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Biomass response and changes in composition of ephemeral macroalgal assemblages along an experimental gradient of nutrient enrichment

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Abstract

Most conceptual marine eutrophication models predict that ephemeral and epiphytic macroalgae will become substantially more abundant with increasing nutrient richness. This expectation is based on the fact that most of these fast-growing algae possess high requirements for inorganic N and P and, therefore, suffer from nutrient limitation under nutrient poor conditions. We tested the hypothesis that nutrient enrichment will stimulate the abundance of ephemeral macroalgae by studying the abundance and species composition of these algae on several types of substrata along an artificial nutrient gradient.

The total biomass of ephemeral macroalgae differed considerably among different types of substrata. The total ephemeral load was significantly higher on consolidated substrata than on large perennial algae, but we were unable to detect any systematic increase in the abundance of these ephemerals with increasing nutrient richness. We found, however, indications that the composition of the ephemeral assemblage changed with nutrient richness. Hence, corticated filamentous algae (mostly red algae) were more abundant at low nutrient richness while thin foliose algae (mainly green species) tended to become more abundant with increasing nutrient richness in most of the surveyed assemblages.

Keywords: Epiphytes; Coastal eutrophication; Nutrients; Rocky shores; Seaweeds; Mesocosm

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1. Introduction

Increasing availability of inorganic nutrients (especially N and P) is known to stimulate the abundance of ephemeral and epiphytic macroalgae in shallow coastal waters (Sand-Jensen and Borum, 1991; Duarte, 1995; Valiela et al., 1997). Mass accumulations of fast-growing, ephemeral algae is most often due to the foliose or uniserate filamentous green algae belonging to the genera *Ulva*, *Enteromorpha* or *Cladophora* (Fletcher, 1996; Raffaelli et al., 1998) although blooms of red and brown uniserate filamentous algae have been reported occasionally (Valiela et al., 1997). The accumulation of ephemeral algae under eutrophic conditions is often followed by a concomitant decline in slower growing, perennial macrophytes such as seagrasses and larger, perennial macroalgae (Borum and Sand-Jensen, 1996; Duarte, 1995; Valiela et al., 1997; Schramm, 1999).

The stimulation of ephemeral algae with increasing nutrient richness is related to ecophysiological traits, which are linked to algal morphology. Traits such as growth rates, nutrient requirements and uptake rates are scaled to the surface area to volume ratio (SA:V) of the algae such that thin algae (with high SA:V) tend to grow faster (Odum et al., 1958; Nielsen and Sand-Jensen, 1990), require more nutrients per unit of time and biomass (Pedersen and Borum, 1996) and exert higher nutrient uptake rates (Odum et al., 1958; Wallentinus, 1984; Rosenberg and Ramus, 1984; Hein et al., 1995; Taylor et al., 1998) than thick algae with a lower SA:V. A comparison of the balance between nutrient requirements and uptake rates across species has shown that the nutrient concentration needed to saturate growth is also scaled to SA:V such that thin algae tend to require much higher nutrient concentrations than thick algae in order to grow without nutrient limitation (Pedersen and Borum, 1997).

Most studies on the nutritional ecophysiology of macroalgae have compared slow-growing perennial species with ephemeral species. Although ephemeral algae, as a group, are considered more responsive to nutrient enrichment than perennial macroalgae, it is important to realise that these algae constitute a morphologically diverse group. Hence, SA:V ratios may vary considerably among different types of ephemeral algae (Nielsen and Sand-Jensen, 1990; Taylor et al., 1998; M.F. Pedersen, unpublished data) and it is therefore, expected that ecophysiological attributes and the response to nutrient enrichment may vary accordingly. Based on the relationships outlined above, we expect that thin corticated filamentous algae (e.g. *Rhodomela*, *Polysiphonia*, *Ceramium* etc., mean $\mathrm{SA}:V = 221\,\mathrm{cm}^{-1}$, range $57–409\,\mathrm{cm}^{-1}$, data from Nielsen and Sand-Jensen, 1990 and M.F. Pedersen, unpublished data) should be less sensitive to nutrient poor conditions and, therefore, should be able to dominate assemblages of ephemeral algae at low nutrient concentrations. Foliose algae, in contrast, have higher SA:V ratios (e.g. *Ulva*, *Enteromorpha*, *Porphyra* etc., mean $\mathrm{SA}:V = 413\,\mathrm{cm}^{-1}$, range: $196–628\,\mathrm{cm}^{-1}$) and should therefore, suffer from nutrient limitation under nutrient poor conditions and, thus, become more abundant with nutrient enrichment. Most uniserate filamentous algae have very high SA:V ratios (e.g. *Cladophora* sp. *Ectocarpus* sp., *Pilayella* sp. etc., mean $\mathrm{SA}:V = 891\,\mathrm{cm}^{-1}$, range $226–1737\,\mathrm{cm}^{-1}$) and are consequently expected to benefit from substantial nutrient enrichment given that other controlling factors (e.g. salinity, light, temperature, physical disturbance and grazing) remain constant. Increasing dominance of foliose and uniserate filamentous algae over corticated filamentous algae along gradients of nutrient richness has been reported in a few cases (e.g. Littler and Murray, 1975; Rönnberg et al., 1992; Lopez-Rodriguez et al., 1999; Middelboe and Sand-Jensen, 2000; Diaz et al., 2002). The effect of nutrient enrichment on the composition of natural algal assemblages is, however, often confounded by strong and inverse correlations between nutrient richness and salinity and the observed changes can, therefore, rarely be attributed solely to changes in nutrient availability (Middelboe et al., 1998).

