Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms

Heike K. Lotze, Boris Worm and Ulrich Sommer

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Destructive macroalgal mass blooms threaten estuarine and coastal ecosystems worldwide. We asked which factors regulate macroalgal bloom intensity, distribution and species composition. In field experiments in the Baltic Sea, we analyzed the relative effects of nutrients, herbivores and algal propagule banks on population development and dominance patterns in two co-occurring bloom-forming macroalgae, *Enteromorpha intestinalis* and *Pilayella littoralis*.
Both species were highly affected by the combined effects of a propagule bank, herbivory and nutrients. The magnitude of effects varied with season. The propagule bank was an important overwintering mechanism for both algae, and allowed for recruitment two months earlier than recruitment via freshly dispersed propagules. This provided a seasonal escape from intense herbivory and nutrient limitation later in the year. Favored by massive recruitment from the propagule bank, *Enteromorpha* was the superior space occupier in early spring, thereby reducing recruitment of *Pilayella*. Elimination of the propagule bank and recruitment via freshly dispersed propagules favored *Pilayella*. Strong and selective herbivory on *Enteromorpha* supported *Pilayella* in the presence, but not in the absence of the propagule bank. Nutrient enrichment in summer counteracted herbivore pressure on *Enteromorpha*, thereby negatively affecting *Pilayella*. Herbivore and nutrient effects were more pronounced for early life stages than adult algae.
These results show that recruitment processes and forces affecting early life stages at the beginning of the vegetation period determine development and dominance patterns of macroalgal blooms. Herbivores naturally suppress blooms but increasing nutrient enrichment can override this important control mechanism. The propagule bank plays a previously unrecognized role for population and community dynamics.

H. K. Lotze, B. Worm and U. Sommer, Institut für Meereskunde, Düsternbrooker Weg 20, D-24105 Kiel, Germany (present address of HKL: Biology Dept, Dalhousie Univ., Halifax, NS, Canada, B3H 4J1 [hlotze@is.dal.ca]).

Over the last four decades, increasing anthropogenic nitrogen fixation and phosphorus mobilization have caused severe changes in community composition and ecosystem functioning in terrestrial and aquatic habitats (Vitousek et al. 1997, Carpenter et al. 1998). As a consequence of increased nutrient input, macroalgal blooms frequently occur in eutrophicated estuarine and coastal ecosystems, harming the epi- and endobenthic fauna and perennial flora (Fletcher 1996, Valiela et al. 1997, Raffaelli et al. 1998). These blooms are per-formed by fast-growing opportunistic annuals which are characterized by high productivity rates and are strongly favored by nutrient enrichment (Duarte 1995, Raffaelli et al. 1998). However, the extent, distribution, and species composition of blooms vary strongly among systems of similar nutrient loading, which compromises our ability to predict these events based on information about nutrient status alone (Bonsdorff 1992, Schories 1995a, Schramm and Nienhuis 1996). Thus, additional factors may play a role in the control

of macroalgal blooms. Their relative influences are best assessed using experimental manipulations in the field (Nixon 1990, Raffaelli et al. 1998). Here, we present results from factorial field experiments in the Baltic Sea analyzing population development and dominance patterns in two cosmopolitan bloom-forming macroalgae, the filamentous brown alga *Pilayella littoralis* [L.] Kjellm. and the foliose green alga *Enteromorpha intestinalis* L.

Pilayella, as adult biomass, dominates blooms in the Baltic Sea whereas *Enteromorpha* is much less abundant (Lotze et al. 1999). This species dominance pattern could not be explained by ecophysiological traits of adult stages (Lotze 1998, Lotze and Schramm in press) as has been proposed for other bloom-forming macroalgae (Lavery and McComb 1991, Peckol and Rivers 1995, Fong et al. 1996). However, germination experiments in the laboratory have shown that *Pilayella* may gain a seasonal advantage over *Enteromorpha* in early spring by germinating at lower temperatures (Lotze et al. 1999). In contrast, the higher abundance of overwintering stages in *Enteromorpha* may support spring recruitment of this species (Lotze et al. 1999). Strong and selective herbivory on *Enteromorpha*, as demonstrated in laboratory experiments (Lotze 1998, Lotze et al. 1999), could be a further advantage for *Pilayella*. The relative importance of these processes for population development and species dominance in the field is as yet unclear.

Temporal and spatial variability in propagule supply caused by variations in reproductive output, dispersal, settlement and survival are important structuring factors in terrestrial (Lavorel et al. 1994, Dalling et al. 1998, Hubbell et al. 1999) and marine plant assemblages (Reed et al. 1988, Reed 1990, Santelices 1990, Vadas et al. 1992, Worm and Chapman 1998). In temperate ecosystems with pronounced seasonality, population development of annual plants depends on an overwintering mechanism and a recruitment source in the following vegetation period. This is provided by soil seed banks in terrestrial systems (Leck et al. 1989, Fenner 1992, Crawley 1997). In marine macroalgae, "banks of microscopic forms" (sensu Chapman 1986) consisting of settled propagules, microrecruits and microscopic life stages have been recently characterized (Santelices et al. 1995, Lotze et al. 1999), but the functioning and ecological role of these "marine seed banks" is not well understood (Hoffmann and Santelices 1991). We tested for the effects of the presence or absence of a macroalgal propagule bank for recruitment and population development of *Pilayella* and *Enteromorpha*. In addition to variability in propagule supply, consumers and resources are important determinants of plant population and community structure. Herbivore consumers directly reduce algal biomass, and this can indirectly affect species competition (Lubchenco 1978, Paine 1990). Nutrient enrichment

supports growth and can counteract herbivore effects (Williams and Ruckelshaus 1993, Hauxwell et al. 1998). We use factorial experiments to determine potentially interactive effects of herbivores ("top-down"), nutrients ("bottom-up"), and sources of propagule supply (dormancy versus dispersal). Rather than assessing the effects of single factors, we used this macroalgal system to test the more general idea that species distribution and abundance are determined by potentially complex interactions among ecophysiological constraints, resource availability, herbivory, competition, and factors affecting propagule supply (Diamond and Case 1986, Roughgarden et al. 1988, Keddy 1989, Reed et al. 1997). We hypothesized that (1) availability of a propagule bank as a recruitment source in spring, and (2) seasonal patterns of herbivory and nutrient supply control species abundance and dominance patterns among bloom-forming macroalgae.

