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Strong bottom-up and top-down control of early life stages of macroalgae

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Abstract

In contrast to most pelagic primary producers, benthic macrophytes pass through morphologically distinct life stages, which can be subject to different ecological controls. Using factorial field experiments, we investigated how grazing pressure (three levels) and nutrient supply (four levels) interact in controlling the passage of marine macroalgae through an apparent recruitment ''bottleneck'' at the germling stage. In comparative experiments, we asked whether relative bottom-up and top-down effects on early life stages (<4 week germlings) vary (1) between the eutrophic Baltic Sea and the oligotrophic NW Atlantic, (2) across seasons in the NW Atlantic, and (3) among annual and perennial macroalgae. In both systems nutrient enrichment favored and grazers suppressed recruitment of green and brown annual algae; however, enrichment effects were much more pronounced in the Baltic, whereas grazer effects dominated in the NW Atlantic. Grazers induced a shift from grazer-susceptible green to more resistant brown algae in the Baltic without reducing total germling density. In the NW Atlantic, grazers strongly reduced overall recruitment rate throughout all seasons. Effects on perennials were similar in both systems with moderate losses to grazing and no effects of nutrient enrichment. Recruit densities and species composition shifted with season in the NW Atlantic. We conclude that the relative effects of grazers and nutrient enrichment depended on the nutrient status of the system, algal life history strategy, and season. Strong bottom-up and top-down controls shape benthic community composition before macroalgae reach visible size.

Benthic macrophyte communities represent important links in marine nutrient and carbon cycles, form a base of nearshore food webs, and provide crucial habitat and nursery area for many associated plants and animals (Smith 1981; Duggins et al. 1989; Duarte 1995; Worm et al. 2000*a*). In recent decades, coastal ecosystems and their related functions have become impaired by increasing nitrogen loading from various anthropogenic sources (NRC 2000). Increasing nutrient availability often favors fast-growing annual algae over perennial vegetation with consequences for community structure, diversity, and functioning (Duarte 1995; Valiela et al. 1997; Worm et al. 1999, 2000*a*). Recent studies have demonstrated that grazing pressure can counterbalance the effects of moderate nutrient enrichment on macroalgal communities (Geertz-Hansen et al. 1993; Hauxwell et al. 1998; Worm et al. 1999; Lotze et al. 2000). As shown earlier for pelagic food webs (e.g., Sommer 1988; McQueen et al. 1989), bottom-up and top-down forces simultaneously influence macrobenthic populations and communities (Menge et al. 1997; Worm et al. 2000a). Their relative strength, however, may vary under different environmental conditions.

Almost all of our scant knowledge on the interactions of consumer and resource control of marine macroalgal communities comes from studies on adult life stages (Geertz-Hansen et al. 1993; Neckles et al. 1993; Hauxwell et al. 1998). However, in contrast to pelagic primary producers, macroalgae have complex life cycles where different life stages of the same species are part of the planktonic, microbenthic, and macrobenthic communities (Santelices 1990). Different factors can affect population development at different life stages, with potentially important implications for community dynamics. As in many organisms on land and in the sea (Underwood and Fairwether 1989; Grosberg and Levitan 1992; Baskin and Baskin 1998), early life stages likely represent the most vulnerable phases in the population development of seaweeds (Santelices 1990; Vadas et al.

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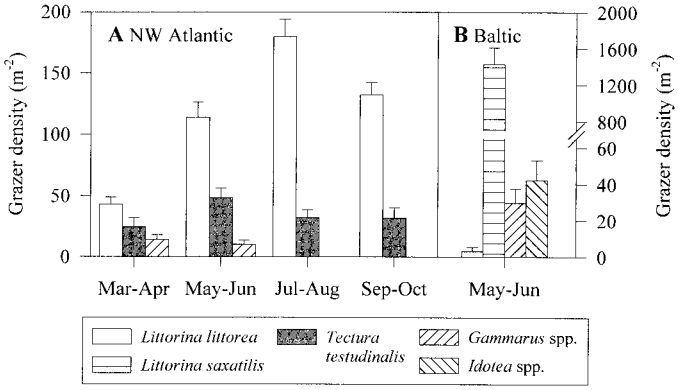

Fig. 1. Grazer densities per m^2 during the five experimental runs in (A) NW Atlantic and (B) Baltic. Densities are means of grazer and cage control plots (± 1 SE, $n = 16$). For *Gammarus* and *Idotea* species identification refer to text.

1992). We were interested how the passage of macroalgae through this recruitment bottleneck is ecologically controlled by grazing and nutrient availability.

Macroalgal propagules and germlings are delicate structures often lacking mechanisms of protection or resistance against physical and biological stresses found in adults (Lubchenco 1983; Brawley and Johnson 1991). Thus, both presettlement and postsettlement stages suffer from high losses to mortality due to consumption, competition, or disturbance (Santelices 1990; Vadas et al. 1992). Furthermore, they strongly respond toward changes in their abiotic environment (Santelices 1990), sometimes in different ways compared with adult algae (Lotze et al. 1999). Nutrients can control germination rate, thereby counteracting on grazer effects (Lotze et al. 2000).

In this study, we used factorial field experiments in order to investigate the response of early life stages of macroalgae following manipulation of grazer presence and nutrient enrichment. We asked whether bottom-up and top-down effects on macroalgal recruitment differ (1) among annual and perennial species and (2) across four seasons, and (3) we compared how experimental effects varied between an oligotrophic and a eutrophic site. We performed five factorial field experiments: one in spring in the eutrophic Baltic Sea, and four from early spring to fall in the oligotrophic NW Atlantic. Algal propagules settled, germinated, and grew on ceramic tiles exposed over a period of 4 weeks before we determined germling density, germling length, and macroalgal species composition.

