

## GRAZING REGULATES THE SPATIAL VARIABILITY OF PERIPHYTON BIOMASS

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**Abstract.** The presence of consumers not only alters the mean biomass of the prey assemblage, but also affects the spatial heterogeneity of biomass distribution. Whereas the mean prey biomass is generally reduced by consumer presence, the effect on spatial heterogeneity is less clear-cut. A meta-analysis of almost 600 field experiments manipulating the presence of benthic invertebrate or vertebrate grazers was conducted to analyze the effect of grazers on both the absolute spatial variability of periphyton biomass and the relative variability, which was standardized to the mean. Effects on absolute variability were measured as the log response ratio of the standard deviation of biomass (LR-SD), whereas effects on relative variability were measured as the log response ratio of the coefficient of variation of biomass (LR-CV). The overall magnitude and range of LR-SD and LR-CV indicated that grazers not only reduced periphyton biomass, but also substantially altered their spatial distribution. However, grazer effects differed strongly for absolute and relative variability. On average, grazers reduced the absolute spatial variability in prey biomass by 50% (average LR-SD =  $-0.68$ ) but increased the relative variability by 24% (average LR-CV =  $0.22$ ). The magnitude of LR-SD strongly depended on the efficiency of grazing, with strong biomass removal leading to strong homogenization. Moreover, LR-CV and LR-SD were significantly affected by habitat type (freshwater vs. coastal) and substrata. Given the importance of spatial heterogeneity for resource uptake, competition and the maintenance of diversity, grazer presence has potentially strong indirect effects on the interactions within prey assemblages.

**Key words:** *coefficient of variation; grazer efficiency; meta-analysis; periphyton biomass; spatial heterogeneity; standard deviations.*

### INTRODUCTION

Trophic interactions are a primary regulating force of community structure and ecosystem functioning. The presence of a consumer tends to have strong (and mostly negative) effects on the average biomass, growth, and survival of the prey assemblage. Several meta-analyses analyzed the efficiency of biomass removal by consumers in a variety of ecosystems, with special emphasis on the relative effects of resource supply and consumer presence (Brett and Goldman 1997, Hawkes and Sullivan 2001, Hillebrand 2002, 2005, Shurin et al. 2002, Hughes et al. 2004, Borer et al. 2005).

However, consumption is rarely evenly distributed in space, and consumers tend also to affect the spatial distribution of prey biomass. Whereas average effect sizes of consumers on prey biomass have been analyzed frequently, there is little evidence on general effects of consumers on the variability of biomass. Acknowledging the variance of consumer effects may help to understand ecological patterns in natural communities (Benedetti-Cecchi 2000, Benedetti-Cecchi et al. 2005). In a marine field experiment, Benedetti-Cecchi et al. (2005) manip-

ulated both the average grazing pressure and the variability of grazing and found strong independent effects of both aspects of grazing on the spatial distribution of algae. In a spatially explicit freshwater experiment, Peters et al. (2007) found strong variation in grazing pressure on periphyton in few meters distance despite macroscopical uniformity of the habitat. Within the autotroph community, consumer-induced spatial heterogeneity has important consequences for the functioning of communities and for plant coexistence (Pacala and Crawley 1992, Chase et al. 2002).

Despite the potential importance, few studies have explicitly analyzed the degree of consumer-induced heterogeneity on plants, although the importance of spatial patterns in grazer-dominated systems has long been recognized (McNaughton 1983, 1985, Milchunas and Lauenroth 1993). In a recent review, Adler et al. (2001) concluded that the presence of herbivores can either increase or decrease the spatial heterogeneity of terrestrial vegetation. They used simulation models and literature data to show that the effect of grazer presence on plant spatial heterogeneity depends on the spatial pattern of grazing and the preexisting spatial pattern of the vegetation.

In aquatic communities, consumer-induced heterogeneity has been proposed to be especially important in periphyton communities, as grazing may alter commu-

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nity physiognomy, nutrient uptake, and competition (Steinman et al. 1992, Hillebrand and Kahlert 2001, Wellnitz and Rader 2003). Patchy distribution of periphyton biomass affects nutrient flow and uptake (Riber and Wetzel 1987), competition for light (Hillebrand 2005), as well as the ability of grazers to recognize and select food patches (Vaughn 1986, Kawata and Agawa 1999). Additionally, spatial heterogeneity also affects important ecosystem processes performed by periphyton such as production (Cardinale et al. 2002).