Here we wanted to test the prediction that the biomass of ephemeral macroalgae is stimulated by nutrient enrichment and we wanted further to evaluate whether thin foliose and uniserate filamentous algae are favoured more by increasing nutrient richness than corticated filamentous algae. We did so by measuring total biomass and species composition of the ephemeral algal assemblage on a variety of substrata in eight large littoral mesocosms exposed to different levels of inorganic nutrients, whilst controlling salinity.

2. Materials and methods

2.1. Study site

The investigations were conducted in eight land-based mesocosms containing rocky shore littoral communities at the Marine Research Station, Solbergstrand (Oslofjord, Norway, 59°39′N, 10°40′E). Each mesocosm contained from 6 to 12 m^3 of seawater (low and high tide) and was fed with 5 $m^3\,h^{-1}$ fjord water (mean water residence time of about 2 h). A wave generator provided for continuous water movement and mixing. A technical description of the mesocosm facility is presented in Bokn et al. (2001). Littoral communities, resembling that of the littoral zone in the Oslofjord, were established in 1996 by introducing small boulders with attached macroalgae and associated fauna from the Oslofjord into each mesocosm. These communities were continuously supplied with larvae and spores imported from the Oslofjord with the inflowing water. The resulting macroalgal assemblage in the mesocosms was strongly dominated by perennial brown algae such as *Fucus vesiculosus*, *Fucus serratus* and *Ascophyllum nodosum*.

Nutrient enrichment was initiated in May 1998 and inorganic N and P was added continuously to six of the eight basins from stock solutions of H_3PO_4 and NH_4NO_3 at target concentrations of 1, 2, 4, 8, 16 and 32 μM DIN and 0.06, 0.13. 0.25, 0.5, 1.0 and 2.0 μM DIP above background concentrations of the inflowing water. Bokn et al. (2001) provide details on the nutrient manipulation of the mesocosms.

2.2. Sampling schemes

Five data sets on total biomass and species composition of ephemeral macroalgae were sampled on various substrata in 1999 and 2000. Data set 1 was the only one to which snails and other exclusively crawling grazers had access. The mountings of the other substrata were constructed so that snails were prevented from reaching the algae. In contrast, swimming herbivores (mostly isopods and amphipods) had access to all surveyed substrata.

Table 1
Summary of the data sets included in the present analysis

Data set	Substratum	Data subsets	Units per mesocosm	Sampling date or exposure time (exposure duration)
1	*Fucus vesiculosus*: individuals sampled from the *Fucus* assemblage on the N-wall of each mesocosm	(a) (b) (c)	4 10 10	(a) 11th May 1999 (>1 year) (b) 29th July 1999 (>1 year) (c) 3rd October 1999 (>1 year)
2	*Fucus vesiculosus*: introduced individuals	(a)	12	(a) 5th May–21st July 1999 (11 weeks)
		(b)	20	(b) 30th July–28th September 1999 (8 weeks)
3	*Fucus serratus*: introduced individuals		6	7th May–25th July 1999 (11 weeks)
4	*Polyvinylchloride frames*: area: 688 cm^2 per mesocosm		1	28th September 1999–10th August 2000 (44 weeks)
5	*Ceramic tiles*: area: 345 cm^2 per mesocosm		1	20th April 1999–7th August 2000 (67 weeks)

The data sets contain data on biomass and species composition of ephemeral macroalgae sampled on various substrata in the mesocosm.

2.3. Data set 1

Macroscopic epiphytes were sampled from ‘native’ *F. vesiculosus* individuals inhabiting the dense *Fucus* assemblage on the northern wall of each mesocosm in spring, summer and autumn 1999 (providing data sets 1a, 1b and 1c, respectively; Table 1). From each basin, 4–10 specimens of *F. vesiculosus* were harvested randomly from the area just emergent at low tide. The epiphytes were carefully removed from the host algae and identified. Dry weight biomass of each species/type was determined after drying at 80 °C for 24–48 h. Each of the examined host algae was photocopied, the copy scanned and the area calculated with the computer program Cirrus 1.5 (Canto GmbH, Berlin).

