Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading

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Abstract

By factorial field experiments we analyzed the relative effects of increased nutrient (N+P) loading and natural grazing pressure on species composition, carbon storage, and nitrogen retention in the Baltic Sea littoral food web, composed of macroalgae, grazers (snails, isopods, amphipods), and predators (shrimps, crabs, fish). Nitrogen was depleted relative to phosphorus throughout most of the year. Increasing nitrogen (6–200% over ambient concentrations) enhanced algal productivity and cover of fast-growing annual algae, grazer, and predator densities, suggesting a three-level bottom-up effect. With increasing nitrogen loading, annual algae increasingly blocked perennial algal recruitment (65–98% decrease) and growth. Grazers counteracted the effects of nutrient enrichment on algal species composition through selective consumption of annual algae. Grazer exclusion had equivalent negative effects on perennial recruitment as a 85% increase in nitrogen loading. Nutrient enrichment increased algal nitrogen content and decreased tissue C : N ratios in spring and summer but not in fall. Carbon storage and nitrogen retention, measured as C and N retained in plant biomass at the end of the growth season, were increased by grazers (C: 39%, N: 24%) but decreased with increasing nitrogen loading (C: −71%, N: −74%). Our results emphasize the important role of grazers in buffering moderate eutrophication effects and illustrate how food web interactions and shifts in species composition are tightly linked to coastal ecosystem function.

Currently, humans are more than doubling the rate at which nitrogen and phosphorus enter the global biogeochemical cycles (Schlesinger 1991; Vitousek et al. 1997). Through river, groundwater, and atmospheric transport, a large fraction of these excess nutrients passes through estuarine and coastal ecosystems (Howarth et al. 1996; Nixon et al. 1996; Jickells 1998). Primary producers in these systems can act as efficient filters and largely control nutrient cycling and the export of nutrients to the open ocean (Jickells 1998). This function has been pointed out as one of the most important ecosystem services provided by marine ecosystems (Costanza et al. 1997). However, increasing nutrient loading can change primary producer abundance and species composition, with feedbacks on the cycling and processing of nutrients. In this study, we asked how the effects of increasing nutrient loading are mediated by food web interactions in the Baltic Sea coastal system.

Detailed experimental work in freshwater systems showed that nutrients and consumer strongly influence algal abundance, biogeochemical cycling, and fisheries production (e.g., Carpenter et al. 1985, 1996; Sommer 1985, 1992; Power 1990; Brett and Goldman 1997). In contrast, very few studies in the marine environments considered nutrient and consumer effects simultaneously. Experimental evidence for coastal phytoplankton assemblages (Kivi et al. 1993; Metaxas and Scheibling 1996) and seagrass–epiphyte assemblages (Neckles et al. 1993; Williams and Ruckelshaus 1993) indicates generally strong nutrient and grazing effects on plant species composition and biomass, together with pronounced seasonal variability. Macroalgal assemblages that dominate biomass and productivity of most of the worlds rocky shores (Mann 1973) have been studied intensively for consumer effects (Lubchenco and Gaines 1981; Menge and Farrell 1989; Worm and Chapman 1998), but these were rarely weighed against the effects of nutrients (Menge et al. 1997). Recent work on Baltic macroalgal communities (Lotze et al. 1999, 2000; Worm et al. 1999) indicated interactive effects of grazers, nutrients, and algal propagule supply during summer nutrient limitation. The purpose of this study was to assess the relative effects and possible interactions between nutrients and consumers throughout an entire growth period (February–November) and model changes in species composition, carbon storage, and nitrogen retention (measured as C and N retained in plant biomass at the end of the growth period) along a nutrient gradient. Using factorial field experiments, we tested the hypotheses that (1) increasing N and P loading, grazers and predators interact in controlling macroalgal abundance and species composition; and (2) that changes in algal and grazer abundance feed back on higher trophic levels. Moreover, we hypothesized (3) tight links between changes in species composition and ecosystem functioning (primary productivity, carbon storage, and nitrogen retention) in the coastal zone.

Methods

Study site and food web—Experiments were conducted in the littoral zone close to the Maasholm field station of the Institut für Meereskunde, outer Schlei Fjord (54°41′N, 10°0′E), Western Baltic Sea, Germany. The site is protected
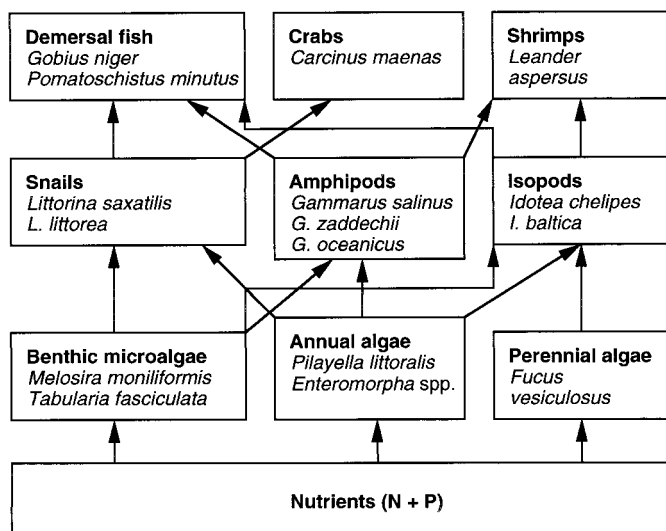
Fig. 1. Primary components of the coastal hard-bottom food web at the study site Maasholm, Western Baltic Sea. Within a functional group, abundant species are listed before rare species. Second-level carnivores (gulls *Larus* spp.; cod *Gadus morhua*) and filter feeders (*Mytilus edulis, Balanus improvisus*) were present but are not shown because of their low abundance throughout the experiment.

from severe wave action (maximum fetch is 5 km). Tides are unimportant, but irregular wind-driven sea-level changes reach an amplitude of ±0.5 m around mean water level. Salinity fluctuates between 12–18 PSU in summer and 14–20 PSU in winter. Water temperature ranges between -1 to $2°C$ in winter and 16–25°C in summer. The bottom consists of sand, gravel, and boulders. Hard substrata are dominated by dense stands (84 $\pm$ 7.3% cover on rocks, mean ±1 SE) of the perennial brown seaweed *Fucus vesiculosus* (*Fucus* hereafter). Annual macroalgae (mostly the filamentous brown *Pilayella littoralis,* hereafter *Pilayella,* and the foliose green *Enteromorpha* spp., hereafter *Enteromorpha*) and benthic microalgae (mostly diatoms) co-occur with *Fucus* (Lotze et al. 1999). These primary producers are consumed by a species-rich grazer guild, which is consumed by crustacean and fish predators (Fig. 1). We compiled data from feeding experiments (Sommer 1997; Lotze 1998; B. Worm unpubl. data) and >100 h of field observations to map major feeding links in this tritrophic food web (Fig. 1).

Experimental design—The relative effects of grazers and nutrient enrichment on macroalgal abundance and subsequent changes in food web structure and ecosystem function were investigated in factorial field experiments from February to November 1998 at 0.8 m of water depth. Throughout this period, grazers (present at natural densities or absent) and nutrient concentrations (NO enrichment, LOW, MED, and HIGH enrichment; *see below*) were manipulated in a 2 $\times$ 4 orthogonal design with four replicates. Our experiment was designed to test for the main effects and interactions among nutrient enrichment and grazing by factorial analysis of variance (ANOVA) and to model algal response to nutrient enrichment through regression analysis.