Consequently, the spatial effects of invertebrate or vertebrate grazers have been analyzed in a number of studies with quite disparate results. Some studies showed an increase in spatial heterogeneity of periphyton (Sommer 2000, Kawata et al. 2001, Alvarez and Peckarsky 2005), whereas in others grazers reduced spatial and temporal heterogeneity (Gelwick and Matthews 1997, Sommer 2000). A number of hypotheses have been put forward to explain the disparate results. The increase in spatial heterogeneity of stream periphyton biomass was connected to more mobile consumers (Alvarez and Peckarsky 2005). Sommer (2000) explained the heterogeneity enhancing effects of a snail by its bulldozer type of grazing, whereas the presence of an isopod grazer did not enhance prey heterogeneity as this species distributed its grazing pressure more evenly (see also Gelwick and Matthews 1997). The supply of resources (light or nutrients) strongly affected how grazer presence altered periphyton patchiness (Pringle 1996, Wellnitz and Rader 2003). Flecker and Taylor (2004) used herbivorous fishes as consumer to test whether spatial heterogeneity might be enhanced at intermediate densities. They argued that very low densities may not alter spatial heterogeneity, whereas very strong grazing pressure might reduce prey variability, proposing a unimodal relationship with strongest increase in spatial heterogeneity at intermediate densities. They found such a unimodal relationship, but only at the start of their experiment. After two weeks, all consumer densities led to an increase in spatial heterogeneity of the periphyton.

In order to generally analyze how consumer presence affects prey heterogeneity, I performed a meta-analysis of grazer-periphyton experiments. The standard deviation (SD) of periphyton biomass and its coefficient of variation (CV) were used to measure the absolute and relative spatial heterogeneity in algal biomass, respectively. SD and CV are simple and spatially non-explicit measures of biomass heterogeneity, which can be calculated for all replicated experiments manipulating grazer presence. Both have been criticized as measures of spatial heterogeneity as they give only one measure of overall variability, which is sensitive to different scales of observation and is not informative per se as many different underlying biomass distributions can give the same variability (Cooper et al. 1997). Other measures of spatial variability like the Morisita index (Alvarez and

Peckarsky 2005), landscape indices (Flecker and Taylor 2004), or other geostatistical approaches (Cooper et al. 1997) contain more information on the spatial distribution of periphyton biomass and its dependence on spatial distance. However, the information necessary to calculate these measures is rarely published in experiments. By using simple measures such as SD and CV, grazer effects on periphyton heterogeneity could be obtained from almost 600 field experiments. Moreover, the use of a coarse measure of variability can be justified in this analysis, as I analyze the relative change in SD and CV with grazing rather than absolute values.

For this analysis, both absolute and relative spatial variability in algal biomass are addressed, which is warranted as altered CV or SD may have different ramifications (Cooper et al. 1997). Herbivores aggregate on biomass-rich periphyton patches (Lamberti and Resh 1983, McAuliffe 1983), which will depend on absolute rather than relative biomass amounts. Also microbial processes, which often scale to algal biomass in periphyton (Romani and Sabater 1999) will rather be affected by absolute variation in algal biomass. On the other hand, relative variability will affect competitive interactions within the periphyton, as competition for light (Hillebrand 2005) and relative access to water column nutrients (Riber and Wetzel 1987) is affected by the relative biomass within a patch compared to the surrounding rather than by the absolute biomass. It has been shown for terrestrial plants that competitive advantage in light competition depends on the relative height advantage compared to competitors rather than the absolute height (Falster and Westoby 2003). Similarly, small relative increases in height will foster light and nutrient uptake for periphyton.

Using the broad experimental information on grazer effects on CV and SD, I first analyzed the general tendencies of grazer effects on relative heterogeneity and absolute heterogeneity. I calculated mean effect sizes and 95% confidence interval (CI) to test how grazer presence affects the absolute and relative variability of periphyton biomass. In a second step, I tested whether grazer effects on spatial heterogeneity differ between broad habitat types (lotic, lentic, or coastal), substrata, consumer groups, and experimental approaches. Finally, I analyzed whether grazer effects on spatial heterogeneity were related to factors potentially affecting consumer-induced related spatial heterogeneity such as the efficiency of the grazers (Gelwick and Matthews 1997, Alvarez and Peckarsky 2005), the resource supply in the ecosystem (Pringle 1996, Wellnitz and Rader 2003), or the spatial and temporal scale of the experiment (Flecker and Taylor 2004).

## METHODS

### *Data*

The data were derived from a database containing >800 experiments, where grazer presence was manipulated and the mean and standard deviation of periph-

yton biomass was analyzed in replicated 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\*).” Experiments were included when they contained replicated grazed and ungrazed treatments and provided estimates of periphyton abundance or biomass. For this analysis, only field experiments ( $N = 593$  experiments) were used as laboratory experiments were considered to have too artificial setups and small size to analyze spatial heterogeneity. These experiments originate from 127 publications, which are listed in Appendix A together with the main categorical variables obtained from these studies.