Methods

Study sites—This study was carried out in 1998 in Maasholm Bay (54°41′N, 10°0′E), outer Schlei Fjord, Germany, western Baltic Sea and in 1999 in Bald Rock (44°28.3′N, 63°34.7′W), Sambro Harbor, Nova Scotia, NW Atlantic. Both sites are located in sheltered embayments and have similar habitat structure and species composition. The bottom at both sites consists of sandy sediment with scattered rocks and boulders. These hard substrata are mainly covered by perennial seaweeds (*Fucus vesiculosus* L. in the Baltic, *F. vesiculosus, F. spiralis* L., *Ascophyllum nodosum* L. in the NW Atlantic) and an associated assemblage of epiphytic and epilithic annual algae. In the Baltic, bloom-forming *Pilayella littoralis* L. and *Enteromorpha intestinalis* Link dominate the annual flora and epiphytize much of the perennial vegetation in spring and summer (Lotze et al. 2000). In the NW Atlantic, only *P. littoralis* is seasonally abundant as an epiphyte on *Fucus.* The numerically dominant grazers at both sites are littorinid snails. Amphipods (both sites), isopods (Baltic), and small limpets (NW Atlantic) are less abundant (Fig. 1). Temperature range in the Baltic in 1998 was -0.5 to 21.3°C with maxima in July and August and minima in January and February with sporadic ice coverage. In the NW Atlantic in 1999, temperature ranged from -0.5 to 22.8°C with maxima in August and September and minima in January and February with sporadic ice coverage. Salinity fluctuated seasonally between 12 and 20 PSU at the Baltic site and 22 and 31 PSU at the NW Atlantic site. The Baltic site is tideless, but frequent wind-driven water level fluctuations have amplitudes of 1.5 m around mean water level. The NW Atlantic site shows maximum tidal amplitudes of 2.1 m. The experiments were set up at 0.8 m depth in the Baltic and 1 m below mean water level in the NW Atlantic. Thus the experiments were not exposed to air except for brief periods during spring tides in the NW Atlantic. Summer nutrient concentrations in the water column typically remain close to the detection limit at both sites (0.0–0.3 μmol L^{-1}), phosphate remains detectable at 0.1–0.6 μmol L^{-1} (Worm 2000). Winter nutrient concentrations are much higher at the Baltic site, reaching 10–15 μmol L^{-1} ammonium, 100–150 μmol L^{-1} nitrate, and 2 μmol L^{-1} phosphate, compared with the NW Atlantic site (1–2 μmol L^{-1} ammonium, 2–6 μmol L^{-1} nitrate, and 0.6 μmol L^{-1} phosphate).

Experimental design—We investigated the relative effects of nutrient enrichment and grazer presence on macroalgal recruitment in factorial field experiments in the Baltic Sea 1998 (one run) and in the NW Atlantic 1999 (four runs). Macroalgal recruitment was assessed by monitoring the establishment of germlings on ceramic tiles. Here recruitment is defined as the establishment of germlings that are visible at 25–40 power magnification under a dissecting microscope. Recruitment includes the processes of propagule settlement, germination, and germling growth over an experimental period of 4 weeks for each experimental run. We used a larger, year-round experimental study (Worm 2000; Worm et al. 2000*a*) as a platform for our short-term (4 week) experimental runs. In this larger setup, grazer presence and nutrient enrichment were manipulated with cages and nutrient diffusers to study their effects on benthic community structure and function. Our experimental run in the Baltic was performed during the main recruitment period of the three dominant algal species, which occurred from mid-May to mid-June in 1998 (Worm et al. 1999; Lotze et al. 1999, 2000). In the NW Atlantic, we carried out four runs across four seasons, early spring (mid-March to mid-April), late spring (mid-May to mid-June), summer (mid-July to mid-August), and fall (mid-September to mid-October), because

it was not clear when the main settlement event(s) would occur.

In our experiments, we established a 2 × 4 orthogonal design for factorial ANOVA with the factors grazers (present, absent) and nutrient enrichment (no, low, medium, high level) and four replicates per treatment combination. This approach allowed testing for the main and interactive effects of nutrient enrichment and grazer presence on macroalgal recruitment.

Grazer presence was manipulated with cages (25 × 25 × 25 cm), which were made from a stainless steel frame covered with a clear 1-mm polyethylene mesh to effectively exclude all small-bodied mesograzers (*see below*) that dominated at our sites. Completely closed cages excluded grazers (no grazer treatment), whereas cages with one site cut open allowed grazer access (grazer treatment). All cages were brushed weekly, which was sufficient to prevent significant fouling on the mesh. Replicated light measurements revealed that inside the cages, light intensity was reduced by only 8% (LI-COR LI-192SA). Besides this main experiment, we conducted a control experiment to evaluate potential cage effects on algal recruitment, grazer density, and nutrient enrichment. Therefore, we compared grazer treatments with uncaged plots (cage control treatments), which were also combined with nutrient enrichment and replicated fourfold. Individual experimental units were placed within macroalgal communities and were separated 3–4 m to avoid interactions. Grazer densities were estimated once during each experimental run by visual underwater counts within open cages and around uncaged plots (25 × 25 cm area). Each plot was carefully inspected, including close examinations of the algal canopy and the rocks. These field counts may only represent first-order estimates for some of the smaller amphipods and isopods; however, their relative abundance in the various treatment should be assessed accurately.

Nutrient availability was manipulated with nutrient diffusers made of polyethylene mesh rolls and filled with a slow-release NPK-fertilizer (Plantacote Depot™ 6M, Urania Agrochem). This fertilizer consisted of pellets with a semipermeable polyurethane layer and contained 14% N (5.7% NO_3, 8.3% NH_4), 9% P (P_2O_5), and 15% K_2O. The effectiveness of this type of fertilizer was verified in a series of field tests by Worm et al. (2000*b*). That study revealed that nutrient release rates in seawater decline after 6 weeks. Thus, we replaced pellets in 6-week intervals. Diffusers were 3.5 cm in diameter with variable length according to the nutrient enrichment levels: no diffuser (no), 2.5 and 5 cm diffusers (low), 10 and 20 cm (medium), 40 and 80 cm (high) with 0, 10, 20, 40, 80, 160, 320 g fertilizer pellets, respectively. Averaged over the year, diffusers enriched water column inorganic nitrogen concentrations by 6–200%, depending in a linear fashion on diffuser length and fertilizer mass (Worm 2000; Worm et al. 2000*b*). The diffusers were placed inside the cages or fixed with steel tent pegs on cage control plots. Treatments without enrichment were replicated fourfold, each diffuser length was replicated twofold (resulting in four replicates for low, medium, and high enrichment levels). To test whether diffusers were releasing nutrients and to estimate enrichment levels, nutrient background and enrichment concentrations were analyzed once during each 4-week experimental run. We collected water samples with 30-ml plastic syringes 10–15 cm above each experimental plot. Samples were filtered immediately (Whatman GF/F filters) and analyzed within 3 h for dissolved ammonium, nitrate, and orthophosphate on a Technicon autoanalyzer.

