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Benthic microalgal diversity enhanced by spatial heterogeneity of grazing

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Abstract This study presents model experiments on the effect of the spatial pattern of herbivory on primary producer diversity. Microalgal biofilms (periphyton) were exposed to different mixtures of two benthic herbivores, the isopod *Idothea chelipes* and the gastropod *Littorina littorea*. The herbivores are similar in their feeding selectivity but differ strongly in the spatial pattern of grazing. *Idothea* did not increase the spatial heterogeneity of algal cell densities beyond the level of ungrazed controls (<1 order of magnitude between local minima and maxima at the 1 mm^2 scale). *Littorina* grazing, in contrast, created a pronounced spatial heterogeneity with maximum:minmum ratios of almost 3 orders of magnitude. When algae were exposed to mixtures of both gazers, the spatial heterogeneity of microalgal cell densities increased with an increasing proportion of *Littorina* in the herbivore mixture. Algal species richness, diversity and evenness also increased with increasing proportions of *Littorina*, and was highly significantly correlated with the spatial heterogeneity of cell densities.

Key words Diversity · Herbivory · Periphyton ·*Idothea* · *Littorina*

Introduction

The effect of herbivory on primary producer diversity is still controversial (Olff and Ritchie 1998). High grazing pressure seems to reduce plant diversity while moderate grazing pressure seems to increase it (Paine and Vadas 1969; Lubchenco 1978; McNaughton 1985; Milchunas et al. 1988). However, there is also circumstantial evidence that spatial heterogeneity of the grazing pressure might be more important for the maintenance of plant diversity than the mean intensity of grazing, as indicated by a comparison between the grazing impacts of digging rodents and ungulates (Huntly and Reichman 1994; Olff and Ritchie 1998). However, the difference between the spatial effects of rodents and ungulates might have been confounded by other differences, e.g. in feeding selcectivity. Therefore, I used an experimental model system consisting of benthic microalgae and different mixtures of two benthic herbivores that are similar in their feeding selectivity but differ strongly in the spatial pattern of grazing.

The isopod *Idothea chelipes* (Salemaa 1987; Schaffelke et al. 1995) and the gastropod *Littorina littorea* (Steneck and Watling 1982) feed on benthic macroalgae and on microalgae growing on solid substrates ("periphyton"). Both are important herbivores in the littoral of the Western Baltic Sea. They feed rather unselectively on a wide variety of microalgal species. Gelatinous coverage of algae and tight attachment to the substratum offer a relative protection (25–50% reduction of mortality) against both grazers (Sommer 1997, 1999a,1999b). The similarity in feeding selectivity is contrasted by pronounced differences in the spatial distribution of grazing pressure (Sommer 1999c). Biofilms grazed by *Idothea* look quite homogenous macroscopically without visible bite marks ("lawn-mower" type of herbivory) while *Littorina* moves slowly over the biofilm producing a macroscopically visible feeding track ("bulldozer" type of herbivory). After some days, there is a diverse mosaic of fresh grazing tracks, old grazing tracks in different stages of recolonization, and untouched biofilm. Both herbivores produced a periphyton diversity optimum at intermediate grazer densities but the optimum was more pronounced in the *Littorina* experiments (Sommer 1999c). Tentatively, I attributed this difference to spatial heterogeneity, but intermediate levels of heterogeneity were lacking in those monospecific experiments. Therefore, the experiments reported here used different *Littorina*:*Idothea* mixtures to produce a continuous gradient of spatial heterogeneity.

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Methods

Prior to the grazing experiment, natural periphyton assemblages were permitted to grow on artificial substrata. The substrata consisted of transparent plastic sheets (ContiFol 50; normally used for overhead transparencies) of 580 cm^2. This type of sheets was chosen because it is the roughest available, but still clear enough to permit direct microscopy of the algae. Biofilms were produced by exposing the artificial substrata at 1 m depth at the dock of the Institut für Meereskunde (Kiel, Germany) for several weeks until a macroscopically visible but still transparent biofilm had developed. After incubation, the biofilms were placed in 15-l aquaria filled with sterile filtered water from the Baltic Sea together with the experimental animals.

