EFFECTS OF NUTRIENTS, HERBIVORY, AND DEPTH ON THE MACROALGAL COMMUNITY IN THE ROCKY SUBLITTORAL

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Abstract. We studied the interacting roles of nutrient availability and herbivory in determining the macroalgal community in a rocky littoral environment. We conducted a factorial field experiment where we manipulated nutrient levels and herbivory at two sublittoral depths and measured macroalgal colonization and the following young assemblage during the growing season. At the community level, grazing reduced algal colonization, though the effect varied with depth and its interaction with nutrient availability varied in time. In shallow water, the total density of macroalgae increased in response to nutrient enrichment, but the ability of grazers to reduce macroalgal density also increased with the nutrient enrichment, and thus, the community could not escape from the top-down control. In deep water, the algal density was lower, except in July when nutrient enrichment caused a very dense algal growth. Grazing at the greater depth, though effective, was generally of smaller magnitude, and in July it could not limit algal recruitment and growth. Species richness peaked at the intermediate nutrient level in deep but not in shallow water during most of the growing season. Grazing had no effect on diversity of the algal community at either depth and only a minor effect on species richness at the greater depth. Opportunistic and ephemeral algae benefited from the nutrient enrichment but were also grazed to very low densities. Slowly growing and/or perennial species colonized poorly in the nutrient enriched treatments, and depending on the species, either suffered or indirectly benefited from herbivory. For all species, effects of nutrients on colonization depended on depth; usually both nutrient and herbivory effects were more pronounced at the shallow depth. We conclude that grazers are able to reduce macroalgae over a large range of nutrient availabilities, up to 12-fold nutrient enrichment in the current experiment, and that the sublittoral depth gradient generates variation in the algal community control exerted by both herbivory and nutrient availability. Thus temporal and spatial variability in both top-down and bottom-up control and in their interaction, especially along the depth gradient, may be crucially important for producer diversity and for the successional dynamic in a rocky sublittoral environment.

Key words: Baltic Sea; bottom-up; community control; depth gradient; eutrophication; Fucus vesiculosus; macroalgal colonization; macroalgal consumption; nutrient enrichment; sublittoral herbivory; top-down.

INTRODUCTION

Top-down control, the ability of predators to determine the distribution and abundance of their prey, is considered to be more prevalent in aquatic than terrestrial environments; in the marine littoral, herbivore impacts on macroalgae are particularly strong (Pace et al. 1999, Shurin et al. 2002). Herbivory modifies competitive interactions among species of marine algae through selective grazing and, by generating disturbance, can explain species composition better than nutrient availability (Worm et al. 2000*a*). On the other hand, rather than considering bottom-up and top-down influences as alternatives, it is more fruitful to explore how these controlling mechanisms may interact (Menge 1992, Menge et al. 1997, Lotze et al. 2001, Nielsen 2001,

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Worm et al. 2002) and how their relative strength and interaction varies in space and time and at different scales of each (e.g., Menge 2000, Lotze et al. 2001, Boyer et al. 2003).

The effects of herbivory on plant communities have been studied extensively and with varying outcomes (reviewed in Proulx and Mazumder 1998, Worm et al. 2002). Reported effects on plant species richness have been positive, negative, or unimodal. Over a range of ecosystems, the outcomes of herbivory depend on nutrient availability in the environment: in unproductive environments plant species richness is decreased by grazing pressure, but in productive environments it is increased (Proulx and Mazumder 1998). Consistent with the empirical finding by Proulx and Mazumder (1998), a simulation model predicts that the positive effect of disturbance on species richness will increase with productivity level (Kondoh 2001). According to Kondoh (2001) in low-resource environments regrowth after grazing is limited, while in high-resource environments

the disturbance due to grazing prevents competitive exclusion (Proulx et al. 1996, Hillebrand et al. 2000; however, see Abrams 1995). Thus the effects of nutrients and herbivory are not independent; it is their interactive effects that determine species richness.

In several sheltered coastal areas and marginal seas, increased human action has led to a eutrophication process characterized by increased nutrient availability and primary production (Ryther and Dunstan 1971, Kautsky et al. 1986, Rönnberg and Bonsdorff 2004). The resulting new assemblage of benthic primary producers is not only more massive in terms of biomass (Valiela et al. 1997), but also has different species composition and new dominant species (Lotze and Schramm 2000, Lotze et al. 2001). While grazing by mesoherbivores may efficiently reduce algal growth and change species composition at low or intermediate nutrient levels (e.g., Lubchenco 1978, Lubchenco and Gaines 1981, Duffy and Hay 2000, Worm et al. 2002), such control may break down at high nutrient levels, after which opportunistic algae will prosper (Pace et al. 1999, Lotze et al. 2001, Lotze and Worm 2002, Worm et al. 2002, Lapointe et al. 2004). Thus the efficiency of herbivory in limiting plant communities may be linked to resource levels (Pace et al. 1999, Lotze et al. 2001, Worm et al. 2002). For example, Lotze et al. (2001) suggest that herbivory is less effective in determining the algal assemblage in the nutrient-rich Baltic Sea than in the nutrient-poor northeast Atlantic, implying that the sublittoral community in the Baltic Sea may be driven by bottom-up control.

Depth gradients may generate variation in the relative importance of top-down and bottom-up control. Due to the zonation of algal and faunal species (e.g., Kautsky et al. 1986, Kautsky and Kautsky 1989, Underwood et al. 1991, Nielsen et al. 2003) and the consequent differences in species identities between the zones, interspecific interactions may differ along the depth gradient. Light levels attenuate and water motion declines with increasing depth, causing reduced photosynthesis, reduced nutrient uptake rates (reviewed in Hurd [2000]), increased sedimentation, and increased herbivore density and grazing efficiency (e.g., Lubchenco and Menge 1978, Nielsen 2001, Robles et al. 2001). Consequently, the relative importance of top-down control may increase with the increasing depth.