Macroalgal recruitment was assessed on the unglazed, rough side of sterilized ceramic tiles (7.5 × 7.5 cm) over a period of 4 weeks in each run. Tiles were fixed to the cage frame near the bottom and placed in a slightly tilted position to prevent sediment deposition on the tile surface. On cage control plots, tiles were fixed in the same position to steel tent pegs. After 4 weeks, abundance of macroalgal germlings (>100 μm length) was counted at the species level with a dissecting microscope. If necessary, a compound microscope was used for species identification. We counted 10 subsamples (4 × 4 mm) per tile. Maximum height of the overall germling canopy and thus maximum germling length was measured with a ruler to a resolution of 1 mm and served as an estimate of maximum growth response. We calculated single-species and total germling density per cm^2.

Data analysis—We used fixed-factor ANOVA to analyze main and interactive effects of grazers (no grazer, grazer) and nutrient enrichment (no, low, medium, high) on the dependent variables total germling density and germling length. Moreover, we tested differences among the four seasonal runs in NW Atlantic. As further dependent variables, we chose nutrient concentration and grazer density to test for efficacy of experimental manipulation. The effects of diffusers on water column nutrient concentrations were also assessed by linear regression models. The control experiment for cage artifacts was analyzed like the main experiment, except that the effect cage (grazer, cage control) replaced the effect of grazers. For post hoc comparisons among enrichment levels, we used Tukey-Kramer's procedure at the $\alpha = 0.05$ significance level. Homogeneity of variances was checked by Cochran's test. Data were log transformed or square root transformed if necessary. The relative effect size of main effects and interactions in the ANOVA was calculated as percent variance explained using the ω^2 measure, as recommended for fixed-factor models (Howell 1992). Treatment effects on species composition were analyzed by MANOVA using the Pillai trace statistics, which is most robust against violations of model assumptions (Johnson and Field 1993; Scheiner 1993). This approach was chosen because it takes cross correlations among species abundances into account. Since most tests for multihomoscedascicity are discussed controversially by statisticians, we followed the advice of Scheiner (1993) and checked for univariate homogeneity of variances by Cochran's test and visually inspected our data set for possible correlations between dependent variables that differ among groups. Data were log transformed. When MANOVA results were significant, we explored effects on selected abundant species by protected univariate ANOVA. Therefore, α levels were Bonnferoni-adjusted in cases where more than one analysis was performed (Scheiner 1993).

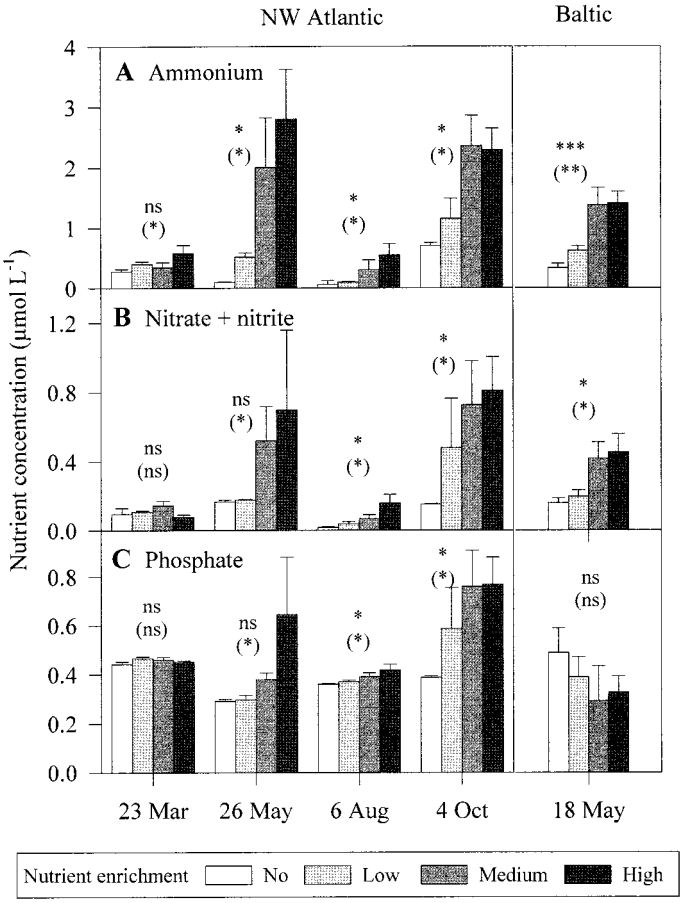

Fig. 2. Water column nutrient concentrations in the experimental runs in the NW Atlantic (left) and the Baltic (right) for (A) ammonium, (B) nitrate and nitrite, and (C) phosphate. Significant increases of water column nutrient concentrations in enriched treatments were assessed by ANOVA (no versus low, medium, high enrichment) and are indicated with asterisks. Significant linear regression results are given in brackets (one asterisk, $P < 0.05$; two asterisks, $P < 0.001$; three asterisks, $P < 0.0001$). Data are means (± 1 SE, $n = 4$). Note that these single measurements per experimental run can only be a rough estimate for average values during the 4-week periods.

