

## ECOPHYSIOLOGICAL TRAITS EXPLAIN SPECIES DOMINANCE PATTERNS IN MACROALGAL BLOOMS<sup>1</sup>

Heike K. Lotze<sup>2,3</sup> and Winfrid Schramm

Institut für Meereskunde, Düsternbrooker Weg 20, 24105 Kiel, Germany

Macroalgal blooms are a growing environmental problem in eutrophic coastal ecosystems world wide. These blooms are dominated typically by only one out of several co-occurring opportunistic species, which are all favored by increased nutrient loads. We asked whether pronounced dominance of filamentous *Pilayella littoralis* Kjellm. (Phaeophyceae) over foliose *Enteromorpha intestinalis* L. (Chlorophyceae) in the Baltic Sea can be explained by interspecific physiological differences. In laboratory experiments, we analyzed uptake kinetics of nitrate, ammonium, and phosphate and the time dependency of uptake rates for both species. We further examined growth rates and nutrient assimilation in relation to single and combined enrichment with nitrate and phosphate, and three different nitrogen sources. Overall, we did not detect distinct differences in uptake, growth, and assimilation rates between *P. littoralis* and *E. intestinalis*. Minor differences and the related advantages for single species are discussed. Highest maximal uptake rates were found for ammonium, followed by nitrate and phosphate. Strong time dependency of uptake occurred, with the highest rates during the first 15 to 30 min. Nitrate enrichment had far more of an effect on growth than phosphate. Enrichment with urea, ammonium, and nitrate significantly increased growth rates without interspecific differences. A larger surface area to volume (SA/V) ratio in *Pilayella* compared with *Enteromorpha* did not translate into greater physiological capacity. We conclude that species dominance patterns in macroalgal blooms are not always a direct result of different ecophysiological traits among species. Ecological traits such as susceptibility to herbivory are important factors in determining species distribution in the field.

**Key index words:** *Enteromorpha*; eutrophication; functional form; growth; nutrient source; *Pilayella*; surface area to volume ratio; time dependency; tissue content; uptake kinetics

**Abbreviations:**  $K_m$ , half-saturation constant; RGR, relative growth rate; SA/V, surface area to volume;  $V_{max}$ , maximal uptake rate;  $\alpha$ , initial slope ( $V_{max}/K_m$ )

In recent decades, increasing cultural eutrophication has changed the structure and diversity of marine benthic communities (Ryther and Dunstan 1971, Raffaelli et al. 1989, Nixon 1990, Duarte 1995, Schories et al. 1997). Most visibly, mass blooms of opportunistic fast-growing species now occur frequently in eutrophic coastal waters worldwide (Cederwall and Elmgren 1990, Bonsdorff 1992, Schramm and Nienhuis 1996, Raffaelli et al. 1998). These macroalgal blooms are generally explained by increased nutrient loads which selectively favor filamentous and foliose macroalgae because of their physiological traits (Larsson et al. 1985, Duarte 1995, Pedersen and Borum 1996, Raffaelli et al. 1998). Characterized by high rates of nutrient uptake, photosynthesis, and growth, these opportunistic species gain competitive advantage over the perennial, late-successional vegetation in the course of increasing nutrient loading (Wallentinus 1978, 1984, Sand-Jensen and Borum 1991, Duarte 1995). Moreover, the high tolerance of opportunists to changes in salinity, temperature, light, and dissolved oxygen levels enhances the success of these algae in eutrophic estuaries and lagoons, which are often characterized by highly fluctuating abiotic conditions (Peckol et al. 1994, Peckol and Rivers 1995a, Fong et al. 1996, Raffaelli et al. 1998). In many coastal areas, macroalgal blooms are dominated by one or two green algal species of the genera *Enteromorpha*, *Ulva*, *Cladophora*, or *Chaetomorpha* (overview in Fletcher 1996, Raffaelli et al. 1998). Distinct differences in physiological capacity or tolerance may explain dominance patterns among co-occurring opportunistic species as suggested by the few existing attempts that have been made to test this hypothesis (Lavery and McComb 1991, Lotze 1994, Peckol and Rivers 1995b, Fong et al. 1996). Still, our ability to predict species dominance among bloom-forming macroalgae is slight (Raffaelli et al. 1998).

In contrast to the common dominance of green tides (Fletcher 1996), the filamentous brown alga *Pilayella littoralis* dominates mass blooms over co-occurring *E. intestinalis* in many parts of the Baltic Sea (Wallentinus 1984, Kruk-Dowgiallo 1991, Norkko and Bonsdorff 1996, Kiirikki and Lehvo 1997, Lotze et al. 1999). This dominance of *P. littoralis* cannot be related to different productivity levels over a range of temperature and light conditions, despite advantageous germination of *P. littoralis* at lower temperatures (Lotze et al. 1999). Furthermore, productivity levels of both species are not reduced in brackish conditions (Bolton 1979, Reed and Russell 1979).

In this paper, we asked whether distinct differences in nutrient use and preference between the two bloom-

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<sup>2</sup> Author for reprint requests; e-mail hlotze@ifm.uni-kiel.de.

<sup>3</sup> Present address and address for correspondence: Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 4J1; e-mail hlotze@is.dal.ca.

forming macroalgae *P. littoralis* and *E. intestinalis* may explain the dominance of the former in the Baltic Sea. *Pilayella littoralis*, with its filamentous, highly branched thalli, has a greater SA/V ratio than the foliose *E. intestinalis* (Nielsen and Sand-Jensen 1990). Because increased SA/V ratio is generally thought to translate into higher productivity levels (Rosenberg and Ramus 1984, Duke et al. 1989, Carpenter 1990), we tested whether greater surface area in *P. littoralis* translates into greater nutrient uptake and growth rates compared with *E. intestinalis*. In laboratory experiments, we studied (1) time-dependent uptake kinetics of ammonium, nitrate, and phosphate; (2) growth rates in relation to enrichment with different nitrogen sources (ammonium, nitrate, urea), as well as interactions in a combined enrichment with nitrate and phosphate; and (3) assimilation rates of N and P during the growth experiments.