For regression analysis, we established a nutrient gradient across seven levels ($n = 2$ for enriched treatments, $n = 4$ for controls), corresponding to exponentially increasing nutrient diffuser length (2.5–80 cm) and nutrient supply. In order to achieve a balanced and statistically powerful ANOVA design, we combined these nutrient enrichment treatments into four categories: NO (no diffusers), LOW (2.5, 5 cm diffusers), MED (10, 20 cm diffusers), and HIGH (40, 80 cm diffusers) each replicated fourfold.

Grazers were manipulated with exclusion cages (25 $\times$ 25 $\times$ 25 cm), made from a stainless steel frame covered with a clear 1-mm polyethylene mesh (NO GRAZER treatment). Half of these cages had one open side to allow grazer access (GRAZER treatment). All cages were brushed weekly in order to remove fouling algae on the mesh, to check closed cages for grazer intrusion, and to remove intruders from these cages. Photon flux inside the cages was reduced by only 8% (Li-Cor LI-192SA). To evaluate potential cage effects on algal, grazer, or predator density, we conducted a control experiment where we compared GRAZER treatments with uncaged plots (GRAZER CONTROL). These treatments were also combined with nutrient enrichment and replicated fourfold.

Nutrient enrichment was performed with a slow-release NPK-fertilizer (Plantacote Depot 6M, Urania Agrochem) consisting of pellets with a semipermeable polyurethane layer. Detailed comparisons of this and other methods for in situ nutrient enrichment are provided by Worm et al. (2000). Pellets contained 14% N (5.7% NO_3 and 8.3% NH_4), 9% P (P_2O_5), and 15% K_2O; the latter we assumed to have no effect because of the high K level of seawater. Nutrients are released over a 6-month period (in soil). Previous tests of this method at our site have shown that release rates in seawater drop after 6 weeks; thus, we replaced pellets in 6-week intervals. Fertilizer pellets were enclosed in polyethylene mesh rolls (diffusers) 3.5 cm in diameter and 2.5, 5, 10, 20, 40, or 80 cm in length (10, 20, 40, 80, 160, 320 g pellets). Diffusers were placed inside cages or fixed with a steel tent pick on uncaged plots. Treatments without enrichment were replicated fourfold; each diffuser length was replicated twofold. All treatments were arranged in a randomized block design with two blocks. Blocks measured 10 $\times$ 30 m and were separated by 20 m. Individual plots were separated by 3–4 m to avoid interactions.

To monitor nutrient release through time, we collected water samples 10–15 cm above a set of control plots ($n = 5$) with intermediate diffuser length (20 cm) every 3 weeks. In August, we sampled all plots to reveal how nutrient availability changes with increasing diffuser length. Water samples were obtained with 30-ml plastic syringes, immediately filtered (Whatman GF/F filters), and analyzed within 3 h for dissolved ammonium, nitrate, nitrite, and phosphate on a Technicon autoanalyzer.

As experimental substrata, we used granite rocks (ca. 20 cm in diameter) from the experimental site. Rocks were collected in the shallow subtidal on 10 February 1998, cleared from *Fucus* cover, and randomly assigned to the experimental plots. The percentage cover of algal species was determined in monthly intervals using a 15 $\times$ 15 cm Plexiglas sheet with 50 random dots. Further, we monitored recruit-

Table 1. Average concentrations (μmol L^{-1}) of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) in nutrient-enriched versus control plots during the experiment.

Date	Diffuser length (cm)	Enrichment category	n	DIN control	DIN enriched	DIP control	DIP enriched
02 Mar			5	35.76		0.64	
26 Mar	20	MED	5	10.68	22.90	0.39	0.95
19 Apr	20	MED	5	9.53	10.16	0.09	0.16
18 May	20	MED	5	0.72	1.64	0.21	0.24
10 Jun	20	MED	5	0.50	0.66	0.10	0.36
09 Jul	20	MED	5	0.29	0.61	0.10	0.22
28 Jul	20	MED	5	4.91	5.24	0.31	0.36
12 Aug	20	MED	5	0.46	0.68	0.32	0.35
31 Aug	20	MED	5	1.19	2.27	0.29	0.43
21 Sep	20	MED	5	5.81	6.75	0.73	0.64
14 Oct	20	MED	5	9.54	11.63	0.58	0.62
12 Aug	2.5	LOW	6	0.46	0.50	0.32	0.34
12 Aug	5	LOW	6	0.46	0.44	0.32	0.34
12 Aug	10	MED	6	0.46	0.59	0.32	0.34
12 Aug	20	MED	6	0.46	0.68	0.32	0.35
12 Aug	40	HIGH	6	0.46	1.38	0.32	0.44
12 Aug	80	HIGH	6	0.46	1.25	0.32	0.43

ment of *Fucus* because this species is usually dominant at our site but may be particularly vulnerable to competition from other species and grazing at the recruitment stage (Worm and Chapman 1996, 1998; Worm et al. 1999). *Fucus* recruits became visible in June. Germlings >1 mm in length were counted in five random 2 × 2–cm subsamples within a central 10 × 10 area on all experimental rocks. Grazer and predator densities were assessed in 4–6-week intervals by visual underwater counts within open cages and around uncaged plots (25 × 25–cm area). Each plot was inspected very carefully, including close examinations of the algal canopy and below the rocks (partially buried crabs). These field counts may only represent first-order estimates for some of the smaller amphipods and isopods; however, their relative abundance in the various treatments should be assessed accurately.

In order to reveal changes in algal tissue carbon and nitrogen levels in response to nutrient enrichment and grazing, we obtained samples (ca. 0.5 g wet weight) of the two most abundant algae, *Fucus* and *Enteromorpha.* Samples were taken in May, July, and October from all experimental plots, dried for 48 h at 80°C, ground to powder, and analyzed in two subsamples per plot on an automated C:N analyzer. On 26 October 1998, the central 10 × 10–cm area was harvested from all plots sorted by species, dried, weighed, and analyzed for tissue C:N ratios as above.

Data analysis—Data were analyzed by factorial ANOVA including "grazers" (GRAZER vs. NO GRAZER) and "nutrients" (NO, LOW, MED, HIGH enrichment levels) as the main effects. The control experiment was analyzed like the main experiment, only that the effect "cage" (GRAZER vs. GRAZER CONTROL) replaced the "grazers" effect. The spatial block effect did not explain significant portions of the variance ($P > 0.2$) and hence was excluded from the analyses. Species cover data were angular transformed (Sokal and Rohlf 1995) and analyzed by multivariate multirank

analysis of variance (MANOVA), using the Pillai trace statistic (Johnson and Field 1993). This approach was chosen because it takes cross correlations among species abundances into account. In order to optimize the power of the analysis, the number of variables was limited to species with an average cover >1% (across all plots) or >5% cover on any plot. Three MANOVA runs were performed for spring (30 March), summer (28 June), and fall (6 October) because different sets of species colonized during these seasons. When MANOVA results were significant, we used univariate ANOVA to explore changes in the abundance of individual species. Total plant cover, grazer, and predator abundances were analyzed by factorial repeated-measures (RM) ANOVA, including "grazers" and "nutrients" as the main effects and "time" (monthly sampling February–October) as the repeated measure. Cover data were angular transformed and consumer abundance data ($\log + 1$) transformed in order to achieve homogeneity of variances, which was checked by Cochran's test. Student–Newman–Keuls (SNK) procedure was used for comparisons among nutrient treatments. In addition to ANOVA, we modeled the quantitative response of selected dependent variables across all seven nutrient enrichment treatments. We employed linear and second-order polynomial regression analysis (fitted with a nonlinear regression procedure). Polynomial regression results are only reported if significantly better fits were achieved using this method compared with the linear model.

