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# Opposing effects of grazing and nutrients on diversity

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Conceptual models predict counteractive effects of herbivores and nutrient enrichment on plant diversity and reversed effects of grazers under different nutrient regimes. I tested these hypotheses in 11 field experiments with periphyton communities in three different aquatic habitats (a highly eutrophic lake, an meso-eutrophic lake, and an meso-eutrophic part of the Baltic Sea coast) and in different seasons. Grazer access and nutrient supply were manipulated in a factorial design. Species richness and evenness were chosen as response variables. Both manipulated factors had significant and contrasting effects on diversity, with variable effect strength between sites and seasons. From the two aspects of diversity, evenness well reflected the changes in community composition. Fertilization tended to increase the dominance of few species and thus to decrease evenness, whereas grazers counteracted these effects by removing dominant life forms. The response of species richness was not as expected, since grazers decreased richness throughout, whereas nutrients had weaker effects but tended to increase richness. Species richness rather reflected changes in periphyton architecture. Grazers reduced algal richness presumably by co-consumption of rare species in the tightly connected periphyton assemblages, whereas enrichment may increase richness by providing more structure via increased dominance of filamentous species. Although grazer and nutrient effects on richness and evenness were opposing, there was no change in the effect of one factor by manipulation of the other.

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## Introduction

The diversity of autotrophic organisms is affected by mechanisms operating on different scales of time and space. Large-scale processes such as speciation, dispersal, and connectivity act in combination with small-scale processes such as grazing, facilitation, and competition to shape local plant diversity (Tilman and Pacala 1993, Huston 1999, Loreau and Mouquet 1999, Godfray and Lawton 2001, Hillebrand and Blenckner 2002). The relative importance of regional and local processes for diversity has received wide attention (Zobel 1997, 2001, Lawton 1999) and resulted in an on-going debate on the strength of ecological interactions in determining diversity (Shurin 2001, Hillebrand and Blenckner 2002).

Nutrient supply and herbivory represent major local influences, which may be strongly interdependent. Previous studies from aquatic (Lubchenco and Gaines 1981, Hillebrand et al. 2000) and terrestrial ecosystems (Wardle and Barker 1997) indicated complex changes in diversity with manipulation of both herbivory and competition. To explain these divergent effects of local interactions, conceptual models aim at counteractive mechanisms in the plant-herbivore-nutrient interaction (Lubchenco and Gaines 1981, Proulx and Mazumder 1998).

Grazing removes prey biomass and thus also certain species from the local assemblage, i.e. grazing primarily reduces species richness. If grazers impose higher mortality on the most dominant species though, competitive exclusion of inferior species will be prevented. This

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positive effect of grazing can outweigh the grazer-related removal of species in the plant assemblage (Lubchenco 1978, Lubchenco and Gaines 1981, Proulx and Mazumder 1998, Worm et al. 1999, Hillebrand et al. 2000). The net effects of grazers on community structure depend on their selectivity and the spatial distribution of grazing pressure (Lubchenco 1978, Sommer 1999), and also on grazer density, with highest prey diversity often related to "intermediate" mortality (Huston 1979, Sommer 1999, Abrams 2001).

The grazing effect on diversity also depends on the productivity of the habitat, which will determine the rates of competitive exclusion and of recovery after grazing (Huston 1979, Kondoh 2001). On the one hand, increasing nutrient supply generally increases the dominance of few plant species (Lubchenco and Gaines 1981, Proulx and Mazumder 1998), allowing for more positive effects of grazer presence (Worm et al. 1999). On the other hand, the ability of plants to withstand mortality such as grazing and regrow afterwards correlates to nutrient input (Proulx and Mazumder 1998). Thus, the nutrient supply sustaining maximum plant diversity will increase with increasing mortality (Huston 1979, Hillebrand et al. 2000) and the effects of nutrients on diversity change with grazer presence or absence. Therefore, Proulx and Mazumder (1998) suggested reversed effects of grazers on diversity under contrasting nutrient richness, which is in concordance with model predicitions (Huston 1979, Kondoh 2001).

Also for periphyton, positive and negative trends of diversity have been observed following nutrient enrichment or grazing (Steinman 1996, Hillebrand et al. 2000). However, in studies with simultaneous manipulations of grazer presence and nutrients, the diversity of periphyton has rarely been assessed (but see Mulholland et al. 1991, Hillebrand et al. 2000). Here, I use data from 11 field experiments spread over different sites and seasons to investigate the combined influence of nutrients and grazers on algal diversity. I tested two hypotheses: (1) grazers and nutrients have significant and contrasting effects on algal diversity, and (2) grazer and nutrient effects are reversed by the manipulation of the other factor.

