



ORIGINAL ARTICLE

Comparisons of individual and community photosynthetic production indicate light limitation in the shallow water macroalgal communities of the Northern Baltic Sea

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Keywords

Baltic Sea; *Cladophora glomerata*; community production; *Fucus vesiculosus*; individual production; photosynthesis; primary production.

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Accepted: 13 December 2012

doi: 10.1111/maec.12074

Abstract

Primary production is of special importance in ecology, since it fuels other trophic levels with energy and biomass. In aquatic ecosystems, almost all primary production is performed by algae. The primary production of aquatic macrophytes has been mainly quantified using detached phyto-elements (fronds and algal thalli) or whole plants, whereas the community level is usually ignored. In a field experiment we evaluated macroalgal photosynthesis at individual and community levels. We used natural communities dominated by the ephemeral green alga *Cladophora glomerata* (L.) Kützting and the perennial brown alga *Fucus vesiculosus* L. *Fucus vesiculosus* had temporally stable and *C. glomerata* highly variable photosynthetic production. On a biomass basis, net and gross photosynthetic production was always higher at the individual level than at the community level. The ratio of individual photosynthetic production to community photosynthetic production increased with light intensities. The observed relationships give clear evidence that in shallow water, where light is supposedly plentiful, macroalgae are nevertheless strongly light-limited. Although photosynthetic production estimates at individual levels are traditionally extrapolated to the community level, such estimates largely overestimate reality and give a false impression of the potential photosynthetic production of macroalgae.

Introduction

Primary production in the sea is the major process that supplies energy and matter to marine organisms. In coastal ecosystems, macroalgae constitute the most productive habitats and virtually all primary production is performed by them (Field *et al.* 1998; Mann 2000). Primary production is limited by abiotic and biotic factors (Field *et al.* 1998; Hauxwell *et al.* 2003), with abiotic constraints being the most important in natural ecosystems (Hill *et al.* 1995).

The availability of light is known to play a crucial role in regulating primary production of macroalgae (e.g. Pagnall & Rudy 1985; Field *et al.* 1998; Hauxwell *et al.* 1998; Duffy & Hay 2000; Binzer *et al.* 2006). The hyperbolic tangent function has been traditionally used to describe the relationship between light and photosynthetic production

(Jassby & Platt 1976) as it can easily represent the transition from one state (light limitation) to another (light saturation). Light limitation may arise from the amount of irradiance arriving at the sea surface but more likely from self-shading. Thus, in addition to the light environment above the algal canopy, macroalgal density and structure determine overall community photosynthetic production. Therefore, it is not only the total light availability but also the distribution of light photons between different parts of the algal thalli that largely determine the community photosynthetic production (Binzer & Sand-Jensen 2002). Often the light is unevenly distributed and most of the photons are absorbed in the upper layers of photosynthetic tissue. Even though algal photosynthesis will be saturated locally with increasing irradiance, community photosynthesis will not become saturated because the lower photosynthetic tissue in the community will have an unused photosynthetic

potential (Binzer & Middelboe 2005). In general, light availability is inversely related to algal densities, is highest in tips and decreases with distance from the tip along the thallus. Shaded algal parts are subject to less seasonal variation in irradiance (Stengel & Dring 1998; Binzer & Sand-Jensen 2002) and, due to photoacclimation, their photosynthetic performance may differ from that of the upper thallus (Middelboe & Binzer 2004; Binzer & Middelboe 2005; Binzer *et al.* 2006).

The shape of irradiance–production curves may vary among macroalgae. Measurements of individual photosynthetic production have shown that thin, sheet-like and filamentous algae are capable of fast growth, which is coupled to high photosynthetic rates per unit biomass (Johansson & Snoeijs 2002). On the other hand, perennial bush-like macroalgae grow slowly and have low photosynthetic rates per unit biomass (King & Schramm 1976; Wallentinus 1984; Middelboe & Binzer 2004; Sand-Jensen *et al.* 2007). Moreover, the relationship and variability between irradiance and photosynthetic production may change with seasonal variations in thallus photosynthesis (King & Schramm 1976; Wallentinus 1978; Stengel & Dring 1998; Middelboe *et al.* 2006).

