

Invited review: Direct and indirect effects in herbivore – periphyton interactions

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With 3 figures

Abstract: In this article we review the indirect interactions prevailing in littoral communities and compare their importance to direct trophic interactions. We focus on the interaction between benthic algae and their herbivorous consumers, i. e. invertebrate grazers and herbivorous fish. In addition to the effects of grazers on periphyton biomass and production, we categorise and describe the types of indirect interactions observed and we present a quantitative meta-analysis to compare the effect magnitude of indirect and direct effects. Our review shows that herbivore-plant interactions comprise considerable complexity beyond consumption. We identify and review three different indirect interactions, which play important roles for periphyton-grazer interactions in benthic food webs. These are keystone predation, trophic cascading and habitat facilitation. Direct negative effects were stronger than indirect positive effect, because grazing leads in almost all studies to a decrease in algal biomass. We found positive effects of grazing on algal nutrient content, biomass-specific productivity and evenness. We found negative overall effects on species richness and area-specific productivity. Moreover, spatial heterogeneity was on average increased by grazing. The magnitudes of direct and indirect effects were often correlated.

Key words: Grazing, periphyton, indirect effects, meta-analysis, diversity, productivity, heterogeneity, nutrient content.

Introduction

Littoral communities belong to the most productive assemblages in aquatic ecosystems (DAEHNICK et al. 1992, PINCKNEY & ZINGMARK 1993). Despite

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this fact, littoral communities have been investigated less extensively compared to the pelagic community. Littoral is here generally defined as shallow benthos in streams, lakes and costal areas providing enough light for algal growth. The basis of the benthic littoral food web is periphyton, an assemblage of algae, bacteria and eukaryotic micro-organisms covering almost all substrates. The second trophic level is mainly occupied by different grazers (gastropods, insect larvae, herbivorous fish), which ingest periphyton. A third and fourth level may or may not exist and is occupied by predatory macroinvertebrates or predatory fish.

Previous studies have shown that growth and architecture of periphytic biofilms is often constrained by the availability of light (HILL 1996) and nutrients (BORCHARDT 1996, HILLEBRAND & SOMMER 1997), and by consumption from herbivores (FEMINELLA & HAWKINS 1995, HILLEBRAND et al. 2000, NICOTRI 1977). Nutrients, light and grazers play important antagonistic roles for the development of algal biomass. Reviews about the influence of grazers on periphyton through consumption show that algal biomass almost always declines in the presence of herbivores (FEMINELLA & HAWKINS 1995, STEINMAN 1996). But there are also indirect effects of herbivores on periphyton, which can in some cases lead to an increase of algal biomass of some or all species of the algal community in the presence of grazers. As yet no review exists to

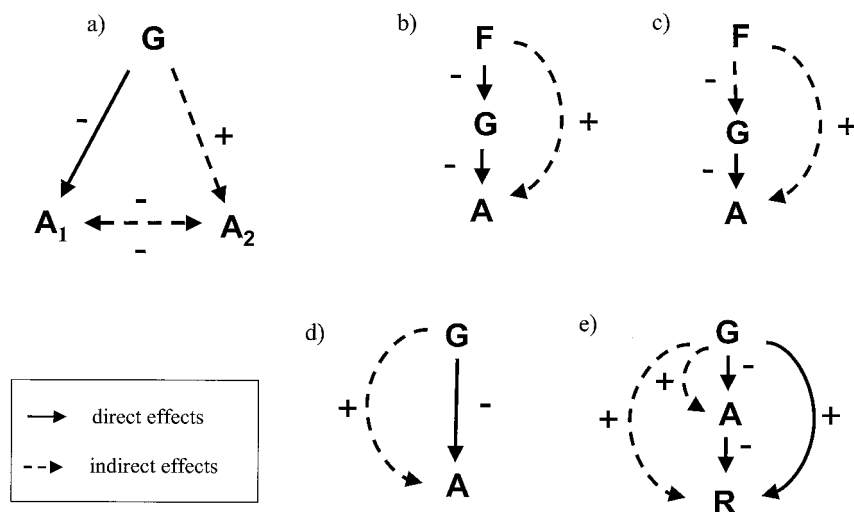


Fig. 1. Models of indirect effects in littoral food webs. G: grazer; A: algae; F: fish; R: resource. Solid arrows represent direct effects, dashed arrows represent indirect effects. +: positive effect; -: negative effect. The indirect effects in littoral food webs are **a)** keystone predation, **b)** trophic cascades, **c)** trophic cascades through behavioural changes, **d)** habitat facilitation and **e)** habitat facilitation through nutrient cycling.

what extent indirect effects are important in littoral communities and under which circumstances they show detectable results.

Here we will identify the indirect effects that grazers have on periphyton biomass, growth rate and community composition. In a second step we will quantitatively estimate the effect strength of indirect effects in a meta-analysis.

Direct effects are relatively easy to define. Common direct effects are predation and interference competition (MENGE 1995). In the interactions between predator and prey, the only direct effect is predation. All other (non-lethal) effects of predators on prey are regarded as indirect effects. Our focus is on indirect interactions in littoral habitats, i. e. shallow benthic stream-, lake- and coastal areas. In the case of the littoral food web, herbivores mostly have direct negative effects on algae through consumption and algae have direct positive effects on herbivores. The indirect effects are harder to identify, but previous models have identified at least seven different indirect effects (MENGE 1995), three of which are found in grazer-periphyton interactions (Fig. 1):

1. *Keystone predation* (Fig. 1 a), where a consumer indirectly increases the abundance of its preys competitor by consumption of the prey (PAINE 1966). In the periphyton-grazer interaction, keystone predation happens when one algal species has an advantage under grazed conditions because their competitors are reduced. Whether or not this process leads to greater diversity and spatial heterogeneity shall be reviewed here.
2. *Trophic cascading* (Fig. 1 b) or an increase in plant abundance caused by the control of herbivores by their predator (HAIRSTON et al. 1960). In the littoral food web, this means that grazer abundance can be reduced by fish predation. Fish preying on grazers have, therefore, an indirect positive effect on periphyton. A special case of trophic cascading (Fig. 1 c), which is trait-mediated, is the alteration in behaviour of organisms in one trophic level, induced by the trophic level above, which leads to higher biomass in the trophic level below. This happens when grazers alter their behaviour and become less successful consumers in the presence of fish (MCCOLLUM et al. 1998).
3. *Habitat facilitation* (Fig. 1 d) occurs when one organism indirectly improves the habitat of a second by altering the abundance of a third interactor (FAIRWEATHER 1990). In the littoral food web, the most common case of habitat facilitation is through nutrient regeneration by grazers (Fig. 1 e), where the abiotic environment of the algae is improved though the availability of more nutrients. How much improvement is gained and for which algal species is very dependent upon the ratio (C:N:P) of the recycled nutrients in relation to limiting nutrients in the system (ELSER & HASSETT 1994).