## Methods

Nutrient supply and grazer access to periphyton were experimentally manipulated at three sites in Sweden, two freshwater lakes (Lake Erken and Lake Limmaren) and one brackish water coastal site (at the south tip of the island Väddö). Characteristics of the sites and the experimental design were described in detail elsewhere (Hillebrand and Kahlert 2001). Information on the sites is briefly summarized in Table 1. The sites differ in productivity and herbivore composition. Lake Limmaren is highly eutrophic (mean total phosphorus TP = 1.8 μmol $l^{-1}$, mean total nitrogen TN = 70 μmol $l^{-1}$), whereas Lake Erken (mean TP = 0.9, mean TN = 45.5 μmol $l^{-1}$) and the coastal site at Väddö (mean TP = 0.79, mean TN = 20.6 μmol $l^{-1}$) are meso-eutrophic. In spite of the high total nutrient content, the dissolved nutrient concentrations varied and were at time very low even in the most productive site (Table 1). Regarding the herbivore fauna present at the three sites, the overall variation is small except for Väddö. Gastropods were important at all three sites (Table 1), together with trichopteran larvae (Lake Erken),

Table 1. Characteristics of the experimental sites, two lakes and one coastal site. The table lists the concentrations of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) as well as phytoplankton biomass. The nutrient and phytoplankton data are from the Erken Laboratory's monitoring program. For Väddö, the nearby Singöfjärden was used as reference site. For the grazer fauna, ambient total density at the experimental sites and main groups are given (Hillebrand and Kahlert 2001). The values are reported for each experimental season, autumn 1999 (Aut), early spring 2000 (Espr), late spring 2000 (Lspr) and summer 2000 (Sum). n.d. = not determined.

| Site | Nutrient | | | Grazer | |
|---|---|---|---|---|---|
| Season | DIN (μmol $l^{-1}$) | DIP (μmol $l^{-1}$) | Phytoplankton (μg $l^{-1}$) | Abundance (Ind. $m^{-2}$) | Main groups |
| Lake Erken | | | | | |
| Aut | 4.07 | 0.87 | 6.3 | n.d. | Gastropoda, Isopoda |
| Espr | 0.87 | 0.46 | 2.8 | 1257 | Gastropoda, Trichoptera |
| Lspr | 2.44 | 0.12 | 3.5 | 1193 | Gastropoda, Trichoptera |
| Lake Limmaren | | | | | |
| Aut | 4.64 | 0.29 | 28.2 | n.d. | Gastropoda |
| Espr | 0.02 | 0.01 | 16.0 | 751 | Gastropoda, Trichoptera |
| Lspr | 0.40 | 0.11 | 12.8 | 1056 | Ephemeroptera |
| Sum | 1.79 | 0.04 | 31.9 | 1507 | Chironomidae, Ephemeroptera, Gastropoda |
| Väddö | | | | | |
| Aut | 1.31 | 0.42 | 6.2 | n.d. | Amphipoda, Gastropoda |
| Espr | 2.58 | 0.19 | 3.2 | 182 | Gastropoda |
| Lspr | 0.30 | 0.01 | 8.5 | 870 | Gastropoda, Amphipoda |
| Sum | 1.31 | 0.03 | 5.5 | 421 | Gastropoda, Amphipoda |

ephemeropteran larvae (Lake Limmaren) and crustacean grazers (Väddö). Chironomids were highly abundant but are regarded as less effective grazers (Steinman 1996).

The experimental setup consisted of cages with nets of 1 mm mesh size to exclude grazers (see Hillebrand and Kahlert 2001 for details). The cage consisted of a concrete base plate and a metal frame cage, onto which the net was placed. In grazer exclusions, the net covered the complete cages, whereas in grazer access cages, two adjacent sites of the cage were open. To control for cage artifacts, cage-free control plots with grazer access were established on concrete plates without cages. Nutrient enrichment was by 30 g of granulose NPK-fertilizer, which was added to half of the exclusion, access and control treatments, respectively. The fertilizer slowly releases nitrogen and phosphorus to the water column with a nearly constant rate, as was shown in previous experiments (Worm et al. 2000). The fertilization resulted in a 2–5 fold enrichment of both dissolved phosphorus and nitrogen in the water column as measured at the end of the experiments (Hillebrand and Kahlert 2001). Grazer and nutrient treatments were factorially crossed and replicated fourfold, resulting in a $3 \times 2 \times 4$ design at each site and for each season. The cages and cage-free control plots were placed at a distance of ca 1 m at a depth of 70–90 cm (Hillebrand and Kahlert 2001).