In this study, we explored the relative and interactive effects of grazing and nutrient availability in determining the species composition, diversity and structure of a macroalgal assemblage. We conducted a factorial experiment in the field, where we manipulated nutrient availability and the occurrence of herbivores at two depths and measured the colonization of macroalgae on artificial substrates. To our knowledge, this is the first study testing the effects of nutrient concentration and grazing at two sublittoral depths in a manipulative experiment. We hypothesized that (H_1) nutrient enrichment (bottom-up) will first enhance diversity and species

richness due to an increase in opportunistic species, but at a higher nutrient level will cause a species-poor algal assemblage due to the predominance of the opportunistic species and competitive exclusion (Proulx and Mazumber 1998, Kassen et al. 2000, Kondoh 2001, Worm et al. 2002). Second, we hypothesized that (H_2) herbivory generates disturbance (top-down), thus inhibiting competitive exclusion and increasing species richness and diversity; selective feeding of dominant species particularly enhances this effect (Lubchenco 1978, Kautsky and Kautsky 1989, Proulx and Mazumber 1998, Ojeda and Munoz 1999, Kondoh 2001, Worm et al. 2002). We further expected certain interactions of nutrients, herbivory, and depth: (H_3) Mesoherbivores may strongly reduce algal colonization at natural levels of nutrients, thus decreasing species richness; with increasing nutrient levels the effect of grazers on species richness will turn positive; at the highest nutrient level herbivores may be unable to control algal densities leading to a drop in species richness (Proulx and Mazumber 1998, Kondoh 2001, Worm et al. 2002). Grazing may be more efficient in deep water, where the environmental stress for grazers, in terms of wave action, is less severe and algae, due to reduced photosynthesis, can utilize nutrients less efficiently than close to the surface (Lubchenco and Menge 1978, Robles et al. 2001, Nielsen et al. 2003). Thus, (H_4) we expected the grazing effects on algal colonization to be more pronounced in deep than in shallow environment. As a corollary, herbivory may decrease species richness more at greater water depth because resource limitation constrains regrowth and colonization. Conversely, (H_5) we expected bottom-up control to be more prominent in shallow water. There the nutrient enrichment may increase algal density despite the presence of herbivores, which is likely to lead to dominance competition and decreased species richness. Abiotic disturbances, however, are likely to be more frequent in the shallow than in the deep environment and they may counteract such a decrease of species richness.

Methods

Study site and community

Our experiment was located in a moderately waveexposed bay on Jurmo Island in the Archipelago Sea in southwest Finland (northern Baltic Sea; $59^{\circ}49'31''$ N, $21^{\circ}35'16''$ E). This is a brackish-water sea (surface water salinity range, 5.5–6 psu) with no tide. The rocky reef extends to a depth of 3 m, where it abuts a sandy, less steep substratum. Based on weekly scuba dives, wave action was usually clearly perceivable at the one-meter depth but not at the three-meter depth. The significant wave height offshore ranged between <1 m in May and August and 2–3 m in the autumn (Finnish Institute of Marine Research), but the swell on the shore was weaker due to protecting skerries. Although the coastal area is affected by anthropogenic eutrophication, the outer archipelago, including our study site, can be considered "mesotrophic" (see description in Rönnberg and Bonsdorff [2004]). In the summer and autumn, the surface water concentrations of inorganic nitrogen and phosphate vary between 2–200 μ g/L and 1–40 μ g/L, respectively (Finnish Environment Institute); the low concentrations prevail between June and August increasing in the autumn.

The natural macroalgal assemblage in our study area consists of only a few common species, all of which colonized our experimental substrates and were included in the analysis. Fucus vesiculosus (L.) is the only fucoid species, and also the only species forming a distinct, permanent zone at 1-3 m depth. The bush-like Ceramium tenuicorne (Kütz) Waern is abundant especially during the autumn, but occurs during most of the summer. The filamentous species-the green algae Cladophora glomerata (L.) Kütz and Enteromorpha spp. and the brown algae Pilayella littoralis (L.) Kjellm and Ectocarpus siliculosus (Dillwyn) Lyngbye-are abundant during the ice-free period, and overwinter as spores or diminutive forms (C. glomerata and P. littoralis; Kiirikki and Lehvo 1997). Other species are rare and in low abundance in our study site.

Mesoherbivores in our study area are dominated by four species of gastropods (*Hydrobia ulvae* [Pennant], *H. ventrosa* [Montagu], *Potamopyrgus antipodarum* [Gray], and *Theodoxus fluviatilis* [L.]), by four amphipod species of the genus *Gammarus*, and by the isopods *Idotea baltica* (Pallas) and *I. chelipes* (Pallas). The crustacean mesoherbivores have a generalist diet of filamentous macro- and microalgae (Salemaa 1987, Worm et al. 2000*a*, Jormalainen et al. 2001; S. Korpinen, V. Jormalainen, and T. Honkanen, *personal observations*). Feeding preferences of snails include periphyton and microalgae and possibly the spores and germlings of macroalgae (Malm et al. 1999, Blanchard et al. 2000), but data on possible preferences are lacking.

Experimental design

We used a factorial design to evaluate the effects of grazing (three levels), nutrient enrichment (three levels), and depth (two levels) on the density and species composition of macroalgae. We used empty rough-faced concrete tiles of 10×20 cm as colonization surfaces. The tiles were attached to cages, 10 tiles in each. The cages in each treatment combination were replicated three times, giving a total of 54 cages.

