Journal of Sea Research 45 (2001) 95–103

Reversal of density dependence of juvenile Littorina littorea (Gastropoda) growth in response to periphyton nutrient status

Ulrich Sommer

Institut für Meereskunde Düsternbrooker Weg 20 24105 Kiel
Germany

Received 5 September 2000;accepted 23 November 2000

Abstract

Experimental periphyton communities were grown in aquaria receiving media of differently enriched seawater (fully enriched, without Si enrichment, without N and P enrichment) and supplied differently with medium (batch and weekly replacement). Periphyton was subject to grazing by 1–6 individuals of juvenile Littorina littorea. Periphyton biomass was higher in the replacement aquaria than in the batch aquaria and higher in the full and the –Si medium than in the –NP medium. The N:C ratio of the periphyton increased with Littorina number in the batch aquaria and was unaffected by Littorina number in the replacement aquaria. Diatoms were most dominant in the –NP treatments and rarest in the –Si treatments. Chlorophytes were dominant in the –Si and the fully enriched treatments, but also Cyanobacteria contributed significantly to periphyton biomass in those treatments under nutrient replacement. Somatic growth of Littorina was negatively correlated to Littorina density in the replacement aquaria and positively density dependent in the batch aquaria. The latter is explained by improved food quality under stronger grazing pressure.

KeYwords: Herbivory; Littorina;Periphyton; Food quality; Benthos

1. Introduction

During the last decade, it has become increasingly clear that the growth and reproduction of herbivorous animals might not only be limited by the total amount or energy content of their food but also by its chemical composition (Muller-Navarra and Lampert, 1996). Essential organic constituents, particularly highly unsaturated fatty acids (Brett and Muller-Navarra, 1997;Mu ller-Navarra et al., 2000) and mineral nutrients, particularly nitrogen and phosphorous (Hessen, 1992;Urabe and Watanabe, 1992;Sterner, 1993) have received attention. In some cases, correlations between the content of mineral nutrients and essential organic constituents make the distinction between the two types of 'food quality limitation' difficult (Muller-Navarra, 1995;Sterner and Schulz, 1998). In the case of unicellular algae, mineral nutrient content of biomass is closely related to the extent of algal nutrient limitation (Droop, 1973, 1985). Micro-algal nutrient status can be co-determined by grazing because of animal nutrient excretion and because less algae can share the same supply of mineral nutrients if grazing reduces biomass (Sterner, 1989, 1990). The resulting negative correlation between grazing and nutrient limitation could lead to an improved food quality at higher grazing pressure. If food quality limitation limits herbivore growth, the traditional view of a negative relationship between population densities and growth rates would be turned upside down. More grazers would reduce the amount of food but improve its nutritional quality. This

Email address: usommer@ifm.uni-kiel.de (U. Sommer).

reversal of density dependence has been shown by continuous culture experiments with the freshwater zooplankter ap nia ealeata and the P-limited planktonic green alga cenedes'1'ts acttts (Sommer, 1992) as food organism. A reversal of density-dependent regulation would require substantial changes in tradi- tional models of population interactions, which frequently rest on the assumption of negative density dependence.

Here, I present laboratory experiments with juveniles of the common periwinkle (Littorina littorea) and Baltic Sea periphyton which show a reversal of density dependence induced by nutrient limitation of periphyton. Littorina littorea is an important herbivore on Northern European and American coasts, feeding on a wide array of benthic food items. If given a choice, they prefer periphytic microalgae, filamentous macroalgae or microscopic germlings of macroalgae over leathery macroalgae (Lubchenco, 1978;Steneck and Watling, 1982;Worm et al., 1999;Lotze et al., 2000). There is no pronounced selectivity in periphyton feeding, except for some relative protection of algae attached tightly to the substratum and gelatinous algae (Sommer, 1999a,b).

2. Material and methods

The experiments were performed in 36 aquaria with a bottom area of 1.5 dm^2 and a volume of 2.3 dm^3. The bottom of each aquarium was covered by 28 sandstone tiles (of 5.29 cm^2 each), which could be removed individually for subsampling. The aquaria were filled with 1.5 dm^3 growth medium. Periphyton for the experiments was obtained by incubating rough, transparent plastic sheets at ca. 1 m depth in Kiel Fjord (western Baltic Sea) from 3 May to 11 June 1999. After incubation, periphyton was scratched from the plastic sheets, suspended in 250 cm^3 sterile seawater, mixed well and distributed equally to the 36 aquaria. The algae were permitted to settle and start growth on the tiles until 22 June. Then juvenile Littorina individuals (1.8–2.3 mm shell height) were placed in the aquaria. Those snails had been kept under abundant food supply in an aquarium for two months before the start of the experiment. Every four weeks, one randomly selected tile was removed for sampling and replaced by a fresh one. The experiment was terminated after 16 weeks. The day-light cycle was 14:10 hrs;photon flux density was ca. 40 J.E cm^{-2} s^{-1};the experimental temperature was 15°C.