Unglazed ceramic tiles, which had been pre-colonized for $>6$ months, were used as standard substrates and glued to the base plate. Four experiments were conducted at each site (autumn 1999, early spring, late spring and summer 2000), but one experiment had to be removed from the analysis (intrusion of grazers, summer, Lake Erken). For the different seasons, the same habitats within the three study sites were used. After 4–5 weeks, I sampled the substrates, scraped off the periphyton and separated conglomerates carefully with scissors and forceps. The biomass was suspended in a defined volume of water, which had previously been taken from the vicinity of the experiments and filtered (0.2 μm filter). Counting was done in a 3 ml Utermöhl chamber under an inverted microscope ($400\times$ magnification). For taxonomic identification, I additionally used permanent slides for diatoms and live samples for non-silicified algae ($1000\times$ magnification). Periphyton biovolume was determined using microscopic measurements and best fitting geometric models (Hillebrand et al. 1999).

Two aspects of diversity were employed, species richness and evenness. Raw estimates of species richness varied with the number of cells counted, which ranged from a minimum of 1000 to up to 3000. Therefore, species richness was adjusted by counting only species contributing $>0.1\%$ of algal biovolume ($S_{1000}$ sensu Sommer 1999). This measure avoids bias related to the detection of more rare species with increased counting effort. Evenness (Pielou's J) was calculated from biovolume proportions (Hillebrand and Sommer 2000). In a recent review, Smith and Wilson (1996) found Pielou's J less suitable because it relates to species richness. However, this correlation was seen only at very low species richness, which always was exceeded in my experiments.

To relate the effects on diversity to changes in community structure, the algae were categorized in five different growth forms. These comprised sessile single cells, motile single cells (mostly diatoms), monofilaments (unbranched filaments, diatom chains), branched filaments (including also other upright thalli), and colonies, which mostly were characterized by gelatinous spheres (e.g. cyanobacteria).

For statistical analysis, three-factorial (seasons, grazing, nutrient enrichment) ANOVA was conducted for each site and each of the two diversity measures. Due to the missing summer experiment in Lake Erken, I conducted the analyses separately for each site to avoid unequal ANOVA design. Independent factors comprised season ($N=4$ for Väddö and Limmaren, $N=3$ for Erken), grazer presence ($N=2$, closed and open cages) and nutrient enrichment ($N=2$, enriched and ambient). The impact of cages was estimated with an analogous design, where the factor grazer presence was replaced by cage presence ($N=2$, open cage and control). Untransformed data were homoscedastic and normally distributed, only for Väddö, evenness data were arcsine-square-root transformed. Due to the known variation in benthic communities, I discuss results with significance levels $p<0.05$ as significant effects and with $0.05<p<0.1$ as non-significant trends.

Pearson correlations were used to check for significant relations between diversity measures and log-transformed algal biovolume.

To test for significant treatment effects on the biovolume of the different growth forms, I conducted a multivariate analysis of variance (MANOVA). The MANOVA comprised the same independent factors as described above. The log-transformed biovolumes in all five groups separated by growth were used as dependent variables. In MANOVA, the eigenvalues of error and treatment matrices comprise the test statistic to calculate the multivariate F-value. I used the Pillai's trace statistic, which is recommended to test for significant effects in MANOVA due to its robustness (Scheiner 1993). To investigate which of the algal growth types was affected by the experimental manipulation, I conducted univariate ANOVAs for the significant treatment effect on all five groups. Here, significance levels were Bonferroni-adjusted to account for the multiple testing (indicated as $p_{adj}$ in the Results section).

## Results

Both nutrients and grazers affected the total algal biovolume (Hillebrand and Kahlert 2001) and the biovolume of the different growth forms (Fig. 1, Table 2). In addition to large and significant seasonal variation at all three sites, grazer presence and nutrients had distinct effects on different parts of the periphyton assemblage.

Grazer effects were significant in Lake Limmaren and at Väddö (significant main effect) and partially also in Lake Erken (significant grazer × season interaction) (Table 2). The presence of grazers reduced the biovolume of mono-filamentous algae at all three sites (Fig. 1), which was significant in Lake Limmaren ($F = 16.4$, $p_{adj} = 0.001$) and Väddö ($F = 24.7$, $p_{adj} < 0.001$) and – restricted to the autumn experiment – also in Lake Erken (grazer × season, $F = 9.3$, $p_{adj} = 0.016$). Single

