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Algal propagule banks modify competition, consumer and resource control on Baltic rocky shores

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Abstract We hypothesized that supply from macroalgal propagule banks may influence the relative abundance of annual and perennial algae and that this may alter the effects of grazers and nutrients on species composition. In a factorial field experiment in the Baltic Sea littoral system we tested the effects of manipulating propagule banks, the abundance of crustacean and gastropod grazers, and nutrient supply on recruitment and growth of macroalgae over a year. Moreover, we determined seasonal patterns of macroalgal propagule dispersal at the experimental site and quantified algal abundance and recruitment at 25 locations throughout the Baltic Sea. Experimental manipulations had minor effects on adults of the dominating perennial alga, *Fucus vesiculosus*. Instead, we found that species composition was determined by processes operating at early life stages. Propagule supply from a propagule bank strongly favored the fast-growing annual alga *Enteromorpha* spp. which then blocked settlement and recruitment of *Fucus*. Grazers reduced the abundance of annual algae and indirectly favored *Fucus* recruitment. There was an apparent trade-off between gains from the propagule bank and losses to herbivory in five of seven colonizing species. Nutrient enrichment overrode grazer control of annual algae and accelerated the decline of *Fucus* only when annual algae had already achieved high densities through the propagule bank. Corroborating the experimental findings, field surveys across the Baltic showed that *Fucus* recruit densities can be predicted from the cover of annual algae during the period of *Fucus* reproduction and settlement. Recruitment inhibition by annual algae, which is driven by the abundance of annuals in the propagule bank, increasing nutrient levels, and declining consumer control,

is suggested as a mechanistic explanation of the current decline of perennial algae in the Baltic Sea.

Keywords Dormancy · Eutrophication · *Fucus vesiculosus* · Grazing · Nutrients

Introduction

Dispersal and dormancy of propagules are critical processes that contribute to the persistence of plant populations in a variable environment (Harper 1977). Dispersal reduces the risk of local extinction by spreading propagules spatially. Contrarily, investment into banks of dormant propagules can provide temporal escapes from adverse conditions. Although dormant propagule banks occur in all major habitats, they have mostly been studied in higher land plants (Leck et al. 1989; Fenner 1992). Among land plants, differential investment into the propagule bank is related to species life-history patterns: opportunistic annuals invest orders of magnitude more propagules into soil seed banks than most perennial species (Grime 1979) and have more persistent seeds than related perennials (Thompson et al. 1998). Such traits may translate into a competitive advantage for opportunistic annuals in frequently disturbed environments (ruderal strategy, Grime 1979), which has consequences for the structure of plant assemblages.

In the marine environment, macroalgal propagule banks have only recently been described in detail and little is known about the factors that determine their composition, density, and ecological role (Santelices et al. 1995; Lotze et al. 1999). These “banks of microscopic stages” (Chapman 1986) consist of settled spores, micro-recruits, or other microscopic forms which suspend growth when environmental conditions are unfavorable and can survive for up to 10 months (Hoffmann and Santelices 1991; Schories 1995). It is thought that macroalgal propagule banks are transient in a sense that they persist only for some months (e.g., through winter) until environmental conditions improve and all propagules

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germinate or are lost to grazing or other sources of mortality (Lotze et al. 1999). Recently, it has been shown that bloom-forming annual algae use the propagule bank as an overwintering mechanism and as an important "seed source" for the annual spring bloom (Schories 1995; Lotze et al. 1999, 2000), and that these blooms can interfere with the establishment of perennial algae (Worm et al. 2000a). In addition to propagule supply, nutrient availability and herbivory have strong effects on plant species composition in littoral communities ("bottom-up" versus "top-down" control, Menge 1992; Worm et al. 2000a). The responses of individual species to these forces are linked to life-history patterns: increasing nutrient supply tends to increase the dominance of fast-growing annuals, whereas increasing herbivore pressure favors well-defended perennials (Steneck and Dethier 1994; Duarte 1995; Worm et al. 2000a). However, these effects may rarely be independent, as herbivore effects can depend on nutrient supply (Proulx and Mazumder 1998) and the effects of nutrient enrichment can depend on herbivore abundance (Lotze et al. 2000; Worm et al. 2000a). Therefore we chose to study the effects of a propagule bank in combination with factorial manipulation of grazers and nutrient supply.

We hypothesized that the presence of a propagule bank increases the abundance of annual relative to perennial algae and that this may decrease the relative magnitude of reported strong impacts of grazers and resources on species composition in the Baltic littoral community (Worm et al. 2000a). Moreover, building on previous work from North America (Lubchenco 1986; Worm and Chapman 1996), we hypothesized that annual-perennial competition may be particularly intense at the recruitment stage, rather than at the adult stage. To test these hypotheses, we manipulated the presence of grazers and the propagule bank as well as nutrient supply in a factorial field experiment, monitoring algal recruitment and growth of adult algae. In order to relate patterns of macroalgal recruitment in the experiment to seasonal patterns of propagule supply, we also monitored settlement and recruitment of macroalgal propagules over a 2-year period. In order to test the generality of concepts that emerged from our small-scale field experiments, we conducted a large-scale field survey throughout the Baltic Sea where we quantified patterns of macroalgal abundance and recruitment.

Materials and methods

Study area and species

The experiments and observations were carried out at Maasholm, a shallow embayment which is part of a nature reserve in the outer Schlei Fjord (54°41'N, 10°0'E), western Baltic Sea, Germany. The study area is protected from severe wave action (maximum fetch is 5 km). Lunar tides are unimportant, compared with irregular wind-driven sea level changes with an amplitude of ± 0.5 m around mean water level. Salinity fluctuates irregularly following water exchange with the more saline Kattegatt Sea and ranges between 12 and 18 PSU (practical salinity units) in summer and 14 and

20 PSU in winter. Formation of sea ice is common in January and February. Water temperature ranges between -1 and 4°C in winter and 16 and 25°C in summer. Like most regions of the Baltic Sea, the Schlei Fjord is eutrophicated by human activity. Winter concentrations at Maasholm reach $160 \mu\text{mol l}^{-1}$ nitrate, $12 \mu\text{mol l}^{-1}$ ammonium and $2 \mu\text{mol l}^{-1}$ phosphate from January to March (Schramm et al. 1996). From mid-May to mid-August, ammonium and nitrate are largely depleted and typically remain close to the detection limit (0.0 – $0.3 \mu\text{mol l}^{-1}$). Soluble reactive phosphate remains between 0.1 – $0.6 \mu\text{mol l}^{-1}$. In September, ammonium regeneration starts and nutrient concentrations rise rapidly throughout the fall.

In shallow water (0–1 m depth), rocks and boulders provide abundant substratum for seaweed colonization. From a previous study (Lotze et al. 1999), we knew that colonization by various species can either occur from new reproduction (dispersal), or from overwintering banks of microscopic stages (dormancy) which can be found on various substrata, most densely on rocks. The established hard-bottom community at our site is dominated by dense stands ($84 \pm 7.3\%$ cover on rocks, $\text{mean} \pm \text{1SE}$, $n=10$) of the perennial brown seaweed *Fucus vesiculosus* (simply called *Fucus* hereafter). A suite of annual macroalgae (species names listed in figures and tables, Results), benthic diatoms and benthic invertebrates (*Mytilus edulis*, *Balanus improvisus*, various hydroids and bryozoans) co-occur epilithically or epiphytically with *Fucus*. Large macrograzers such as urchins or limpets are absent from the Baltic but mesoherbivorous gastropods and crustaceans are common (species names and densities given in tables, Results).

