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Control of macroalgal blooms at early developmental stages: *Pilayella littoralis* versus *Enteromorpha* spp.

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Abstract Although blooms of opportunistic fast-growing macroalgae now occur frequently in coastal ecosystems affected by eutrophication, their initiation and control is little understood. Most previous studies have focused on the ecophysiology of adult algae only. We show that spores and/or germlings may represent critical stages in the life cycles and mass-developments of co-occurring opportunistic macroalgae in the Baltic (*Pilayella littoralis* and *Enteromorpha* spp.). We investigated the overwintering of spores, timing of germination, subsequent growth, and grazing on spores and germlings, in order to explain the initiation of mass blooms and species dominance patterns. In the field, *Enteromorpha* spp. showed 10- to 50-fold higher abundances of overwintering microscopic forms (up to 330 individuals cm^{-2}) than *P. littoralis*. Moreover, we found continuous production of spores (up to 1.2 million settling spores m^{-2} h^{-1}) from April to October in *Enteromorpha* spp., while there was evidence of only a short reproductive period in *Pilayella*. However, in spring, germlings and adults of *P. littoralis* appeared earlier in the field and reached a 10-fold higher biomass than *Enteromorpha* spp. In factorial laboratory experiments including temperature and light, there were clear differences in timing of germination. *P. littoralis* germinated at 5°C whereas *Enteromorpha* spp. required temperatures of 10–15°C for germination. In contrast, we detected only minor differences in growth response among adults of *P. littoralis* and *Enteromorpha* spp. Germination, not growth of adults, appeared to be the ecophysiological bottleneck for initiating mass spring development. Following the spring *Pilayella* bloom, *Enteromorpha* germlings occurred massively in the field (April–September), but rarely developed into adults. In laboratory feeding experiments we tested whether crustacean mesograzers common in summer may control development of *Enteromorpha* germlings. Both germination of settled spores and growth of germlings were reduced by 93–99% in the presence of grazers (*Idotea chelipes* and *Gammarus locusta*). Thus in addition to ecophysiological constraints, grazers, if present, may play a decisive role in the early life stages of macroalgal mass developments. These results mirror patterns of overwintering of seeds, germination control, seed and seedling predation in terrestrial plant communities.

Key words Baltic Sea · Coastal eutrophication
Crustacean grazers germination · Overwintering
propagules

Introduction

Although change in community configuration has been the norm throughout the history of the planet's ecosystems, anthropogenic influences have enormously increased the rates and scales of change (Vitousek 1994). In the marine realm, bodies of seawater with restricted flushing have been most visibly affected by anthropogenic forces. The Baltic Sea is such a body of water, but others, such as the Black Sea or the Mediterranean Sea, also fall into this category. The distributions and abundances of species in benthic communities of the Baltic Sea have changed conspicuously, which is generally attributed to the effects of eutrophication (e.g. Cederwall and Elmgren 1990; Kruk-Dowgiallo 1991). The distributions of large macrophytes such as *Fucus vesiculosus* and *Zostera marina* are more restricted than several decades ago (Kautsky et al. 1986; Vogt and Schramm 1991). Concomitantly, there have been marked increases in abundances of annual filamentous and foliose algae (Kautsky 1991; Kruk-Dowgiallo 1991).

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According to the strategic resource allocation concept of Littler and Littler (1980), such algal forms may be regarded as opportunistic species characterized by high rates of mineral nutrient uptake (Wallentinus 1984) and enhanced reproductive capability (Hoffmann and Ugarte 1985). Following coastal eutrophication, mass developments of filamentous and foliose algal species occur in many parts of the world (Ryther and Dunstan 1971; Schramm and Nienhuis 1996). Spring blooms of such opportunistic species often develop rapidly into unusually thick, drifting mats of detached algae. In some cases, these algal mats persist throughout the summer and often oxygen deficiency upon decomposition, which leads to increasing mortality of epi- and endobenthic fauna and perennial flora (Hull 1987; Norkko and Bonsdorff 1996).

In many coastal areas, macroalgal blooms are dominated by green algal species of the genera *Enteromorpha*, *Ulva* and *Cladophora* (Reise 1983; Schramm and Nienhuis 1996). Conspicuously, mass developments in the Baltic Sea mainly consist of the filamentous brown alga *Pilayella littoralis* (personal observations; Kruk-Dowgiallo 1991; Kiirikki and Lehvo 1997). In addition to *P. littoralis*, several species of *Enteromorpha* co-occur in the Baltic (South and Tittley 1986). Since in both genera productivity of adults is not reduced under Baltic salinity conditions, and rates of growth and photosynthesis are similar (Bolton 1979; Reed and Russell 1979), other factors may explain the observed dominance of *Pilayella*.

