

Light regime and consumer control of autotrophic biomass

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Summary

1 Autotrophic biomass is often regulated by resource supply and consumer presence. Most studies on top-down vs. bottom-up control of plant biomass focus on nutrients as basal resources, whereas light has received considerably less attention.

2 Effects of light and nutrients may differ because light represents a vertical resource and plant adaptations to acquire light might counteract or facilitate consumer effects. I tested the interaction between light supply and consumer presence in a meta-analysis of experiments that manipulated both these factors factorially and measured the biomass of benthic algae (periphyton).

3 Both grazer removal and light enhancement had positive effects on algal biomass. These two factors showed strong interactions, which exceeded previously observed interaction terms between nutrient supply and grazer removal. Positive light effects on algal biomass were primarily observed in the absence of grazers. Grazer effects became stronger at high light supply, which indicated that high light favours algal growth types that are easily ingested.

4 Further analyses showed that light effects increased with trophic state of the habitat and with algal biomass, indicating enhanced importance of light limitation and self-shading at high nutrient supply. Grazer effects depended on grazer biomass and varied with type of experimental manipulation.

5 This study implies that light is of similar importance as nutrients in resource control of benthic algal biomass. High light levels simultaneously enhance consumer control of algal biomass, resulting in strong resource vs. consumer interactions. Light competition and consumer presence pose a trade-off on algal growth, where growth form may distinguish between adaptations to acquire light and to avoid consumption.

Key-words: benthic food webs, consumer vs. resource control, grazing, growth forms, irradiance, meta-analysis, periphyton, trade-off

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Introduction

Autotrophic biomass is generally controlled by factors regulating from the bottom up (resources) and from the top down (herbivory). The long-standing debate over which type of factors prevail has been replaced by the view that they interact (Leibold *et al.* 1997). Recent meta-analyses have shown that both resource supply and grazing significantly affect plant biomass in a range of ecosystems including terrestrial grasslands (Hawkes & Sullivan 2001), phytoplankton (Brett & Goldman 1997) and periphyton (Hillebrand 2002).

Most investigations have used nutrients as the basal resource (Brett & Goldman 1997; Hillebrand 2002),

and light has received much less attention in this context (Harley 2002). Light is the only energy source for all photoautotrophic organisms and therefore light limitation may be as important as nutrient limitation for primary production (Hill 1996). Light limitation can be particularly strong for periphyton, the dominant photoautotroph community in streams and lake littorals, due to the absorption of light by the water column, the asymmetric competition for light with phytoplankton and the shading by terrestrial vegetation along the stream or the shoreline.

Therefore, many experimental studies found an increase in periphyton biomass with increasing light supply (Hill 1996), mediated by an increase in photosynthesis and carbon fixation. The relationships between light and both photosynthesis and growth are non-linear. The typical photosynthesis-irradiance (P-I)

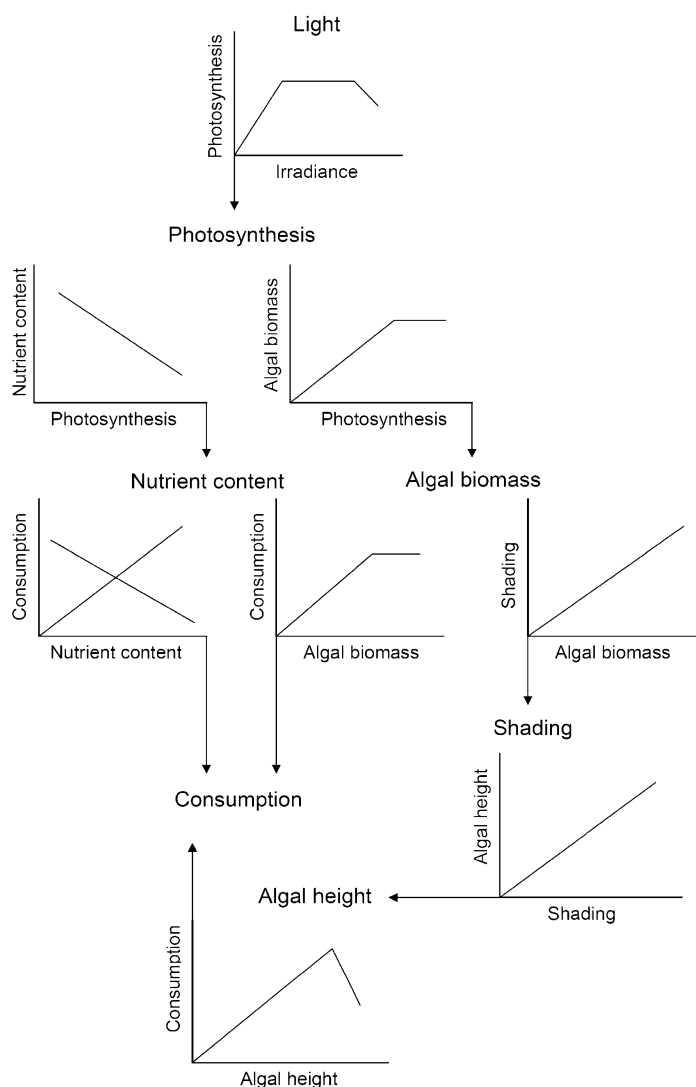


Fig. 1 Model for effects of light on algal physiology, growth and biomass as well as the consumption of algal biomass. The diagrams represent sketches of the quantitative relations between the variables connected by the respective arrow.

curve is characterized by increase, saturation and inhibition phases (Fig. 1) although for periphyton, photo-inhibition seems to be rare (Hill 1996). In the absence of other growth constraints, higher photosynthesis will increase plant biomass, which can best be described by a saturation function (Fig. 1). It can therefore be presumed that at high light conditions more algal biomass is available to herbivores (Fig. 1).