Qualitative analyses of indirect effects

Keystone predation

Keystone predation depends crucially on the ability of the consumer to select between prey species or prey types. Selectivity leads to an alteration in species composition through two mechanisms: by actively preferring food items (active choice), or by passively ingesting more of the species which are structurally more available (passive preference) (HILLEBRAND et al. 2000, NICOTRI 1977, SOMMER 1997).

Active choice is often not possible because of unselective mouth parts and prey which are small compared to grazer size. There is little evidence that freshwater benthic grazers possess the sensory equipment necessary for discriminating among algal taxa (STEINMAN 1996). Exceptions are large prey (macroalgae) or small grazers such as protists, which, for example, can select for diatoms. McCORMICK (1991) examined the feeding behaviour of protozoa and found that all three species exhibited a preference for the dominant diatom species. Since protozoa appear to be selective, they can influence the diatom community structure. On the other hand, snails are known to have different efficiencies (passive preference) for different types of algae. Differential efficiencies can be due to mouth part morphology or grade of satiation (STEINMAN 1996).

Grazing can change the competitive advantages of growth strategies. In ungrazed or lightly grazed algal assemblages, filamentous algae have a competitive advantage. Being long and sticking out of the algal matrix, they have easy access to light and nutrients. The same traits constitute a disadvantage under grazed conditions because some grazers can easily remove filamentous algae (STEINMAN et al. 1992). For this reason, grazing tends to change community structure and especially the relation of understory to overstory growth. Grazing by larger bodied snails or fish usually leads to an increase in the percentage of understory forms. This response results from the removal of the (to most grazes) more vulnerable overstory forms, which may result in either increased proportion of less vulnerable understory forms or in more resources available for understory forms (STEINMAN 1996).

Several studies show that grazers reduce overstory abundance and facilitate understory growth (HART 1985, MARKS & LOWE 1989, McCORMICK & STEVENSON 1991). There is further a general tendency towards reduction of grazing susceptible algae and an increase in resistant taxa (DENICOLA et al. 1990, HILLEBRAND et al. 2000, STEINMAN et al. 1987, STEINMAN et al. 1991, WELLNITZ & WARD 1998). Filamentous algae are easier to ingest than adnate algae and often suffer strongly from herbivory through large bodied grazers. On the other hand, grazers may also increase overstory biomass when their basal at-

tachment and coarse thallus texture make them harder to ingest for smaller grazers as for example chironomid and mayfly larvae (SARNELLE et al. 1993). Additionally, the removal of epiphyton from macroalgae by grazers may benefit the host and result in enhanced biomass (DUDLEY 1992). Grazer resistant taxa and growth forms, such as cyanobacteria and the basal cells of the chlorophyte *Stigeoclonium* tend to dominate the periphyton community under grazed conditions (DENICOLA et al. 1990, HILL et al. 1992, STEINMAN et al. 1987).

Herbivorous fish also modify the community composition of algal assemblages. Basal cells of the grazer resistant species *Stigeoclonium* (Chlorophyta) comprised a larger portion of algal assemblages on substrates accessible to grazing fishes compared to fish exclusions (FLECKER et al. 2002).

In marine habitats it was found that the grazer *Idothea chelipes* could shift marine periphyton community composition from more edible to less edible algae (SOMMER 1997). Grazers may also select for rapidly dividing taxa and so diminish biomass but enhance productivity (HILL et al. 1992) or enhance per capita productivity of grazer resistant taxa (LAMBERTI 1996, STEINMAN 1996).

Whereas clear patterns, consistent with keystone predation, are visible for growth forms, generalisations regarding the effect of herbivory on algal diversity and taxonomic composition are difficult to make. It is, however, quite obvious that grazers can modify community composition. Whether species diversity and richness increase or decrease can be dependent on herbivore abundance and species composition. The Intermediate Disturbance Hypothesis (IDH) (CONNELL 1978) predicts that diversity will be greatest at intermediate levels of mortality, i. e. either disturbance or grazer density. According to this hypothesis, grazers at intermediate densities should increase species diversity through the creation of higher habitat heterogeneity or when the dominant algae is grazed more heavily (LUBCHENCO 1978). The applicability of the IDH hypothesis to littoral communities has rarely been tested, and showed that algal diversity peaked at intermediate grazer densities in ambient and nitrate enriched treatments (McCORMICK & STEVENSON 1989). Grazing increased habitat heterogeneity and through this algal diversity.

Spatial heterogeneity can be influenced by grazers. Generally, heterogeneity is expected to increase in the presence of grazers, because grazing will not happen everywhere at the same time. This leads to newly emptied patches which are colonised by a different community than patches that are harder to discover or to reach for grazers. If grazer density becomes too high, however, an evenly grazed substrate can result, and spatial heterogeneity declines (HILLEBRAND et al. 2000). KAWATA & AGAWA (1999) found that spatial heterogeneity in algal biomass increased with grazing. With increasing grazing pressure the coefficient of variation of periphyton biomass per area (patchiness) increased. However, this is not true for all grazers, but depends on the behaviour of herbivores. SOMMER (2000) examined the influence of different grazers

(*Idothea chelipes* and *Littorina littorea*) on spatial heterogeneity. *Idothea* did not increase spatial heterogeneity of periphyton density, but *Littorina* increased spatial heterogeneity significantly.

Trophic cascading

Trophic interactions are important in determining distribution and abundance of organisms. But ecologists are still debating whether the primary control is by resources (bottom-up forces) or by predators (top-down forces). This debate is reviewed in detail by POWER (1992).

HAIRSTON et al. (1960), in their famous theory about “why the world is green” (HSS), envisioned food webs as consisting of three trophic levels: producers, herbivores, and predators. The theory states that abundant green plants dominate terrestrial landscapes because herbivores are limited by predators. Producers are consequently limited by their resources (bottom-up limitation).

Several models have been developed to attempt a mathematical explanation of trophic cascades: OKSANEN et al. (1981) based their “top-down and bottom-up” model on the assumption that each trophic level acts as a single exploitative population. The structure of ecosystems is determined by the number of trophic levels, which increase along a productivity gradient. The model predicts herbivory pressure to be most severe in environments with two trophic levels. Herbivores are food limited (“bottom-up” limitation). The addition of a third trophic level leads to stronger predation pressure on herbivores, thus releasing plants from grazing pressure. Herbivores are limited through predation (“top-down” limitation). The model predicts bottom-up limitation for ecosystems with even numbers of trophic levels and top-down limitation for odd numbers of trophic levels.