#### MATERIALS AND METHODS

**Plant material and field site.** Adult thalli of *Pilayella littoralis* and *Enteromorpha intestinalis* were collected in the outer Schlei Fjord (lat 54°41'N, long 10°0'E), Western Baltic Sea, Germany. Here, the perennial vegetation, consisting of *Fucus vesiculosus* L., *Potamogeton pectinatus* L., and *Zostera marina* L., becomes overgrown regularly in spring and summer by epiphytic *P. littoralis* and to a lesser extent by *E. intestinalis*. In 1995, maximum biomass of *Pilayella* and *Enteromorpha* was 16 and 1.4 g·m<sup>-2</sup> dry weight basis, respectively (Lotze et al. 1999). Winter nutrient concentrations in 1995 reached maxima of 160 μM nitrate N, 12 μM ammonium N, and 2 μM phosphate P; minimum summer concentrations in nitrate and ammonium varied between undetectable and 0.3 μM; in phosphate, between 0.1 and 0.6 μM (Schramm et al. 1996). Nutrient supply at the field site varies greatly on a time scale of hours to days because of wind-driven water exchanges with either nutrient-rich water from the inner, highly eutrophic Schlei Fjord or comparatively nutrient-poor water from the adjacent Kiel Bight (Schramm et al. 1996). We collected fresh plant material 1 day prior to our laboratory experiments in June 1995, when both species were abundant in the field and previously observed high epiphytic diatom loads on *Pilayella* had disappeared (Lotze 1998). Thus, a possible confounding of physiological properties from the epiphytic diatoms was avoided. Algal thalli were then kept in 20-L tanks filled with freshly collected and 0.2-μm filtered seawater from the field site. Tanks were illuminated by fluorescent light tubes at 100 μmol photon·m<sup>-2</sup>·s<sup>-1</sup> in a 14 h light:10 h dark cycle at 15° C.

**Growth rate and nutrient assimilation.** In June 1995, nutrient effects on growth rates of *E. intestinalis* and *P. littoralis* were tested over a 12-day period in a batch mode experiment. Nutrient-enriched media were replaced every 2 days. Levels of nutrient enrichment were chosen as high, short-time pulse concentrations that were about five times greater than maximum winter concentrations measured in the outer Schlei (see above). These high nutrient levels represented nutrient pulses occurring through (1) wind-driven water exchange, (2) flux from the sediment, and (3) increased land runoff after a rainfall (Riisgard et al. 1995, Fong et al. 1996, Schramm et al. 1996). In the first experiment, thalli of *Enteromorpha* and *Pilayella* were exposed to single and combined enrichment with nitrate and phosphate. Enrichment concentrations correspond to 500 μM nitrate N (as NaNO<sub>3</sub>) and 30 μM phosphate P (as KH<sub>2</sub>PO<sub>4</sub>). A treatment without enrichment served as a control. Compared with the control treatment with a background N:P ratio of 43:1, P was added in surplus to the enrichment treatment (N:P ratio of 16.6:1) to avoid P limitation during the experiment. To test effects of other nitrogen sources in a second parallel experiment, we enriched treatments with 50 μM ammonium N (as NH<sub>4</sub>Cl), and 10 μM urea N (=5 μM CO(NH<sub>2</sub>)<sub>2</sub>). To prevent P limitation in these treatments, 30 μM

phosphate P (as KH<sub>2</sub>PO<sub>4</sub>) was added. Each treatment was started in five replicates, with a standard algal weight of 0.1 g wet weight in 750 mL freshly collected, 0.2-μm filtered seawater with nutrients added from stock solutions. Algal wet weight was determined in a standardized procedure with a specially constructed centrifuge, operating as a spin dryer to remove adherent water for 30 s with constant rotation speed. Background seawater levels were 0.09 μM phosphate P, 3.49 μM nitrate N, 0.80 μM ammonium N, and 0.61 μM urea N. All tests were run at 15° C, 100 μmol photon·m<sup>-2</sup>·s<sup>-1</sup> in a 14 h light:10 h dark cycle. After 12 days, algal material was reweighed and relative growth rates were calculated: RGR = (ln w<sub>1</sub> - ln w<sub>2</sub>)/(t<sub>2</sub> - t<sub>1</sub>), where *w* is wet weight and *t* is time.

After the growth experiment, three randomly chosen replicates per treatment were used to analyze C-N-P tissue content of treated algae and compared with those of untreated algae. Algal thalli were dried for 48 h at 70° C for dry weight determination. Afterwards, C-N content of dried material was determined using a C/N Analyzer (Fisons Instruments, NA 1500 N). For the analysis of P content, dried algal material was combusted (550° C for 2 h), eluted with 5 mL H<sub>2</sub>O and 0.1 mL H<sub>2</sub>SO<sub>4</sub> (4.5 n) and then PO<sub>4</sub>-P was photometrically analyzed with an autoanalyzer using the methods of Grasshoff et al. (1986).

Statistical analysis was performed by three-way ANOVA (factors: species, nitrate, and phosphate, 2 × 2 × 2) and two-way ANOVA (factors: species and nitrogen source, 2 × 2) with RGR and tissue N and P content as the dependent variables. Untransformed data met the assumption of homogeneity of variances (Cochran's Test). Relative effect size of the experimental factors was calculated as omega-squared for a fixed-factor model and transformed to the percentage of explained variance (Howell 1992). Linear regression analyses were performed to check for linear correlations between RGR and N content versus molar N concentration in different nitrogen enrichments.