Light also affects relative nutrient content and the representation of different growth forms in the community (Fig. 1). High light conditions often relate to high C : nutrient ratios in the algae, which then represent poorer food for the herbivores (Urabe *et al.* 2002; Hillebrand *et al.* 2004). This lowered nutritional quality can be expressed as changes within species (increased cellular C : nutrient ratios) as well as by changes in species composition, because growth forms favoured at high light contain more structural carbon (Fig. 1). Light effects on species composition are often related to different growth forms (Steinman *et al.* 1992), as, with increasing algal biomass, small and prostrate algal

species are heavily shaded, whereas erect growth forms are superior competitors for light. The filamentous and chain-forming algal species that therefore tend to dominate at high light are often more prone to grazing (Steinman *et al.* 1992; Hillebrand *et al.* 2000), as the dominant herbivores (snails, insect larvae) are large compared with their algal prey and tend to graze preferentially on the upper layers of the periphyton community (Steinman 1996). However, single algal species may grow into a size refuge (Hart 1992), which can reduce grazer effectiveness at greatest prey height. If such inedible prey gains dominance in the plant assemblage, grazer effects decrease at greatest plant height (see non-linear response in Fig. 1).

From a consumer perspective, increasing light thus results in more algal biomass, which, moreover, is dominated by easily ingestible growth forms, although these have poor nutritional quality. By contrast, nutrient enrichment tends to increase plant biomass and quality and there are therefore strongly contrasting ways in which nutrient and light effects can be propagated to

the consumer level. The effects of changes in nutritional quality may also depend on the ability of the grazers to choose food. High light may result in less algal biomass consumed if grazers selectively avoid food of lower quality, or in more biomass consumed if grazers increase their intake to compensate for the low quality (Cruz-Rivera & Hay 2000).

Patterns described for grazer–periphyton interactions may also be relevant in other plant–herbivore interactions. Grasslands grazed by large mammals such as ungulates reveal a similar size ratio between consumer and prey. Consequently, grazer presence also affects plant biomass and plant size structure in these ecosystems (McNaughton 1984). Despite several differences in community functioning between periphyton and grasslands (e.g. the importance of below-ground processes in terrestrial communities), results on light vs. consumer control of algal biomass may be important beyond the community analysed.

To test for the relative effects of light and consumer presence on algal biomass, I conducted a meta-analysis of experiments that manipulated light supply and grazer presence in a factorial design and monitored the effect on periphyton biomass. This study therefore represents a general test for significant interactions between light supply and grazer presence in determining algal biomass. Comparison with a previous analysis of nutrient vs. grazer control (Hillebrand 2002), further enables evaluation of the relative importance of light and nutrients as basal resources and the identification of abiotic and biotic factors regulating the relative role of light and consumer effects on periphyton biomass.

Following the recommendations of Lajeunesse & Forbes (2003), two different types of effect sizes were analysed. First, a recently proposed factorial meta-analysis (Gurevitch *et al.* 2000) on the standardized difference (measured as Hedges' *d*) between the manipulated factor and the control was used to compare the overall effect sizes of light enhancement and grazer removal and to test for significant interactions. Secondly,

the proportional effects (measured as log response ratio, *LR*) of light enhancement and grazer removal were calculated for either level of the other variable. These analyses were used to test the following hypotheses.

- 1 Grazer removal and light enhancement both have significant positive effects on algal biomass.
- 2 The interaction between grazer and light manipulation is significant, i.e. light enhancement increases grazer effect size, whereas grazer presence reduces light effects.
- 3 The interaction between grazer and light is stronger than that previously determined (Hillebrand 2002) for the interaction between grazer and nutrient manipulations.
- 4 Light effects are stronger in situations of high nutrient supply or high algal biomass.
- 5 Grazing effects are stronger at high algal biomass and/or high grazer biomass.
- 6 The effect sizes depend on characteristics of the experimental design such as (a) experiment type, (b) degree of light enhancement, (c) manipulated grazer group, and (d) duration of the experiment.

Materials and methods

DATA

Searching the literature for experiments in benthic communities that manipulated light supply in factorial combination with grazer presence revealed 14 studies with a total of 35 experiments (Table 1). The terms 'algae', 'periphyton', 'microphytobenthos', 'light', 'irradiance', 'grazing' and 'herbivory' were used to search literature data bases such as Aquatic Science and Fisheries Abstracts (ASFA) and ISI Web of Science. Studies were only included if (i) the experimental manipulations had been replicated to calculate effect sizes, (ii) manipulations of grazer presence were direct (i.e. not by manipulating other trophic levels in order to reduce grazer density), and (iii) mean and standard deviation of algal biomass were reported for four different treatment combinations:

Table 1 Experiments used for meta-analysis of grazer vs. light effects on periphyton. The different studies were performed in lotic or lentic waters. Consumer group, type of light treatment and experimental unit, the productivity of the habitat, and experiment duration are given. *n* = number of experiments reported in each study

Authors	Habitat	Consumer	Light treatment	Duration Units	(days)	<i>n</i>
Hill <i>et al.</i> (1995)	Lotic	Gastropoda	Shade-removal	<i>In-situ</i> channels	40	1
Hillebrand <i>et al.</i> (2004)	Lentic	Gastropoda	Bulbs	Aquaria	16	2
Holomuzki (1998)	Lentic	Amphibia	Shading	Enclosures	23	1
Lamberti <i>et al.</i> (1989)	Lotic	Gastropoda	Shading	Laboratory channels	59	2
Pringle (1996)	Lentic	Decapoda	Natural gradient	Naturally non-available	1	1
Rosemond (1993)	Lotic	Gastropoda	Bulbs	<i>In-situ</i> channels	49	2
Rosemond <i>et al.</i> (2000)	Lotic	Gastropoda	Bulbs	<i>In-situ</i> channels	50	4
Steinman (1992)	Lotic	Gastropoda	Bulbs	<i>In-situ</i> channels	49	1
Steinman <i>et al.</i> (1989)	Lotic	Gastropoda	Bulbs	Laboratory channels	64	2
Steinman <i>et al.</i> (1995)	Lotic	Gastropoda	Bulbs	Laboratory channels	15	2
Wellnitz & Rader (2003)	Lotic	Ephemeroptera	Shading	<i>In-situ</i> channels	21	2
Wellnitz & Ward (1998)	Lotic	Ephemeroptera	Shading	Laboratory channels	16	5
Wellnitz & Ward (2000)	Lotic	Ephemeroptera, Trichoptera	Shading	<i>In-situ</i> channels	18	6
Wellnitz <i>et al.</i> (1996)	Lotic	Ephemeroptera	Shading	<i>In-situ</i> channels	22	4