Results

Grazer density—Total grazer abundance was 10 times higher in the Baltic compared to the NW Atlantic (Fig. 1), and species composition differed between the two sites. In the Baltic, *Littorina saxatilis* Olivi was by far the most abundant grazer (Fig. 1B), followed by *Idotea* spp. (>95% *I. chelipes* Pallas, <5% *I. baltica* Pallas) and *Gammarus* spp. (*G. locusta* L., *G. salinus* L., *G. zaddachi* Sexton). In the NW Atlantic, *Littorina littorea* L. was the most abundant species followed by the limpet *Tectura testudinalis* Müller and *Gammarus oceanicus* Segerstrale (Fig. 1A). Total grazer abundance differed significantly between the four seasonal runs in the NW Atlantic (ANOVA, $F_{3,96} = 28.34$, $P = 0.0001$) with significantly lower grazer densities in March–April than in the following months (Tukey-Kramer, $P < 0.05$).

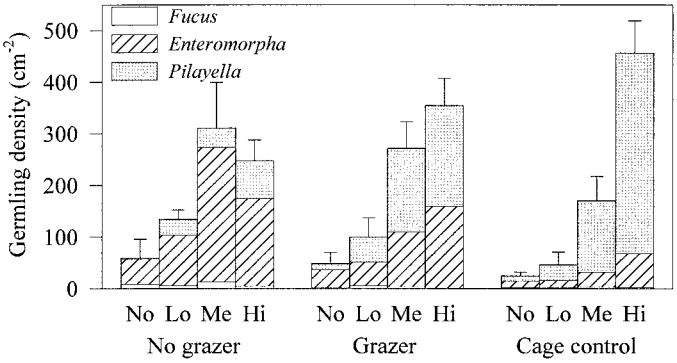

Fig. 3. Effects of grazers (no grazer, grazer, cage control) and nutrient enrichment (no, low [lo], medium [me], high [hi]) on macroalgal recruitment in the Baltic, in May–June 1998. Germling densities were estimated after 4 weeks (means ± 1 SE, $n = 4$). Temperature range during the experiment was 12.7–19.9°C (mean 17.3°C $\pm$ 1.3 SE).

Manipulation of grazer presence by cages was successful. Grazers were excluded from no grazer treatments with closed cages, which were checked weekly in order to remove rare intruders (mostly small amphipods). Comparison of grazer (open cages) and cage control (uncaged) treatments, however, revealed that abundances of slow-moving snails (*L. saxatilis, L. littorea*) were reduced by 30–60% in grazer treatments compared to cage controls, which was most likely an effect of the weekly cage-cleaning procedure, after which slow-moving snails needed time to reinvade. Abundances of mobile crustaceans (*Idotea, Gammarus*) were slightly higher in grazer treatments compared to cage controls, which might be a result of higher food supply and protection in open cages. In the Baltic, total grazer density was significantly reduced by 61% in grazer treatments compared to cage controls (ANOVA, $F_{1,24} = 9.10$, $P = 0.006$). In NW Atlantic, total grazer densities in grazer treatments were significantly reduced by 30–40% compared to cage controls in all seasons (ANOVAs, $P < 0.02$) except fall ($F_{1,24} = 0.241$, $P = 0.63$). Thus overall, grazer effects were conservatively estimated in both experiments. Nutrient enrichment had no effects on grazer densities during any experimental run (ANOVA, $P > 0.05$).

Nutrient enrichment—Overall, nutrient background and enrichment concentrations during the experimental runs were comparable between the Baltic and NW Atlantic (Fig. 2). Ammonium concentrations were significantly elevated by nutrient diffusers in all experimental runs (Fig. 2A), whereas nitrate enrichment was successful in all runs except for March–April (Fig. 2B), and phosphate enrichment was successful in all runs except for March–April in the NW Atlantic and in May in the Baltic. There were no cage or grazer effects on nutrient concentrations (ANOVAs, $P > 0.05$).

Baltic 1998—The Baltic experiment was run during the main reproductive period of the three dominant species in this system, *Fucus vesiculosus, Enteromorpha intestinalis,* and *Pilayella littoralis.* All three species recruited on experimental tiles (Fig. 3). Species composition was significantly

Table 1. MANOVA results (Pillai trace statistics) of grazer and nutrient effects on macroalgal species composition in the Baltic 1998 and in three seasonal runs in NW Atlantic (NWA) 1999. Because only one species (*Fucus vesiculosus*) recruited in the NW Atlantic in May–June, this run was not analyzed by MANOVA (for ANOVA results on *Fucus* germling density *see Table 2*). G, grazer; N, nutrients, **bold** *P* values are $P < 0.05$. Significant cage effects are indicated with asterisks (one, $P < 0.05$; two, $P < 0.001$).

Site and season	Source	*df*	Pillai trace	*F*	*P*	Cage effect
Baltic, May–June	grazer	3, 22	0.536	8.483	**0.0006**	**
	nutrients	9, 72	0.980	3.883	**0.0005**	
	G × N	9, 72	0.259	0.754	0.6582	
NWA, March–April	grazer	2, 23	0.709	28.073	**0.0001**	*
	nutrients	6, 46	0.365	1.784	0.1225	
	G × N	6, 46	0.377	1.856	0.1082	
NWA, July–August	grazer	7, 18	0.790	9.667	**0.0001**	
	nutrients	21, 60	0.877	1.181	0.2998	
	G × N	21, 60	0.695	0.862	0.6360	
NWA, September–October	grazer	10, 15	0.905	14.262	**0.0001**	
	nutrients	30, 51	1.268	1.245	0.2410	
	G × N	30, 51	1.493	1.684	**0.0497**	