We manipulated the access of grazers to the colonization substrates by enclosing the substrates in mesh-net cages. We had three treatment levels: no grazers present (fully closed cage, CC), free entry for grazers to a cage with only the roof mesh net present (roofed cage, RC), and free entry for grazers in a cage without mesh nets (open cage, OC). For closing the cages to herbivory, and for the roofs, we used translucent polyamide net (mesh size 1 mm, width 50 cm, length 70 cm, height 30 cm). The roofed cage and the cage without mesh net were used to control for the decrease in light due to the mesh net. The effect of the mesh net on light availability varied with the duration of the experiment and with the weekly cleaning cycle of the nets. In newly assembled cages, the amount of light inside the cage was $95 \pm 2.3\%$ (mean \pm SE, n=3 cages); in cages with fouled mesh-nets just before the weekly cleaning, only $52 \pm 5.0\%$ (n=9 cages) of that at the sea bottom. The possible effect of cages on water motion was not controlled except for the weekly cleaning that kept the mesh nets open for water motion.

The manipulation of nutrient availability had three levels: ambient concentration, low nutrient enrichment, and high nutrient enrichment. We used a controlledrelease fertilizer (Osmocote Exact Standard 3-4M, 16N:5P:9K, Scotts Company, Marysville, Ohio, USA), packed in elongated diffusion pouches (see Worm et al. [2000b] for methodology). The initial amounts of fertilizer were 0.5 and 1 kg for the low- and highnutrient enrichment treatments, respectively. The nutrient samples were taken by scuba-diving from inside the cages. The nutrient concentrations obtained in the ambient, low-enrichment, and high-enrichment cages were 8.14 \pm 0.14 (mean \pm SE, n = 7 cages), 40.8 \pm 13.3 (n = 24 cages), and 108.3 ± 35.7 $(n = 21 \text{ cages}) \mu g \text{ DIN/L}$ and 10.6 \pm 3.4 (*n* = 7 cages), 12.5 \pm 2.6 (*n* = 24 cages), and 25.6 \pm 5.6 (n = 22 cages) µg DIP/L, respectively (DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus), pooled over three successive samples between July and September. The enriched nutrient levels correspond to approximately fivefold and 12-fold concentrations of inorganic nitrogen, when compared to the corresponding ambient concentration and are within the concentrations found from the study area between summer and autumn (see Study site and *community*). The highest enrichment level corresponds to DIN concentrations of eutrophied areas in the Baltic Sea. The nutrient concentrations peaked in mid-July and differed among the three enrichment treatments (twoway ANOVA; DIN $F_{2,24} = 5.1$, P < 0.05; DIP $F_{2,25} =$ 3.9, P < 0.05) and among sampling dates (DIN $F_{2,24} =$ 9.9, P < 0.001; DIP $F_{2,25} = 21.5$, P < 0.0001). Although we attempted to take water samples during calm weather, minor differences in water motion and temperature between the dates are likely to explain these temporal differences. Inorganic nitrogen concentrations did not differ between the two depths, whereas the phosphate values were higher in September in deep water (two-way ANOVA, depth \times date $F_{2,25} = 8.6$, P <0.01), the latter probably being attributable to differences in water motion between the depths and consequent faster spreading of solute nutrients close to the surface. The fertilizer pouches were replaced with new ones at four- to five-week intervals. The old pouches were dried and weighed to ensure a sufficiency of the fertilizer over the treatment period; over 30% of the original weight of the fertilizer remained in all pouches at the time of their replacement.

We wanted to safeguard against possible contamination from the nutrient additions and, therefore, left at least a 10-m distance between the cages belonging to different nutrient levels. Due to limited availability of homogeneous littoral area we had to slightly aggregate the cages within each nutrient treatment level: instead of 54 cages, we had 25 aggregates being separated by at least 10-m distance. Within each aggregate we had one

to three cages, belonging to the same nutrient treatment and depth level but to a random herbivory treatment level, placed 1–5 m apart. Preliminary data analysis indicated that this loose aggregation did not compromise interpretations of the nutrient and herbivory effects (see *Statistical analyses*).

We placed half of the cages at the shallow end (0.5-1 m) and the rest at the deep end (2.5-3.5 m) of the F. vesiculosus belt for algal colonization. We chose these depths because the most diverse algal community is found in this area, the wave action diminishes steeply within this range (due to protecting islands and relatively low wave heights in the region), and the amount of light quickly decreases with depth. In our study area, in July on a sunny day, the proportion of photosynthetically active light at the bottom, out of that at the surface, was $86.0 \pm 4.1\%$ (*n*=3 measurements) and $25.1 \pm 3.6\%$ (*n*=4 measurements) in shallow and deep water, respectively; measured with a Li188B integrating photometer; LI-COR, Lincoln, Nebraska, USA). The actual light intensities, 677 ± 14 and $143 \pm 12 \ \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in shallow and deep water, respectively, differed significantly between the depths ($F_{1,5} = 878, P < 0.001$).

We quantified the densities of herbivorous invertebrate species at the study site in order to better interpret the herbivory treatment effects. We did this separately for the three nutrient levels and two depths. The methods and results for this are presented in Appendix A.

Measuring algal density and diversity

We started the experiment in early June 2003; two tiles were removed for analysis on subsequent dates, five weeks apart, in early July, mid-August, mid-September, and early November. The macroalgae colonized the tiles during the whole experimental period; therefore the data on the first sampling date concerns mainly colonization success while those of the last three sampling dates describe both the succession of the initial algal assemblage and the successive colonization. We counted the attached macroalgae in four random 2×2 cm squares on each of the two tiles per sampling date. The algae were identified and counted under a dissecting microscope. When the algal density on a square was very high, a subsample the size of the microscope view $(\sim 0.25 \text{ cm}^2)$ was taken randomly from the square and densities were extrapolated to the whole square. We started counting the algae immediately after the transfer from the growing site; during the counting process of up to six days the tiles were stored underwater in a dark room at 4°C. When the filaments were too tiny for identification, they were pooled to the nearest taxon possible. For example, small individuals of *P. littoralis* and *E. siliculosus* were pooled as filamentous brown algae. Since some species were handled at the genus level and some taxa were combined, estimates of diversity and species richness represent minimum values.

