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NOTE

Rapid direct and indirect effects of a single nutrient pulse in a seaweed-epiphyte-grazer system

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ABSTRACT: In the Baltic Sea, we tested how short nutrient pulses of different lengths and frequencies affect macroalgae, epiphytes, grazers and their interactions. We hypothesized that even small-scale variations in nutrient supply may have significant impacts by favoring fast-growing epiphytes which can cause large-scale declines of canopy-forming macroalgae. In a factorial field experiment single plants of the canopy-forming macroalga *Fucus vesiculosus* with and without epiphytes were exposed to pulses of elevated nutrients (N and P) over 25 d. Five 1 h pulses given every 5 d had no significant effects. A single 5 h pulse increased the epiphyte load but not *F. vesiculosus* growth rate. In contrast, increasing epiphyte load caused *F. vesiculosus* growth rate to decline and attracted higher densities of gastropod grazers. These results indicate that a single nutrient pulse can have rapid direct and indirect effects on macroalgae and their associated epiphytes and grazers. Temporal variability of nutrient supply (five 1 h vs one 5 h pulse) plays a significant role in determining the response of primary producers and consumers to elevated nutrients.

KEY WORDS: Competition · Grazing · Eutrophication · Nutrient supply · Bottom-up control · Macroalgae · *Fucus vesiculosus*

Nutrient supply is an important variable that regulates primary productivity and species composition in aquatic ecosystems (Hecky & Kilham 1988, Pedersen & Borum 1996, Worm et al. 2000). Under most conditions, nutrient supply is spatially and temporally variable and occurs in irregular pulses. Such pulses are generated on small spatial scales by animal excretion (Lehmann & Scavia 1982, Reusch et al. 1994), on intermediate scales by leaching of sediment porewater or mineralization of decomposing organisms (Hanisak 1993), and on large scales by land run-off and wind-induced mixing and upwelling (Pedersen et al. 1995, Kiirikki & Blomster 1996, Schaffelke & Klumpp 1998). In addition to pulse scale and frequency, pulse concentrations can be extremely variable, ranging for example from <1 to 1500 µmol l^{-1} for dissolved inorganic nitrogen (DIN) (Lehmann & Scavia 1982, Hanisak 1993, Jürgensen 1995, Schramm et al. 1996). Primary producers have evolved different strategies to exploit heterogeneity in nutrient supply. Microalgae and filamentous macroalgae have a relatively high surface area to volume ratio that results in rapid nutrient uptake and fast growth (Rosenberg & Ramus 1984, Hein et al. 1995), but low nutrient storage capacity (2 to 8 d for filamentous algae; Fujita 1985, Pedersen & Borum 1996). Perennial, canopy-forming macroalgae have thick, corticated thalli, and low surface area to volume ratios. They have slower nutrient uptake and growth rates (Wallentinus 1984, Pedersen & Borum 1996) but higher nutrient storage capacities compared with phytoplankton and filamentous algae (weeks to several months; Chapman & Craigie 1977, Pedersen & Borum 1996). These physiological differences may translate into variable responses to nutrient pulses of different duration and frequency (Rosenberg et al. 1984).

Most work on the effects of nutrient pulses has focused on phytoplankton assemblages (Lehmann & Scavia 1982, Sommer 1985) or single species of macroalgae (Rosenberg et al. 1984, Lapointe 1985, Schaffelke & Klumpp 1998). Here, we were interested in how small-scale variations in pulse duration and frequency affect competition between perennial algae and their filamentous epiphytes, and whether the effects of short nutrient pulses are transmitted to higher trophic levels. Competition for light and nutrients may be particularly intense between filamentous algal epiphytes and their hosts. Work in seagrass meadows has shown that increased nutrient supply can increase epiphyte loads with negative conse-