A comprehensive understanding of factors controlling macroalgal blooms is currently lacking. We will argue that merely studying the ecophysiology of adult thalli is insufficient to explain observed ecological abundances. Rather, we show that a knowledge of the population dynamics of all life history stages (from spores to adults) is required. Some recent studies have shown that processes affecting production, development, growth and survival of early developmental stages can be as important as, or more important than, processes affecting adult thalli (reviewed in Santelices 1990; Vadas et al. 1992). Early developmental stages such as spores and germlings are very delicate structures, often lacking resistance mechanisms found in adult individuals (Lubchenco 1983; Brawley and Johnson 1991). Therefore, they are likely to represent critical phases in the life cycle of macroalgae. Physical stress, competition and grazing have all been identified as key processes which, alone or in combination, can suppress early developmental stages (Vadas et al. 1992). Attempts to quantify the relative importance of these processes are rare (Worm and Chapman 1998). Furthermore, almost all field studies which have specifically addressed early stages have dealt with perennial brown algae such as fucoids (Brawley and Johnson 1991; Worm and Chapman 1996) or kelps (Chapman 1984; Reed 1990). Other important groups like mass-occurring filamentous and foliose algae have largely been neglected. In contrast to terrestrial plant communities, for which a large body of empirical work on germination control, seed and seedling ecology exists (Fenner 1992), similar questions have received little attention in marine plants.

In this paper, we present data on the phenology, overwintering of spores, and the combined effects of light and temperature on germination and growth of the opportunistic macroalgae *P. littoralis* and *Enteromorpha* spp. in the Baltic Sea. We also tested whether abundant mesograzers can control germination rate and growth of germlings of *Enteromorpha* spp.

Material and methods

Study area and species

This study was carried out in 1995 in the outer Schlei (54°41′N, 10°0′E), in the western Baltic Sea, Germany. The Schlei is a tideless, 40-km-long fjord-like inshore water system of glacial origin with an average depth of 2.4 m. Salinity fluctuates seasonally between 12 and 20 PSU. Wind-induced water exchanges occur with nutrient-rich water from the inner fjord and comparatively nutrient-poor water from Kiel Bight. Nutrient loads are high and reached maxima of 160 μmol l^{-1} nitrate, 35 μmol l^{-1} ammonium and 2 μmol l^{-1} phosphate in the outer Schlei from January to March 1995 (Schramm et al. 1996). From mid-May to August, nitrate and ammonium are depleted and often close to zero, but irregular, wind-induced nutrient pulses with up to 10 μmol l^{-1} ammonium occur. Average summer phosphate concentrations remain between 0.1 and 0.6 μmol l^{-1} (up to 2 μmol l^{-1} during pulses).

The bottom of the outer Schlei is dominated by sand with scattered rocks and boulders. The dominant submersed macrophytes are *Fucus vesiculosus*, *Potamogeton pectinatus* (0–1.5 m) and *Zostera marina* (below 1.2 m water depth). In this study we consider only the *Fucus*/*Potamogeton* zone. In spring and early summer, macrophytes are overgrown with epiphytic *Pilayella littoralis* and *Enteromorpha* spp., which also occur on rocks, boulders and mussel shells. We identified several *Enteromorpha* species in our study area. At the spore and germling stage, the numerically dominant species were *E. intestinalis* and *E. prolifera*, whereas only *E. intestinalis* was found at the adult stage. In the following, we assume that these two species behave similarly in their ecophysiology and phenology during early developmental stages. Thus, the species are not separated, and are treated as *Enteromorpha* spp. In late spring and summer, mesograzers are abundant at our site, reaching peak densities of several thousand individuals per square meter. The main species are isopods (*Idotea chelipes*), amphipods (*Gammarus* spp., mainly *G. locusta*) and periwinkles (*Littorina saxatilis* and *L. littorea*).

Field studies

Abiotic environment

For correlation of field observations and laboratory experiments, water temperature was measured to the nearest 0.1°C every 2–3 weeks 20 cm below the water surface. Light intensity was continuously recorded as global flux density (J m^{-2} day^{-1}) at Kiel lighthouse by the meteorological station at Kiel. We transformed weekly means of global flux density to photosynthetically active radiation (PAR, 400–700 nm, μmol photons m^{-2} day^{-1}) after Lüning (1985).

Phenology of different life stages

We quantified distribution and abundance of early developmental stages of *P. littoralis* and *Enteromorpha* spp. from January to December 1995 in the outer Schlei. To obtain a relative measure of the amount of viable macroalgal spores in the water column, we sampled spore settlement on ceramic tiles at monthly intervals. We used ceramic tiles because of their surface structure which is suitable for algal settlement. Six titles (10 × 10 cm) were hung in the water column 50 cm above sediment surface (water depth was 70 cm) for 4 h (10.00 a.m.–2.00 p.m.). After transportation to the laboratory in a cooler, tiles were maintained in 500 ml Provasoli enriched seawater (PES, Starr and Zeikus 1987) at constant temperature of 15°C and light intensity of 100 μmol photons m^{-2} s^{-1} in a 14:10 h light:dark (L:D) rhythm. Germanium dioxide (GeO_2) was added to suppress diatom growth. After 7 days of cultivation, germlings (> 200 μm length) were counted using a dissecting microscope with an integrated grid (ten randomly chosen subsamples of 4 × 4 mm per tile).

Germling cover in the field was determined every 4 weeks on 30 randomly collected rocks (*c.* 5 cm in diameter) from 30–70 cm water depth along a 200-m transect. In contrast to germlings that developed on tiles, germlings on rocks were mostly growing too densely to allow good estimates of individual numbers. Instead we estimated percent cover of germlings using a dissecting microscope in five randomly chosen subsamples (10 × 10 mm) per rock.