The final database covered a broad variety of habitats, experiment types, consumer groups and substrata for periphyton growth. A rough one-third of the included experiments were performed in coastal marine sites ( $N = 191$  experiments), the others were lotic (289 experiments) or lentic (113 experiments). Most experiments were either enclosure (347) or exclosure (222) experiments. Enclosures represent confined environments stocked with the target grazer such as buckets, mesocosms, and streamside channels. Exclosures represent setups preventing grazer access to a confined environment (cages, in-situ channels). Only a minority of the studies were removal experiments, e.g., via insecticides (23 studies). All major groups of potentially important grazers on periphyton were included, most frequently gastropods (183 studies), insect larvae (119 studies), crustaceans (53 studies), amphibians (69 studies), and fish (16 studies). More than one grazer group was used in 146 experiments, and seven focused on other animal groups. All kinds of benthic microalgal assemblages were used in this analysis. The overwhelming majority grew on hard substrates (i.e., epilithic, 491 experiments), but other experiments considered epiphytes on plants (57) or sediment-dwelling microalgae (44). Habitat, experiment type, consumer type and substratum were used as categorical variables in the statistical analyses (Appendix A).

Additionally, the following information was obtained for each experiments when given in the original contribution: the size of the experimentally manipulated unit ( $\text{cm}^2$ ), the duration of the experiment (days), the concentrations of dissolved phosphate and dissolved nitrogen ( $\mu\text{g/L}$ ), the mean irradiance ( $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), the grazer biomass ( $\text{mg dry mass}/\text{m}^2$ ) and the periphyton biomass. This measure of prey biomass had to be derived in order to avoid using absolute values (which would confound this variable with the effect sizes). As different measures of algal biomass were used in the original studies, I calculated dimensionless units of algal biomass relative to the mean (across all experiments) of that measure (Hillebrand 2005). Therefore, the ungrazed 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  $j$ .

It turned out that information on resource supply (phosphate, nitrogen, and light) was rarely given completely in the original contributions. To reduce the effect of missing data, I obtained an aggregate index of resource supply by standardizing each log-transformed concentration (light, available P, available N) as a proportion of the mean for this variable across all studies. Aggregated resource supply was then expressed as the average of all standardized resource values obtained from that study, i.e., was based on one to three values. This aggregated index was strongly linearly correlated to the original values for each of the three resource variables ( $r = 0.41\text{--}0.86$ ,  $P < 0.001$ ).

### *Effect sizes*

For each experiment, three different effect sizes were calculated, all as log response ratios (LR). LR are standard effect sizes in meta-analyses (Hedges et al. 1999) and grazer effects are calculated as  $\text{LR} = \ln(\text{grazed}/\text{ungrazed})$ . Since LR measure the relative change in the target variable due to the treatment, they are independent of the units of measurement, and are frequently employed in ecological meta-analysis (Goldberg et al. 1999, Shurin et al. 2002, Lajeunesse and Forbes 2003, Hillebrand 2005).

To measure the effect of consumer presence on average periphyton biomass, I calculated LR-B as the natural-log-transformed ratio of mean biomass in the grazed treatment to mean biomass in the ungrazed treatment. Negative values of LR-B indicate that grazer presence reduced periphyton biomass, positive values that grazing increases periphyton biomass (Fig. 1).

The second LR measures the effect of grazer presence on the absolute variability of periphyton biomass, using the standard deviation (SD) for grazed and ungrazed periphyton, respectively. The effect size (LR-SD) was calculated as the natural log transformed ratio of SD in the grazed treatment to SD in the ungrazed control. A negative LR-SD indicates that grazer presence decreases the absolute variability of prey biomass; a positive LR-SD indicates that the biomass in replicate treatments becomes more dissimilar. All combinations of LR-B and LR-SD are possible, i.e., grazers can have positive effect on biomass, but negative on SD or neutral effects on biomass, but strong effects on SD (Fig. 1).