However, measurements of community photosynthetic production have shown a much more stable photosynthetic production than predicted from their individual photosynthetic production (Middelboe *et al.* 2006). Thus, macroalgae seem not to realize their individual potential at community level due to impoverishment in the light environment within the algal canopy. This allows us to conclude that a three-dimensional structure of communities and high species-richness can make community photosynthetic production more stable and predictable because different parts of the algal canopy and different species complement each other in utilizing all of the available light (Middelboe & Binzer 2004; Middelboe *et al.* 2006).

In a factorial field experiment, we evaluated the photosynthetic production of different species at individual and community levels in the Northern Baltic Sea in May, June and August 2008. The experiment involved shallow-water communities dominated either by the ephemeral green alga *Cladophora glomerata* (L.) Kützinger or the perennial brown alga *Fucus vesiculosus* L. Our hypotheses were as follows: (i) per unit biomass photosynthetic production is higher at an individual level than at community level; (ii) elevated algal biomasses increase light limitation, as shown by larger differences in individual and community level photosynthetic production; (iii) due to higher structural and species diversity, the *F. vesiculosus* community has a more stable community photosynthetic production than the *C. glomerata* community. To date, most of the studies on macroalgal photosynthesis have been con-

ducted under fully marine conditions (e.g. Middelboe & Binzer 2004; Binzer & Middelboe 2005; Middelboe *et al.* 2006). The current study reports the photosynthetic production of macroalgae at a reduced salinity.

Study Area

The study was conducted in the shallow semi-enclosed Kõiguste Bay, Gulf of Riga, Northern Baltic Sea (58°22.10'N, 22°58.69'E). In general, the bottom relief of the area is quite flat, gently sloping towards deeper areas. The prevailing substrate types of the bay are sandy clay mixed with pebbles, gravel or boulders, at between 1 and 4 m. The Gulf of Riga receives fresh water from a huge drainage area and therefore Kõiguste Bay has a reduced and stable salinity of 4.0–6.5 psu and elevated nutrient levels (Kotta *et al.* 2008). The benthic vegetation is well developed (Kersen *et al.* 2011) and an extensive proliferation of ephemeral macroalgae has been reported from the area in the recent years (Lauringson & Kotta 2006).

Material and Methods

In situ experiments were performed adjacent to Kõiguste Marine Biological Laboratory in May, June and August 2008. During the course of the experiment the macroalgal community had 50–70% algal coverage and consisted mainly of *Cladophora glomerata*, *Pilayella littoralis* and *Fucus vesiculosus*.

Stones with growing macroalgae were collected from a shallow (1 m) area and were placed in experimental mesocosms, with replicates in separate chambers. Experimental treatments consisted of communities dominated either by *F. vesiculosus* or *C. glomerata*. Both macroalgae had small amounts of epiphytes, mainly *P. littoralis*, *Ceramium tenuicorne* and *Ulva intestinalis*.

Algal photosynthetic production was estimated each month at individual and community levels over 4 days. On each day, three replicates were made for each combination of treatments. The individual-level photosynthetic production was measured in transparent and dark incubation bottles. About 0.5 g (dry weight) of algal material was incubated in 600-ml transparent and dark glass bottles, filled with the unfiltered seawater and incubated horizontally on special trays at 0.5 m depth. Bottles without algae served as the controls. The community-level production was measured in transparent and dark chambers holding 29 l of water. The surface area of the chamber was 0.08 m². Macroalgal communities were placed in the chamber at coverage relevant to field conditions. The chambers were deployed on the sea floor at 1 m depth, i.e. close to the site of individual-level photosynthetic production estimates.

Oxygen concentration in the incubation bottles and chambers was measured using a calibrated Optode type oxygen sensor (Aanderaa Instruments) connected to a data logger (Compact-Optode data recorder by Alec Electronics). Changes in dissolved oxygen per g dry weight of algal tissue were used as a proxy of photosynthetic production and respiration. Rates of change in the light (includes both primary production and community respiration) indicated community net photosynthesis and rates of change in the dark represented community respiration. Community gross photosynthesis was a sum of community net photosynthesis and respiration. Production experiments lasted 40 min and dark respiration experiments 20 min, respectively. During deployment, the irradiance above the canopy was measured every second 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 and subsequent sorting, counting and determination of algal species were performed in the laboratory using a stereomicroscope. All species were determined to species level. The dry weight (dw) of species was obtained after drying the individuals at 60°C for 2 weeks.