affected by nutrients and grazers (Table 1). Grazers caused a shift from dominance of *Enteromorpha* in the absence of grazers to dominance of *Pilayella* in the presence of grazers (ANOVA, grazer effect on *Enteromorpha*, $F_{1,24} = 3.71$, $P = 0.0661$; *Pilayella*, $F_{1,24} = 8.36$, $P = 0.0080$). There was no significant grazer effect on total germling density (Fig. 3, Table 2). *Fucus* recruits were of low abundance compared with annual algae and were significantly reduced by grazers (Fig. 3, ANOVA, $F_{1,24} = 15.19$, $P = 0.0007$). Nutrient enrichment favored *Enteromorpha* and *Pilayella* (ANOVA, nutrient effect on *Enteromorpha*, $F_{3,24} = 11.64$, $P = 0.0001$; *Pilayella*, $F_{3,24} = 23.02$, $P = 0.0001$) and hence increased total germling density (Table 2). However, the nutrient effect was more pronounced in *Pilayella*, resulting in a shift in species composition (Table 1). There was no nutrient effect on *Fucus* (ANOVA, $F_{3,24} = 1.55$, $P = 0.23$). In the control experiment, comparison of cage controls and grazer treatments revealed no cage effects on total germling density ($P > 0.1$), but there was a cage effect on species composition (MANOVA, $F_{3,22} = 7.55$, $P = 0.0012$), resulting from higher densities of *Enteromorpha* in grazer treatments than in cage controls (Fig. 3, ANOVA, cage effect: $F_{1,24} = 21.69$, $P = 0.0001$). This was likely caused by the reduced grazer densities in open cages (*see above*). There were no significant cage effects on *Pilayella* (ANOVA, $F_{1,24} = 0.01$, $P = 0.93$) and *Fucus* (ANOVA, $F_{1,24} = 0.75$, $P = 0.40$).

Maximum germling length in *Enteromorpha* and *Pilayella* (88–568 mm after 28 d) indicated very high growth rates of 0.4–0.5 d^{-1}, assuming exponential growth and an initial propagule size of 10 μm. Germling length increased with nutrient enrichment primarily in the absence of grazers (Fig. 4), whereas grazers reduced germling length consistently only in cage control plots. The reduction of germling length by grazers was accompanied by the shift from a longer (*Enteromorpha*, maximal length 220 mm) to a shorter (*Pilayella*, maximal length 98 mm) germling turf (Fig. 3), which may have caused the unimodal response in grazer treatments. These differences in grazing effects resulted in significant grazer × nutrient (Table 2) and cage × nutrient interactions ($F_{3,24} = 5.89$, $P = 0.004$). Relative effects sizes, calculated as ω^2, showed that in the Baltic nutrient enrichment explained the largest part of the variance in total germling den-

Table 2. ANOVA results of grazer and nutrient effects on total germling density and germling length of new recruits. G, grazer; N, nutrients; S, season, ω^2, explained variance in percent for significant effects. Significant cage effects are indicated with asterisks (one, $P < 0.05$).

			Total germling density				Germling length			
Site	Source	*df*	MS	*F*	*P*	ω^2	MS	*F*	*P*	ω^2
Baltic	grazer	1	0.01	0.07	0.7885		11,858	13.70	0.0011	11.3
	nutrients	3	1.38	18.06	0.0001	63.1	12,858	14.85	0.0001	36.8
	G × N	3	0.14	0.61	0.6123		8,528	9.85	0.0002*	23.5
	residual	24	1.84				865			
NWA	season	3	5.27	102.90	0.0001	49.0	0.866	37.02	0.0001	17.3
	grazer	1	9.25	180.50	0.0001	28.3	7.64	326.83	0.0001	52.2
	nutrients	3	0.17	3.37	0.0216	1.2	0.22	9.56	0.0001	4.1
	S × G	3	0.02	0.31	0.8220		0.22	9.26	0.0001	4.0
	S × N	9	0.08	1.57	0.1362		0.04	1.81	0.0769	
	G × N	3	0.03	0.48	0.6956		0.01	0.52	0.6711	
	S × G × N	9	0.06	1.24	0.2806		0.04	1.73	0.0925	
	residual	96	0.05				0.02			

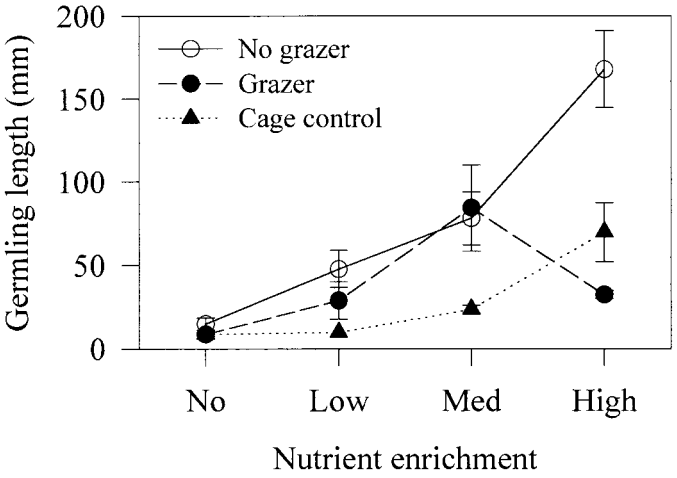

Fig. 4. Effects of grazers and nutrient enrichment on macroalgal germling length in the Baltic. Lengths were measured after 4 weeks of algal recruitment and growth (means ± 1 SE, $n = 4$).

sity (63.1%) and germling length (36.8%), compared to grazing (0%, 11.3%) and the interaction between the two factors (0%, 23.5%, Table 2).

NW Atlantic 1999—Overall, recruit densities in the NW Atlantic were only 2–20% of those in the Baltic (Fig. 5), and maximum length of the germling canopy reached only 10–20% of that in the Baltic (Fig. 6). Species reaching highest germling length were *Ulothrix flacca* Thuret, *Callithamnion tetragonum* S. F. Gray, and *Pilayella littoralis.* Calculated maximum relative growth rates of these annuals were <0.3 d^{-1}. There was no main recruitment period in spring or summer (as found in the Baltic), but recruit densities and species composition differed between seasonal runs, whereas germling length was more similar among runs. Fucoids, which dominated the adult community, recruited from mid-March to mid-June. In March–April, all recruits were subtidal *Fucus evanescens* Agardh, whereas *F. vesiculosus* recruited in May–June. The only spring annual was *Ulothrix flacca* in March–April. In May–June, tube-dwelling diatoms (*Berkeleya* sp.) cooccurred with *Fucus.* In July–August, macroalgal recruitment was low, but there was high settlement of colonial cyanobacteria (*Calothrix* sp.) on the experimental tiles. A variety of green, red, and brown annuals recruited in summer and fall, with highest recruitment rates in fall.