The third LR quantifies grazer effects on the relative variability of periphyton biomass, which is reflected by the coefficient of variation (CV) for grazed and ungrazed periphyton, respectively. CV is standardized to the mean by giving the SD as percentage of the mean. The effect size (LR-CV) was calculated as the natural-log-transformed ratio of CV in the grazed treatment to CV in the ungrazed control. A negative LR-CV indicates that grazer presence decreases the relative variability of prey biomass; a positive LR-CV indicates that grazers

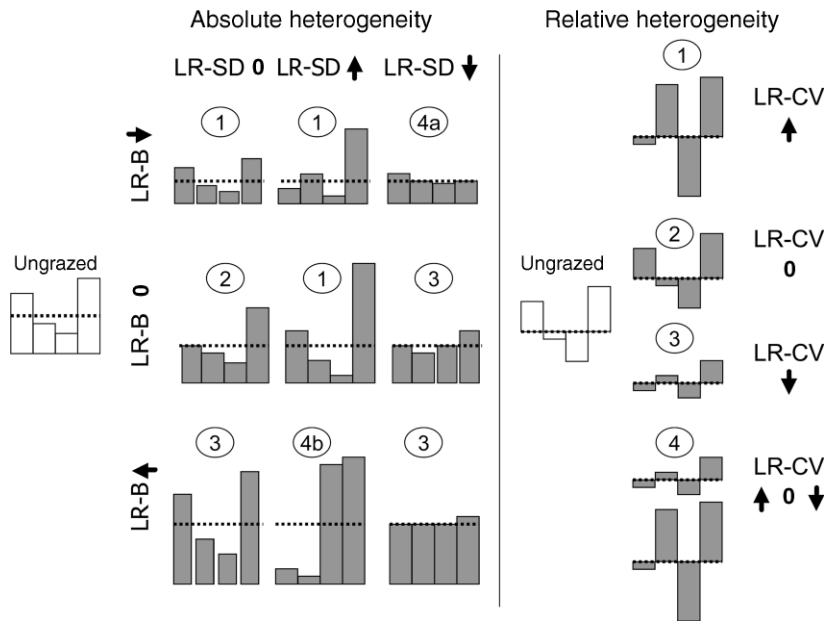


FIG. 1. Potential effects of grazers on average biomass and on absolute and relative biomass variability. Each panel with four bars represents the replicates of a hypothetical treatment, with white bars for ungrazed algal biomass and gray for grazed algal biomass. The mean is indicated by a horizontal dotted line. Left-hand panels show grazer effects on mean biomass (log response ratio, LR-B) and the standard deviation (LR-SD) as a measure of absolute variability of biomass. Grazer presence can a priori have independent effects on biomass and its standard deviation, i.e., each can increase (up-pointing arrow), decrease (down-pointing arrow), or remain unchanged (zero). Based on these effects, the response of periphyton coefficient of variation as a measure of relative variability of biomass (log response ratio, LR-CV) can be categorized into four different cases (circled numbers), depicted in the right-hand panels. In cases 1–3, the sign of the grazer effect on periphyton CV is predetermined by the effects on biomass and its standard deviation. In case 4, increasing or decreasing CV depends on the relative magnitude of grazer effects. If LR-B and LR-SD are both negative (case 4, top), periphyton CV increases if the reduction of biomass is stronger than the reduction in standard deviation but decreases if LR-SD is more negative than LR-B. If LR-B and LR-SD are both positive (case 4, bottom), stronger LR-B than LR-SD decreases the CV of periphyton biomass, whereas periphyton CV increases if biomass increases less than standard deviation.

enhance the relative heterogeneity of biomass distribution. LR-CV depends on both LR-SD and LR-B, leading to many cases where the response of periphyton biomass CV to grazing is predetermined (Fig. 1). When LR-B is positive and LR-SD negative or neutral, LR-CV has to be negative, whereas negative LR-B and neutral to positive LR-SD always leads to positive LR-CV. However, if both LR-SD and LR-B are either positive or negative, flexible LR-CV are possible depending on the relative strength of the effects on SD and mean biomass (Fig. 1).

#### Analyses

Unweighted meta-analyses were performed as the sampling variance of LR-SD and LR-CV could not be calculated. Average effect sizes and 95% confidence intervals (CI) were calculated for both LR-CV and LR-SD. Significant difference from zero was concluded if zero was not included in the 95% CI.

To test variation of effect sizes with important predictor variables, two statistical approaches were used. First, an analysis of heterogeneity (Rosenberg et al. 2000) was performed on univariate predictor

variables comprising categorical factors such as habitat, experiment type, consumer type and substratum as well as continuous factors such as the duration and size of the experiments, resource supply, algal biomass, grazer biomass, and the effect of grazers on mean algal biomass LR-B. The analysis on LR-B could only be performed for LR-SD, as LR-CV is strongly autocorrelated to LR-B as both effect sizes employ the mean biomass in their calculations. To account for the multiple significance tests in the meta-analysis, a sequential Bonferroni adjustment of *P* values was used (Quinn and Keough 2002).

