ECOLOGY

Effect of short-term elevated nutrients and mesoherbivore grazing on photosynthesis of macroalgal communities

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Abstract. Marine macroalgal communities are among the most productive habitats worldwide. They provide energy and matter to higher trophic levels and support other important functions for ecosystems and services for human society. To date it is not clear to what extent irradiance, nutrient loading, and mesoherbivores regulate the primary productivity of a community. In a factorial field experiment we evaluated the interactive effect of short-term pulses of elevated nutrients and of the activity of grazers on the photosynthesis (in terms of the rate of oxygen production per unit mass) of communities dominated by the perennial *Fucus vesiculosus* and the ephemeral *Cladophora glomerata* in the northern Baltic Sea. This experimental manipulation had no effect on the community dominated by *F. vesiculosus*. A 12-hour addition of herbivores decreased the photosynthetic production of the macroalgal community dominated by *C. glomerata* in spring but increased its production in summer. The simultaneous addition of nutrients and herbivores in summer reversed the effect. A 4-times longer manipulation had no effect on the *C. glomerata* production. Differences in the responses between separate and interactive effects imply that the photosynthetic production of a community cannot be predicted by separate effects of the same variables. Our experiment also indicated that macroalgal communities dominated by *F. vesiculosus* covered by epiphytic macrophytes performed stably under different stress regimes and could buffer moderate short-term disturbances due to elevated nutrient loads and/or herbivory of either natural or human origin.

Key words: photosynthetic production, macroalgae, mesoherbivore grazing, nutrient loading.

INTRODUCTION

Primary production is of special importance in ecology as it fuels other trophic levels with energy and matter. In order to understand the functioning of an ecosystem one has to characterize the key processes that regulate its primary production. In the aquatic ecosystems almost all primary production is performed by algae (Field et al., 1998). Algae encompass a diverse range of organisms, ranging from single floating cells to attached seaweeds. Aquatic macrophyte communities occupy coastal environments and are among the densest and the most productive habitats worldwide (Mann, 2000). The availability of light and level of mineral nutrients are known to play crucial roles in regulating primary production of

macroalgae; upwelling, turbulence, turbidity, and grazing intensity can be important as secondary factors (e.g. Field et al., 1998; Hauxwell et al., 1998; Duffy and Hay, 2000).

However, it is not clear how these factors contribute to the primary productivity of macroalgal communities because relationships between the ambient environment and primary productivity are largely inferred from community composition, e.g. from changes in species biomasses (Pedersen and Borum, 1996; Worm and Sommer, 2000; Worm et al., 2000). The accumulation of algae is a result of a number of factors, and biomass is not necessarily a good indicator of the primary productivity of a community. The biomass at a site at any particular time is the net effect of growth, import, export, and decompositional and grazing losses. Consequently, a population may have a high growth rate but

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low biomass if newly formed material is removed rapidly by herbivory or transported to a different location by wind and currents in the case of ice scraping or drifting algae.

The studies in which the primary production of aquatic macrophytes has been directly quantified have usually involved detached pieces of algal thalli or individuals. Few have investigated primary production at the community level, like multiple individuals or epiphytic communities, in the laboratory (e.g. Middelboe and Binzer, 2004; Middelboe et al., 2006; Sand-Jensen et al., 2007) and even fewer in situ in the constantly varying coastal environment (Carpenter, 1985; Cheshire et al., 1996; Copertino et al., 2006). As a consequence, under most experimental conditions the algae had good light regimes, giving rise to the concept that primarily supplies of both nitrogen and phosphorus limit macroalgal primary production (Elser et al., 2007, but see also Field et al., 1998) and production is often saturated by light. Within natural macroalgal beds, however, community production may be either light limited or inhibited at the highest irradiances (Falkowski and LaRoche, 1991; Binzer and Middelboe, 2005; Tait and Schiel, 2011).

Different species of macroalgae also require certain light intensities for the onset of photosynthetic production. Above this level increasing light intensities favour algal production, but extremely high light intensities may have again significant deleterious effects on macroalgae. Therefore, reduced or excess availability of light restricts productivity even if nutrients are abundant (Falkowski and LaRoche, 1991). Likely, resource limitation modifies the macroalgal responses to irradiation and constrains their photoacclimation responses (Chalup and Laws, 1990). Additionally, the movement of light photons in different parts of macroalgae could determine the photosynthetic performance (Binzer and Sand-Jensen, 2002). Due to the availability of light and the flux of light photons the photosynthetic production may be higher in the upper parts of thalli (Middelboe and Binzer, 2004; Binzer and Middelboe, 2005; Binzer et al., 2006) and lower in the shaded parts of macroalgae (Stengel and Dring, 1998; Binzer and Sand-Jensen, 2002). In general, filamentous algae are able to give higher photosynthetic rates per unit biomass (Johansson and Snoeijs, 2002) than perennial macroalgae with a slower growth rate (King and Schramm, 1976; Wallentinus, 1984; Middelboe and Binzer, 2004; Sand-Jensen et al., 2007).