**Nutrient uptake.** Nutrient uptake was studied with three different nutrient sources: nitrate, ammonium, and phosphate. We used a combination of the perturbation and the multiple flask methods as recommended by Pedersen (1994). While the multiple flask incubation with different substrate concentrations and short incubation time is the best method for estimation of initial uptake, the combination with the perturbation method provides important information on the time dependency of nutrient uptake (Harrison et al. 1989, Pedersen 1994). Because of the transient nature of nitrogen uptake, the Michaelis-Menten equation is inadequate to describe the entire uptake kinetics, but can be applied when uptake rates are obtained over analogous time intervals (Pedersen 1994). Time intervals and concentrations used in the following experiments were chosen according to the results of a pilot study (unpublished data). Uptake experiments with nitrate (NaNO<sub>3</sub>) and ammonium (NH<sub>4</sub>Cl) were started with initial N concentrations of 0, 5, 10, 20, 50, 100, 200, and 500 μM. To avoid P shortage of nitrogen uptake (Björnsäter and Wheeler 1990), all experiments received a precautionary phosphate addition of 3 μM. Uptake rates were followed by analyzing nitrate concentrations in the media at 0, 30, 60, 120, and 180 min in the nitrate experiment and ammonium at 0, 15, 30, 45, 60, and 120 min in the ammonium experiment. The phosphate uptake experiment was started with initial phosphate-P concentrations of 0, 3, 6, 12, 18, and 30 μM (KH<sub>2</sub>PO<sub>4</sub>), and an additional 50 μM nitrate N and 50 μM ammonium N, and was sampled at 0, 60, 120, and 240 min. Uptake rates measured with this experimental design represent transient responses to nutrient pulses with surge uptake during the first time intervals and assimilation uptake during the later time intervals, and should be distinguished from acclimated (steady state) uptake rates measured in continuous culture. We chose this approach to detect differences between *Enteromorpha* and *Pilayella* in their rapid response (minutes to hours) to nutrient pulses, whereas their responses over a longer time scale (12 days) were investigated in our growth experiments.

Freshly collected and 0.2-μm filtered seawater was used for

the uptake experiments with corresponding background nutrient levels of 0.54  $\mu\text{M}$  phosphate P, 0.41  $\mu\text{M}$  nitrate N, and 0.56  $\mu\text{M}$  ammonium N. Nutrient concentrations in seawater samples were determined with a continuous flow analyzer using the methods of Grasshoff et al. (1986). All uptake tests were run at 15° C and 200  $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  between 1200 and 1500 hours. Nitrate and ammonium uptake rates were determined in 1-L sterilized glass bottles, phosphate uptake was determined in 1-L sterilized PETG (polyethylene terephthalate copolyester, Nalgene) bottles because of phosphate absorption by glass. For adaptation of algae to experimental conditions, we filled beakers with 1 L of 0.2- $\mu\text{m}$  filtered seawater and added 1 g wet weight (entire, freshly collected thalli) 2 hours in advance. Aeration provided continual mixing of the medium. After this adaptive period, we removed the algal thalli carefully with a sieve, added nutrients from a concentrated stock solution, mixed carefully, took the first nutrient sample (1 mL) with an Eppendorf pipette (using 1 tip per sample), and put the algae back into the beaker. Nutrient samples were diluted and analyzed immediately with an autoanalyzer. After final sampling, algae were dried for 48 h at 70° C for dry weight determination. In each uptake experiment, a control without algal material and with additions of 100  $\mu\text{M}$  nitrate N or ammonium N or 12  $\mu\text{M}$  phosphate P was run. No autogenic changes in substrate concentrations were detected over the experimental period.

Uptake rates ( $V$ ) were calculated from changes in substrate concentrations during each sampling interval as  $\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$  dry weight:  $V = [(S_0 \times \text{vol}_0) - (S_t \times \text{vol}_t)] / (t \times w)$ , where  $S_0$  is the actual substrate concentration at the beginning and  $S_t$  at the end of a sampling interval,  $\text{vol}_0$  is the water volume at the beginning and  $\text{vol}_t$  at the end of a sampling interval,  $t$  is the time of the sampling interval and  $w$  is the algal biomass as grams dry weight. Uptake rates were plotted against  $S_0$  for each time interval separately and fitted to the Michaelis–Menten equation,  $V = (V_{\text{max}} \times S_0) / (K_m + S_0)$ , using nonlinear least-squares regression (we used the Marquardt–Levenberg algorithm; the process is iterative). This provided estimates of  $V_{\text{max}}$  (maximum uptake rate) and  $K_m$  (half-saturation constant), which allowed calculation of  $\alpha$  (initial slope =  $V_{\text{max}}/K_m$ ).