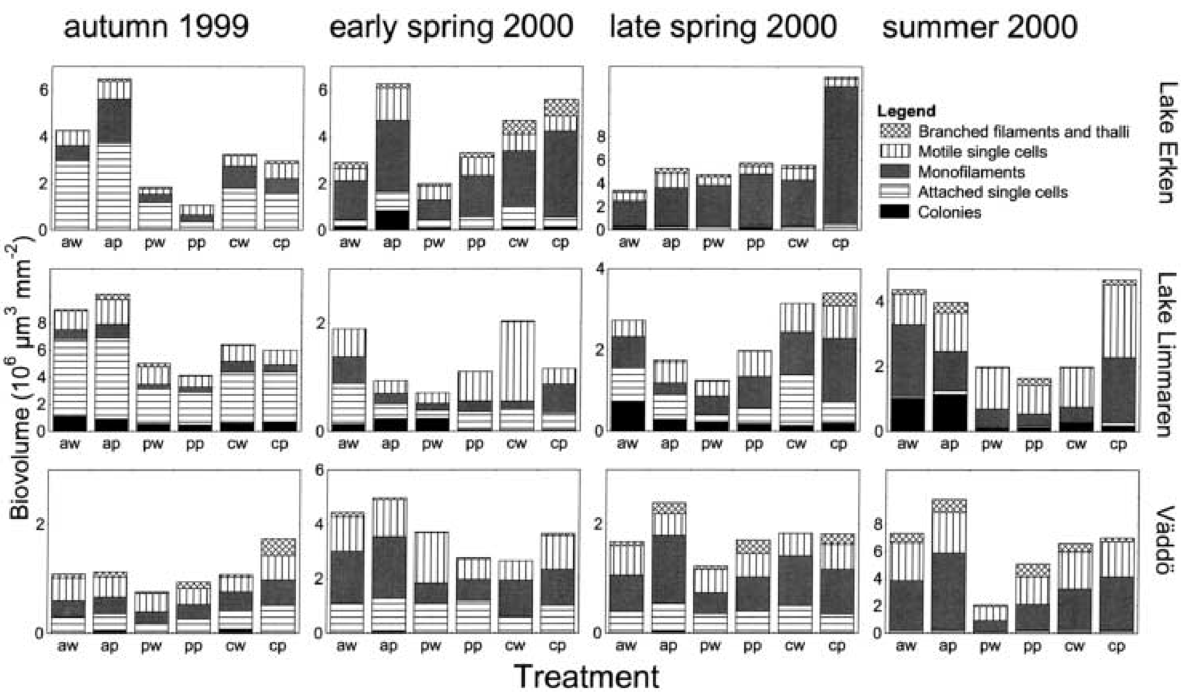


Fig. 1. Mean biovolume of algal growth forms in experiments with grazer and nutrient manipulation. The diagrams are separated in columns by seasons and in rows by site (Lake Erken, Lake Limmaren and Väddö). The five growth forms are given for each of 6 treatment combinations in each of the 11 experiments. The treatment codes represent grazer absent without enrichment (aw), grazer absent plus enrichment (ap), grazer present without or plus enrichment (pw and pp, respectively) and uncaged control plots with both nutrient levels (cw and cp, respectively).

Table 2. Results of multivariate three-factorial ANOVA on periphytic composition, represented by the biovolume of single attached cells, single motile cells, monofilaments, branched filaments, and colonies. The table gives the degrees of freedom for each analysis, Pillai's trace (PT) values and the F-ratio (with significance levels in parentheses) for the main factors and all interactions for each of the three sites. Log-transformed data were used for all sites.

| Factor | Erken | | | Limmaren | | | Väddö | | |
|---|---|---|---|---|---|---|---|---|---|
| | df | PT | F | df | PT | F | df | PT | F |
| Season (S) | 10;56 | 1.04 | 6.04 (<0.001) | 15;126 | 1.83 | 13.11 (<0.001) | 15;135 | 1.63 | 10.8 (<0.001) |
| Grazing (G) | 5;27 | 0.40 | 3.56 (0.013) | 5;40 | 0.48 | 7.51 (<0.001) | 5;43 | 0.35 | 4.70 (0.002) |
| Nutrient (N) | 5;27 | 0.45 | 4.36 (0.005) | 5;40 | 0.03 | 0.29 (0.918) | 5;43 | 0.32 | 4.10 (0.004) |
| S × G | 10;56 | 0.74 | 3.32 (0.002) | 15;126 | 0.35 | 1.10 (0.360) | 15;135 | 0.37 | 1.29 (0.270) |
| S × N | 10;56 | 0.21 | 0.66 (0.754) | 15;126 | 0.17 | 0.51 (0.933) | 15;135 | 0.14 | 0.44 (0.963) |
| G × N | 5;27 | 0.10 | 0.63 (0.681) | 5;40 | 0.21 | 1.41 (0.241) | 5;43 | 0.06 | 0.53 (0.754) |
| S × G × N | 10;56 | 0.34 | 1.13 (0.355) | 15;126 | 0.36 | 1.15 (0.319) | 15;135 | 0.22 | 0.70 (0.785) |
| Cage (C) | 5;25 | 0.55 | 6.09 (0.001) | 5;32 | 0.31 | 2.85 (0.031) | 5;39 | 0.39 | 4.90 (0.001) |
| S × C | 10;52 | 0.24 | 0.71 (0.708) | 15;102 | 0.35 | 0.91 (0.558) | 15;123 | 0.33 | 1.02 (0.435) |
| N × C | 5;25 | 0.06 | 0.29 (0.913) | 5;32 | 0.17 | 1.33 (0.278) | 5;39 | 0.16 | 1.45 (0.228) |
| S × N × C | 10;52 | 0.19 | 0.54 (0.852) | 15;102 | 0.65 | 1.87 (0.035) | 15;123 | 0.24 | 0.70 (0.781) |