Results

Nutrient dynamics—During our experiment, dissolved inorganic nitrogen (DIN; DIN = NO_3^- + NH_4^+ + NO_2^-) showed strong seasonal trends with generally high concentrations in early spring and fall and low concentrations (<1 μmol L^{-1}) in the summer (Table 1). Only on 28 July did DIN show a strong summer peak (Table 1). This was due to

high NH_4^+ concentrations following the decomposition of the annual *Pilayella* bloom, which breaks down in late June–July (Lotze et al. 1999). Dissolved inorganic phosphorus (DIP; DIP = PO_4^{3-}) showed less pronounced seasonal patterns than DIN. Throughout the experiment, N:P ratios ranged from 104 in April to 1.5 in August (mean 19.0 ± 9.7 SE). N:P ratios were <20 from May to October and <10 from May to July. These data strongly suggest nitrogen rather than phosphorus depletion with respect to macroalgal nutrient requirements (average tissue N:P ratios range between 30:1, Atkinson and Smith 1983; and 49:1, Duarte 1992). Nutrient diffusers filled with coated fertilizers increased nutrient availability for DIN and DIP over the experimental period (Table 1). Averaged over the year, medium-sized (20 cm) diffusers increased DIN concentrations by 49.9 ± 17.6%, and DIP by 68.8 ± 27.5%, relative to background levels (Table 1). N:P ratios in enriched plots averaged 15.0 (±5.8) and were not significantly different from control plots (ANOVA, $F_{1,18}$ = 0.122, P = 0.73). Sampling nutrient concentrations across all diffusers in August revealed that DIN and DIP availability was not affected by the presence of cages or grazers (ANOVA: DIN, $F_{2,30}$ = 2.5, P = 0.1; DIP $F_{2,30}$ = 0.5, P = 0.61), but increased with diffuser length and fertilizer mass (Table 1, ANOVA: DIN $F_{2,30}$ = 30.2, P < 0.0001; DIP $F_{2,30}$ = 22.4, P < 0.0001). A linear regression model (DIN = 0.492 + 0.0118x, r^2 = 0.51, P < 0.0001, n = 44) predicted that DIN availability increased by 51% at intermediate diffuser length (20 cm), which was almost exactly the value we obtained when we averaged relative increases across the whole experimental period (50%; *see above*). This value doubled with every doubling of diffuser length (100% increase at 160 g fertilizer, 198% at 320 g). DIP availability was predicted to increase by 9% at intermediate fertilizer mass (DIP = 0.333 + 0.0015x, r^2 = 0.50, P < 0.0001, n = 44), which did not correspond well with a measured average increase of 68.8%.

Algal cover and recruitment—Grazers and nutrients had strong but seasonally variable effects on macroalgal species composition and abundance (Fig. 2). Grazing significantly changed species composition from spring to fall; nutrients had strong effects in summer and weaker effects in fall (Table 2). In summer, the impact of nutrients on species composition depended on grazing pressure, as indicated by a significant interaction term (Table 2). Together, nutrient enrichment and grazing explained between 44% and 58% of total variance in species composition and 48% of variance in total plant cover throughout the year.

In February–March, colonial benthic diatoms (mixed with minor amounts of filamentous green *Ulothrix flacca*) and the green foliose winter annual *Ulvopsis grevillei* colonized (Fig. 2). Species composition was affected by grazers but not by nutrients (Table 2). Grazers strongly suppressed the cover of diatoms (ANOVA: $F_{1,24}$ = 16.5, P = 0.0004) but had no effects on *U. grevillei* (P = 0.94). In late spring and summer, the bloom-forming macroalgae *Pilayella* and *Enteromorpha* spp. (>80% *E. intestinalis*) rapidly colonized and dominated most plots (Fig. 2). Species composition was strongly influenced by the interactive effects of grazers and nutrients (Table 2). *Enteromorpha* dominated NO GRAZER treatments

but was strongly suppressed in GRAZER treatments (ANOVA: $F_{1,24}$ = 98.91, P < 0.0001). In contrast, *Pilayella* was more abundant in GRAZER treatments ($F_{1,24}$ = 91.18, P < 0.0001). Nutrient enrichment strongly increased cover of *Pilayella* in GRAZER treatments and cover of *Enteromorpha* in NO GRAZER treatments respectively (G × N interaction, Table 2, *Pilayella* $F_{3,24}$ = 3.7, P = 0.025; *Enteromorpha* $F_{3,24}$ = 9.3, P = 0.0003). Response of *Pilayella* to nutrient enrichment in GRAZER and of *Enteromorpha* in NO GRAZER treatments were best described by simple linear models (*Pilayella* cover = 48.22 + 0.16 N, r^2 = 0.21, P = 0.07; *Enteromorpha* cover = 35.03 + 0.35 N, r^2 = 0.74, P = 0.0011, n = 16, N = percentage increase in DIN). The only perennial alga was *Fucus,* which recruited in June and dominated all treatments in fall (Fig. 2). Species composition in October was significantly affected by grazers (Table 2), which increased cover of *Fucus* by an average of 36% ($F_{1,24}$ = 4.68, P = 0.0408). In contrast, nutrient enrichment gradually decreased *Fucus* cover by 18 to 62%, from LOW to HIGH enrichment levels ($F_{3,24}$ = 4.7, P = 0.0023). These effects were independent (G × N interaction, P = 0.66). In the control experiment, cages significantly affected species composition in summer ($F_{4,21}$ = 21.2, P < 0.0001) and fall ($F_{4,21}$ = 21.2, P < 0.0001). Positive grazer effects on *Fucus* and negative effects on *Enteromorpha* tended to be stronger in uncaged GRAZER CONTROL plots compared with caged GRAZER plots (*Fucus*: $F_{1,24}$ = 37.7, P < 0.0001; *Enteromorpha*: $F_{1,24}$ = 3.7, P = 0.067). Also, the cover of *Pilayella* decreased on GRAZER CONTROL compared with GRAZER plots ($F_{1,24}$ = 5.2, P = 0.0068). These effects were probably caused by the increased density of grazers in uncaged plots as compared to open cages (*see below*).