The experimental treatments differed in the number of snails (6 levels from 1 to 6 individuals per aquarium), the composition of the medium (3 levels; full, -Si, -NP) and the supply mode of the medium (replacement of 2/3 each week;no replacement). There was a fully factorial combination of all treatments. The full medium consisted of filtered (0.2 J.m) Baltic Sea water enriched with 20 J.M Si, 15 J.M N (supplied as NH_4NO_3), and 2 J.M P. The -Si medium contained no Si enrichment and the -NP medium contained no enrichment with N and P. The background concentrations in the filtered seawater were variable, but always <10% of the enrichments. The two supply modes were intended to contrast scenarios where nutrient supply to the algae was dominated by external sources (replacement) and by excretion by snails (no replacement = batch).

Periphyton was scratched from the sample tiles and suspended in filtered seawater in order to be split into subsamples for the analysis of particulate C, N, P, and cell counts. Chemical analysis was performed on periphyton filtered onto precombusted glass fiber filters. Particulate C and N were analysed in a CN analyser (Fisons NA 1500 N), particulate P was measured according to oceanographic standard methods (Grasshoff, 1976) in an autoanalyser after muffling the filters at 545°C and dissolving the ash in H_2S0_4. Subsamples for cell counts were treated like plankton samples and counted under the inverted microscope (Utermohl, 1958). At least 400 individuals were counted, which gives 95% confidence limit of ±10% for the estimated cell number (Lund et al., 1958). Taxonomic identification was performed according to Pankow (1990). Cell volumes were calculated according to the geometric formulae suggested by Hillebrand et al. (1999) after measurements of 20 individuals per taxon.

Littorina growth was measured as per capita gain of soft-body organic substance (ash-free dry mass = AFDM) during the experiment (16 weeks). AFDM for the end point of the experiments

Table 1
AN0VAs of response variables with medium composition (M) and supply mode (S) as categorial factors and Littorina number as quantitative factor. Response variables: periphyton biomass [ln (J.g C cm^{-2})], periphyton N:C ratio [ln (mol N/mol C)], relative biomass of higher taxa [arcsine$(B_i/B_{tot})^{-1/2}$], Littorina growth [mg AFDM/ind];significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ****$p < 0.0001$

Dependent variable	Significant main effects (F-ratio, significance)	Significant interactions (F-ratio, significance)
Biomass	M (12.75****) S (84.4****) L (238.5****)	M X S (6.5**)
N:C	M (35.1****) S (159.7****) L (22.2****)	M X S (4.6*) S X L (25.6****)
Diatoms	M (1226****) S (9.7**)	M X S (9.6**)
Green algae	M (476****) S (64.0****)	M X S (19.3****)
Cyanobacteria	M (6.1**) S (6.3*) L (5.6*)	M X S (7.1**)
Littorina growth	M (9.3**) S (66.4****)	M X S (5.9**) S X L (17.9***)

was measured directly while start values were estimated from a shell height (mm)-mass (mg) regression:

$$AFDM = 0.05525H^{2.96};$$

$$r^2 = 0.72;\ d.f. = 35;\ p < 0.00001$$

This regression had been obtained with Littorina individuals from the same source as the experiments.

The experimental results were first analysed by a multifactor AN0VA (general linear models, Stagraphics) with three independent variables: medium composition and supply mode as categorial factors and Littorina number as quantitative factor (Table 1). The number of cases entered in each AN0VA was 36. Mean values over the entire duration of the experiment were chosen for the periphyton parameters, because the calculation of Littorina growth refers to the same period. The response of dependent variables (periphyton C, perphyton N:C ratio, Littorina growth) to Littorina number was then analysed by individual