2.4. Data set 2

Individuals (96–160) of *F. vesiculosus* were sampled randomly from the littoral zone of the Oslofjord and transplanted into all basins in April and July 1999, respectively. Individual algae were attached by thin silicone tubes to a screw protruding from a stainless steel weight. These weights were then arranged on platforms (43 cm × 32 cm PVC) fixed in each mesocosm in a way that shading and whiplashing (i.e. the adverse mechanical effect of thalli in motion, see e.g. Kiirikki, 1996) were minimised. At low tide, the algae were submerged by a 20 cm water column, at high tide by 60 cm. The first set of introduced algae was harvested in July 1999 (2a) while the second set was harvested in October 1999 (2b). The samples were treated as described for data set 1 above.

2.5. Data set 3

Eighty individuals of *F. serratus* were collected randomly from the littoral zone of Oslofjord and introduced to the mesocosms (10 individuals in each) in April 1999. The algae were placed on a platform (16 cm × 43 cm) situated 20 cm deeper than for *F. vesiculosus* (data set 2). These algae were harvested in July 1999 and treated as described above.

2.6. Data set 4

The platforms holding the introduced fucoids remained in the basins for 10 months after the last harvest of introduced host algae. In August 2000, we harvested all the macroalgae that had settled and developed on these platforms and analysed the species composition and biomass of each species/group as described for data sets 1–3.

2.7. Data set 5

Fifteen ceramic tiles (4.8 cm × 4.8 cm) were installed in each mesocosm in April 1999 for settling and development of algal spores. The tiles were arranged vertically so that the uppermost of three tiles (in each of five columns) was just submerged at low tide. By August 2000, after 16 months of exposure, the tiles were removed and the attached algae harvested and treated as described for data sets 1–4 above.

2.8. Statistical analyses

Prior to statistical analyses, we grouped the ephemeral macroalgae into the following morphological groups: thin corticated filamentous algae (e.g. *Ceramium* sp., *Polysiphonia* sp. and *Rhodomela* sp.), foliose algae (e.g. *Ulva* sp. and *Enteromorpha* sp.) and uniserate filamentous algae (e.g. *Pilayella* sp., *Ectocarpus* sp., *Elachista* sp. *Cladophora* sp.). Data from subunits (thalli or tiles, refer to Table 1) were pooled per mesocosmos. The relationships between total algal biomass or the biomass of each morphological group and concentrations of dissolved inorganic phosphorus in the water prior to harvest were analysed using Pearson correlation analysis (Sokal and Rohlf, 1995). Data were log-transformed prior to analysis when needed to obtain a linear relationship between the variables. The generated *P*-values were sorted in ascending order (i.e. $P_{i=1} < P_{i=2}, \dots, < P_{i=m}$) and subsequently compared to significance levels which had been adjusted for multiple comparisons ($\alpha/(m - i + 1)$, with m being the total number of comparisons and i the rank of the respective *P*-value) using the method of Holm (1979). Comparisons of biomass among different substrata or seasons were carried out using Student's *t*-test for dependent samples (Sokal and Rohlf, 1995).

3. Results

3.1. Nutrient concentrations

A detailed presentation of the concentrations of dissolved inorganic N (DIN) and P (DIP) in the mesocosms during the entire mesocosm experiment (1998–2000) can be found in

Table 2
Concentrations of dissolved inorganic N (DIN) and P (DIP) in the mesocosms during the time of exposure for the various substrata

Treatment	Data set					
	1a (μM DIN/ μM DIP)	1b (μM DIN/ μM DIP)	1c (μM DIN/ μM DIP)	2a and 3 (μM DIN/ μM DIP)	2b (μM DIN/ μM DIP)	4 and 5 (μM DIN/ μM DIP)
+0/+0.00	11.06/0.19	11.98/0.18	21.99/0.53	11.60/0.16	20.19/0.51	3.58/0.22
+0/+0.00	11.12/0.21	10.82/0.21	16.40/0.42	11.41/0.21	14.96/0.41	3.69/0.20
+1/+0.06	11.08/0.24	11.23/0.23	16.18/0.44	11.62/0.19	14.64/0.46	4.26/0.23
+2/+0.13	13.03/0.30	12.96/0.31	17.91/0.52	13.24/0.29	16.96/0.52	5.20/0.29
+4/+0.25	13.70/0.39	14.58/0.36	20.24/0.66	14.86/0.32	18.46/0.65	6.57/0.40
+8/+0.50	18.48/0.65	20.03/0.68	26.23/0.97	20.34/0.63	24.85/0.98	13.58/0.88
+16/+1.00	27.24/1.09	27.25/1.11	32.98/1.36	27.70/1.08	31.55/1.36	16.93/1.03
+32/+2.00	38.90/1.89	36.81/1.77	45.89/2.22	37.23/1.74	44.76/2.19	30.67/1.92

Nutrient concentrations for data sets 1, 4 and 5 represent average values for a period 3 months prior to harvest.