In addition to species shown in Fig. 2, several rare annual species (mean cover <5% at any time) occurred: the green algae *Blidingia minima* (April–June), *Cladophora rupestris* (June–October), and *Chaetomorpha linum* (July–August), the red algae *Ceramium strictum* (June–November) and *Polysiphonia violacea* (September–October), and the brown *Scytosiphon lomentaria* (April–June). Grazer presence and nutrient enrichment did not have significant effects on the abundance of any of these species, with the exception of weak positive grazer effects on *C. strictum* in fall ($F_{1,24}$ = 7.8, P = 0.010).

Averaged over the year, total plant cover was reduced by grazers (by 8.3% relative to NO GRAZER treatments), but note that this effect represents only an insignificant trend with P = 0.059 (Table 3). In contrast, total plant cover was significantly increased by nutrient enrichment (18–28% relative to NO enrichment treatments). There were no significant differences among LOW, MED, and HIGH enrichment levels on total plant cover (SNK, P > 0.05). Both grazer and nutrient effects changed over time (T × G and T × N interactions; Table 3). Graphical inspection of total cover data indicated strong negative grazer effects in March–April, weak effects on total cover from May to August, and positive effects on total cover in September–October (due to a positive effect on *Fucus,* the dominant species in fall). Nutrient enrichment strongly increased algal cover in May, June, and July, but not in the other months. Cages had no effects on total plant cover (P = 0.45).
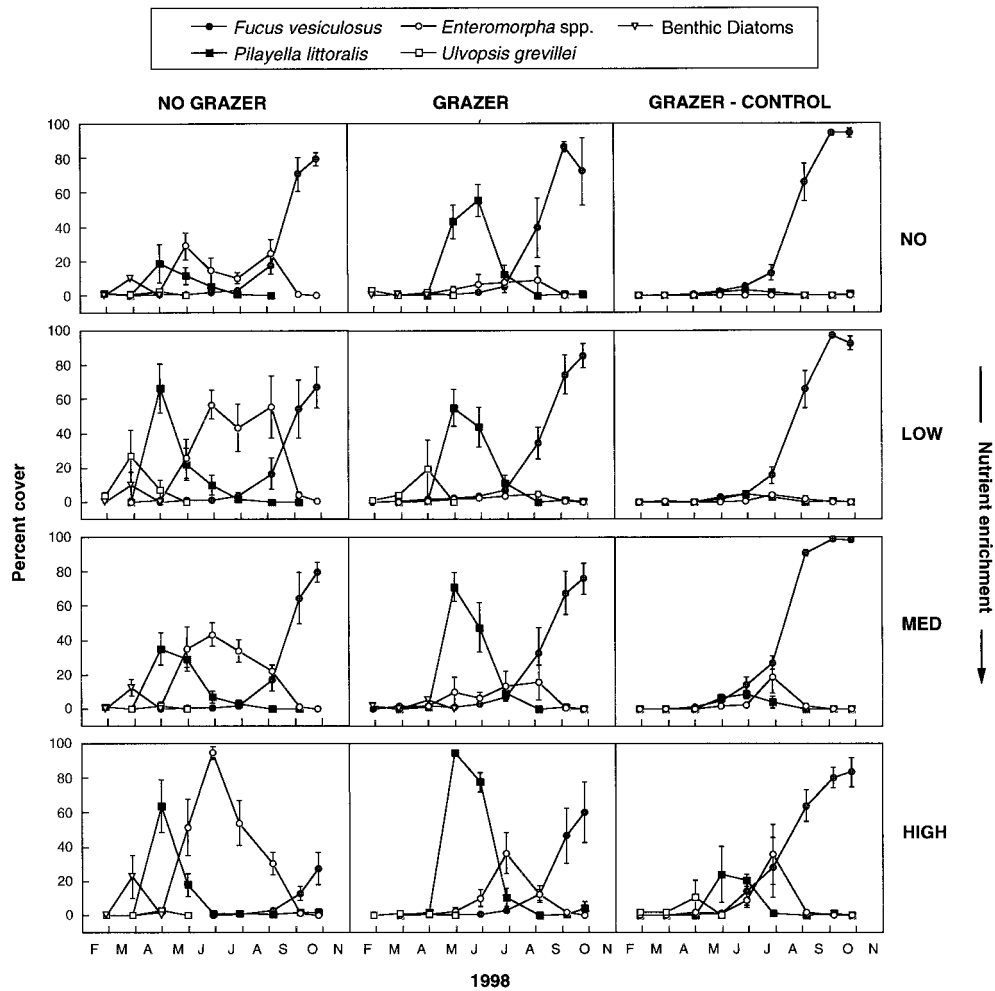
Fig. 2. Effects of grazer presence and nutrient enrichment on algal species composition and abundance (mean cover ±1 SE) over time. Shown are NO GRAZER (closed cages, grazer absent), GRAZER (open cages, grazer present) and GRAZER CONTROL (no cage, grazer present) treatments at increasing nutrient enrichment levels. For actual nutrient concentrations refer to Table 1. For ANOVA results, refer to Tables 2 and 3.

Table 2. MANOVA. Analysis of changes in macroalgal species composition in response to grazer removal and nutrient enrichment. Data were angular transformed.

Season	Dominant species	Source	df	Pillai Trace	F	P
Spring	*Ulvopsis grevillei*	Grazer	2, 23	0.42	8.18	0.0021
	Benthic diatoms	Nutrients	6, 48	0.37	1.82	0.1144
		G × N	6, 48	0.24	1.09	0.3808
Summer	*Enteromorpha* spp.	Grazer	4, 21	0.89	43.07	0.0001
	Pilayella littoralis	Nutrients	12, 69	0.92	2.56	0.0072
		G × N	12, 69	1.01	2.91	0.0025
Fall	*Fucus vesiculosus*	Grazer	4, 21	0.36	2.99	0.042
		Nutrients	12, 69	0.72	1.81	0.0642
		G × N	12, 69	0.57	1.35	0.2138

Table 3. Repeated-measures ANOVA. Effects of grazer removal and nutrient enrichment over time (Feb–Oct) on total plant cover. Data were angular transformed.

Source	df	MS	F	P
Grazer	1	0.24	3.93	0.0591
Nutrients	3	0.23	3.83	0.0225
G × N	3	0.13	2.23	0.1104
Error	24	0.06		
Time	8	3.81	74.92	0.0001
T × G	8	0.45	8.84	0.0001
T × N	24	0.26	5.17	0.0001
T × G × N	24	0.06	1.25	0.2472
Error	192	0.05		

Positive grazer effects and negative effects of nutrient enrichment on *Fucus* were most pronounced at the recruitment stage. Nutrient enrichment caused an exponential decline in recruitment success of *Fucus* (Fig. 3, Table 4), probably because of increased annual algal cover that blocks *Fucus* settlement and recruitment. Counteracting the nutrient effect, grazers favored *Fucus* recruitment. The relative influence of grazers increased with increasing nutrient loading. This was even more pronounced in GRAZER CONTROL compared with GRAZER treatments (Fig. 3). A linear regression model (Table 4) predicted that a 85% increase in nitrogen concentrations in GRAZER plots caused the same decline in *Fucus* recruitment as grazer exclusion. A 200% increase was predicted to cause a 97.6% drop in *Fucus* recruit densities in NO GRAZER treatments, as opposed to 93.7% in GRAZER treatments and 65.3% in GRAZER CONTROL treatments.