Adult algal biomass (mg dry weight m^{-2}) was determined monthly within the *Fucus*/*Potamogeton* zone (30–150 cm water depth). Six quadrats (25 × 25 cm) were placed randomly along a 100-m transect line and sampled with a framed sampling net. We detached all epiphytic and epilithic macroalgae from their substratum, sorted them by species which were then dried for 48 h at 70°C for dry weight determination.

Laboratory experiments

Overwintering of spores

We investigated whether *Enteromorpha* spp. and *P. littoralis* differed in their overwintering strategy. Since we did not observe overwintering of adult thalli, there must be a "bank of microscopic forms" (Chapman 1986), comparable with a seed bank, from which spring blooms are initiated (Hoffmann and Santelices 1991). In this paper, we refer to overwintering microscopic forms as settled but not germinated spores. Because no germlings were visible with a dissecting microscope (40×) prior to cultivation, we assume that spores did not germinate in winter or that they overwintered in the stage of spores or germlings composed only of a few cells. Five different kinds of substrata: (1) shells of *Mytilus edulis*, (2) sand grains from surface up to 5 mm sediment depth, (3) rocks, (4) thalli of *Fucus vesiculosus*, and (5) leaves of *Zostera marina*, were sampled in the field in December 1994. Substrata were cultivated, each with six replicates, in 500 ml PES at 15°C and a light intensity of 100 μmol photons m^{-2} s^{-1} in 14:10 h L:D. After 2 weeks, all germlings (> 200 μm length) on the various substrata were counted and densities per square centimetre were calculated.

Germination of spores

To explain the different temporal patterns of distribution and abundance of *Enteromorpha* spp. and *P. littoralis*, we tested whether germination rates of the species differed as a function of temperature or light intensity, or a combination of these factors. In February 1995, shells of *M. edulis* with attached overwintering spores were collected in the field and cultivated in 500 ml PES at three temperatures (5, 10, 15°C) combined with three light intensities (50, 100, 200 μmol photons m^{-2} s^{-1} in 14:10 h L:D) in a completely crossed design (n = 5 for each treatment combination). The chosen light intensities correspond to daily sums of 2.52, 5.04 and 10.08 mol photons m^{-2} and thus to natural conditions from late autumn to spring. After 12 days of cultivation, germlings were counted in three subsamples (4 × 4 mm) per shell with a dissecting microscope. Two-way analysis of variance (factors: light, temperature, 3 × 3) was performed for each species separately. Data were log-transformed to achieve homogeneity of variances (Cochran's test). Post hoc comparisons were done after Tukey-Kramer. The relative effect size of the experimental factors was calculated as omega-squared (ω^2) as recommended for a fixed-factor model by Howell (1992).

Adult growth rates

We were interested to determine whether ecophysiological demands differed among life stages. Therefore, in a test very similar to the germination experiment (previous section), we checked growth rates of adult thalli of *E. intestinalis* and *P. littoralis* with the same treatment combinations. Each treatment (n = 5) was started with a standard weight of 0.1 g algal wet weight in 750 ml of PES with GeO_2 added. With a specially constructed centrifuge, operating as a spin drier, algal wet weight was determined in a standardized manner, removing adherent water for 30 s at a constant rate of revolution (rpm). Media were changed every 2 days. After 10 days, algal material was reweighed and relative growth rates [$RGR = (\ln w_1 - \ln w_2)/(t_2 - t_1)$, where w is wet weight and t is time] were calculated. Statistical analysis was performed by three-way ANOVA (factors: light, temperature, species, 3 × 3 × 2). Post hoc comparisons and calculations of relative effect sizes were done as described in the previous section.

Grazing on germlings and spores

To determine whether abundant mesograzers are effective in controlling spores and germlings of *Enteromorpha* spp. we performed simple laboratory feeding experiments. To investigate grazer effects on spore germination, 18 ceramic tiles were hung in the water column in June 1995 for 4 h (10.00 a.m.–2.00 p.m.) for spore settlement. Individuals of *Idotea chelipes* and *Gammarus locusta* were collected at the same time and site. Each tile was placed in 500 ml of PES, with GeO_2 added, at 15°C, 100 μmol photons m^{-2} s^{-1} in 14:10 h L:D. One *Idotea* or two *Gammarus* were added to the tiles. A treatment without grazers served as a control for autogenic changes. Each treatment was run with six replicates. After 7 days of cultivation, germlings (> 200 μm length) were counted in ten subsamples (4 × 4 mm) on each tile using a dissecting microscope. To determine whether grazers removed the settled spores totally, or only suppressed their germination and growth, all tiles were cultivated for another 7 days in new medium without grazers. Germling density was determined again after this second cultivation period.