Whether or not the models for trophic cascading hold true and changes in abundance of one level propagate through the whole food chain or only affect the adjacent trophic levels is dependent on the factor limiting primary production.

The effectiveness of the grazers and predators determines whether predation limits grazer abundance or grazers limit periphyton biomass. Thus streams with 3 trophic levels (algae – grazer – fish) can react to nutrient enrichment and predator addition in different ways. If algae are controlled by grazing pressure, as in the case of low predation, nutrient addition will only lead to an increase in grazer biomass. On the other hand, if grazers are controlled by intense predation, nutrient addition will lead to increased algal biomass. This hypothesis was tested by BIGGS et al. (2000) using different streams with inefficient predators in half the streams and efficient predators in the others. Nutrient addition led to an increase in total invertebrate densities, but these increases were greater in streams with inefficient predators. Algal

biomass was higher in streams with efficient predators. That predators can increase periphyton biomass, by limiting grazer abundance, was also shown by DAHL (1998).

Further, increase in one trophic level can affect more than one other trophic level. This means that bottom-up and top-down forces are at work simultaneously, as was demonstrated in an enrichment experiment (MOELLER et al. 1998). Grazers could not consume all extra algal growth due to nutrient enrichment and both trophic levels, periphyton and grazers, increased in biomass. HANSSON (1992) showed that differences in number of trophic levels in different lakes had a negligible effect on the biomass of the periphyton.

These studies show the difficulty of finding one general mechanism to explain regulation of food webs. The relative strength of top-down and bottom-up effects cannot be generalised among benthic systems, and the effects of either force appear to diminish with distance down or up the food web. Still, some patterns appear more often than others: LAMBERTI (1996) reviewed the role of periphyton in benthic food webs and came to the conclusion that benthic grazers appear to be food-limited by either abundance or quality of food, rather than being predator controlled.

Besides the direct effects that fish have on grazers, there are indirect effects of predator induced behavioural changes of prey. DIEHL et al. (2000) investigated the consequences of multiple behavioural responses of grazers which are faced with a trade off between foraging return and predation risk. Their model predicted that predators have a positive effect on benthic algae biomass mediated through grazer behaviour (emigration, change of surface use) rather than through consumptive reductions of grazer numbers. This prediction was experimentally confirmed (McCOLLUM et al. 1998). Another study supports this notion. Here, fish-predators were found to inhibit snail reproduction and suppress grazing activity (GELWICK 2000). At the same time behavioural responses of prey can be dependent on the identity of the predators species (BERNOT & TURNER 2001, TURNER et al. 1999). Recently, SHURIN et al. (2002) analysed the strength of the trophic cascade and found that benthic communities revealed strong cascades both in marine and freshwater systems.

Habitat facilitation

Grazers can indirectly improve the habitat of the algae by increasing the availability of space. Large armoured catfish (*Ancistrus spinosus*) in Panamanian streams clear nutrient poor, fine sediment from rock surfaces, thereby creating new habitats for epilithic algae (POWER 1984). But the most common case of habitat facilitation by grazers is through nutrient regeneration. Mathematical models suggest that grazing can increase the rates of nutrient cycling (DE ANGELIS 1992) and improve the abiotic environment of the algae. Many studies

also show that herbivores and other consumers recycle nutrients via excretion, thereby augmenting rates of nutrient supply (GRIMM 1988, STERNER 1986, VANNI 1987, 1996, ELSEER 1992). Herbivory results in nutrient regeneration from within the periphyton matrix, so in cases of greater nutrient limitation, the positive response of greater nutrient flux may outweigh the negative response of herbivory (McCORMICK & STEVENSON 1991). But this window where the indirect positive effects outweigh the direct negative effects is very narrow (MULHOLLAND et al. 1991, STEWART 1987) and restricted mostly to situations with low grazer density (STEINMAN 1996).

These dynamics can act differently on different parts of the community. Grazers may influence the nature of the supply of limiting nutrients to understory algae by removing overlying senescent cells that can diminish nutrient transport rates into even a thin periphyton layer (McCORMICK & STEVENSON 1991). Grazers may also increase nutrient supply by excretion, and those nutrients may stimulate the growth of grazer resistant species. For example, enhanced growth by *Stigeoclonium* (grazing resistant) exceeds grazing loss (McCORMICK & STEVENSON 1991). McCOLLUM et al. (1998) come to a similar conclusion. Their data suggest that fish can have an important indirect effect on algae through the resupply of nutrients and by altering the competitive outcome among taxa and growth forms. Only one study was found to show an enhancement of nutrient limitation with grazing. The degree of N-limitation was more than 2.5 times greater on substrates grazed by herbivorous fishes compared to substrates inaccessible to macroherbivores (FLECKER et al. 2002).

It is obvious from enrichment experiments that nutrient addition can greatly reduce the direct negative effect through consumption that grazers have on primary producers. McCORMICK (1994) found that snails had a negative impact on algal abundance through the removal and consumption of algal biomass. At the same time they had a positive effect, stimulating growth by increasing the availability of nutrients to remaining cells. However, consumptive losses far outweighed stimulating effects on algal abundance under ambient nutrient conditions. Both positive and negative effects of grazing on algae were equal under enriched conditions; even though grazers probably consumed more biomass under enriched conditions.

The main limiting nutrients in littoral communities are nitrogen and phosphorous. Here it is important to note that the facilitating effect of nutrient regeneration depends very strongly on the ratios (nutrient stoichiometry) in which these nutrients are resupplied, and on nutrient limitation conditions. ELSEER & HASSETT (1994) studied nutrient limitation and cycling in marine and lacustrine habitats. P-limitation seems to be an important feature of lakes, but not of marine sites. They also found that the N:P ratio of consumers and their food determines the recycling rates. Thus, when consuming food with an N:P ratio higher than their body N:P, animals will retain P and recycle N. This

model incorporates a homeostatic regulation of grazer tissue composition. Algal communities receiving nutrients primarily from homeostatic grazers are expected to become limited by either N or P, but not by both (STERNER 1990).