Species composition in March–April, July–August, and September–October was significantly affected by grazers, but not by nutrients except for September–October (Fig. 5, Table 1), when we detected a significant nutrient × grazer interaction on species composition (Table 1). This interaction indicated that the green annuals *Cladophora* sp. Kuetz. and *Rhizoclonium riparium* Kuetz. increased with nutrient enrichment in grazer-exclusion plots but not in grazer-access plots, where their numbers remained very low whether nutrients were added or not. All green annuals (*Ulothrix flacca, Cladophora* sp., *Rhizoclonium riparium, Bryopsis plumosa* Agardh, *Enteromorpha intestinalis*) were strongly reduced by grazers (Fig. 5). Among red annuals, grazers reduced *Callithamnion tetragonum* and *Polysiphonia harveyi* J. Bailey,

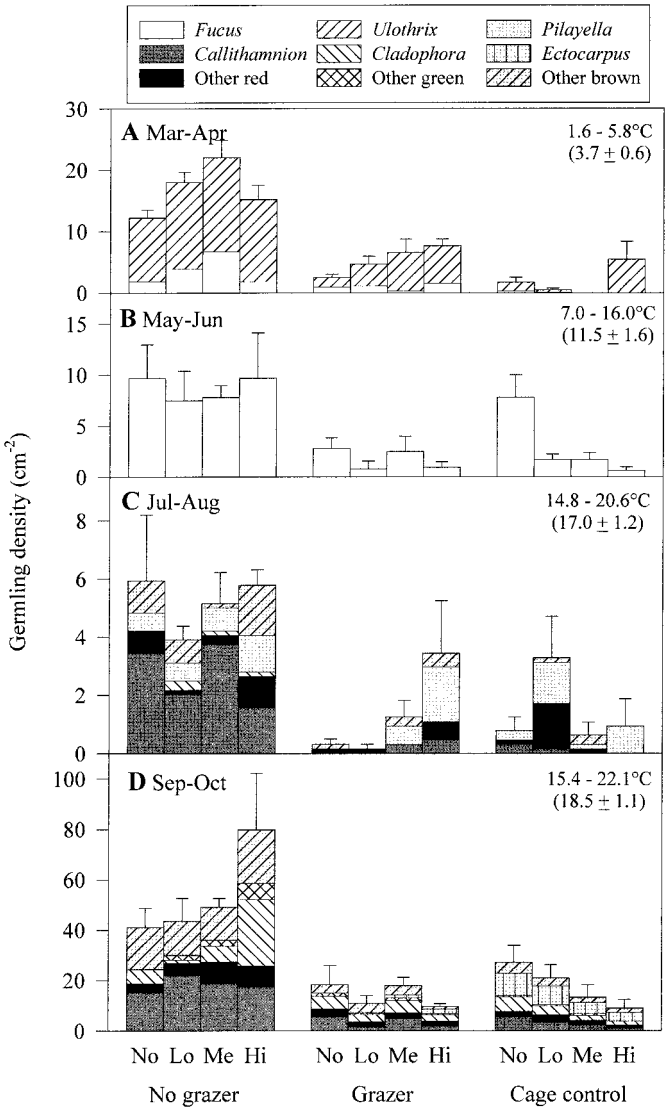

Fig. 5. Effects of grazers (no grazer, grazer, cage control) and nutrient enrichment (no, low [lo], medium [me], high [hi]) on macroalgal recruitment in four seasonal runs (A–D) in NW Atlantic. Germling densities were estimated after 4 weeks (means ± 1SE, $n = 4$). Temperature range and means during the individual runs are given in upper right corners. Different algal groups are indicated as follows: red annuals (dark gray and black), brown annuals (light gray), green annuals (white with pattern), perennials (plain white). *Fucus* in March–April is mainly *F. evanescens* and in May–June mainly *F. vesiculosus.* Other brown is mainly *Sphacelaria,* other green is mainly *Rhizoclonium,* other red is mainly *Polysiphonia* in grazer absence and *Erytrotrichia* and *Ceramium* in grazer presence.

but *Erytrotrichia carnea* Agardh and *Ceramium strictum* Harey increased in grazer-inclusion plots. Among brown annuals, grazers induced a shift from *Sphacelaria cirrosa* Agardh in grazer-exclusion plots to *Pilayella littoralis* (July–August) or *Ectocarpus fasciculatus* Harvey (September–October) in grazer-inclusion plots. Also, perennial *Fucus* recruits were reduced by grazing throughout their recruitment period (March–June, Fig. 5).