Repeated measures ANOVA was used to compare total macroalgal biomass, community species number and light intensities among macrophyte communities (levels: *Cladophora glomerata*, *Fucus vesiculosus* community) and months (levels: May, June, August). Repeated measures ANCOVA was used to compare the effect of organizational level (levels: individual, community) and macroalgal community (levels: *Cladophora glomerata*, *Fucus vesiculosus* community) on the photosynthetic production of macroalgal communities among months (levels: May, June, August). In the ANCOVA models, light and temperature were included into analysis as time-varying covariates. *Post-hoc* Bonferroni tests were used to analyse which treatment levels were statistically different from each other. Multiple regression analysis was used to learn more about the relationship between light, total macroalgal biomass and the ratio of individual net photosynthetic production to community net photosynthetic production.

Results

On a sample basis the *Fucus vesiculosus* community had on average about fivefold higher biomasses (Fig. 1, repeated measures ANOVA, *post-hoc* Bonferroni test $P < 0.001$) and higher number of macrophyte species compared to the *Cladophora glomerata* communities (Fig. 2, repeated measures ANOVA, *post-hoc* Bonferroni test $P < 0.001$). However, due to more equal spread of biomasses among species, the Shannon diversity values were

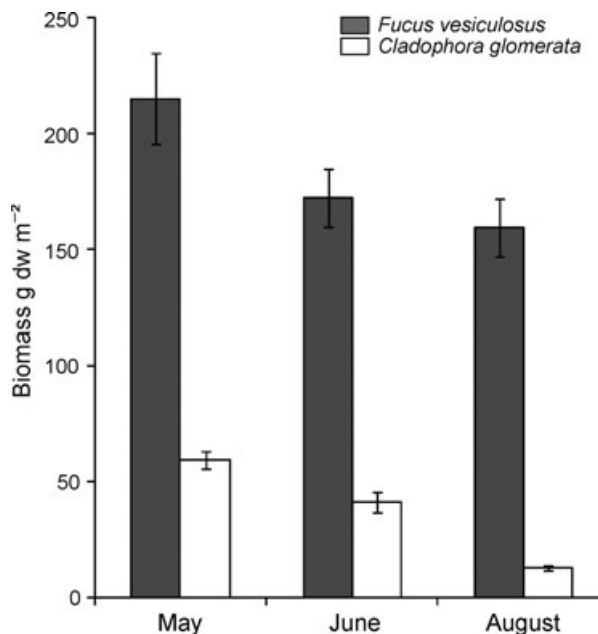


Fig. 1. Average biomasses of the *Fucus vesiculosus*- (F) and *Cladophora glomerata*- (C) dominated communities (means \pm SE) ($\text{g} \cdot \text{dw} \cdot \text{m}^{-2}$) in different months calculated on a sample basis.

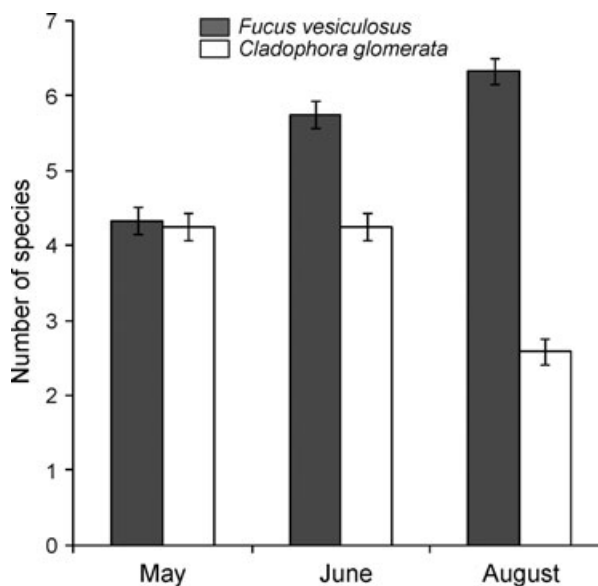


Fig. 2. Average number of species in the *Fucus vesiculosus* and *Cladophora glomerata* dominated communities (means \pm SE) in different months calculated on a sample basis.

higher in the *C. glomerata* community than in the *F. vesiculosus* community (Fig. 3, repeated measures ANOVA, *post-hoc* Bonferroni test $P < 0.01$). When all samples were pooled together, the number of species within the studied macroalgal communities was almost equal (Table 1).