Bokn et al. (2003), but average concentrations of DIN and DIP during exposure of the various substrata are presented in Table 2. The concentrations of DIN were relatively high in the inflowing water (Table 2, Fig. 1) but concentrations of DIP were very low and suggest P-limitation. Nutrient enrichment enhanced the concentrations of both DIN and DIP substantially (Table 2).

3.2. Data set 1: macroepiphytes on *Fucus vesiculosus* from the mesocosm communities

The total epiphyte load on 'native' *F. vesiculosus* was relatively low in spring and summer (spring mean = 1.86 mg DW cm^{-2}, summer mean = 0.55 mg DW cm^{-2}), and decreased further in fall when almost no epiphytes were present on the host algae (mean = 0.09 mg DW cm^{-2}, Fig. 2). Total epiphyte biomass was strongly correlated to nutrient treatment level in spring and summer ($r = 0.80$, $P = 0.018$ and $r = 0.82$, $P = 0.013$, Table 3), while no such relationship existed in fall. The biomass of corticated filamentous algae, foliose algae and uniserate filamentous algae did not vary systematically along the nutrient gradient, but corticated filamentous algae tended to increase with nutrient richness in spring ($r = 0.77$, $P = 0.025$) while foliose algae tended to be more abundant at high nutrient levels in summer ($r = 0.77$, $P = 0.027$, Table 3, Fig. 3).

3.3. Data set 2: macroepiphytes on introduced *Fucus vesiculosus*

Final epiphyte load on transplanted *F. vesiculosus* individuals exposed in the basins from spring to summer (mean = 5.37 mg DW cm^{-2}) was higher (t-test, $P = 0.0039$) than on those exposed from summer to autumn (mean = 1.57 mg DW cm^{-2}, Fig. 3). Total epiphyte load on transplanted *F. vesiculosus* did not vary systematically with nutrient treatment level ($P > 0.219$). The biomass of corticated filamentous algae tended to be inversely related to nutrient richness during both periods, albeit not significantly so ($r = -0.56$ and $r = -0.61$;

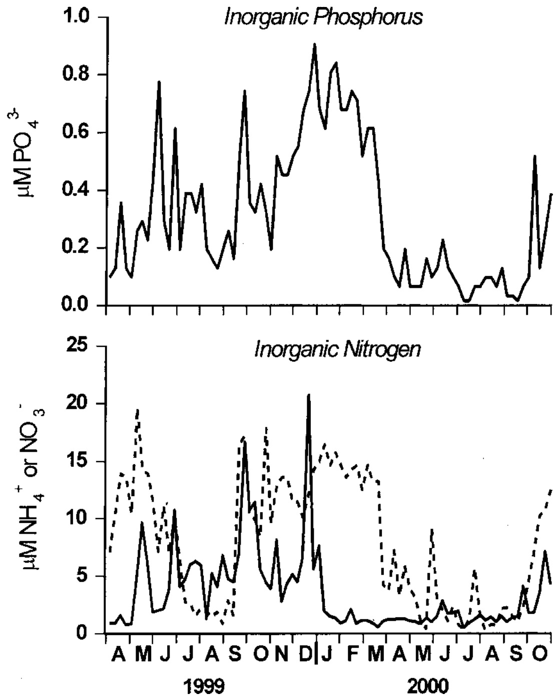

Fig. 1. Concentrations of dissolved inorganic P (upper panel) and N (lower panel, solid line: NH_4^+, broken line: NO_3^-) in the water flowing into the mesocosms from the Oslofjord during the period from April 1999 to October 2000.

Table 3). The amount of foliose algae increased marginally with nutrient richness on those basiophytes exposed from spring to summer ($r = 0.71$, $P = 0.048$).

3.4. Data set 3: macroepiphytes on introduced *Fucus serratus*

Final epiphyte biomass on transplanted *F. serratus* exposed in the mesocosms from spring to summer 1999 was low (mean = 0.31 mg DW cm^{-2}) and not correlated to nutrient treatment level ($r = -0.64$, $P = 0.088$). The epiphyte assemblage on *F. serratus* was dominated by corticated filamentous algae, which became less abundant at high nutrient levels ($r = -0.84$, $P = 0.009$). The biomass of foliose and uniserate filamentous algae was very low on *F. serratus* and did not vary systematically with nutrient richness (Table 3).