Because the study site, and the northern Baltic Sea in general, supports relatively few macroalgal species (see *Study site and community*), the responses of single species have a considerable effect on the whole macroalgal community. Therefore, we present species or taxon-specific analyses for the five dominant algae, belonging to three algal groups. These groups represent different life-history modes and/or types of responses to the manipulations: (1) perennial, non-opportunistic, readily consumed (*Fucus vesiculosus*); (2) ephemeral, opportunistic, readily consumed (*Cladophora glomerata*, filamentous brown algae, and *Enteromorpha* spp.); and (3) ephemeral, non-opportunistic, not reduced by herbivores (*Ceramium tenuicorne*).

Statistical analyses

Dzensities of each species are count data that were non-normally distributed. Therefore, we used generalized linear models to analyze the main and interactive effects of herbivory (OC, RC, CC), depth (shallow, deep), and nutrient enrichment (ambient, low, and high enrichment). We ran all the analyses, except the diversity variables, using SAS GENMOD procedure (SAS Institute 1999). Generalized linear models are more flexible than general linear models; they allow various sample distributions and do not assume homoscedasticity of variances (Dobson 2003). Our data fit well to the negative binomial distribution, and we used it as the sample distribution. In the case of a negative binomial sample distribution, SAS uses logarithmic link function that models the log of the mean. The analysis is based on the maximum likelihood estimation and the hy pothesis testing on the χ^2 distribution. The model fit was evaluated separately for each data set by observing the ratio between deviance and degrees of freedom; a value of close to one indicates a good fit (Dobson 2003). In addition, we checked the normality of the residual variation.

We further reduced the models by removing all possible nonsignificant (P > 0.1) interactions and rerunning the analysis. We checked that the reduction did not significantly decrease the model fit, on the basis of a nonsignificant difference (P > 0.1) of the deviances of the full and reduced models (Myers and Montgomery 1997). We used cages as the units of replication (each variable summed over two tiles per cage); in the figures we have transformed the densities to individuals per square centimeter.

Our experimental design had a loose aggregation of cages within the nutrient treatment levels (see *Experimental design*), which, if the aggregates differ in the spore availability or in growing conditions (i.e., the

macroalgal community at the experimental area is heterogeneous at the spatial scale of the aggregate placement), could potentially confound the statistical inference of the nutrient factor. In order to assess this possibility we reran all the analyses by SAS MIXED ANOVA (SAS Institute 1999) with and without the random factor "aggregation." We checked the significance of the random factor by calculating the difference between the -2 res log likelihood values of the two models, one including and the other excluding the aggregation factor, and comparing it to χ^2 tables (df = 1; Littel et al. 1996). The aggregation factor did not improve the model fit (P > 0.1) indicating that the aggregation had no detectable effect on algal densities or the number of species. We, therefore, did not take it into account in the final analyses.

Since the colonization of filamentous species is highly dynamic and interactions with "date" are therefore difficult to interpret, we ran the analyses of the four filamentous taxa separately for the four dates. To present the density of each species over the course of the experiment, we chose one representative sampling date for each filamentous algal species on the basis of its abundance in the community (Fig. 1). Additional figures and corresponding analyses of algal densities for other dates are presented in the appendices. In the case of the perennial F. vesiculosus, colonization occurred in the beginning of the experiment and inclusion of the temporal trend (date factor) in the analysis could have been plausible. However, the generalized linear model with date as a repeated factor did not converge in this case; we, therefore, analyzed each date separately, similarly to the filamentous taxa.

In analyzing the community variables (total filament density summed over all taxa, diversity, and species richness), we included date (early July, mid-August, mid-September, and early November) as a factor in the analysis. We analyzed the total filament density using the repeated measures approach in the SAS GENMOD procedure; date was treated as the repeated measures and cage as the subject. The unit for the calculation of the community variables was the cage (summed over two tiles per cage, total observed area 32 cm^2). The data on species richness were normally distributed, and their variances were homoscedastic according to Levene's test. We therefore used repeated measures ANOVA with date as a repeated factor and nutrient enrichment, herbivory and depth as the between subject factors (SAS GLM procedure; SAS Institute 1999). The analysis of the Shannon-Wiener diversity (H') is presented in Appendix B.

In order to estimate the difference between the two cages allowing herbivore entry (OC, RC), we tested a priori contrasts for the five dominant macroalgal species between OC and RC at every depth \times nutrient level for the four dates. Although the mesh-net periodically decreased the availability of light (see above), the grazer entry cages without a net (OC) and with a roof-net (RC)

produced roughly similar results. In a total of 96 tests (four combinations were non-testable), only 11% of the results showed a significant (P < 0.05) difference between the OC and RC treatment levels. Therefore we have in some analyses contrasted OC + RC vs. CC, within depth, nutrient, and date, in order to clarify certain interactions.

RESULTS

Effects at the community level

Even without the over-wintered spore bank, the colonization of macroalgae was rapid and a large quantity of early-stage algae were found from the cages in the first sampling, five weeks after initiation. The first dominants in the nutrient enrichment treatments were the filamentous browns (*P. littoralis* or *E. siliculosus*) in early July (Fig. 1). In contrast, the perennial brown alga, *F. vesiculosus*, and the red alga, *C. tenuicorne*, were the predominant colonizers of the ambient nutrient level at the shallow depth (Fig. 1a). From mid-August through the remainder of the experiment, *C. glomerata* was the most abundant species at all nutrient and depth levels (Fig. 1).