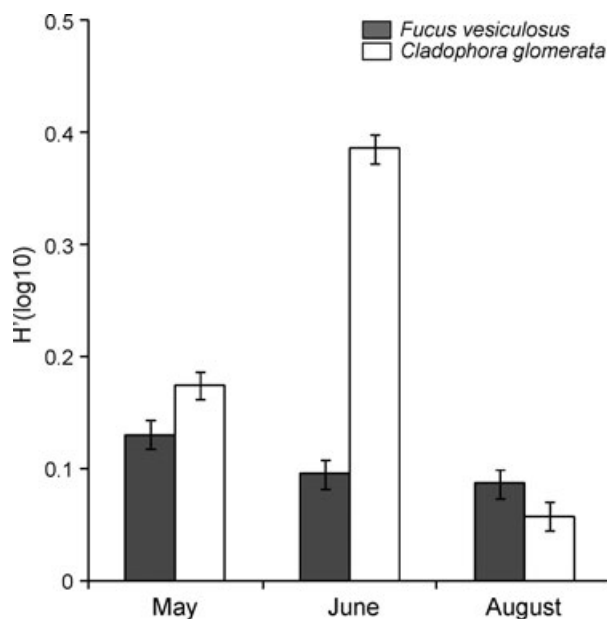


Fig. 3. Shannon diversity index on a log-base-10 scale in the *Fucus vesiculosus* and *Cladophora glomerata* dominated communities in different months calculated on a sample basis.

In terms of dominant species the *F. vesiculosus* and *C. glomerata* communities did not differ largely among months. Thus, seasonal differences were mostly due to the sporadic occurrence or absence of rare species (Table 1). On a sample basis, both studied communities had higher biomasses in May than in August (*post-hoc* Bonferroni test $P < 0.001$) (Fig. 1). Similarly, the *C. glomerata* community had a higher number of macrophyte species in May and June than in August, whereas the *F. vesiculosus* community had a lower number of macrophyte species in May than in June and August (Fig. 2; repeated measures ANOVA, *post-hoc* Bonferroni tests $P < 0.001$). The Shannon diversity of the *C. glomerata* community was highest in June, intermediate in May and lowest in August. The Shannon diversity value in the *F. vesiculosus* community was opposed to the seasonal patterns of species number (Fig. 3; repeated measures ANOVA, *post-hoc* Bonferroni tests $P < 0.001$). In May the studied communities had a similar number of macroalgal species, whereas in June and August the species number of the *F. vesiculosus* community exceeded the values in the *C. glomerata* community (Fig. 2). In May and August there was no difference in the Shannon diversity of the studied communities. In June, however, the *C. glomerata* community had higher Shannon diversity values compared with the *F. vesiculosus* community (Fig. 3; repeated measures ANOVA, *post-hoc* Bonferroni tests $P < 0.001$).

During the measurements of photosynthetic production, light levels within benthic chambers were between

273 and 1929 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Light levels did not differ statistically among macrophyte communities and months (Fig. 4; Table 2; repeated measures ANOVA, *post-hoc* Bonferroni test $P > 0.05$).

The net photosynthetic production of macrophytes (NPP) was significantly affected by almost all studied factors and interactions. The NPP was mostly higher at the individual level than at the community level (Table 2; repeated measures ANOVA, *post-hoc* Bonferroni test $P < 0.05$), estimated at 0.017–0.048 and 0.004–0.037 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ for *F. vesiculosus*, and at 0.011–0.400 and 0.005–0.309 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ for *C. glomerata*, respectively (Fig. 5).