Material and methods

Study site and species

This study was carried out in 1997 in Maasholm Bay, outer Schlei Fjord (54°41′N, 10°0′E), western Baltic Sea, Germany. This tideless bay experiences irregular wind-driven water exchanges with nutrient-rich water from the inner part of the fjord and comparatively nutrient-poor water from Kiel Bight. Salinity fluctuates with season between 12–18 PSU in summer and 14–20 PSU in winter. Water temperature varies between -1–2°C in winter and 16–25°C in summer. Thin sea ice is common in January and February. Winter nutrient concentrations reach maxima of 160 µmol l^{-1} nitrate, 12 µmol l^{-1} ammonium and 2 µmol l^{-1} phosphate from January to March (Schramm et al. 1996). From mid-May to August, nitrate and ammonium levels mostly remain close to the detection limit (0.0–0.3 µmol l^{-1}), whereas phosphate remains between 0.1 and 0.6 µmol l^{-1}. In September, ammonium regeneration starts and concentrations rise rapidly, while nitrate levels remain low until winter. In the shallow Maasholm Bay (0–1.5 m), the sandy bottom is scattered with rocks and boulders providing abundant substrata for seaweed colonization. Here, the perennial brown rockweed *Fucus vesiculosus* L. dominates the benthic community. Regularly in spring and early summer, *Fucus* plants become overgrown with epiphytic *Pilayella littoralis* and *Enteromorpha* spp., which also occur abundantly on rocks, and later in free-floating stages. Within the genus *Enteromorpha*, *E. intestinalis* is the dominant species, but *E. prolifera* (O. F. Müller) J. Agardh and *E. clathrata* (Roth) Greville co-occur in summer. At early life stages (propagules, germlings), these species can hardly be distinguished and are therefore treated hereafter as *Enteromorpha* spp.

Dispersal rate

To monitor the amount of viable macroalgal propagules in the water column, we quantified propagule settlement on ceramic tiles at 2–4-wk intervals. Six sterilized ceramic tiles (10 × 10 cm) were fastened to six steel rods and exposed vertically in the water column 0.5 m above the sediment surface (water depth was 0.7 m) for 24 h. Replicates were 30 m apart. This method allows settlement of positively phototactic zoids and gametes on their way to the water surface and of negative phototactic zygotes on their way down from the water surface. After transportation to the laboratory in a cooler, tiles were maintained in 500 ml Provasoli enriched seawater (Starr and Zeikus 1987) at a constant temperature of 10°C and light intensity of 100 μmol photons m^{-2} s^{-1} in a 14:10 h light:dark cycle. Germanium dioxide (GeO_2) was added to the medium at 0.5 mg l^{-1} in order to suppress growth of diatoms. We chose a low GeO_2 concentration to avoid inhibitory effects on *Pilayella* (Wang 1993). Still, this treatment effectively kept the cultures free of diatoms over the short cultivation period that we used. After 7 d, germlings (> 200 μm length) were counted using a dissecting microscope with an integrated grid (pooling 10 randomly chosen subsamples of 4 × 4 mm per tile). This method does not provide an absolute measure of the amount of propagules produced by the algal community because of potential mortality during settlement and early recruitment. However, it provides a maximum estimate of the availability of viable and recruiting propagules in the system because inhibiting effects in the field such as nutrient limitation and herbivory were eliminated during cultivation.

Adult biomass and herbivore abundance

Adult algal biomass and herbivore abundance were determined monthly within the zone dominated by *Fucus vesiculosus*. We placed six quadrats (25 × 25 cm) randomly along a 100-m transect line (parallel to the coast line, 0.7 m water depth) and sampled all algae and herbivores within each quadrat with a framed sampling net. Abundance of herbivores (individuals m^{-2}) was determined to the species level. We detached all epiphytic and epilithic macroalgae from their substratum (mostly epiphytes on *Fucus*), sorted them by species and determined dry weight after 48 h at 70°C (g dry weight m^{-2}).

Experimental design

From February to December 1997, we performed a factorial field experiment where we analyzed the combined effects of the propagule bank, herbivory and nutrient enrichment on population development of co-occurring *Pilayella* and *Enteromorpha*. The three experimental factors were combined in a completely crossed design (2 × 2 × 2) with 48 experimental units and four replicates per treatment combination arranged in a "randomized block design" (Hurlbert 1984). The experimental units were 3 m apart to ensure independence between plots especially with respect to nutrient enrichment (see below). The experiment was located at 0.7 m water depth in the zone dominated by *Fucus vesiculosus*. The experimental units were flat granite rocks (15–20 cm in diameter) which were collected in February 1997 at the study site (10–40 cm depth). At that time, the rocks had no macroscopic vegetation.

Herbivore presence was manipulated with cages (25 × 25 × 25 cm) made of a stainless steel frame covered with 1-mm transparent polyethylene mesh. Herbivores > 1 mm were excluded from closed cages, while open cages with one side cut open allowed free access for herbivores. Plots without cages (open plots) served as controls for cage artifacts. Cages were brushed weekly to prevent fouling. Light measurements (LI-COR underwater quantum sensor LI-192SA) inside and outside the cages revealed that light intensity was reduced by only 8% by the polyethylene mesh. We judged this to be negligible. To determine whether herbivore densities were similar in open cages and uncaged plots, we estimated herbivore densities within a central 10 × 10 cm area on the experimental rocks at the end of July.

For manipulation of the propagule bank, half of the experimental rocks were selected at random and heat sterilized for 48 h at 100°C, killing microscopic stages. The other rocks were left untreated. Within the study area, *Enteromorpha* (330 ± 30 recruits cm^{-2}) and *Pilayella* (6.67 ± 6.67 cm^{-2}) were the main species recruiting from the natural propagule bank on rocky surfaces (Lotze et al. 1999).

Nutrient enrichment was performed on one half of the experimental plots from June to September when nutrient pools at the study site reached their seasonal low (see above). Nutrient diffusers were pipes (400 × 25 mm) of 1-mm polyethylene mesh filled with 160 g N-P-K coated slow-release fertilizer (Plantacote™ 6M, Urania Agrochem, Hamburg). Detailed tests of this method showed that it provides a tool for dynamic, long-term, gradual release of nutrients at realistic enrichment levels. Moreover, the enrichment effect is confined to < 1 m from the source, avoiding cross-fertilization among plots (Worm et al. in press a). Water column ammonium and phosphate concentrations were determined on all plots every 3–4 wk 10 cm above plots. Samples were taken with 10 ml polyethylene syringes, immediately filtered over Watman GFC filters (pre-combusted at 550°C to remove possible contaminations), and determined colorimetrically using the methods of Grasshoff et al. (1986). Nitrate is released

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at a fixed molar ratio of 0.69:1 to ammonium (Urania Agrochem pers. comm.) and was not determined in this study.