celled attached species were significantly reduced by grazing both in Lake Limmaren ($F = 22.5$, $p_{adj} < 0.001$) and Lake Erken, in autumn and early spring (grazer × season, $F = 5.6$, $p_{adj} = 0.043$). Except for a significant reduction in motile diatom species in Lake Erken ($F = 9.5$, $p_{adj} = 0.022$), no other group was significantly affected by grazing.

The impact of nutrient enrichment on the biovolume of the different growth types was significant for Väddö and Lake Erken (Table 2), whereas Lake Limmaren showed no nutrient effect at all. Nutrient enrichment increased the biomass of monofilaments ($F = 13.4$, $p_{adj} = 0.005$) and motile species ($F = 10.7$, $p_{adj} = 0.013$) in Lake Erken. Similar trends were observed in branched filaments (Fig. 1), but were non-significant at all sites. Colonial species were significantly favored by nutrient enrichment at Väddö ($F = 15.0$, $p_{adj} = 0.002$).

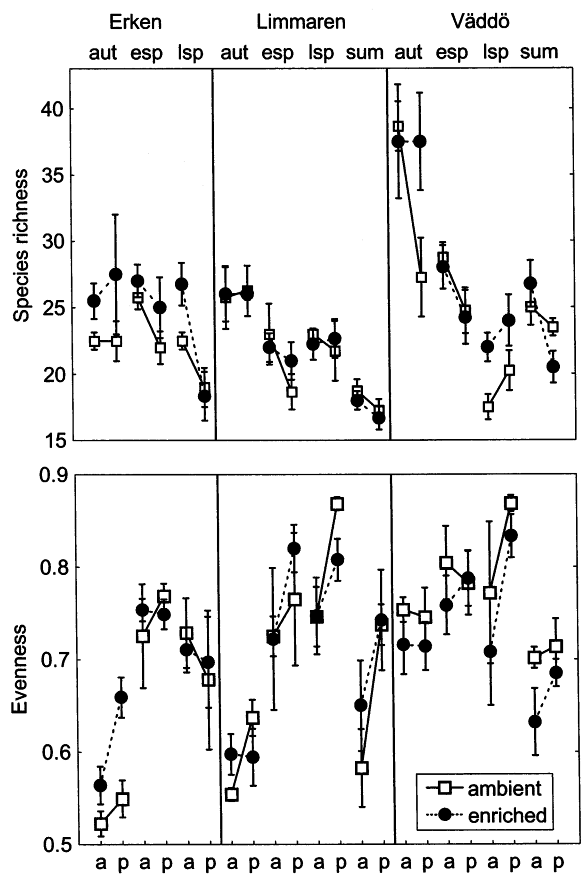


Fig. 2. Species richness ($S_{1000}$) and evenness of periphyton in experiments with grazer and nutrient manipulation. At three sites (Erken, Limmaren, Väddö) and in four different seasons (aut = autumn, esp = early spring, lsp = late spring, sum = summer), in total 11 experiments were conducted. For each experiment, the diversity measures are given for ambient (squares) and enriched (closed circles) nutrient levels and for grazers absent (a) and present (p).

Significant cage effects were found at all three sites (Table 2) and the reduction in filamentous species in open cages ($F > 10$, $p_{adj} < 0.02$) was the most striking difference to uncaged controls.

Evenness had a strong negative relationship to algal biovolume in the presence ($r = -0.425$, $p < 0.001$, $N = 79$) and absence ($r = -0.495$, $p < 0.001$, $N = 85$) of grazers. No such correlation was found for $S_{1000}$, neither at grazer presence ($r = 0.129$, $p = 0.256$, $N = 79$) nor absence ($r = 0.175$, $p = 0.109$, $N = 85$).

Grazers and nutrients had significant but seasonally differing effects on both aspects of diversity. Both for $S_{1000}$ and evenness, the seasonal differences were strong and significant at all three sites, but the seasonal patterns differed between measures and sites (Fig. 2, Table 3). $S_{1000}$ was high in autumn (Limmaren, Väddö) and low in late spring (Erken, Väddö) or summer (Limmaren). Evenness was low in summer (Väddö) or autumn (Erken, Limmaren) and highest in spring at all sites.

