

## Spatial variation of grazer effects on epilithic meiofauna and algae

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**Abstract.** Periphyton is a key component of shallow littoral zones of lakes and streams because it is an important source of primary production and a food resource for herbivores. Meiofauna are abundant in periphyton, but macroinvertebrate grazer (macrograzers) effects on periphytic meiofauna have not been studied so far. We used a spatially structured field experiment (hierarchical nested design consisting of 3 subsites at each of 3 sites) in Lake Erken (Sweden) to investigate the effect of macrograzers on epilithic meiofauna and algae in periphyton by controlling macrograzer access to littoral periphyton communities. Overall, we found a strong negative effect of macrograzer presence on algal biomass and some evidence for negative macrograzer effects on meiofaunal abundance and community composition. The impact of macrograzers on both algae and meiofauna were highly variable between sites and subsites. The largest spatial differences were for macrograzer effects on meiofaunal abundance and composition. We also investigated the ability of macrograzers to reduce spatial heterogeneity of periphyton biomass, but the presence of macrograzers did not alter the variation in algal biomass and associated meiofauna among replicates. We conclude that strong local variability in algal biomass and meiofauna abundance exists between neighboring sites even in the presence of strong overall macrograzer effects. This local variability could be based on factors known to cause spatial heterogeneity, such as hydrodynamics, nutrients, substrate characteristics (size, texture, exposure), or biotic interactions.

**Key words:** algal biomass, herbivory, indirect effects, macroinvertebrates, meiofauna, nematodes, periphyton, spatial heterogeneity.

Periphyton is a complex community of bacteria, fungi, algae, protozoa, and meiofauna and other organic and inorganic components that covers all kinds of aquatic substrates (*sensu* Wetzel 2001). Periphyton communities are ubiquitous, but the biomass and composition of benthic algal assemblages on hard substrates can vary substantially over spatial scales from millimeters to kilometers (Harrison and Hildrew 1998, 2001, Kahlert et al. 2002). Spatial heterogeneity of periphyton biomass and species composition is driven by a number of single factors affecting periphyton, e.g., hydrodynamics, light re-

gime, nutrient concentrations (Cattaneo 1990, Feminella and Hawkins 1995, Stevenson 1997, Ledger and Hildrew 1998, Kahlert et al. 2002), and grazing (Gelwick and Matthews 1997, Nisbet et al. 1997, Harrison and Hildrew 1998, 2001, Sommer 1999, Kawata et al. 2001), which, in turn, are often highly variable in space. The spatial variation in periphyton communities also may be affected by the interaction of factors (e.g., nutrients vs grazing; Hillebrand 2003) or multiple resource limitations on the periphyton (e.g., light and nutrients; Rosemond et al. 2000).

Consumer–resource interactions between macroinvertebrates and periphyton have been studied intensively, especially in the past 2 decades (Nicotri 1977, Lamberti and Resh 1983, McCormick and Stevenson 1989, Cattaneo and Mousseau 1995, Feminella and Hawkins 1995, Steinman 1996, Hillebrand 2002), with

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a broad consensus that grazing by macroinvertebrate herbivores (macrograzers; e.g., gastropods, insect larvae, crustaceans) leads to a reduction of periphyton biomass and changes in composition and physiognomy. Herbivory can be affected by a variety of factors leading to spatially heterogeneous impacts on the periphyton. If macrograzer community composition is spatially homogeneous, changes in the impact of grazing can be caused by predator-induced behavioral changes (Power 1992, Turner et al. 2000) or differences in physical conditions (e.g., flow velocity; DeNicola and McIntire 1991). If the macrograzer community composition is spatially variable, spatial heterogeneity of grazing effects can be a consequence of differences in grazing efficiency determined by feeding modes of single grazer species (Steinman 1996).

Periphyton also serves as habitat for many meiobenthic taxa, some of which inhabit periphyton in high abundances (nematodes and rotifers) and moderate to high species diversity (nematodes; Meschkat 1934, Pieczynska 1964, Traunspurger 1992, Peters and Traunspurger 2005). Surprisingly little information about periphytic meiofauna is available, and interactions between benthic macroconsumers and meiofauna in freshwater ecosystems (i.e., meiofauna as prey for macroinvertebrates) have been insufficiently investigated (summarized in Schmid and Schmid-Araya 2002). The few freshwater studies on predator-prey relationships involving meiofaunal taxa show that meiofauna are subject to macroinvertebrate (Hildrew et al. 1985, Feminella and Stewart 1986, Sephton 1987, Tokeshi 1991, Lancaster and Robertson 1995, Beier et al. 2004) or fish predation (Adamicka 1991, Rundle and Hildrew 1992), and that fish can have strong effects on meiofaunal abundance (Hakenkamp and Palmer 2000).

Detailed analyses of effects of macrograzers on meiofaunal organisms or on whole meiofaunal communities in the periphyton are lacking. However, a preliminary study of the effects of macrograzers on different components of the periphyton provides an indication of the capacity of macrograzers to influence epilithic meiofaunal abundance (Hillebrand et al. 2002). In addition, studies on epilithic meiofauna in freshwater and marine systems show that meiofaunal abundance is closely connected to epilithic algal biomass and total organic matter content (Hall and Bell 1988, Peters and Traunspurger 2005, Peters et al. 2005). Therefore, we predict that macrograzers will influence meiofaunal abundance and community composition directly by consumption or indirectly by altering periphyton size and structure.

We present results of an experiment on macrograzer-periphyton interactions that analyzed the

spatial distribution of macrograzer effects on epilithic meiofauna and algae in the littoral zone of Lake Erken, Sweden. We manipulated macrograzer access to periphyton and associated meiofauna in a hierarchical nested spatial design focusing on mesoscale variation (i.e., variation of effects within a single ecosystem). We addressed 3 basic questions in this experiment: 1) Do macrograzers affect meiofaunal abundance and community structure in the periphyton? 2) Are grazing impacts variable in space? 3) Does grazing affect food resource variability?

## Methods

### Study site

Lake Erken (lat 59°50'N, long 18°35'E) covers an area of 23.7 km<sup>2</sup> within a catchment area of 141 km<sup>2</sup>. Mean depth is 9.0 m, pH is ~8.0, and mean conductivity is 280 µS/cm. The lake is mesotrophic to eutrophic, with a mean total P concentration of 27.0 µg/L and a mean total N concentration of 657 µg/L. The littoral zone of the lake is characterized by cobblestones of different sizes, inhabited by a rich grazer fauna dominated by gastropods (especially *Theodoxus fluviatilis*, *Bithynia tentaculata*, and *Viviparus viviparus*) and trichopteran larvae, with additional important contributions by isopods (*Asellus aquaticus*) and ephemeropteran larvae (Hillebrand and Kahlert 2001).