Carbon storage and nitrogen retention—The two most abundant algae over the experimental period, *Enteromorpha* and *Fucus,* responded similarly to nutrient enrichment with a seasonal increase in N ($P < 0.05$ in May, July, $P > 0.2$ in October) but not C tissue contents ($P > 0.2$ at any time). The increased N content caused tissue C:N ratios to decline with increasing nutrient enrichment (Fig. 4). Again, we found weak nutrient effects in spring, pronounced effects in summer, and no effects in fall (Fig. 4). Grazers and cages had no effects on tissue C:N ratios ($P > 0.2$ at any time).

At the end of the growth period, we harvested all macroalgal biomass from our plots in order to determine how grazing and nutrient enrichment changed total particulate or-
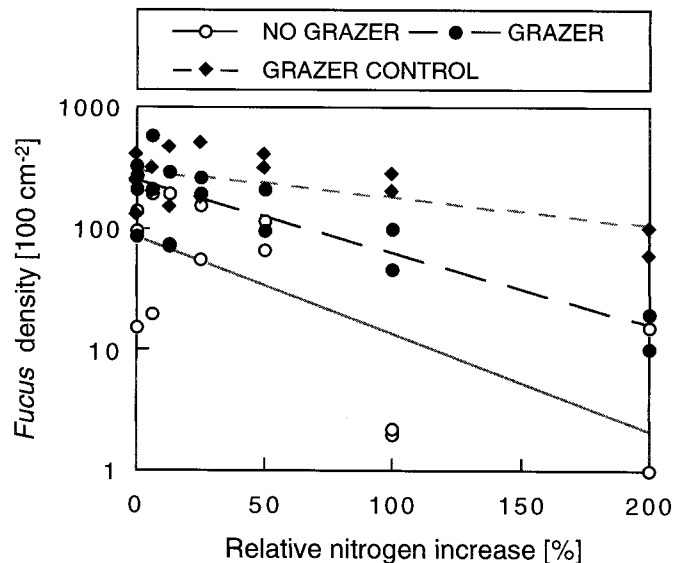

Fig. 3. Effects of grazers and nutrient enrichment on recruitment (germling density per 100 cm²) of the only perennial species, *Fucus.* Note the logarithmic scale. For regression analyses, refer to Table 4.

ganic carbon (POC) storage and particulate organic nitrogen (PON) retention by the algal community. We found that almost all (96.7%) of the biomass was *Fucus,* and a minor portion (2.3%) was *C. strictum, Pilayella* (1%), and *Enteromorpha* (0.0003%). Total POC and PON in macroalgal biomass increased with the presence of grazers (ANOVA: POC, $F_{1,23} = 6.84$, $P = 0.015$; PON, $F_{1,23} = 4.41$, $P = 0.046$). These increases were more pronounced on GRAZER CONTROL compared with GRAZER plots (POC: $F_{1,23} = 40.02$, $P < 0.0001$; PON: $F_{1,23} = 35.46$, $P < 0.0001$). Nutrient enrichment strongly decreased POC and PON in NO GRAZER and GRAZER treatments. In GRAZER CONTROL treatments POC and PON increased at LOW–MED enrichment but decreased at high enrichment levels (Fig. 5, Table 4).

Grazer and predator densities—Grazers and predators showed strong but contrasting seasonal trends in abundance (Fig. 6). Predators were most abundant in summer (10.5 ± 2.5 individuals m^{-2} in July) as opposed to spring and fall (<3 m^{-2}). Grazer densities were low in summer (44 ± 14

Table 4. Linear and second-order polynomial regressions of *Fucus* recruit densities (RD), total particulate carbon (POC) and nitrogen (PON) on relative nitrogen increase (N), $n = 16$.

Treatment	Regression	r^2	P
NO GRAZER	log *Fucus* RD = 1.93 − 0.0081 N	0.52	0.0017
GRAZER	log *Fucus* RD = 2.39 − 0.0060 N	0.86	0.0001
CONTROL	log *Fucus* RD = 2.47 − 0.0023 N	0.38	0.0113
NO GRAZER	POC = 68.28 − 0.29 N	0.32	0.0248
GRAZER	POC = 93.18 − 0.36 N	0.46	0.0039
CONTROL	POC = 154.1 + 1.55 N − 0.0085 N²	0.37	0.0131
NO GRAZER	PON = 4.83 − 0.021 N	0.36	0.0149
GRAZER	PON = 6.14 − 0.023 N	0.32	0.0217
CONTROL	PON = 10.262 + 0.067 N − 0.00042 N²	0.34	0.0183

MAY   JULY   OCTOBER

y = 29.18 - 0.037x
P=0.013, r^2=0.17

y = 29.09 - 0.069x
P=0.0004, r^2=0.25

y = 15.88 + 0.005x
not significant

y = 27.94 - 0.059x
P=0.003, r^2=0.26

y = 24.65 - 0.083x
P<0.0001, r^2=0.41

y = 8.43 + 0.024x
not significant
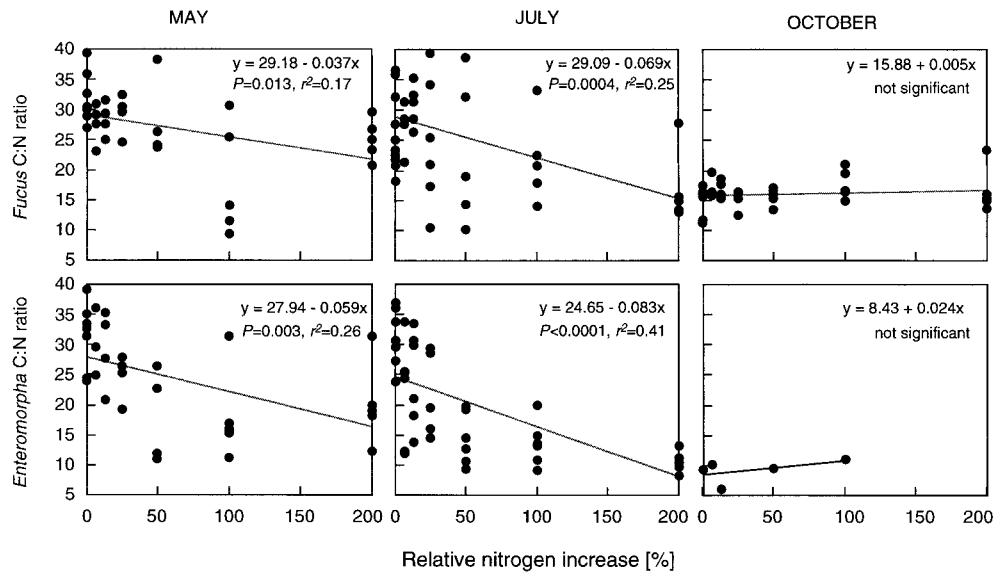
Fucus C:N ratio

Enteromorpha C:N ratio

Relative nitrogen increase [%]

Fig. 4. Effects of nutrient enrichment on C:N–tissue ratios of *Fucus* and *Enteromorpha* in spring, summer, and fall. Nutrient enrichment had significant effects in spring and summer, but not in fall. Grazers and cages had no effects on C:N ratios at any time (ANOVA: $P > 0.2$).