Grazers reduced $S_{1000}$ significantly in Erken and Väddö (Fig. 2, Table 3). At both sites, the effects were more evident in some seasons (significant grazer × season interactions) and the effect was even reversed in one experiment (Väddö, late spring). Grazer effects on richness were non-significant in Limmaren (Fig. 2, Table 3). Nutrients increased $S_{1000}$ significantly in Lake Erken, whereas no nutrient effect was detected in Limmaren (Table 3). In Väddö, the pattern was more complex. Both the nutrient effect and the nutrient × grazer × season interaction were marginally non-significant. These trends reflected an increase in $S_{1000}$ with enrichment, which was detected at both grazer treatments (late spring) or only at grazer presence (autumn). However, in the other seasons no effect (early spring) or even a decrease of richness at grazer presence (summer) was observed.

Grazer had significant positive effects on evenness in Lake Limmaren (Fig. 2, Table 3). Similar trends were visible in Väddö, where both the main grazer effect and the season × grazer interaction were marginally non-significant. At this coastal site, evenness increased with grazing in late spring and – restricted to enriched treatments – in early spring and summer. Nutrients had no significant impact on evenness in Erken and Limmaren. By contrast, nutrient enrichment significantly reduced evenness in Väddö (significant main effect, Table 3).

Neither cages nor any interaction of cages with seasons or nutrients, respectively, had significant effects on $S_{1000}$ (ANOVA, $p > 0.15$). For evenness, however, there was a significant increase in the cages in Lake Limmaren (ANOVA, $p = 0.049$) and at Väddö ($p < 0.001$), whereas in Lake Erken the positive effects of cages was restricted to the autumn experiment (ANOVA, cages × season, $p = 0.022$).

Table 3. Results of three-factorial ANOVA on algal species richness and evenness. The table gives the F-ratios (with significance levels in parentheses) for the main factors and all interactions for each of three sites. The degrees of freedoms for the effect terms are given in parentheses for each effect (note: for Erken, all terms involving seasons have 2 d.f.), for the error term in the row on top of the analysis. Untransformed data were homoscedastic and normally distributed; only for Väddö evenness data were arcsine-square-root transformed.

| Factor | Erken | Limmaren | Väddö |
|---|---|---|---|
| Species richness | 31 | 44 | 47 |
| season (3) | 5.57 (0.009) | 20.48 (<0.001) | 33.20 (<0.001) |
| grazing (1) | 8.16 (0.008) | 1.88 (0.177) | 6.95 (0.011) |
| nutrient (1) | 8.34 (0.007) | 0.01 (0.979) | 3.11 (0.084) |
| seas × graz (3) | 4.47 (0.020) | 0.69 (0.565) | 2.84 (0.048) |
| seas × nut (3) | 0.50 (0.611) | 0.12 (0.945) | 1.86 (0.150) |
| graz × nut (1) | 0.05 (0.833) | 0.57 (0.456) | 0.54 (0.467) |
| seas × graz × nutr (3) | 1.62 (0.214) | 0.31 (0.818) | 2.62 (0.061) |
| Evenness | 31 | 44 | 47 |
| season (3) | 18.12 (<0.001) | 21.28 (<0.001) | 9.11 (<0.001) |
| grazing (1) | 0.43 (0.515) | 18.31 (<0.001) | 3.87 (0.055) |
| nutrient (1) | 0.97 (0.331) | 0.16 (0.592) | 4.81 (0.033) |
| seas × graz (3) | 1.08 (0.352) | 0.91 (0.476) | 2.23 (0.097) |
| seas × nut (3) | 0.93 (0.405) | 0.68 (0.688) | 0.16 (0.924) |
| graz × nut (1) | 0.14 (0.707) | 1.41 (0.253) | 0.73 (0.396) |
| seas × graz × nutr (3) | 0.51 (0.607) | 1.06 (0.392) | 0.08 (0.970) |

## Discussion

Local conditions and interactions (seasonal setting, grazing and nutrient supply) significantly influenced periphyton diversity, but the effects of grazing and nutrients were variable between sites and seasons. Nutrient and grazing effects were clearly counteractive with opposing directions for each response variable (supporting hypothesis 1). Additionally, the main direction of both effects was reversed between richness and evenness. A reversal of grazer effects with contrasting nutrient enrichment (and vice versa) was not detected (refuting hypothesis 2).

The absence of a significant correlation between species richness and biomass shows that changes in $S_{1000}$ were not simply a consequence of changes in algal biomass. On the other hand, a negative correlation between biomass and evenness has consistently been observed (Drobner et al. 1998, Weiher and Keddy 1999, Hillebrand and Sommer 2000). It has been attributed to inherent characteristics of evenness indices related to the distribution of abundances on species (Drobner et al. 1998).

