funding of the universities of Uppsala (Sweden), Kiel (Germany), and Cologne (Germany).

- Alvarez, M. & Pardo, I. 2007. Factors controlling epilithon biomass in a temporary, karstic stream: the interaction between substratum and grazing. *J. North Am. Benthol. Soc.* 26:207–20.
- Blumenshine, S. C., Vadeboncoeur, Y., Lodge, D. M., Cottingham, K. L. & Knight, S. E. 1997. Benthic–pelagic links: responses of benthos to water-column nutrient enrichment. *J. North Am. Benthol. Soc.* 16:466–79.
- Borchardt, M. A. 1996. Nutrients. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology – Freshwater Benthic Ecosystems*. Academic Press, San Diego, California, pp. 183–227.
- Borer, E. T., Seabloom, E. W., Shurin, J. B., Anderson, K. E., Blanchette, C. A., Broitman, B., Cooper, S. D. & Halpern, B. S. 2005. What determines the strength of a trophic cascade? *Ecology* 86:528–37.
- Bourassa, N. & Cattaneo, A. 1998. Control of periphyton biomass in Laurentian streams (Quebec). *J. North Am. Benthol. Soc.* 17:420–9.
- Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L. F., Blanchard, J. L., et al. 2006. Consumer-resource body-size relationships in natural food webs. *Ecology* 87:2411–7.
- Burkholder, J. M. 1996. Interactions of benthic algae with their substrata. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology – Freshwater Benthic Ecosystems*. Academic Press, San Diego, California, pp. 253–97.
- Cebrian, J. 1999. Patterns in the fate of production in plant communities. *Am. Nat.* 154:449–68.
- Cebrian, J. & Lartigue, J. 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecol. Monogr.* 74:237–59.
- Cruz-Rivera, E. & Hay, M. E. 2000. Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. *Ecology* 81:201–19.
- De Mazancourt, C., Loreau, M. & Abbadie, L. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology* 79:2242–52.
- DeNicola, D. M. 1996. Periphyton responses to temperature at different ecological levels. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology – Freshwater Benthic Ecosystems*. Academic Press, San Diego, California, pp. 149–81.
- Fairchild, G. W. & Lowe, R. L. 1984. Artificial substrates which release nutrients: effects on periphyton and invertebrate succession. *Hydrobiologia* 114:29–37.
- Feminella, J. W. & Hawkins, C. P. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. *J. North Am. Benthol. Soc.* 14:465–509.
- Frost, P. C., Hillebrand, H. & Kahlert, M. 2005. Low algal carbon content and its effect on the C : P stoichiometry of periphyton. *Freshw. Biol.* 50:1800–7.
- Gruner, D. S., Smith, J. E., Seabloom, E. W., Sandin, S. A., Ngai, J. T., Hillebrand, H., Harpole, W. S., et al. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecol. Lett.* 11:740–55.
- Gurevitch, J., Morrison, J. A. & Hedges, L. V. 2000. The interaction between competition and predation: a meta-analysis of field experiments. *Am. Nat.* 155:435–53.
- Hedges, L. V., Gurevitch, J. & Curtis, P. S. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–6.
- Hill, W. R. 1996. Effects of light. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology – Freshwater Benthic Ecosystems*. Academic Press, San Diego, California, pp. 121–48.
- Hill, W. R., Ryon, M. G. & Schilling, E. M. 1995. Light limitation in a stream ecosystem – responses by primary producers and consumers. *Ecology* 76:1297–309.
- Hillebrand, H. 2002. Top-down versus bottom-up control of autotrophic biomass – a meta-analysis on experiments with periphyton. *J. North Am. Benthol. Soc.* 21:349–69.
- Hillebrand, H. 2005. Light regime and consumer control of autotrophic biomass. *J. Ecol.* 93:758–69.
- Hillebrand, H., de Montpelier, G. & Liess, A. 2004. Effects of macrograzers and light on periphyton stoichiometry. *Oikos* 106:93–104.
- Hillebrand, H., Kahlert, M., Haglund, A. L., Berninger, U. G., Nagel, S. & Wickham, S. 2002. Control of microbenthic communities by grazing and nutrient supply. *Ecology* 83:2205–19.
- Hillebrand, H., Worm, B. & Lotze, H. K. 2000. Marine microbenthic community structure regulated by nitrogen loading and grazing pressure. *Mar. Ecol. Prog. Ser.* 204:27–38.
- Hughes, A. R., Bundo, K. J., Rodriguez, L. F. & Williams, S. L. 2004. Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. *Mar. Ecol. Prog. Ser.* 282:87–99.
- James, M. R., Hawes, I. & Weatherhead, M. 2000. Removal of settled sediments and periphyton from macrophytes by grazing invertebrates in the littoral zone of a large oligotrophic lake. *Freshw. Biol.* 44:311–26.
- Lamberti, G. A. 1996. The role of periphyton in benthic food webs. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology – Freshwater Benthic Ecosystems*. Academic Press, San Diego, California, pp. 533–72.
- Lamberti, G. A., Gregory, S. V., Ashkenas, L. R., Steinman, A. D. & McIntire, C. D. 1989. Productive capacity of periphyton as a determinant of plant herbivore interactions in streams. *Ecology* 70:1840–56.
- Liess, A. & Hillebrand, H. 2004. Direct and indirect effects in herbivore–periphyton interactions. *Arch. Hydrobiol.* 159:433–53.
- Mosisch, T. D., Bunn, S. E. & Davies, P. M. 2001. The relative importance of shading and nutrients on algal production in subtropical streams. *Freshw. Biol.* 46:1269–78.
- Munoz, I., Real, M., Guasch, H., Navarro, E. & Sabater, S. 2000. Resource limitation by freshwater snail (*Stagnicola vulnerata*) grazing pressure: an experimental study. *Arch. Hydrobiol.* 148:517–32.
- Oksanen, L., Fretwell, S. D., Arruda, J. & Niemelä, P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118:240–61.