Combining all four runs, total germling density and max-

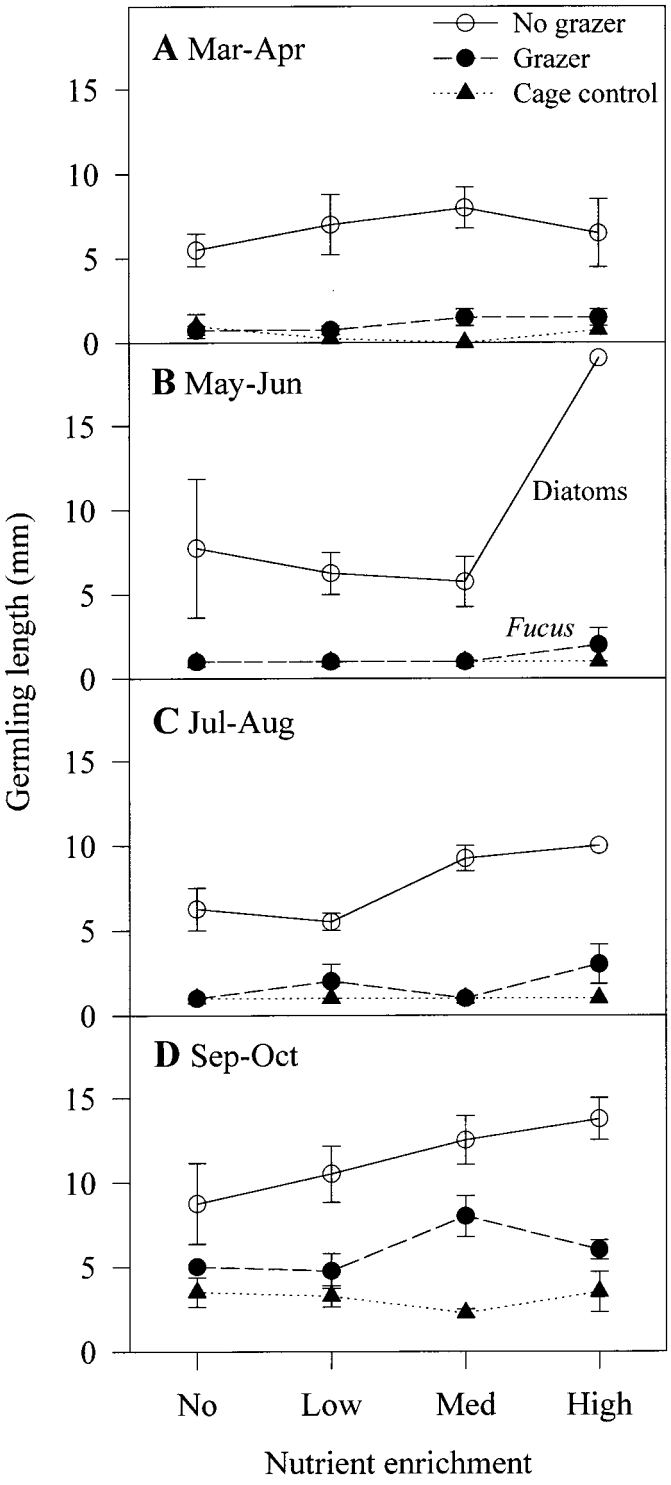

Fig. 6. Germling length of recruiting macroalgae as a function of nutrient enrichment and grazer presence in four seasons (A–D) in NW Atlantic. In (B) May–June, the germling length in no grazer plots was related to tube-dwelling diatoms, in plots with grazers present it was related to *Fucus vesiculosus*, the only macroalga recruiting in this season. Data are means (±1 SE, $n = 4$).

imum germling length were significantly affected by season, grazers, and nutrients (Table 2). A significant season × grazer interaction indicated decreased grazing effects on germling length (but not density) in fall compared to the three earlier runs (Tukey-Kramer, $P < 0.05$). Compared to grazing (explained variance $\omega^2 = 28.3\%$) and season (49.0%), nutrient enrichment explained only a very small fraction of variance (1.2%) in germling density. Germling length was slightly more affected by nutrients (explained variance 4.1%), but still, variation attributed to seasons and grazer treatments was much greater (17.3 and 52.2% respectively, Table 2).

The control experiment revealed a cage effect on total germling density in March–April (ANOVA, $F_{1,24} = 22.23$, $P = 0.0001$) due to reduced germling densities in cage controls compared to grazer treatments. This effect was not found in the following three runs ($P > 0.05$). Germling length was always slightly higher in grazer treatments compared to cage controls, which was significant in March–April (ANOVA, $F_{1,24} = 5.0$, $P = 0.035$) and September–October ($F_{1,24} = 22.93$, $P = 0.0001$). There was a cage effect on species composition in March–April (MANOVA, $F_{2,23} = 10.58$, $P = 0.0006$), which reflects the relatively stronger reduction of *Fucus* compared to *Ulothrix* by increased grazer pressure in cage controls (Fig. 5A).

Discussion

Our experiments revealed that nutrients and consumers have strong effects on marine macroalgal populations before they reach visible size. Because early life stages and recruitment processes represent critical phases in the population development of marine benthic organisms (Underwood and Fairwether 1989; Grosberg and Levitan 1992; Vadas et al. 1992; Lotze et al. 1999, 2000), invisible bottom-up and top-down controls likely bear important consequences on the structure and dynamics of benthic communities.

In our Baltic Sea experiment, nutrient enrichment strongly stimulated recruit density and growth of annual algae, whereas grazers had more limited effects. Among the annual algae, grazers induced a shift in community composition from dominance of *Enteromorpha* to dominance of *Pilayella.* In a previous study at our Baltic site, we have shown that *Enteromorpha* is the dominant space competitor (Lotze et al. 2000) but is also more susceptible to herbivory compared with *Pilayella* (Lotze and Worm 2000). Because grazers simply induced the replacement of a grazer-susceptible alga by a more resistant one, no significant decline in total germling density occurred (Fig. 3). However, the dominant grazers at the Baltic site (*Littorina saxatilis, Idotea* spp., *Gammarus* spp.) were shown to be potentially highly effective in diminishing populations of annual macroalgae (Lotze and Worm 2000), and it was suggested that grazer control could be a major counteracting force that prevents destructive macroalgal blooms by intercepting bloom development at early life stages (Lotze et al. 1999, 2000). The present results indicate, however, that grazer control at the earliest life stages may become less efficient when nutrient loads further increase and more grazer-resistant bloom-forming species like *Pilayella* become dominant.