Monitoring of settlement

We applied a recently developed monitoring technique in order to obtain a qualitative estimate of seasonal patterns of propagule dispersal and settlement at the experimental site (Kiirikki and Lehvo 1997). Propagule settlement was estimated from observations of a sequence of settlement substrata (concrete blocks) which were submerged at discrete time intervals at the research site. Concrete is a suitable substratum for settlement of Baltic macroalgae (Kiirikki and Lehvo 1997). We exposed a sequence of 50 concrete blocks ($30 \times 30 \times 5$ cm) at intervals of 14 days (February–July 1997) or 10 d (August 1997–October 1998). One block per time interval was added to the sequence and installed adjacent to the cage experiment at 0.8 m water depth. Every 1–2 months, all blocks were inspected and average canopy height of each attached species was measured with a ruler in 0.5 cm intervals. In addition, percent cover of all attached species was estimated using a 25×25 cm plexiglas sheet with 50 random dots. Algal samples were obtained to verify species identification.

The beginning of a settlement period can be estimated by comparing the average canopy height of colonizing species over time: blocks which were exposed prior to the settlement period of a species are colonized simultaneously while the following blocks will be colonized in discrete time intervals according to the sequence of exposure. When these colonizing propagules grow into macroscopic recruits, plant height is similar among simultaneously colonized blocks and gradually declines throughout the following sequence of blocks. The last block that is colonized marks the end of the settlement period (Kiirikki and Lehvo 1997). Comparison of plant cover among blocks may allow a crude estimate of settlement intensity. When only single algae were visible ($<2\%$ cover) we classified this as "low settlement", and higher abundance was classified as "high settlement". This method allows only minimum estimates of the settlement period and settlement intensity of a species because it requires recruitment and growth of settled propagules to macroscopic germlings of at least 2–3 mm length. However, various factors (herbivory, competition, unfavorable abiotic conditions) can suppress recruitment of settled propagules to macroscopic stages (Vadas et al. 1992; Worm and Chapman 1998).

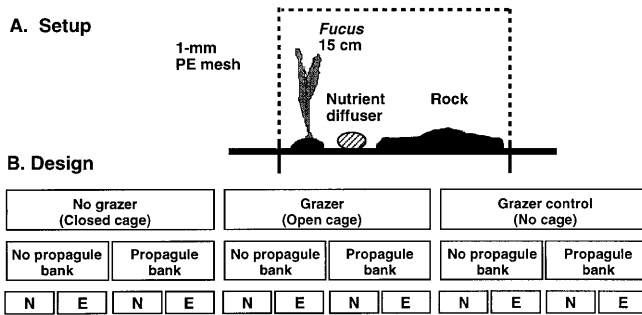


Fig. 1 **A** Experimental setup and **B** experimental design of a factorial field experiment testing for interactions among grazers, a macroalgal propagule bank, and summer nutrient enrichment (*N* not enriched, *E* nutrient-enriched). Each of the 12 treatment combinations had 4 replicates. The design allowed us to test for grazer effects (main experiment: comparing No Grazer and Grazer treatments) and to control for cage effects (control experiment: comparing Grazer and Grazer Control plots). The experiment was run from February to December 1997; nutrient enrichment was maintained from June to August 1997

Field experiment

We performed a factorial field experiment from February to December 1997 where we manipulated the presence of a macroalgal propagule bank, grazer presence and nutrient enrichment (Fig. 1). The experiment was conducted at Maasholm in a natural stand of *F. vesiculosus* at 0.8 m water depth. The experimental manipulations (propagule bank, grazer, nutrients) were combined in a 3×2×2 completely crossed design (Fig. 1) with randomized blocks (4 replicates per treatment combination arranged in 4 blocks of 12 plots each, Mead 1997). All plots were 3 m apart from each other and blocks were 5 m apart.

The experimental units were flat granite rocks (*c.* 15–20 cm in diameter). These rocks were collected from the shallow-water zone at the study site after break-up of sea ice in February and were initially bare of macroscopic vegetation. To remove the microscopic propagule bank, half of the rocks were heat-sterilized for 48 h at 100°C in order to kill all microscopic macroalgal stages; the other half were left untreated.

Grazers were manipulated with cages (25×25×25 cm). These were made from a stainless steel frame covered with transparent polyethylene mesh (1 mm mesh size). This mesh size is necessary in order to exclude mesograzers (2–15 mm body size), which dominate the grazer fauna of the Baltic Sea. Repeated light measurements (LI-COR LI-192SA) indicated that photon flux through the mesh was reduced by only 8%. Half of the cages were completely closed (“No Grazer” treatment), the other half of the cages had one side cut open to allow free access for grazers (“Grazer” treatment). In addition, we established uncaged “Grazer Control” plots to test for potential cage artifacts. All cages were brushed weekly to prevent fouling and closed cages were checked weekly for grazer intrusion. In July, we compared grazer densities within a central 10×10 cm area between Grazer and Grazer Control plots to evaluate possible cage artifacts on grazer abundance.

Nutrient enrichment was performed on one half of the experimental plots during the period of summer nutrient depletion (20 June–30 September 1997). We used nutrient diffusers which were rolls of polyethylene mesh (40×2.5 cm, 1 mm mesh size) filled with 160 g NPK slow-release fertilizer pellets (Plantacote Depot 6 M, Urania Agrochem, Hamburg, Germany). Pellets are covered with a semi-permeable polyurethane membrane and contain 14% N (5.7% NO₃ and 8.3% NH₄), 9%P (P₂O₅) and 15% K₂O, the last of which presumably had no effect due to the high K concentrations in seawater. This method is probably the most reliable technique for *in situ* nutrient enrichment of benthic communities; for detailed discussion and comparisons with other methods

see Worm et al. (2000b). To control treatment levels, we monitored water column nutrient concentrations on all plots at 3-week intervals. We obtained water samples with 10-ml polyethylene syringes at a central position within the cages. All samples were immediately filtered over Whatman GF/F filters (pre-combusted at 550°C to remove possible contaminations) and analyzed colorimetrically for ammonium and phosphate (Grasshoff et al. 1986). Release of nitrate was not quantified in this experiment. Independent tests of this enrichment method showed that these diffusers increase nitrate availability on average by 120% relative to background concentrations (Worm et al. 2000b). Using this relationship, we estimated nitrate enrichment levels from water column nitrate levels which were sampled at the experimental site every 2 weeks. Nitrate samples were obtained with 1-l polyethylene bottles, filtered (Whatman GF/F), frozen and subsequently analyzed on a Technicon autoanalyzer.

As the main dependent variable, percent cover of all species on the experimental rocks was estimated monthly with a 10×10 cm plexiglas sheet marked with 50 random dots. Furthermore, we estimated *Fucus* recruit densities in May, June, August and October in five 2×2 cm subsamples within a central 10×10 cm area on all experimental rocks. In September and November, the biomass (grams dry weight per 10×10 cm area on the rocks) of *Fucus* recruits was estimated with a non-destructive method (Kiirikki 1996). Percentage cover of each species was multiplied by canopy height (measured with a ruler in 0.5 cm intervals). This value (*x*) can be transformed into grams dry weight per 100 cm² (*y*) using an empirical relationship ($y = -0.0084 + 0.0057x$, $n = 43$, $r^2 = 0.75$, $P < 0.0001$), which was derived from measurements in *Fucus* stands at our experimental site (Worm 2000).