3.5. Data set 4: ephemeral macroalgae on PVC platforms

The biomass of ephemeral algae on the PVC platforms was very high (mean = 39.71 mg DW cm^{-2}) when compared to the epiphytic load on *Fucus* and did not vary with nutrient level ($P = 0.383$). The assemblage of ephemeral algae was dominated by corticated filamentous

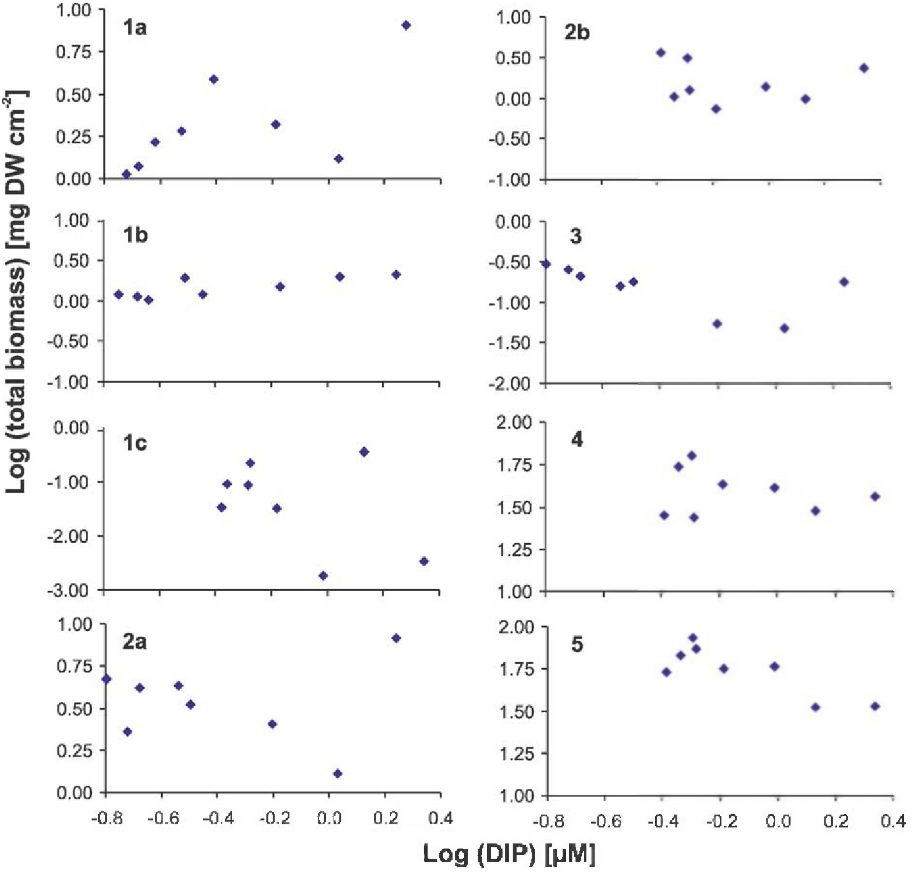

Fig. 2. Logarithm of total biomass (g DW cm^{-2}) of ephemeral macroalgae on various substrata along a gradient of nutrient addition, presented here as logarithm of measured dissolved inorganic phosphorus (DIP). Bold numbers indicate data sets (refer to Table 1).

algae which tended to become less abundant at high nutrient levels ($r = -0.67$, $P = 0.072$) while foliose algae became more abundant ($r = 0.71$, $P = 0.047$).

3.6. Data set 5: ephemeral macroalgae on ceramic tiles

The biomass of ephemeral algae on the ceramic tiles which had been exposed in the basins for 16 months was high (mean = 56.12 mg DW cm^{-2}) and inversely related to nutrient treatment level ($r = -0.83$, $P = 0.011$). The algal assemblages on the tiles were dominated by foliose algae (especially *Ulva*) which tended to become more abundant with increasing nutrient richness ($r = 0.74$, $P = 0.035$). Corticated filamentous algae were less abundant and the abundance of these algae was inversely related to nutrient richness ($r = -0.85$, $P = 0.008$).

Table 3
Correlations between the biomass of ephemeral macrolagae and mean concentrations of dissolved inorganic phosphorus (from Table 1).