### Experimental setup

We manipulated grazer access to the periphyton in an experiment with a hierarchical nested spatial design. A nested design is recommended for examination of spatial variation in ecological processes (Cooper et al. 1997). We focused on spatial scales of meters and kilometers and avoided small-scale heterogeneity by using unglazed ceramic tiles (4.7 × 4.7 cm) as substrates. We chose 3 sites (kilometer scale, designated according to their geographic position NW, NE, and SE) that were separated by 3.2 km (NW-NE), 3.9 km (NW-SE), and 2.5 km (NE-SE) (Fig. 1A). Site SE was examined in a previous study on grazing effects on periphyton in Lake Erken (Hillebrand and Kahlert 2001). The sites represent a range of wind exposure, with site NE being the least exposed and site SE being highly exposed to the predominantly westerly winds. Within each site, we chose 3 subsites (meter scale) 10 m apart at the same water depth (70–90 cm). We placed a set of 3 experimental units (blocks = replicates) in each subsite.

Each experimental unit consisted of a concrete plate (40 × 40 cm) with 1 replicate of each of 3 different treatments: 2 caged treatments and 1 uncaged treat-

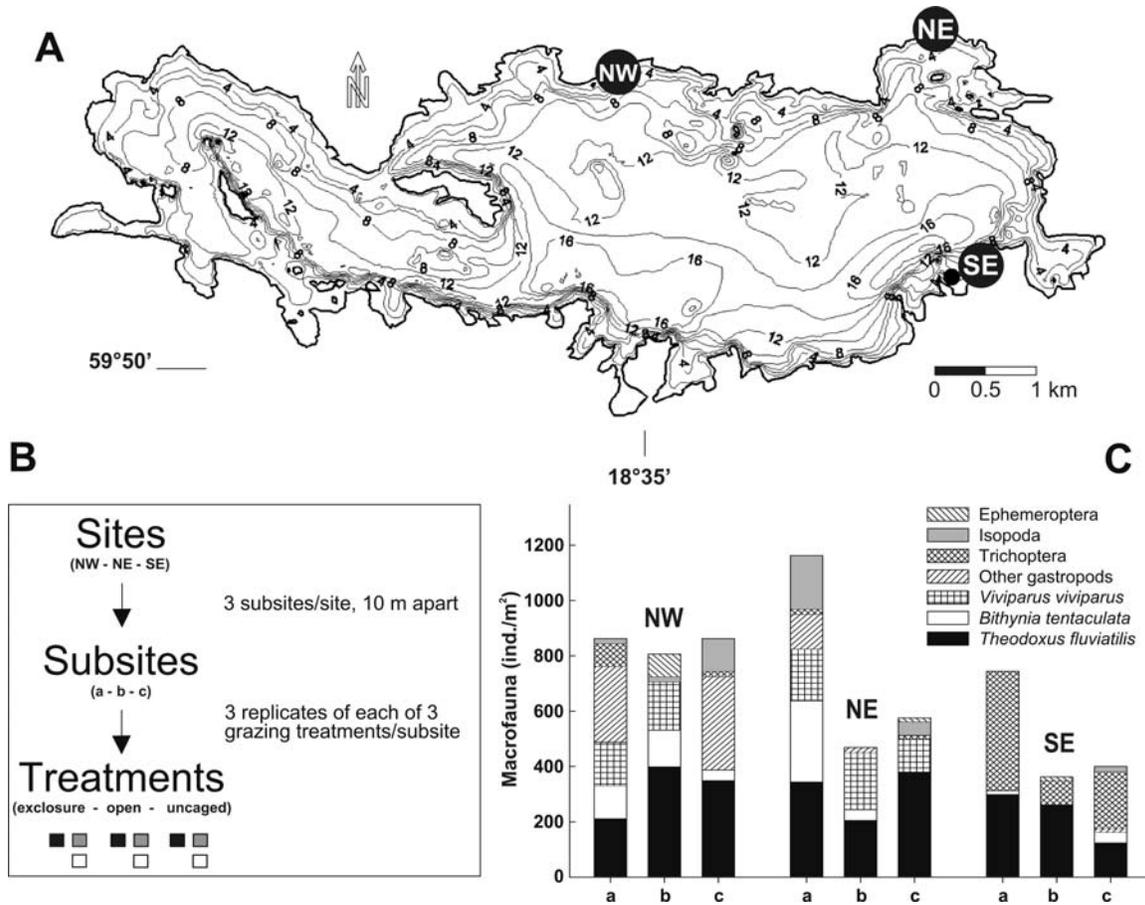


FIG. 1. A.—Lake Erken with depth structure and experimental sites (NW, NE, SE). B.—Experimental design: at each site, 3 subsites (a, b, c) were randomly chosen. Each subsite had 3 replicates of 3 grazing treatments (exclosure, open cages, uncaged). C.—Macrograzer faunal composition at each subsite.

ment. Cages were 15 × 15 × 15 cm and were made of metal frames and a tightly adhered 1-mm screen (Hillebrand and Kahlert 2001). Exclosure cages (excl) were fully enclosed, open cages (open) had 2 adjacent sides cut out to allow grazer access, and uncaged treatments (con) were controls for cage artifacts. We equipped each treatment on each concrete plate with 1 ceramic tile (resulting in 3 tiles/concrete plate) that had been pre-incubated in the lake at one site for 6 mo (December 2000–June 2001) and was overgrown by periphyton at the start of the experiment. Thus, the complete experiment consisted of 3 sites × 3 subsites × 3 blocks (replicates) × 3 treatments = 81 samples (Fig. 1B).

We started the experiment on 18 June 2001 when tiles were glued to the concrete plates and screens were placed on top of the metal frames. The top screens were removable so that they could be replaced to prevent shading caused by algal colonization of the screens. During the experiment, we exchanged and cleaned the screens weekly until we sampled the

concrete plates on 16 July 2001. We considered the 4-wk duration of the experiment long enough to permit detection of grazing effects (Feminella and Hawkins 1995, Hillebrand and Kahlert 2001, Hillebrand et al. 2002), but short enough that the periphyton communities would retain sufficient meiofauna for analysis of abundance and community composition.

*Sampling and analyses*

We analyzed macrograzer density and composition on the concrete plates (1600 cm<sup>2</sup>) once at each subsite. On 9 July 2001, we carefully removed one concrete plate from each subsite and picked all macroscopically visible organisms (>1 mm) from the upper side of the plate. Plates were then carefully put back on the lake bottom, avoiding disturbance of the experimental tiles. We fixed the macrograzers in 70% ethanol, and counted and identified them to species (gastropods) or order (crustaceans, insects).