Both diversity measures showed significant variation between seasons and also between sites. The seasonal variation in diversity was not correlated between the three sites and the effects of the two manipulated factors neither showed synchronous variation. The variation in diversity was higher between seasons within a site than between sites. The differences between sites in productivity or in grazer composition did not consistently alter the response of diversity to the manipulations. Only the absence of nutrient effects in the highly eutrophic Lake Limmaren could obviously be related to the high nutrient availability. Similar results were found for the effects of nutrients and grazing on algal biovolume and nutrient content in these experiments (Hillebrand and Kahlert 2001). It was concluded earlier (Hillebrand and Kahlert 2001) that no single overriding factor controls the importance of grazing or nutrients in these aquatic ecosystems. Also the diversity of benthic algal assemblages and its response to grazing and fertilization was highly context- (site and season) specific.

The effects of grazing and nutrients counteracted each other, as predicted from the conceptual (Lubchenco 1978, Proulx and Mazumder 1998) and analytical models, describing bivariate unimodal responses of diversity to both resource richness and disturbance levels (Huston 1979, 1994, Kondoh 2001). However, the main trends of both effects diverged for richness and evenness, and in spite of the counteraction, no significant interaction terms between grazing and nutrients were observed (Table 3).

The evenness of the periphyton assemblages was mainly increased by grazing (Limmaren and partly Väddö) and – in a less consistent manner – negatively affected by nutrients (Väddö). This pattern is consistent with the observed changes in the community composition (Fig. 1, Table 2). Nutrient enrichment significantly increased total periphyton biomass in Erken and Väddö (Hillebrand and Kahlert 2001) and affected also the growth type biovolume at both sites (Table 2). The growth types favored by fertilization in Lake Erken, monofilaments and motile diatoms, were also those significantly removed by grazing. For coastal periphyton, Hillebrand et al. 2000 found a similar strong correlation between the responsiveness of a species to nutrient enrichment and to grazing, respectively. In Lake Limmaren, which was the most productive site, grazing had strong positive effects on evenness by reducing monofilaments and attached single cells, which were the dominant growth forms already under ambient nutrient concentrations. At Väddö, again the largely dominating filamentous growth forms were reduced by grazing, but here the very subdominant colonial forms increased with fertilization. Thus, across all sites grazing affected mainly the most dominant growth forms, and in Lake Erken grazing directly counteracted the nutrient-related changes. These counteracting effects of grazing and nutrients on species composition and evenness are well in line with observations on plant diversity in both terrestrial and aquatic ecosystems (Lubchenco 1978, Collins et al. 1998, Proulx and Mazumder 1998, Worm et al. 1999, Hillebrand et al. 2000). They also reflect the predicted impact of growth form on the performance of periphytic algae (Steinman et al. 1992, Hillebrand et al. 2000).

However, the results of this study were not only characterized by a high variability between seasons and sites. Moreover, no significant grazer × nutrient interactions on evenness were found, and in contrast to predictions (Proulx and Mazumder 1998) the direction of grazer effects on evenness was not reversed by nutrient enrichment. This led to the refutement of the hypothesis of interdependent reversal of nutrient and grazer effects. However, all sites in this study had rather high total nutrient concentrations and none could be classified as oligotrophic. In a recent contribution, Worm et al. (2002) increased the range of sites for this analysis from very nutrient-poor to highly nutrient-rich. With this extended dataset, grazing effects on prey diversity switched from negative in oligotrophic to positive in eutrophic habitats. A reversed switch (positive with grazing and negative without grazing) was observed for nutrient enrichment effects on algal diversity at these sites. Thus, in a wider prespective the data presented here fit into the context of increasing competitive dominance of few species with fertilization and the counteractive action of mortality events (Huston 1979, Kondoh 2001). At a finer resolution variability in effects was observed, which points at complicating aspects regarding the effects of grazing and nutrient availability on diversity, such as the strong seasonal variation in evenness and in grazer effect strength (see Hillebrand and Kahlert 2001 for a further discussion of variability on biomass-related effects).

Conversely, effects of grazing and enrichment on $S_{1000}$ did not follow the pattern expected from conceptual models (Proulx and Mazumder 1998). Taking into account the medium to low overall abundances of grazers in our experiments (compared to grazer densities reported elsewhere, see Feminella and Hawkins 1995), an increase in species richness could be expected from hypotheses related to the intermediate disturbance hypothesis (Sommer 1999, Abrams 2001). In my experiments, the grazer effects on $S_{1000}$ were negative throughout and no grazer × nutrient interactions were found. Also regarding the prediction that nutrients reduce species richness via accelerated competitive exclusion was not met in my experiments. Nutrients had positive effects on $S_{1000}$ in Lake Erken and mostly positive effects at Väddö, revealing another difference between species number and evenness.