Both the total density and the species richness of the macroalgal community responded strongly to nutrient enrichment, herbivory and growing depth, as could be seen from the significant main effects as well as second order interactions (Table 1). Both the main effects and their interactions also varied temporally as indicated by the several interactions with date (Table 1). Nutrients increased total algal density particularly in shallow water, and the total density decreased towards November (Fig. 2; the significant depth \times nutrient \times date interaction in Table 1). In early July, the low nutrient enrichment increased the algal density in all the herbivory treatment levels, while later on and in the high nutrient enrichment the density increased in the absence of herbivores only (CC) (nutrient \times herbivory \times date in Table 1 and Fig. 2). In early July, the algae colonized the deep-water tiles better than the shallowwater ones at low nutrient addition (Fig. 2), but later on the shallow-water habitat supported higher density (depth \times nutrient \times date in Table 1).

The effect of herbivory depended on the growing depth and date (depth \times herbivory \times date interaction in Table 1). Herbivores reduced the macroalgae even by 90% in the shallow-water, high-nutrient-enrichment community (Fig. 2). In deep water, however, grazing effects were of smaller magnitude and algae temporarily escaped grazing in early July. In August, herbivores reduced the deep-growing algae in all nutrient concentrations and in September this happened in the low nutrient enrichment treatment (Fig. 2b, d, f). All grazing effects on total density ceased by November (Fig. 2).

The response of species richness (S) to nutrients was dependent on depth and this interaction varied with date: Species richness showed a general decrease from July onwards (Fig. 3; main effect "date" in Table 1), but in the high enrichment in deep water (Fig. 3f) and in the



FIG. 1. Density (percentage, mean \pm SE) of green algae *Cladophora glomerata* and *Enteromorpha* spp., filamentous brown algae (pooled filaments of *Pilayella littoralis* and *Ectocarpus siliculosus*), the red alga *Ceramium tenuicorne*, and *Fucus vesiculosus* in the macroalgal assemblage in shallow and deep water at three nutrient levels. Values are derived from algal densities in the open cages.

ambient concentration in shallow water (Fig. 3a) this trend did not occur (depth \times nutrient \times date in Table 1). In July, S was high on the shallow-water tiles in both nutrient enrichments (Fig. 3c, e), but later on the response was more variable, often leading to a decrease in S in the nutrient enrichment treatments (Fig. 3c, e). In deep water, the low enrichment treatment produced the highest S values; thus species richness formed a unimodal response to nutrient availability but such a pattern was not evident in the shallow water (Fig. 3d; depth \times nutrient in Table 1).

The lack of a nutrient \times herbivory interaction in Table 1 indicates that grazers did not have a contrasting impact on species richness at different nutrient levels.

There was an indication of an interaction of depth and herbivory that, however, varied with the date (depth × herbivory × date in Table 1). Generally, herbivory decreased species richness in deep but not in shallow water (Fig. 3, a priori contrast tests, OC + RC vs. CC; P< 0.01 in deep water and P > 0.1 in shallow water).

Effects at the algal species level

Separate macroalgal taxa showed contrasting responses to the manipulations of herbivory, nutrients, and depth. *F. vesiculosus* was more abundant by about two orders of magnitude in shallow than in deep water (deep-water densities were very low; all means < 0.1individuals/cm², and are thus not shown in Fig. 4 nor

		Tota	Total density		Species richness			
Source	df	χ^2	Р	MS	F	Р		
Depth	1	21.58	< 0.0001	3.91	19.94	< 0.0001		
Nutrient	2	21.46	< 0.0001	1.08	5.49	< 0.01		
Herbivory	2	25.52	< 0.0001	0.63	3.23	0.05		
Date	3	34.05	< 0.0001	2.11	30.70	< 0.0001		
Depth \times nutrient	2	16.28	< 0.001	0.61	6.45	< 0.01		
$Depth \times herbivory$	2	5.62	0.06	0.36	1.82	NS		
Nutrient \times herbivory	4	3.33	NS	0.07	0.38	NS		
Depth \times date	3	5.09	NS	0.18	2.69	0.05		
Nutrient \times date	6	20.99	< 0.01	0.13	1.90	0.09		
Herbivory \times date	6	19.65	< 0.01	0.02	0.28	NS		
Depth \times nutrient \times date	6	15.62	< 0.05	0.45	6.50	< 0.0001		
$\hat{\text{Depth}} \times \text{nutrient} \times \text{herbivory}$	4	6.95	NS	0.11	0.56	NS		
Depth \times herbivory \times date		12.75	< 0.05	0.14	2.06	0.06		
Nutrient \times herbivory \times date 1		25.29	< 0.05	0.04	0.61	NS		
Depth \times nutrient \times herbivory \times date 12		18.73	0.09	0.11	1.65	0.09		

TABLE 1. Statistical analyses of total algal density and species richness across all sampling dates.

Notes: Total algal density consists of the pooled number of individual stems and filaments of all macroalgae and was analyzed using a generalized linear model, with dates treated as repeated measures. The ratio of deviance to degrees of freedom (226/143) evaluates the model fit (see *Methods: Statistical analyses*). Species richness was analyzed accordingly using the repeated-measures ANOVA. In this ANOVA, the between-subjects error is df = 35, and the within-subject error is df = 105. The summary statistics are presented in Figs. 2 and 3. NS indicates that effects were not significant.

included in the statistical analyses). In deep water, the treatments did not affect *Fucus* density when analyzed separately for each date (all P > 0.1). In the shallow environment, the density of *F. vesiculosus* was highest in July (Fig. 4), reflecting the end of its reproductive season at that time. From early July to mid-August it decreased to about one third, and at subsequent dates its density decreased yet further (Fig. 4). *F. vesiculosus* colonized well at ambient nutrient concentrations when grazers were excluded, whereas in the nutrient-enriched environments colonization was poor regardless of the type of herbivore treatment (Fig. 4, nutrient × herbivory interaction in Table 2). This indicates that *F. vesiculosus* density was reduced by both grazers and nutrient enrichment.