To test grazing pressure on epiphytic germlings, several thalli of *Fucus vesiculosus* (about 5 g wet weight) were collected in January 1995 and cultivated to obtain epiphytic germlings. Each *Fucus* thallus was kept in a glass beaker with 1 l of 0.2 μm filtered freshly collected nutrient-rich winter seawater. Water was exchanged every 2–3 days. After 14 days, germlings (> 200 μm length) were counted with a dissecting microscope; most germlings (> 99%) belonged to the genus *Enteromorpha*. One *Idotea*, two *Gammarus* or no grazers were added to each *Fucus* thallus (n = 6). After 7 days, *Enteromorpha* germlings were counted again and grazing rates were calculated. No statistical analysis was performed because overwhelming treatment effects rendered this unnecessary.

Results

Abiotic environment

Water temperature reached a maximum of 23.9°C in August and a minimum of −0.7°C in January (Fig. 1). In 1995, there was no ice cover on the Schlei. PAR showed a maximum at the end of June (weekly mean of 66.29 mol photons m^{-2} day^{-1}), and a minimum at the end of December (weekly mean 1.77 mol photons m^{-2} day^{-1}).

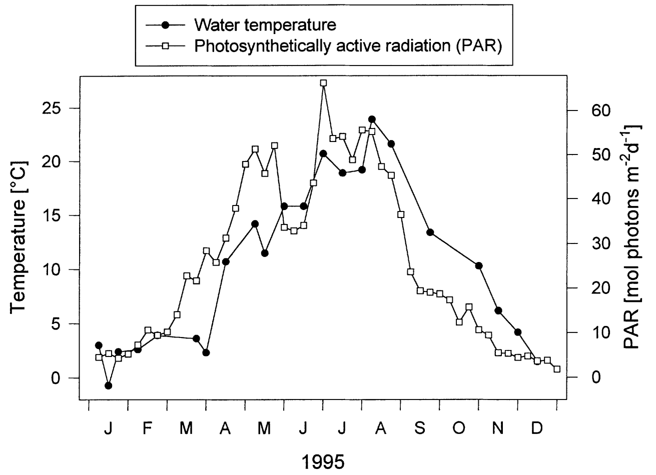

Fig. 1 Water temperature and photosynthetically active radiation (PAR, 400–700 nm) above water surface in the outer Schlei 1995. Temperature was measured every 2–3 weeks. PAR was recorded continuously. Calculated weekly means are shown

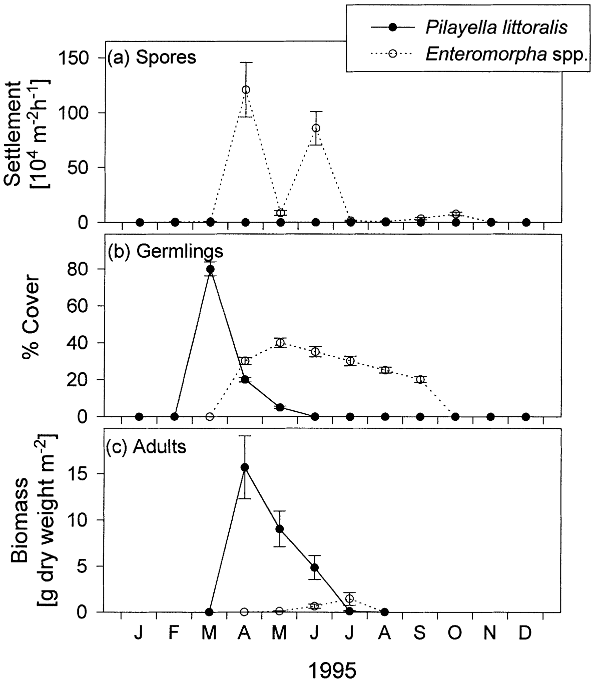

Fig. 2a–c Occurrence of three life stages of *Enteromorpha* spp. and *Pilayella littoralis* in the outer Schlei fjord in 1995. **a** Spore densities sampled from the water column. Data are mean densities of viable spores on ceramic tiles exposed for 4 h. No spores of *P. littoralis* were detected using this method. **b** Percent cover of germlings on rocks. **c** Biomass of adults. Symbols are means ± 1 SE (n = 6 for **a**, **c**; n = 30 for **b**)

Phenology of different life stages

Over the entire vegetation period from March to October, viable spores of *Enteromorpha* spp. occurred in the water column (Fig. 2a). Peak densities were reached in April with 1.2 million settling spores m^{-2} h^{-1}. We were unable to detect spores of *P. littoralis* in any month. At the beginning of the vegetation period in March and April 1995, *Pilayella* germlings occurred earlier than *Enteromorpha* germlings (Fig. 2b) and covered up to 80% of space of hard substrata. Whereas *Pilayella* germlings had disappeared by June, *Enteromorpha* germlings persisted with 20–40% cover throughout the summer until October. *P. littoralis* reached a maximum biomass of 15.68 g dry weight m^{-2} in April (Fig. 2c). Later in the year, adult biomass declined steadily and *Pilayella* disappeared in July. Adult *Enteromorpha* spp. reached a maximum biomass of only 1.44 g dry weight m^{-2} in July and disappeared in August.