(a) grazed, low light, (b) grazed, high light, (c) ungrazed, low light, and (d) ungrazed, high light.

In all the experiments included in this analysis, grazing was reduced by removing the herbivores (i.e. grazer absence and presence were compared). Light was manipulated by setting different light intensities in the laboratory or by shading natural assemblages (contrasting high light and low light, rather than presence and absence). Light is a continuous resource with a large natural range and algal traits show non-linear responses to irradiance (see Fig. 1). The high vs. low light contrast employed here is a necessary simplification, but I tested for the different effects of light in relation to the strength of the manipulation. The published experiments differed in how grazer presence and light supply were manipulated, in the type of grazers manipulated, the biomass of grazers and algae present, and in the duration of the experiments. To test for the consequences of such differences for effect sizes of either light or grazing, I obtained the following information from each study (see also Table 1).

I classified the habitat as either lotic or lentic. The consumer groups present in two or more experiments were Trichoptera, Ephemeroptera and Gastropoda, whereas other groups occurred only once (Table 1). All grazer manipulations had absent and present levels, but the grazer biomass differed strongly between studies. Therefore, grazer biomass was included in the analysis as log-transformed dry mass m^{-2} . The type of experimental unit used was most often *in-situ* channels or laboratory channels, although aquaria were used in two experiments and two other unit types each occurred once. The nutrient status of the system (productivity) was reported in very different measures (dissolved or total nutrients), which prevented using a continuous variable of nutrient availability. Instead, I characterized the study system as either oligotroph or eutroph (only one mesotroph system was present). This assessment was based on the nutrient concentrations given in the original studies, using threshold values successfully implemented in a previous meta-analysis (Hillebrand 2002). Some studies did not report any nutrient data, leading to their omission for this particular analysis.

Light manipulation was either by shading (ambient light vs. shaded), by removing shade (ambient light vs. enhanced light) or by using light bulbs of different irradiance or wattage. In all cases, the calculation of light effects was between high light (HL) and low light (LL). Note that high light can represent the manipulated (shade removal) or ambient (unshaded) treatment in different studies. The variable light manipulation also represents a contrast between laboratory and field experiments. From the light measurements in the original study, the relative light enhancement was calculated as the log-transformed ratio between irradiance at HL vs. LL (measured as $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). The range of photon flux density across experiments was 5–590 at LL, and 90–1700 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at HL,

respectively. The duration of the experiments was given in days. Finally, I obtained measures of algal biomass in ungrazed, low-light treatments. 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) and to summarize the different measures of algal biomass used in the original studies. 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.

EFFECT SIZES

The raw data for the calculations were the means and the standard deviations of algal biomass as well as the number of replicates for each of the four treatment combinations: (a) grazed, low light, (b) grazed, high light, (c) ungrazed, low light, and (d) ungrazed high light.

I used the factorial meta-analysis implemented by Gurevitch *et al.* (2000) to calculate overall effect sizes for grazer removal and light enhancement as well as their interactions. These effect sizes are based on Hedges' d and reflect the standardized difference in algal biomass due to the experimental manipulations. Positive effect sizes pertain to higher algal biomass with grazer removal (positive d_G) or with light enhancement (positive d_L). Positive interaction effect sizes (d_I) show increased grazer effects at high light and vice versa. The grazer removal effect (d_G) represents the standardized mean difference between grazed and ungrazed treatments $((c + d) - (a + b))$. Correspondingly, d_L is calculated by contrasting both high-light treatments against low-light treatments $((b + d) - (a + c))$. The interaction term is calculated by subtracting the mean difference of high light minus low light at grazed conditions from the mean difference at ungrazed conditions $((d - c) - (b - a))$. The standardization of the mean difference is a function of the standard deviation and replication of the respective treatments. Calculation details for the effect sizes and their sampling variances can be found elsewhere (Gurevitch *et al.* 2000; Hillebrand 2002).

My second approach involved proportional effect sizes, which are measured as log-response ratios (LR) (Hedges *et al.* 1999). LR represents the naturally log-transformed ratio of treatment mean over control mean. As no factorial design is available for LR , I calculated the four effect sizes: LR_{GLL} , the proportional effect of grazer removal at low light; LR_{GHL} , the corresponding effect of grazer removal at high light; LR_{LGA} , the effect size of light enhancement in the absence of grazers; and LR_{LGP} , the effect size of light in the presence of grazers.

These two effect metrics reflect different aspects of the response of algal biomass to grazer and light manipulations. Hedges' d represents the standardized difference between treatment and control means in

units of standard deviations. *LR*, however, measures the response in algal biomass in the treatment relative to the control. For reasons of conciseness, I will call these metrics standardized (*d*) and proportional (*LR*) effects throughout the text. Combining these two analyses allows stronger generalizations to be made about the processes under investigation (Lajeunesse & Forbes 2003).

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. Measures of sampling variance can be calculated for both types of effect sizes (Hedges *et al.* 1999; Gurevitch *et al.* 2000; Rosenberg *et al.* 2000; Hillebrand 2002).