Data set	Variable	r	P-value	$\alpha/(m-i+1)$	Result
1a	Total biomass	0.797	0.018	0.013	ns
	Corticated	0.770	0.025	0.017	ns
	Foliose	0.440	0.276	0.025	ns
	Uniserate	−0.088	0.835	0.050	ns
1b	Total biomass	0.819	0.013	0.013	Significant
	Corticated	0.137	0.746	0.050	ns
	Foliose	0.766	0.027	0.017	ns
	Uniserate	0.672	0.068	0.025	ns
1c	Total biomass	−0.057	0.890	0.050	ns
	Corticated	−0.064	0.881	0.025	ns
	Foliose	0.380	0.354	0.017	ns
	Uniserate	−0.770	0.026	0.013	ns
2a	Total biomass	0.468	0.219	0.025	ns
	Corticated	−0.564	0.145	0.017	ns
	Foliose	0.711	0.048	0.013	ns
	Uniserate	−0.208	0.622	0.050	ns
2b	Total biomass	−0.183	0.665	0.050	ns
	Corticated	−0.614	0.106	0.013	ns
	Foliose	0.526	0.181	0.025	ns
	Uniserate	0.583	0.129	0.017	ns
3	Total biomass	−0.639	0.088	0.025	ns
	Corticated	−0.840	0.009	0.013	Significant
	Foliose	0.619	0.101	0.050	ns
	Uniserate	−0.659	0.076	0.017	ns
4	Total biomass	0.358	0.383	0.025	ns
	Corticated	−0.665	0.072	0.017	ns
	Foliose	0.714	0.047	0.013	ns
	Uniserate	–	–	0.050	ns
5	Total biomass	−0.831	0.011	0.017	Significant
	Corticated	−0.848	0.008	0.013	Significant
	Foliose	0.742	0.035	0.025	ns
	Uniserate	−0.395	0.333	0.050	ns

Data sets 1–3 comprise ephemeral algae on *Fucus*, data sets 4 and 5 on consolidated substrata (PVC, ceramic tiles). r is Pearson correlation coefficient and P is the probability that H_0 (i.e. no relationship) is true. The level of significance was adjusted for multiple comparisons (with an overall level of $\alpha = 0.05$) using the method described by Holm (1979).

Overall, we were not able to detect a systematic increase in total biomass of ephemeral algae with nutrient enrichment. Our results do, however, indicate that the composition of the assemblage changed with nutrient enrichment, since the abundance of corticated filamentous algae tended to be highest at low nutrient levels, whereas foliose algae tended to be more abundant with increasing nutrient richness. These tendencies were, however, rarely strong enough to reveal clear and significant relationships. The abundance of uniserate filamentous

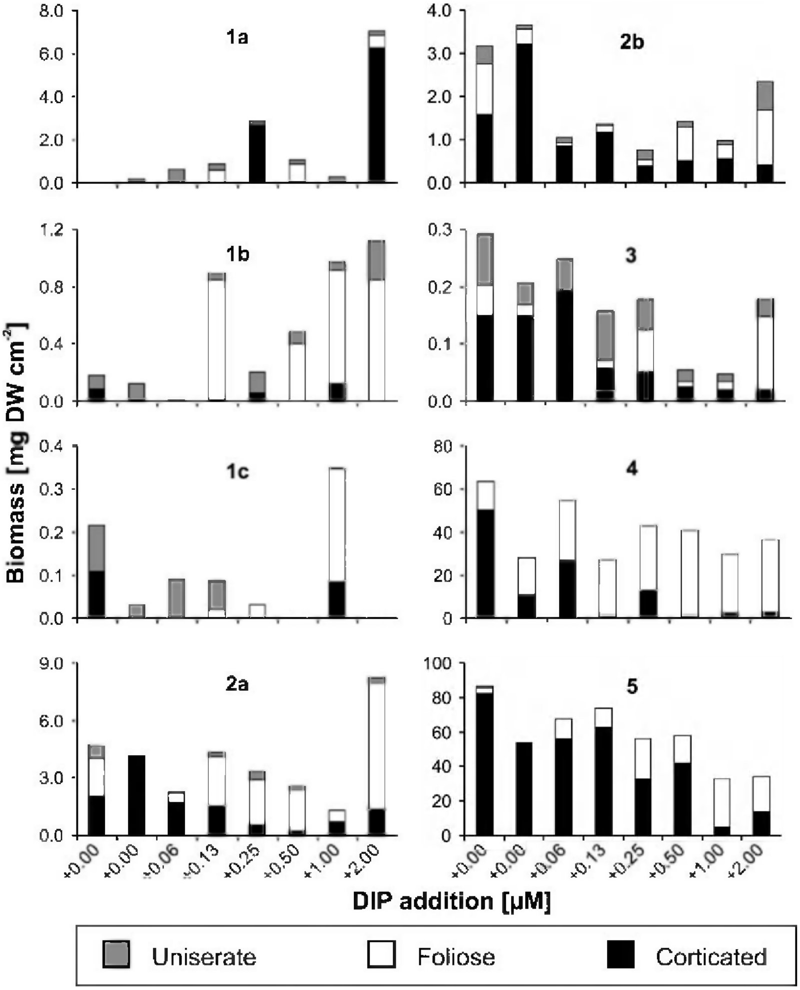

Fig. 3. Biomass (g DW cm^{-2}) of corticated filamentous, foliose and uniserate filamentous algae on various substrata along a gradient of nutrient addition. Here only DIP addition is shown, but there was also 16-fold addition of DIN. Bold numbers indicate data sets (refer to Table 1).