The experimental temperatures were similar to those in situ during the outdoor growth of the biofilms (experiment 1:7–11 August 1998, 18°C; experiment 2:28 September–19 October 1998, 16°C). *Littorina*:*Idothea* mixtures consisted of 0:12; 3:3; 2:6; 1:9; 1:12 individuals of *c*. 2 cm size. Each grazer mixture was employed in triplicate. Experiment 1 lasted for 4 days and experiment 2 for 21 days, respectively. At the end of the experiments, the biofilms were collected and fixed with Lugol's iodine. Twenty small random subsamples (1 mm^2) were pierced from the substratum for the analysis of spatial heterogeneity by direct microscopic analysis. Then the biofilm was scratched from the substratum and suspended in water. A 10-ml subsample of the suspension was permitted to settle in 10-ml sedimentation chambers for identifying, counting and measuring of the algae under an inverted microscope (Lund et al. 1958; Utermöhl 1958). In some cases it was necessary to make frustule preparations for the species identification of diatoms. For that purpose, subsamples were soaked for 3 days in H_2O_2 to oxidize the organic matter and thereafter mounted in Naphrax. Diversity and species richness were obtained from the 10-ml subsamples.

In order to test for the robustness of the diversity response, several measures of diversity were used (Washington 1984). Diversity was expressed as the raw species number (*S*) including all species identified, as the standardized species number (S_{1000}) excluding all species with a relative abundance <0.1%, and as the Shannon index of diversity:

$H' = -p_i . \ln p_i$

where p_i is the relative abundance of species *i*. Evenness (*E*) was claculated as the quotient H'/H'_{max}, where H'_{max} is the theoretical maximum of *H'* at a given number of species, which would be obtained if all species had equal abundances.

The rationale for the 1:3 equivalence of *Littorina* to *Idothea* in the grazing mixtures was based on previous experiments, where the impact of different densities of both species had been studied (Sommer 1999c). In those experiments, the grazing impact of *Littorina* had been *c*. 3–4 times as strong as the grazing impact of *Idothea*, as assessed by the slope of a linear regression of log algal biomass on grazer density. The total density of animals (207 *Idothea* equivalents m^{-2}) in the present study was chosen because it is close to the grand mean of diversity optima (185±107 *Idothea* equivalents m^{-2}) calculated for two grazers, two experiments, and two diversity measures in the monospecific experiments of Sommer (1999c).

Results

Mean algal cell densities showed no trend across the mixture gradient, while there was a pronounced response of patchiness (Figs. 1,2). Local minima differed from local maxima by <1 order of magnitude in the *Idothea*-only treatments and the ungrazed controls, while they differed by almost 3 orders of magnitude in the *Littorina*-only treatments. For statistical purposes, the SD of $\log_{10}$ cell densities (calculated from 20 subsamples of 1 mm^2) was used as a measure of spatial heterogeneity. Spatial heterogeneity increased linearly with the number of *Littorina* individuals in the herbivore mixture (r^2=0.95 for experiment 1; r^2=0.90 for experiment 2; P<0.0001 for both experiments). The slopes of the linear regression were remarkably similar for biofilms subject to 4 days of grazing and for biofilms subject to 3 weeks of grazing (0.123±0.008 SE for experiment 1; 0.159±0.015 for experiment 2).

The composition of the herbivore mixture had a strong impact on the species richness of periphyton algae (Figs. 3,4). Compared to the starting conditions, the number of species dropped clearly in the controls and in the *Idothea*-only treatments, while it was maintained in the *Littorina*-only treatments of experiment 1 and showed even a slight increase in the *Littorina*-only treatments in experiment 2. The species richness in the mixed treatments showed an intermediate response with a tendency towards increased species richness with an increasing share of *Littorina*. A linear regression of four

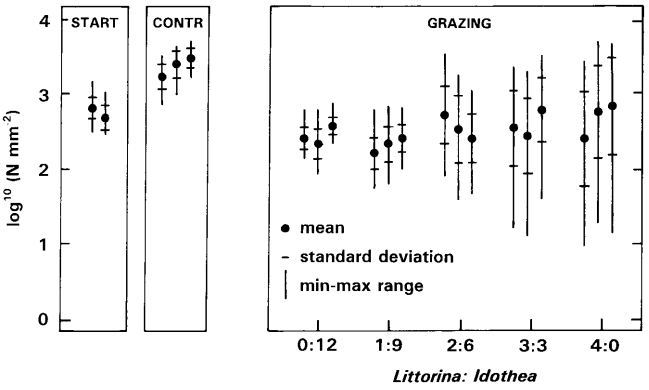

Fig. 1 Effect of grazer composition on the spatial variability of algal abundances (experiment 1). Log cell density (mean, SD, minimum to maximum range) of benthic microalgae as a function of grazer mixture after 4 days of grazing (*START* before incubation in aquaria, *CONTR* 4 days incubation without grazers)