On 16 July 2001, we removed the tiles from each

concrete plate and immediately placed the tiles in plastic bags with filtered lake water. We transferred the plastic bags to the laboratory, where we stored them at 4°C in the dark until all processing was completed (<4 h). We carefully removed all epilithic material from the tiles with water and razor blades. We separated algal conglomerates with scissors and forceps to attain suspensions that were as homogenous as possible. We adjusted the suspensions to a defined volume (100–150 mL) and subsampled them by stirring and sampling with a 5-mL pipette. We filtered 1 aliquot (10–20 mL) onto glass-fiber filters (Whatman GF/C, 25-mm diameter; Whatman, Maidstone, UK) for the analysis of chlorophyll *a* (Chl *a*). We stored all filtered samples at –18°C until analyzed. We extracted Chl *a* with acetone (90%) at 4°C in the dark for 24 h. We measured Chl *a* concentrations spectrophotometrically and used pheophytin-uncorrected values to calculate Chl *a* concentrations (Stich and Brinker 2005). We sieved the remainder of each sample (80–140 mL) through a 30- $\mu$ m-mesh net. We fixed all organisms retained on the net with formaldehyde (4% final concentration) and stained them with rose Bengal. We counted all meiofaunal organisms at 40 $\times$  using a stereomicroscope and classified them into major taxonomic groups (nematodes, rotifers, crustaceans [harpacticoid, cyclopoid, and calanoid copepods, copepod nauplii, and ostracods], and others [oligochaetes and tardigrades]).

#### Statistical design

We assessed the effect of grazer presence on algal biomass (as Chl *a*) and meiofaunal abundance with a mixed-model nested analysis of variance (ANOVA) design (Cooper et al. 1997, Underwood 1997). We contrasted grazer treatments (excl, open, con) and sites (NE, NW, SE), and nested subsites (a, b, c) within sites. Subsites were used as random factors, whereas grazing and site were considered fixed.  $\text{Log}_e(x)$  transformation of the dependent variables resulted in homogeneous variances. We used Tukey's Honestly Significant Difference (HSD) test for post hoc comparison of grazer treatments, sites, and subsites. We used Spearman rank correlations on subsite data ( $n = 9$ ) for analyses of correlations between algal biomass and meiofaunal abundance.

We investigated the effect of grazer presence on the variability of algal biomass by calculating coefficients of variation (CV). CV is not a spatially explicit measure of variability; it describes variation around the mean using all replicates of one treatment combination. However, we regard CV as a suitable measure of variability in our study because we focused on mesoscale variability (within-ecosystem variability).

At the centimeter scale, we calculated the CV for the 3 replicates of each treatment at each subsite. At the meter scale, we calculated the CV for the 3 subsite means for each treatment at each site. At the kilometer scale, we calculated the CV for the 3 site means for each treatment. Thus, the CVs followed a nested hierarchy and relied on 3 replicates at each scale. We used a 2-factor ANOVA on CV with scale (cm, m, km) and grazing (excl, open, con) as independent factors to test whether variability between replicates was affected by distance or grazer access. Untransformed data were homoscedastic. We did all ANOVAs and correlations using Statistica software (version 6; StatSoft, Tulsa, Oklahoma).

We used nonmetric multidimensional scaling (NMDS) to analyze the effects of grazing on meiofaunal group composition and spatial differences in group composition. The Bray–Curtis coefficient *S* was used to compute similarities based on absolute group abundance/cm<sup>2</sup>. *S* ranges from 100% for 2 samples that are completely similar to 0% for 2 samples that have no species in common. *S* has the advantage of not being influenced by joint absences of species in 2 samples, a circumstance under which many other coefficients fail (Clarke and Green 1988). We transformed meiofaunal abundance data ( $\sqrt{x}$ ) before calculating Bray–Curtis similarities (Clarke 1993). Distances in NMDS ordination plots are relative because they are based on rank abundances in samples. The relative dissimilarity between samples is reflected in the relative distances in the plot. Therefore, NMDS plots can be arbitrarily rotated and scaled and do not possess defined axes. The larger the distance between 2 points (samples) in an NMDS plot, the lower the similarity between the 2 samples and vice versa. If samples are clustered and clusters are separated in an NMDS plot, then the differences in community structures among clusters are larger than the differences among samples within each cluster. The quality or reliability of a 2-dimensional NMDS plot is indicated by the stress value, which gives good or excellent representation of the similarities between samples when <0.1 or <0.05, respectively (Clarke 1993).

We used a 2-way analysis of similarities (ANOSIM) test for differences in meiofaunal group composition between subsites (a, b, c) and treatments (excl, open, con). We used 1-way ANOSIM to test for differences in meiofaunal group composition between sites (NW, NE, and SE). The ANOSIM procedure compares the ranked similarities for differences within and between groups. The resulting *R*-value usually lies between 0 and 1, but can lie within a range of –1 to +1. A large *R*-value indicates separation of the groups, and small values close to 0 imply little or no separation (Clarke and Warwick 2001). Negative *R*-values  $\ll 0$  can occur

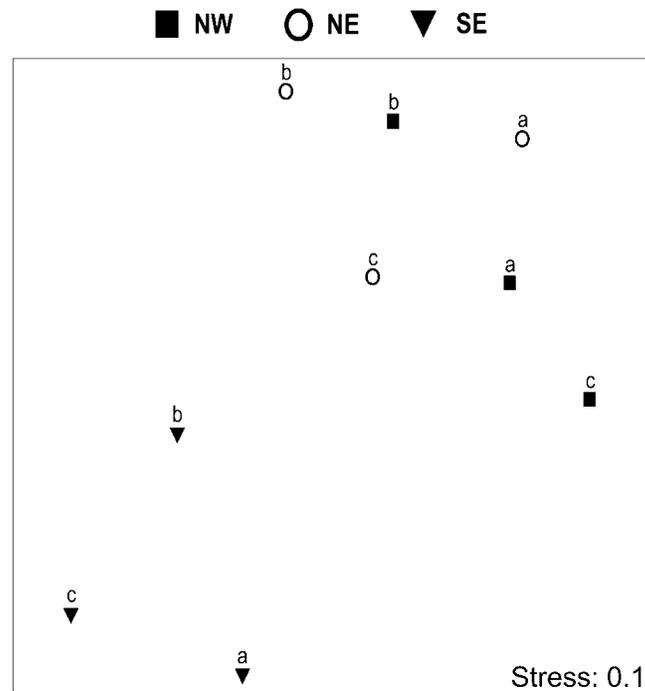


FIG. 2. Nonmetric multidimensional scaling (NMDS) plot of macrofaunal composition at 3 sites (NW, NE, SE) and 3 subsites (a, b, c) in Lake Erken. NMDS calculations are based on Bray–Curtis similarity with untransformed abundance (ind./m<sup>2</sup>) data.

when a community is species-poor or when the individuals have a strongly clustered spatial or temporal distribution, so that replicates are very variable, but each sample has similar amounts of variability among replicates (Chapman and Underwood 1999). In contrast to standard Z-type statistics,  $R$  has an absolute interpretation of its value that is potentially more meaningful than its statistical significance. As with standard tests,  $R$  can be significantly different from 0 with a difference too small to be important if there are enough replicates. A global  $R$  exists for the analyses based on the ANOVA result and for pairwise comparisons based on multiple post hoc tests. We considered  $R$ -values  $>0.5$  indicative of pronounced differences between groups. We analyzed differences in the macrograzer community between sites using a 1-way ANOSIM with one randomly chosen concrete plate per subsite as replicate ( $n = 9$ ). These analyses were carried out using the PRIMER software package (version 6; PRIMER-E, Plymouth, UK).