A large number of experimental field studies demonstrate that marine herbivores play key roles in the organization of marine benthic communities (e.g. Hayward, 1988; Kotta and Orav, 2001; Sala and Graham, 2002; Kotta and Witman, 2009). Herbivores have a high potential for mediating effects that cascade up and down trophic chains in ecosystems (Kotta et al., 2000, 2004; Schmitz, 2008; Orav-Kotta et al. 2009;

Tomczak et al., 2009; Kotta et al., 2010). The way these effects are mediated depends on constraints determining resource availability, herbivore feeding mode, the adaptive trade-off to balance nutrient intake, and predation risk avoidance. We remain largely ignorant of the ecological roles of herbivores in the primary productivity of macroalgae as previous studies in aquatic ecosystems have generally assessed the impacts of herbivores on community composition (e.g. Pedersen and Borum, 1996; Worm and Sommer, 2000; Worm et al., 2000). Grazing depletes the population of primary producers and may lead to a decline in productivity. In some instances, however, grazers selectively feed on the senescent tissue of plants (Kotta et al., 2006) and, thus, may facilitate photosynthetic production per unit algal mass. We are not aware of studies quantifying such impacts on community functions, including photosynthetic production. Therefore, there is a need to gather additional empirical evidence on the photosynthesis of macroalgal communities and to re-evaluate the roles of light and nutrients as well as the roles of secondary factors, e.g. grazing intensity.

In a factorial field experiment we evaluated the separate and interactive effects of short-term pulses of elevated nutrients and grazing activity on the photosynthesis of macroalgal communities in the northern Baltic Sea in spring and summer 2008. The northern Baltic Sea area is strongly seasonally characterized, macroalgae are periodically nutrient depleted, nutrient additions are temporally variable and occur in irregular pulses in our study area (Kotta et al., 2008a). Such nutrient pulses have potentially an important role in regulating photosynthetic production and growth and species composition of macroalgal communities (Carpenter, 1985; Pedersen and Borum, 1996; Field et al., 1998; Schaffelke, 1999; Worm and Sommer, 2000; Worm et al., 2000). As shown by Worm and Sommer (2000), a single nutrient pulse can have drastic direct and indirect effects on macroalgae and their associated epiphytes and grazers. Although this study focussed on community structure only, the mechanism behind the observed changes is plausibly related to the elevated photosynthetic production of ephemeral species (Pedersen and Borum, 1996). In the long run, the facilitation of ephemeral species may lead to a shift in the dominance pattern or species composition (Carpenter, 1985; Field et al., 1998; Schaffelke, 1999). Although there is strong experimental evidence on the role of nutrient addition to the community structure and growth of macroalgae (e.g. Fujita and Edwards, 1989), we have no empirical evidence on the photosynthesis and nutrient relations in the coastal marine environments.

In our experiment we used natural communities dominated by the ephemeral green alga *Cladophora glomerata* (L.) Kützing and the perennial brown alga *Fucus vesiculosus* L. *Cladophora glomerata* is a fast

growing species, and we expect that its production depends on the immediate supply of nutrients and that the effect size increases with the duration of the enrichment pulse (Middelboe et al., 2006; Ylla et al., 2007). *Fucus vesiculosus* in turn is a slowly growing species with a slower nutrient uptake (Wallentinus, 1984; Pedersen and Borum, 1996; Worm and Sommer, 2000). The species can store nutrients for the periods of nutrient depletion and its production is likely less coupled with nutrient levels in the ambient environment (Hemmi et al., 2005).

In recent decades, elevated levels of eutrophication have been supporting a large fraction of benthic primary production and development of drift algal mats in the study area. Such drift algae are also known to host a dense community of mobile benthic herbivores (Paalme et al., 2002; Lauringson and Kotta, 2006; Kotta et al., 2008b). Due to varying wind conditions the drifting algae are constantly displaced and usually do not cover the same area longer than a week. However, herbivores of the drift algae are expected to migrate into adjacent macrophyte communities, which leads to a manifold increase of the density of herbivores within hours only (authors' personal observations). Such a dramatic increase in herbivory pressure most likely affects the photosynthesis of the macroalgal community. In our experiment we expected that the effect of herbivores on the photosynthesis of the macroalgal community would increase with the duration of herbivory enrichment. We also expected that herbivores would reduce the photosynthetic production of the macroalgal community dominated by *C. glomerata* under low nutrient levels but not under high nutrient levels. Due to the slow recovery rate of the macroalgal community dominated by *F. vesiculosus* because of its perenniality, the negative effects of herbivores would most likely occur both in a low and a high nutrient environment.