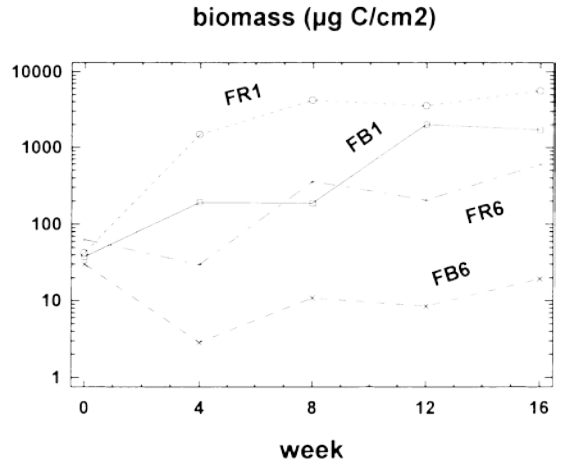

Fig. 1. Time course of periphyton biomass (P0C) in the full medium;FB1: full medium, batch, 1 Littorina;FB6: full medium, batch, 6 Littorina;FR1: full medium, replacement, 1 Littorina;FR6: full medium, replacement, 6 Littorina.

regression analysis for each combination of medium composition and supply mode.

3. Results

3 Perip Yton nio'1'ass and stoic io'1'etrY

Already after four weeks a clear response of periphyton biomass measured as P0C to the different treatments could be observed. Those differences were maintained throughout the entire duration of the experiment (Figs 1-3). In the AN0VA, biomass showed a significant response to medium composition, supply mode and Littorina densities (Table 1). Interaction effects between medium composition and supply mode were also significant. Biomass levels were lower in the batch than in the replacement treatments and lower in the -NP treatments than in the other two nutrient treatments which formed a homogeneous group according to Scheffe's multiple range test. Log biomass declined linearly with Littorina density (Table 2).

The relationship between particulate P and particulate N was examined by a regression analysis according to the model

$$N = aP^n$$

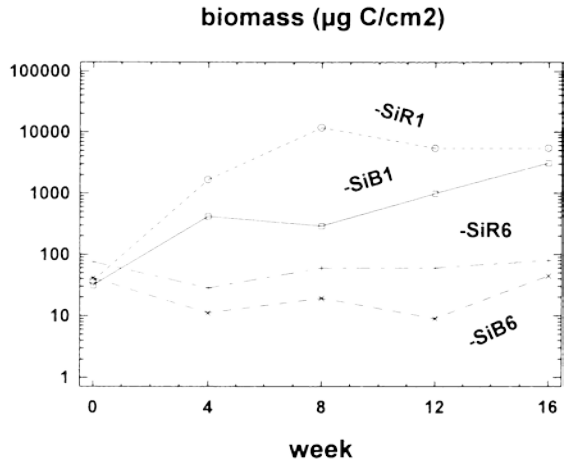

Fig. 2. Time course of periphyton biomass (P0C) in the medium without Si-enrichment;-SiB1: without Si, batch, 1 Littorina; -SiB6: without Si, batch, 6 Littorina;-SiR1: without Si, replacement, 1 Littorina;-SiR6: without Si, replacement, 6 Littorina.

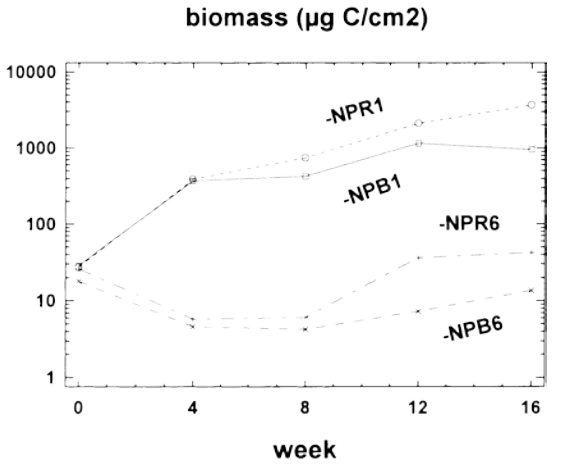

Fig. 3. Time course of periphyton biomass (P0C) in the medium without N- and P enrichment;-NPB1: without N and P, batch, 1 Littorina;-NP6: without N and B, batch, 6 Littorina;-NPR1: without N and P, replacement, 1 Littorina;-NPR6: without N and B, replacement, 6 Littorina.

which showed an almost linear relationship (Table 3). At exponents close to 1, parameter a is an estimate of the N:P ratio in algal biomass. This was clearly below the Redfield-ratio (16:1), indicating that N rather than P was the potentially limiting nutrient (Hillebrand and Sommer, 1999). Therefore, and because of the close and linear relationship between N and P, only the N:C ratios will be analysed as indicators of algal nutrient status. They were significantly influenced by all experimental factors (Table 4, Fig. 4). Biomass N content was higher under medium replacement than under batch conditions and lower in the -NP medium than in the other two media (Scheffe's multiple range test). In the batch experiments N:C increased with Littorina density but it was not significantly influenced by Littorina density under nutrient replacement (Table 4).