## Results

### Macrograzer fauna

The survey of macrograzer composition revealed no differences in total abundances (1-way ANOVA:  $MS = 91,458.0$ ,  $F_{2,6} = 1.48$ ,  $p = 0.3$ ; Fig. 1C), but perceivable

differences in the proportion of major groups between sites (Figs 1C, 2). The 1-way ANOSIM resulted in significant overall differences in the macrograzer community between sites (global  $R = 0.498$ ,  $p < 0.05$ ), with site SE tending to have a different macroinvertebrate composition from sites NW ( $R = 1.0$ ,  $p = 0.1$ ) and NE ( $R = 0.852$ ,  $p = 0.1$ ); no differences were found between sites NW and NE ( $R = -0.333$ ,  $p = 0.9$ ) (Fig. 2). The most abundant macrograzers were the gastropod species *T. fluviatilis*, *B. tentaculata*, and *V. viviparus*, and mayfly and caddisfly larvae (Fig. 1C). Trichopteran larvae were important only at site SE, whereas the communities at other sites were largely dominated by gastropods. *Theodoxus fluviatilis* were evenly abundant at all subsites, whereas *V. viviparus* and *B. tentaculata* were differentially distributed among sites and subsites.

### Algal biomass and meiofaunal abundance

A comparison between open cages and uncaged control plots showed that algal biomass (ANOVA:  $MS = 0.46$ ,  $F_{1,50} = 0.54$ ,  $p = 0.47$ ) and meiofaunal abundance (ANOVA:  $MS = 1.23$ ,  $F_{1,50} = 0.79$ ,  $p = 0.38$ ) did not differ between the 2 grazing treatments. Thus, no cage artifacts were found, and both open cages and uncaged treatments were included in the remaining analyses. Algal biomass differed among sites, with significant differences between sites NE and NW ( $p <$

TABLE 1. Three-factor nested analysis of variance (ANOVA) on  $\log_e(x)$ -transformed algal biomass (as chlorophyll *a*) and meiofaunal abundance. Independent factors were grazing (open and enclosure cages and uncaged controls) and sites (NE, NW, SE), with subsites (a, b, c) nested within sites in Lake Erken. A mixed-model ANOVA with fixed (f) and random (r) factors was used.

Effects	Chlorophyll <i>a</i>				Meiofaunal abundance			
	df	MS	<i>F</i>	<i>p</i>	df	MS	<i>F</i>	<i>p</i>
Grazing (f)	2	11.96	15.00	<0.001	2	1.60	1.66	0.230
Site (f)	2	4.81	6.19	0.034	2	14.86	5.69	0.041
Subsite (site) (r)	6	0.78	0.97	0.483	6	2.63	2.71	0.067
Grazing × site (f)	4	1.91	2.39	0.108	4	2.41	2.50	0.098
Grazing × subsite (r)	12	0.80	1.64	0.110	12	0.97	2.21	0.025
Error	51	0.49			51	0.44		

0.01) and sites NE and SE ( $p < 0.001$ ), and no difference between sites SE and NW ( $p = 0.96$ ; Table 1, Fig. 3). Grazing had a significant negative effect on algal biomass (Table 1), with significant differences between enclosures and open cages (Tukey's HSD,  $p < 0.001$ ) and enclosures and uncaged controls ( $p < 0.001$ ). No interaction between grazer presence and spatial scale was found for algal biomass (Table 1), although grazing was especially prominent at site NW, where algal biomass was largely removed from the

tiles (Fig. 3). At sites NE and SE, the effect of grazing on algal biomass differed among subsites.

Meiofaunal abundance was highly variable and differed among all sites ( $p < 0.01$ ), but differed between subsites only at site SE ( $p < 0.01$ ; Table 1, Fig. 4). Grazing had no overall effect on meiofaunal abundance (Table 1), but affected meiofaunal abundance at subsites a and b at site NW, based on significant differences between enclosures and open cages (Tukey's HSD,  $p < 0.001$ ) and between enclo-

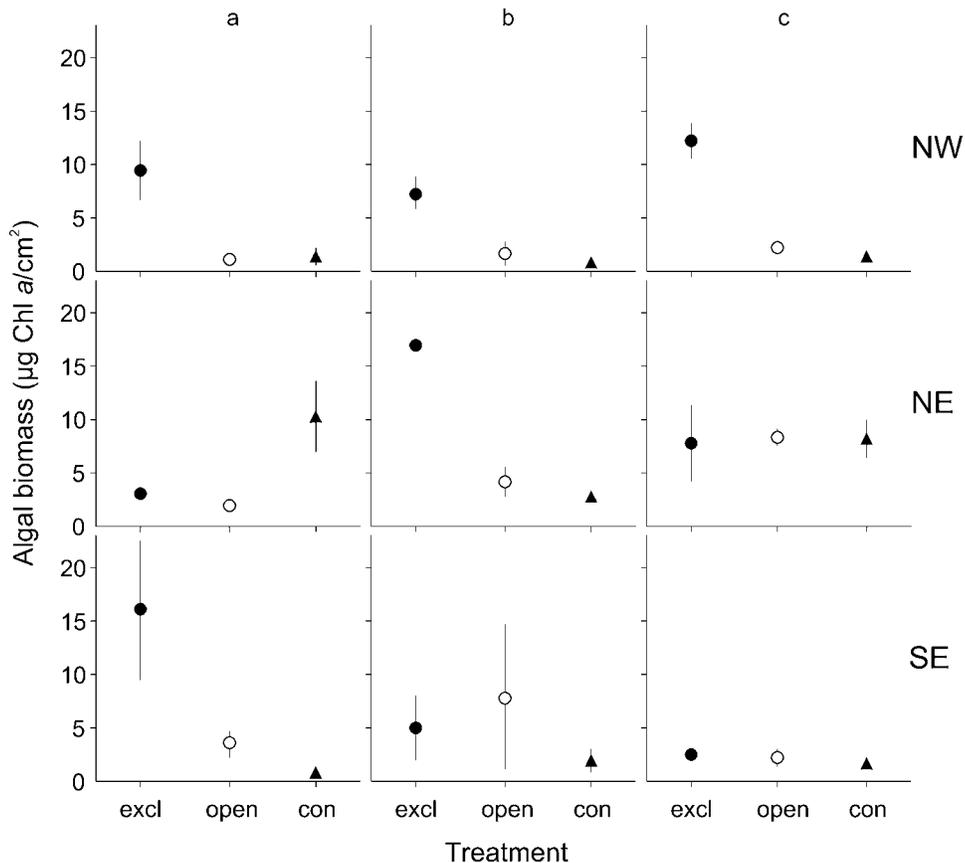


FIG. 3. Mean ( $\pm 1$  SE) algal biomass ( $\mu\text{g}$  chlorophyll *a* [Chl *a*]/ $\text{cm}^2$ ) in 3 grazing treatments (enclosures [excl], open cages [open], and uncaged controls [con]) at 3 subsites (a, b, c) within 3 sites (NW, NE, SE) in Lake Erken.