MATERIAL AND METHODS

The study was conducted in the shallow semi-enclosed Kõiguste Bay, Gulf of Riga, northern Baltic Sea. The prevailing sediment types are sandy clay mixed with pebbles, gravel, or boulders. The prevailing depths are between 1 and 4 m. The area is influenced by a diffuse nutrient load from the moderately eutrophicated Gulf of Riga (Kotta et al., 2008a). The benthic vegetation is well developed and extensive proliferation of ephemeral macroalgae has been reported from the area in recent years (Lauringson and Kotta, 2006). Due to the short geological history of the Baltic Sea, prominent macro-grazers are absent and predominant herbivores are small crustaceans such as isopods and gammarid amphipods. In general mesograzers are abundant but their densities are highly variable in the study area (Kotta et al., 2008a).

The experiments to assess the photosynthetic production of the macroalgal communities were performed at 1 m depth adjacent to Kõiguste Marine Biological Laboratory (58°22.10′N, 22°58.69′E) in May and July 2008. Prior to the experiment the macroalgae attached to stones were collected from a shallow (1–2 m) area and placed in on-land transparent chambers holding 200 L of water, with replicates in separate chambers. The surface area of the chambers was 1485 cm^2 and the coverage of the macroalgae in the holding tanks varied between 50% and 70%, which is equal to the macroalgal densities in field conditions. The water in the chambers was regularly changed. The water temperature was coupled with the seawater temperature, which ranged from 11.6 to 15.1 °C in spring and from 17.5 to 19.9 °C in summer.

Treatments consisted of communities dominated by *F. vesiculosus*, *C. glomerata*, and an equal mixture of these species (coverages were estimated visually). The mixed community was included into the experimental design because mixed algal communities are as common as monospecific communities in our study area (Kotta et al., 2008a). Macroalgal communities dominated by *F. vesiculosus* had small amounts of epiphytes, mainly *Pilayella littoralis* (L.) Kjellman, *Ceramium tenuicorne* (Kützing) Waern, and *Ulva intestinalis* L. Half of the treatments were kept at natural seawater nutrient levels (25 μmol N L^{-1} and 1 μmol P L^{-1}), others were kept at elevated nutrient levels (125 μmol N L^{-1} and 5 μmol P L^{-1}) either for 12 or 48 hours. Nutrient delivery represented the typical upwelling conditions in the study area (Kotta et al., 2008a). Half of the treatments were kept at natural mesoherbivore densities (the gammarid amphipods at 400 ind. m^{-2} and the isopods at 200 ind. m^{-2}). To the other half of the treatments meso-herbivores were added at 5 times higher densities than natural but at natural proportions, either for 12 or 48 hours. Herbivores were collected by shaking the algae harvested from the study area. They were added randomly to the treatments at appropriate densities. The mesoherbivore community consisted mainly of amphipods (*Gammarus salinus* Spooner, *G. oceanicus* Segerstråle, *G. duebeni* Liljeborg) and isopods (*Idotea balthica* (Pallas), *I. chelipes* (Pallas)). There were 42 treatments in total. Three replicates were made for each combination of treatments (Fig. 1).

The photosynthetic production of algal communities was measured in a transparent chamber holding 29 L of water. The chamber consisted of a transparent Plexiglas dome and a 28 cm × 28 cm steel base. An airtight seal between the chamber and the base was achieved using a rubber sealing and steel wing nuts. Shortly before the measurement of photosynthetic production, the stones with attached macroalgae were taken from premanipula-tion chambers. Each stone was vigorously shaken in sea water to remove any attached macroinvertebrates and then placed into the production chambers at coverages
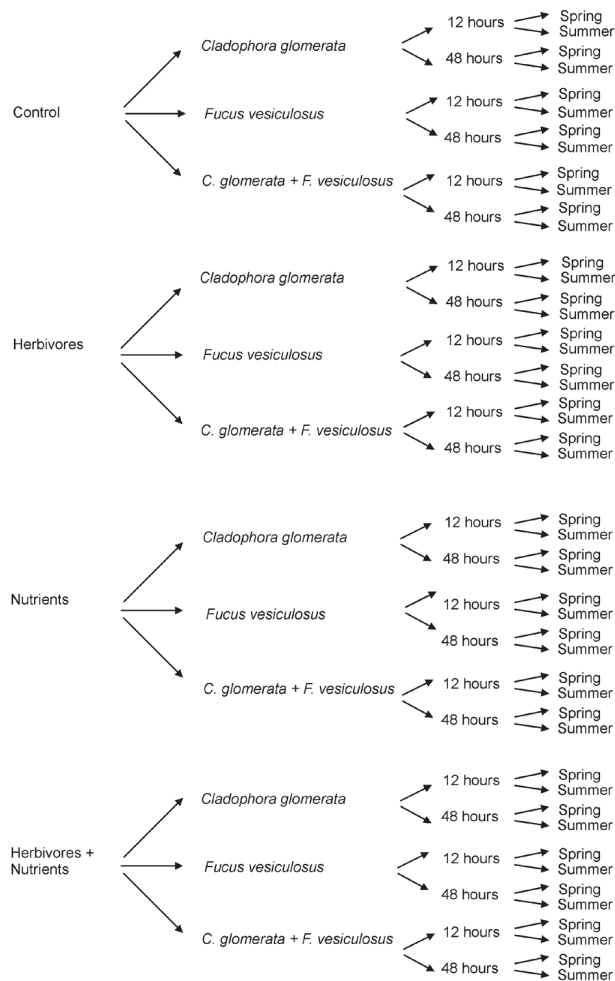
Fig. 1. Experimental design with treatments and levels. Factors and levels were as follows: treatments (control, herbivore addition, nutrient addition, nutrient + herbivore addition), community (*Cladophora glomerata*, *Fucus vesiculosus*, mixture of *C. glomerata* and *F. vesiculosus*), pretreatment duration (12 hours, 48 hours), season (spring, summer). Three replicates for each combination of treatments were used.