algae remained very low in most data sets and did not vary systematically with nutrient enrichment. The macrofauna was monitored regularly in all mesocosms for other purposes (Kraufvelin et al., 2002), but data for the two most important groups of herbivores are presented in Fig. 4. Swimming crustaceans (mainly isopods and amphipods) were strongly dominated by the amphipod *Gammarus locusta* (L.), which at times made up ca. 80% of the total mesograzer biomass (Christie and Kraufvelin, in press). The abundance of *G. locusta*, which had access to all surveyed substrata, tended to increase insignificantly with nutrient enrichment except for autumn 1999. The common periwinkle *Littorina littorea* (L.) was dominant among the crawling grazers and the abundance of this herbivore increased

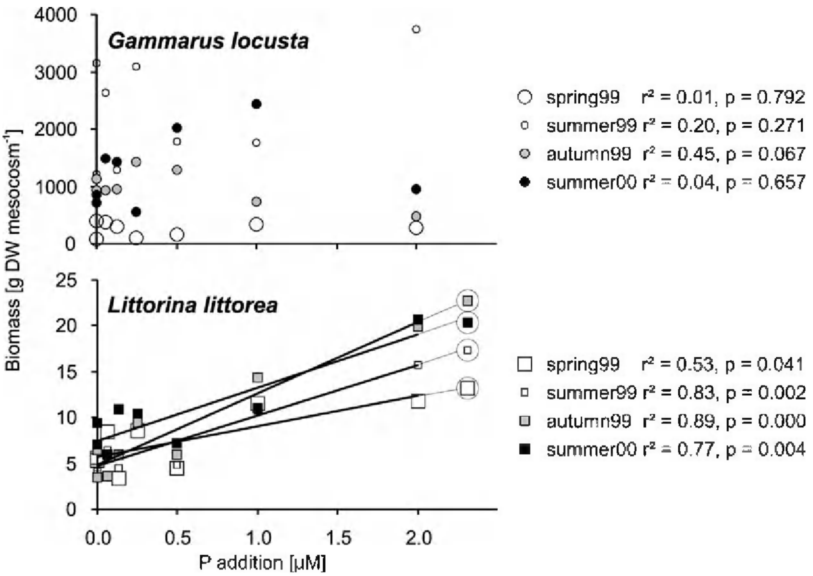

Fig. 4. Linear regressions of biomass of the most important mesograzers in the mesocosms (from Krauvelin et al., unpublished data) against DIP addition. Upper panel: *Gammarus locusta*, lower panel: *Littorina littorea*. Encircled symbols indicate the respective regression line.

significantly with nutrient enrichment (Fig. 4). *L. littorea* and other crawling herbivores had, however, only access to the ‘native’ algae of data set 1.

4. Discussion

Contrary to our expectations, total biomass of ephemeral algae did not increase with the nutrient gradient. The amount of ephemeral algae differed considerably among the various types of substrata surveyed in the present study. Stable substrata such as the PVC-frames and the ceramic tiles supported a very high biomass of ephemeral algae corresponding to about 500 g DW m^{-2}. The epiphytic load on ‘native’ fucoids collected in the mesocosms was, in contrast, much lower, most probably due to immense shading and/or due to whiplash effects (Kiirikki, 1996) within the dense fucoid assemblages. Transplanted *F. vesiculosus* carried significantly more epiphytes than ‘native’ *Fucus*, which supports the notion that shading and/or whiplash effects may limit the abundance of epiphytes within the denser established fucoid assemblages, since the transplanted fucoids were arranged so that neighbouring effects were minimised. The low epiphytic biomass observed on transplanted *F. serratus* cannot be explained by shading and/or whiplash effects, but these thalli were shaded by additional 20 cm water column and a species-specific basibiont or substratum effects can neither be ruled out.

Total biomass was strongly influenced by the season of exposure of substrata, which could be seen when the same substratum type was harvested at various dates. In the ephemeral algae communities on 'native' *Fucus*, notable amounts were mainly found in summer and obviously season was the overriding factor here. Stable substrata, which moreover were exposed for almost or more than one year, respectively, hosted so much more biomass that probably the time for biomass accumulation and succession to proceed was more important. However, the negative trend of total biomass and the shift from corticated to foliose algae were especially visible in these mature communities of ephemeral algae.

Comparisons of the nutritional ecophysiology of different types of ephemeral algae led to the expectation that nutrient enrichment would stimulate the abundance of foliose and uniserate filamentous algae much more than corticated algae. The impression from the analysis of our five data sets is that nutrient enrichment tended to stimulate an increase in foliose algae and a decline of corticated filamentous algae, while the amount of uniserate filamentous algae remained low and unrelated to nutrient level. These changes were especially obvious when basins of low and high nutrient loading were compared visually but could, however, rarely be verified statistically.