HILLEBRAND & KAHLERT (2001) examined how the presence of grazers influenced algal nutrient content and found that it decreased the C:N and C:P ratios of algae. More grazing experiments support the view that grazing improves algae nutrient status. FROST & ELSER (2002) and FROST et al. (2002) measured C:P ratios of epilithic periphyton under different grazing intensity and confirmed that C:P ratios of periphyton at high grazer densities were significantly lower than their C:P ratios in ungrazed treatments. HUNTER & RUSSELL-HUNTER (1983) did the same for C:N ratios and with the result that the C:N ratio of benthic algae decreased with grazer density. Experiments by ROSEMOND (1993) in streamside flow-through channels showed that the cellular nutrient content of the algae community increased when grazers were present. Moreover, algae produced more chlorophyll per biomass in the presence of grazers, maybe in order to compensate for grazing losses.

Indirect versus direct effects

Grazing is primarily a process where algal biomass is ingested and incorporated into grazer biomass. This reduction of algal biomass through consumption has a direct negative effect on periphyton biomass. But we showed that herbivores affect their prey in more complex ways than the classic view of the plus-minus relationship between predator and prey suggests. The question that remains to be answered is how much of the negative effect of grazing is compensated by the long list of indirect effects reviewed above. Positive effects sometimes overwhelm negative ones especially for relatively inedible algal taxa.

The two parameters which we use as a measure of positive and negative effects on periphyton are algal biomass and productivity. Most publications detected a decrease in biomass due to grazing. FEMINELLA & HAWKINS (1995) examined over 100 studies to estimate the effects of grazers on periphyton biomass. Almost 70 % of studies reported significant effects of grazers on periphyton ash free dry matter (AFDM). These effects were negative in all except one case (McCORMICK 1990). The effects of grazers on chlorophyll-a were slightly less frequent but still significant. In another review, STEINMAN (1996) examined 95 studies and showed that biomass decreased in 73 studies as a result of grazing by different types of herbivores, whereas 7 studies grazing resulted in an increase in biomass.

Grazing can have opposite effects on algal biomass and productivity. Losses from grazing can be significant, but grazers may select for rapidly dividing

taxa (HILL et al. 1992) and so diminish the biomass but enhance the biomass-specific productivity.

The quantitative importance of indirect effects

From the previous sections, the importance of indirect effects in the relation between macrograzers and periphyton has become evident. However, it is not clear, whether the indirect effects found in single experiments have an overall significance and whether their effect size is of similar magnitude to the direct effect of biomass consumption. Therefore, we conducted a quantitative summary of indirect effects by using meta-analysis techniques.

Methods

We conducted a quantitative meta-analysis of published experiments on grazing on periphyton (lentic and lotic freshwater as well as coastal periphyton). We obtained the relevant literature searching the Aquatic Sciences and Fisheries Abstracts (ASFA) and the ISI Web of Science databases (covering the years 1978 – June 2002). Earlier publications were found by searching the bibliography of the abstracted publications. Moreover, we were able to use information from three recent reviews (FEMINELLA & HAWKINS 1995, HILLEBRAND 2002, STEINMAN 1996).

We included experiments in our database if they fulfilled the following criteria: Experiments had to be replicated and grazers had to be manipulated directly, thus studies manipulating grazer access by removing or adding predators were not included (HILLEBRAND 2002). Moreover, the manipulation of grazer density had to result in a minimal 90 % decline in grazer abundance or grazer biomass. Means and some measure of variation (standard error or standard deviation) had to be reported for at least one of the response variables (see below). In total, more than 300 publications were searched for relevant information after reading the abstract, with finally 116 studies included in this analysis, reporting the results of 495 experiments.

For the calculation of effect sizes, a common metric was used for direct and indirect effects. We used the log response ratio $\ln(R)$, which is an established effect size in meta-analysis (HEDGES et al. 1999) and allows conducting a weighted meta-analysis (ROSENBERG et al. 2000). For a weighted meta-analysis, each experiment-wise effect size is divided by its variance, thus giving more impact to studies with higher replication and thus higher “reliability” of effects (GUREVITCH & HEDGES 1993, 1999).

The log response ratio $\ln(R)$ is calculated as

$$\ln(R) = \ln\left(\frac{X_G}{X_C}\right)$$

and its variance is calculated as

$$v_{\ln(R)} = \frac{(SD_G)^2}{(N_G) \cdot (X_G)^2} + \frac{(SD_C)^2}{(N_C) \cdot (X_C)^2}.$$

Here, the subscripts C and G denote the ungrazed Control and the Grazed treatment, respectively. \bar{X} is the mean, N the number of replicates, and SD the standard deviation of C and G, respectively.

From all the experiment-wise effect sizes, an overall effect size (grand mean effect size, E^{++}) is calculated as

$$E^{++} = \frac{\sum_{i=1}^{i=n} w_i \cdot E_i}{\sum_{i=1}^{i=n} w_i}$$

where E_i is the effect size and w_i is the weight for each study i .

For this grand mean effect size, 95 % confidence intervals (CI) can be calculated (ROSENBERG et al. 2000). Effect sizes with 95 % CI differing from 0 are regarded significant. Moreover, the magnitudes of the E^{++} for different variables can be compared, where non-overlapping CI indicate significantly different effects. We also used Pearson's correlation to identify relations between the experiment-wise effect sizes on different response variables.

Effect sizes and variances were calculated for the following response variables:

Direct effects: The removal of biomass was used as a direct effect, with biomass mainly measured as biovolume, chlorophyll-a, (ash-free-) dry mass, cell counts (total $N = 492$). We expected a significant negative deviation from zero of the grand mean effect on biomass.

Indirect effects: Not all indirect effects on periphyton described above were quantifiable, leading our focus in this section on nutrient content, productivity, species composition and spatial heterogeneity. We did not do an analyses on trophic cascades which was done just recently (SHURIN et al. 2002).

Nutrient content

From the 495 experiments, 57 reported the effect of grazer presence on the C:N ratio, 49 on the C:P ratio and 47 on the N:P ratio. Additionally, 10 experiments reported the phosphorus content as % P in dry weight, which also was used as a response variable. For nitrogen content as % N, not enough data were present. We expected that grazing would increase periphytic nutrient content, resulting in significant negative effect sizes for all ratios and a significant positive effect size for % P.

Productivity

Productivity has been reported in two different ways, per area (P_{area}) and per biomass (P_{biom}). Both were measured either from carbon incorporation or from oxygen production. Due to the consumption of biomass, we expected a reduction of P_{area} with grazing (significant negative effect size). Due to the increase in nutrient content and light availability (see above), we expected a positive effect size for P_{biom} . For P_{area} , we obtained results from 62 experiments. Only 28 experiments reported P_{biom} directly, but another 30 experiments allowed its calculation from P_{area} and biomass. Since no var-

iance could be calculated for these effect sizes, we used an unweighted meta-analysis for P_{biom} ($N = 58$).