Table 2
Linear regressions of periphyton biomass (ln J.g C cm^{-2}) on Littorina number per vessel, for treatment codes see text and legend of Fig. 4

Treatment	a ± SE	n ± SE	r^2	p
FR	8.29 ± 0.59	−0.53 ± 0.15	0.75	0.0260
-SiR	9.04 ± 0.40	−0.82 ± 0.10	0.94	0.0013
-NPR	7.70 ± 0.40	−0.82 ± 0.10	0.94	0.0013
FB	7.06 ± 0.58	−0.83 ± 0.15	0.88	0.0052
-SiB	7.12 ± 0.51	−0.73 ± 0.13	0.89	0.0051
-NPB	7.16 ± 0.23	−0.89 ± 0.06	0.98	0.0001

3 Perip Yton taxono'1'ic co'1'position

Throughout the experiment, the bulk of algal biomass was composed of three higher taxa, Bacillariophyceae (diatoms), Chlorophyta (green algae) and Cyanobacteria (blue-green algae), while other groups were negligible. Medium composition exerted the greatest influence, while supply mode had a significant influence only in some cases (Table 1). Littorina density was not an important factor in determining higher level taxonomic composition. Diatoms were dominant in the -NP treatments, contributed less to total biomass in the F treatments, and still less in the -Si treatments (Fig. 5). Green algae (mainly Entero'1'orpa intestinalis, Cladophora pYe'1'aea,

Table 3
Regression of particulate N on particulate P (both molar) according to the model $N = aP^n$

Time (weeks)	a ± SE	n ± SE	r^2	p
4	8.33 ± 1.95	0.95 ± 0.05	0.90	< 0.00001
8	9.49 ± 2.10	1.00 ± 0.05	0.92	< 0.00001
12	7.97 ± 1.52	0.94 ± 0.05	0.91	< 0.00001
16	7.88 ± 1.06	0.92 ± 0.04	0.94	< 0.00001

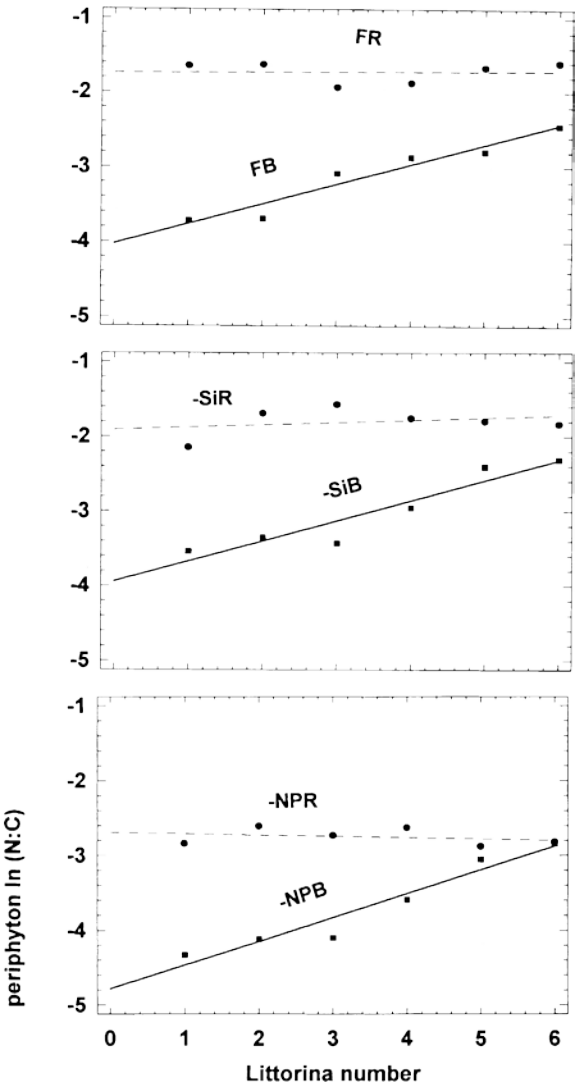

Fig. 4. Periphyton N:C ratio (log transformed) in response to Littorina density. F: full enrichment;-Si: enrichment without Si;-NP: enrichment without N and P;B: batch;R: replacement.