## RESULTS

**Growth rate and nutrient assimilation.** In our growth experiments, all treatments with nitrogen enrichment significantly increased the growth rate of *E. intestinalis* and *P. littoralis* compared with the control treatments (Fig. 1), but no significant differences between the two species were detected (factor species, nitrate enrichment:  $F_{1,16} = 2.037$ ,  $P = 0.1727$ ; ammonium:  $F_{1,16} = 0.223$ ,  $P = 0.6432$ ; urea:  $F_{1,16} = 0.342$ ,  $P = 0.5671$ ). Nitrate enrichment more than doubled growth rate ( $F_{1,16} = 55.74$ ,  $P = 0.0001$ ) in *Enteromorpha* (2.1-fold) and *Pilayella* (2.4-fold). Ammonium enrichment resulted in 1.7- and 1.4-fold increases ( $F_{1,16} = 7.46$ ,  $P = 0.0148$ ), and urea enrichment in 1.6- and 1.3-fold increases ( $F_{1,16} = 5.53$ ,  $P = 0.0319$ ) in growth rate of *Enteromorpha* and *Pilayella*, respectively. A regression analysis over the different nitrogen sources indicated a significant increase of RGR with increasing molar N concentration ( $F_{1,37} = 30.753$ ,  $P = 0.0001$ ,  $R^2 = 0.45$ ), but again there was no significant difference between the two species ( $F_{1,37} = 0.20$ ,  $P = 0.8876$ ). Tissue N content was significantly enhanced by enrichment with nitrate ( $F_{1,8} = 262$ ,  $P = 0.0001$ ) and ammonium ( $F_{1,8} = 19.4$ ,  $P = 0.0023$ ), whereas urea enrichment caused a slight decrease in tissue N ( $F_{1,8} = 6.3$ ,  $P = 0.0366$ ). Regression analysis revealed a significant correlation between tissue N

content and molar N concentration in the medium ( $F_{1,21} = 160$ ,  $P = 0.0001$ ,  $R^2 = 0.88$ ) without interspecific difference ( $F_{1,21} = 0.015$ ,  $P = 0.9029$ ). Phosphorus content remained unaffected ( $P > 0.3$ ) by all nitrogen enrichment treatments and no interspecific differences occurred ( $P > 0.1$  for all nitrogen sources).

In a combined enrichment experiment, no interaction between nitrate and phosphate enrichment was detected ( $N \times P$ ,  $P = 0.0761$ ; Table 1; Fig. 2). Nitrate enrichment had the main effect on growth rate, explaining 45% of variance without a significant difference between species ( $S \times N$ ,  $P = 0.526$ ). While growth of *Enteromorpha* was not affected by phosphate enrichment, phosphate slightly increased growth of *Pilayella*, indicated by a significant species  $\times$  phosphate interaction ( $S \times P$ ,  $P = 0.0148$ ). However, this interaction effect explained only 6.3% of the total variance (Table 1). Combined enrichment of nitrate and phosphate resulted in a 3.5-fold increase of RGR in *Pilayella* and a 1.6-fold increase in *Enteromorpha* (Fig. 2). After combined enrichment, however, maximal RGRs were not significantly different between species ( $t$ -test,  $F_{1,32} = 1.858$ ,  $P = 0.1824$ ). Tissue N content was significantly enhanced by nitrate enrichment ( $F_{3,16} = 153$ ,  $P = 0.0001$ ), as well as tissue P by phosphate enrichment ( $F_{3,16} = 14.2$ ,  $P = 0.0001$ ), but no interspecific differences occurred (factor species, tissue N:  $F_{1,16} = 3.219$ ,  $P = 0.0917$ ; tissue P:  $F_{1,16} = 0.864$ ,  $P = 0.3663$ ) (Fig. 2). Prior to the experiments, N contents were 1.44% ( $\pm 0.03$  SE) of dry weight in *E. intestinalis* and 2.22% ( $\pm 0.03$ ) in *P. littoralis*, P contents were 0.15% ( $\pm 0.01$ ) and 0.25% ( $\pm 0.01$ ), respectively, resulting in

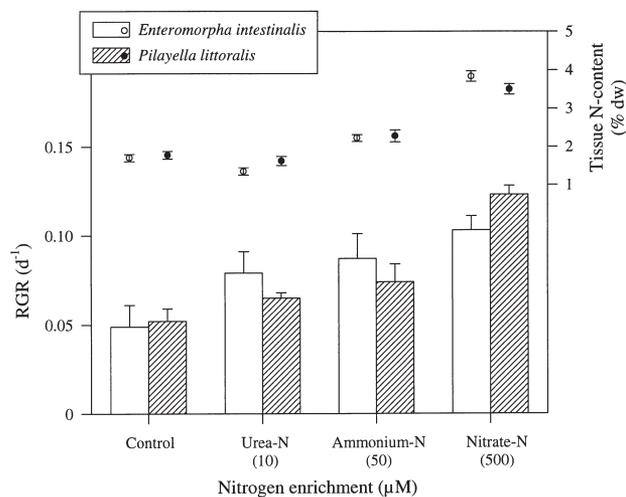


FIG. 1. Growth of adult thalli and tissue N assimilation of *Enteromorpha intestinalis* and *Pilayella littoralis* in relation to enrichment with different sources of nitrogen: nitrate N (500  $\mu\text{M}$ ), ammonium N (50  $\mu\text{M}$ ), urea N (10  $\mu\text{M}$ ), and a control. Phosphate was enriched in all treatments (30  $\mu\text{M}$ ). Relative growth rate per day (RGR· $\text{d}^{-1}$ ,  $\pm 1$  SE,  $n = 5$ ) was determined by increase of wet weight after 12 d. Final tissue N content of *Enteromorpha* (open circles) and *Pilayella* (filled circles) are shown for each treatment ( $\pm 1$  SE,  $n = 3$ ).

molar N:P ratios of 21 in *Enteromorpha* and 19 in *Pilayella*. After 12 days in combined N and P enrichments with media N:P ratios ranging from 0.1 to 5000, tissue N:P ratios ranged from 11.55 to 46.98 (Table 2).