ANALYSIS

A fixed effect model was used for the factorial meta-analysis on Hedges' *d*, whereas a mixed-model analysis was used for *LR*. The use of mixed models is advantageous as it avoids the assumption of fixed effect models that there is a true common effect size for all studies (Gurevitch & Hedges 1993). However, this procedure is not yet available for the factorial analysis, which therefore has to be calculated as fixed effect model (Gurevitch *et al.* 2000).

To test hypotheses 1–3, grand mean effect sizes were calculated for each effect metric. The weighted average effect size and its 95% confidence interval (CI) were calculated using bootstrapping with 9999 randomizations (Rosenberg *et al.* 2000). This grand mean effect size was significantly different from zero if the CI did not overlap zero.

To test hypotheses 4–6, weighted meta-analysis was used to test for significant changes in effect sizes due to one of the explanatory variables. For categorical variables (habitat, productivity, consumer group, light manipulation, experimental units), the analysis separates the overall heterogeneity in effect sizes into that between group levels (Q_b) and that within groups (Q_w). For continuous variables (algal biomass, grazer biomass, light enhancement, duration of experiment), a weighted regression approach is available for meta-analyses (Rosenberg *et al.* 2000), which separates the overall heterogeneity into that explained by the regression (Q_b) and residual heterogeneity (Q_w).

The degrees of freedom for these tests vary because not all studies gave the information necessary to attain values or levels for the grouping variables and because the number of grazer treatments per study differed, which resulted in a lower number of light effect sizes without grazers (LR_{LGA}) than with grazers (LR_{LGP}).

To account for the multiple significance tests, a sequential Bonferroni adjustment of *P*-values was used for each of the effect sizes (Quinn & Keough 2002). I report on significant effects for adjusted *P*-values < 0.05 and on trends for adjusted *P*-values < 0.1, as Bonferroni adjustments are known to be overly conservative (Quinn & Keough 2002).

Results

OVERALL EFFECTS AND INTERACTIONS

The overall effect size for grazer removal (d_G) and light enhancement (d_L) were both positive and significantly different from zero (Fig. 2a). Thus, algal biomass increased in the absence of grazers and in the presence of more light. Moreover, the interaction term (d_I) was also significantly positive (Fig. 2a), indicating a significantly greater biomass response to grazing in high light than in low light. The average magnitude of the interaction effect was 1.15, c. 50% larger than the average interaction between grazer removal and nutrient enrichment (0.78) obtained from a previous meta-analysis (Hillebrand 2002).

The overall proportional effect sizes (*LR*) for grazer removal were positive and significantly different from zero (Fig. 2b). Grazer effects were higher (+20%) at high light compared with low light, but this difference was not significant. The grand mean proportional effect for light was significantly positive only in the absence of grazers (Fig. 2b). When consumers were present, the average light effect was only slightly positive and no longer significantly different from zero.

Significant heterogeneity in effect sizes (for terminology, see Gurevitch & Hedges 1993) was observed for all three effect sizes in the factorial meta-analysis of *d*, i.e. for grazer removal, light and their interaction (Table 2). Similarly, the analyses of heterogeneity revealed significant differences in relative effects sizes (*LR*) for light and grazing (Table 3).

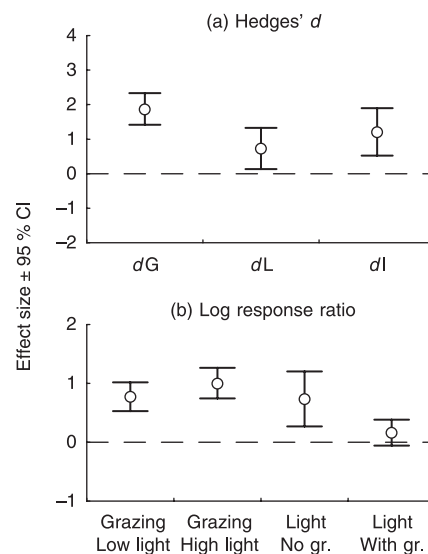


Fig. 2 Overall effects of grazer and light manipulation on algal biomass represented as mean effect size \pm 95% confidence intervals. (a) Standardized effects of grazer removal (d_G), light enhancement (d_L), and their interaction (d_I). (b) Proportional effects of grazer removal at low (LR_{GLL}) and high light (LR_{GHL}) as well as light at grazer absence (LR_{LGA}) and presence (LR_{LGP}). Proportional effects are log-transformed response ratios. Dashed lines represent zero effects.

Table 2 Results of tests of heterogeneity on effect-sizes of grazer removal (d_G), light enhancement (d_L), and of the interaction between both factors (d_t) on algal biomass. The table lists the degrees of freedom (d.f.), the heterogeneity (Q) between (B) and within (W) groups, respectively, and the adjusted significance level (P) of the heterogeneity explained by the variable

	d_G			d_L			d_t		
	d.f.	Q	P	d.f.	Q	P	d.f.	Q	P
Habitat									
B	1	3.37	NS	1	6.08	NS	1	8.60	NS
W	33	200.32		33	411.73		33	100.61	
Consumer group									
B	2	28.76	NS	Not applicable			2	13.85	NS
W	30	162.38					30	86.11	
Productivity									
B	1	4.21	NS	1	82.59	0.016	1	22.85	0.042
W	19	127.06		18	135.90		18	43.70	
Light manipulation									
B	Not applicable			1	3.60	NS	1	3.20	NS
W				31	400.68		31	97.50	
Experimental units									
B	2	38.84	NS	2	159.41	0.005	2	29.25	0.042
W	30	152.30		30	243.68		30	70.72	
Duration									
B	1	2.00	NS	1	36.85	< 0.001	1	13.01	0.002
W	33	201.69		33	380.97		33	96.21	
Grazer biomass									
B	1	37.00	< 0.001	Not applicable			1	33.88	< 0.001
W	33	166.69					33	75.34	
Algal biomass									
B	1	2.24	NS	1	56.26	< 0.001	1	3.79	NS
W	29	174.73		29	231.06		29	95.04	
Light enhancement									
B	Not applicable			1	31.83	< 0.001	1	0.05	NS
W				31	371.26		31	99.91	