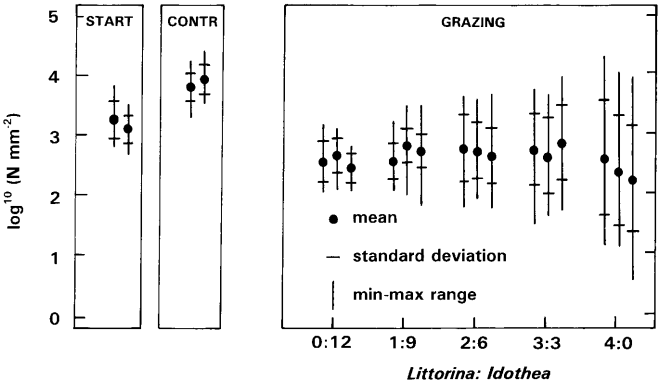

Fig. 2 Effect of grazer composition on the spatial variability of algal abundances (experiment 2). Log cell density (mean, SD, minimum to maximum range) of benthic microalgae as a function of grazer mixture after 21 days of grazing (*START* before incubation in aquaria, *CONTR* 4 days incubation without grazers)

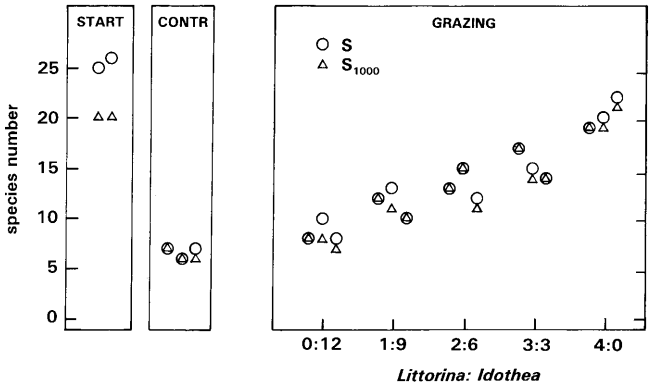

Fig. 3 Effect of grazer composition on algal species richness (experiments 1). Raw species number (*S*) and standardised species number (S_{1000}) of benthic microalgae as a function of grazer mixture after 4 days of grazing (*START* before incubation in aquaria, *CONTR* 4 days incubation without grazers)

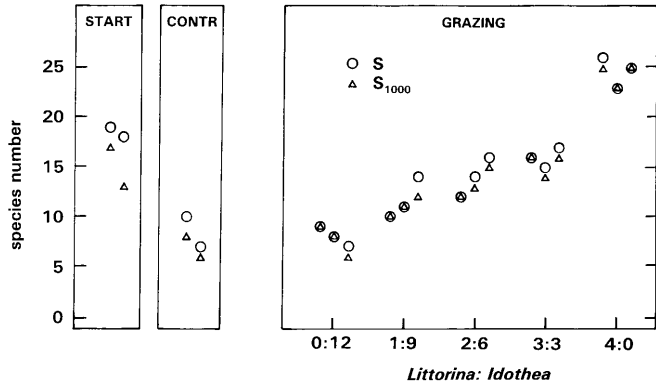

Fig. 4 Impact of grazer composition on algal species richness (experiments 2). Raw species number (*S*) and standardised species number (S_{1000}) of benthic microalgae as a function of grazer mixture after 21 days of grazing (*START* before incubation in aquaria, *CONTR* 4 days incubation without grazers)

different measures of diversity (*S*, raw species number; S_{1000}, standardized species number; *H'*, Shannon's diversity index; *E*, evenness) on spatial heterogeneity (Table 1) confirmed the working hypothesis that spatial heterogeneity of herbivory should increase algal diversity.

Discussion

The agreement between the responses of species richness and the response of evenness indicates that the diversity-heterogeneity relationship should be robust against the choice of a particular diversity index. Different diversity indices are distinguished from each other primarily by the relative weight which they give to species richness and evenness (Washington 1984). As indicated by the close similarity of the results of experiments 1 and 2, the responses of spatial heterogeneity and of diversity seem also to be robust against differences in the duration of exposure to grazing, at least under conditions where grazing and algal growth are almost in balance. The absence of a strong imbalance between grazing and algal growth can be inferred from the fact that algal density changes during the experiment were rather small for organisms with potential growth rates of 1–2 doublings day^{-1} (Figs. 1,2).