Single *Fucus vesiculosus* plants (12–18 cm length) were added to all plots to provide a habitat for herbivores and a dispersal source for *Fucus* propagules. We determined percent cover of all species developing on rocks over monthly intervals, and species canopy height every 2 mo as the dependent variables. Percent cover was determined with a 10×10 cm Plexiglas sheet with 50 random dots (1 dot = 2% cover). Canopy height of each species was measured with a ruler.

Statistical analyses were performed using fixed-factor, two- and three-way factorial ANOVA models for randomized block design with percent cover and canopy height of *Pilayella* and *Enteromorpha* as the dependent variables. Homogeneity of variances was checked using Cochran's test. Percent cover data were arcsin (sqrt $(x + 1)$) transformed as recommended by Sokal and Rohlf (1995). We calculated omega-squared (ω^2) for the relative magnitude of effects as recommended for a fixed-factor model by Howell (1992). We checked for linear correlation among the densities of

Pilayella and *Enteromorpha* with linear regression analysis on percent cover data of both species in the end of May. The effects of nutrient enrichment on water column ammonium and phosphate concentrations were analyzed by three-way ANOVAs. Similarly, herbivore densities within caged and uncaged plots in July were compared by three-way ANOVAs (cage, nutrients, propagule bank) for each species separately. Both nutrient concentrations and herbivore data were log-transformed to achieve homogeneity of variances.

New recruitment

In the end of June 1997, we studied the combined effects of herbivory, propagule bank presence and nutrient enrichment on new recruitment of *Enteromorpha* spp. and *Pilayella littoralis* out of the water column via newly produced and dispersed propagules. In this experiment, the presence or absence of the propagule bank had only indirect effects on new recruitment via differential propagule supply from algal stands on plots with and without the propagule bank. One sterilized ceramic tile (5×10 cm) per plot was exposed as a settlement substratum in cages (closed and open) and on uncaged control plots of the factorial field experiment described above. After 14 d, germling abundance was determined with a dissecting microscope (mean of 6 subsamples of 4×4 mm). *Enteromorpha* and *Pilayella* were the main species settling on the tiles. In addition, we detected a few germlings of *Ceramium strictum* Harvey. Statistical analyses were performed by three-way ANOVA ($2 \times 2 \times 2$) on germling densities per cm^2 for *Pilayella* and *Enteromorpha* separately. Data were log-transformed to achieve homogeneity of variances.
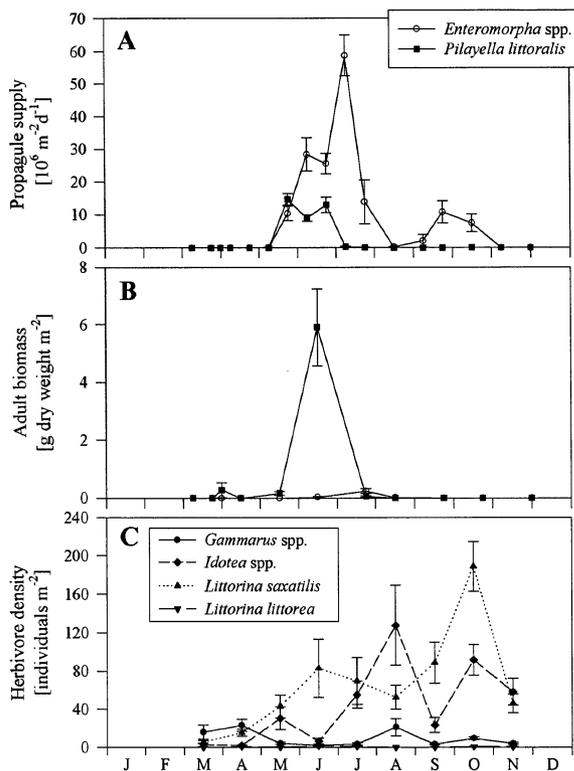

Fig. 1. Seasonal propagule supply and adult biomass of *Enteromorpha* spp. and *Pilayella littoralis*, and herbivore abundance in 1997: (A) Densities of viable propagules settling over 24 h from the water column onto ceramic tiles. (B) Biomass of adult algae and (C) density of main herbivore species associated with the *Fucus vesiculosus* community per m². Data are means $\pm$ 1 SE ($n = 6$).

Results

Dispersal rate

Both species initiated reproduction in May 1997 (Fig. 1A). The reproductive period of *Pilayella* was short and ended in July whereas *Enteromorpha* propagules were detectable until the end of October. In *Pilayella*, there was a maximum of 15 million settling propagules m^{-2} d^{-1} in May, which was only a quarter of the maximum densities in *Enteromorpha* (60 million m^{-2} d^{-1}) in July.

Adult biomass and herbivore abundance

Pilayella first appeared in March 1997 at low biomass (0.3 g dry weight m^{-2}). Maximum bloom biomass was achieved in June with 6 g dry weight m^{-2} (Fig. 1B). Similar blooms that were largely dominated by *Pi-*
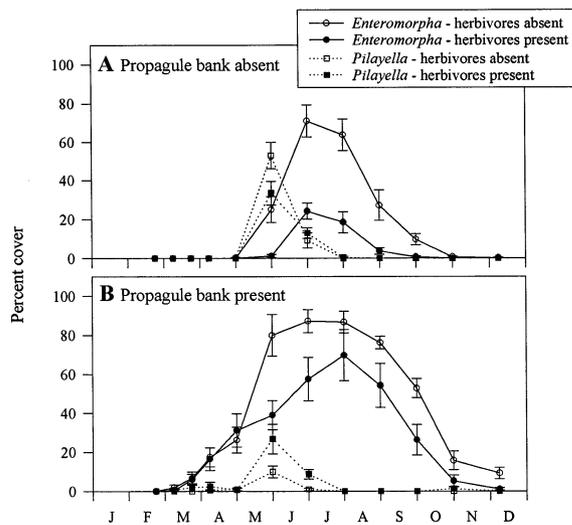
Fig. 2. Effects of the propagule bank and herbivory on population development of *Enteromorpha* spp. and *Pilayella littoralis* on rocks. The treatment combinations are indicated as (A) the propagule bank is absent (sterilized rocks) or (B) present (untreated rocks), herbivores are absent (exclusion cages) or present (herbivore-access cages). Data were analyzed as percent cover (mean ± 1 SE, *n* = 8).

layella were observed in previous years (Lotze et al. 1999) and at a number of different sites across the Baltic Sea (H. K. Lotze and B. Worm pers. obs., Worm et al. 1999). Adult *Enteromorpha* spp. (> 80% *E. intestinalis*) only appeared in July with a biomass of 0.2 g dry weight m^{-2}. Most of the bloom biomass was found epiphytically on *Fucus vesiculosus*. Lower amounts of biomass were found on rocks.