Diversity

Effects on species composition were quantified by three diversity parameters, which were the ones most often reported: species richness ($N = 90$), Shannon-Wiener's diversity index H' ($N = 83$) and evenness J ($N = 36$). Other aspects of species composition and community structure were difficult to quantify and thus not included. For diversity, predictions were less straightforward than for other indirect effects. However, we assume that grazing increases evenness since grazing most often decreases the dominance of few species. For species richness, the effects depend on the counteractive influences from removing biomass and structure (decreasing S) and preventing competitive exclusion (increasing S). For H' , we expected an intermediate response.

Spatial heterogeneity

Heterogeneity was quantified in few studies directly with a variety of measures, which in contrast to the different measures for variables described above could not be unified in one analysis. Instead, we decided to calculate the coefficient of variation (CV) for the biomass in controls and treatments and to calculate the effect of grazing on this overall measure of variability. In this way, results from 494 experiment could be used for this calculation, which was then analysed in an unweighted meta-analysis. Our expectation was that grazing would tend to increase heterogeneity, at least at lower grazer pressure.

Results

Summarised over all 492 experiments, grazing clearly affected the periphytic biomass negatively with $E^{++} = -0.661$ (Fig. 2). Although the overall effect was clearly negative, there was a significant number of experiments reporting positive effects ($N = 53$, 10.8 % of all experiments).

The effect of grazing on periphytic nutrient content was significantly positive both for N and P (Fig. 2). However, the C:P ratio was much more affected than the C:N ratio, for which the effect was significantly different from zero, but E^{++} was only -0.023 . The higher impact on P than on N became also evident from a significant negative effect of grazing on the resulting N:P ratio, showing that P-content was more increased than N-content. The E^{++} on C:P ratio and N:P ratio was -0.141 and -0.118 , respectively. The effect of grazing on both these ratios was positively correlated to the effect of grazing on biomass (Fig. 3 a), indicating that grazers increased the P-content more when their rate of biomass removal was higher. A similar relation could not be found for C:N (Fig. 3 a).

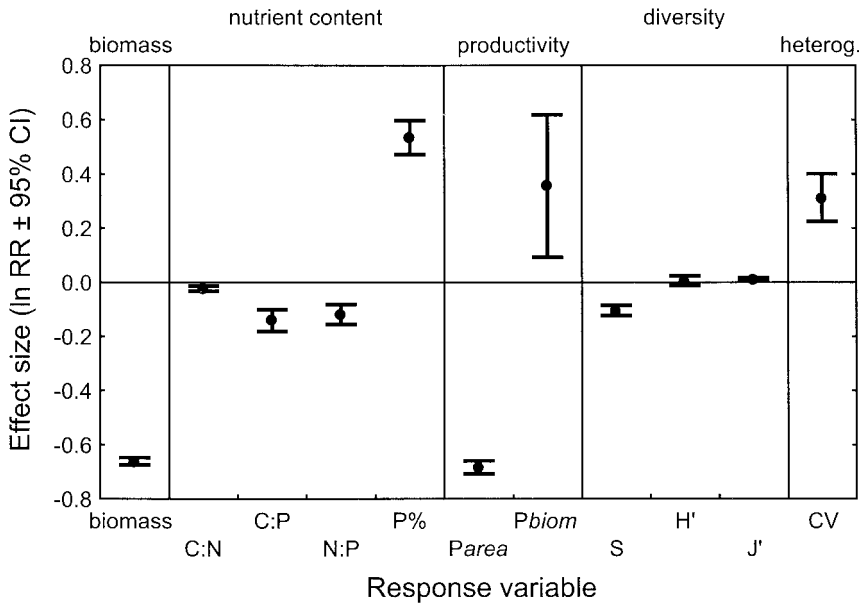


Fig. 2. Grand mean effect sizes (I 95% confidence intervals) for grazer effects on algal biomass, nutrient content, productivity, diversity and heterogeneity.

Effects on productivity were significant, but with contrasting signs for area-specific and biomass-specific productivity (Fig. 2). Grazers reduced P_{area} to a similar extent than biomass ($E^{++} = -0.683$) and the two effects were closely correlated (Fig. 3 b). Grazing increased P_{biom} , the effect magnitude being slightly smaller ($E^{++} = 0.355$) than for biomass. Also for P_{biom} , effect sizes became stronger (more positive) when effects on biomass were stronger (more negative) (Fig. 3 b).

Grazing significantly reduced species richness (S) and had a strong effect on diversity ($E^{++} = -0.104$), but this reduction in S was not correlated to the direct consumption of biomass (Fig. 3 c). Grazing had a significant positive effect on evenness, but with low overall effect size ($E^{++} = 0.010$). Effects on evenness however, were strongly correlated with biomass effects. H' was affected both positively and negatively, being the sum of the effects on S and J' , and the effect size did not differ significantly from 0 (Fig. 2).

The variability of algal biomass (measured as CV) was overall positively affected by grazer presence ($E^{++} = 0.312$). Nevertheless the variation in effects was high, with almost a third of the experiments showing negative effects of grazing on CV. There was a weak correlation between effects of grazing on biomass and on variability, which was significant though due to the high number of observations (Fig. 3 d). There was thus a weak tendency that increased grazing pressure leads to increased positive effects on heterogeneity.

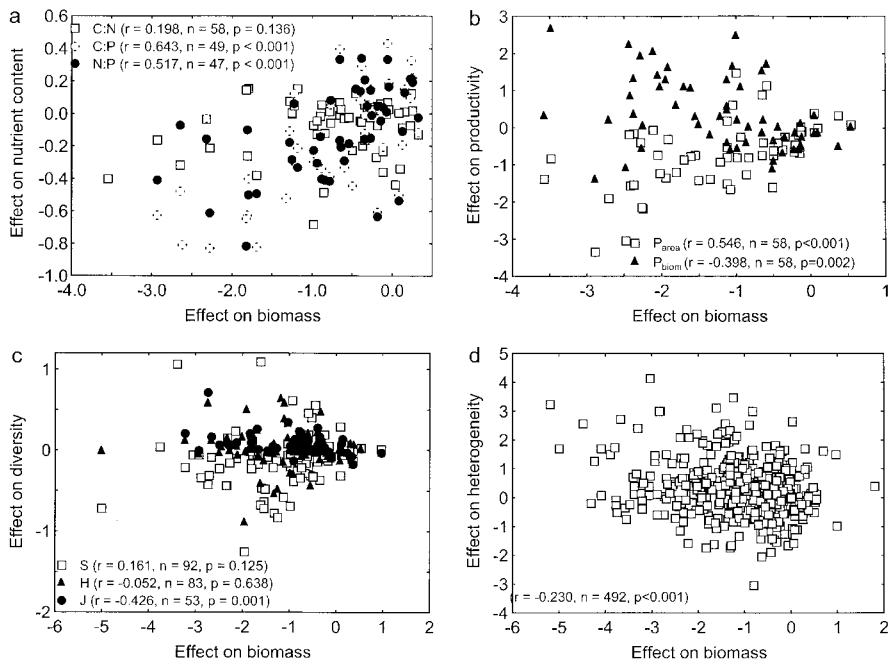


Fig. 3. Experiment-wise indirect effect sizes were correlated to experiment wise direct effect sizes on biomass. The indirect effects are **a)** nutrient content, **b)** productivity, **c)** diversity and **d)** heterogeneity.