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quences for the host plant (Sand-Jensen 1977). On the other hand, most grazers prefer to feed on the epiphytes and may increase in abundance when food supply increases (Worm et al. 2000). Increased grazing pressure may thereby counteract nutrient effects on epiphyte growth (Neckles et al. 1993, Williams & Ruckelshaus 1993). Here, we focus on the perennial brown alga *Fucus vesiculosus* (*Fucus* hereafter) and its filamentous epiphytes. In the Baltic Sea *Fucus* used to dominate hard substrata from 0 to >10 m depth, but has declined by 50 to 95% over the last decades, depending on the region considered (reviewed by Schramm 1996). This severely altered the associated food web and decreased the ability of the coastal ecosystem to retain carbon, nitrogen and phosphorus (Worm et al. 2000). Using field experiments and surveys, the decline of *Fucus* in the Baltic has been linked to nutrient overloading causing increased competition from filamentous and foliose annual algae (Worm et al. 1999, 2000) and phytoplankton (Kautsky et al. 1986). The role of temporal variability in nutrient supply, however, is not clear. Here we tested the hypotheses that (1) small-scale nutrient pulses affect epiphyte cover depending on pulse duration and frequency, (2) effects of nutrient pulses on *Fucus* depend on the cover of epiphytes, and (3) as a feedback, grazer densities may increase with increased epiphyte cover.

Methods. A factorial field experiment was conducted in a sheltered embayment at Maasholm, at the mouth of Schlei Fjord, Western Baltic Sea, Germany (54° 41′ N, 10° 00′ E). A detailed site description is given by Worm et al. (2000). The experiment lasted for 25 d from 22 May to 15 June 1997. *Fucus* individuals with 2 different levels of epiphytes (epiphytes removed every 5 d, no epiphyte removal) were exposed to 3 different nutrient pulse levels (no pulses, five 1 h pulses, one 5 h pulse over a 25 d period). Individuals assigned to 1 h nutrient pulses were treated on Days 2, 7, 12, 17, and 22; individuals that were assigned to 5 h pulses were treated once on Day 12. Six replicates were used for each of the 6 treatments. While pulse frequency and duration were manipulated, pulse concentration was constant at 200 µmol l^{-1} nitrate and 15 µmol l^{-1} phosphate added to ambient seawater. Average background concentrations at this site in May are <10 µmol l^{-1} DIN, <1 µmol l^{-1} DIP (Worm et al. 2000), but irregular nutrient pulses can occur through wind-induced mixing with water masses from the hypertrophic inner fjord (Schramm et al. 1996). *F. vesiculosus* individuals were collected from 3 different stands of 1 yr old specimens (25 to 35 cm length). The algae with attached small pieces of substratum were chiseled from the rocks. All individuals had significant epiphyte loads, typical for the time of year (filamentous brown *Pilayella littoralis* and *Elachista fucicola*). In the laboratory, epiphytes were cut back with scissors to 3–5 mm length in order to standardize initial epiphyte load among replicates and to estimate *Fucus* wet mass (WM). WM was estimated to the nearest mg after carefully blotting individuals and attached rocks for 10 s between 2 pieces of paper tissue. All *Fucus* were fastened on six 1 × 1 m PVC grids with attached plastic clothes pins. Clothes pins were numbered and treatments were assigned to individual algae using random number tables. One replicate of each treatment was assigned to each grid. Grids were submerged at 0.8 m water depth and anchored with steel rods. Individual grids were separated by 2 m; *Fucus* individuals on a grid were separated by 35 to 50 cm.

All grids were retrieved at Days 2, 7, 12, 17 and 22 of the experiment and half of the *Fucus* individuals were manually cleaned of epiphytes. Only 1 individual was damaged and excluded from further analysis. Individuals that were assigned to a particular nutrient pulse treatment were placed in a large tub, filled with 30 l freshly collected seawater, enriched with 200 µmol l^{-1} $NaNO_3$ and 15 µmol l^{-1} NaH_2PO_4. The tub was placed at the beach close to the experiment at natural irradiance levels. The water was exchanged and newly enriched with a concentrated stock solution every 20 min in order to keep pulse concentration approximately constant. Individuals that were not assigned to pulses were handled in a similar manner and placed in shallow water at similar irradiance levels as the pulsed plants (procedural control).

After 25 d, all *Fucus* individuals were collected with mesh bags (500 µm mesh) in order to catch all associated mesograzers. In 2 cases, grazers escaped from the mesh bags during sampling; these individuals were excluded from analysis of grazer densities. In the laboratory, grazers were counted, epiphytes were removed, and *Fucus* was blotted dry for 10 s before determining WM. Rocks were removed from all individuals and weighed. Epiphytes and *Fucus* individuals were dried separately at 80°C for 48 h and dry mass (DM) was measured to the nearest mg.