Main herbivores in the field were amphipods, isopods, and littorinid snails (Fig. 1C). *Idotea* spp. (> 95% *I. chelipes* Pallas, < 5% *I. balthica* Pallas) and *Littorina saxatilis* Olivi showed strong seasonal trends with low densities in early spring and higher densities in summer and fall, reaching maxima of 120 and 200

individuals m^{-2}, respectively. *Gammarus* spp. (*G. locusta* L., *G. salinus* Spooner, *G. zaddachi* Sexton) and *Littorina littorea* L. were less abundant (0 to 20 individuals m^{-2}) throughout the vegetation period.

Population development of *Pilayella* and *Enteromorpha*

Populations of *Enteromorpha* and *Pilayella* clearly differed in their response to the combined effects of herbivory and the presence of a propagule bank. Nutrient enrichment from June to September had only minor effects on adult populations compared with the two other factors, but strongly affected new recruitment in summer (see below). Overall, *Pilayella* showed a distinctly shorter period of occurrence (March to July) than *Enteromorpha* which occurred from March to December (Figs 2, 3).

Development of *Enteromorpha* and *Pilayella* began in early March, given the propagule bank was present (Fig. 2B). In the absence of this recruitment source, i.e. on sterilized rocks (Fig. 2A), population development depended on supply of newly dispersed propagules, which started in May (Fig. 1A). Thus, population development of both species was delayed by 2 mo when the propagule bank was absent. The beneficial effects of the propagule bank were much stronger in *Enteromorpha*, allowing this species to reach 30% cover by May (Fig. 2B). In this month, the propagule bank had a significant positive effect on *Enteromorpha* cover (Table 1). In contrast, only a few thalli of *Pilayella* appeared from the propagule bank (< 5% cover). This species started its main development in May, subsequent to new recruitment from dispersed propagules.

In May, herbivores, mainly *Idotea* spp., *Gammarus* spp., *Littorina saxatilis* and *L. littorea* became abundant (Fig. 1C). Their effects became clearly visible as indicated by a sudden divergence of herbivore inclusion and exclusion treatments (Fig. 2B). In late May, herbi-

Table 1. Results of two-way ANOVAs on combined effects of herbivores and propagule bank on percent cover of *Enteromorpha* spp. and *Pilayella littoralis* in late May. Relative effect size is shown as explained variance in percent. Data were arcsin (sqrt $(x+1)$) transformed. Significant cage artifacts ($p = 0.0020$ in *Enteromorpha*, $p = 0.0001$ in *Pilayella*) occurred in the control experiment caused by reduced herbivore densities in open cages compared to open plots.

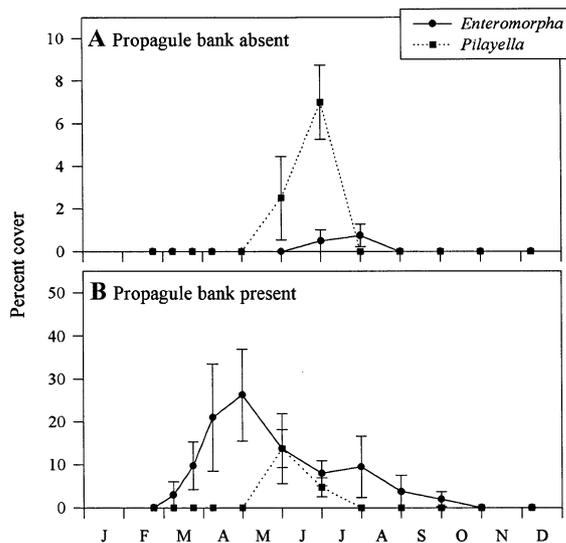| Source	df	MS	F-ratio	p-value	Variance (%)
Enteromorpha spp.					
Herbivory (H)	1	1.875	24.765	0.0001	24.6
Propagule bank (P)	1	3.386	44.711	0.0001	45.3
H × P	1	0.015	0.204	0.6554	
Block	3	0.016			
Residual	25	0.076			
Pilayella littoralis					
Herbivory (H)	1	0.005	0.118	0.7341	
Propagule bank (P)	1	0.599	13.033	0.0013	25.4
H × P	1	0.339	7.379	0.0118	13.5
Block	3	0.013			
Residual	25	0.046			

Fig. 3. Population development of *Enteromorpha* spp. and *Pilayella littoralis* on uncaged control plots with natural herbivore pressure without (A) and with (B) propagule bank. Data were analyzed as percent cover (mean ± 1 SE, n = 8).
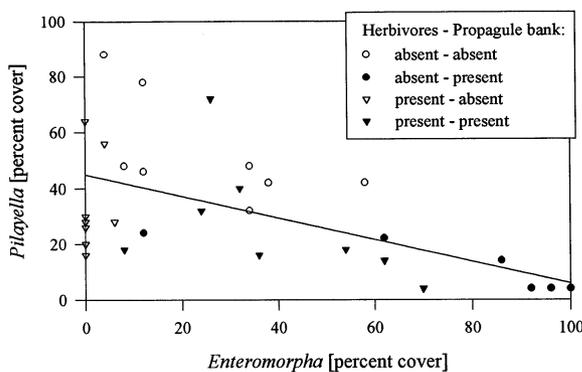

Fig. 4. Linear regression of percent cover of *Pilayella littoralis* versus percent cover of *Enteromorpha* spp. in May. Regression analysis revealed the following equation: $f(x) = -0.390x + 44.988$; $r^2 = 0.363$, $p = 0.0003$.

vores significantly reduced *Enteromorpha* cover (Fig. 2, Table 1). In *Pilayella*, herbivore effects depended on the presence of the propagule bank, as shown by a significant herbivore × propagule bank interaction in the analysis (Table 1). If the propagule bank was present (high *Enteromorpha* abundance), *Pilayella* was favored by the presence of herbivores which reduced *Enteromorpha* cover (Fig. 2B). In contrast, herbivores negatively affected *Pilayella* cover in the absence of the propagule bank (Fig. 2A, low *Enteromorpha* abundance). These pronounced herbivore effects were even stronger on the control plots without cages (Fig. 3). Both species, *Pilayella* ($F_{1,25} = 30.12$, $p = 0.0001$) and *Enteromorpha* ($F_{1,25} = 11.92$, $p = 0.0020$) had decreased cover on uncaged plots compared with open cages. In

the presence of the propagule bank, *Enteromorpha* was strongly reduced on control plots after herbivores became active in May (Fig. 3B) and *Pilayella* was able to co-occur with *Enteromorpha* until mid-July. In contrast, on control plots without a propagule bank, herbivores strongly reduced both species, but *Pilayella* dominated over *Enteromorpha* (Fig. 3A). This was the only treatment with a clear dominance of *Pilayella* over *Enteromorpha*. Reduced herbivore densities are the most likely cause for the observed differences between caged and uncaged plots (see below). Percent cover of *Pilayella* in May was significantly ($F_{1,30} = 17.11$, $p = 0.0003$, Fig. 4) negatively correlated with percent cover of *Enteromorpha*. This may support the idea that direct effects of herbivores and the propagule bank on *Enteromorpha* indirectly influenced *Pilayella* cover.