similar to field conditions, i.e. at 50–70%. The chamber was deployed on the seafloor close to the site of algal collection in the natural sea water. The photosynthetic production of replicate plots was measured in batches with treatments and replicates assigned to the batches randomly.

Oxygen concentration in the chamber was measured every second using a calibrated Optode type oxygen sensor (Aanderaa Instruments) connected to a data logger (data recorder by Alec Electronics). This instrument also provides data on water temperature. Changes in dissolved oxygen averaged over minute intervals were used as a proxy of the community's net photosynthetic production. Production experiments lasted 40 min. During deployment irradiance above the canopy was measured every minute using a calibrated spherical

quantum sensor connected to a data logger (ultra miniature logger for light intensity by Alec Electronics).

After the experiment, all algae were stored in a deep freezer at −20 °C. The subsequent sorting, counting, and determination of species were performed in the laboratory using a stereomicroscope. The dry weight of species was obtained after drying the individuals at 60 °C for two weeks.

Analysis of covariance (ANCOVA) was used to compare the effect of nutrient addition (levels: added, ambient), herbivores (levels: added, ambient), pretreatment duration (levels: 12, 48 hours prior to experiment), and macroalgal community (levels: community dominated by *C. glomerata*, community dominated by *F. vesiculosus*, a mixed community co-dominated by *C. glomerata* and *F. vesiculosus*) and light (continuous variable) on the photosynthetic production of macroalgal communities between seasons (spring and summer conditions). Post-hoc Bonferroni tests were used to analyse which treatment levels were statistically different from each other. The ANCOVA combines factorial analysis of variance with linear regression (General Linear Model) and the post-hoc Bonferroni test can be used to identify the significant differences between group means in an analysis of variance setting (StatSoft, 2008).

RESULTS

The studied macrophyte communities had a comparatively stable species composition through spring and summer. The macroalgal community dominated by *F. vesiculosus* had a higher number of macrophyte species in spring than in summer, whereas its total biomass was higher in summer than in spring. In contrast, the macroalgal community dominated by *C. glomerata* had a higher number of macrophyte species in summer than in spring and its total biomass was higher in spring than in summer. The macroalgal community dominated by *C. glomerata* had 10-fold lower biomasses compared to the community dominated by *F. vesiculosus* (Table 1). The studied macroalgae had similar net photosynthesis per unit algal mass across communities and through seasons. Only the community dominated by *C. glomerata* had a significantly higher net photosynthesis in summer compared to the spring value (ANCOVA post-hoc Bonferroni test $p < 0.001$). During the experiment the light intensity varied from 534.9 to 2244.3 μmol m^{-2} s^{-1} in spring and from 309.7 to 2222.4 μmol m^{-2} s^{-1} in summer. Within the observed range, light had no effect on the photosynthetic production of the macroalgal community dominated by *F. vesiculosus* (Fig. 2), whereas a clear photoinhibitory effect was observed for the community dominated by *C. glomerata* (Fig. 2).

Table 1. Average biomasses (g dw m^{-2}) $\pm$SE of macroalgal species in the experimental *Fucus vesiculosus* and *Cladophora glomerata* dominated communities in spring and summer