We correlated *Fucus* WM and DM with a linear regression model (DM = 1.1369 + 0.149 WM, $r^2 = 0.89$, $p < 0.0001$). Using this model, *Fucus* initial WM was transformed into DM. We estimated *Fucus* relative growth rate as RGR = $(\ln M_2 - \ln M_2)/(t_2 - t_1)$, with M = DM of *Fucus* (g) and t = time (d). Data were analyzed by 2-way fixed-factor ANOVA with nutrient pulsing and epiphytes as independent variables and *Fucus* RGR as the dependent variable. Epiphyte DM data were normalized to the DM of *Fucus* and analyzed by 1-way ANOVA with nutrient pulsing as the independent variable. Grazer data were also normalized to the mass of *Fucus* and analyzed separately for treatments with and without epiphytes by 1-way

ANOVA with nutrient pulsing as the independent variable. Separate analyses were performed for grazer data from individuals with epiphytes present and removed, because epiphyte removal probably also reduced grazer densities precluding direct comparison of these treatments. A Student-Newman-Keuls test (SNK) was used for post-hoc comparisons. All data were log-transformed in order to fulfill the assumption of homogeneous variances tested by Cochran's test. In a subsequent analysis, we used linear regression models to test for correlations among (1) epiphyte load and grazer densities and (2) epiphyte load and growth rates of *Fucus* individuals.

Results. The mean growth rate of *Fucus* individuals in the experiment was 0.016 ± 0.006 d^{-1} (mean ± 1 SE, n = 35). Growth rates were not significantly affected by epiphyte removal (ANOVA, $F_{1,29}$ = 0.14, p = 0.71) or nutrient pulsing ($F_{2,29}$ = 1.32, p = 0.28), but there was an insignificant trend towards interactive effects between these 2 factors (Pulse × Epiphytes, $F_{2,29}$ = 2.81, p = 0.0766). This trend may indicate that nutrient pulsing increased the growth rate of *Fucus* in the absence of epiphytes (Fig. 1A) but decreased growth rates in the presence of epiphytes (Fig. 1B).

Epiphyte biomass ranged from 0.2 to 7.4% of the *Fucus* biomass at the end of the experiment (mean 3.1 ± 0.5% SE). Epiphyte species composition did not change over the course of the experiment (i.e. ca 70% *Pilayella littoralis* and ca 30% *Elachista fucicola*). Microscopic examinations revealed that both species were fouled by benthic diatoms (mostly *Tabularia fasciculata*). Nutrient pulses increased epiphyte biomass (Fig. 2A, ANOVA, $F_{2,15}$ = 4.25, p = 0.0344). However, repeated 1 h pulses increased epiphyte biomass only by 31% (not significant: SNK, p > 0.05), while a single 5 h pulse significantly increased epiphyte biomass by 153% compared with controls (SNK, p < 0.05).

The grazer fauna (Table 1) was dominated by small snails (*Littorina saxatilis* 44% of total, *Hydrobia ulvae* 48%) as compared to crustacean mesograzers (*Idotea* spp. 6%, *Gammarus* spp. 2%). Grazer densities ranged from 9 to 118 ind. $plant^{-1}$ (mean 40.2 ± 5.3) or 3 to 22 ind. g^{-1} *Fucus* DM (mean 8.6 ± 0.9). Following the increase in epiphyte biomass, grazers occurred at significantly higher densities on nutrient-enriched *Fucus* individuals (Fig. 2C, ANOVA, $F_{2,13}$ = 4.74, p = 0.0284). The differences between controls and 1 h pulse treatments were not significant (SNK, p > 0.05), while the 62% increase in grazer density in the 5 h pulse treatments was significant (SNK, p < 0.05). There was no effect of nutrient pulsing on grazer densities in treatments without epiphytes (Fig. 2B, ANOVA, $F_{2,15}$ = 2.91, p = 0.0856), but this could also be an artifact of the epiphyte removal procedure.