In addition to *Fucus* recruitment, we were interested to test for treatment effects on growth and survival of adult *Fucus*. Therefore we included single *Fucus* individuals into all cages and on uncaged plots (Fig. 1A). In February we collected *Fucus* individuals (12–18 cm length) that were growing on small rocks at Maasholm. All specimens were initially free of epiphytes. Algae with rocks were blotted dry with paper tissue for 15 s and weighed to the nearest 1 mg. We assumed that dormant propagules on *Fucus* could not be manipulated in a similar manner as on the experimental rocks without damaging *Fucus*. Instead, we removed all germinating epiphytes on half of the algae during a first sub-experiment from February–June. Hence, during this period grazers and epiphytes were manipulated in a 3×2 design. In June, *Fucus* individuals were collected, separated from epiphytes and rocks and all three parts were weighed separately. The dry weight of *Fucus* and epiphytes was determined after drying at 80°C for 48 h. A second, independent set of *Fucus* individuals was run from July–November. During this sub-experiment, grazers and nutrient enrichment were manipulated (3×2). Epiphyte cover on *Fucus* remained very low in the second sub-experiment and was not manipulated. Individuals were weighed together with their rock substrate in September. In November, the algae were separated from rocks and both parts were weighed separately. Then dry weight of *Fucus* was determined as above. As dependent variables, we estimated *Fucus* relative growth rate in the two sub-experiments as $RGR = (\ln DW_2 - \ln DW_1) / (t_2 - t_1)$, where DW = dry weight of *Fucus* (g), t_1 = time at start, and t_2 = time at end (d).

All data from the field experiment were analyzed by factorial fixed-factor ANOVA including “Grazer” (Grazer vs. No Grazer) and “Propagule Bank” (No Propagule Bank vs. Propagule Bank) as the main effects. Over the period of enrichment, “Nutrients” were added as an additional factor to test for the effects of summer nutrient enrichment. The control experiment was analyzed like the main experiment, except that the effect “Cage” (Grazer vs. Grazer Control) replaced the Grazer effect. When it explained a significant portion of variance, the spatial block effect was included as a non-interactive variable (Mead 1997). Percentage cover data were generally treated with an angular transformation (Sokal and Rohlf 1995). Recruit biomass and nutrient data and grazer densities were $\log(x+1)$ -transformed to fulfill the assumption of homogeneity of variances (checked by Cochran’s test). We also tested for a linear relationship between $\log(x+1)$ -transformed *Fucus* recruit densities

and the cover of *Enteromorpha* in the experiment by linear regression analysis (Sokal and Rohlf 1995).

Field survey

Using a large-scale field survey we attempted to predict average recruit densities of *Fucus* from the cover of annual algae on rocky substrata during the period of *Fucus* spring reproduction at a given site. *Fucus* reproduction usually occurs during May in the western Baltic, June in the central Baltic, and July in the eastern Baltic (see Results; C. Boström and R. Engkvist, personal communications). We sampled 15 predominantly rocky sites in Kiel Bight, Germany (54°12'N 11°03'E–54°55'N 9°48'E), 4 sites at the Swedish east coast (56°14'N 16°02'E–57°21'N 16°37'E), 4 sites in the Åland archipelago, Finland (60°20'N 19°36'E–60°23'N 19°43'E) and 2 sites along the Lithuanian open shore (55°50'N 21°03'E–55°55'N 21°02'E). These regions were 400–1000 km apart, and sites within regions were at least 5 km apart. At each site, ten replicate measurements were done along 100- to 150-m transects located at 0.8–1.2 m water depth. Replicates were placed randomly on rocky substrata and separated by 10–15 m. We determined annual algal cover in spring with a 25×25 plexiglas frame with 50 random dots. The sites were revisited after 3 months and the density of visible (>2 mm) *Fucus* recruits was determined within a 10×10 cm frame. Results were analyzed by linear regression analysis. Replicate measurements along transects were pooled for each site.

Results

Monitoring of settlement

Eight species of macroalgae showed dense settlement and recruitment on the settlement blocks (Fig. 2). Additional rare species which recruited too sparsely to estimate their settlement periods were *Ceramium nodulosum*, *Polysiphonia violacea*, *Dumontia contorta* and *Chaetomorpha linum*. Among the annual species a clear temporal distinction between six species of summer annuals (*Enteromorpha intestinalis*, *E. prolifera*, *E. clathrata*, *Pilayella littoralis*, *Ceramium strictum*, *Cladophora rupestris*) and three species of winter annuals (*Ulvopsis grevillei*, *Petalonia fascia*, *Scytosiphon lomentaria*) was observed (Fig. 2). The length of the settlement period varied among species and years between 1 and 5.5 months. The only perennial species, *F. vesiculosus*, was characterized by a short and intense settlement period from late April to late May in 1997 and from early May to late June in 1998. Some minor *Fucus* settlement

occurred on blocks exposed from September to November 1997 and in September 1998. *Fucus* propagules that were generated in fall overwintered as microscopic forms in the propagule bank and recruited to the macrobenthos in the following spring. Similar spring recruitment of overwintering microscopic forms was observed in *Enteromorpha* spp. *Cladophora rupestris* and *Pilayella littoralis*. In addition, adult thalli of *Fucus*, *Ceramium strictum* and (only a few individuals) *Cladophora rupestris* overwintered at Maasholm.

Field experiment: species composition

Macroalgae were the dominant colonizers on all experimental rocks. Benthic invertebrates (*Mytilus edulis*, *Balanus improvisus*) showed very low recruitment (2% cover or less). Benthic microalgae (mostly tube-dwelling diatoms: *Berkeleya rutilans*) mixed with some fine filaments of the winter annual *Ulothrix flacca* occurred abundantly 1–2 months after initiation of the experiment, but disappeared thereafter. Depending on the treatment combination, the macroalgal community was dominated by the green annual *Enteromorpha* spp. (Fig. 3A) or *F. vesiculosus* (Fig. 3B). *Enteromorpha* spp. (*Enteromorpha* hereafter) was mostly (>80%) *E. intestinalis*. In July and August *E. prolifera* and *E. clathrata* co-occurred with *E. intestinalis*. Diatoms and brown, green, and red annual macroalgae colonized the rocks in a successive seasonal sequence at low to intermediate densities (Fig. 3C–E). Other macroalgae that occurred at low densities (<2% mean cover at any time) were *Chaetomorpha linum* and *Ceramium nodulosum*.

Enteromorpha recruited abundantly from overwintering propagules in March–April and dominated treatments with propagule bank thereafter (Fig. 3A). *Enteromorpha* cover remained significantly lower in treatments

Fig. 2 Estimated periods of propagule dispersal and settlement for eight abundant macroalgal species at the experimental site. Settlement plates were submerged every 10–14 days from February 1997 to October 1998. Filled circles indicate high settlement (>2% cover of visible recruits), open circles low settlement (<2% cover). *Enteromorpha* spp. was mostly (>80%) *E. intestinalis*; during July and August, *E. prolifera* and *E. clathrata* co-occurred with *E. intestinalis*