Discussion

The quantitative meta-analysis highlighted two main points on the importance of indirect effects: first, most indirect effects investigated were clearly significant, whereas the effect magnitude mainly was smaller than for the direct consumption of biomass. Second, most effect sizes on diversity, productivity, nutrient content and heterogeneity were clearly correlated to the magnitude of biomass consumption with 7 out of 10 correlations being highly significant.

Grazing significantly reduced algal biomass, which was expected from previous reviews on this topic (FEMINELLA & HAWKINS 1995, HILLEBRAND 2002, STEINMAN 1996). In spite of the high negative effects of grazing on algal biomass, 10 % of the studies actually showed positive grazing effects. Nutrient supply might affect the impact of grazing, where low grazing pressure and low external nutrient concentrations might lead to positive grazing effects on prey biomass (HILLEBRAND 2002, STEINMAN 1996). In a recent meta-analysis, HAWKES & SULLIVAN (2001) showed the influence of nutrient supply for the overcompensation of terrestrial plants, that is, the increase in plant biomass following herbivory. Their results indicated that different plant groups reacted

differently to nutrient supply under herbivory, some overcompensating at low, others at high resource availability.

Grazers decreased clearly C:P and C:N ratios in periphyton. Although effects on C:P ratios were stronger than for C:N ratios, both were significant, which was clearer than expected. We expected more variation since the experiments were conducted in a wide range of habitats (marine to freshwater, oligotrophic to eutrophic) with highly different limitation scenarios and the mechanisms, by which nutrient content can be increased in the presence of grazers, are highly variable (see Habitat facilitation). The consistency of the effects corroborates results of a meta-analysis on experiments increasing lotic nutrient supply, which showed that both N and P have positive effects on algae, although in single experiments mostly one nutrient effect is detected due to limited statistical power (FRANCOEUR 2001). Thus, even under strong limitation by one nutrient, both nutrients will be taken up and incorporated into periphytic biomass.

Effects on productivity sustained the hypotheses that grazers would decrease area-specific productivity due to biomass consumption, exemplified by the correlation between effect sizes on biomass and P_{area} , and increase biomass-specific productivity due to increased biomass-specific access to nutrients and light.

The impact on species richness was significantly negative and the impact on evenness positive. The reduction in species richness showed that the local extinction of algal species due to grazing was not balanced by a reduced competitive exclusion. Several aspects of periphyton community structure may contribute to the weaker role of competitive exclusion compared to biomass loss (HILLEBRAND 2003). First, even though competition for nutrients might be intense in periphyton, most experiments have been conducted in the field, with free access of propagules to the sampled substrates. Thus, local extinction of species is rather transient, as has been observed in a coastal eutrophication study investigating microalgal diversity (HILLEBRAND & SOMMER 2000). Second, the removal of biomass often affects filamentous, rather large algal species (HILLEBRAND et al. 2000, STEINMAN 1996), resulting in less three-dimensional structure in grazed assemblages. In a vote-counting review, STEINMAN (1996) found divergent effects of grazing on diversity, with almost 50 % of the studies finding reduced algal species richness with grazing. Therefore, grazed assemblages have been described as simplified (MUNOZ et al. 2000, POFF & WARD 1995), and new colonisers, especially epiphytes will find less available structure to settle. In contrast to species richness, the dominance of single or few species is clearly counteracted by grazer presence, thus evenness increased with grazing. The contrasting effect on species richness can also be explained from the dominance of certain growth forms (filamentous algae) in

ungrazed periphyton, which also are highly susceptible to grazing (HILLEBRAND *et al.* 2000, STEINMAN 1996).

The impact of grazing on spatial complexity is highly divergent depending on mouthpart morphology, grazer density and activity (see above). This is mirrored by the large variability in CV associated with grazing effects as shown in our analysis. Still, a quite consistent pattern could be detected with grazers mainly increasing CV (i.e., increasing the variability between replicates), especially if negative effects on algal biomass were high. Negative effects on heterogeneity were found at low grazing pressure. Thus, effects on heterogeneity depend on overall grazing pressure, explaining contrasting results in previous studies on algal variability (HILLEBRAND *et al.* 2000). Moreover, CV is the simplest measure of heterogeneity, whereas other aspects may give more detailed results on spatial effects (GELWICK & MATHEW 1997, SARNELLE *et al.* 1993).

In conclusion, indirect effects, that is effects of grazers other than biomass consumption, are not marginal, and might contribute to structuring littoral communities. This result of the meta-analysis is evident even by comparing only two trophic levels, grazers and their prey. More indirect effects would be expected by including more complete food webs. Whereas some studies show that indirect effects in tritrophic systems propagate on algal and grazer biomass and grazer behaviour, there are almost no studies showing how the presence of a predator affects other aspects of the grazer-periphyton interaction such as effects on diversity or nutrient content. Not all of these indirect interactions will be of equal importance as the effects analysed here, but weak interactions may contribute largely to the stability of food webs (McCANN *et al.* 1998).

Many questions are still unanswered. We present a list of specific questions worth pursuing in future research:

1. How do trait mediated effects propagate through the benthic food web? Which part does nutrient regeneration play in such indirect interactions?
2. How do stoichiometric constraints affect indirect consumer-prey interactions?
3. What regulates the effects of consumers on diversity? Are ecosystem productivity, disturbance history and consumer diversity important in this context?
4. Which influence has the addition of a third trophic level on indirect consumer-prey interactions? Does this influence the stoichiometry of producers and consumers?