In June, nutrient enrichment was introduced as an additional factor. Ammonium was significantly enriched until mid-August on average 2.82-fold, and phosphorus until mid-September on average 1.35-fold (Table 2). Nutrient enrichment levels were not affected by cages and presence of the propagule bank (ANOVAs, $p > 0.05$). On average, ammonium enrichment did not exceed 4 µmol l^{-1}, and phosphate enrichment did not exceed 1.5 µmol l^{-1} compared to background nutrient concentrations. Nitrate, which is released in a fixed molar ratio to ammonium (0.69:1), may not have exceeded 2.5 µmol l^{-1} due to enrichment.

At the end of June, herbivore effects on percent cover of *Enteromorpha* were more important (34.8% of variance explained, Table 3) than in May (24.6%, Table 1) whereas the propagule bank effect decreased in importance (June 15.2%, May 45.3%). Nutrient enrichment had no effect on percent cover of *Enteromorpha* (Table 3). However, nutrient enrichment significantly increased canopy height of *Enteromorpha* and this effect was stronger in treatments without propagule bank compared to treatments with propagule bank (nutrient enrichment × propagule bank interaction, $F_{1,21} = 4.47$, $p = 0.0466$, cage effect on canopy height, $F_{1,21} = 62.08$, $p = 0.0001$). In *Pilayella*, biomass strongly decreased towards the end of June and canopy height was not analyzed. However, percent cover of *Pilayella* was significantly increased by herbivores and negatively affected by the propagule bank (Table 3). Furthermore, nutrient enrichment had significant negative effects on percent cover of *Pilayella* in June (Table 3).

Herbivore densities within open cages were reduced compared to control plots without cages (Table 4). This was most probably caused by the weekly cleaning procedure which was necessary to prevent fouling of cages. This significantly reduced the density of slow-moving *Littorina saxatilis* (Table 4). A similar but non-significant trend was visible in *L. littorea*, whereas mobile *Idotea* slightly preferred open cages compared to open plots. In *Gammarus*, there was no trend visible. Re-

Table 2. Ammonium and phosphate background and enrichment concentrations in the field experiment (means ± 1 SE, $n = 24$), and ANOVA results on nutrient enrichment. Cages and the presence of the propagule bank had no effect on nutrient enrichment ($p > 0.05$ in all analyses). Data were log-transformed to achieve homogeneity of variances.

Date	Background		Enrichment		p-value	$F_{1,33}$-value	MS_{error}
	Mean	SE	Mean	SE			
Ammonium (μmol l^{-1})							
5.7.97	0.11	0.05	0.83	0.32	0.0091	7.692	0.029
24.7.97	4.28	0.14	7.18	0.93	0.0001	19.609	0.019
15.8.97	0.80	0.15	1.02	0.28	0.7186	0.132	0.290
12.9.97	3.15	0.21	2.94	0.32	0.1043	2.790	0.012
Phosphate (μmol l^{-1})							
5.7.97	0.40	0.02	0.71	0.07	0.0001	37.643	0.002
24.7.97	2.09	0.05	2.74	0.21	0.0004	15.199	0.007
15.8.97	1.33	0.03	1.55	0.08	0.0059	8.656	0.006
12.9.97	0.68	0.03	0.79	0.05	0.2102	1.633	0.013

duced herbivore densities in open cages compared to uncaged control plots are assumed to be the main factor causing significant cage artifacts in our analyses on algal percent cover and canopy height. In open cages, the three-fold reduction of *L. saxatilis* which is an important consumer of algal germlings (Lotze 1998) may be not compensated for by the two-fold increase of *Idotea*. All cage artifacts resulted in increased performance of algae in open cages compared to uncaged control plots. The cages did not affect the other experimental variables (nutrients, propagule bank) in any of the analyses (ANOVAs, $p > 0.05$). We found no hints of further cage artifacts such as reduced light level (see above), reduced nutrient supply (see above), or enhanced sedimentation rate due to possible reduced water motion (H. K. Lotze and B. Worm pers. obs.). All these effects would have decreased algal performance within cages in contrast to the observed increase. Be-

cause of the reduction of herbivore pressure in open cages herbivore effects were conservatively estimated in the experiment.

New recruitment

New recruitment of algal propagules included settlement from the water column, germination and subsequent growth of germlings. These processes were strongly controlled by the combined effects of herbivory and nutrient enrichment in our experiment (Fig. 5). Nutrient enrichment resulted in significantly increased abundances of visible germlings in *Enteromorpha* and *Pilayella* (Table 5), and was the factor with the largest relative effect size (33.6% and 16.2% of variance explained for the two species, respectively). Nutrient enrichment had stronger effects on new re-

Table 3. Results of three-way ANOVAs on combined effects of herbivory, propagule bank and nutrient enrichment on percent cover of *Enteromorpha* spp. and *Pilayella littoralis* in late June. Significant cage artifacts ($p = 0.0001$ in *Enteromorpha*, $p = 0.0522$ in *Pilayella*) occurred in the control experiment caused by reduced herbivore densities in open cages compared to open plots. Data were arcsin (sqrt $(x+1)$) transformed.

Source	df	MS	F-ratio	p-value	Variance (%)
Enteromorpha spp.					
Herbivory (H)	1	1.849	21.105	0.0002	34.8
Propagule bank (P)	1	0.853	9.739	0.0052	15.2
Nutrient enrichment (N)	1	0.016	0.181	0.6753	
H × P	1	0.014	0.163	0.6906	
H × N	1	0.005	0.052	0.8216	
P × N	1	0.127	1.447	0.2424	
H × P × N	1	0.268	3.059	0.0949	
Block	3	0.001			
Residual	21	0.088			
Pilayella littoralis					
Herbivory (H)	1	0.194	8.969	0.0069	16.0
Propagule bank (P)	1	0.181	8.404	0.0086	14.8
Nutrient enrichment (N)	1	0.102	4.735	0.0411	7.5
H × P	1	0.020	0.938	0.3438	
H × N	1	0.005	0.220	0.6442	
P × N	1	0.006	0.295	0.5928	
H × P × N	1	0.029	1.356	0.2573	
Block	3	0.020			
Residual	21	0.022			

Table 4. Herbivore densities per m² in uncaged control plots (natural herbivore density) and open cages (herbivore access) in July (means ± 1 SE, n = 16), and ANOVA results of the cage effect on herbivore density. Nutrient enrichment and the propagule bank had no effects on herbivore densities (p > 0.05 in all analyses).