**Nutrient uptake.** Nutrient uptake rates of *E. intestinalis* and *P. littoralis* following initial pulses of nitrate, ammonium, and phosphate were analyzed over several time intervals (Fig. 3). Overall, no distinct differences between the two species were detected in uptake rates of any nutrient tested, but minor differences occurred. *Enteromorpha* showed greater nitrate uptake in later time intervals (60–120, 120–180 min) compared with *Pilayella* (Fig. 3; Table 3). Ammonium uptake in the first 30 minutes was similar in both species, but *Pilayella* showed higher uptake rates in intermediate time intervals (30–45, 45–60 min). There were no distinct differences between species in phosphate uptake. Strong time dependency in the uptake of all three nutrients occurred, with  $K_m$  and  $V_{max}$  declining with increasing incubation time. Hence, values of  $\alpha$  were highly variable and did not change consistently with time; the increase in  $\alpha$  for nitrate uptake of *Pilayella* and the decrease in  $\alpha$  for phosphate uptake of both species may be artifacts due to the high variability of both  $K_m$  and  $V_{max}$  values (Table 3). Surge uptake of ammonium during the first time interval was 7-fold greater than assimilation uptake during the last time interval in *Enteromorpha* and 8-fold greater in *Pilayella*. Surge uptake was 3- and 5-fold greater than the assimilation uptake for phosphate and 2.5- and 9-fold greater for nitrate in *Enteromorpha* and *Pilayella*, respectively.

The actual uptake data (Fig. 3, symbols) for all three nutrients showed distinct deviations from the Michaelis–Menten fit (Fig. 3, lines) in both species, especially in the early time intervals. Our data show a saturation level at lower concentrations than predicted by the Michaelis–Menten equation, and slightly reduced uptake rates at highest substrate concentrations.

#### DISCUSSION

Our results show that dominance patterns among opportunistic bloom-forming macroalgae are not always a direct result of different ecophysiological traits

TABLE 1. Results of 3-way ANOVA on single and combined effects of phosphate (30  $\mu\text{M}$ ) and nitrate (500  $\mu\text{M}$ ) enrichment on growth of adult thalli of *Enteromorpha intestinalis* and *Pilayella littoralis* (factor: species). Relative effect size is shown as explained variance in %.

Source of variation	df	MS $\times$ 10 <sup>3</sup>	F-ratio	P-value	Variance (%)
Species (S)	1	0.562	0.984	0.3287	
Nitrate (N)	1	23.771	41.623	0.0001	45.0
Phosphate (P)	1	2.243	3.927	0.0562	
S $\times$ N	1	0.235	0.411	0.5260	
S $\times$ P	1	3.789	6.634	0.0148	6.3
N $\times$ P	1	1.920	3.361	0.0761	
S $\times$ N $\times$ P	1	0.143	0.251	0.6199	
Residual	32	0.571			

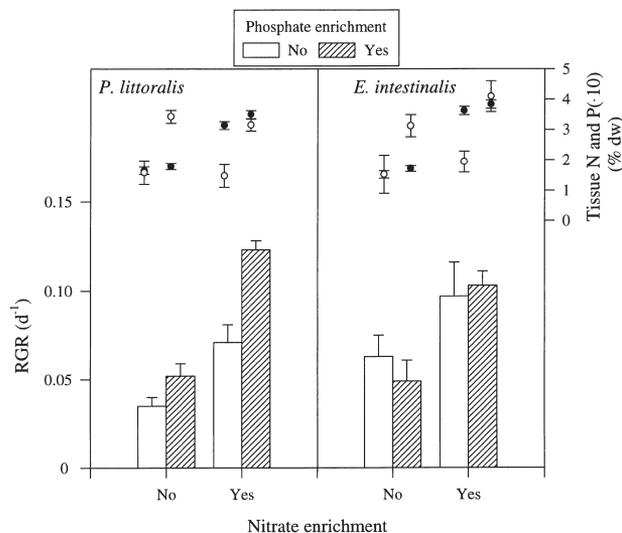


FIG. 2. Growth of adult thalli and tissue N and P assimilation of *Enteromorpha intestinalis* and *Pilayella littoralis* in relation to single and combined enrichment with phosphate (30  $\mu\text{M}$ ) and nitrate (500  $\mu\text{M}$ ). Relative growth rate per day (RGR- $\text{d}^{-1}$ ,  $\pm 1$  SE,  $n = 5$ ) was determined by measuring increase of wet weight after 12 d. Final tissue N content (filled circles) and P content (open circles) are shown for each treatment ( $\pm 1$  SE,  $n = 3$ ).

as reported from other studies (Fujita 1985, Lavery and McComb 1991, Lotze 1994, Peckol and Rivers 1995b, Fong et al. 1996). The co-occurring filamentous brown alga *Pilayella littoralis* and foliose green alga *Enteromorpha intestinalis* showed closely similar nutrient uptake, nutrient assimilation, and growth rates at various nutrient enrichment treatments. Surprisingly, distinct differences in thallus morphology and SA/V ratio between the two species did not translate into different physiological capacities as suggested by a functional-form model.

Growth rates of adult *E. intestinalis* and *P. littoralis* were significantly increased by enrichment with urea, ammonium, and nitrate, but no interspecific differences occurred. In addition, the two species did not differ in N and P assimilation over the experimental period. We therefore assume no preference or niche differentiation between the two species regarding the use of different nitrogen sources as reported for other macroalgae (DeBoer et al. 1978, Fujita et al. 1989, Floreto et al. 1996). In combined enrichment treatments, phosphate slightly increased growth in *Pilayella*, whereas

TABLE 2. Molar N:P ratios of media and algal tissue after 12 days of growth in treatments with single and combined enrichments with nitrate (500  $\mu\text{M}$ ) and phosphate (30  $\mu\text{M}$ ).