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References

- BERNOT, R. J. & TURNER, A. M. (2001): Predator identity and trait-mediated indirect effects in a littoral food web. – *Oecologia* **129**: 139–146.
- BIGGS, B. J. F., FRANCOEUR, S. N., HURYN, A. D., YOUNG, R., ARBUCKLE, C. J. & TOWNSEND, C. R. (2000): Trophic cascades in streams: effects of nutrient enrichment on autotrophic and consumer benthic communities under two different fish predation regimes. – *Can. J. Fish. Aquat. Sci.* **57**: 1380–1394.
- BORCHARDT, M. A. (1996): Nutrients. – In: STEVENSON, R. J., BOTHWELL, M. L. & LOWE, R. L. (eds): *Algal Ecology – Freshwater Benthic Ecosystems*. – Academic Press, pp. 183–227.
- CONNELL, J. H. (1978): Diversity in tropical rain forests and coral reefs. – *Science* **199**: 1302–1310.
- DAEHNICK, A. E., SULLIVAN, M. J. & MONCREIFF, C. A. (1992): Primary production of the sand microflora in seagrass beds of Mississippi Sound. – *Botanica Marina* **35**: 131–139.
- DAHL, J. (1998): Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. – *Oecologia* **116**: 426–432.
- DEANGELIS, D. L. (1992): Dynamics of nutrient cycling and food webs. – Chapman and Hall, London, UK.
- DENICOLA, D. M., MCINTIRE, C. D., LAMBERTI, G. A., GREGORY, S. V. & ASHKENAS, L. R. (1990): Temporal patterns of grazer-periphyton interactions in laboratory streams. – *Freshwat. Biol.* **23**: 475–489.
- DIEHL, S., COOPER, S. D., KRATZ, K. W., NISBET, R. M., ROLL, S. K., WISEMAN, S. W. & JENKINS, T. M. (2000): Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. – *Amer. Nat.* **156**: 293–313.
- DUDLEY, T. L. (1992): Beneficial effects of herbivores on stream macroalgae via epiphyte removal. – *Oikos* **65**: 121–127.
- ELSER, J. J. (1992): Phytoplankton dynamics and the role of grazers in Castle Lake, California. – *Ecology* **80**: 1157–1167.
- ELSER, J. J. & HASSETT, R. P. (1994) A stoichiometric analysis of the zooplankton-phytoplankton interaction in marine and freshwater ecosystems. – *Nature* **370**: 211–213.
- FAIRWEATHER, P. G. (1990): Is predation capable of interacting with other community processes on rocky reefs? – *Austral. J. Ecol.* **15**: 453–464.
- FEMINELLA, J. W. & HAWKINS, C. P. (1995): Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. – *J. N. Amer. Benthol. Soc.* **14**: 465–509.
- FLECKER, A. S., TAYLOR, B. W., BERNHARDT, E. S., HOOD, J. M., CORNWELL, W. K., CASSATT, S. R., VANNI, M. J. & ALTMAN, N. S. (2002): Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. – *Ecology* **83**: 1831–1844.
- FRANCOEUR, S. N. (2001): Meta-analysis of lotic nutrient amendment experiments: detecting and quantifying subtle responses. – *J. N. Amer. Benthol. Soc.* **20**: 358–368.

- FROST, P. C. & ELSEY, J. J. (2002): Growth responses of littoral mayflies to the phosphorus content of their food. – *Ecol. Letters* **5**: 232–240.
- FROST, P. C., ELSEY, J. J. & TURNER, M. A. (2002): Effects of caddisfly grazers on the elemental composition of epilithon in a boreal lake. – *J. N. Amer. Benthol. Soc.* **21**: 54–63.
- GELWICK, F. P. (2000): Grazer identity changes the spatial distribution of cascading trophic effects in stream pools. – *Oecologia* **125**: 573–583.
- GELWICK, F. P. & MATTHEWS, W. J. (1997): Effects of algivorous minnows (*Camposotoma*) on spatial and temporal heterogeneity of stream periphyton. – *Oecologia* **112**: 386–392.
- GRIMM, N. B. (1988): Role of macroinvertebrates in nitrogen dynamics of a desert stream. – *Ecology* **69**: 1884–1893.
- GUREVITCH, J. & HEDGES, L. V. (1993): Meta-analysis: combining the results of independent experiments. – In: SCHEINER, S. M. & GUREVITCH, J. (eds): *Design and analysis of ecological experiments*. – Chapman & Hall, New York, pp. 378–398.
- (1999): Statistical issues in ecological meta-analyses. – *Ecology* **80**: 1142–1149.
- HAIRSTON, N. G., SR., SMITH, J. E. & SLOBODKIN, L. B. (1960): Community structure, population control, and competition. – *Amer. Nat.* **94**: 421–424.
- HANSSON, L. A. (1992): Factors regulating periphytic algal biomass. – *Limnol. Oceanogr.* **37**: 322–328.
- HART, D. D. (1985): Causes and consequences of territoriality in a grazing stream insect. – *Ecology* **66**: 404–414.
- HAWKES, C. V. & SULLIVAN, J. J. (2001): The impact of herbivory on plants in different resource conditions: A meta-analysis. – *Ecology* **82**: 2045–2058.
- HEDGES, L. V., GUREVITCH, J. & CURTIS, P. S. (1999): The meta-analysis of response ratios in experimental ecology. – *Ecology* **80**: 1150–1156.
- 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, pp. 121–148.
- HILL, W. R., BOSTON, H. L. & STEINMAN, A. D. (1992): Grazers and nutrients simultaneously limit lotic primary productivity. – *Can. J. Fish. Aquat. Sci.* **49**: 504–512.
- HILLEBRAND, H. (2002): Top-down versus bottom-up control of autotrophic biomass – a meta-analysis on experiments with periphyton. – *J. N. Amer. Benthol. Soc.* **21**: 349–369.
- (2003): Opposing effects of grazing and nutrients on diversity. – *Oikos* **100**: 592–600.
- HILLEBRAND, H. & KAHLERT, M. (2001): Effect of grazing and nutrient supply on periphyton biomass and nutrient stoichiometry in habitats of different productivity. – *Limnol. Oceanogr.* **46**: 1881–1898.
- 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**: 2205–2219.
- HILLEBRAND, H. & SOMMER, U. (1997): Response of epilithic microphytobenthos of the Western Baltic Sea to in situ experiments with nutrient enrichment. – *Mar. Ecol. Progr. Ser.* **160**: 35–46.
- (2000): Diversity of benthic microalgae in response to colonization time and eutrophication. – *Aquat. Bot.* **67**: 221–236.