Overwintering of spores

In December 1994, both species overwintered in the form of settled spores on all substrata tested, but *Enteromorpha* spores always outnumbered *Pilayella* spores by 10- to 50-fold (Table 1). Maximum spore densities were found on rocks, which seemed by far the most suitable substratum for settling and/or overwintering (with up to 330 spores cm^{-2} for *Enteromorpha*, and only up to 6.7 spores cm^{-2} for *Pilayella*).

Germination of spores

In February 1995, we investigated germination of *Enteromorpha* spp. and *P. littoralis* in relation to the combined effects of temperature and light intensity. *P. littoralis* showed no significant differences among treatments (Fig. 3, Table 2). Mean germling density averaged

Table 1 Overwintering of *Enteromorpha* spp. and *Pilayella littoralis* in the form of settled spores on different substrata in the field. Six replicate samples per substratum type were collected in December 1994. Substrata were cultivated in the laboratory to induce germination. After 2 weeks, germinated and grown spores were counted

Substratum type	Density of germinated spores cm^{-2}			
	Enteromorpha spp.		*Pilayella littoralis*	
	Mean	SE	Mean	SE
Fucus vesiculosus	7.122	1.842	0.140	0.140
Zostera marina	0.686	0.304	0.000	0.000
Sand grains (0–5 mm sediment depth)	21.881	1.440	0.095	0.095
Rocks	330.000	30.000	6.667	6.667
Shells of *Mytilus edulis*	59.375	15.040	1.743	0.425

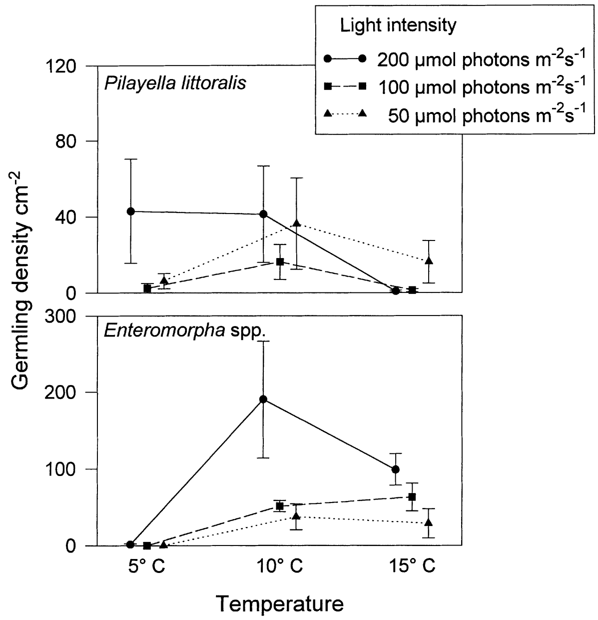

Fig. 3 Germination of *Enteromorpha* spp. and *P. littoralis* at three temperatures and light intensities. Shells of *Mytilus edulis* were used as a source of overwintering spores. After 7 days of cultivation, new germlings were counted. Data are means with standard error (n = 5). Refer to Table 2 for statistical analysis

over all treatments was 2.91 ± 0.85 SE cm^{-2} (n = 45). In contrast, germination of *Enteromorpha* spp. was positively affected by temperature and light intensity (Fig. 3, Table 2). Maximum germling density of 190.0 ± 76.31 cm^{-2} was reached at 10°C and 200 µmol photons m^{-2} s^{-1}. In *Enteromorpha* spp., post hoc comparisons among temperature treatments showed significantly higher ($P < 0.01$) germination rates at 10 and 15°C than at 5°C. Light intensity positively influenced germination rates which were significantly higher ($P < 0.01$) at 200 µmol photons m^{-2} s^{-1} than at 50 µmol photons m^{-2} s^{-1}.

Comparing both species, *Enteromorpha* spp. showed distinctly higher germination rates at higher temperatures (10 and 15°C) in combination with higher light intensities (100 and 200 µmol photons m^{-2} s^{-1}) than *P. littoralis*. At a low light intensity of 50 µmol photons m^{-2} s^{-1} no difference between species was visible, independent of the temperature. At low temperature (5°C) *P. littoralis* showed distinctly higher germination rates at all light intensities with a maximum of 42.92 ± 27.35 germlings cm^{-2} at 200 µmol photons m^{-2} s^{-1} while *Enteromorpha* spp. had only 1.25 ± 1.25 germlings cm^{-2}. Within the experimental treatments, temperature was the factor with the greatest effect in both species (Table 2). The results from this laboratory experiment are in agreement with our findings from the field, where germlings of *P. littoralis* appeared earlier in spring than those of *Enteromorpha* spp.

Adult growth rates

In June 1995, we examined growth of *E. intestinalis* and *P. littoralis* as a function of temperature and light intensity in a laboratory experiment. Temperature had highly significant, positive effects on relative growth rate, but there was no difference between the two species (Fig. 4, Table 3). The relative growth rate of both species was significantly higher at 10°C than at 5°C and again significantly higher at 15°C than at 10°C ($P < 0.01$). Light intensity showed a slight interaction with species. Relative growth rate of both species was significantly higher at 100 and 200 µmol photons m^{-2} s^{-1}, with no difference between species, but at 50 µmol photons m^{-2}s^{-1} *P. littoralis* showed higher growth rates at 10 and 15°C than *E. intestinalis*. However, this was only a small effect (1.8% of variance explained) compared with the main effects of light (29.7%) and temperature (27.9%) regardless of species. Therefore, the interaction is less important than the main factors.