GRAZER EFFECT SIZES (D_G AND LR_G)

Grazer removal effects (d_G) significantly increased with grazer biomass (Table 2, Fig. 3a). A significant increase of grazer removal effects with grazer biomass was also observed in the proportional effect sizes, but this was significant only for LR_{GHL} (Table 3, Fig. 4a). Thus, more abundant grazers not only reduce algal biomass more in absolute terms, but also consume a higher percentage of the algae present. Different consumer groups showed no distinctive effects on algal biomass irrespective of the effect metric used (Tables 2 and 3), indicating that gastropods, trichopterans and ephemeropterans had similar effects.

d_G was high in aquaria and low in laboratory channels (Fig. 3e), but this difference was non-significant (Table 2). The grazer log response ratio varied significantly between experimental units and with grazer biomass (Table 3). The proportional effect of grazer removal at low light (LR_{GLL}) was significantly higher in aquaria than in other experimental units (Fig. 4b). The same trend prevailed at high light, but was no longer significant (Table 3). This contrast between aquaria and channels presumably also caused the contrast in LR_{GLL} between habitats, which was observed as a trend at low

light (Table 3). No such difference between habitats was observed for d_G (Table 2).

There was no significant difference in grazer removal effects with algal biomass, with habitat productivity or with the duration of the experiment (Tables 2 and 3). This similarity in effect sizes was consistent for both d_G and LR_G .

LIGHT EFFECT SIZES (D_L AND LR_L)

The standardized effect size of light (d_L) varied with experimental unit, but, in contrast to consumer effects, higher effect sizes were observed in laboratory channels than in *in-situ* channels and aquaria (Table 2, Fig. 3e). Proportional light effects showed only minor variation between experimental units (Table 3, Fig. 4b). The standardized light effects decreased slightly, but significantly, with the duration of the experiment (Table 2, Fig. 3b). There was no corresponding effect of duration on the proportional light effects (Table 3).

Whereas no difference was observed between lotic and lentic habitats (Tables 2 and 3), the standardized light effect size depended significantly on the productivity of the habitat, being much greater in eutrophic than in oligotrophic habitats (Table 2, Fig. 3f). Neither

Table 3 Tests of heterogeneity on effect-sizes of grazer removal (LR_G) and light enhancement (LR_L) on algal biomass. The different analyses were conducted on light effects at grazer absence (GA) and grazer presence (GP), and grazer removal effects at low (LL) and high (HL) light. The table lists the degrees of freedom (d.f.), the heterogeneity (Q) between (B) and within (W) groups, respectively, and the adjusted significance level (P) of the heterogeneity explained

	LR_{GLL}			LR_{GHL}			LR_{LGA}			LR_{LGP}		
	d.f.	Q	P	d.f.	Q	P	d.f.	Q	P	d.f.	Q	P
Habitat												
B	1	13.92	0.060	1	7.15	NS	1	2.86	NS	1	0.25	NS
W	33	55.90		33	77.55		21	55.88		33	68.46	
Consumer group												
B	2	1.24	NS	2	6.31	NS	Not applicable			2	1.52	NS
W	30	49.99		30	54.31					30	63.85	
Productivity												
B	1	0.14	NS	1	0.01	NS	1	0.67	NS	1	1.59	NS
W	18	12.90		18	37.77		13	28.56		18	27.24	
Light manipulation												
B	Not applicable			Not applicable			1	0.15	NS	1	0.28	NS
W							19	27.37		31	64.40	
Experimental units												
B	2	25.10	0.049	2	6.46	NS	1	2.53	NS	2	8.69	NS
W	30	45.55		30	55.12		18	21.93		30	66.71	
Duration												
B	1	1.15	NS	1	0.17	NS	1	0.01	NS	1	0.61	NS
W	33	53.50		33	82.30		21	51.28		33	72.88	
Grazer biomass												
B	1	0.03	NS	1	14.03	< 0.001	Not applicable			1	1.24	NS
W	33	53.89		33	69.10					33	68.12	
Algal biomass												
B	1	0.04	NS	1	0.60	NS	1	0.11	NS	1	6.96	0.064
W	29	41.43		29	68.93		17	53.59		29	59.51	
Light enhancement												
B	Not applicable			Not applicable			1	17.16	< 0.001	1	14.75	< 0.001
W							19	64.24		31	51.58	

habitat nor productivity resulted in differences in LR_L (Table 3).

Concordantly, both d_L and LR_L increased with increasing algal biomass (Figs 3c and 4c). This contrast was significant for d_L (Table 2) and marginally significant for LR_{LGP} (Table 3). Thus, light enhancement was more effective in situations of high algal standing stock, indicating a higher potential for light limitation if biomass was high.

Light effects did not differ between shading experiments and those using artificial light sources. Instead, light effects increased significantly with increasing light enhancement ratio (Tables 2 and 3), i.e. effect size metrics were higher when high and low light intensities differed more (Figs 3d and 4d). The change in irradiance (light enhancement ratio) was therefore important for the effect size of light rather than the source of the light.