Species	C. glomerata		F. vesiculosus	
	Spring	Summer	Spring	Summer
Ceramium tenuicorne	0	0.008±0.005	0.029±0.018	0
Cladophora glomerata	25.709±2.011	18.101±4.153	0.040±0.026	0.760±0.212
Fucus vesiculosus	0	0	307.487±29.023	418.058±77.806
Pilayella littoralis	0	0.977±0.508	0.071±0.015	1.954±1.201
Ruppia maritima	0	0	0.062±0.040	0
Ulva intestinalis	0.002±0.001	0.003±0.002	0	0
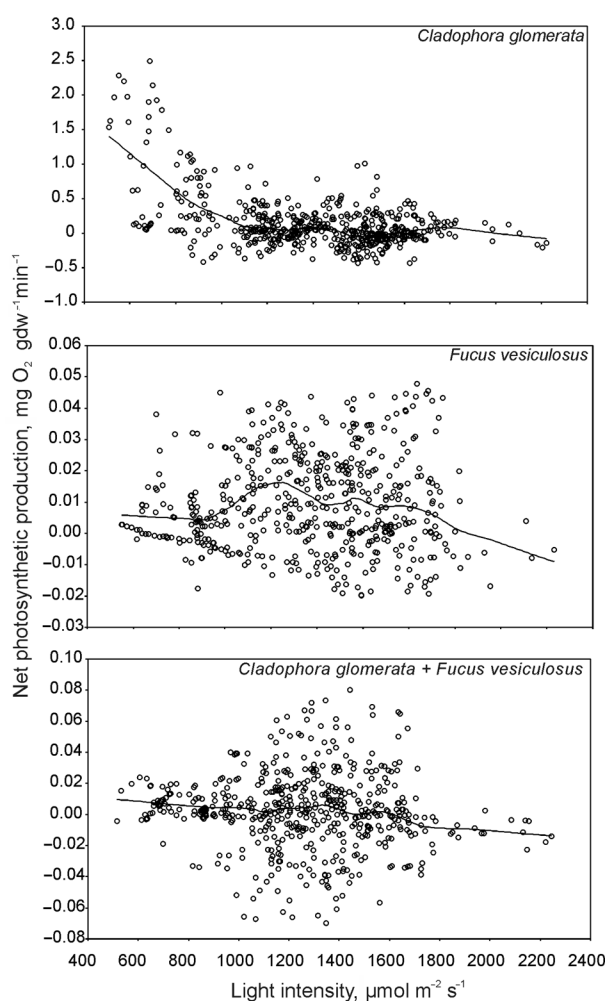
Fig. 2. Relationship between light intensities and net community photosynthetic production of the studied macroalgal communities.

Table 2. ANCOVA analysis on the separate and combined effects of the studied factors and interactions on net community photosynthesis. Factors and levels were as follows: treatments (control, nutrient addition, herbivore addition, or nutrient + herbivore addition), community (*Cladophora glomerata*, *Fucus vesiculosus*, mixture of *C. glomerata* and *F. vesiculosus*), season (spring, summer), pretreatment duration (12 hours, 48 hours). Abbreviations: *SS* – sum of squares, *Df* – degrees of freedom, *MS* – mean square, *F* – F-statistic, *p* – statistical significance level

Effect	*SS*	*Df*	*MS*	*F*	*p*
Intercept	1.155	1	1.155	42.183	<0.001
Light	0.548	1	0.548	20.011	<0.001
1: Treatment	2.493	3	0.831	30.360	<0.001
2: Community	6.830	2	3.415	124.781	<0.001
3: Season	1.171	1	1.171	42.791	<0.001
4: Pretreatment duration	0.003	1	0.003	0.119	0.730
1 x 2	4.606	6	0.768	28.048	<0.001
1 x 3	2.758	3	0.919	33.588	<0.001
2 x 3	5.720	2	2.860	104.495	<0.001
1 x 4	1.651	3	0.550	20.106	<0.001
2 x 4	1.096	2	0.548	20.024	<0.001
3 x 4	1.059	1	1.059	38.680	<0.001
1 x 2 x 3	5.858	6	0.976	35.671	<0.001
1 x 2 x 4	3.939	6	0.657	23.987	<0.001
1 x 3 x 4	2.087	3	0.696	25.419	<0.001
2 x 3 x 4	5.090	2	2.545	92.995	<0.001
1 x 2 x 3 x 4	5.149	6	0.858	31.353	<0.001
Error	42.915	1568	0.027		