Grazing on germlings and spores

The two grazers *Idotea chelipes* and *Gammarus locusta* had distinct effects (Table 4) on spore abundance and germination of *Enteromorpha* spp. In the presence of *Idotea*, only 4.4% (*Gammarus* 6.9%) of spores developed to visible germlings compared to the control treatment. Both grazers were highly effective in suppressing germination and/or growth of germlings. After

Table 2 Two-way ANOVAs: germination of *Enteromorpha* spp. and *P. littoralis* in relation to temperature and light intensity. Data were log-transformed to meet the assumption of homogeneity of variances. Relative treatment effects (ω^2) are shown for significant factors only

Source of variation	*df*	MS	*F*-ratio	*P*	ω^2
Enteromorpha spp.					
Temperature	2	4.181	41.737	0.0001	0.567
Light intensity	2	0.827	8.260	0.0011	0.101
Temperature × light intensity	4	0.166	1.655	0.1819	
Residual	36	0.100			
Pilayella littoralis					
Temperature	2	0.363	1.851	0.1718	
Light intensity	2	0.146	0.744	0.4822	
Temperature × light intensity	4	0.136	0.694	0.6012	
Residual	36	0.196			

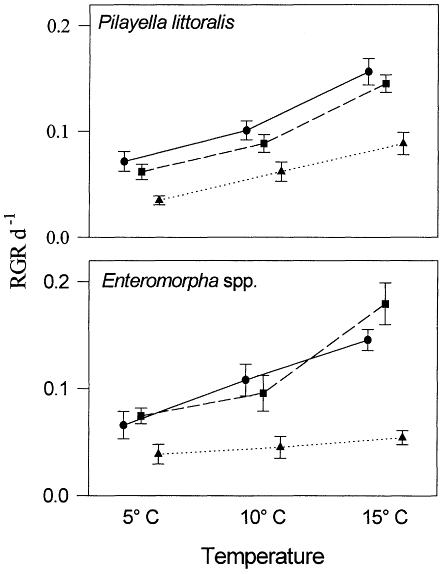

Fig. 4 Growth of adult thalli of *E. intestinalis* and *P. littoralis* at three temperatures and light intensities (symbols as in Fig. 3). Relative growth rate (RGR) per day was determined by measuring increase of wet weight. Means with standard error are shown ($n = 5$). Refer to Table 3 for statistical analysis

grazer removal and further cultivation for another 7 days, the amount of germinated spores in the control treatment increased 6-fold, which could be due to new reproduction from fertile cells and/or new germination of settled but not yet germinated spores on the tile. The density of germlings in treatments with *Gammarus* increased 8-fold, similar to the control treatments. In contrast, germlings in treatments with *Idotea* increased 30-fold. This second part of the experiment indicated that grazing mechanisms may differ between *Idotea* and *Gammarus*. *Gammarus* seemed to be effective in reducing germlings and/or spores completely by removing them from their substratum, and, after removal of *Gammarus*, only new germination of hitherto ungerminated spores, or newly produced spores, occurred at a rate comparable to the control treatment. *Idotea* seemed to suppress growth of germlings by consuming the growing erect filament but not the basal parts. After removal of *Idotea*, both already existing germlings and newly germinated spores grew to visible size.

In January 1995, grazing on established germlings of *Enteromorpha* spp. was tested. Both grazer species conspicuously reduced germlings of *Enteromorpha* spp. (99% for *Gammarus*, 98% for *Idotea*) whereas in the control treatment, density of germlings increased up to 444% (Fig. 5). Without grazers, further germination of settled, but not yet germinated, spores of *Enteromorpha* spp. occurred within the experimental period. *Fucus vesiculosus*, the host plant, showed slight grazing marks in the presence of *Idotea* only.

Discussion

Our observations and experiments suggest that early life-cycle stages may be of critical importance for population dynamics of opportunistic macroalgae in the Baltic Sea. Based on our results, we propose that the timing of germination of overwintering spores in early spring, and grazing of spores and germlings by mesograzers in late spring and summer, may be important processes con-

Table 3 Three-way ANOVA: effects of temperature and light intensity on growth of adult thalli of *Enteromorpha* spp. and *P. littoralis* (factor "species"). Relative treatment effects (ω^2) are shown for significant factors only

Source of variation	*df*	MS*10^3	*F*-ratio	*P*	ω^2
Species	1	1.038	1.296	0.2587	
Temperature	2	29.679	37.054	0.0001	0.279
Light intensity	2	31.576	39.422	0.0001	0.297
Species × temperature	2	1.661	2.074	0.1331	
Species × light intensity	2	2.698	3.369	0.0399	0.018
Temperature × light intensity	4	2.690	3.358	0.0141	0.037
Species × temperature × light intensity	4	1.396	1.743	0.1500	
Residual	72	0.800			