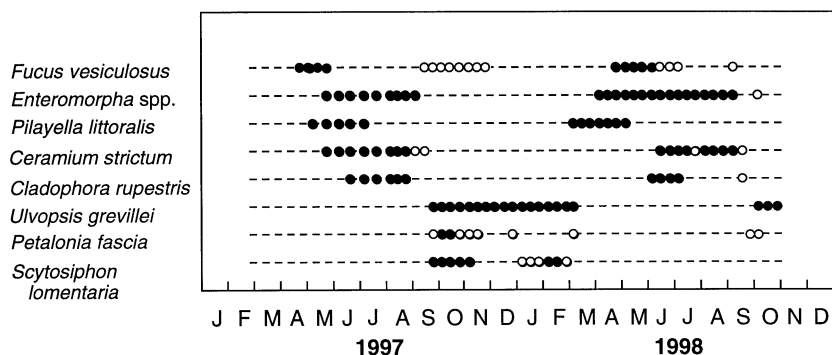
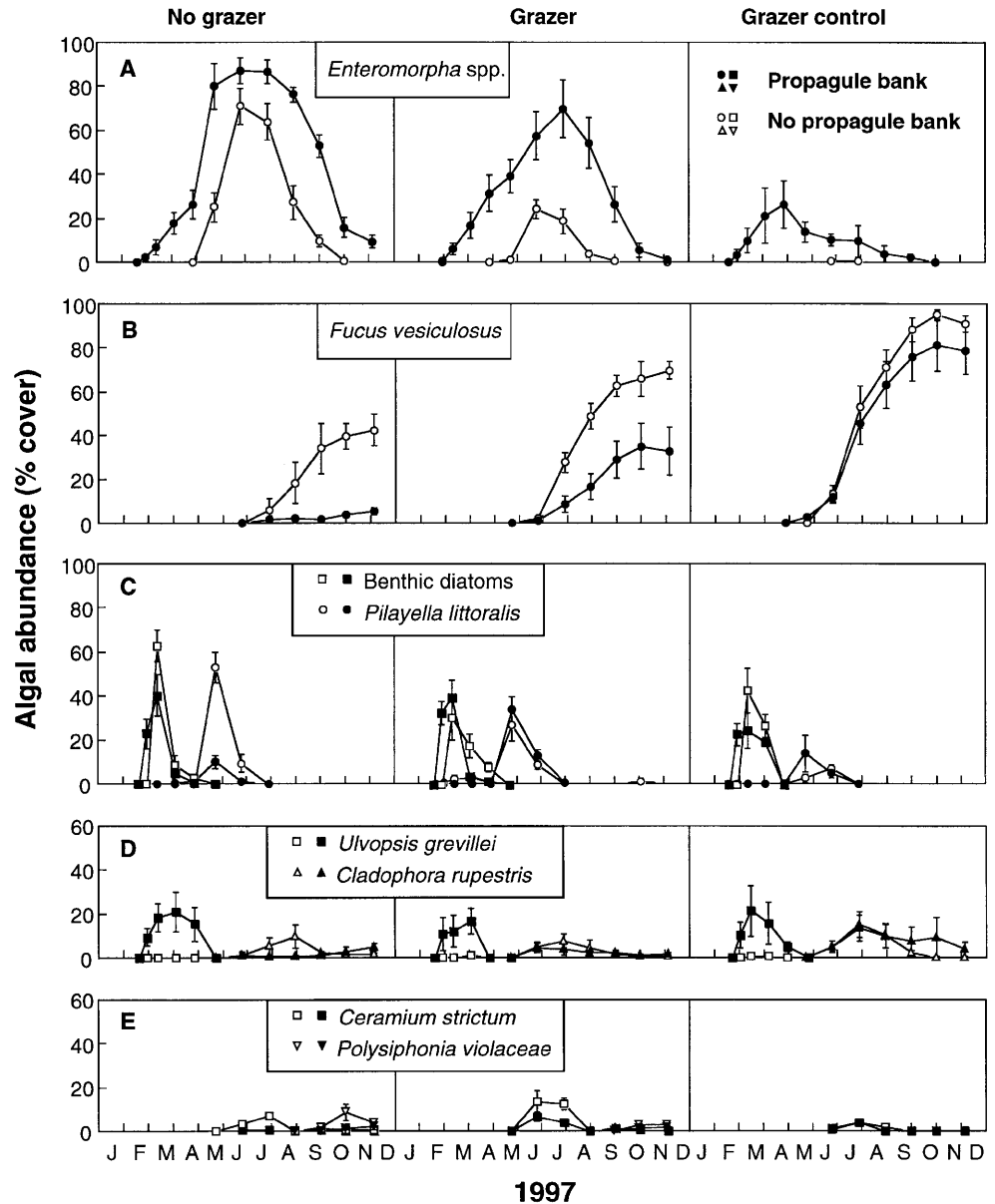


Fig. 3A–E Species composition in the experiment. Effects of grazers and an algal propagule bank on population development of 8 abundant macroalgal species (means \pm 1SE, $n=8$). Percentage cover is shown throughout the year for **A** the annual green alga *Enteromorpha* spp., **B** the perennial alga *Fucus vesiculosus*, **C** diatoms and ephemeral brown algae, **D** ephemeral green algae, and **E** ephemeral red algae. For ANOVA results see Table 1



without propagule bank (Table 1). In contrast, *Fucus* recruited mostly from spring reproduction (April–May, Fig. 2) and dominated treatments without propagule bank (Fig. 3B, Table 1). Similarly, *Pilayella littoralis* and *Cladophora rupestris* were significantly more abundant in treatments without propagule bank (Fig. 3C, D, Table 1). The winter annual *Ulvopsis grevillei* dominated treatments with propagule bank in February and March (Fig. 3D), but was replaced by *Enteromorpha* thereafter. Grazers had no significant effect on any of the species from February–April, but pronounced effects throughout the following months (Fig. 3). *Enteromorpha* and *Pilayella littoralis* were reduced by grazing (Fig. 3, Table 1), but note that the grazer effect on *Pilayella* depended on the propagule bank (as indicated by an interaction in the analysis, Table 1): *Pilayella* was reduced by grazing when the propagule bank was absent, but increased in grazed plots when the propagule bank was present, prob-

ably because grazers preferred *Enteromorpha*, which was most abundant in plots with the propagule bank (Lotze et al. 2000; Lotze and Worm 2000). More grazer-resistant species such as *Ceramium strictum* and *Fucus* always significantly increased in abundance when grazers were present (Table 1).

In the control experiment (Grazer vs. Grazer Control treatments), we detected significant cage artifacts on several colonizing species (Fig. 3, Table 1). These species were also significantly affected by grazers in the main experiment (Table 1). The grazer-susceptible species *Enteromorpha* and *Pilayella* had increased in Grazer cages, whereas *Fucus* and *Ceramium strictum* which were indirectly favored by grazing had increased on Grazer Control plots. This suggests that cage artifacts may be linked to changes in grazer abundance or activity and not by other possible factors such as reduction of photon flux or water flow or increased sedimentation in-

Table 1 Results of two-way ANOVAs on percentage cover of species in the main (*above*) and control (*below*) experiment. Values are *F*-ratios. Analyses were performed for the one month when each species reached its maximum mean abundance (aver-

aged over all plots) (Table 3). Summer nutrient enrichment had no significant effect ($P>0.1$) on the cover of individual species during these months. Thus this effect was pooled with the error term

Main experiment Species	Grazer <i>df</i> =1	Propagule Bank <i>df</i> =1	G×PB <i>df</i> =1	MS block <i>df</i> =3	MS error <i>df</i> =28
<i>Enteromorpha</i> spp.	20.50***	9.46**	0.16n.s.	0.001	0.090
<i>Fucus vesiculosus</i>	18.01***	34.23***	0.28n.s.	0.014	0.049
Benthic diatoms	2.70n.s.	0.66n.s.	2.48n.s.	0.017	0.106
<i>Pilayella littoralis</i>	0.12n.s.	13.03**	7.37*	0.013	0.046
<i>Ulvopsis grevillei</i>	0.13n.s.	9.28**	0.30n.s.	0.133	0.076
<i>Cladophora rupestris</i>	0.05n.s.	4.68*	1.12n.s.	0.063	0.028
<i>Ceramium strictum</i>	9.94**	4.12n.s.	0.02n.s.	0.021	0.026
<i>Polysiphonia violacea</i>	1.53n.s.	3.93n.s.	1.94n.s.	0.006	0.019
Control experiment Species	Cage <i>df</i> =1	Propagule Bank <i>df</i> =1	C×PB <i>df</i> =1	MS block <i>df</i> =3	MS error <i>df</i> =28
<i>Enteromorpha</i> spp.	32.16***	12.04**	3.78n.s.	0.007	0.008
<i>Fucus vesiculosus</i>	17.72***	8.382**	1.24n.s.	0.052	0.088
Benthic diatoms	0.05n.s.	0.27n.s.	0.26n.s.	0.028	0.111
<i>Pilayella littoralis</i>	30.12***	0.401n.s.	3.52n.s.	0.196	0.040
<i>Ulvopsis grevillei</i>	0.01n.s.	5.932*	0.01n.s.	0.051	0.088
<i>Cladophora rupestris</i>	1.38n.s.	0.29n.s.	0.06n.s.	0.008	0.057
<i>Ceramium strictum</i>	15.96***	1.115n.s.	1.42n.s.	0.019	0.024
<i>Polysiphonia violacea</i>	3.62n.s.	0.006n.s.	0.55n.s.	0.004	0.004