The net photosynthesis of the macroalgal communities was affected by all studied factors and interactions except for a separate effect of the duration of manipulation (Table 2). There were clear differences between the communities in the responses (Fig. 3). The experimental manipulation had no effect on the community dominated by *F. vesiculosus* and the mixed community co-dominated by *F. vesiculosus* and *C. glomerata* (ANCOVA post-hoc Bonferroni test $p_{\text{control vs other treatments}} >$ 0.05). In spring the 12-hour addition of herbivores decreased the photosynthetic production of the macroalgal community dominated by *C. glomerata* from a net positive production to respiration (ANCOVA post-hoc Bonferroni test $p_{\text{control vs herbivores}} = 0.007$). In summer, in contrast, the addition of herbivores increased the net production of the community dominated by *C. glomerata* about six times (ANCOVA post-hoc Bonferroni test $p_{\text{control vs herbivores}} < 0.001$).
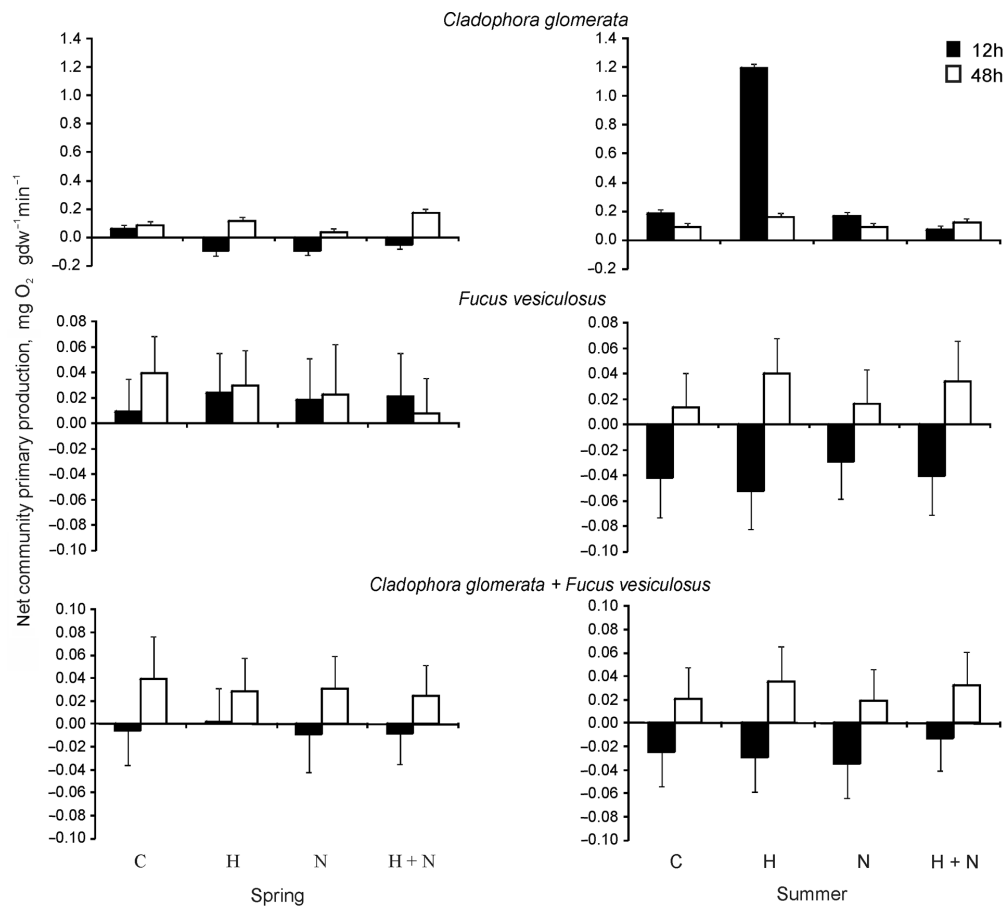
Fig. 3. Net photosynthetic production of macroalgal communities (mean±SE) for each combination of treatments. The code of treatments is as follows: C – control, H – herbivore addition, N – nutrient addition, H + N – herbivore and nutrient addition, 12h – 12 hour pretreatment, 48h – 48 hour pretreatment.

In general, the interactive effect of added herbivores and nutrients on the net photosynthesis of the macroalgal communities was not significant (ANCOVA post-hoc Bonferroni test $p_{\text{herbivores+nutrients vs other treatments}} > 0.05$). In summer, however, the simultaneous addition of nutrients and herbivores reversed a separate effect of added herbivores with photosynthetic production estimated as 2.5 times lower than the control value (ANCOVA post-hoc Bonferroni test $p_{\text{herbivores+nutrients vs control}} = 0.046$). However, this effect was only marginally significant.

All significant effects were observed when the pulse duration did not exceed 12 hours. A 4-times longer manipulation (48 hours) had no effect on the net photosynthesis of the macroalgal community compared to the control values (ANCOVA post-hoc Bonferroni test $p_{\text{control vs other treatments}} > 0.05$).

DISCUSSION

We expected that nutrient enrichment would support elevated macroalgal photosynthetic production, especially the photosynthetic production of ephemeral species, and that the effect would increase with the duration of the enrichment pulse. The hypothesis was not confirmed as nutrient addition did not increase the photosynthetic production of macroalgal communities in any of the nutrient pulse treatments. As shown earlier, *F. vesiculosus* can store nutrients for the periods of depletion (Hemmi et al., 2005), which may explain why its production was not coupled with nutrient levels in the ambient environment. Moreover, a fucoid community may exert a negative feedback on the nutrient enrichment even under short-term exposure (Bergström et al., 2003). On the other hand, *C. glomerata* is thought to be dependent on the immediate supply of nutrients (Wallentinus, 1984; Paalme et al., 2002; Middelboe et al., 2006; Ylla et al., 2007), and strong responses are likely.

Based on previous nutrient pulsing experiments (Lapointe, 1985; Pickering et al., 1993), Worm and Sommer (2000) suggested that the pulse duration should exceed 6 hours in order for macroalgae to effectively raise internal nutrient pools to a critical level required to

sustain a significant response in their growth. Our experiment suggested that this might not be enough and longer exposure to a nutrient pulse, possibly on a time scale of week(s), would be needed in order for macroalgae to effectively increase their photosynthetic productivity.