INTERACTION EFFECT SIZES (D_I)

More positive interaction effect sizes (d_I) were revealed at higher grazer biomass (Fig. 3a) and in eutrophic rather than oligotrophic habitats (Fig. 3f). Both

contrasts were significant (Table 2). Therewith, d_I reflects the increase in light effects with productivity and the increase in grazer effects with higher grazer biomass. The interaction effect size decreased with the duration of the experiment (Fig. 3b), as did the light effects. Moreover, d_I varied significantly between experiment units, with interactions in laboratory channels > *in-situ* channels > aquaria (Fig. 3e). Thus, the heterogeneity in interaction effect sizes was a consequence of heterogeneity in the main effects. None of the other factors analysed (habitat, consumer group, light treatment, algal biomass or light enhancement ratio) affected d_I (Table 2).

For the proportional effect sizes, no direct measure of interaction could be obtained. However, the change in effect sizes between the two levels of the other factors can shed light on the interactions present. Light levels altered how grazer effects were related to grazer biomass: grazer effects increased with grazer biomass at high light, but not when light levels were low (Table 3, Fig. 4a). This contrast indicates a strong effect of light limitation on the consumable biomass: increasing grazer biomass is only able to intensify the consumption of algae at high light, but not at low light. Grazer

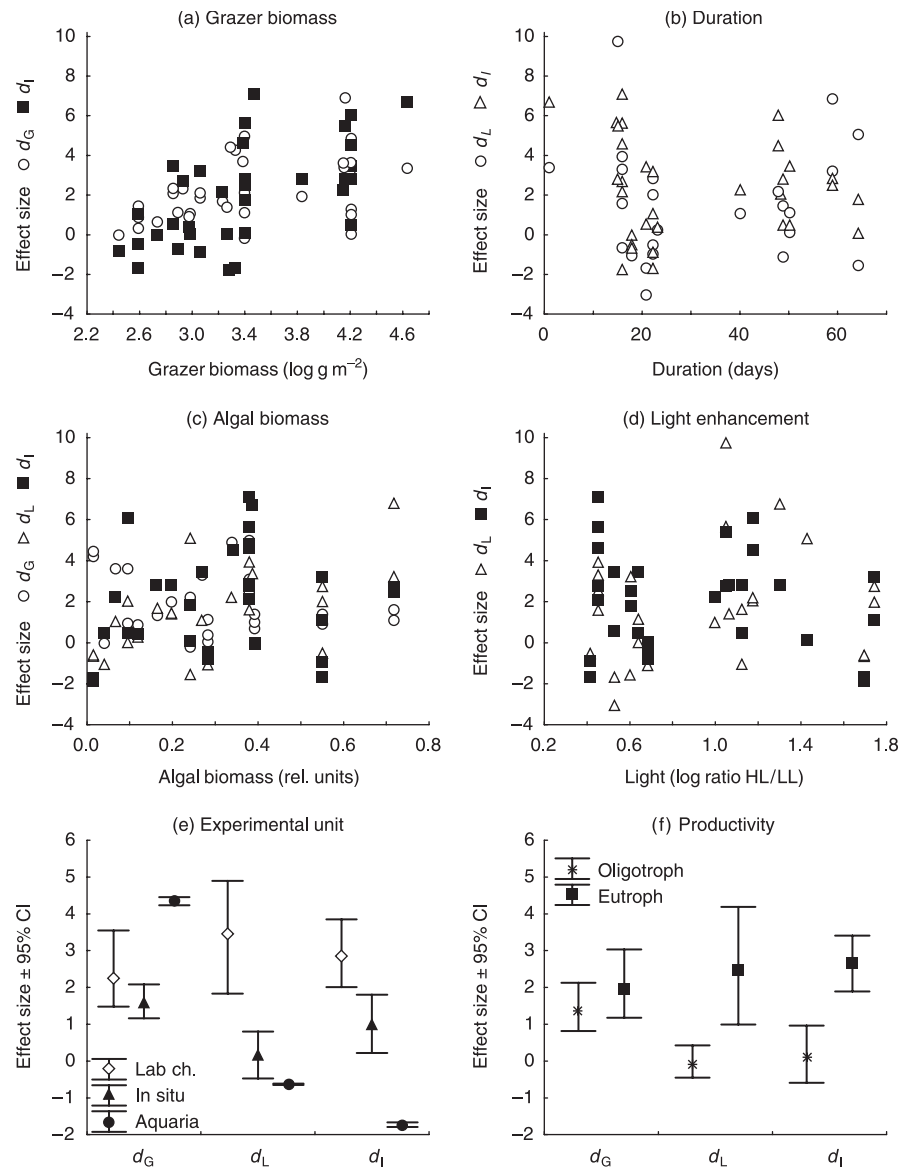


Fig. 3 Heterogeneity in standardized grazer and light effects on algal biomass. Experiment-wise standardized effects of grazer removal (d_G), light enhancement (d_L), and grazing–light interaction (d_I) in relation to grazer biomass (a), experiment duration (b), algal biomass (c) and light enhancement ratio (d). Mean effects \pm 95% confidence intervals of grazer removal (d_G), light enhancement (d_L) and grazing–light interaction (d_I) in relation to experimental units and the productivity of the habitat (e–f).

absence affected how light effects increased with algal biomass (Table 3, Fig. 4c): only with grazers present did LR_L increase with algal biomass.

Discussion

This meta-analysis of experiments on benthic herbivore–algae interactions revealed strong interactive effects of grazer and light treatments on autotrophic biomass. The presence of consumers counteracted the effects of light treatments, whereas the grazers profited from light enhancement. Moreover, the grazer effects depended mainly on grazer biomass, whereas light effects varied with the productivity of the habitat, algal biomass and light enhancement ratio. The experimental unit affected mainly the light effects, but also influenced the interaction between light and grazing. Results were generally

similar for the two different effect metrics used (Hedges d' , LR).

MAIN EFFECTS OF LIGHT AND GRAZING

Both grazer removal and light enhancement have significant positive effects on algal biomass (accepting hypothesis 1) for both standardized and proportional metrics. The overall effect size of grazer removal (d_G) observed in this data set was similar to previously observed effect sizes (Hillebrand 2002). Light enhancement had, on average, lower effect sizes than grazer removal, which may be caused by the immediate impact of grazing compared with the physiological and growth responses required by resource effects (Hillebrand 2002).