Table 4
Linear regressions of log^e periphyton N:C ratio on Littorina number per vessel

Treatment	a ± SE	n ± SE	r^2	p
FR	−1.74 ± 0.16	−0.005 ± 0.038	0.005	0.896
-SiR	−1.92 ± 0.19	0.03 ± 0.5	0.09	0.564
-NPR	−2.60 ± 0.11	0.02 ± 0.03	0.09	0.559
FB	−4.03 ± 0.13	0.27 ± 0.03	0.94	0.0014
-SiB	−3.95 ± 0.18	0.27 ± 0.05	0.89	0.0045
-NPB	−4.78 ± 0.16	0.32 ± 0.04	0.94	0.0015

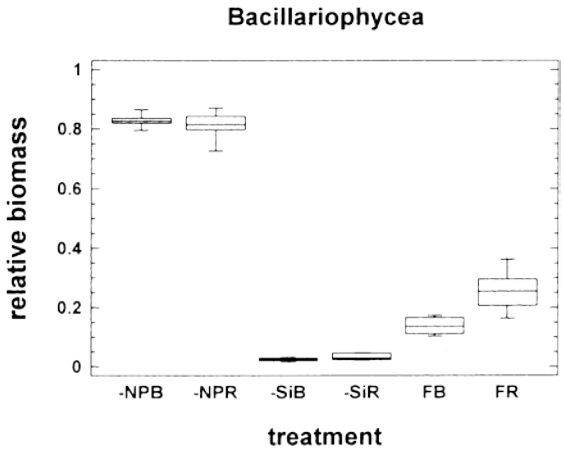

Fig. 5. Relative biomass (taxon biomass/total biomass) of Bacillariophyceae in response to nutrient treatments, box-and-whisker plots showing medians, quartiles and full range of data;F: full enrichment;-Si: enrichment without Si;-NP: enrichment without N and P;B: batch; R: replacement.

lot rix i'1'plexa, and unidentified flagellates/zoospores) and Cyanobacteria (mainly Ananaena naltica) performed best in the -Si medium, second best in the full medium and worst in the -NP medium (Figs 6 and 7). Medium replacement favoured Cyanobacteria while the batch supply mode favoured the green algae. Individual species responded to the different media in the same way as the higher taxa to which they belonged. However, there were some differences in the response of diatom species/genera to the supply mode. A positive response to medium replacement was found in Fraeilaria tantlata, Ac nant es lone ipes, A'1'p ora co aei or'1'is, and tatroneis con stricta. A negative response to medium replacement was found in unidentified, small centric diatoms, BerseleYa (= A'1'p ipletra) rttilans, and Nitzsc ia spp. elosira '1'onili or'1'is responded neutrally to the supply mode.

3 3 Littorina erowt

The gain of ash-free dry mass responded significantly to the medium composition and the supply mode (Table 1). Littorina density did not show up as a significant main effect, but there was a significant interaction between Littorina density and supply mode. Although individual regressions of Littorina growth on Littorina number were insignificant in

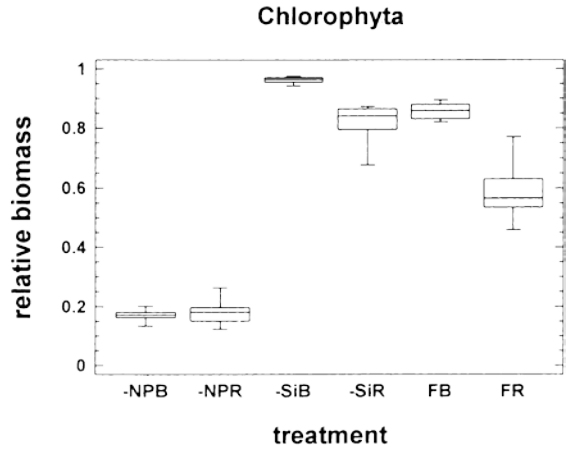

Fig. 6. Relative biomass (taxon biomass/total biomass) of Chlorophyta in response to nutrient treatments, box-and-whisker plots showing median, quartiles and full range of data;F: full enrichment; -Si: enrichment without Si;-NP: enrichment without N and P; B: batch;R: replacement.