* $P<0.05$, ** $P<0.01$, *** $P<0.001$, n.s. $P>0.05$

Table 2 Densities of grazer species in the cage experiment (individuals per 100 cm²±1SE, $n=16$). *Gammarus* spp. was *G. salinus*, *G. locusta* and *G. zaddachi*. *Idotea* spp. was *I. chelipes* and *I. baltica*. Grazer (open cages) and Grazer Control plots (no cage) were compared by ANOVA

Species	Open cage	SE	No cage	SE
<i>Littorina saxatilis</i>	4.46***	0.77	13.06	2.27
<i>Littorina littorea</i>	0.04n.s.	0.04	1.27	0.63
<i>Idotea</i> spp.	4.97*	1.16	2.12	0.48
<i>Gammarus</i> spp.	3.39n.s.	0.67	3.02	0.76
All species combined	12.85*	1.29	18.32	2.40

* $P<0.05$, ** $P<0.01$, *** $P<0.001$, n.s. $P>0.05$

side cages (this would have reduced the performance of all species inside cages as compared with uncaged plots). In accordance with this hypothesis, grazer counts revealed that the abundance of the snail *Littorina saxatilis* was significantly reduced in the Grazer compared with Grazer Control plots (Table 2, ANOVA, $F_{1,28}=23.6$, $P<0.0001$). This was most likely an artifact created by the weekly cage brushing procedure, after which slow-moving snails needed time to re-invade Grazer cages. Fast-moving crustacean grazers (*Idotea chelipes* and *I. baltica*) occurred at higher densities in Grazer compared with Grazer Control plots (Table 2). Gammarid amphipods and the snail *Littorina littorea* were not affected by the presence of cages. Overall, grazer densities were significantly reduced by 30% in the Grazer compared with Grazer Control plots (Table 2). Weekly examinations revealed that grazer exclusion cages (No Grazer treatment) remained practically free of grazers throughout the experiment.

When we compared the effects of grazer exclusion and elimination of the propagule bank among the colonizing macroalgae we found that grazers and the propagule bank had opposing effects on species abundance: species which were negatively affected by grazers tended to be positively affected by the propagule bank and vice versa (Table 3). Also, we found an apparent trade-off between losses to herbivory and microrecruit densities in the propagule bank among the three most abundant species (Table 3).

Nutrient enrichment from June to September significantly enhanced water column nutrient concentrations on the experimental plots (Table 4). Nutrient concentrations were not different among caged and uncaged treatments (ANOVA, $P>0.2$). Ammonium concentrations were strongly enhanced after 1 month of enrichment, but declined thereafter. Phosphate remained enriched for 2 months (Table 4). Nitrate background concentrations ranged between 0.77 and 4.3 $\mu\text{mol l}^{-1}$ (mean 1.35 ± 0.29 $\mu\text{mol l}^{-1}$, $n=21$) during the period of enrichment (June–September). From this, we estimate that nitrate concentrations on enriched plots averaged 2.97 $\mu\text{mol l}^{-1}$ (120% increase, Worm et al. 2000b). The enrichment procedure did not significantly enhance percentage cover of individual species, except for *Enteromorpha*. By September, nutrient enrichment had increased the cover of *Enteromorpha* by 54% (relative to unenriched plots) in treatments with the propagule bank, but cover decreased by 60% in treatments without the propagule bank (ANOVA, Propagule Bank×Nutrients, $F_{1,21}=4.56$, $P=0.044$, Table 5).

Table 3 Experimental effects, estimated propagule densities in the propagule bank and maximum cover of macroalgal species in the cage experiment. To compare experimental effects among species, we calculated a simple index $I=(\text{treatment density-control density})/\text{control density}$ (Paine 1992) for the month when the species

reached its maximum mean cover, averaged over all plots. Positive or negative values identify net positive or negative effects of grazers or the propagule bank, as averaged over all treatments. AN-OVA results are reported in Table 1. Propagule density data were compiled from Lotze et al. (1999)

Species	Grazer effect	Propagule effect	Propagule density (± 1 SE)	Maximum cover (%) (± 1 SE, $n=8$)	Month with maximum cover
<i>Enteromorpha</i> spp.	-0.48	0.52	33,000 ($\pm 3,000$)	87.3 (± 5.8)	June
<i>Ulvoopsis grevillei</i>	-0.23	27.8	No data	20.8 (± 9.2)	April
<i>Polysiphonia violacea</i>	-0.21	-0.36	No data	3.5 (± 1.9)	October
<i>Pilayella littoralis</i>	-0.04	-0.58	667 (± 667)	53.0 (± 6.9)	May
<i>Cladophora rupestris</i>	0.91	-0.69	No data	9.5 (± 5.4)	August
<i>Ceramium strictum</i>	1.03	-0.78	No data	13.3 (± 5.1)	June
<i>Fucus vesiculosus</i>	1.55	-0.68	1.7 (± 0.8)	69.8 (± 4.2)	December

Table 4 Phosphate and ammonium concentrations ($\mu\text{mol l}^{-1}$) in non-enriched versus enriched plots during summer nutrient enrichment ($n=24$, ± 1 SE). Significance levels for the effect of nutrient enrichment were tested by three-way ANOVA

Date	Not enriched	SE	Enriched	SE	Percent increase
Phosphate					
5 July	0.40	0.02	0.71***	0.07	76.62
24 July	2.09	0.05	2.74***	0.21	30.82
15 August	1.33	0.03	1.55**	0.08	16.80
12 September	0.68	0.03	0.79n.s.	0.05	15.50
Mean	1.13	0.07	1.45	0.10	34.94
Ammonium					
5 July	0.11	0.05	0.83*	0.32	637.20
24 July	4.28	0.14	7.18***	0.93	67.81
15 August	0.80	0.15	1.02n.s.	0.28	27.69
12 September	3.15	0.21	2.94n.s.	0.32	-6.48
Mean	2.08	0.19	2.99	0.37	181.56