Species	Control plots		Open cages		p-value	$F_{1,21}$-value	MS_{error}
	Mean	SE	Mean	SE			
Littorina saxatilis	1306.4	226.8	446.4	76.8	0.0002	20.570	0.052
Littorina littorea	12.7	6.3	4.2	4.2	0.2911	1.173	0.006
Idotea spp.	211.5	18.0	498.6	108.0	0.0417	4.707	0.083
Gammarus spp.	301.9	89.5	338.7	63.2	0.3910	0.767	0.060

cruitment of *Enteromorpha* (4.4- to 7.3-fold increase, Fig. 5) than on *Pilayella* (1.6- to 2.5-fold). Herbivores counteracted the nutrient effect and significantly reduced recruitment of the two species (Table 5). Herbivore presence explained 14.0% and 8.5% of total variance in *Enteromorpha* and *Pilayella*, respectively. These herbivore effects, however, may be underestimated in the cage experiment (see above) as indicated by significant cage effects on *Enteromorpha* ($F_{1,21}$ = 20.36, p = 0.0002) and *Pilayella* ($F_{1,21}$ = 52.16, p = 0.0001). In *Enteromorpha*, there was an additional effect of the propagule bank, resulting from manipulations of the propagule bank on adjacent rocks (Fig. 2). The propagule bank had a significant positive effect on new recruitment of *Enteromorpha* on the tiles (Table 5). Since the propagule bank increased *Enteromorpha* cover on the rocks (Fig. 2) this may have caused higher propagule supply on the tiles. This suggests that propagule supply can vary with the proximity and size of the propagule source.

Discussion

Population development and dominance patterns of the co-occurring bloom-forming macroalgae *Pilayella littoralis* and *Enteromorpha intestinalis* were controlled by the combined effects of a propagule bank, herbivore consumption and nutrient enrichment. Recruitment processes and forces affecting early life stages at the beginning of the vegetation period represented a bottleneck for population development of these two algae. Our results demonstrate a previously unrecognized ecological role of a macroalgal propagule bank for population dynamics of annual algae and the formation of macroalgal blooms. Furthermore, the propagule bank affected processes of population and community regulation via interactions with consumers and resources.

The propagule bank

The propagule bank was an important overwintering mechanism and a major source of spring recruitment for *Enteromorpha* and *Pilayella* at our study site. Whereas bloom-forming macroalgae have been shown

to overwinter as adult thalli in some areas (Vermaat and Sand-Jensen 1987, Schories 1995b, Kamermans et al. 1998), settled propagules or microscopic stages have been proposed to be the major or only source of overwintering when adult stages are absent in winter (Schories 1995b, Lotze et al. 1999). This important role of a propagule bank in the life cycle of annual algae may be comparable to the overwintering of annual land plants in the form of seeds or bulbs (Fenner 1992, Crawley 1997, Baskin and Baskin 1998). As in many other organisms which invest into banks of resting eggs, cysts, seeds, seedlings or other dormant stages
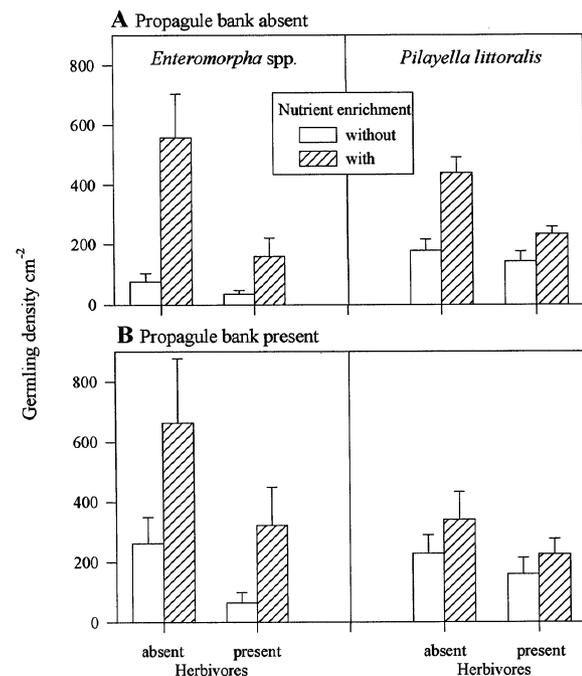

Fig. 5. Combined effects of herbivores, propagule bank, and nutrient enrichment on new recruitment of *Enteromorpha* spp. and *Pilayella littoralis* in June. New recruitment was examined on sterilized ceramic tiles which were exposed to all treatment plots of the field experiment. The presence/absence of the propagule bank in this part of the experiment is not directly manipulated, but the direct effect of the propagule bank on the algal canopy on rocks (Figs 2, 3), which acts as a propagule source, causes an indirect effect on recruitment rate. Germling density was quantified after 14 d (means + 1 SE, n = 4).

(Hairston and De Stasio 1988, Leck et al. 1989, Hoffmann and Santelices 1991, Fenchel et al. 1997) this "marine seed bank" allows algal populations to persist through unfavorable conditions and sudden disturbances in a variable environment.

However, not all species are favored by a propagule bank and different recruitment strategies may enable species coexistence (Lavorel et al. 1994). We observed alternating dominance patterns between *Enteromorpha* and *Pilayella* depending on the recruitment source. Massive recruitment from the propagule bank on rocks favored *Enteromorpha* and had strong negative effects on *Pilayella*. This may be a result of the 10- to 50-fold higher density of *Enteromorpha* in the propagule bank (330 cm^{-2} on rocks) compared to *Pilayella* (7 cm^{-2}) (Lotze et al. 1999). When both species initiated new reproduction in May, *Pilayella* clearly dominated over *Enteromorpha* through dispersal of new propagules on substrata without the propagule bank (sterilized rocks), although it showed only slightly higher propagule supply than *Enteromorpha* at this time (Fig. 1A). In the field, such substrata without propagule banks are mainly provided by thalli of perennial plants such as *Fucus vesiculosus* on which only few propagules overwinter (Lotze et al. 1999). Clearly, the importance of the propagule bank (dormancy) versus dispersal for population development may depend not only on species-specific investment rates, but also on forces affecting successful recruitment. Competitive interactions within the recruitment stage and the modifying effects of herbivores, nutrients and other abiotic or biotic factors may alter the relative impact of the propagule bank.