- Pan, Y., Stevenson, R. J., Hill, B. H., Kaufman, P. R. & Herlihy, A. T. 1999. Spatial patterns and ecological determinants of benthic algal assemblages in mid-Atlantic streams, USA. *J. Phycol.* 35:160–8.
- Planas, D. 1996. Acidification effects. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology – Freshwater Benthic Ecosystems*. Academic Press, San Diego, California, pp. 497–530.
- Pringle, C. M., Blake, G. A., Covich, A. P., Buzby, K. M. & Finley, A. 1993. Effects of omnivorous shrimp in a montane tropical stream – sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. *Oecologia* 93:1–11.
- Rosenberg, M. S., Adams, D. C. & Gurevitch, J. 2000. *MetaWin Version 2.0 Statistical Software for Meta-Analysis*. Sinauer Associates, Sunderland, Massachusetts.
- Ruesink, J. L. 2000. Intertidal mesograzers in field microcosms: linking laboratory feeding rates to community dynamics. *J. Exp. Mar. Biol. Ecol.* 248:163–76.
- Steinman, A. D. 1996. Effects of grazers on benthic freshwater algae. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology – Freshwater Benthic Ecosystems*. Academic Press, San Diego, California, pp. 341–73.
- Steinman, A. D., Mulholland, P. J. & Hill, W. R. 1992. Functional responses associated with growth forms in stream algae. *J. North Am. Benthol. Soc.* 11:229–43.
- Stevenson, R. J. 1996a. An introduction to algal ecology in freshwater benthic habitats. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology – Freshwater Benthic Ecosystems*. Academic Press, San Diego, California, pp. 3–30.
- Stevenson, R. J. 1996b. The stimulation and drag of current. In Stevenson, R. J., Bothwell, M. L. & Lowe, R. L. [Eds.] *Algal Ecology – Freshwater Benthic Ecosystems*. Academic Press, San Diego, California, pp. 321–40.
- Vadeboncoeur, Y., Lodge, D. M. & Carpenter, S. R. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. *Ecology* 82:1065–77.
- Vander Zanden, M. J. & Vadeboncoeur, Y. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83:2152–61.
- Vanni, M. J. 1996. Nutrient transport and recycling by consumers in lake food webs: implications for algal communities. In Polis, G. A. & Winemiller, K. O. [Eds.] *Food Webs: Integration of Patterns and Dynamics*. Chapman Hall, New York City, New York, pp. 81–95.
- Verity, P. G. 1985. Grazing, respiration, excretion, and growth-rates of tintinnids. *Limnol. Oceanogr.* 30:1268–82.
- Wetzel, R. G. 2001. *Limnology*, 3rd ed. Academic Press, San Diego, California, 850 pp.

Supplementary Material

The following supplementary material is available for this article:

Appendix S1. List of papers included in the meta-analysis on grazing effects on periphyton biomass.

This material is available as part of the online article.

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