* $P<0.05$, ** $P<0.01$, *** $P<0.001$, n.s. $P>0.05$

Field experiment: *Fucus* recruitment

When we monitored *Fucus* recruitment throughout the experiment (Fig. 4A), we found very low recruitment from the propagule bank in May (1.7 ± 0.8 visible germlings per 100 cm^2 when grazers were present). Moreover, a statistically insignificant trend indicated that recruitment from the propagule bank was even lower when grazers were excluded (0.2 ± 0.14 germlings per 100 cm^2 , $F_{1,25}=3.9$, $P=0.068$). Following spring reproduction, a new cohort of *Fucus* germlings became visible on most plots in June. Densities of new recruits as estimated on 26 June 1997 strongly depended on manipulations of grazers and the propagule bank (Grazer $F_{1,25}=3.7$, $P=0.064$, Propagule Bank $F_{1,25}=35.6$, $P<0.0001$, $G\times PB$ $F_{1,25}=3.1$, $P=0.091$). Grazer presence increased *Fucus* germling density while the presence of the propagule bank decreased germling density. This general pattern did not change through the year (June–December, Fig. 4A) which indicates lack of further propagule supply. However, by December, the previously insignificant interaction term had become significant ($G\times PB$ $F_{1,25}=10.3$, $P=0.0037$), indicating that grazers had more pronounced effects on *Fucus* recruit densities when the

propagule bank was present (Fig. 4A). This was probably an indirect effect of strong grazer effects on the dominant *Enteromorpha* in these treatments. Overall, recruitment of *Fucus* was strongly depressed in treatments dominated by *Enteromorpha*, and highest densities occurred in treatments where *Enteromorpha* cover was low. Regression analysis suggested that recruitment success of *Fucus* was a function of *Enteromorpha* cover during the time of *Fucus* settlement (Fig. 4B). Experimental cages and summer nutrient enrichment had no significant effects on the density of *Fucus* recruits (ANOVA, $P>0.2$). However, when we estimated the biomass of *Fucus* recruits after 2.5 months of nutrient enrichment (Fig. 5B) we found that the direction of the effects of nutrient enrichment on *Fucus* depended on the manipulation of grazers and propagule banks as shown by a significant three-way interaction in the analysis (Table 5). Nutrients significantly enhanced *Fucus* recruit biomass (t -test, $P=0.0063$) when the propagule bank was absent and grazers were present. In contrast, nutrients had a strong negative effect on *Fucus* when the propagule bank and grazers were both present (t -test, $P=0.0067$). In the absence of grazers, *Fucus* recruit biomass remained low regardless of whether nutrients were added or not. This

Table 5 Three-way ANOVA table for the effects of grazers, a propagule bank, and nutrient enrichment on percent cover of *Enteromorpha* spp. and biomass (g dry weight per 100 cm² area) of

Source	df	<i>Enteromorpha</i> cover			<i>Fucus</i> biomass		
		MS	F	P	MS	F	P
Grazer (G)	1	0.645	19.56	0.0002	0.391	49.53	0.0001
Propagule Bank (PB)	1	1.905	57.76	0.0001	0.119	15.10	0.0009
Nutrients (N)	1	0.011	0.34	0.5661	0.004	0.55	0.4661
G×PB	1	0.025	0.77	0.3914	0.025	3.20	0.0879
G×N	1	0.002	0.05	0.8305	0.000	0.04	0.8497
PB×N	1	0.150	4.56	0.0447	0.050	6.39	0.0195
G×PB×N	1	0.000	0.00	0.9989	0.084	10.70	0.0037
Block	3	0.095			0.037		
Error	21	0.008			0.008		

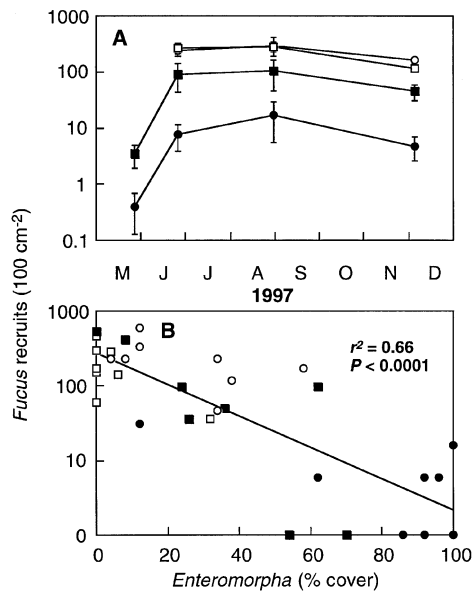


Fig. 4A, B Recruitment of *F. vesiculosus*. Symbols identify Grazer treatments with (■) and without propagule bank (□) and No Grazer treatments with (●) and without (○) propagule bank. **A** Effects of grazers and propagule bank on recruit densities on rocks. Recruits in May originate from the propagule bank, recruits on subsequent dates from the propagule bank plus new reproduction. **B** Relationship between *Enteromorpha* cover during the period of *Fucus* settlement (May) and *Fucus* recruit densities on the experimental rocks. Linear regression showed $\log(y+1)=2.436-0.021x$

indicated that under natural conditions (propagule bank and grazers both present) nutrient enrichment depressed the growth of *Fucus* germlings, presumably by favoring fast-growing *Enteromorpha*, but this effect depended on the magnitude of *Enteromorpha* cover, as determined by the presence of grazers and a propagule bank (Fig. 5A, Table 5). This strong interactive effect of grazers, nutrients and the propagule bank on *Fucus* persisted at least until November 1997 (Grazer×Propagule Bank×Nutrients $F_{1,21}=17.9$, $P=0.0004$).

Fucus vesiculosus recruits after 2.5 months of nutrient enrichment. Primary data are in Fig. 5

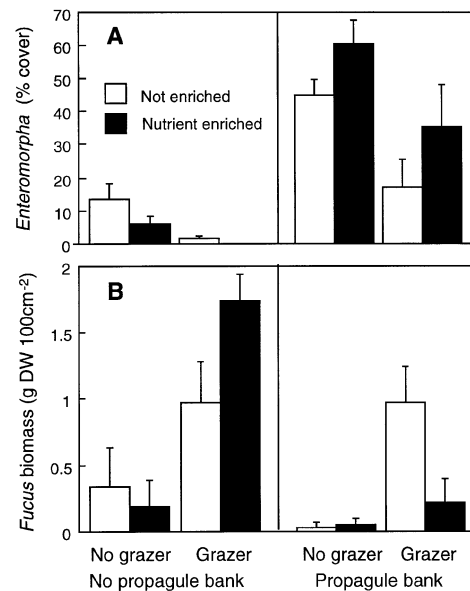


Fig. 5 Effects of nutrient enrichment, herbivory and the propagule bank on **A** cover of *Enteromorpha* spp. and **B** biomass of *F. vesiculosus* recruits (estimated as grams dry weight per 100 cm²). Measurements were made in September 1997 after 2.5 months of nutrient enrichment. For analysis see Table 5

Field experiment: growth of adult *Fucus*

In striking contrast to *Fucus* early life stages, the effects of epiphytes (mainly *Pilayella littoralis*), grazers and nutrients on growth of adult *Fucus* were weak (Fig. 6). All individuals in the experiment survived, grew at similar rates and developed fertile receptacles. During the spring experiment, we detected a significant interaction between the effects of grazers and epiphytes on *Fucus* growth rate (Grazer×Epiphytes $F_{1,25}=6.6$, $P=0.016$). Grazers slightly reduced *Fucus* growth when epiphytes were removed, but enhanced growth when epiphytes were present (Fig. 6A). However, we could not detect an

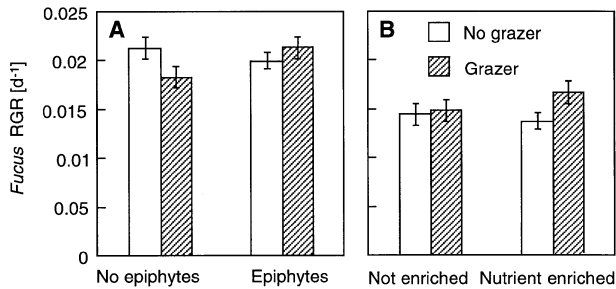


Fig. 6A, B Growth of adult *Fucus* individuals in relation to the presence of grazers, epiphytes and nutrient enrichment. **A** Spring experiment from February–June: effects of grazers and epiphytes on *Fucus* relative growth rate (RGR=relative biomass increase per day) **B** Summer experiment from July to September: effects of herbivory and nutrient enrichment on relative growth rate. For analysis see Results