- HILLEBRAND, H., WORM, B. & LOTZE, H. K. (2000): Marine microbenthic community structure regulated by nitrogen loading and grazing pressure. – *Mar. Ecol. Progr. Ser.* **204**: 27–38.
- KAWATA, M. & AGAWA, H. (1999): Perceptual scales of spatial heterogeneity of periphyton for freshwater snails. – *Ecol. Letters* **2**: 210–214.
- 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, pp. 533–572.
- LUBCHENCO, J. (1978): Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. – *Amer. Nat.* **112**: 23–39.
- MARKS, J. C. & LOWE, R. L. (1989): The independent and interactive effects of snail grazing and nutrient enrichment on structuring periphyton communities. – *Hydrobiologia* **185**: 9–17.
- MCCANN, K., HASTINGS, A. & HUXEL, G. R. (1998): Weak trophic interactions and the balance of nature. – *Nature* **395**: 794–798.
- MCCOLLUM, E. W., CROWDER, L. B. & MCCOLLUM, S. A. (1998): Complex interactions of fish, snails, and littoral zone periphyton. – *Ecology* **79**: 1980–1994.
- MCCORMICK, P. V. (1990): Direct and indirect effects of consumers on benthic algae in isolated pools of an ephemeral stream. – *Can. J. Fish. Aquat. Sci.* **47**: 2057–2065.
- (1991): Lotic protistan herbivore selectivity and its potential impact on benthic algal assemblages. – *J. N. Amer. Benthol. Soc.* **10**: 238–250.
- (1994): Evaluating the multiple mechanisms underlying herbivore-algal interactions in streams. – *Hydrobiologia* **291**: 47–59.
- MCCORMICK, P. V. & STEVENSON, R. J. (1989): Effects of snail grazing on benthic algal community structure in different nutrient environments. – *J. N. Amer. Benthol. Soc.* **8**: 162–172.
- (1991): Grazer control of nutrient availability in the periphyton. – *Oecologia* **86**: 287–291.
- MENGE, B. A. (1995): Indirect effects in marine rocky intertidal interaction webs: patterns and importance. – *Ecol. Monogr.* **65**: 21–74.
- MOELLER, R. E., WETZEL, R. G. & OSENBURG, C. W. (1998): Concordance of phosphorus limitation in lakes: Phytoplankton epiphytes and rooted macrophytes. – *Ecol. Stud.* **131**: 318–325.
- MULHOLLAND, P. J., STEINMAN, A. D., PALUMBO, A. V., ELWOOD, J. W. & KIRSCHTEL, D. B. (1991): Role of nutrient cycling and herbivory in regulating periphyton communities in laboratory streams. – *Ecology* **72**: 966–982.
- 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**: 517–532.
- NICOTRI, M. E. (1977): Grazing effects of four marine intertidal herbivores on the microflora. – *Ecology* **58**: 1020–1032.
- OKSANEN, L., FRETWELL, S. D., ARRUDA, J. & NIEMELÄ, P. (1981): Exploitation ecosystems in gradients of primary productivity. – *Amer. Nat.* **118**: 240–261.
- PAINE, R. T. (1966): Food web complexity and species diversity. – *Amer. Nat.* **100**: 65–75.
- PINCKNEY, J. & ZINGMARK, R. G. (1993): Modelling the annual production of intertidal benthic microalgae in estuarine ecosystems. – *J. Phycol.* **29**: 396–407.

- POFF, N. L. & WARD, J. V. (1995): Herbivory under different flow regimes: a field experiment and test of a model with a benthic stream insect. – *Oikos* **72**: 179–188.
- POWER, M. E. (1984): Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. – *J. Animal Ecol.* **53**: 357–374.
- (1992): Top-down and bottom-up forces in food webs: Do plants have primacy? – *Ecology* **73**: 733–746.
- ROSEMOND, A. D. (1993): Interactions among irradiance, nutrients, and herbivores constrain a stream algal community. – *Oecologia* **94**: 585–594.
- ROSENBERG, M. S., ADAMS, D. C. & GUREVITCH, J. (2000): Sinauer Associates, Sunderland, USA.
- SARNELLE, O., KRATZ, K. W. & COOPER, S. D. (1993): Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat. – *Oecologia* **96**: 208–218.
- SCHMID-ARAYA, J. M., HILDREW, A. G., ROBERTSON, A., SCHMID, P. E. & WINTERBOTTOM, J. (2002): The importance of meiofauna in food webs: Evidence from an acid stream. – *Ecology* **83**: 1271–1285.
- SCHMID-ARAYA, J. M. & SCHMID, P. E. (2000): Trophic relationships: integrating meiofauna into a realistic benthic food web. – *Freshwat. Biol.* **44**: 149–163.
- SHURIN, B. J., BORER, E. T., SEABLOOM, E. W., ANDERSON, K., BLANCHETTE, C. A., BROITMAN, B., COOPER, S. D. & HALPERN, B. S. (2002): A cross-ecosystem comparison of the strength of trophic cascades. – *Ecol. Letters* **5**: 789–791.
- SOMMER, U. (1997): Selectivity of *Idothea chelipes* (Crustacea, Isopoda) grazing on benthic microalgae. – *Limnol. Oceanogr.* **42**: 1622–1628.
- (2000): Benthic microalgal diversity enhanced by spatial heterogeneity of grazing. – *Oecologia* **122**: 284–287.
- 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, pp. 341–373.
- STEINMAN, A. D., MCINTIRE, C. D., GREGORY, S. V., LAMBERTI, G. A. & ASHKENAS, L. R. (1987): Effect of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. – *J. N. Amer. Benthol. Soc.* **6**: 175–188.
- STEINMAN, A. D., MULHOLLAND, P. J. & KIRSCHTEL, D. B. (1991): Interactive effects of nutrient reduction and herbivory on biomass, taxonomic structure, and P uptake in lotic periphyton communities. – *Can. J. Fish. Aquat. Sci.* **48**: 1951–1959.
- STEINMAN, A. D., MULHOLLAND, P. J. & HILL, W. R. (1992): Functional responses associated with growth forms in stream algae. – *J. N. Amer. Benthol. Soc.* **11**: 229–243.
- STERNER, R. W. (1986): Herbivores' direct and indirect effects on algal populations. – *Science* **231**: 605–607.
- (1990): The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and the algal competitive arena. – *Amer. Nat.* **136**: 209–229.
- STEWART, A. J. (1987): Responses of stream algae to grazing minnows and nutrients: a field test for interactions. – *Oecologia* **72**: 1–7.
- TURNER, A. M., FETTEROLF, S. A. & BERNOT, R. J. (1999): Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail. – *Oecologia* **118**: 242–247.

- VANNI, M. J. (1987): Effects of nutrients and zooplankton size on the structure of a phytoplankton community. – *Ecology* **68**: 624–635.
- WELLNITZ, T. A. & WARD, J. V. (1998): Does light intensity modify the effect mayfly grazers have on periphyton? – *Freshwat. Biol.* **39**: 135–149.

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