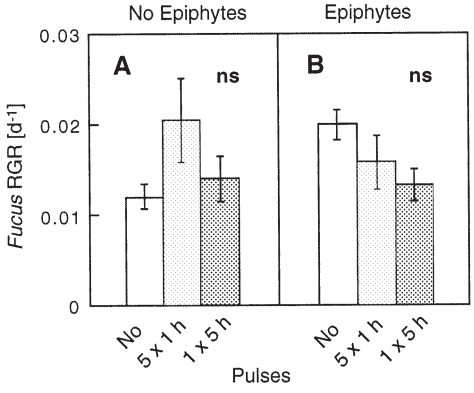

Fig. 1. Effects of nutrient pulsing (frequency × duration) and epiphyte removal on the relative growth rate (RGR) of *Fucus vesiculosus* in the experiment. Data are means ± 1 SE (n = 6). See 'Results' for ANOVA results (ns = not significant)

There was a positive linear relationship between epiphyte load and grazer density ($y = 6.2 + 129.9x$, r^2 = 0.28, p = 0.0354) and a negative relationship between epiphyte load and *Fucus* growth rate ($y = 0.02 - 0.130x$, r^2 = 0.26, p = 0.0371) in treatments with epiphytes present (Fig. 3).

Discussion. These results suggest that a single nutrient pulse can have pronounced direct and indirect effects on macroalgae, epiphytes and grazers during the spring epiphyte bloom when epiphyte loads on *Fucus* in the Western Baltic typically reach their annual maximum (Lotze et al. 2000). Throughout this

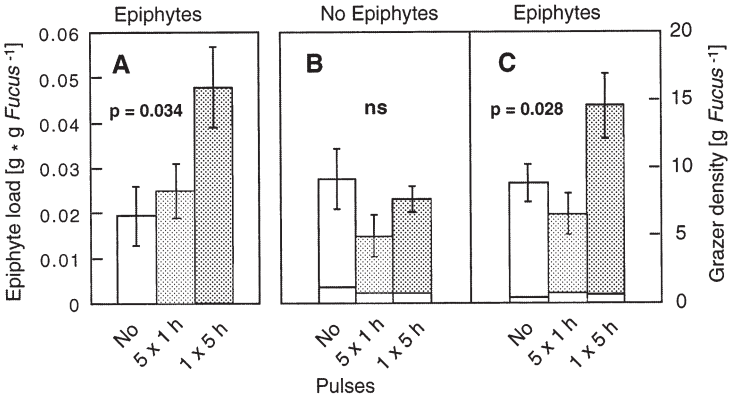

Fig. 2. Effects of nutrient pulsing on (A) epiphyte load on *Fucus vesiculosus* (*Pilayella littoralis*, *Elachista fucicola*), (B) grazer densitiy on *F. vesiculosus* in treatments without epiphytes, and (C) grazer density in treatments with epiphytes. Data are normalized to the dry mass of the *F. vesiculosus* host individual. Bars represent means ± 1 SE (n = 6). p-values are derived from 1-way ANOVA models (see 'Results' for details). Horizontal lines in grazer density columns indicate the relative proportions of gastropods (upper part of column) and crustaceans (lower part of column)

Table 1. Grazer densities on *Fucus vesiculosus* (ind. g^{-1} *F. vesiculosus* DM) in treatments with and without epiphytes (n = 18). *Idotea* spp. were *I. chelipes* and *I. baltica*; *Gammarus* spp. were *G. salinus* and *G. oceanicus*

Species	No epiphytes		Epiphytes	
	Mean	± SE	Mean	± SE
Littorina saxatilis	3.49	0.53	4.10	0.73
Hydrobia ulvae	2.90	0.52	5.51	0.92
Littorina littorea	0	0	0.02	0.02
Idotea spp.	0.54	0.11	0.49	0.10
Gammarus spp.	0.24	0.08	0.12	0.05
Jaera albifrons	0.09	0.06	0	0
Total	7.25	0.99	10.25	1.37

period, grazer densities increase and nutrient concentrations decline rapidly towards low summer values (<0.5 µmol l^{-1} DIN and phosphorus, Worm et al. 2000). Work in pelagic food webs has shown that intense grazing and increasing nutrient limitation regulate the abundance of phytoplankton under these conditions (Sommer et al. 1986). We examined whether variations in nutrient supply had effects on the abundance of filamentous epiphytes, and whether this triggered responses in grazers and the perennial host plants. Nutrient pulses such as those simulated in the experiment are common in eutrophic coastal systems. At the study site, irregular nitrate pulses (70 to 160 µmol l^{-1}) can occur on a time scale of hours to days between February and May through wind-driven transport of hypertrophic waters from the inner Schlei Fjord (Schramm et al. 1996). On similar time scales, wind-driven mixing or upwelling of deep water increased total N 10-fold in a Danish fjord (Pedersen et al. 1995) and caused mass occurrences of filamentous epiphytes along the Finnish southwest coast (Kiirikki & Blomster 1996).