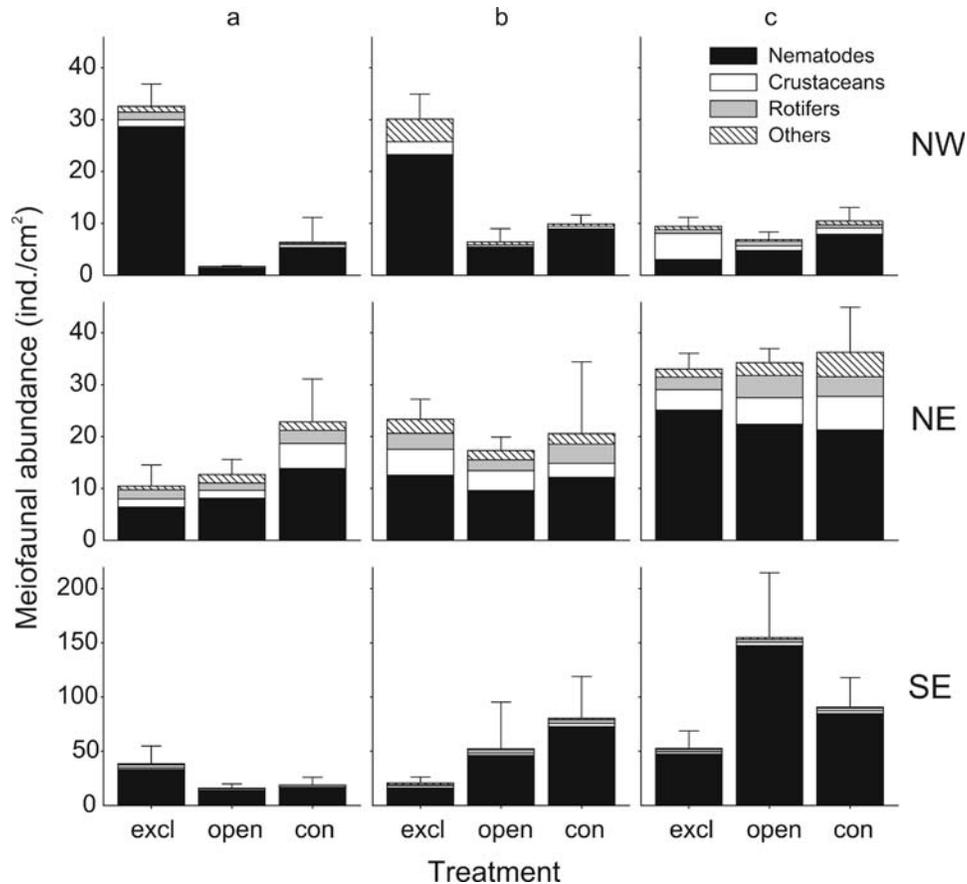


FIG. 4. Cumulative mean ( $\pm 1$  SE) meiofaunal abundance (ind./cm<sup>2</sup>) and abundance of each taxonomic group in 3 grazing treatments (exlosures [excl], open cages [open], and uncaged controls [con]) at 3 subsites (a, b, c) within 3 sites (NW, NE, SE) in Lake Erken.

exlosures and uncaged controls ( $p < 0.05$ ; Fig. 4). At sites NE and SE, grazing had no effect on meiofaunal abundance. Grazing effects on meiofaunal abundance varied on both spatial scales (Fig. 4), and interactions of grazing effects with subsite were significant. The interaction of grazer effects with site was not significant (Table 1).

We found a strong relationship between meiofaunal abundance and algal biomass at 4 subsites (Spearman rank correlation, NW, a:  $R = 0.85$ ,  $p < 0.01$ , b:  $R = 0.73$ ,  $p < 0.05$ ; NE, c:  $R = 0.75$ ,  $p < 0.05$ ; SE, b:  $R = 0.68$ ,  $p < 0.05$ ). Correlations at all other subsites were positive but not significant. At site NW (subsites a and b), the highest meiofaunal abundances were associated with the highest algal biomasses in the exlosures.

Neither distance (ANOVA,  $MS = 911.8$ ,  $F_{2,30} = 1.03$ ,  $p = 0.368$ ) nor grazing ( $MS = 76.1$ ,  $F_{2,30} = 0.09$ ,  $p = 0.917$ ) had an effect on the variability of algal biomass measured as CV (Fig. 5A), and neither distance ( $MS = 12.4$ ,  $F_{2,30} = 0.01$ ,  $p = 0.986$ ) nor grazing ( $MS = 478.3$ ,  $F_{2,30} = 0.51$ ,  $p = 0.605$ ) had an effect on the variability of meiofaunal abundance (Fig. 5B). The interaction

between the 2 factors was not significant for both algal biomass ( $MS = 253.0$ ,  $F_{4,30} = 0.29$ ,  $p = 0.884$ ) and meiofaunal abundance ( $MS = 1071.5$ ,  $F_{4,30} = 1.15$ ,  $p = 0.354$ ).

#### Grazing effects on meiofaunal group composition

The meiofaunal community was largely dominated by nematodes, especially at site SE (Fig. 4), where nematodes constituted  $86.6 \pm 8.0\%$  of the meiofauna. At sites NW and NE, nematodes constituted  $73.3 \pm 17.0\%$  and  $60.4 \pm 12.3\%$ , respectively, of all meiofauna (means across all subsites and treatments  $\pm$  SD; NW:  $n = 27$ , NE:  $n = 24$ ). At site NE, crustaceans ( $17.0 \pm 6.6\%$ ) and rotifers ( $13.3 \pm 7.0\%$ ) contributed considerably to the meiofauna, and at site NW, crustaceans ( $13.7 \pm 14.0\%$ ) were the 2<sup>nd</sup>-most frequent group because of their dominance in exlosures at subsite c.