On the other hand, a short-term nutrient pulse together with the addition of herbivores resulted in a reduced photosynthetic production of the macroalgal community dominated by *C. glomerata* in summer. While earlier field experiments established negative links between nutrient addition and the growth of *F. vesiculosus* (Pedersen and Borum, 1996; Worm and Sommer, 2000; Worm et al., 2000), the reduced photosynthetic productivity of *C. glomerata* at the elevated nutrient level is not corroborated by any field experiment that considered structural elements of the community only.

The wide disparities between photosynthetic production of a community and growth estimates derived from the community's composition may also suggest that there is an additional time lag between a nutrient pulse and the photosynthetic production of the community. It is plausible that the elevated internal nutrient pools do not trigger an immediate response in the photosynthetic productivity of the community, but the productivity is rather a function of interactive effects of multiple extrinsic and intrinsic factors, possibly including the nutrient level in sea water and in macroalgal tissues as well as light and the condition of macroalgae. Specifically, when pulses are of very high concentration, the opportunistic algae can delay growth in favour of saving energy to maximize nutrient uptake and storage (Fong et al., 2004). The explanation of such a relationship is that under a high concentration of nutrients macroalgae prioritize allocation of the available energy and carbon to nutrient uptake and have no energy and fixed carbon left over for growth. It is also plausible that nitrate may inhibit the phosphate uptake directly, for example, by binding to and blocking the phosphate transporter, which results in phosphorus limitation for macroalgae (Lundberg et al., 1989; Turpin, 1991). Moreover, macroalgae, especially their filamentous forms, show the capacity to utilize, quickly absorb, and metabolize different forms of inorganic nitrogen. In chloroplasts nitrate is quickly reduced to ammonium. Under high external nutrient supplies the stored ammonium may reach toxic levels and suppress the photosynthetic production of macroalgae (Lobban and Harrison, 1994; Kevekordes, 2001). In order to detect the exact mode of inhibition, detailed kinetic experiments should be made. Finally, it is also possible that micro-scale ammonium regeneration within the community dominated by *C. glomerata* meets its nutritional needs and therefore its productivity is not coupled with the external supply of nutrients.

We expected that herbivores would have a severe effect on the *F. vesiculosus* community and a moderate effect on the macroalgal community dominated by *C. glomerata* and that nutrient loading might release filamentous algae from the stress induced by herbivores. In our experiment, on the contrary, herbivores affected only the net photosynthetic production of the macroalgal community dominated by *C. glomerata* and nutrient loading did not induce a significant positive feedback.

In spring herbivores had a weak negative effect on the photosynthetic production of the macroalgal community dominated by *C. glomerata*. During this period the community dominated by *C. glomerata* is in its active growth phase, the concentration of nutrients is high in the ambient sea water and low in the algal tissues. Thus, the acquisition of nutrients is energetically demanding and algae may lack resources to cope with such extra herbivory damage. Minor negative effects are also due to low temperatures hindering the recovery of the macroalgal community dominated by *C. glomerata* (Ensminger et al., 2000; Necchi, 2006). Nevertheless, our experiment showed that the filamentous algal community was not too sensitive to elevated herbivory and its growth rates were sufficient to compensate for major grazing impacts, corroborating results of earlier studies (Kotta et al., 2006; Bracken et al., 2007).

Moreover, in summer herbivores strongly promoted the photosynthetic production of the macroalgal community dominated by *C. glomerata*. In the northern Baltic Sea the proportion of senescent and decomposing tissues within filamentous algal communities largely varies among seasons with highest values measured in summer (Kotta et al., 2008a). Considering that herbivores in the study area forage preferentially on ephemeral algae over perennial species (Orav-Kotta and Kotta, 2004) and senescent tissues over fresh algae (Kotta et al., 2006), a short-term grazing would result in the removal of senescent tissues of filamentous algae, promote the photosynthetic production of *C. glomerata*, and prolong the seasonal occurrence of *C. glomerata* in the coastal sea of the eastern Baltic Sea. However, a more intensive grazing would also lead to the removal and/or damage of healthy tissues and thus a decline of the photosynthetic production of the community. The nitrogen excretion by invertebrates (as demonstrated in Bracken and Nielsen, 2004) is not a likely mechanism for the observed mutualistic interaction demonstrated by the lack of positive generic responses of nutrient addition on the net photosynthetic production of the macroalgal community dominated by *C. glomerata*.

In general, our study showed that the addition of nutrients and herbivores had no interactive effect on the net photosynthetic production of macroalgal communities despite the presence of some significant separate effects. The only exception was the simultaneous addition of nutrients and herbivores in summer, which reversed a

separate effect of added herbivores. Nevertheless, this effect was only marginally significant. Although the exact mechanism underlying this discrepancy is not clear, multiple stressors are known to reduce, buffer, or amplify environmental stress due to shifting interactions among species and therefore changing community performance in unpredictable ways (e.g. Pugnaire and Luque, 2003; Kikvidze et al., 2006), i.e. multiple factors may have either synergistic or antagonistic effects if the stress imposed by one factor renders the community more or less susceptible to the other.