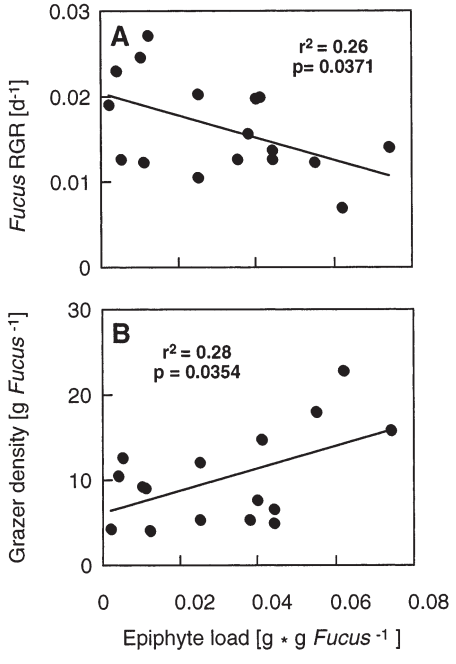

Fig. 3. Linear relationships between epiphyte load and (A) *Fucus vesiculosus* growth rate and (B) total grazer densitiy in the experiment. Epiphyte and grazer data are normalized to the dry mass of the *F. vesiculosus* host individual

In our experiment, a single 5 h nutrient pulse increased growth of epiphytes, which led to increased grazers densities. In contrast, five 1 h pulses had no significant effects. Although nutrient uptake occurs on a time scale of minutes (Thomas & Harrison 1987, Lotze & Schramm 2000), longer exposure to a nutrient pulse may be necessary to elevate internal nutrient pools to a critical level which is needed to sustain a significant growth response (Fujita et al. 1989, Pedersen & Borum 1996). In 2 other nutrient pulsing experiments, increases in pulse frequency had positive effects on algal growth rates, but pulse duration was always 6 h (Lapointe 1985, Pickering et al. 1993) and increases in frequency were confounded with increases in total nutrient input. Our results indicate that pulse duration is a key factor that can be more important than pulse frequency on a time scale of hours.

Manipulations of epiphyte densities allowed us to test for direct effects of nutrient pulses on *Fucus* as well as indirect effects through increased epiphyte cover. We did not detect a significant direct effect on *Fucus* growth rate (Fig. 1A). This could indicate the lack of nutrient limitation of *Fucus* in spring because of significant nitrogen storage in winter and spring (Pedersen & Borum 1996). However, a statistically insignificant trend (p = 0.076) indicated that nutrient pulsing tended to decrease growth of *Fucus* in the presence of epiphytes (Fig. 1). This most likely represents an indirect effect which is mediated through increased competition from epiphytes. Indeed, 5 h nutrient pulses increased epiphyte load (Fig. 2) and high epiphyte load decreased *Fucus* growth rate by up to 50% (Fig. 3). Extrapolation of the regression line in Fig. 3 suggests that *Fucus* growth rate approaches zero when epiphyte load exceeds 0.15 g per g *Fucus*, a value which is often exceeded in the study area (Schramm et al. 1996). Although deleterious effects of epiphytes on macrophytes have been demonstrated before (Sand-Jensen 1977, Neckles et al. 1993), this is the first evidence that single pulses on a scale of hours can affect epiphyte-macrophyte competition. However, the relative roles of light and nutrient competition have yet to be revealed.

In seagrass communities, grazers limit epiphyte biomass and can thereby mediate competition between epiphytes and seagrass (Neckles et al. 1993, Williams & Ruckelshaus 1993). In this experiment, however,

grazer density correlated positively with epiphyte biomass (Fig. 3) and increased significantly with nutrient enrichment. This indicates prevailing bottom-up effects from nutrients to epiphytes to grazers on the temporal and spatial scale of this experiment. A significant top-down feedback through increased grazing pressure was not detected but may occur on longer time scales or later in the season when epiphytes become increasingly nutrient limited. Increases in grazer densities with increasing nutrient supply have also been indicated on a large spatial scale by comparisons across entire coastlines (Bustamante et al. 1995, Menge et al. 1997) and by a long-term enrichment experiment (Worm et al. 2000). This study suggests that similar patterns can be found at very small temporal and spatial scales such as single plants subjected to single pulses of elevated nutrients.

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