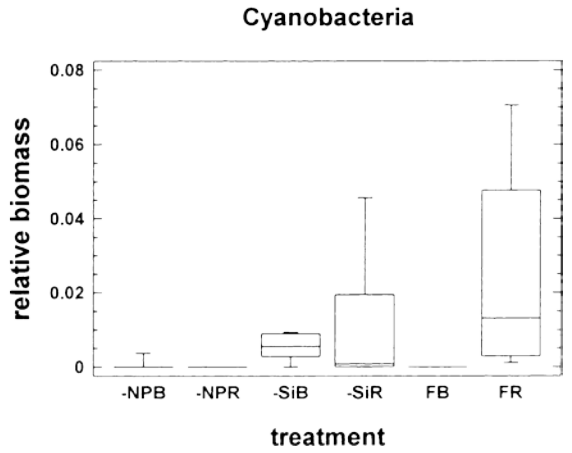

Fig. 7. Relative biomass (taxon biomass/total biomass) of Cyanobacteria in response to nutrient treatments, box-and-whisker plots showing median, quartiles, and full range of data;F: full enrichment;-Si: enrichment without Si;-NP: enrichment without N and P;B: batch;R: replacement.

most cases a consistent contrast in the sign of the regression coefficient between the different nutrient supply modes could be found (Table 5). The regression lines for the replacement and the batch mode were significantly different from each other. In the batch experiments, Littorina growth responded positively to density while it responded negatively under nutrient replacement (Fig. 8).

4. Discussion

The N:C stoichiometry of periphyton biomass spans one order of magnitude from 0.01 to 0.21. The lowest margin is ca. one half of the minimum value (0.022) reported by Hillebrand and Sommer (1999) from a growth experiment in the western Baltic Sea and indicates severe nitrogen limitation of growth. In their study, a C:N:P ratio of 119:17:1 was found to indicate optimal growth, which is remarkably similar to the analogous Redfield-ratio for phytoplankton (106:16:1;Goldman et al., 1979). Due to the scatter of data, Hillebrand and Sommer (1999) have suggested N:C < 0.1 as 'safe' indication of N limitation, provided that N:P < 13. Using this criterion, periphyton growth has to be considered N saturated in the full and the -Si media under the replacement supply mode and N limited in the other treatments, including the possibility of Si limitation of diatoms. The absence of a response of algal N:C to Littorina density under medium replacement indicates, that external nutrient supply was sufficient to

Table 5
Linear regressions of Littorina growth (in mg AFDM ind^{-1}) on Littorina number;probabilities of error: p_{ind}: for individual regression; p_a: for comparison of intercepts; p_b: for comparison of slopes

Treatment	a ± SE	n ± SE	r^2	p_{ind}	p_a	p_b
FR	2.41 ± 0.46	−0.16 ± 0.12	0.31	0.896	0.0059	0.0041
FB	0.06 ± 0.17	0.09 ± 0.04	0.52	0.107		
SiR	2.95 ± 0.33	−0.33 ± 0.175	0.48	0.126	0.0046	0.0476
-SiB	0.36 ± 0.17	0.08 ± 0.04	0.47	0.131		
-NPR	1.34 ± 0.26	−0.15 ± 0.07	0.56	0.087	< 0.0001	0.0825
-NPB	−0.08 ± 0.09	0.13 ± 0.02	0.88	0.0085		