Nutrient enrichments affected C. glomerata positively (Fig. 5a, b), but the strength of the effect varied temporally (see Appendix C: Table C1). In September, halfway through the period of its predominance, the negative effect of grazing on C. glomerata was present in the two nutrient enrichment levels in shallow water and, in deep water, in the ambient nutrient and low nutrient enrichment levels (nutrient \times herbivory \times depth in Table 3; Fig. 5a, b; a priori contrast tests, OC + RC vs. CC; in shallow water, P > 0.1, < 0.01, and < 0.0001 for ambient concentration, low, and high enrichments, respectively, and in deep water, P < 0.05, < 0.0001, and >0.1 for the same nutrient levels, respectively). The nutrient \times herbivory \times depth interaction indicates that both top-down and bottom-up processes affected the species, but differently between depths. In September, C. glomerata did not colonize or grow well in the high nutrient enrichment in deep-water closed cages (Fig. 5b). In the early phase of colonization (early July), C. glomerata grew denser at the 3 m than at the 1 m depth, but by mid-August depth was irrelevant and later the density was slightly higher in shallow water (Fig. 5a, b; see Appendix C: Table C1, Fig. C1).

Filamentous browns responded positively to nutrient enrichment, were more abundant in the deep water, and were readily consumed by the herbivores in the shallow water (Fig. 5c, d; Table 3). In July and August, their abundance increased by two to three orders of magnitude even in the low enrichment (Figs. 1, 5c, d; Table 3; see also Appendix C: Table C2, Fig. C2). Grazers reduced the density of filamentous browns to 20% of that in the closed cages in shallow water in the high nutrient enrichment in early July. However, the grazing effect varied between depths at the time of its peak occurrence in early July (for other dates, see Appendix C: Table C2, Fig. C2), implying that grazing decreased colonization in shallow water but not in deep water (Fig. 5d; depth \times herbivory in Table 3). In the ambient nutrient concentration, filamentous brown algae were rare (Fig. 5c, d); together with the depthdependent herbivory effect, this resulted in the depth \times nutrient \times herbivory interaction (Fig. 5c, d). In August, grazing reduced the algae at both depths (see Appendix C: Table C2, Fig. C2a, b). Later in the autumn the density was very low and the grazing impact was negligible (see Appendix C: Table C2, Fig. C2c-f). Obviously both the bottom-up and top-down processes affected the density of filamentous brown algae, though differently at the two depths.

Enteromorpha spp. increased greatly in abundance on the nutrient enriched substrates. The exclusion of herbivores caused dense stands in the low and especially in the high nutrient enrichment treatments ("nutrient" main effect in Table 3; Fig. 5e, f; Appendix C: Table C3, Fig. C3), but the species was rare at the ambient nutrient level even in the absence of herbivory (nutrient \times herbivory interaction in Table 3; Fig. 5e, f). However, at



FIG. 2. Total density of all macroalgal species in (a, c, e) shallow and (b, d, f) deep water in the three nutrient and herbivory treatments (open, herbivory [OC]; roofed, herbivory [RC]; and closed, no herbivory [CC]). Values are least-square means \pm SE of the model (see *Methods: Statistical analyses*).

the time of its highest abundance in mid-August and mid-September, and later in November, the density of *Enteromorpha* increased in the high nutrient enrichment in shallow but not in deep water, as indicated by the depth \times nutrient interaction (Fig. 5e, f; Table 3; Appendix C: Table C3, Fig. C3). The abundance of *Enteromorpha* spp. was strongly reduced by herbivory at both depths (Fig. 5e, f; Table 3). Herbivores were able to reduce this species to very low levels even in the high nutrient treatments (Fig. 5e, f; Table 3). The red alga *Ceramium tenuicorne* benefited from the presence of herbivores in shallow water, as indicated by its increase in density and reflected in the marginally significant depth × herbivory interaction (Table 3, Fig. 5g, h; a priori contrast test, OC + RC vs. CC, in shallow water, P < 0.05, 0.001, not significant, <0.01 for the four dates, respectively; see Appendix C: Table C4, Fig. C4). The density of *C. tenuicorne* decreased with nutrient enrichment in shallow water (Fig. 5g, h; depth × nutrient in Table 3). The species was clearly less abundant in deep than in shallow water (Figs. 1, 5g, h; Table 3).



FIG. 3. Species richness of macroalgal community in shallow and deep water in the three nutrient and herbivory treatments (open, herbivory [OC]; roofed, herbivory [RC]; and closed, no herbivory [CC]). Values are least-square means \pm SE of the model (see *Methods: Statistical analyses*).