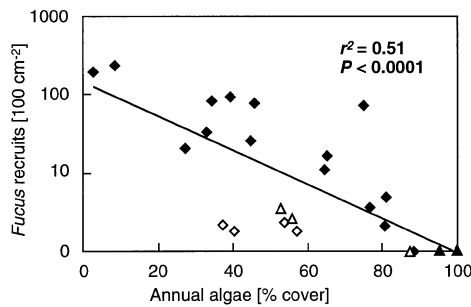


Fig. 7 Relationship between the cover of annual algae estimated during the period of *F. vesiculosus* settlement and *Fucus* recruit densities at 24 sites in Germany (solid diamonds), Finland (open diamonds), Lithuania (solid triangles) and Sweden (open triangles). Linear regression analysis showed $\log(y+1)=2.16-0.022x$

effect of grazers on epiphyte dry weight, which averaged 0.047 g per *Fucus* individual in June ($F_{1,14}=0.027$, $P=0.84$). In the summer experiment from July to September (Fig. 6B), *Fucus* growth rate averaged 0.015 ± 0.002 day⁻¹ which was a 25% decrease compared with the spring experiment (mean 0.020 ± 0.003 day⁻¹). Manipulations of grazers and nutrients had no effect on *Fucus* growth rate from July to September ($P>0.2$). From September to November, *Fucus* growth rate declined by another 40% to 0.0089 ± 0.0004 day⁻¹. Experimental manipulations had no effect ($P>0.2$). However, the two latter analyses should be interpreted with caution, because of the loss of eight replicates from the experiment. No cage effects on adult *Fucus* were detected in the spring ($P>0.2$), but a trend towards increased *Fucus* growth rates on Grazer Control plots was found in the summer experiment ($F_{1,6}=5.2$, $P=0.064$).

Field survey

When we combined data from Finland, Lithuania, Sweden, and Germany, we found that 51% of the variance in *Fucus* recruit densities across the Baltic could be predict-

ed from annual algal cover during the period of *Fucus* spring reproduction and settlement (Fig. 7). The dominant annual algae during the *Fucus* settlement period were *Enteromorpha intestinalis* (Germany), *Cladophora glomerata* (Finland, Lithuania) and *Pilayella littoralis* (all regions). The relationship between annual algal cover and *Fucus* recruit densities closely resembled the relationship that we found in the field experiment (Fig. 4B). Recruit densities in Germany were consistently higher than in the other regions (Fig. 7). If results from German sites were analyzed separately, we found almost the same relationship between cover of annual algae and *Fucus* recruit density as in our field experiment [$\log(y+1)=2.485-0.022x$, $r^2=0.68$, $P=0.0002$, $n=15$].

Discussion

In our experiments algal recruitment from propagule banks clearly favored opportunistic fast-growing annuals which prevented colonization of long-lived perennials. Strong effects of herbivory and nutrient enrichment upon competition among the two groups depended on the presence or absence of the propagule bank. These results suggest that plant recruitment from propagule banks directly affects competitive interactions among primary producers and indirectly the structuring roles of consumers and resources. Interactions among these processes may reinforce observed shifts from high-diversity mixtures to low-diversity assemblages of fast-growing annuals upon eutrophication.

In contrast to terrestrial ecologists, who have been fascinated by seed banks for more than a century (Darwin 1855), aquatic ecologists are only beginning to realize the importance of propagule banks formed by pelagic (Hairston and DeStasio 1988; Madhupratap et al. 1996) and benthic (Santelices et al. 1995; Lotze et al. 1999) organisms. Macroalgal propagule banks in particular have rarely been investigated. In Chile, a species-rich (25 taxa) macroalgal propagule bank showed low species turnover over the year and removal of the propagule bank had no significant effect on the performance of colonizing species (Santelices et al. 1995; but note that only one replicate per season was analyzed). In California, the presence of a propagule bank did not contribute significantly to recruitment of large kelps, but enhanced spring recruitment of a filamentous annual alga, *Desmarestia ligulata* (Reed et al. 1997). In contrast to these studies we found strong and persistent effects of a propagule bank on species composition and the competitive balance among annual and perennial algae in the Baltic Sea. Furthermore, the intensity and composition of destructive macroalgal blooms were strongly affected by the presence of a macroalgal propagule bank (Lotze et al. 1999, 2000).

How may these differences among studies in Chile, California, and the Baltic be explained? Dormancy can occur in winter or summer depending on the life strategy of the organisms in relation to climatic variability. In the

Baltic, most summer annuals (*Enteromorpha*, *Pilayella littoralis*, *Polysiphonia violacea*) were not or rarely (*Cladophora rupestris*) found as macroscopic thalli during the winter months. In contrast, erect thalli of winter annuals (*Ulvopsis grevillei*, *Petalonia fascia*, *Scytosiphon lomentaria*) were absent over the summer. Moreover, we found strong seasonality of spore production and settlement (Fig. 2) in all species at our site. Thus, most species must rely on banks of microscopic forms in order to persist through unfavorable seasonal conditions. This contrasts with aseasonal (Chile) and less seasonal systems (California) where spore production and settlement occur year-round (Santelices et al. 1995; Reed et al. 1997). Based on these limited comparisons for macroalgal propagule banks we hypothesize that the importance of dormancy will increase with increasing seasonality of abiotic and possibly biotic factors that limit the period of plant growth, reproduction and survival. In addition to pronounced seasonality, strong species-specific differences in the abundance of dormant propagules (Table 3; Lotze et al. 1999) may explain the strong effect of the propagule bank at our site. In our experiment, competitive dominance of the opportunistic annual *Enteromorpha* was apparently mediated through its extreme dominance in the propagule bank. This species was 500 to 20,000 times more abundant in the propagule bank than *Pilayella* and *Fucus*. This massive investment into overwintering propagules enabled *Enteromorpha* to recruit in high densities in early spring. During this period, competition from other species is minimal because winter annuals decline in abundance and other summer annuals are absent or rare. Moreover, growing germlings benefit from high nutrient levels in spring while germination is severely nutrient limited later in the year (Lotze et al. 2000). Importantly, grazers only begin to have an effect on algal cover in May. Thus, recruitment from a propagule bank early in the year can provide a seasonal escape from herbivory for grazer-susceptible species. Overall, recruitment from the propagule bank enabled *Enteromorpha* to use favorable conditions in early spring and to form a dense canopy before perennial *Fucus* initiated reproduction.

This canopy acted as a settlement barrier that strongly interfered with recruitment of perennial *F. vesiculosus*. *Fucus* recruited very poorly from the propagule bank (0.005% propagule density compared with *Enteromorpha*). New propagules were generated during a short but intense reproductive period in late spring (Fig. 2; Grütz-macher 1983). During this period, settlement of *Fucus* zygotes and recruitment to macroscopic germlings depended critically on the degree of space preemption by *Enteromorpha*. Initial differences between treatments persisted throughout the year (independently of the seasonal decline of *Enteromorpha* in summer) and resulted in a >20-fold difference for the mean cover of *Fucus* among treatment combinations at the end of the growth period. A minor recruitment event of *Fucus* in the fall (Fig. 2) was not strong enough to alter patterns of recruit abundance in the experiment (Fig. 4A). However, it

could be hypothesized that fall-reproducing *Fucus* has a selective advantage over spring-reproducing individuals because it may largely escape competition from summer annuals such as *Enteromorpha*. Whether this selective advantage translates into increasing cover of fall-reproducing *Fucus* in the Baltic remains to be shown over the long term.