Treatment	Molar N:P ratio		
	Medium	<i>E. intestinalis</i>	<i>P. littoralis</i>
$\text{NO}_3^-$	5000	41.32	46.98
$\text{NO}_3^- / \text{PO}_4^-$	16.6	20.71	24.57
$\text{PO}_4^-$	0.1	12.18	11.55
Control	43	22.13	23.13

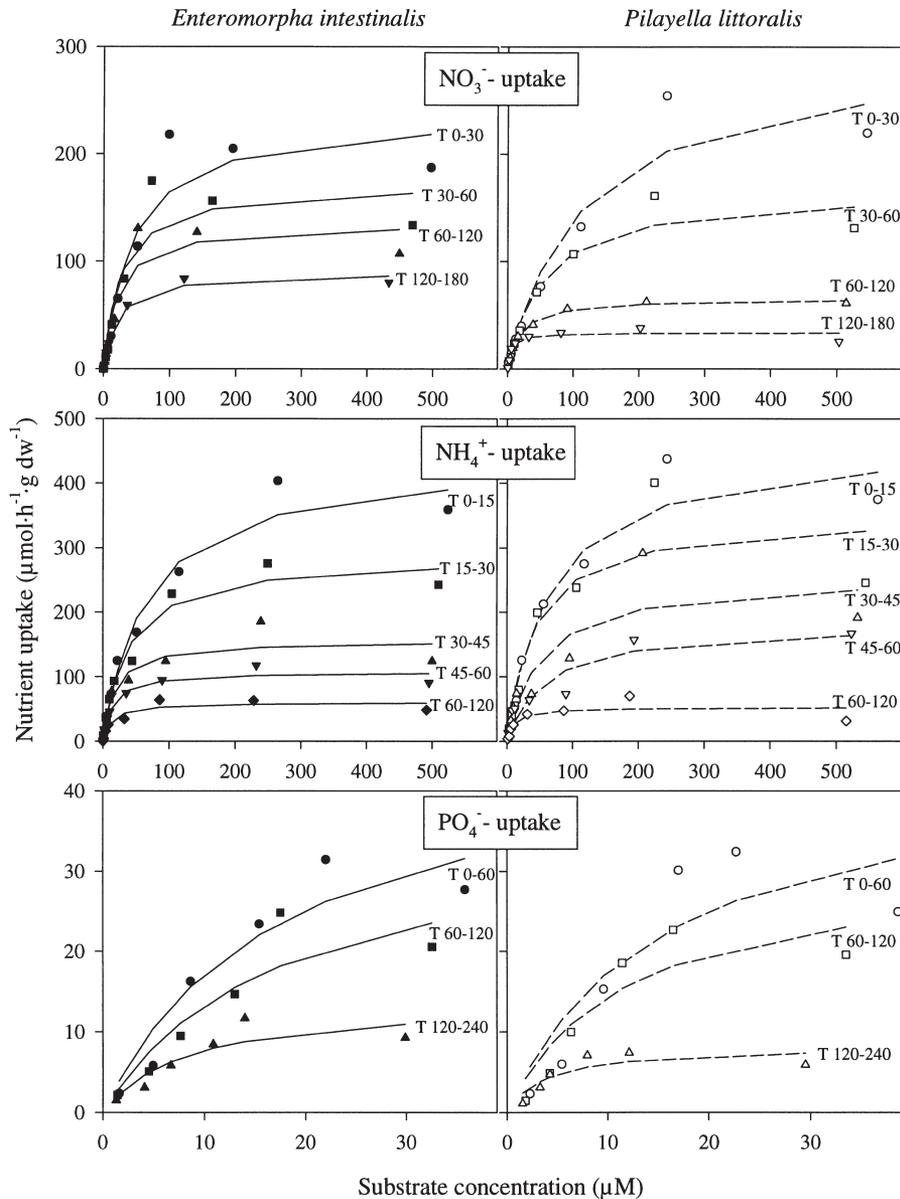


FIG. 3. Nutrient uptake of *Pilayella littoralis* and *Enteromorpha intestinalis* in relation to substrate concentration at different time intervals. Symbols follow increasing time interval ( $T$ , in minutes) in the order circle, square, triangle up, triangle down, diamond. Data of each time interval were fitted to Michaelis-Menten equation using nonlinear regression analyses (solid lines). For parameter estimation ( $V_{\max}$ ,  $K_m$ ,  $\alpha$ ), see Table 3.

*Enteromorpha* remained unaffected. However, this difference as indicated by a significant phosphate  $\times$  species interaction explained only a small portion of total variance compared with the dominant nitrate effect, which did not differ among species (Table 1). Moreover, *Pilayella* did not reach higher maximal RGR than *Enteromorpha*. We further suggest that selective phosphate effects on *Pilayella* may not be ecologically relevant. During the main growing period of the two species in spring and summer, nitrogen limitation in the field (see below) overrides the phosphate effect, while in winter and early spring, temperature and light conditions are the main limiting factors for growth (Lotze et al. 1999).