Table 1 Dependence of periphyton diversity on spatial heterogeneity: linear regression of diversity measures (*S* raw species number, S_{1000} number of species with p_i>0.001, *H'* Shannon index of diversity, *E* evenness) on spatial heterogeneity of of periphyton cell densities (measured as standard deviation of $\log_{10}$ cells mm^{-2})

Experiment 1
$\log_{10}$ S=0.865+0.695 SD ($\log_{10}$ *n*); r^2=0.91; *n*=15; *P*<0.00001
$\log_{10}$ S_{1000}=0.82+0.756 SD ($\log_{10}$ *n*); r^2=0.91; *n*=15; *P*<0.00001
H'=0.454+2.81 SD ($\log_{10}$ *n*); r^2=0.82; *n*=15; *P*<0.00001
E=0.30+0.719 SD ($\log_{10}$ *n*); r^2=0.71; *n*=15; *P*<0.0001
Experiment 2
$\log_{10}$ *S*=0.809+0.638 SD ($\log_{10}$ *n*); r^2=0.81; *n*=15; *P*<0.00001
$\log_{10}$ S_{1000}=0.775+0.668 SD ($\log_{10}$ *n*); r^2=0.94; *n*=15; *P*<0.00001
H'=0.575+2.045 SD ($\log_{10}$ *n*); r^2=0.86; *n*=15; *P*<0.00001
E=0.389+0.426 SD ($\log_{10}$ *n*); r^2=0.69; *n*=15; *P*<0.0005

The positive impact of environmental heterogeneity on species richness and diversity agrees with theoretical models which have been proposed to explain the persistence of numerous species in spite of competitive exclusion (Grubb 1977; Connell 1978; Levins 1979; Hastings 1980). Heterogeneity can be produced even in a physically and chemically quite homogeneous environment by biological processes, e.g. by gaps resulting from the death of sessile organisms (Shmida and Ellner 1984; Pacala 1986; Pacala and Silander 1990; Tilman 1994). In my experiments, the beneficial effect of *Littorina* on microalgal diversity probably resulted from creation of a diverse mosaic of microhabitats (feeding tracks of different age, untouched biofilm) where different species are superior competitors in different places or where good colonizers but poor competitors find local escapes from competitive exclusion. *Idothea* behaves differently and creates no patchiness beyond the extent in ungrazed biofilms (start and controls). In the herbivore mixtures, *Idothea* even seemed to decrease the patchiness created by *Littorina*, as indicated by the continuity of the reponse of heterogeneity to herbivore mixture. The mechanism can easily be imagined if *Idothea* fed prefentially in the biomass-rich untouched parts of the biofilm instead of choosing the biomass-poor grazing tracks.

The slopes of the diversity-heterogeneity relationships (Table 1) should not be transferred to other situations or other measurement protocols. Any measure of spatial heterogeneity depends on the scale of the subsamples from which it is calculated. Here, the small size of 1 mm^2 was chosen in order to match the width of the grazing tracks. Larger subsamples would have been preferable because they would better represent the total biofilm, but this would have masked the difference between tracks and adjacent areas.

Heterogeneity-diversity relationships are frequently discussed under the conceptual umbrella of the intermediate-disturbance-hypothesis (Connell 1978), but it is questionable whether grazing should be called a "disturbance" because it is a normal phenomenon in undisturbed communities. The definition by Grime (1979) of disturbance as a destruction of biomass would include grazing, while that of Picket and White (1985) of disturbance as a temporally or spatally discrete event disrupting communities would exclude it. In a previous study (Sommer 1999c) I have shown that the response of microalgal diversity to the intensity of grazing is indeed "intermediate", i.e. unimodal. Here, diversity in the *Idothea*-alone treatments was not elevated above the control levels even though grazer densities conformed to the diversity optimum of the previous study. In contrast to the unimodal response to grazing intensity, the response of diversity to spatial heterogeneity induced by grazing does not seem to be unimodal. The data presented here do not even support the assumption that diversity would level off at some degree of environmental heterogeneity. A continuous increase of diversity with environmental heterogeneity seems plausible, as long as an increase of heterogeneity adds more microsites with different living conditions. A saturating response should be expected, however, if the range of spatial environmental variability extended into uninhabitable conditions.

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