The strong effect of the *Enteromorpha* canopy in our experiment was closely paralleled by similar effects of *Enteromorpha*, *Cladophora glomerata*, and *Pilayella littoralis* on *Fucus* recruitment in our field survey (Fig. 7). This suggests that in different regions, various annual species have effects on *Fucus* similar to those of *Enteromorpha* at our study site. However, recruit densities at sites in the eastern Baltic were consistently lower than at sites in the western Baltic. This indicates that an additional factor constrains *Fucus* settlement and recruitment in the eastern Baltic. Probably this factor is reduced salinity. Low salinity in the eastern and northern Baltic (5–8 PSU) interferes with reproduction and fertilization in *Fucus*, which severely reduces the recruitment success of this species (Serrão et al. 1996, 1999). Because of this, *Fucus* in the eastern Baltic may be even more susceptible to increased competition from annual algae. In summary, we conclude that settlement and recruitment of dispersed propagules appears to be a population bottleneck for *Fucus*. Similar conclusions were obtained for *Enteromorpha-Fucus* competition in New England (Lubchenco 1986) and equally for *Chondrus crispus-Fucus* competition in eastern Canada (Worm and Chapman 1996, 1998).

In contrast to early life stages, adult *Fucus* (15–20 cm size) appeared to be surprisingly insensitive to experimental manipulations of epiphyte cover, herbivory, and nutrients (Fig. 5). However, epiphyte loads were relatively low on the medium-sized *Fucus* individuals that we used in our experiment, compared with large (1–1.5 m) *Fucus*, which dominate at our site. These multi-year algae often carry significant epiphyte loads (Schramm et al. 1996). Most fucoids constantly shed epidermal cells as a defense against epibiosis. Successful recruitment of epiphytes on *Fucus* typically occurs on eroding stipes or injured thallus parts (Russell and Veltkamp 1984; B. Worm and H.K. Lotze, personal observations). Such recruitment foci were largely absent on the relatively young and healthy specimens that we used, but are more abundant in older individuals. Thus, the effects of annual algae on *Fucus* may be highest during the recruitment stage (through blocking of settlement), low at intermediate life stages and again higher in old individuals (through epiphytism).

Clearly, crustacean and gastropod grazers played a key role in this community. The pronounced effects of grazers in our experiment may be even a conservative estimate of total grazer impact, because of reduced *Littorina saxatilis* abundance in the open cages, compared with uncaged control plots. Through massive and selective consumption of fast-growing annual species, herbivores can prevent their competitive dominance. This se-

lective herbivore pressure indirectly sustains the *Fucus* population. A large-scale positive relationship between grazer densities and *Fucus* cover and a negative relationship between grazer densities and annual algal cover has also been described for the entire Baltic Sea (Worm et al. 1999). These findings provide broad support for the general concept that selective consumption of a competitively dominant species by herbivores (Lubchenco 1978) or carnivores (Paine 1966, 1971) favors species coexistence and prevents space monopolization by a top competitor. As indicated by recent evidence, these interactions can shape species distribution patterns over geographical scales (Worm et al. 1999).

Can strong grazer control in this macroalgal community be compensated by other factors? Seasonal or spatial escapes of grazer-susceptible species appear important in this context. The propagule bank provides such a seasonal escape for *Enteromorpha*. When grazers were present, *Enteromorpha* only reached dominance when the propagule bank was present (Fig. 3A). In treatments without the propagule bank *Enteromorpha* could not compensate herbivore pressure despite strong and continuous propagule supply from May to October (500–6,000 spores settling on replicated ceramic tiles per 1 cm² per day, Lotze et al. 1999). Further, we found a general trade-off among species, comparing losses to herbivory with species microrecruit density in the propagule bank and with the relative effects of a propagule bank on species cover (Table 3). Based on this evidence we suggest that propagule banks could serve as an adaptation to seasonal variation in herbivory in addition to their important role for overwintering (Lotze et al. 1999). A similar adaptive value was proposed for small encrusting or boring life stages which alternate with large erect thalli in some herbivore-susceptible intertidal species (Lubchenco and Cubitt 1980).

The effects of grazers on the structure of plant assemblages may also be altered by changes in nutrient supply (Proulx and Mazumder 1998). Anthropogenic nutrient enrichment is a global-scale phenomenon that fundamentally alters the dynamics of terrestrial and aquatic ecosystems (Vitousek et al. 1997; Carpenter et al. 1998). In the marine realm, few studies have experimentally analyzed the effects of nutrient enrichment on plant-herbivore interactions. In eelgrass meadows, water column nutrient enrichment promotes epiphytes which suppress eelgrass growth (Neckles et al. 1993; Williams and Ruckelshaus 1993). Isopods alone (Williams and Ruckelshaus 1993) or isopods, amphipods, and snails together (Neckles et al. 1993) can increase eelgrass productivity through consumption of epiphytes, but their effects vary strongly with season. These general conclusions apply in our system, although grazing effects on epiphytes seemed less important compared with grazer effects on epilithic algae that block *Fucus* recruitment. Despite the mitigating influence of grazers, further increases in nutrients can overcompensate grazer control of annual algae (Worm et al. 2000a; this study) which has negative effects on *Fucus* recruitment. One interesting result was

that these effects depended strongly on manipulations of the propagule bank in our experiment. The strongest negative effects of nutrient enrichment on *Fucus* were seen in treatment combinations with grazers and a propagule bank both present (note that this is the natural situation). When the propagule bank was excluded, nutrients had no effects or even increased perennial recruit biomass, depending on the presence of grazers (Fig. 5). Similar interactions were found for nutrient effects on species diversity in this community (Worm et al. 1999). We conclude that the balance and magnitude of resource (“bottom-up”) and consumer (“top down”) control can depend on patterns of propagule supply which are linked to dormancy and dispersal strategies of the organisms.

These subtle interactions can have important ecosystem consequences. In eutrophied coastal ecosystems throughout the world, spring blooms of annual macroalgae frequently uncouple from grazer control and persist through the summer, with strong negative effects on the perennial flora and fauna (Raffaelli et al. 1998). In the Baltic Sea, shifts in macroalgal diversity have been reported from Finland (Kangas et al. 1982), Sweden (Baden et al. 1990), Lithuania (Olenin and Klovaite 1998), Poland (Kruk-Dowgiallo 1991) and Germany (Vogt and Schramm 1991), but also from the Skagerrak (Bokn and Lein 1978) and the Mediterranean Seas (Munda 1993). At most of these sites, *Fucus* spp. is being replaced by turfs of fast-growing annuals. This process impairs critical ecosystem functions such as nitrogen retention and carbon storage by the coastal community (Worm et al. 2000a) and the provision of fish breeding and juvenile habitat (Kautsky et al. 1992). We suggest that the decline of *Fucus* may be at least partly explained by recruitment inhibition caused by annual algae and that this process is mediated through the abundance of annuals in the propagule bank, increasing nutrient levels (Nehring 1987), and declining consumer control.

Do higher-order interactions among propagule banks, herbivores and nutrients play a role in the response of terrestrial communities to eutrophication? We propose that this generalization should be critically evaluated, ideally using factorial field experiments. To date we know of no experiment where soil seed banks and herbivores or nutrients were manipulated in combination. Evidence from single-factor experiments suggests that (1) seed banks can be of greater importance than seed dispersal for plant recruitment in natural grasslands (Thompson 1992) and that many annuals have more persistent seeds than related perennials (Thompson et al. 1998); (2) herbivores and granivores can strongly affect seed bank dynamics, plant recruitment and plant community composition in desert, grassland, and forest ecosystems (overview in Davidson 1993); and (3) nutrient enrichment typically increases competitive dominance of one or few fast-growing species with negative effects on plant diversity in grasslands, forests, wetlands and heathlands (Tilman 1987; Bobbink et al. 1998). Moreover, sustained nutrient enrichment may shift seed bank composition towards dominance of a few nutrient-responsive

species (Kirkham and Kent 1997). These generalizations are in accordance with our results from a marine macroalgal community.

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