NMDS ordination of samples for each of the 3 sites revealed that the largest differences in meiofaunal community composition were between subsites and treatments at site NW (Fig. 6A), and that some

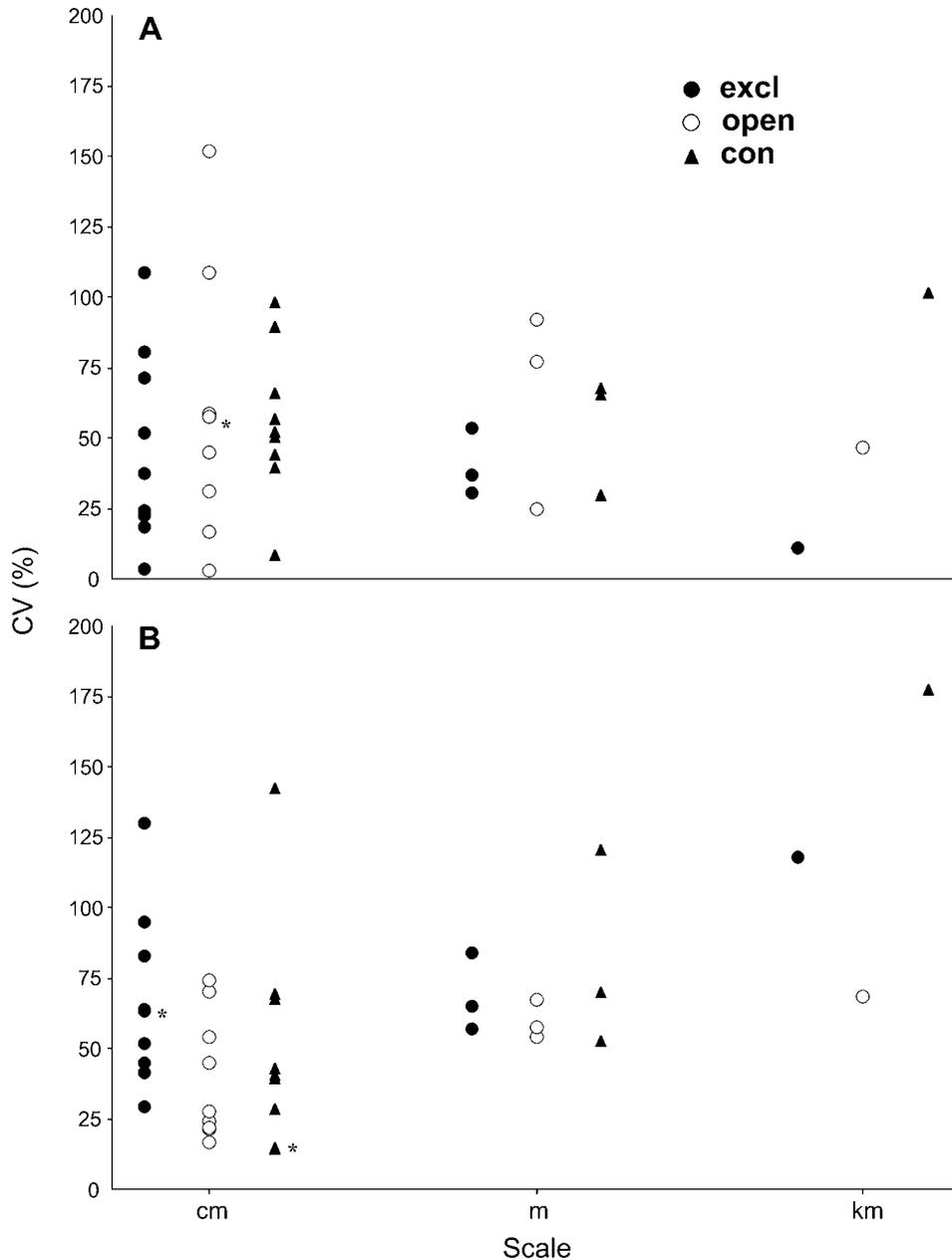
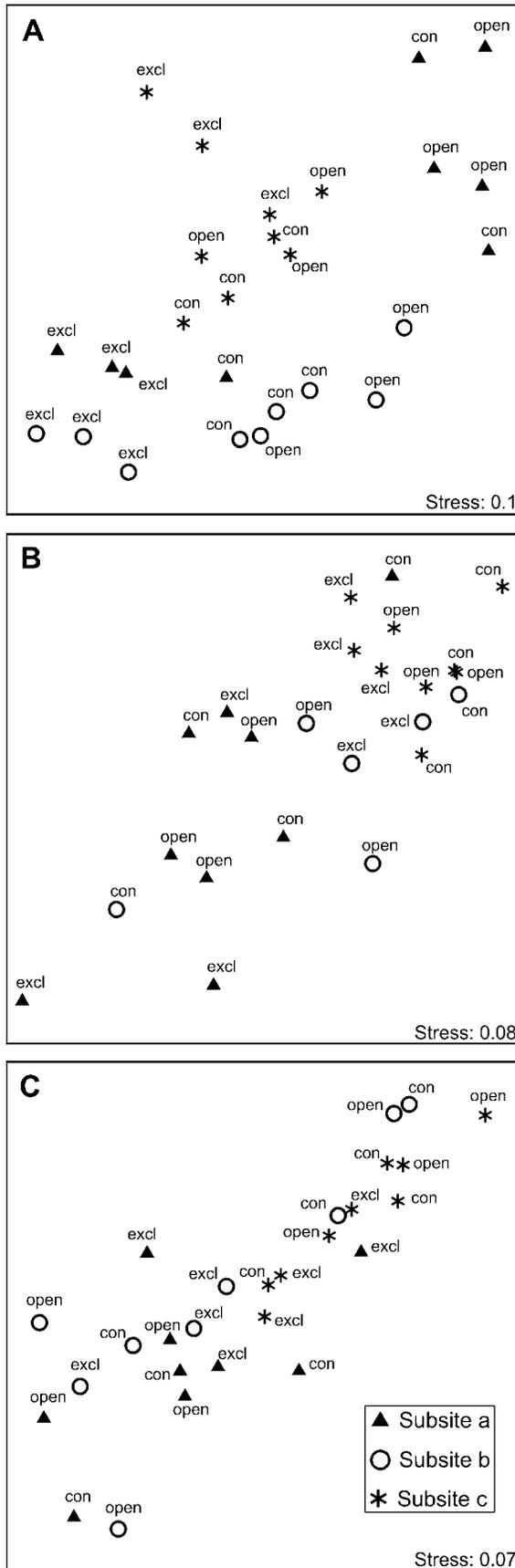


FIG. 5. Coefficients of variation (CVs) of algal biomass (A) and meiofaunal abundance (B) in 3 grazing treatments (exlosures [excl], open cages [open], and uncaged controls [con]) at 3 spatial scales (cm, m, km) in Lake Erken.  $n = 3$  for each CV for each treatment and at each spatial scale (see text for details). Overlapping points are marked with \*.

differences existed between subsites a and c at sites NE and SE (Fig. 6B, C). At site NW, replicates of grazed (uncaged control, open cages) and ungrazed (exclosure) treatments at each subsite clustered together with clearly observable distances between grazed and ungrazed treatments in the NMDS plot (Fig. 6A). These differences were most pronounced at the subsites a and b and showed a tendency to be different at subsite c. At sites NE and SE, no such patterns were

found, indicating little effect of macrograzers on meiofaunal community structure (Fig. 6B, C).