Note that not all information could be obtained from each paper, leading to different degrees of freedom for each univariate test. The univariate meta-analyses made use of the largest possible database for each test, but did not account for collinearity between the explanatory variables. Therefore, I compared the meta-analysis to a multivariate model, which accounted for the collinearity at the expense of a reduction in the data set, as studies lacking information on one of the predictor variables had to be deleted from the multivariate analysis ( $N = 246$  studies). I used a model selection procedure employing

Akaike information criteria (AIC; Johnson and Omland 2004) to identify the most parsimonious general linear model (GLM) for variation in LR-CV and LR-SD. For both analyses, GLM and meta-analysis, full statistical results are reported in Appendix B. Within the text, statistical tests are summarized with a focus on factors significant in both analyses.

## RESULTS

### *Overall effect sizes*

The average grazer effect on absolute heterogeneity of periphyton biomass (LR-SD) was  $-0.68$  and significantly different from zero (Fig. 2a). That is, grazers on average decreased the spatial heterogeneity of periphyton biomass by 50% (back-transformed from the mean effect size). The effect sizes of single experiments on absolute biomass variability ranged from  $-6$  to  $+3$  (Fig. 2b), which corresponds to effect magnitudes of more than 400-fold decrease or 20-fold increase in spatial biomass heterogeneity, respectively. LR-B for the same set of experiments varied between  $-6$  and  $+2$  with a significantly negative average of  $-0.90$ , which corresponds to 60% biomass reduction by grazer presence.

Grazer effects on absolute biomass variability were thus equivalent to grazer effects on mean biomass, with respect to both average magnitude and range of the effect sizes. However, as LR-B was on average stronger than LR-SD, the resulting effect on the CV of biomass was positive (cf. Fig. 1). The average LR-CV was  $0.22$  (Fig. 2a) and differed significantly from zero, which means that grazers on average increased the relative spatial heterogeneity of periphyton biomass by 24%. Single values for LR-CV ranged from  $-4$  to  $+5$ , which corresponds to effect magnitudes ranging between a 50-fold decrease and a 150-fold increase in relative biomass heterogeneity (Fig. 2b).

### *Variation in grazer effects on biomass variability*

Both statistical analyses led to the conclusion that LR-SD was significantly affected by grazer effects on biomass (LR-B) and differed between habitats and substratum types (Table 1). Coastal periphyton showed stronger reductions in SD by grazing than lotic or lentic periphyton (Fig. 3a). Stronger reductions in SD were also observed for periphyton on plants (epiphytes) than for epilithic or sediment microalgae (Fig. 3b). Despite these contrasts, LR-SD remained significantly negative for all three habitats and all three substrata. LR-SD and LR-B were strongly positively correlated (Fig. 3c), with strong biomass removal (negative LR-B) leading to strong homogenization of biomass variability (negative LR-SD). The slope of this relationship was almost invariant between the meta-analysis and the general linear model (Table 1). The final GLM was highly significant and explained 57% of the variance in LR-SD (see Appendix B for full statistical details).

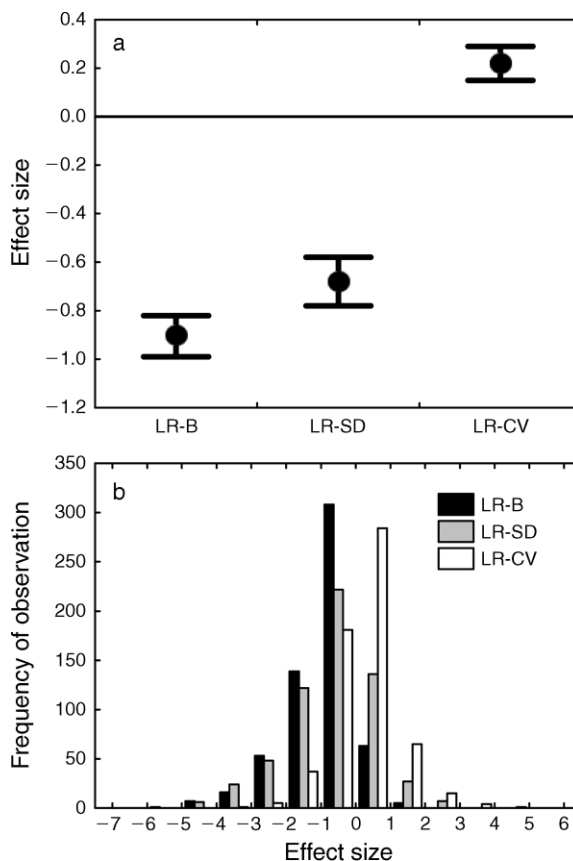


FIG. 2. (a) Effect sizes (mean and 95% CI) of grazer presence on average periphyton biomass (LR-B) as well as the absolute (LR-SD) and relative (LR-CV) variability of periphyton biomass. (b) Frequency distribution of effects sizes of grazer presence on average periphyton biomass (LR-B) as well as the absolute (LR-SD) and relative (LR-CV) variability of periphyton biomass.