Table 4 Effects of the two grazers *Idotea chelipes* and *Gammarus locusta* on germination of *Enteromorpha* spp. Spores settled on tiles were cultivated for 7 days with and without grazers and developed germlings counted (*A*). Afterwards, all tiles were cultivated for another 7 days without grazers. All germlings were counted again (*B*). Means with standard errors are shown ($n = 6$)

Cultivation	Grazer treatment					
	Control		*Idotea chelipes*		*Gammarus locusta*	
	Mean	SE	Mean	SE	Mean	SE
A: days 1–7 (+ grazer)	15.417	0.875	0.683	0.310	1.067	0.457
B: days 7–14 (– grazer)	95.233	6.542	21.900	3.564	9.150	2.423

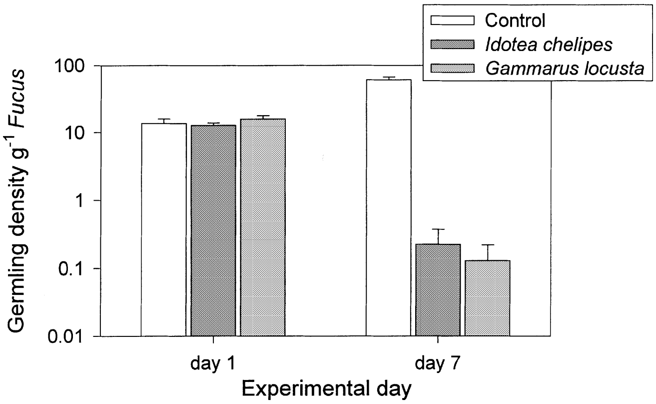

Fig. 5 Grazing on germlings of *Enteromorpha* spp. by grazers (*Idotea chelipes* and *Gammarus locusta*) within 7 days of cultivation. Germlings were growing as epiphytes on *Fucus vesiculosus*. Means and SEs are shown ($n = 6$)

trolling the initiation of annual macroalgal blooms and species dominance patterns within these blooms.

Spring blooms of the brown alga *P. littoralis* appear almost every year at our study site, and at various sites in the Baltic (personal observations, Kruk-Dowgiallo 1991; Kiirikki and Lehvo 1997). *Enteromorpha* spp., which commonly forms blooms in many other coastal water systems affected by eutrophication (Warwick et al. 1982; Reise 1983; Pregnall and Rudy 1985), remains subordinate in the western Baltic. At our study site, *E. intestinalis* reached only < 10% of the peak biomass of *Pilayella* in 1995. Attributes of opportunistic life style (e.g. high rates of nutrient uptake, growth, reproductive output) have been studied mainly in adult plants which have been of principal research interest for decades. In this study, we tried to explain the dominance pattern of *P. littoralis* over *Enteromorpha* spp. by examining early developmental stages. We differentiated among four life cycle processes: (1) overwintering of spores, (2) germination of spores, (3) growth of adults, and (4) reproduction.

Overwintering of spores (or seeds) is a strategy for surviving unfavorable conditions in an environment with pronounced seasonality. In so-called aseasonal annuals (Sears and Wilce 1975), some adult thalli may survive in the subtidal zone and act as a source for a new generation. Seasonal annuals survive with thallus fragments buried in the sediment (Schories 1995), with crustose life phases (Lüning 1985), or with cryptic microscopic forms which may have analogous functions to terrestrial seed banks (Chapman 1986; Hoffmann and Santelices 1991). Investigations of these "banks of microscopic forms" are rare. A detailed characterization of such an assemblage of microscopic forms, their species composition and turnover, was done for tide pools in Chile (Santelices et al. 1995). In these tide pools, both perennial and annual species (a total of 25 taxa) were present as microscopic forms, and the bank seemed more important for the survival of populations of perennial species. At our study site, neither *P. littoralis* nor *Enteromorpha* spp. were observed as macroscopic thalli in winter, but overwintered in the form of cryptic microscopic forms (Table 1). These forms may be settled but germinated spores, or spores which have developed into microscopic thalli which suspend growth while environmental conditions are unfavorable. Other dormancy strategies involve gametophytes, germlings and algal embryos (reviewed by Hoffmann and Santelices 1991). Some of these forms may persist for extended periods. Settled spores of *Enteromorpha* spp. survived >10 months in darkness at 5°C and 15°C, but survival rate decreased with time and increasing temperature (Schories 1995).

On five substrata, we found 10- to 50-fold higher overwintering spore densities for *Enteromorpha* than *Pilayella*. This could have resulted from continual and massive production of *Enteromorpha* spores from April to October. We did not detect *Pilayella* spores in the water column, which was probably due to a shortcoming of our method (e.g. timing of sampling), but we observed fertile cells in *Pilayella* from March to June as well as cells which had already released spores. Since germlings only occurred from March to May, and adults disappeared in July, we may assume that the reproductive period of *Pilayella* was shorter and earlier in the year than that of *Enteromorpha*. Hence, fewer microscopic stages may survive until next spring. Given the relatively low densities of overwintering spores and the high observed cover of germlings in early spring, it is likely that *Pilayella* initiated reproduction shortly after germination. Indeed, laboratory cultures reproduced within < 1 month after germination (Müller and Stache 1989).