m^{-2} in July) and high in spring (2,671 $\pm$ 341 in May) and fall (1,184 $\pm$ 96 in October). Snails dominated grazers by number in spring, crustaceans in late summer and fall. Crustaceans (crabs, shrimps) always dominated predators by number, as opposed to fish. On average, predators had increased densities in caged GRAZER treatments (0.56 $\pm$ 0.08 vs. 0.28 $\pm$ 0.06 m^{-2}), whereas herbivores were more abundant in uncaged GRAZER CONTROL treatments (1,080 $\pm$ 136 vs. 610 $\pm$ 56 m^{-2}), but these effects tended to change over time (T $\times$ C interactions, Table 5; graphical inspection revealed strongest effects in May and July [grazers] and April, June, and August [predators]). Cage effects were most pronounced on the slow-moving snails *Littorina saxatilis* (731 $\pm$ 141 vs. 302 $\pm$ 51 m^{-2}). Small-bodied grazers were occasionally found in low numbers (<5 individuals per cage) in closed cages (NO GRAZER treatment, checked weekly and grazers removed). Larger grazer individuals and predators were never found in closed cages. This demonstrates the effectiveness of grazer-exclusion cages in this experiment.

Nutrients significantly increased grazer and predator densities in GRAZER and GRAZER CONTROL plots (Table 5). Analyzing the responses of individual species to nutrient enrichment, we found overall significant increases in isopods *Idotea* spp. (RM-ANOVA: $F_{3,24} = 7.83$, $P = 0.0008$), and in shrimps *Leander aspersus* (RM-ANOVA: $F_{3,24} = 4.33$, $P = 0.014$). Increased densities of these species upon nutrient enrichment scaled well to parallel increases in *Enteromorpha* (Fig. 7), suggesting a three-level bottom-up effect.

Discussion

Grazers and nutrients had strong and antagonistic effects on algal species composition and abundance, and carbon and nitrogen cycling in the studied macroalgal food web. Results

of this and a previous study (Lotze et al. 1999; Worm et al. 1999) provide detailed experimental evidence that increasing N loading causes shifts in macroalgal diversity, loss of consumer control, increased intensity of destructive algal blooms, and the disruption of important ecosystem functions, and that these responses are tightly linked.

Algal abundance—This experiment was performed in order to quantify the relative effects of grazers and nutrients in a natural macroalgal community. We found that the magnitude of effects depended on whether populations (cover of individual species) or the entire community (total plant cover) were examined. Species abundance and composition were strongly altered by grazing throughout the experiment. Nutrient effects on species composition were less pronounced and significant only during summer nutrient limitation (Table 2). On the contrary, despite dramatic changes in species abundances, total plant cover was not significantly reduced by grazers (decline by 8%, $P = 0.059$) but increased up to 28% ($P = 0.023$) in response to nutrient enrichment. No interaction among the effects of grazers and enrichment on plant cover occurred, suggesting that these factors have independent effects on algal productivity. However, nutrient effects on species composition can depend on grazing pressure. Nutrient enrichment increased the abundances of fast-growing annual algae, but grazers determined whether *Pilayella* or *Enteromorpha* were enhanced, corroborating results of an earlier study (Lotze et al. 1999). In contrast, perennial algae (*Fucus*) were independently favored by grazers and suppressed by nutrient enrichment. The magnitude of grazer and nutrient effects changed with season (Tables 2, 3). This was likely driven by seasonal patterns of nutrient supply (Table 1) and grazer density (Fig. 6). We conclude that grazers represent a seasonal, but an overall important, ecological force that can partly override the effects of eutro-
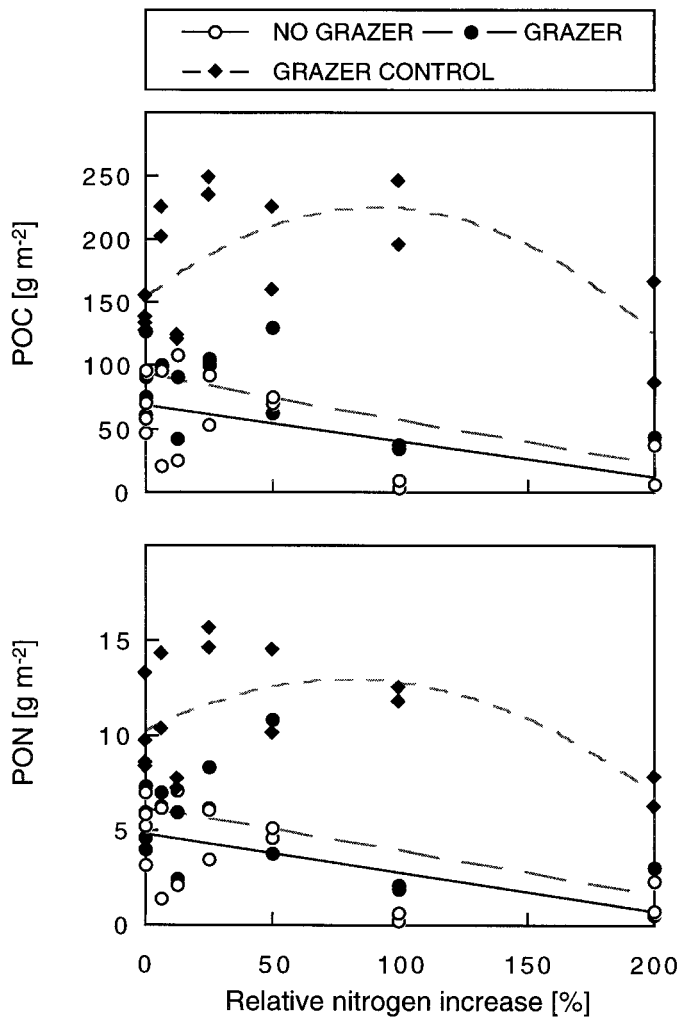
Fig. 5. Grazer and nutrient effects on carbon storage and nitrogen retention, measured as POC and PON retained in plant biomass at the end of the growth season. For regression analyses, refer to Table 4.