The univariate meta-analyses also highlighted that LR-SD was mainly negative at high grazer biomass, large size of the experimental units and low supply of resources (Table 1). Moreover, insects and crustaceans had a stronger reducing effect on SD than amphibians and gastropods (Table 1). None of these differences was included in the final GLM.

Also for LR-CV, GLM and meta-analysis results were highly congruent as both detected significant effects of habitat and substratum type (Table 1). Positive LR-CV were more pronounced in both freshwater systems (lentic and lotic) than in coastal marine systems, where the average effect size was not significantly different from zero (Fig. 4a). Moreover, LR-CV were more positive for periphyton on hard substratum than for epiphytes and sediment microalgae (Fig. 4b). Thus, grazer presence tended to increase the relative spatial heterogeneity of the algae mainly in freshwater habitats on hard substrates. The final GLM was significant and explained 15% of the variance in LR-CV. Neither the

TABLE 1. Summary of statistical results on variation in grazer effects on the absolute (LR-SD) and relative (LR-CV) spatial variability of algal biomass.

Factor	LR-SD			LR-CV		
	MA		GLM	MA		GLM
	Contrast/slope	$P_{adj}$		Contrast/slope	$P_{adj}$	Contrast/slope
Habitat†	Lo $\geq$ Co*	ns	Lo = Le > Co***	Lo = Le > Co*	ns	Lo = Le > Co**
Experimental unit	ns	ns	—	ns	ns	—
Substratum‡	Se = Ha > Pl**	**	Se = Ha > Pl***	Se = Ha > Pl**	ns	Se = Ha > Pl***
Consumer group§	Am = Ga > In = Cr**	*	—	*	ns	—
Grazer biomass (log[g dry mass/m <sup>2</sup> ])	-0.15**	*	—	ns	ns	—
LR-B¶	0.84***	***	0.88***	na	na	na
Duration (log[days])	ns	ns	—	ns	ns	—
Experiment size (log[cm <sup>2</sup> ])	-0.22***	***	—	ns	ns	—
Resource supply (relative units)	0.59**	*	—	ns	ns	—
Algal biomass (relative units)	ns	ns	—	ns	ns	—

Notes: The table lists results for the univariate meta-analysis (MA) and the general linear model (GLM). For the MA, the table lists the significant contrast for categorical variables or the slope for continuous variables and their significance levels as well as the Bonferroni-adjusted  $P$  values ( $P_{adj}$ ). For the GLM, contrasts or slopes are given with significance levels (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; ns, nonsignificant; na, not applicable; —, not included).

† Lo, lotic; Le, lentic; Co, coastal.

‡ Se, sediment; Ha, hard; Pl, plant.

§ Am, amphibia; Ga, gastropods; In, insects; Cr, crustaceans; fish; other; diverse.

¶ Natural-log-transformed ratio of mean biomass in the grazed treatment to mean biomass in the ungrazed treatment.

consumer group nor the scaling of the experiment, nor resource supply altered the effect of grazers on relative biomass heterogeneity (Appendix B).

## DISCUSSION

Grazers had strong negative effects on the absolute variability of periphyton biomass, whereas effects on the relative variability of periphyton biomass were on average positive, but more heterogeneous. The spatial distribution of periphyton biomass was strongly homogenized by grazer presence, but standardized to the biomass present, grazed periphyton shows higher heterogeneity than ungrazed periphyton. These effects were comparable in magnitude to the main effects on average algal biomass. Especially the ranges of LR-SD (from -6 to +3) and of LR-CV (from -4 to 5) found in this meta-analysis are astonishing as it corresponds to orders of magnitudes differences in biomass variability. This range and the significant difference of average effect sizes from zero indicate that organism-induced effects on heterogeneity in biomass distribution is an underestimated process in periphyton and probably also in many other trophic interactions. On a very general level, this meta-analysis corroborates the presence of consumer-induced relative variability in biomass found in previous single studies (Sommer 2000, Kawata et al. 2001, Alvarez and Peckarsky 2005). However, the present analysis amends this conclusion by showing that grazer presence homogenizes the biomass distribution of periphyton in absolute terms.