DISCUSSION

Effects of nutrient availability and grazing on the macroalgal community

Ecological models predicting the impact of nutrients on a plant community have stressed the unimodal response of species richness (Worm et al. 2002, reviewed by Rajaniemi 2003, Herbert et al. 2004, and references therein). The prediction from these models is that an increase in nutrient availability at first favors several species, thus increasing species richness; later on superior competitors outcompete other species and species richness and diversity decline (cf. Suding et al. 2005). In this study, fertilization caused a unimodal response in species richness in deep water in all levels of the grazer treatment (i.e., supporting hypothesis H_1) while, in shallow water, the response to fertilization



FIG. 4. Density of *Fucus vesiculosus* stems in shallow water in the three nutrient enrichments and in the three herbivory treatment cages (open, herbivory [OC]; roofed, herbivory [RC]; and closed, no herbivory [CC]). Values are least-square means \pm SE of the model (see *Methods: Statistical analyses*).

varied over time from increasing to decreasing. The theoretical model by Kondoh (2001) predicts that the peak in species richness will move to higher nutrient levels as the disturbance, e.g., grazing pressure, increases. Similarly, the relationship between herbivory and species richness is unimodal, and the peak moves to higher grazing pressure with an increase in productivity. We found that grazing pressure, though being strong, did not enhance species richness (i.e., contrary to hypothesis H_2). We did not find the effect of herbivores on species richness to increase with the increasing nutrient enrichment (contrary to hypothesis H_3). Instead, at the deeper depth species richness was higher in the absence of grazers (supporting hypothesis H_4). Thus, the ecological models concerning the effects of grazing and productivity on plant community were not supported in this study: we did not find that herbivory increased species richness or diversity along the nutrient gradient. We suggest that in species-poor environments, such as the northern Baltic Sea, the species pool has very few new species to fill the grazer-generated empty patches and, therefore, grazing does not necessarily increase species richness. Furthermore, certain common algal species respond negatively even to moderate nutrient enrichment thus hindering the increase of species richness with nutrient availability.

Worm et al. (1999) found that an increased nutrient concentration reduced algal diversity in the absence of herbivory, but caused no change in the presence of herbivory. However, isopods (grazers) increased in abundance in increased nutrient concentrations; thus enhanced nutrient availability caused changes at a higher trophic level (Worm et al. 1999). In this study, hydrobid gastropods were very abundant on nutrientenriched surfaces (Appendix A). Such a shift in mesograzer abundance probably reflects increased periphyton growth and the hydrobids' feeding preference for periphyton; macroalgal propagules may share a common doom with microalgae and periphyton. Hydrobids were also six times more abundant in the deep than shallow sublittoral. We suggest that these very abundant gastropod grazers in sublittoral habitats of the Baltic Sea are important and relatively non-selective consumers of the macroalgal assemblage at the early colonization phase, and their effect may be especially strong in the depths where waves do not impede grazing.

Grazers also reduced total algal density in the shallow water in all nutrient conditions (i.e., contrary to hypothesis H_4). Although grazing was stronger in deep water, the greater wave action was not sufficient to inhibit grazing at shallow depths. We suggest that the

TABLE 2. Statistical analyses of the density of bladderwrack (Fucus vesiculosus).

		Early July		Mid-August		Mid-September		Early November	
Source	df	χ^2	Р	χ^2	Р	χ^2	Р	χ^2	Р
Nutrient	2	9.95	< 0.01	35.18	< 0.0001	25.30	< 0.0001	32.32	< 0.0001
Herbivory	2	5.56	0.06	6.12	< 0.05	0.27	NS	0.86	NS
Nutrient \times herbivory	4	1.66	NS	10.46	< 0.05	2.54	NS	11.10	< 0.05

Notes: The ratio of deviance to degrees of freedom (early July, 29/18; mid-August, 27/18; mid-September, 23/18; early November, 26/18) evaluates the model fit (see *Methods: Statistical analyses*). The summary statistics are presented in Fig. 4. NS indicates that effects were not significant.

top-down control of macroalgal density in shallow water was due to combined grazing pressure by hydrobid and *T. fluviatilis* snails and by crustacean mesograzers that increased in abundance in the shallow depth with the progressing season (Appendix A). Thus, grazers capable of feeding on propagules and early colonization stages of macroalgae are very abundant in sublittoral of the northern Baltic Sea. Lack of large grazer species, such as sea urchins and large gastropods, hinders the grazing impact on adult algae. We therefore suggest that the majority of grazing effects on macroalgal assemblages occur at early colonization stages (cf. Lotze et al. 1999); grazing of adult algae is important in some alga–grazer interactions, e.g., between isopods and the bladderwrack (Hemmi and Jormalainen 2002).

Recent studies indicate that herbivores may be inefficient in reducing macroalgal abundance in highly eutrophic environments (Lotze et al. 2001, Lotze and Worm 2002, Morgan et al. 2003, Lapointe et al. 2004). In previous studies, herbivores were unable to reduce macroalgae at enriched, even 25-fold, nutrient levels (Lotze et al. 2001, Lotze and Worm 2002, Morgan et al. 2003). In this study, the highest concentration was about 12-fold the average background level, and close to the maxima of nutrient concentrations detected in the study area. Herbivores reduced algal densities regardless of the nutrient level (contrary to hypothesis H_3); in the case of opportunistic filamentous brown algae, down to 7-22% of that on the herbivore exclosure substrates depending on the nutrient level. The strong herbivore impact in this study is most likely explained by high herbivore densities; amphipods, for example, were 20 times denser in our study area than in the southern Baltic Sea (Lotze et al. 2001). However, we found momentary macroalgal escape from herbivore control due to enhanced nutrient availability: in July, grazers did not reduce filamentous browns in deep water. Instead, these algae seemed to benefit from the grazers in the nutrient enriched environment, probably due to a release from competition. However, the top-down control of macroalgae at their colonization and early life stages by herbivory may prevail even in the highest natural nutrient concentrations (see also Nielsen 2001). Variable results in studies conducted at different regions stress the significance of knowing the identities and interactions of herbivores and their hosts, as well as the differences in ambient nutrient levels and grazer abundance.