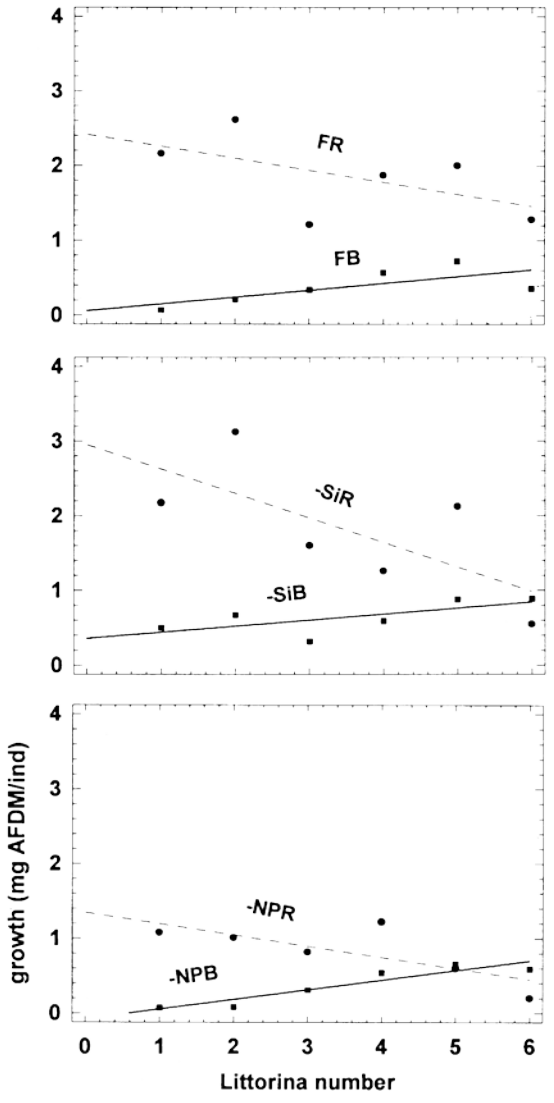

Fig. 8. Littorina growth (mg AFDW gained per individual) in response to Littorina density. F: full enrichment;-Si: enrichment without Si;-NP: enrichment without N and P; B: batch; R: replacement.

obscure any effect on algal N:C by the herbivores. Conversely, in the batch treatments biomass reduction by Littorina and nutrient supply by excretion significantly alleviated N limitation;however, this did not lead to N-replete conditions (Fig. 7).

The performance of diatoms in the different media conforms to the resource ratio hypothesis developed in the context of Tilman's (1982) competition theory and confirmed for periphyton communities by Sommer (1996) and Hillebrand and Sommer (1997). In both studies, an increasing importance of diatoms with increasing Si:N ratios had been found. In the present study, the largest relative biomass of diatoms was found in the -NP medium (highest Si:N ratio) and lowest in the -Si medium (lowest Si:N ratio). However, there is one surprise that cannot be explained at present. The potentially N_2-fixing Cyanobacterium Ananaena naltica was favoured by medium exchange (no N limitation), while it would have been expected to be most strongly favoured under the most severe N limitation. However, Ananaena growth might have been restricted by P shortage in the -NP treatments without medium exchange.

The shift from a negative to a positive density dependence of Littorina growth indicates poor food quality under nutrient-limited conditions. Here, I use the biomass specific cell quota of nitrogen (N:C) as an index of chemical food quality. The choice does not necessarily imply that I assume nitrogen limitation of Littorina growth. 0ther substances correlated with cellular N might also have been limiting for Littorina growth, as has been suggested by Muller-Navarra (1995) for a case of apparent P limitation of the freshwater zooplankter ap nia. In their review, Sterner and Schulz, 1998 propose two possible ways in which limitation by food quality and food quantity could interact. Poor food quality can reduce growth rates at any level of food quantity, or poor food quality could be compensated by enhanced ingestion at high food concentrations. This would permit maximal growth rates even with suboptimal food with a later transition from food limitation to saturation for the low quality food. Compensatory feeding cannot be tested with the data of the present study, because the highest periphyton biomass levels were attained under experimental condition without N limitation (medium replacement, full or -Si medium). Therefore, the combined influence of food quantity and food quality was tested by a multiple regression analysis. A multiplicative effect of food quantity and of food quality would show up as an additive effect if both measures are transformed logarithmically. Therefore, $\log^{10}$ of periphyton C (mg/cm^2) and of biomass N:C (mol/mol) were used as independent variables. Additionally, the arcsine-square root transformed values of diatom, green algal, and cyanobacterial relative

biomass were entered as candidate variables to account for taxonomy effects of food quality. Both the forward and the backward stepwise variable selection (F-to-enter = 4.0) removed all candidate independent variables except for $\log^{10}$C and $\log^{10}$(N:C):

$$G = 1.92(\pm 0.34) + 0.39(\pm 0.09)\log^{10}C + 1.54(\pm 0.19)\log^{10}(N\ C);$$

$$r^2 = 0.74; \quad p < 0.0001$$

where G = individual growth.

It should be noted that the experimental system is an highly artificial model system which demonstrates the reversal of density dependence of herbivore growth between open (medium exchange) and closed (batch) systems. Especially the batch systems do not mimic the behaviour of natural periphyton-grazer systems, because those are almost always open systems. A large portion of the nutrients excreted by herbivores will usually be washed away by waves and fertilise phytoplankton rather than periphyton. The other possible beneficial effect (reduction of algae which have to share the same nutrient flux) should be similar in open and closed systems.