Spatial heterogeneity is highly important for processes within the periphyton community. The spatial patchi-

ness of algal biomass is prone to influence nutrient uptake (Riber and Wetzel 1987), the competitive coexistence of algal species (Sommer 1999), within-periphyton trophic interactions by micro- und meiofauna (ciliates, rotifers, nematodes) (Hillebrand et al. 2002), and also the coexistence of grazer species (Chase et al. 2001). These different processes are differentially affected by the absolute or the relative variability in biomass. The selection of food patches by grazers is mainly affected by absolute differences in periphyton biomass (Vaughn 1986), however, at saturating food levels, even large differences in absolute biomass may be unimportant (Cooper et al. 1997). Still, in most cases, patch selection by grazer species and the resulting microdistribution will be affected by how strongly patches differ in absolute biomass (Kawata and Agawa 1999). Grazing itself is of course only one factor affecting the patchiness of periphyton biomass, which occurs on very different spatial scales in both horizontal and vertical dimensions (Kahlert et al. 2002). In addition to biomass, food quality also differs spatially and often independently of total biomass (Kahlert 2002, Kahlert et al. 2002), which also may have important consequences for grazer distribution.

The spatial variability in relation to the biomass present (as reflected by the coefficient of variation) is more informative for the ability of periphyton to access water column nutrients. High relative spatial heterogeneity will decrease boundary layers and increase nutrient uptake (Riber and Wetzel 1987). Nutrient uptake abilities will also affect resource competition and algal coexistence. In consequence strong indirect and propa-

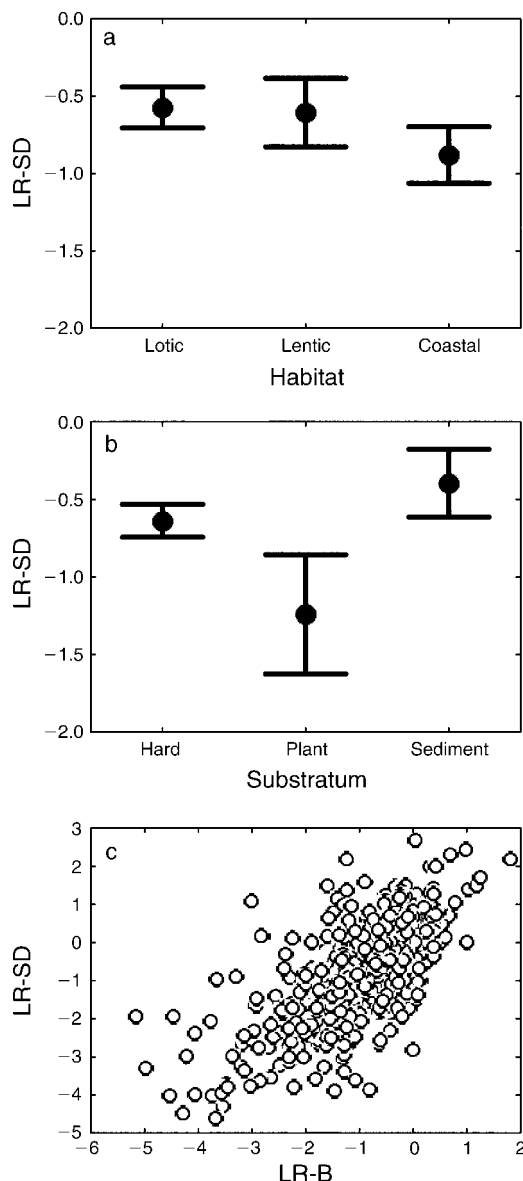


FIG. 3. Mean effects of grazer presence on the absolute variability of periphyton biomass (LR-SD) for (a) different habitats and (b) different substrata as well as (c) the correlation between LR-SD and grazer biomass removal efficiency (LR-B). Error bars are 95% confidence intervals.

gating effects in the microbenthos have to be expected due to induction or reduction of spatial heterogeneity by grazers.

The magnitude of LR-SD was mainly affected by variables relating to grazing pressure, but also by substratum type and habitat. Other variables also affected LR-SD, but only LR-B, habitat and substratum type were retained in the most parsimonious model. The negative effect of grazer presence on the absolute spatial heterogeneity of periphyton biomass was more pronounced in coastal areas than in freshwater and for epiphytic assemblages than for sediment or epilithic

microalgae. The single most important factor regulating LR-SD, however, was the grazers' effect on mean biomass, LR-B. Higher grazing efficiency (more negative LR-B) strongly reduced the difference between replicate treatments, thus homogenized the spatial distribution of periphyton biomass. The strength of the relation to LR-B is based on the fact that LR-B integrates several aspects of grazer efficiency, which have previously been shown to affect organism-induced heterogeneity: the mobility of the consumer (Alvarez and Peckarsky 2005), the grazing type via mouthpart morphology (Sommer 2000) or grazer density (Flecker and Taylor 2004).