Species-level interactions

Herbivory greatly reduced both the opportunistic ephemeral species and the perennial one in this study. In the framework of macroalgal succession, Lubchenco (1983) and Worm et al. (2001) have stressed that severe grazing pressure on opportunistic algae (e.g., *Ulva* or *Enteromorpha*) frees space for fucoids. According to our results, grazing pressure on newly attached zygotes or germlings of *F. vesiculosus* in the summer during the colonization period was almost as heavy as on the



FIG. 5. Density of the green alga *Cladophora glomerata*, filamentous brown algae (pooled filaments of *Pilayella littoralis* and *Ectocarpus siliculosus*), *Enteromorpha* spp., and the red alga *Ceramium tenuicorne* in shallow and deep water in the three nutrient enrichments and in herbivory treatment cages (open, herbivory [OC]; roofed, herbivory [RC]; and closed, no herbivory [CC]) at the moment of their peak abundance. Values are least-square means \pm SE of the model (see *Methods: Statistical analyses*).

opportunistic species. Although germling mortality due to other factors than grazing was considerable, the mortality due to grazing had reduced the density of *F. vesiculosus* to less than half of that in grazer exclosures by the end of the first growing season in November. This indicates that grazing is a significant

Table 3.	Statistical an	alyses of tł	ne density of t	the green al	ga <i>Cladophord</i>	ı glomerata, t	filamentous l	orown algae (pooled filaments of
Pilayell	<i>a littoralis</i> and	d Ectocarp	us siliculosus)	, the green	alga Enterom	orpha sp., ar	nd the red alg	ga Ceramium	tenuicorne.

		C. glomerata, mid-September		Filamentous browns, early July		Enteromorpha, mid-September		C. tenuicorne, mid-August	
Source	df	χ^2	Р	χ^2	Р	χ^2	Р	χ^2	Р
Depth	1	12.18	< 0.001	4.15	< 0.05	0.03	NS	15.82	< 0.0001
Nutrient	2	8.58	< 0.05	59.94	< 0.0001	19.39	< 0.0001	24.54	< 0.0001
Herbivory	2	34.42	< 0.0001	2.26	NS	25.43	< 0.0001	1.34	NS
Depth \times nutrient	2	5.72	0.06	3.58	NS	8.00	< 0.05	23.44	< 0.0001
$Depth \times herbivory$	2	0.42	NS	10.36	< 0.01	1.93	NS	5.09	0.08
Nutrient \times herbivory	4	8.90	0.06	5.42	NS	13.22	< 0.05	5.97	NS
Nutrient \times herbivory \times depth	4	12.79	< 0.05	8.36	0.08	…†	…†	2.20	NS

Notes: The ratio of deviance to degrees of freedom (mid-September, 52/36; early July, 55/36; mid-September, 41/40; mid-August, 27/36) evaluates the model fit (see *Methods: Statistical analyses*). The summary statistics are presented in Fig. 5.

† Reduced model in Enteromorpha (see Methods: Statistical analyses).

mortality factor at the early life stages of this species (cf. Malm et al. 1999).

Nutrient enrichment caused a clear decline in the density of the slowly growing algae F. vesiculosus and C. tenuicorne. This decline occurred also on the herbivorefree substrates, which excludes the role of consumption as the sole cause. We therefore suggest that the slowlygrowing algae were suppressed by competition with the opportunistic ephemerals. The responses of F. vesiculosus and C. tenuicorne to fertilization do not fit those models that predict the number of species first to increase, and later to decrease, with the increasing productivity (Kondoh 2001, Worm et al. 2002). If a large part of the species forming the community is adapted to a low productivity environment, nutrient enrichment is expected to monotonically decrease species richness. This may be particularly true with the several species in the species-poor northern Baltic Sea.

The species benefiting from the herbivory were the red alga C. tenuicorne and, momentarily, the filamentous brown algae in deep water. Although we consider release from the interspecific competition as the likely mechanism behind the observed pattern, this experiment was not designed to reveal such a causal relationship. However, as a slowly growing species, C. tenuicorne may not be able to compete for space with the opportunistic species and herbivory can benefit the alga only if it deters herbivores (e.g., chemical defenses) and thereby redirects feeding to other species. C. tenuicorne is not preferred by isopod grazers (Jormalainen et al. 2001) that are important herbivores in this system. On the other hand, the filamentous brown algae were readily consumed later in the autumn at both the depths and thus the release from grazer control was only momentary and likely linked to changes in grazer abundance and community composition and consequent change in feeding preferences.

The fast recruitment of ephemerals may take place through over-wintering propagules (Lotze et al. 1999), which were not available in this study, or through high spore production and fast-growing sporophytes or zygotes (this paper, Hoffmann and Ugarte 1985) based on rapid nutrient uptake (Wallentinus 1984). According to macroalgal NO₃-N or PO₄-P uptake rates, the species can be ordered as follows: *C. glomerata* > *Enteromorpha* spp. > *P. littoralis* > *C. tenuicorne* > *F. vesiculosus* (Wallentinus 1984). In shallow water, all of the opportunistic species benefited from low and high nutrient enrichment when provided a refuge from herbivory. In deep water, on the contrary, algae could generally not take advantage from the high nutrient enrichment, probably due to low light level. Thus, the bottom-up forces have more potential to affect algal communities in shallow than in deep water (i.e., supporting hypothesis H_5), which, however, does not preclude the actual limitation of algal abundance being exerted by the grazer trophic level.

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APPENDIX A

Herbivore density in enriched and ambient nutrient conditions at two sublittoral depths (Ecological Archives E088-052-A1).

APPENDIX B

Statistical analysis (repeated-measures ANOVA) of macroalgal diversity across the four dates from July to November (*Ecological Archives* E088-052-A2).

APPENDIX C

Treatment effects on macroalgal species at times not presented in the article (Ecological Archives E088-052-A3).