ANOSIM showed that grazing affected the meiofaunal community structure at site NW (global  $R = 0.578$ ,  $p = 0.001$ ), with pronounced differences in the community structure between uncaged controls and exclosures ( $R = 0.65$ ,  $p = 0.001$ ) and between exclosures and open cages ( $R = 0.79$ ,  $p = 0.001$ ) (Table 2). Meiofauna community composition did not differ



←

FIG. 6. Nonmetric multidimensional scaling (NMDS) plots of meiofaunal composition in 3 grazing treatments (exclosures [excl], open cages [open], and uncaged controls [con]) within each of 3 subsites (a, b, c) at the NW (A), NE (B), SE (C) sites in Lake Erken. NMDS calculations are based on Bray–Curtis similarity with  $\sqrt{x}$ -transformed abundance (ind./m<sup>2</sup>) data.

between uncaged controls and open cages, indicating no cage artifacts ( $R = 0.16$ ,  $p = 0.17$ ). At sites NE and SE, no differences in the meiofaunal community composition were found among treatments. Meiofaunal community structure differed between subsites at site NW (global  $R = 0.728$ ,  $p = 0.001$ ), but weak or no differences were found among subsites at sites NE (global  $R = 0.469$ ,  $p = 0.002$ ) and SE (global  $R = 0.182$ ,  $p = 0.08$ ; Table 2). Pairwise comparisons of subsites showed marked differences between all subsites at site NW and differences between subsites a and c ( $R = 0.64$ ,  $p = 0.004$ ) and between subsites b and c ( $R = 0.56$ ,  $p = 0.004$ ) at site NE.

### Discussion

We found generally strong negative effects of macrograzers on algal biomass, but no effect of macrograzers on meiofaunal abundance at the site scale and spatially variable effects at the subsite scale. We found significant differences in algal biomass and meiofaunal abundance among sites and significant interactions between the effects of grazing and spatial scale (subsite) on meiofauna (Table 1). Thus, despite the overall significant main effect of grazing on algal biomass, control of algal biomass by macrograzers varied spatially. Moreover, grazing did not reduce the variability of algal biomass and meiofaunal abundance.

#### *Grazing effects on algal biomass*

Numerous studies on grazer–periphyton interactions have generally shown top-down regulation of periphyton biomass by macrograzers (reviewed in Feminella and Hawkins 1995, Steinman 1996, Hillebrand 2002). Our findings in Lake Erken are consistent with these results and with the results of a previous grazing experiment on periphyton in Lake Erken (Hillebrand and Kahlert 2001). Negative overall effects of grazing on periphyton biomass were present in Lake Erken, but our data clearly pointed out that grazer–periphyton interactions can be spatially variable within a single ecosystem. Spatial differences in grazer effects can result from differences in the macrograzer composition among different parts of an

TABLE 2. Two-way analyses of similarity on Bray–Curtis similarities with  $\sqrt{x}$ -transformed meiofaunal abundance for 3 sites (NW, NE, SE) in Lake Erken. Factor groups were grazing (exclosures [excl], open cages [open], uncaged controls [con]) and subsites (a, b, c). The global  $R$  for each site and factor group and results of a pairwise comparison ( $R$ - and  $p$ -values) within each factor group (subsite averaged across all grazing groups and grazing averaged across all subsite groups) are shown. n.s. = not significant, \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ .

Subsites			Grazing		
Factor group	$R$	$p$	Factor group	$R$	$p$
NW			NW		
Global	0.728	***	Global	0.578	***
a × b	0.77	**	con × excl	0.65	***
b × c	0.96	***	con × open	0.16	n.s.
a × c	0.72	***	excl × open	0.79	***
NE			NE		
Global	0.469	**	Global	0.091	n.s.
a × b	0.25	n.s.	con × excl	0.19	n.s.
b × c	0.56	**	con × open	0.00	n.s.
a × c	0.64	**	excl × open	0.05	n.s.
SE			SE		
Global	0.182	n.s.	Global	-0.108	n.s.
a × b	-0.05	n.s.	con × excl	-0.07	n.s.
b × c	0.14	n.s.	con × open	-0.28	n.s.
a × c	0.46	*	excl × open	0.09	n.s.

ecosystem. These differences can, in turn, be influenced by environmental conditions to which organisms might have adapted. If macrograzer communities differ, then the effect of different grazer types (different mouthpart morphologies or grazing strategies) can lead to differences in the effects of grazing on periphyton biomass and physiognomic complexity (Steinman 1996). In systems with homogeneously distributed grazer abundances or similar grazer community compositions (e.g., our study), the outcome of grazing effects can vary because of factors influencing the efficiency or altering the behavior of macrograzers. For example, nonlethal predator effects alter herbivore behavior and activity and, thus, may reduce grazing pressure on periphyton (Power 1992, McCollum et al. 1998, Diehl et al. 2000, Turner et al. 2000, McIntosh et al. 2004). Physical disturbance, such as flow velocity in streams or wave action in lakes, can influence macrograzer efficiency and is a likely explanation for the kilometer-scale variability in grazing effects among sites in our study. DeNicola and McIntire (1991) examined grazer effects on periphyton in artificial stream channels and showed that stream gastropods reduce periphyton biomass more on sheltered substrates than on substrates exposed to high flow velocity. A similar mechanism also might explain the large differences in grazing effects among sites in Lake Erken. Macrograzers at the wind-exposed site SE might have been affected by more frequent and intense disturbances than grazers at the more sheltered sites NW and NE, resulting in less

intense grazing effects on algal biomass and meiofaunal abundance at site SE than at sites NW or NE.

#### *Effects of grazing on meiofauna*

Macrograzers had less effect on meiofaunal abundance and composition than on algal biomass. The effects of macrograzers on meiofauna also were spatially variable, indicating that other factors might be important regulators of meiofauna communities. Several factors might directly or indirectly influence the abundance and the composition of epilithic meiofauna communities. From the point of view of meiofauna, periphyton has 2 main functions: 1) periphyton is a habitat, and 2) some periphyton components, in particular algae (diatoms), bacteria, and detritus, are the basic food resources of non-predatory meiofauna. If grazing affects either of these functions, meiofauna will be affected by macrograzer activity.

The role of periphyton as a habitat for meiofauna (some authors have considered meiofauna to be part of the periphyton) has been little studied, but a few studies supply evidence for such a function. Peters and Traunspurger (2005) investigated epilithic meiofaunal abundance and community composition in a large number of different lake ecosystems (including Lake Erken) and showed that meiofauna are highly abundant and diverse in the periphyton. Peters and Traunspurger (2005) found a strong positive relationship between periphyton biomass (considered as an estimator of habitat size) and meiofaunal abundance

(Spearman rank correlations for data from Lake Erken at similar subsites to those in our study,  $n = 9$ ; meiofauna vs Chl *a*:  $r = 0.93$ ,  $p < 0.001$ , meiofauna vs organic matter:  $r = 0.80$ ,  $p < 0.01$ ), and they interpreted these results as indicating the importance of habitat size, in accordance with earlier studies (Nagle 1968, Hall and Bell 1988, Danovaro and Fraschetti 2002, Peters et al. 2005).