At the beginning of the vegetation period, the seasonal recruitment windows of *Enteromorpha* and *Pilayella* are opened by rising temperature and light intensity (Lotze et al. 1999), which is a general pattern among many marine and terrestrial plants (Deysher and Dean 1986, Fenner 1992, Baskin and Baskin 1998). Although early recruitment would be a competitive advantage for space occupancy over species that germinate later in the year, the ability of *Pilayella* to germinate at lower temperatures than *Enteromorpha* (Lotze et. al. 1999) did not prove to be a significant advantage in our field experiment. Both species initiated recruitment at the same time. Later in the year, increasing herbivory and depletion of nutrients limit the seasonal window of optimal growth and recruitment conditions (Lotze 1998). Because recruitment from the propagule bank started 2 mo earlier than recruitment from new reproduction and dispersal, there were two major seasonal advantages, (1) a 2-mo escape from herbivory and (2) an opportunity to use high nutrient concentrations in early spring. Both factors may generally favor bloom-forming macroalgae which are supported by high nutrient supply but are susceptible to herbivory (Valiela et al. 1997, Raffaelli et al. 1998), whereas species-specific differences in the responses to these factors may cause the observed dominance patterns among *Enteromorpha* and *Pilayella*.

Herbivory

Herbivory is a dominant factor affecting species performance and competitive interactions (Lubchenco 1978,

Table 5. Results of three-way ANOVAs on combined effects of herbivory, propagule bank and nutrient enrichment on new recruitment of *Enteromorpha* spp. and *Pilayella littoralis* in late June. Significant cage artifacts ($p = 0.0002$ in *Enteromorpha*, $p = 0.0001$ in *Pilayella*) occurred in the control experiment caused by reduced herbivore densities in open cages compared to open plots. Log-transformed data achieved homogeneity of variances.

Source	df	MS	F-ratio	p-value	Variance (%)
Enteromorpha spp.					
Herbivory (H)	1	1.684	10.350	0.0041	14.0
Propagule bank (P)	1	0.799	4.914	0.0378	5.8
Nutrient enrichment (N)	1	3.824	23.505	0.0001	33.6
H × P	1	0.030	0.187	0.6699	
H × N	1	0.007	0.041	0.8416	
P × N	1	0.178	1.096	0.3070	
H × P × N	1	0.262	1.612	0.2180	
Block	3	0.179			
Residual	21	0.163			
Pilayella littoralis					
Herbivory (H)	1	0.235	4.525	0.0454	8.5
Propagule bank (P)	1	0.007	0.139	0.7127	
Nutrient enrichment (N)	1	0.482	9.271	0.0062	16.2
H × P	1	0.003	0.056	0.8158	
H × N	1	0.007	0.140	0.7116	
P × N	1	0.062	1.200	0.2857	
H × P × N	1	0.022	0.418	0.5250	
Block	3	0.095			
Residual	21	0.052			

Paine 1990). At our site, herbivores became abundant and active in May, and strongly altered the performances of *Enteromorpha* and *Pilayella*. Both species were heavily consumed, yet, effects were stronger on *Enteromorpha* which was shown to be a preferred food source in all life stages (Lotze 1998). Dominance of *Enteromorpha* on rocks with the propagule bank was reduced by herbivores, resulting in an indirect positive herbivore effect on *Pilayella*. Strong selective consumption of a superior competitor as in our experiment is known to modify competitive interactions (Lubchenco 1978, 1983, Paine 1990, Menge 1995). However, if *Enteromorpha* was not abundant (as on plots without the propagule bank) the net effect of herbivores on *Pilayella* was negative. Hence, the net herbivore effect on *Pilayella* depended on the relative abundance of *Enteromorpha* which, at this stage, was largely controlled by the presence of the propagule bank. Moreover, herbivore consumption of *Enteromorpha* and *Pilayella* favored recruitment of perennial algae and species diversity in the system (Worm et al. 1999). These strong effects of herbivores as revealed by our cage experiment may even represent a conservative estimate because of reduced snail abundances caused by the weekly brushing procedure. Total herbivore effects were more pronounced on uncaged plots (Fig. 3), but relative effects on *Enteromorpha* and *Pilayella* were not different from caged plots (Fig. 2). Strong community effects of herbivores in the Baltic are caused by a diverse herbivore guild (Table 4, Lotze 1998) rather than a single "keystone species" (Paine 1966, 1995). Such "diffuse predation" (effect shared by several species of similar potential importance) as opposed to "keystone predation" (large effects of one important consumer) has also been identified in various North American rocky shore communities (Robles and Robb 1993, Menge et al. 1994).

Nutrient enrichment

Seasonal shifts in nutrient availability may influence dominance patterns of *Enteromorpha* and *Pilayella* by altering competitive abilities or the degree of competitive asymmetry (Keddy et al. 1997) between species. Recruitment of *Enteromorpha* was more strongly enhanced by nutrient enrichment than in *Pilayella* (Fig. 5). This is an advantage for *Enteromorpha* recruiting from the propagule bank during nutrient-rich conditions in early spring (Fig. 2B). Under nutrient-poor conditions, in summer, recruitment of *Enteromorpha* was reduced compared with *Pilayella*. Germlings of *Pilayella* may use nutrients more efficiently at low summer concentrations. This may favor *Pilayella* over *Enteromorpha* in the course of recruitment of newly dispersed propagules on sterilized substrata from May to June (Fig. 2A). Thus, shifting dominance between

Enteromorpha and *Pilayella* may depend on the recruitment source, herbivore pressure and seasonal nutrient availability. Unexpectedly, nutrient enrichment during summer had only slight effects on the established adult algal canopy in our experiments. Nutrient enrichment significantly increased canopy height of *Enteromorpha* which had negative effects on percent cover of *Pilayella*. This nutrient effect on *Enteromorpha* was more pronounced in the absence of the propagule bank, as indicated by a significant nutrient × propagule bank interaction. Still, the overall nutrient effect on adult populations was small compared to the effects of herbivory and the propagule bank. However, our experiment only considered processes in response to summer nutrient enrichment. In the course of eutrophication, nutrient availability may increase across all seasons. Subsequent experiments revealed that nutrient enrichment during the critical period of algal recruitment and growth in spring has pronounced effects on the development of an adult canopy (Worm et al. in press b).