The availability of light is another factor that is known to play a crucial role in regulating the photosynthetic production of macroalgae. Furthermore, the photosynthesis–irradiance relationship is expected to vary among macroalgal communities (Wallentinus, 1978; Littler, 1980). In our experiment we observed a clear inverse relationship between light irradiance and the net photosynthetic production of the macroalgal community dominated by *C. glomerata*. As the community dominated by *C. glomerata* has moderate biomasses, the algae become quickly oversaturated by light. If this happens, macroalgae are able to protect themselves against an excessive irradiance by decreasing their photosynthetic activity (Häder and Figueroa, 1997; Ensminger et al., 2000). The observed tendency to declined productivity at around 700 μmol photons $m^{-2} s^{-1}$ corresponds well to the earlier observation by Lester et al. (1988) and Dodds (1991). On the other hand, while our experiment demonstrated a clear light-induced photoinhibition of the net photosynthetic production of the macroalgal community dominated by *C. glomerata*, then the photosynthetic production of the community dominated by *F. vesiculosus* was not coupled with light intensities. The likely mechanism behind the observed pattern is that the morphology of *F. vesiculosus* permits effective utilization of the available light in the canopy. Even if upper parts of the thallus are under oversaturated light conditions, the productivity of the rest of the algal thallus compensates for this reduced photosynthetic production (Sand-Jensen et al., 2007). Moreover, although the photosynthetic productivity of macroalgae is known to vary largely among species (Wallentinus, 1978; Littler, 1980), macroalgal communities maintain almost the same production capacity under a highly fluctuating environment (Middelboe et al., 2006). Specifically, the community dominated by *F. vesiculosus* hosts many epiphytic macroalgal species, different species supplement each other and maximize the use of all available resources, thereby keeping the productivity of the community stable over a broad range of light intensities and providing the assurance in our changing environment (Ridder, 2008).

CONCLUSION

Our results suggest that a short-term elevated level of nutrients and herbivores triggers only moderate responses of the net photosynthetic production of macroalgal communities. Namely, (1) the experimental manipulation had significant effects on the community dominated by the ephemeral *C. glomerata* but not on the community dominated by the perennial *F. vesiculosus* and the mixed community co-dominated by *F. vesiculosus* and *C. glomerata*; (2) longer manipulations annulled the effects of elevated nutrients and herbivory. Our study is the first manipulative experiment in a marine ecosystem that directly quantifies how the nutrient and herbivore-mediated structural differences cascade to the community's productivity. The results show that there exist wide disparities between the photosynthetic production of a community and growth estimates derived from its composition. Consequently, the current study helps us to understand the nature of bottom-up and top-down control of ecosystems and to build up a better conceptual framework of interactions between nutrients, grazing intensities, and the photosynthetic production of macroalgal communities. The results point out that there was no generic response of the productivity of the communities to a short-term grazing activity.

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Eutrofeerumise ja herbivooride lühiajaline mõju makrovetikate koosluste fotosünteesile

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Rannikumere makrovetikate kooslused on maailmas ühed kõige produktiivsemad elupaigad ja ühtlasi on need kogu rannikumere ökosüsteemi toimimise alustalaks, mille käigus toodetakse orgaanilisi ühendeid kõrgematele troofilis-tele tasanditele. Vaatamata suhteliselt suurele makrovetikate uuritusele, pole teada valguse, mineraalsete toitainete kättesaadavuse ja herbivooride asustustiheduse mõju põhjataimestiku koosluste fotosünteetilisele aktiivsusele. Väli-

eksperimentide käigus uuriti eutrofeerumise ja herbivooride lühiajalist interaktiivset mõju makrovetikate koosluste fotosünteetilisele aktiivsusele Läänemere põhjaosas. Fotosünteesi mõõdeti põisadru *Fucus vesiculosus* ja karevetika *Cladophora glomerata* koosluses ning kooslustes, kus nimetatud liike oli katvuse alusel võrdselt. Katsetulemused näitasid, et 12-tunnine toitainetega rikastamine või herbivooride lisamine ei muutnud põisadru *F. vesiculosus* koosluse primaarproduktsiooni. Herbivooride lisamine vähendas *C. glomerata* koosluse fotosünteetilist aktiivsust kevadel ja suurendas suvel. Nii toitainete kui ka herbivooride lisamisel suurenes suvel *C. glomerata* fotosünteetiline aktiivsus. 48-tunnine kõrgendatud toitainete või herbivooride foon ei avaldanud *F. vesiculosus*'e ja *C. glomerata* koosluse produktsioonile olulist mõju. Katsetulemused näitavad, et faktorite koosmõju ei ole tuletatav üksikute faktorite eraldi mõjudest. Uuritud makrovetikate koosluses kohanesid üllatavalt kiiresti suurenenud toitainete kontsentratsioonide ja herbivooride asustustihedusega ehk kooslustele oli iseloomulik väga stabiilne fotosünteetiline produktsioon nii ajas kui ka eri keskkonnatingimuste juures.