The greater effect of N over P enrichment may indicate N limitation of growth (Björnsäter and Wheeler 1990). In summer, nitrogen concentrations at the field

site were close to the detection limit, whereas phosphate was still available (Schramm et al. 1996). However, species may use nutrient pulses caused by frequent wind-driven water exchange with the inner, highly eutrophic Schlei Fjord (Schramm et al. 1996). Other potentially important nitrogen sources include nutrient recycling through the detritus food chain (Pregnall and Miller 1988, Lavery and McComb 1991, Hanisak 1993), herbivore excretion (Williams and Carpenter 1988), and nutrient flux from the sediment (Christiansen et al. 1992, Brennan and Wilson 1993). Tissue analyses of field plants indicated increasing N limitation with decreasing N:P ratios from 40 in spring to <20 in summer (Schramm et al. 1996). Prior to our experiments in June, N:P ratios were 19 and 21 for *Pilayella* and *Enteromorpha*, respectively. After 12 days of growth, unenriched (N:P = 43) and combined N- and

TABLE 3. Maximum uptake rate ( $V_{\max}$  in  $\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$  dry weight), half-saturation constant ( $K_m$  in  $\mu\text{M}$ ), initial slope ( $\alpha = V_{\max}/K_m$ ), and correlation coefficient ( $R^2$ ) of nutrient uptake of *Pilayella littoralis* and *Enteromorpha intestinalis* at different time intervals.<sup>a</sup>

Time (min)	<i>Enteromorpha intestinalis</i>						<i>Pilayella littoralis</i>					
	$V_{\max}$	SE	$K_m$	SE	$\alpha$	$R^2$	$V_{\max}$	SE	$K_m$	SE	$\alpha$	$R^2$
<b>NO<sub>3</sub><sup>-</sup> uptake</b>												
0–30	237.3	30.3	43.7	18.5	5.4	0.64	300.1	43.4	116.4	45.9	2.6	0.77
30–60	172.8	24.0	26.9	13.4	6.4	0.56	166.5	16.0	54.5	17.1	3.1	0.65
60–120	135.7	17.6	21.4	10.3	6.3	0.51	65.8	1.5	19.9	1.8	3.3	0.50
120–180	90.1	4.2	20.4	3.7	4.4	0.49	33.6	2.5	5.2	1.9	6.5	0.37
<b>NH<sub>4</sub><sup>+</sup> uptake</b>												
0–15	439.1	33.7	66.4	16.3	6.6	0.67	466.7	43.2	66.6	19.1	7.0	0.67
15–30	286.9	20.1	37.7	9.6	7.6	0.58	351.4	56.2	42.3	22.9	8.3	0.60
30–45	156.0	15.9	17.7	7.6	8.8	0.47	257.5	51.8	53.1	34.9	4.9	0.64
45–60	107.5	6.3	13.3	3.5	8.1	0.42	181.6	27.3	58.2	28.5	3.1	0.66
60–120	60.7	5.5	12.8	5.4	4.7	0.41	52.6	8.1	10.1	6.6	5.2	0.40
<b>PO<sub>4</sub><sup>-</sup> uptake</b>												
0–60	46.9	13.5	17.3	10.6	2.7	0.92	44.2	17.7	15.4	13.9	2.9	0.90
60–120	35.9	14.4	17.1	13.8	2.1	0.93	30.9	9.4	11.6	8.0	2.7	0.87
120–240	13.9	3.9	8.1	5.8	1.7	0.86	8.2	1.8	3.7	2.5	2.2	0.75

<sup>a</sup>Data were fitted to the Michaelis–Menten equation using nonlinear least-squares regression. Shown are means of estimated kinetic parameters ( $\pm 1$  SE,  $n = 7$  for nitrate and ammonium,  $n = 5$  for phosphate).

P-enriched (N:P = 17) treatments resulted in tissue N:P ratios of 21 to 25 in both species, which is close to a balanced internal N:P ratio (Björnsäter and Wheeler 1990). In contrast, tissue N:P ratios exceeded 40 in N-enriched treatments (N:P = 5000); this suggests P limitation comparable to the early spring situation in the field. Tissue N:P ratios around 12 in P-enriched treatments (N:P = 0.1) suggest N limitation comparable to the summer field situation. Our experimental plants thus seemed to be slightly N limited. Compared with *Enteromorpha*, *P. littoralis* had a greater N content. This indicates that *Pilayella* either assimilated more N in the field or had a greater storage capacity than *Enteromorpha*. However, N content of both *Pilayella* and *Enteromorpha* varied greatly during the vegetation period, with no clear patterns between the two species in the field (Schrammet al. 1996). We therefore assume that there is no clear advantage for *Pilayella* resulting from increased N assimilation or storage.

Similar growth responses of *E. intestinalis* and *P. littoralis* are corroborated by the results of our nutrient uptake studies. No distinct interspecific differences occurred in the uptake rates and kinetic parameters for nitrate, ammonium, and phosphate. *Enteromorpha* showed slightly higher nitrate uptake rates at later time intervals (60–120, 120–180 min). In contrast, *Pilayella* showed higher ammonium uptake rates at intermediate time intervals (30–45, 45–60 min). Since nitrogen pulses released from the sediment are mainly in the form of ammonium (Riisgard et al. 1995) there may be a slight net advantage for *Pilayella*. Furthermore, the greater initial tissue N content in *Pilayella* might have lowered its overall uptake rates, since there is a feedback between internal N pools (which reflect past nutritional history) and uptake rates (Fujita 1985, O'Brien and Wheeler 1987). However, the greater N content could also reflect a higher N demand or critical N content in *Pilayella* needed to sustain maximal uptake or growth rate (Fujita et al. 1989, Pedersen and Borum 1996). Import-

tantly, these rather subtle differences did not result in better performance of one species in either our laboratory growth experiments or in field experiments (Lotze et al. 2000, Worm et al. 2000).