The impacts of grazing and fertilization on richness may reflect special features of periphyton assemblages. Steinman (1996) reviewed freshwater grazing experiments and found reduced species richness with grazing reported in 50% of all studies, whereas the others reported no or positive effects of grazing. Positive or neutral effects of nutrients on algal species richness were found in other ecosystems (Pringle 1990, Hillebrand and Sommer 2000).

Monofilaments were most consistently reduced by grazing, showing a preference of grazers for the dominant growth form. However, most grazers of periphyton do not actively select their prey but remove certain life forms due to their mouthpart morphology (Nicotri 1977, Steinman 1996). Due to high ability of periphytic algae to attach to each other (Steinman 1996), the mechanics of grazing leads to increased mortality in dominant growth forms (filaments), but also in associated species (e.g. epiphytes). Thus, there will be a co-consumption of inferior species due to the large grazer-prey size ratio between grazers and periphyton. This co-consumption is exemplified by the significant decrease of single attached species with grazing in both Lake Limmaren and Lake Erken.

The importance of co-consumption has previously been described for macrophyte-grazer-epiphyte interactions (Wahl et al. 1997, Karez et al. 2000) and carnivore-prey interactions (Wahl et al. 1997). Wahl et al. (1997) described the combined consumption as shared doom. While in their study the mortality of a basibiont was increased by the presence of an epibiont attractive to the consumer, in the present study the consumption of the basibiont increases the mortality risk of attached life-forms. Steinman (1996) proposed that the co-consumptive effect of grazer presence are important in periphyton since diversity of periphytic assemblages is generally high, including many rare species and increasing the probability of local extinction. Even though I reduced the number of rare species in my analysis by using $S_{1000}$ instead of raw species richness, most species contributed less than 1% of the total biovolume. It was these species which made the difference between the richness in grazed and ungrazed treatments. Moreover, grazing reduces the three-dimensional structure of periphyton, converting the assemblage into a simpler state (Poff and Ward 1995). This may reduce colonization by epiphytes and thus also species richness. Therefore, grazing had opposite effects on the two aspects of diversity analyzed here, evenness and richness.

Also for the positive effects of nutrients on periphytic species richness, the explanation may be found in the community structure of the periphyton. Increased nutrients are predicted to reduce species richness if the competitive exclusion is accelerated, but the continuous supply of propagules in natural systems may prevent local exclusion (McIntire and Overton 1971, Hillebrand and Sommer 2000). Species richness was therefore found to be less responsive to nutrient enrichment than diversity indices and evenness (Hillebrand and Sommer 2000). Instead, fertilization may even positively affect algal species richness, since nutrient enrichment favors erect growing species, which add structure and thus colonization area to the assemblage, allowing more species to settle (see above). In accordance with these thoughts, the biomass of filamentous algae and attached single cells increased with increased nutrient supply in Lake Erken.

In conclusion, grazers and enrichment had strong and contrasting effects on algal diversity, but the effects were not reversed under manipulations of the respective other factor. The contrasting effects of grazers and nutrients on evenness reflected the changes in community composition and followed predictions from conceptual models. Whereas evenness was a suitable measure of community composition (Smith and Wilson 1996, Hillebrand and Sommer 2000), species richness was more prone to the peculiar characteristics of the assemblage under study.

Despite the variability in effects, a strong control of algal diversity by local interactions (grazing and nutrient competition) and local abiotic conditions (reflected by sites and seasons) could be detected. For higher plants, the importance of local interactions has been critically discussed by promoting the importance of dispersal and regional processes (Pärtel et al. 1996, Zobel 1997, Godfray and Lawton 2001). Clearly, processes on different spatial and temporal scales will act in combination to determine local species richness, but the importance of these different scales is rarely investigated simultaneously (Hillebrand and Blenckner 2002). In a series of experimental and model analyses, Shurin et al. (2000, Shurin 2001, Shurin and Allen 2001) found that both regional and local interactions were important determinants of zooplankton diversity. Strong local interactions structured the diversity of the zooplankton assemblage, even though a strong connection between regional species pools and local diversity was present (Shurin et al. 2000). For small organisms such as unicellular algae or protists, a high dispersal chance is proposed due to their high abundances and high transportability (Finlay et al. 1996, Fenchel et al. 1997, Hillebrand et al. 2001). The emerging hypothesis is that the importance of local interactions for diversity is related to the dispersal ability (and thus proximately to variables such as body size). To my knowledge, there is no experimental test of this hypothesis, but results presented for periphyton (this study) and for other microbial communities (Finlay et al. 1996) are in agreement with these thoughts.

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