This and previous studies demonstrate that early life stages of bloom-forming algae have a greater sensitivity and different reactivity towards factors such as temperature, light, herbivory and nutrients than adult stages (Lotze 1998, Lotze et al. 1999). In our experiment, moderate nutrient enrichment had strong effects on new recruitment of *Enteromorpha* and *Pilayella* in summer that even exceeded the effects of herbivory. Nutrient enrichment mainly allowed *Enteromorpha* to compensate for losses caused by herbivory at the recruitment stage. The general concept of counteracting herbivore and nutrient control of macroalgal blooms is supported by studies from seagrass-dominated systems (McGlathery 1995, Hauxwell et al. 1998). Effective natural herbivore control of macroalgal blooms at early life stages will decrease and probably disappear with increasing nutrient input.

Conclusions and management implications

In conclusion, algal recruitment in spring was the critical period for population development of the bloom-forming macroalgae *Pilayella* and *Enteromorpha*. The recruitment source (propagule bank versus dispersal), in combination with abiotic variables (temperature, light, nutrients) and biotic interactions (herbivory) interactively controlled the extent of blooms and species dominance patterns. The period of optimal growth and recruitment conditions was limited in spring by low temperature and light intensity and in summer by increasing herbivore pressure and low nutrient concentrations. The length of this period may vary from year to year. This may be an important factor that causes the observed variability in the extent of macroalgal blooms. Fig. 6 gives a conceptual model of the main control mechanisms for *Enteromorpha* and *Pilayella*. Massive

Enteromorpha spp.   **Pilayella littoralis**

Propagule bank

Propagule bank

\+ **Temperature** \+
Light

Competition
(for space, light, nutrients)

Germlings ⟷ Germlings

Propagules

Propagules

− **Herbivory** − →
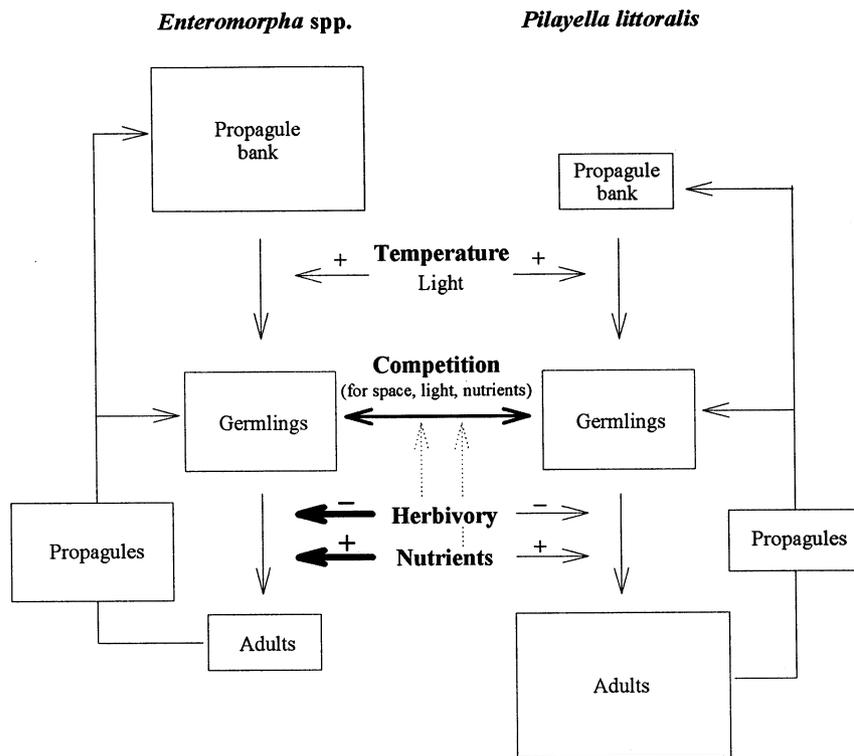\+ **Nutrients** \+ →

Adults

Adults

Fig. 6. Conceptual model of main mechanisms that control population development and species dominance pattern of *Enteromorpha* spp. and *Pilayella littoralis* in macroalgal blooms at the study site. The box size indicates the relative abundance of each life stage. Solid arrows indicate direct effects and transitions from one life stage into another. The thickness of arrows represents the relative importance of effects, +, − the character of direct effects. Dotted arrows indicate modifying indirect effects of herbivory and nutrient concentrations on competitive interactions. For further details refer to the text.

recruitment from the propagule bank favors *Enteromorpha*. The initiation of recruitment of both species in spring is triggered mainly by temperature and to a lesser degree by light (Lotze et al. 1999). Among recruiting germlings competition is likely to occur for space, light and nutrients. Both species are susceptible to herbivory but are supported by nutrients. However, these two factors indirectly affect dominance patterns. Through selective consumption of *Enteromorpha* (Lotze 1998), herbivores promote *Pilayella*. Under actual environmental conditions, this herbivore effect and recruitment on non-propagule bank substrata such as *Fucus* plants, support dominance of *Pilayella* over *Enteromorpha*. But, further increases of nutrient loads, as simulated in our experiments, may allow *Enteromorpha* to overcompensate herbivore pressure and increase *Enteromorpha* dominance over *Pilayella*. Subsequent experiments in different years and at sites in the Baltic and Northwest Atlantic supported the general result, that the ability of annual algae to overcompensate herbivore pressure increases with rising nutrient loading in the adult and early life stages (Worm et al. in press b, H. K. Lotze, B. Worm unpubl.). On the other hand, declines of herbivores will have effects similar to increases in nutrient loads. There is some evidence for decreasing herbivore abundances with increasing eutrophication (Hauxwell et al. 1998). Moreover, herbivores suffer from loss of important habitat such as perennial algae and seagrasses (Salemaa 1987) which

decline in eutrophicated waters worldwide (Schramm and Nienhuis 1996, Raffaelli et al. 1998). Such reduction of natural herbivore pressure in combination with increasing nutrient loads will accelerate macroalgal blooms, with further negative impacts on the perennial flora and fauna. In contrast, reduction of nutrient loads may increase herbivore control of bloom-forming species such as *Enteromorpha* and *Pilayella*, favoring species coexistence and diversity, with proposed general feedbacks on ecosystem function and stability (Schulze and Mooney 1993, Naeem and Li 1997). The reduction of nutrient loads and the conservation of perennial vegetation with their associated high-diversity herbivore fauna will be necessary in order to sustain diverse coastal ecosystems along with their functions and services (Valiela et al. 1997, Vitousek et al. 1997).

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