The overall effect size of light enhancement (d_L) was of similar magnitude to the nutrient effects described

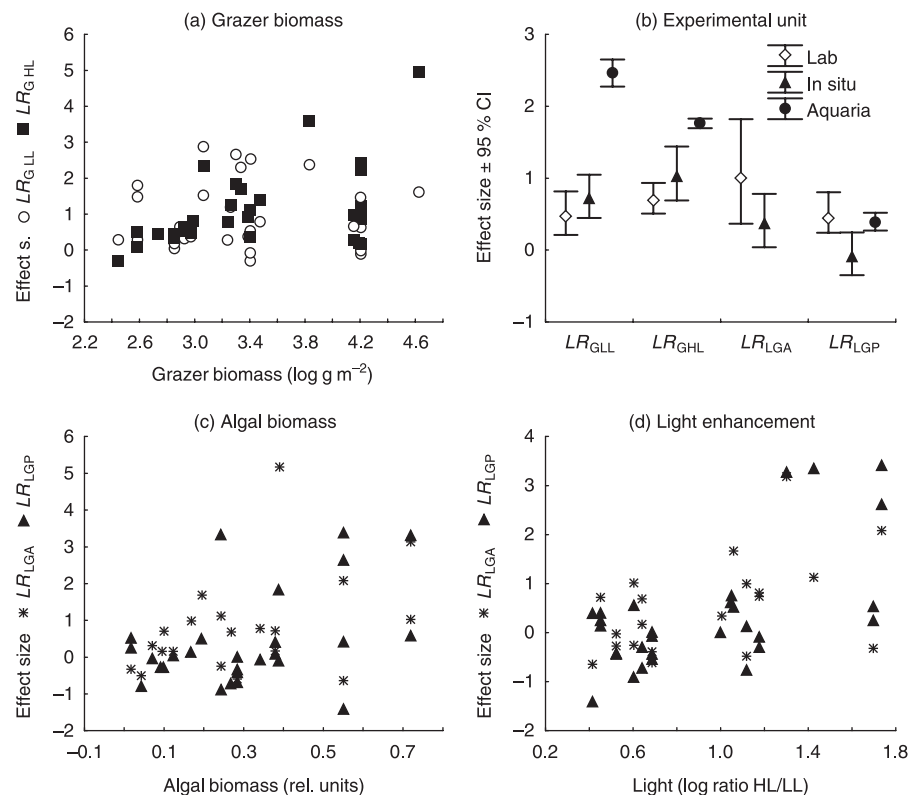


Fig. 4 Heterogeneity in proportional effects (log-transformed response ratios) of grazer removal and light enhancement on algal biomass. (a) Experiment-wise effects of grazer removal at low light (LR_{GLL}) and high light (LR_{GHL}) related to grazer biomass. (b) Mean effects \pm 95% confidence intervals of proportional effect sizes in relation to experimental units. Experiment-wise effects of light in the absence (LR_{LGA}) and presence (LR_{LGP}) of grazers in relation to algal biomass (c) and to light enhancement ratio (d).

previously (Hillebrand 2002), implying that light can limit periphyton biomass to a similar extent to nutrients. As for nutrient limitation (Bothwell 1989), different light intensities have different consequences for various organizational stages. At the cellular level, photosaturation is achieved at relatively low light intensities, compared with the light necessary to saturate the community, determined by the reduced propagation of light through the periphyton mat. Limitation, saturation and inhibition phases (Fig. 1) may thus coexist within a community along the vertical axis from prostrate to intermediate and large algal growth forms.

For both metrics, grazer effects increased with increasing grazer biomass, in line with previous findings on grazer–periphyton interactions in streams (Feminella & Hawkins 1995). However, grazing effect sizes did not vary with algal biomass (and hypothesis 5 was therefore only partly supported). In the previous meta-analysis of grazer vs. nutrient interactions, grazing effects consistently increased with increasing algal biomass (Hillebrand 2002), a difference that is probably due to the more derived measure of algal biomass used in the present study. In the previous analysis, the measure of biomass was directly involved in the calculation of the effect size (Hillebrand 2002), whereas here, this autocorrelation was reduced by transforming algal biomass into relative units.

In contrast to a previous review (Feminella & Hawkins 1995) and an assessment of over 600 grazing

experiments (H. Hillebrand, unpublished data), no difference in grazer effects was observed for the different grazer groups (refuting hypothesis 6c). However, the subset of experiments manipulating both grazer presence and light was small (35 experiments) and this may have precluded the detection of small but real differences.

The type of light treatment had no effect on the magnitude of light effects (partially refuting hypotheses 6a), i.e. light effects were of similar magnitude irrespective of whether light was enhanced in the laboratory or shading was removed in the field. However, the unit used to conduct the experiment had effects on the outcome of both grazer and light manipulation (partially accepting hypothesis 6b). The importance of experimental design has been observed and stressed before (Hillebrand 2002). Rather than a simple dichotomy between laboratory and field experiments, constraints such as system openness and currents are influential, especially in the interaction between resource and grazer control.

Light effects increased if the ratio of high light to low light levels in the experiment was high (accepting hypothesis 6a). This outcome stresses the role of light as a quantitative resource and parallels the increased nutrient effect sizes when the nutrient enrichment ratios increased (Hillebrand 2002). The duration of the experiment reduced the standardized, but not the proportional, light effects (accepting hypothesis 6d). That

is, the increase in algal biomass with light increase was offset in long-term experiments by other processes, such as export of biomass or grazing by (mostly unmanipulated) small fauna (protozoans, meiofauna).