The role of periphyton as a food resource for meiofauna has not yet been investigated in detail, but studies dealing with meiofaunal grazing on microorganisms in soft sediments clearly indicate that meiofauna feed on microorganisms (diatoms, bacteria, protozoa) (Montagna 1995, Bott 1996, Bott and Borchardt 1999). Therefore, macrograzer-induced changes in the physiognomic complexity (Lowe and Hunter 1988), biomass, and composition of the periphyton (Hunter 1980, Lowe and Hunter 1988, Hillebrand et al. 2002, Hillebrand 2003) might indirectly affect the associated meiofauna. On the other hand, several benthic macrograzers (e.g., snails, certain mayflies species) are able to consume the complete periphyton community (Hunter 1980, Hunter and Russel-Hunter 1983, Barnese et al. 1990, Diaz Villanueva et al. 2004) and, thus, will directly influence meiofaunal density and composition. If such grazers ingest or remove most of the vertical strata of the periphyton, meiofaunal organisms also will be ingested or removed. Some of these grazer types (in particular snails) were most abundant at site NW, where grazing led to a marked reduction of algal biomass (habitat size reduction) and meiofaunal abundance and a change in the meiofaunal community structure. The large number of snails at subsites a and b of site NW might explain the large differences between grazed and ungrazed treatments at these subsites.

Other important factors, such as predation, certainly influence meiofaunal abundance and community structure. Predator-prey interactions have been scarcely studied in soft sediments and completely neglected on hard substrates. Thus, it is unclear whether certain macroinvertebrate species prey upon epilithic meiofauna. We cannot completely exclude possible effects of very small predators (e.g., tanypod chironomids, small crustaceans, or leeches) in our experiment, but we are able to exclude the effects of large macroinvertebrate predators known to prey upon sediment meiofauna (Coull 1990, Lancaster and Robertson 1995, Schmid and Schmid-Araya 2002, Beier et al. 2004). Our results suggest that macrograzers affected periphytic meiofauna, but this effect seems to be highly variable on different spatial scales. The factors causing the spatial variability of macrograzer effects

on algal biomass (see *Grazing effects on algal biomass*) probably will also influence the effects of macrograzers on meiofaunal communities.

#### *Spatial variability of periphyton biomass and meiofaunal abundance*

The biomass of benthic algae varies dramatically on different scales (Goldsborough 1994, Saburova et al. 1995, Kahlert et al. 2002, our study). The various causes of this variability include differences in hydrodynamics, light, nutrients, substrate characteristics (size, texture, exposure), disturbance, and biotic interactions such as grazing (Cattaneo 1990, Hart 1992, Ledger and Hildrew 1998, Rosemond et al. 2000, Guichard et al. 2001, Kahlert et al. 2002). The abundance and community composition of meiofauna living in the periphyton also are highly variable among and within lake systems (Peters and Traunspurger 2005, our study). Epilithic meiofauna depend on periphyton biomass accumulated on hard substrates and, therefore, are indirectly affected by factors controlling periphyton biomass. These factors act on different spatial scales and interact with other factors on higher or lower scales. We do not have direct evidence to define the main factors causing the variability among sites and subsites in Lake Erken, but our experimental design allows us to discuss some of the most important mechanisms. We assume that the variability of algal biomass, meiofaunal abundance, and macrograzer efficiency was not simply a consequence of macrograzer community composition because we found only weak differences in grazer communities among sites. We measured macrograzer abundance and composition only once during our experiment, but the composition matched previous results from Lake Erken (Hillebrand and Kahlert 2001) and presumably represents the natural variation found within the lake in summer. The similar macrograzer abundance at all 3 sites did not result in similar grazing pressure, and sites with similar macrograzer fauna did not have similar reductions in algal biomass. Moreover, the spatial variability in algal biomass and meiofaunal abundance was present in all treatments, including macrograzer-free enclosures (significant variability among sites and not among subsites within sites; Table 1), although the communities shared the same preexperimental colonization history and did not differ in microtopography.

A variety of site characteristics other than grazing could have affected the trajectories of periphyton biomass development and, subsequently, meiofaunal abundance and community composition. Differences in wind exposure and ensuing currents and wave

action among the sites certainly would be important, as was previously shown for Lake Erken (Kahlert et al. 2002). Wave action and currents can positively affect periphyton biomass directly by enhancing water renewal and, thus, nutrient availability (Cattaneo 1990). Wave action and currents also can reduce periphyton biomass because of high shear stress (Young 1945, Kairesalo 1983). Other characteristics that vary at spatial scales of meters and kilometers, such as light exposure (Hillebrand and Kahlert 2001) or surrounding vegetation (Harrison and Hildrew 2001), will contribute to the variability in periphyton biomass at scales of meters to kilometers. In addition to heterogeneity in abiotic characteristics of the environment, habitat choice of predators may affect spatial heterogeneity of algae and macrograzers by changing macrograzer presence and behavior (see *Grazing effects on algal biomass*).

The effects of macrograzers on the heterogeneity of the periphyton resource have different implications at small spatial scales (equivalent to the range of individuals) and large spatial scales (equivalent to the effects of the macrograzer population). For example, decapod grazers reduce small-scale patchiness in algal communities, but increase large-scale patchiness (Pringle 1996). At the individual level, the effect of a macrograzer depends on the spatial and temporal distribution of its grazing activities (i.e., grazing tracks). The variability in algal biomass and diversity increased with increasing densities of a snail grazer, but not of a crustacean grazer, because of behavioral differences in spatial grazing patterns (Sommer 1999, 2000). At the population level, individual grazing behavior is integrated over space and time, and the resulting spatial heterogeneity will be density dependent. At low grazer densities, differences in individual grazing tracks may persist and create high spatial heterogeneity. At high grazer densities, individual grazer tracks will overlap and reduce spatial heterogeneity (Gelwick and Matthews 1997, Poff and Nelson-Baker 1997, Hillebrand et al. 2000). In our experiments, low densities of grazing organisms or equal spatial distribution of grazing pressure may explain the absence of effects on the variability of algal biomass and meiofaunal abundance. However, visual inspection of the tiles revealed strong differences in grazing pressure and distinct grazing tracks at different sites. These observations are based on too few data to be generalized. Moreover, heterogeneity in the effects of macrograzers on algal biomass and meiofauna may have a temporal component in addition to the spatial component investigated in our study, and this component should be included in future studies.

## Acknowledgements

We are indebted to Ingrid Gerdin and Monika Feiling for help with field work and sampling, and to Christa and Karl Hillebrand for the construction of the cages. Karen A. Brune edited the English of the manuscript. Two anonymous referees made helpful comments on an earlier version of the manuscript that improved it considerably.

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Received: 28 November 2005

Accepted: 3 August 2006