In spring, the timing of germination may be important since conditions become more unfavorable later in the year. In the Baltic, nutrient concentrations, which are highest in winter, decline steeply in late spring, when the phytoplankton bloom begins (Schramm et al. 1996). Subsequently, high phytoplankton densities attenuate incoming light and light limitation may occur, depending on water depth. Moreover, in late spring, mesograzers, common in the Baltic, increase in abundance and activity (Schramm et al. 1996). With rising temperature, light intensity and daylength, development of spring annuals is initiated, and the limiting factors are probably species-dependent. As long as abiotic and biotic conditions are favourable there may be a "recruitment window" of optimal germination and growth conditions (Deysher and Dean 1986). At our study site, *Pilayella* appeared earlier in the germling and adult stage than *Enteromorpha*. In controlled laboratory experiments, this pattern appeared most likely to be due to an earlier "recruitment window" of *Pilayella* which germinated abundantly at 5°C, a temperature not exceeded in the field until the end of March. Germination of *Enteromorpha* appeared to be largely inhibited at this temperature, but occurred massively at 10°C, a temperature exceeded in the field in the end of April. Thus, *Pilayella* germlings had an advantage of at least 1 month before *Enteromorpha* appeared. Pre-emptive space competition may occur between developing *Pilayella* and *Enteromorpha*. Space pre-emption has been found to be important among other competing macroalgae (Hruby and Norton 1979; Sousa 1979; Reed 1990).

Subtle but important differences detected between germlings of *Pilayella* and *Enteromorpha* cannot be predicted from the behaviour of adult algae, as our growth experiment showed. Growth responses of adult *Pilayella* and *Enteromorpha* to temperature and light were very similar. Only at a light intensity of 50 μmol photons m^{-2} s^{-1} was there a slight advantage for *Pilayella*, but this light intensity is only relevant from November to January. After February, higher light intensities are common. Most importantly, no species × temperature interaction was detected, i.e. differences in responses to temperature found in germlings are not found in adults. Also, nutrient kinetics of adults of the two species showed only minor differences (Wallentinus 1984; Lotze 1998). These results suggest that *Enteromorpha* might well form a mass bloom subsequent to germination in spring. Indeed, germlings occurred massively from April to September, constantly covering 20–40% of the hard substratum. In contrast to *Pilayella*, however, these germlings did not develop into a corresponding amount of adult biomass. Competition by *Pilayella* could play a role in spring, but this does not explain further stagnation of *Enteromorpha* in summer (Fig. 2). We hypothesized that intense grazing of germlings by abundant mesoherbivores suppressed development of adult *Enteromorpha.* In our laboratory experiments, germination and growth of *Enteromorpha* germlings was reduced to near zero when *Gammarus locusta* or *Idotea chelipes* were present. Herbivores may also mediate competitive interactions between adult *Pilayella* and *Enteromorpha* germlings. When we cultivated field-grown adult *Pilayella* thalli in the laboratory (June, July 1995), *Enteromorpha* overgrew *Pilayella* within 1–2 weeks. This overgrowing pattern never occurred in the field. We propose that spores of *Enteromorpha* had settled on *Pilayella*, but development and growth may have been suppressed by grazers present in the field. Following grazer exclusion in the laboratory, germlings developed rapidly. However, these speculations should be regarded with caution. Our laboratory experiments can only give qualitative insights into interactions among grazers and macroalgae. To verify these patterns, manipulative field experiments are necessary. Such field studies involving manipulations of opportunistic macroalgae are scarce and rarely consider different life stages. Evidence from field experiments in New England suggests that *Enteromorpha* is effectively controlled by littornid snails (Lubchenco and Menge 1978). Indirect evidence suggests that grazing control was most effective at the germling stage since the presence of a few snails prevented *Enteromorpha* from colonizing, while high snail densities were required to control an adult *Enteromorpha* canopy (Petraitis 1987). Herbivore-mediated competition among annuals occured in the New England intertidal zone (Lubchenco 1986).

In the control of mass-occurring macroalgae biotic and abiotic factors may alternate in importance, depending on species and season. In our study, germination of *P. littoralis* in spring was controlled by abiotic factors, among which temperature, rather than light, seemed to be limiting. This is in concordance with terrestrial communities where it is predominantly temperature, and to some extent light intensity, that trigger germination of seeds in spring (Fenner 1992). In *Enteromorpha*, the initiation of algal development in early spring also related to abiotic control. After successful germination, however, *Enteromorpha* still remained largely inhibited at the germling stage, which seemed to be a bottleneck in the development of this species. This inhibition of further growth was possibly due to intense grazing and/or nutrient limitation. The pattern of alternating abiotic (mainly temperature, light), biotic (grazing, competition) and/or resource control of spring blooms may be paralleled in other food webs, e.g. during plankton succession in temperate lakes and marine systems (Sommer 1989) or in the development of spring annuals in terrestrial ecosystems (Fenner 1992).

In conclusion, our results suggest that consideration of all life cycle stages is important when determining the importance of environmental factors, including temperature, light and grazing, on population dynamics. Further research may focus on these and other factors, such as effects of different nutrient concentrations on germination and growth of germlings and on the relative importance of environmental stresses, disturbance and biotic interactions.

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