Fig. 6. Densities of grazers and predators in the experiment. Data are means (± 1 SE) pooled over GRAZER and GRAZER CONTROL treatments. Crustaceans are represented by square symbols, fish and snails by circles. Weekly examinations showed that NO GRAZER treatments (not shown) remained practically free of grazers and predators throughout the experiment.

phication on algal community structure. This also holds true for freshwater pelagic food webs, where manipulations of food web structure are used to suppress phytoplankton biomass under eutrophic conditions (Carpenter et al. 1996). It is, however, important to realize the limits of this buffering role. In freshwater webs, blooms of grazer-resistant algae (mostly cyanobacteria) can decouple algal growth from grazer control (Gliwicz 1990; Sommer 1992). Similarly, grazer-induced shifts from fast-growing palatable to unpalatable macroalgae and invertebrates have been demonstrated for warm-temperate algal and coral assemblages (Miller and Hay 1996) and tropical coral reefs (Lewis 1986). In our experiment, a shift from palatable green algae to more grazer resistant (Lotze 1998) brown algae occurred from NO GRAZER to GRAZER and GRAZER CONTROL treatments. The brown annual *Pilayella* was still able to perform an explosive bloom in GRAZER treatments (50-fold cover increase in May). Moreover, the maximum cover of *Pilayella* increased 2- to 12-fold from NO to HIGH nutrient enrich-
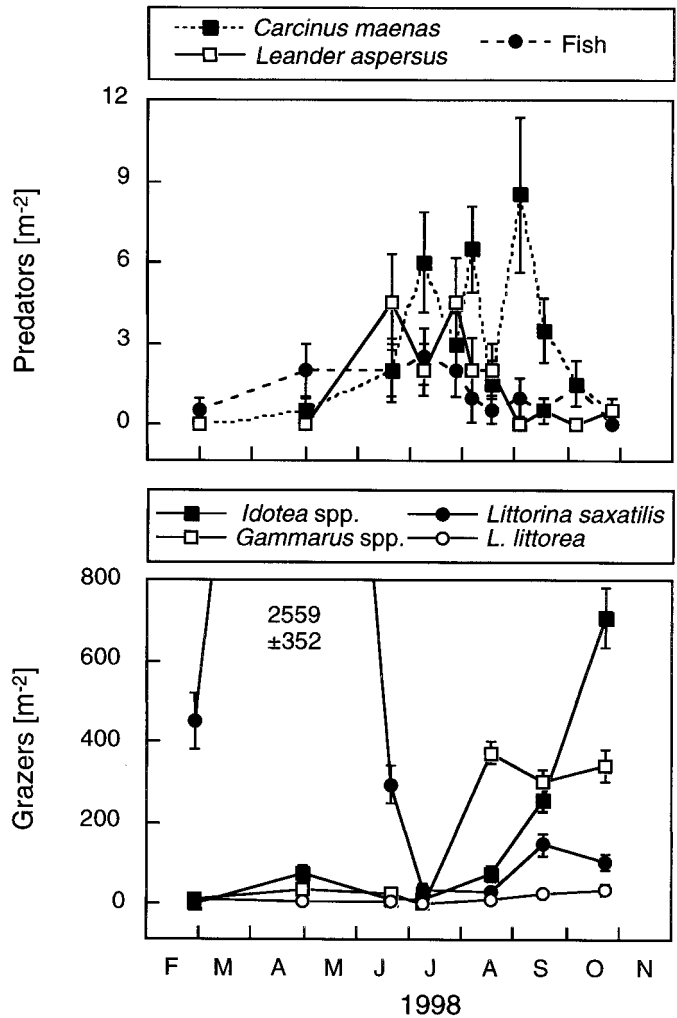
ment levels in GRAZER and GRAZER CONTROL treatments, respectively. Nutrient-stimulated blooms of *Enteromorpha* and *Pilayella* lasted from April to September, with peak biomass from May to July (Fig. 2). This embraces the complete reproductive period of *Fucus* (May–June). By favoring the intensity and duration of blooms, nutrient enrichment caused exponential declines in *Fucus* recruitment. Grazers indirectly enhanced *Fucus* recruitment at ambient nutrient levels and also slowed the rate of decline with increasing enrichment (Fig. 3, Table 4). But even though relative grazer effects increased with enrichment, grazers could not overcompensate the nutrient effect. An 85% increase of nitrogen availability in GRAZER treatments had equal effects as the complete exclusion of grazers. The buffer capacity of grazers was greater in GRAZER CONTROL treatments (Fig. 3), but the trend of an exponential decrease in *Fucus* recruitment remained. Similar patterns were found for softbottom macrophyte assemblages (Neckles et al. 1993;

Table 5. Repeated-measures ANOVA. Effects of cages (open cages versus no cages) and nutrient enrichment on grazer and predator densities in the experiment. Data were (log + 1)-transformed.

Variable	Source	df	MS	F	P
Grazer densities	Cage	1	0.56	1.49	0.2344
	Nutrients	3	1.27	3.39	0.0343
	C × N	3	0.06	0.15	0.9299
	Error	24	0.38		
	Time	6	25.40	66.08	0.0001
	T × C	6	0.89	2.31	0.0823
	T × N	18	0.53	1.38	0.2135
	T × C × N	18	0.27	0.69	0.7159
	Error	144	0.38		
Predator densities	Cage	1	0.23	8.427	0.0078
	Nutrients	3	0.10	3.756	0.0242
	C × N	3	0.03	0.9	0.4554
	Error	24	0.03		
	Time	9	0.11	5.492	0.0001
	T × C	9	0.04	1.957	0.0870
	T × N	27	0.02	1.222	0.2623
	T × C × N	27	0.02	1.043	0.4172
	Error	216	0.02		

Williams and Ruckelshaus 1993). Grazer enhanced seagrass growth by consuming epiphytes, but nutrient enrichment indirectly reduced seagrass growth by favoring fast-growing epiphytes. In one study, however, grazer densities and their impact on seagrass epiphytes declined across three estuaries of increasing nutrient loading (Hauxwell et al. 1998), suggesting an indirect negative effect of nutrient loading on grazers. This could be due to the loss of eelgrass habitat (Salemaa 1987), but may also be caused by other confounding factors in this comparative study.

In our experiment, we found surprisingly similar effects of nutrient enrichment and grazing on macroalgal abundance and microalgal biovolume (Hillebrand et al. unpubl. data). Grazer removal and nutrient enrichment increased microalgal biovolume, and also the dominance of single species that were susceptible to grazing but particularly responsive to nutrient enrichment. Similar growth-resistance trade-offs seem to control the response of coastal micro- and macroalgal and seagrass–epiphyte communities to nutrient enrichment and grazing. Parallel patterns were found in periphyton (Sommer 1997) pelagic (Sterner 1989) and terrestrial plant (Coley et al. 1985) communities.