The reversal of density dependence of herbivore growth because of food quality limitation has previously been reported from zooplankton (Sommer, 1992). The two studies differ from each other in the response variable of the herbivore. In the zooplankton study ap nia reproduction rates were measured as indicator of food limitation, while here only somatic growth of juveniles was measured. It remains to be seen whether limitation of somatic growth would eventually translate into limitation of population growth of Littorina. Traditional predator-prey models frequently include some modification of the logistic growth equation, which assumes negative density dependence of growth rates because of intraspecific competition. For systems where nutrient dynamics are dominated by herbivore recycling, such models should be modified to include intraspecific facilitation (positive density dependence) as well.

Acknowledgements

Technical assistance by Cordula Stilau is gratefully acknowledged.

References

Brett, M.T., Muller-Navarra, D.C., 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. Freshwater Biol. 38, 483–493.

Droop, M.R., 1973. Some thoughts on nutrient limitation in algae. J. Phycol. 9, 264–272.

Droop, M.R., 1985. 25 years of algal growth kinetics. Bot. Mar. 26, 99–112.

Goldman, J.C., McCarthy, J.J., Peavey, D.G., 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature 279, 210–215.

Grasshoff, K., 1976. Methods of Seawater Analysis. Verlag Chemie, Weinheim, Germany.

Hessen, D.0., 1992. Nutrient element limitation of zooplankton production. Am. Nat. 140, 799–814.

Hillebrand, H., Sommer, U., 1997. Response of epilithic microphytobenthos in the Western Baltic Sea to in situ experiments with nutrient enrichment. Mar. Ecol. Prog. Ser. 160, 35–46.

Hillebrand, H., Sommer, U., 1999. The nutrient stoichiometry of benthic microalgal growth. Redfield proportions are optimal. Limnol. 0ceanogr. 44, 440–446.

Hillebrand, H., Durselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. J. Phycol. 35, 404–423.

Lotze, H.K., Worm, B., Sommer, U., 2000. Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. 0ikos 85, 46–58.

Lubchenco, J., 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112, 23–39.

Lund, J.W.G., Kipling, C., LeCren, E.D., 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11, 143–170.

Muller-Navarra, D.C., 1995. Evidence that a highly unsaturated fatty acid limits ap nia growth in nature. Arch. Hydrobiol. 132, 297–307.

Muller-Navarra, D.C., Lampert, W., 1996. Seasonal patterns of food limitation in ap nia ealeata — separating food quantity from food quality effects. J. Plankt. Res. 18, 1137–1157.

Muller-Navarra, C., Brett, M.T., Liston, A.M., Goldman, C.R., 2000. A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. Nature 403, 74–77.

Pankow, H., 1990. 0stsee-Algenflora. Fischer, Jena.

Sommer, U., 1992. Phosphorous limited ap nia: intraspecific facilitation instead of competition. Limnol. 0ceanogr. 37, 966–973.

Sommer, U., 1996. Nutrient competition experiments with periphyton form the Baltic sea. Mar. Ecol. Progr. Ser. 140, 161–167.

Sommer, U., 1999a. The susceptibility of benthic microalgae to periwinkle (Littorina littorea, Gastropoda) grazing in laboratory experiments. Aquat. Bot 63, 11–21.

Sommer, U., 1999b. Periphyton architecture and susceptibility to grazing by periwinkles (Littorina littorea, Gastropoda). Internat. Rev. Hydrobiol., 197–204.

Steneck, R.S., Watling, L., 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Mar. Biol. 68, 299–312.

Sterner, R.W., 1989. The role of grazers in phytoplankton succession. In: Sommer, U. (Ed.). Plankton Ecology: Succession in Plankton Communities. Springer, Berlin, pp. 107–170.

Sterner, R.W., 1990. The ratio of nitrogen to phosphorous resupplied by herbivores: zooplankton and the algal competitive arena. Am. Nat. 136, 209–229.

Sterner, R.W., 1993. ap nia growth on varying quality of cene des'1'ts: mineral limitation of zooplankton. Ecology 74, 2351–2360.

Sterner, R.W., 1998. Zooplankton nutrition: recent progress and a reality check. Aquat. Ecol. 32, 261–279.

Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton.

Urabe, J., Watanabe, Y., 1992. Possibility of N or P limitation for planktonic cladocerans: an experimental test. Limnol. Oceanogr. 37, 244–251.

Utermohl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton Methodik. Mitt. Int. Ver. Theo. Angew. Limnol. 9, 473–485.

Worm, B., Lotze, H.K., Bostrom, C., Engkvist, R., Labanauskas, V., Sommer, U., 1999. Marine diversity shifts linked to interactions among grazers, nutrients and dormant propagules. Mar. Ecol. Prog. Ser. 185, 309–314.