Strong time dependency of uptake rates was found for all nutrients tested and for both species. Initial uptake slopes ( $\alpha$ ) were highly variable and did not change consistently with time, paralleling results from Pedersen (1994) and Pedersen and Borum (1997). Surge uptake was much higher than assimilation uptake in all nutrients tested, which is advantageous in systems with episodic nutrient supply (Pedersen 1994, Pedersen and Borum 1997). Saturation of uptake in our experiments occurred at concentrations greater than reported in earlier studies on *Enteromorpha* and *Pilayella* (Harlin 1978, Kautsky 1982, Wallentinus 1984, Fujita 1985, O'Brien and Wheeler 1987). Both species may have adapted to rich nutrient conditions, accounting for their success in eutrophic waters. The decline of uptake rates at highest substrate concentrations suggests inhibition of algal performance at elevated nutrient levels. This has been reported from growth and uptake of *Cladophora* and *Gracilaria* at ammonium levels of 100  $\mu\text{M}$  (20 times the maximum background level) (Peckol and Rivers 1995a). On the other hand, *Enteromorpha* and *Ulva* have not been depressed at enrichment levels of 840  $\mu\text{M}$  nitrate, which is 56 times the background level (Fong et al. 1996). Depression or inhibition of algal performance under high-nutrient conditions may depend on nutrient type, nutrient concentration, and the degree of tolerance or adaptation to high nutrient levels. The concentrations we chose in our experiments were 4 to 12 times the maximum background levels at our site. These concentrations are realistic with respect to our and other eutrophic systems because (1) high winter concentrations in our system remain until March (Schramm et al. 1996), when annual algal growth is initiated (Lotze et al. 1999, 2000); (2) there is frequent wind-driven transport of nutrient-rich water from the

inner Schlei Fjord (maximum of 350  $\mu\text{M}$  nitrate N, 180  $\mu\text{M}$  ammonium N and 15  $\mu\text{M}$  phosphate P, Schramm et al. 1996); (3) nutrient levels released from the sediment can be very high (e.g. 1300  $\mu\text{mol N}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$  in summer, Riisgard et al. 1995; see also Lohse et al. 1995, Jørgensen 1995, Watson and Frickers 1995); (4) increased land runoff after rainfalls can carry very high nutrient loads (Fong et al. 1996); and (5) nutrient levels within macroalgal mats or blooms are highly elevated compared with the surrounding water (Thybo-Christensen et al. 1993, Krause-Jensen et al. 1996).

Overall, we were surprised not to find distinct differences in physiological capacity of *P. littoralis* and *E. intestinalis*, given marked differences in their morphology. As a measurement of metabolically active area, the SA/V ratio was reported as from 1694 to 1737 in *P. littoralis* and from 369 to 529 in *Enteromorpha* sp. (Nielsen and Sand-Jensen 1990). Since *Enteromorpha* species vary greatly in their morphology, we determined the SA/V ratio for unbranched *E. intestinalis* as 140 (20 individuals measured). Thus, the SA/V ratio is at least 4 to 10 times greater in *P. littoralis* than *E. intestinalis*. A general correlation between SA/V ratio and uptake and growth rates has been found in comparing micro- to macroalgae and angiosperms (Nielsen and Sand-Jensen 1990, Hein et al. 1995), among different functional groups of macroalgae (Rosenberg and Ramus 1984, Duke et al. 1989), and different morphological forms of one genus (Gacia et al. 1996). A difference of 4 to 5 in the SA/V ratio can translate into distinct differences in uptake capacities (Rosenberg and Ramus 1984). On the other hand, 4-fold to 8-fold differences in the SA/V ratio did not result in different maximal growth rates among several filamentous and foliose species (Nielsen and Sand-Jensen 1990). Pedersen and Borum (1997) have reported a weak correlation of uptake capacity to SA/V ratio, with a range from 10 to 560. Combined with our findings, these contrasting results suggest that the SA/V ratio may not be very useful as a comparative index in predicting physiological capabilities for seaweed species co-occurring in a particular habitat, especially when these species belong to similar functional groups. Overlapping diffusion boundary layers may reduce uptake capacities in filamentous algae and thus reduce the advantage of a greater SA/V ratio (Hay 1981). A high SA/V ratio is only one of several morphological factors (such as small size, simple thallus structure, or undifferentiated cells which are all photosynthetic) that are believed to translate into higher physiological capacities, according to a functional-form model (Littler and Littler 1980). However, the physiological capacities of algae belonging to the filamentous (finely branched) and foliose (sheetlike) functional groups often seem to overlap (Wallentinus 1984, Nielsen and Sand-Jensen 1990, Pedersen 1995, Pedersen and Borum 1997). For productivity data, variation within the two groups was often greater than between groups, and maximum productivity levels were reached by either filamentous or foliose species, depending on the study and the parameter measured (Arnold and Murray 1980, Littler 1980, Littler and Arnold 1982, Littler et al. 1983). Very useful as concep-

tual model that outlines general trends in ecophysiological and ecological traits, the functional-group classification (as the SA/V ratio) seems less useful as a predictive model with regards to physiological differences among opportunistic species that form macroalgal blooms.

We conclude that the overwhelming dominance of *P. littoralis* over *E. intestinalis* in the field cannot be explained by interspecific physiological differences. Although strongly reactive to high nutrient loads, bloom-forming macroalgae cannot be viewed as simple growth machines and are subject to complex ecological constraints. Lotze et al. (2000) showed that population dynamics and species distribution of *Enteromorpha* and *Pilayella* in the field were strongly controlled by different overwintering and recruitment strategies, as well as by selective herbivory. Both species suffer from high losses to grazing, but, as long as *Enteromorpha* is present, this species is preferred by herbivores which indirectly favors *Pilayella* (Lotze and Worm 2000). Nutrient enrichment in the field favors both algae in a similar fashion, with *Pilayella* dominating if grazers are present and *Enteromorpha* dominating if grazers are absent (Worm et al. 2000). Clearly, factors other than ecophysiological traits are indicated to explain and predict species distribution and dominance patterns in macroalgal blooms.

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