Carbon storage and nitrogen retention—In addition to changing algal abundance and species patterns, nutrients affected algal tissue chemistry and the ability of the community to retain C and N. Nutrient enrichment increased N content and decreased C : N ratios in *Enteromorpha* and *Fucus* in spring and summer but not in fall. Thus the effect of nutrients on individual organisms were seasonally transient. Grazers did not affect C : N ratios, which may indicate that no structural (C-based) defenses are induced by herbivory in *Enteromorpha* and *Fucus*. Over the period, C and N storage on the community level decreased with nitrogen addition but increased in the presence of grazers. In GRAZER CONTROL treatments there was an increase in C and N storage at LOW and MED enrichment levels, but this decreased again at HIGH enrichment (Fig. 5). These changes in C and N storage were linked to the species shift from perennial to annual algae. Annual algae are short-lived and their tissue nutrients are rapidly regenerated by grazers and bacterial decomposition (Norkko and Bonsdorff 1996). When the annual *Pilayella* bloom decomposed in July at our site, we found that DIN concentrations increased 17-fold (Table 1), which was entirely attributed to increases in ammonium, a product of grazing and decomposition. In contrast, perennial fucoids have a life span of 3 to 5 years. Measurements on replicate concrete settlement plates at our site over an 18-month pe-
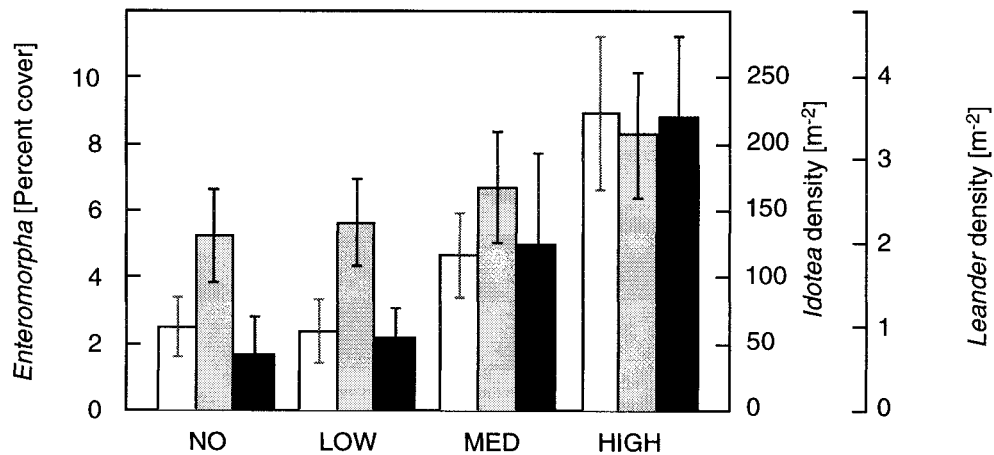

Fig. 7. Proportional increases of foliose annual algae (*Enteromorpha* spp., white bars), isopods (*Idotea* spp., gray bars) and shrimps (*Leander aspersus,* black bars) with increasing nutrient enrichment. *Enteromorpha* is a preferred food source for *Idotea* (Lotze 1998), which is consumed by *Leander.* Data are means (±1 SE) pooled over the experimental period. For ANOVA results, refer to Table 5. Correlation coefficients (r^2) among trophic levels are 0.980 ($P = 0.001$) for nitrogen enrichment–*Enteromorpha*; 0.966 ($P = 0.017$) for *Enteromorpha–Idotea*; and 0.997 ($P = 0.002$) for *Idotea–Leander.*

riod (May 1997–November 1998) revealed that *Fucus* productivity on these surfaces was 907 ± 127 g dry weight m^{-2} month^{-1} ($n = 8$) or 342 ± 47 g C m^{-2} month^{-1} and nitrogen retention of 20 ± 2 g N m^{-2} month^{-1}. These extremely high values are at the upper limit of reported data for macroalgae (Mann 1973) and coral reefs (Sorokin 1995) and grossly exceed the area-specific productivity of terrestrial and marine pelagic systems (Sommer 1998). Because it leads to the decline of perennial macrophytes, nitrogen pollution impairs nitrogen and carbon retention by the coastal macroalgal community, which may result in increased nutrient export to the open ocean. This is most likely the case in the Baltic, where perennial macrophytes have sharply declined on a basinwide scale (Worm et al. 1999). Qualitatively similar declines in nitrogen retention and carbon storage occurred in experimentally fertilized grasslands (Wedin and Tilman 1996), and declines in nitrogen retention can occur in fertilized forests (Aber 1992). These results suggest that reasonable estimates of increasing carbon storage in response to increasing nitrogen deposition (e.g., Schindler and Bayley 1993) need to incorporate nonlinear effects due to changes in species composition.

Higher trophic levels—Nutrient effects in our experiment appeared to be transmitted across three trophic levels. With increasing enrichment, the densities of isopods and shrimps increased in proportion to *Enteromorpha* cover, which is a preferred food of *Idotea* (Lotze 1998). Observations at 15 sites across the Western Baltic corroborated that *Idotea* and shrimps were abundant at sites dominated by *Enteromorpha*, but other consumer species were relatively scarce. Thus, the complex littoral food web (Fig. 1) appears to become gradually impoverished with increasing enrichment and *Enteromorpha* dominance (Worm et al. 1999). Proportional increases of plants, herbivores, and predators are predicted by ratio-dependent predator–prey models, but not by traditional prey-dependent models (Berryman 1992). Our results are in line with ratio-dependent models and also in accordance with large-scale comparative studies in marine benthic (Bustamante et al. 1995; Menge et al. 1997) and pelagic (Aebischer et al. 1990) communities. These generally show increasing grazer and predator abundance with increasing algal abundance or productivity. Our study is the first experimental study to verify these large-scale patterns in a marine benthic community. The only other comparable study we know of (Wootton et al. 1996) found weak effects of nutrient enrichment on micrograzers and no effects on algal biomass, which contradicts our small-scale and other workers' large-scale findings (Bustamante et al. 1995; Menge et al. 1997). Wootton et al. (1996) conducted their experiment at relatively short time scales (2–4 months), which may have influenced conclusions about the community response to enrichment.

How do increased predator densities feed back on lower trophic levels? In freshwater food webs, fish predators usually have strong cascading effects on grazer and algal abundance (Power 1990; Brett and Goldman 1997). For marine food webs, there is very little evidence for trophic cascades in pelagic webs (Micheli 1999), but accumulating evidence in marine benthic webs (Estes et al. 1998: killer whales–sea otters–urchins–macroalgae; Duffy and Hay 2000: fish–amphipods–macroalgae). In our field experiments, cascading predator effects on grazers and algae appeared to be important in summer. Although we did not manipulate predator densities separately, there were apparent negative correlations between grazer densities and predator densities among seasons and among open plots and closed cages. All grazer species showed parallel population crashes (87–100% decline) in June–July, when predators reached their highest densities. During this period, the grazer : predator ratio decreased from $1,068 : 1$ to $4 : 1$ (by number). Grazers recovered again during the fall, when predator numbers declined (grazer : predator ratio $1,184 : 1$). Equally, grazer densities were reduced by 43% in GRAZER cages, where predators were almost twice as abundant compared with uncaged GRAZER CONTROL plots. In addition to increased predation, periodic removal of grazers by the weekly brushing procedure may have reduced grazer density in the GRAZER cages. Differences in grazing pressure could explain changes in algal species composition among these two treatments. More grazer-susceptible species such as *Enteromorpha* and *Pilayella* had increased cover in GRAZER plots compared with GRAZER CONTROL plots, which were more dominated by grazer-resistant *Fucus*. Because of this replacement of annuals by *Fucus*, no cage effects on total plant cover occurred. The strongest species-specific cage effects occurred on *Pilayella* (Fig. 2), which had its maximum development in May, when herbivore densities were extremely high and different between GRAZER and GRAZER CONTROL treatments. Although *Enteromorpha* is more grazer-susceptible than *Pilayella* (Lotze 1998; Lotze et al. 2000), this species was less strongly affected by cages (Fig. 2). *Enteromorpha* had its maximum cover in July when grazer densities had dropped by 98.4% compared with May. We assume that this decline in grazer densities was partly due to seasonally increased predation, indicating a seasonal cascade from predators to algae in summer. In conclusion, these results demonstrate strong trophic links between nutrients, algae, grazers, and predators in this marine benthic food web and pronounced seasonal shifts in the relative importance of bottom-up and top-down control.

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