THE INTERACTION BETWEEN LIGHT AND GRAZING

The interaction effect size (d_i) between grazer and light manipulation was significantly positive (accepting hypothesis 2). A positive interaction means that light enhancement increased grazer effect size, whereas grazer presence reduced light effects. The same pattern was observed with relative effects (LR), with proportional light effects becoming non-significant when grazers were present, and grazer effects being higher at high light. The sign of the interaction between grazers and nutrients (Hillebrand 2002) was the same as that reported here, with higher grazer effects at higher nutrient levels and lower nutrient effects in grazed treatments. However, the average light–grazer interaction effect was 1.15 compared with 0.78 for nutrient–grazer interactions, thus the bi-directional influence was much stronger for light vs. grazers (accepting hypothesis 3). This difference could also be observed in proportional effects: nutrient effects remained significant in the presence of grazers (Hillebrand 2002), but relative light effects did not (this study). Therefore, I tentatively conclude that interactions between light and grazing effects were stronger than between nutrient and grazer effects.

These results have two important implications. First, grazers consumed more biomass at HL in absolute terms. As HL resulted in higher algal biomass, this effect presumably represents a functional response to higher prey density (see Fig. 1), with consumers increasing biomass uptake if more biomass was present. Potential indirect effects of light enhancement, such as changing ultraviolet radiation or changing the visibility of grazers for their predators, did not offset the direct response of grazers to increased prey biomass.

Secondly, the additional increase in proportional grazer effect size (LR) revealed that grazers were also more efficient in removing algal biomass at high light, i.e. they consumed more biomass per biomass present. Grazer effectiveness can be altered by two potential pathways, the change in algal nutritional quality or in algal edibility (Fig. 1). Neither of these were directly assessed in any of the studies included in this analysis, but can be discussed in the light of results from different systems.

The nutritional quality of algae is proposed to decrease with increasing light supply. Thus, grazers may experience food of lower relative nutrient content at high-light conditions (Sterner *et al.* 1997; Urabe *et al.* 2002). Using pelagic model systems, Urabe *et al.* (2002) showed that such lowering in quality might have substantial consequences for consumer growth and survival. The response of benthic grazers to changes

in nutritional quality of their food is less clear. Some grazer species may be able to compensate for low quality by increasing consumption (Cruz-Rivera & Hay 2000), which would result in increased standardized grazer effects. More mobile grazers may avoid patches of lower algal quality and search for food of higher quality (Cruz-Rivera & Hay 2000), resulting in lower standardized effects of grazing at high light in those experiments allowing emigration of grazers. These contrasting changes in grazer behaviour do not explain the changes in proportional effect sizes observed here.

The edibility of the algae can change with light supply in that the availability of light alters the species composition and hence the architecture of the algal assemblage. The algal species dominating at high light may be larger and therefore more prone to consumption. This mechanism reflects a fundamental trade-off in plant growth types, which has also been observed for periphyton. Periphytic algae growing adnate to the substrate have limited access to resources (both nutrients and light) as they become overgrown by larger and more erect growth types. At the same time, the prostrate growth forms are less prone to grazing. These consequences of growth form have been described well for nutrient and grazer interactions on periphyton (Steinman *et al.* 1992; Hillebrand *et al.* 2000). In addition to herbivory, scour and other disturbances also primarily affect erect algal growth forms (Poff & Ward 1995).

For light, this growth form trade-off seems to be even stronger, as light is strictly a vertical resource, whereas nutrients can be regenerated within the periphyton community. At low light, overall biomass will be low and so will the average algal height. At high light supply, biomass and self-shading increase and access to light is only achieved by growing tall (Fig. 1). This mechanism is corroborated by the increasing effects of light enhancement in situations of high productivity (d_L) or high algal biomass (d_L , LR_{LGP}) (accepting hypothesis 4). Both factors reflect the higher importance of light limitation at high nutrient input or high algal biomass.

Similar interactions between light, grazing and plant traits can be found in terrestrial vegetation (Hickey 1961; McNaughton 1984; Painter *et al.* 1993; Hartvigsen & McNaughton 1995). The morphology of single species may differ between grazed (short morphs) and ungrazed (tall morphs) populations (Hartvigsen & McNaughton 1995), and the average plant height was reduced due to grazing by large herbivores (McNaughton 1984). Whereas several processes differ between periphytic algae and grasses, both systems have herbivores that tend to be large compared with their prey. For smaller grazer : prey size ratios, however, the relation of growth form to edibility may be non-linear, as algae may grow into size refuges (Fig. 1), where they can no longer be consumed by the dominant grazers. Some studies on grazer–periphyton interactions found lower edibility for the largest species such as *Cladophora* (Hart 1992), but even these are consumed by at least

some invertebrate grazers (Feminella & Resh 1991). Therefore, growing into a complete size refuge seems to be a rare strategy for periphytic algae.

The strong interaction between grazer avoidance and light acquisition may represent a fundamental trade-off between plant growth strategies. Cautiously extrapolating the results presented here, these considerations correspond closely to two aspects emerging from a recent review of models of evolutionary stable strategies (ESS) to explain plant height in terrestrial vegetation (Falster & Westoby 2003). First, the benefits of height depend on plant biomass (leaf area index in their case), as the optimal height depends on the height of the neighbouring plants, and the latter will increase with biomass. This prediction corresponds well to an increase in light effects at higher algal biomass as observed in this study. Secondly, only one out of 14 models predicted an ESS including a mixture of heights, such as seen in most natural plant assemblages. Here, the higher mortality inflicted on more erect growth forms may allow for coexistence of plants of different height. Oksanen (1990) showed that when grazing exceeds a certain intensity, the most advantageous strategy for height switches abruptly from tall to short. Given the spatial and temporal heterogeneity often observed in grazing studies, herbivory may thus prevent a single height-ESS from monopolizing the plant assemblage.

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