The perennial seaweed *Fucus vesiculosus* suffered moderate grazing losses at the early recruitment stage and did not benefit from nutrient enrichment. The lack of response to nutrient enrichment in *Fucus* was probably the result of slow growth of this species (Pedersen 1995), which never gained more than 1 mm length in 4 weeks (compared to >15 mm for annuals). It is interesting that this study reveals a negative direct effect of grazers on recruiting *Fucus,* whereas longer term and larger scale studies indicated an indirect positive effect of grazers on *Fucus* establishment in the Baltic, caused by grazer-mediated relaxation of competition between *Enteromorpha* and *Fucus* (Worm et al. 1999, 2000*a*). Clearly, our current short-term experiments are not designed to address the outcome of macroalgal competition and may therefore not capture indirect positive effects of grazers on *Fucus.*

In the NW Atlantic, grazers reduced total germling density and maximum height of the germling canopy throughout the year. On a species level, net grazer effects were strongly negative for all species except *Pilayella* and *Ectocarpus,* which likely contain antiherbivore substances (Hay and Fennical 1988). Strong effects of the dominant grazer *Littorina littorea* on macroalgae are common in the NW Atlantic (Lubchenco 1983; Worm 2000), whereas in the Baltic this species has limited effects due to preference for microalgae (Lotze and Worm 2000). Nutrient enrichment had only small beneficial effects on a few annual species in the NW Atlantic, mostly on green annuals (*Ulothrix, Cladophora, Rhizoclonium*). There was a seasonal shift in species composition (Fig. 5) from grazer-susceptible, fast-growing green algae in early spring (i.e., *Ulothrix*) toward more grazer resistant but slower growing red and brown annuals in summer (i.e., *Callithamnion* and *Pilayella*). Interestingly, green algae again appeared late in the year (September–October, Fig. 5), when grazer abundance declined and nutrient concentrations increased (Figs. 1, 2). Thus, seasonal trends of decreasing nutrient availability and increasing grazer abundance toward summer (Figs. 1, 2) appear to restrict recruitment of fast-growing grazer-susceptible species to temporal refuges in early spring and fall (Littler and Littler 1980). Similar seasonal shifts in nutrient and grazer effects and species composition were reported from seagrass-epiphyte assemblages (Neckles et al. 1993) and macroalgal turfs on coral reefs (Hatcher and Larkum 1983).

Although the responses of perennial algae toward grazer and nutrient manipulation were similar at the two study sites (moderate grazing losses, no response to nutrients), responses of annual algae differed markedly (strong nutrient and weak grazer effects in the Baltic, weak nutrient and strong grazer effects in the NW Atlantic). Annual, fast-growing algae have been shown to be more sensitive to nutrient enrichment compared with perennial, slow-growing algae (Pedersen 1995). However, since nutrient background and enrichment concentrations, as well as water temperature and light conditions, were very similar during the experiments in the Baltic and the NW Atlantic (Fig. 2), we would have expected similar responses to nutrient enrichment in annual algae, especially in those species occurring at both study sites (i.e., *Pilayella littoralis, Enteromorpha* spp.). It appears that annual macroalgae adapted to grow in high-nutrient environments show elevated nutrient uptake and maximal growth rates compared with algae growing in low-nutrient environments (Pedersen 1995; Valiela et al. 1997). Consequently, algae in high-nutrient environments can display higher nutrient demands and may experience more pronounced nutrient limitation during summer nutrient depletion compared with species adapted to low-nutrient environments. High growth responses to nutrient enrichment in Baltic algae may also weaken grazer effects (Fig. 3; Duarte 1995). On the other hand, with lower ability to use high nutrient supply, algae growing in the NW Atlantic show lower responses toward nutrient enrichment, which cannot compensate for high grazing losses (Fig. 5; Duarte 1995). Since grazer assemblages differed between the two study sites (Fig. 1), we can only compare relative strengths of grazer effects. However, considering the extremely high abundance of grazers in the Baltic and their demonstrated effectiveness (Lotze et al. 2000; Worm et al. 2000*a*), the weak grazer control may not be easily explained by low grazing pressure.

In contrast to annuals, perennials are typically more strongly adapted to low-nutrient conditions with slow growth rates, low nutrient requirements, high storage capacities, and increased antiherbivore defenses to reduce grazing losses (Littler and Littler 1980; Duarte 1995). These general considerations may explain lack of strong nutrient responses of *Fucus* in both experiments, but not its susceptibility to grazing. It appears that chemical defenses are not sufficiently expressed to prevent grazing losses in the earliest life stages of *Fucus vesiculosus,* as indicated by results from this and several previous reports (Lubchenco 1983; Denton et al. 1990).

Taken together, our results suggest that, at the eutrophic Baltic site, bottom-up control of early life stages may be a predominant structuring force on which grazers can hardly counteract. In turn, at the oligotrophic NW Atlantic site, top-down control may be the dominant structuring force, and nutrient enrichment can hardly overcome this control. Although we admit that no valid generalizations can be drawn from a study involving two sites, we think that our results match similar patterns that emerged in different ecosystems. For example, it was proposed that in lake ecosystems, as productivity increases, top-down control at lower trophic levels should weaken and bottom-up control should become more important (McQueen et al. 1989). Similarly, in salt-marsh ecosystems Van de Koppel et al. (1996) observed that herbivore control of plant biomass weakened at high productivity levels. More experimental studies along gradients of nutrient supply and primary productivity are needed to further substantiate these arguments.

Conclusions—The discussion about bottom-up versus top-down control of primary producers in a wide range of ecosystems revealed the dependence of one control on the other (e.g., Menge et al. 1997; Proulx and Mazumder 1998). We propose that the relative effects of both controls may depend on (1) the nutrient status of the system (oligotrophic systems more strongly top-down controlled than eutrophic systems), (2) seasonal variation in nutrient supply and grazing pressure (high grazing pressure, low nutrient supply in the north-temperate summer), (3) the species life strategies (annuals re-

spond more strongly to shifts in grazing and nutrient supply than perennials), and (4) the life stage of the organisms in study. We demonstrated strong responses of early life stages to nutrient enrichment and grazers indicating their exceptional sensitivity toward these factors. Thus, responses of populations and communities to natural or human-induced changes in the environment are likely to be most evident in the performance of early life stages. These changes can have far-reaching effects on the population and community level, even when a response of adult algae is undetectable (Lotze et al. 1999).

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