The use of correlation analysis requires a rather clear-cut relationship between the variables when the number of treatment levels is low (here $n = 8$) and adjusting the significance level for multiple comparisons makes it even harder to detect any effect of nutrient enrichment or it may even conceal actual effects (Moran, 2003). Hence, many of the correlations between nutrient concentration and the biomass of corticated and foliose algae were not statistically significant even though they could be classified as being strong (i.e. $r > 0.7$).

Another reason for the low degree of correlation between abundance of these algae and nutrient concentration may be the natural high variability in epiphytic biomass even on similar substrata in close proximity. Neighbouring thalli of *Fucus* spp. in the mesocosms, but also in the Oslofjord, could be completely clean or totally covered by epiphytes (R. Karez, personal observation). This high variability in epiphyte load over very short distances may require many more units to be sampled at each nutrient level in order to verify the relationship statistically.

Conceptual eutrophication models predict that the amount of epiphytic algae on host plants and of ephemeral algae on other substrata is stimulated by nutrient enrichment (Sand-Jensen and Borum, 1991; Duarte, 1995; Valiela et al., 1997; Schramm, 1999) and high loads of ephemeral algae have often been observed at eutrophied sites (e.g. Littler and Murray, 1975; Rönnberg et al., 1992; Lopez-Rodriguez et al., 1999; Middelboe and Sand-Jensen, 2000; Diaz et al., 2002). We were, however, unable to detect any consistent increase in total ephemeral biomass along the experimental nutrient gradient and total biomass was even negatively related to nutrient richness in some cases. Ephemeral macroalgal biomass may not be related to nutrient richness if the concentrations of DIN and DIP in the ambient water are too high to render the algae nutrient limited. Even though the inflowing water was very rich in DIN, ambient concentrations of DIP were very low during most of the active growth season (i.e. April–September). Ambient concentrations of DIP during summer were typically below 0.2 μM, which is about 10 times below the average half saturation constant for P-uptake in most ephemeral macroalgae (Wallentinus, 1984) and, hence, low enough to leave most algae susceptible to P-limitation. Measurements carried out in the mesocosm showed accordingly that the growth rate of *Ulva lactuca* L. was stimulated by nutrient enrichment during summer, while the growth of *Polysiphonia fucoides* (Huds.)

Grev. and *Ceramium rubrum* C. Agardh remained largely unaffected by nutrient addition (M.F. Pedersen, unpublished).

The inconsistent relation between total biomass of ephemeral algae and nutrient richness may suggest that herbivores were able to prevent ephemeral algae from developing high biomasses at high nutrient levels. The abundance of mesograzers was generally high in the mesocosms and tended to increase with nutrient enrichment. It is therefore very likely that most ephemeral algae suffered substantial grazing losses in the mesocosms and that the grazing pressure increased with nutrient enrichment. Several studies have shown that mesograzers such as littorinids, isopods and gammarids are able to 'neutralise' the primary effects of nutrient enrichment (i.e. accumulation of ephemeral algae) given that their numbers are high enough (e.g. Brawley and Fei, 1987; Duffy, 1990; Neckles et al., 1993; Williams and Ruckelshaus, 1993). A simple and direct relationship between ephemeral algal biomass and nutrient richness is, therefore, not necessarily to be expected if herbivores respond numerically to nutrient enrichment and the anticipated increase in ephemeral algae biomass with nutrient richness may have been suppressed by grazing effects.

Similarly, the expected changes in dominance patterns may also have been suppressed by the intensified grazing pressure along the nutrient gradient. Several studies have shown that mesoherbivores tend to prefer uniserate filamentous and foliose algae such as *Pilayella*, *Ectocarpus*, *Ulva* and *Enteromorpha* over macroalgae of a more complex morphology (e.g. Lubchenco, 1978; Nicotri, 1980; Watson and Norton, 1985; Lotze et al., 2000; but see Karez et al., 2000). The observed increase in mesograzer abundance and, hence, potential grazing rates, may therefore, explain why the amount of foliose algae and uniserate filamentous algae did not respond more clearly than it did.

The decline of corticated filamentous algae is probably a result from increased competition for light and space among the ephemeral algae at high nutrient levels. Many of the filamentous algae (both uniserate and corticated) found in our study had relatively short thalli when compared to the foliose algae and body length is often seen as key factor for competitive success of plants by exerting asymmetric competition on smaller species and/or individuals (e.g. Gaudet and Keddy, 1988).

In summary, our study did not provide evidence that the abundance of ephemeral algae increases with nutrient enrichment, probably due to a neutralising effect of herbivores. Nutrient enrichment seems to favour thinner algal forms (here especially the foliose algae) more than the thicker corticated filamentous forms, which may even decrease in numbers at high nutrient levels. The opposite pattern in abundance among these two groups may also contribute to explain why the total biomass of the ephemeral algae assemblage did not change more evidently along the nutrient gradient.

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