The relationship between LR-SD and LR-B had a slope less than 1, indicating that stronger biomass removal affected average biomass more than the SD. Thus, the overall positive LR-CV reflected the fact that reduction in average biomass was more substantial than reduction in SD. When the heterogeneity of periphyton biomass was standardized to the average biomass present, the effect sizes were only marginally influenced by habitat type and substratum, leaving a large portion of the variation in this effect measure unexplained.

In contrast to expectations, there were no additional effects on either LR-SD or LR-CV by the scaling of the experiment and variables relating to system productivity, although most interactions are considered to be highly scale-dependent in benthic communities (Cooper

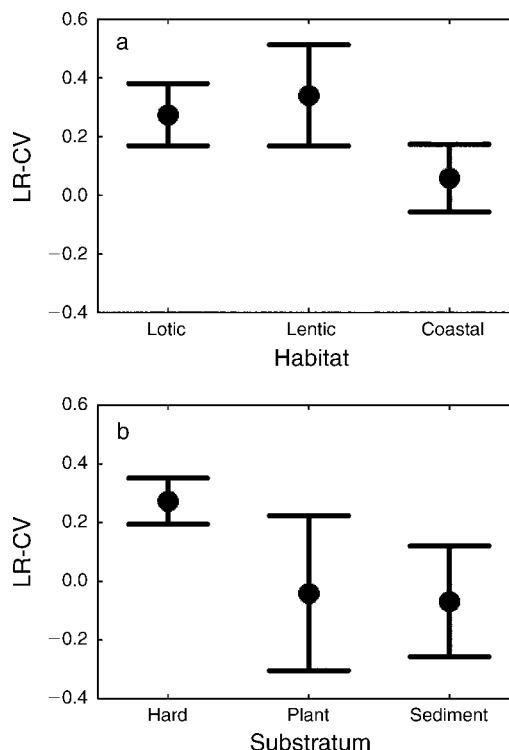


FIG. 4. Mean effects of grazer presence on the relative variability of periphyton biomass (LR-CV) for (a) different habitats and (b) different substrata. Error bars are 95% confidence intervals.

et al. 1998) and previous studies indicated significant effects of resource supply on organism-induced patchiness (Pringle 1996). This contrast may be either due to variation with other variables which were not included in this analysis (climatic variation, etc.) or due to the simplicity of the effect sizes used here.

The present meta-analysis gained its generality through the use of standard deviations as a very coarse measure of overall spatial heterogeneity, which allowed including many experiments. This generality is clearly established at the expense of detailed information. Other measures of heterogeneity are much more explicit in the implementation of space and scale (Cooper et al. 1997). Standard deviations do not allow addressing focus, grain and extent of spatial processes, which are important characteristics in spatial ecology (Rahbek 2005). Especially neighborhood interactions, which are considered important for spatial dynamics (Adler et al. 2001, Kawata et al. 2001, Wahl 2001), can not be addressed by simple measures of variability.

In spite of these caveats, the present meta-analysis provides highly general and basic information on grazer-induced changes in biomass heterogeneity across different aquatic ecosystems. The analysis indicated strong negative effects of grazers on absolute prey heterogeneity and the importance of biomass removal efficiency for explaining these effects. The analysis also revealed that grazer presence on average increases the relative heterogeneity in biomass distribution. These general conclusions and the large unexplained variation (especially for LR-CV) opens the way for more refined analysis of spatially explicit studies. One unresolved aspect is the spatial pattern in the algal vegetation prior to grazing, which has been shown to be important for periphyton (Kawata et al. 2001) and terrestrial vegetation (Adler et al. 2001). A second unresolved aspect is the temporal biomass variability. My analysis focused on spatial variation only, but consumer presence will also affect the temporal variability of prey biomass. Halpern et al. (2005) have analyzed the effect of predators on the temporal variability of herbivore and plant biomass across 40 experiments. They concluded that plant biomass fluctuation was not affected, but herbivore biomass was significantly destabilized by the presence of a predator. This indicates that consumer effects on temporal heterogeneity can be expected to be similar to effects on spatial variability.

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## APPENDIX A

List of studies included in the meta-analysis including citation and information on the habitat, the consumer group, the experimental units, the substratum the algae grew on, and the number of experiments obtained from each publication (*Ecological Archives* E089-009-A1).

## APPENDIX B

Three tables presenting full statistical results for the meta-analysis of grazer effects on the absolute and relative spatial heterogeneity of algal biomass. (*Ecological Archives* E089-009-A2).