There were clear differences in the NPP between macroalgal species level, with *C. glomerata* having significantly higher NPP compared with *F. vesiculosus* (*post-hoc* Bonferroni test: *C. glomerata* vs. *F. vesiculosus* $P < 0.001$). At the individual level *C. glomerata* had higher photosynthetic production than *F. vesiculosus* in all the months studied (*post-hoc* Bonferroni tests: $P < 0.001$), whereas at the community level the difference was statistically important only in August (*post-hoc* Bonferroni tests: $P < 0.05$). The individual NPP of *C. glomerata* was in the range 0.025–0.059, 0.011–0.098 and 0.082–0.400 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ in May, June and August, respectively. The individual NPP values for *F. vesiculosus* were 0.015–0.034 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ in May, 0.021–0.053 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ in June and 0.022–0.048 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ in August (Fig. 5). The community NPP of *C. glomerata* was in the range 0–0.023, 0–0.095 and 0.006–0.309 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ in May, June and August, respectively. The community NPP of *F. vesiculosus* was 0.001–0.037 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ in May, 0.001–0.028 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ in June and 0.0002–0.012 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ in August.

Fucus vesiculosus had quite stable NPP values, both at community and individual levels (*post-hoc* Bonferroni tests: difference among months $P > 0.05$). In contrast, *C. glomerata* had significantly higher production values at community and individual levels in August compared to May and June (*post-hoc* Bonferroni tests: August vs. May and June $P < 0.001$).

Gross photosynthetic production (GPP) showed similar responses to the studied factors, although the effects were more pronounced compared with NPP (Fig. 6, Table 3). The GPP was always higher at the individual than at the community level, estimated at 0.025–0.054 and 0.004–0.038 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ for *F. vesiculosus* and at 0.035–0.416 and 0.006–0.333 $\text{mg O}_2 \text{ min}^{-1} \text{g}^{-1} \text{dw}$ for *C. glomerata*, respectively.

The ratio of individual NPP to community NPP increased linearly with light intensities, whereas total macroalgal biomass had no separate and interactive effects on this ratio (Table 4). Nevertheless, the ratio varied more below 100 g m^{-2} of macroalgal biomass and

Table 1. Average biomasses of macrophyte species calculated from monthly pooled samples (means \pm SE) (g dw m⁻²) in the *Fucus vesiculosus*- and *Cladophora glomerata*-dominated communities.

Species	Taxonomic group	<i>Fucus vesiculosus</i> community			<i>Cladophora glomerata</i> community		
		May	June	August	May	June	August
Total biomass		215.333 \pm 19.834	172.499 \pm 12.439	159.726 \pm 12.421	59.493 \pm 3.518	41.311 \pm 4.210	12.782 \pm 1.090
<i>Fucus vesiculosus</i>	P	202.305 \pm 20.021	163.737 \pm 11.485	154.272 \pm 12.676	5.902 \pm 2.234	0.005 \pm 0.003	0
<i>Cladophora glomerata</i>	C	2.953 \pm 0.277	3.328 \pm 0.726	0.997 \pm 0.123	30.396 \pm 2.602	17.712 \pm 1.240	12.475 \pm 1.110
<i>Pilayella littoralis</i>	P	7.022 \pm 1.047	3.738 \pm 0.740	3.117 \pm 0.688	5.141 \pm 0.509	10.299 \pm 1.203	0.148 \pm 0.081
<i>Ceramium tenuicorne</i>	R	1.813 \pm 0.267	0.699 \pm 0.080	0.238 \pm 0.035	0.341 \pm 0.062	9.994 \pm 2.342	0.034 \pm 0.012
<i>Sphacelaria arctica</i>	P	0.183 \pm 0.102	0.033 \pm 0.011	0	0	0.273 \pm 0.115	0
<i>Ruppia maritima</i>	A	0	0.022 \pm 0.008	0	0.042 \pm 0.021	0.024 \pm 0.007	0
<i>Ulva intestinalis</i>	C	0	0	0.015 \pm 0.003	0.063 \pm 0.015	0	0.089 \pm 0.020
<i>Dictyosiphon foeniculaceus</i>	P	0	0.01 \pm 0.005	0.06 \pm 0.021	0	0.001 \pm 0.000	0
<i>Elachista fucicola</i>	P	0.277 \pm 0.135	0.576 \pm 0.143	1.005 \pm 0.163	0	0	0
<i>Polysiphonia fucoides</i>	R	0.005 \pm 0.003	0	0.001 \pm 0.001	0.004 \pm 0.002	0	0
<i>Polysiphonia fibrillosa</i>	R	0	0	0.006 \pm 0.003	0	0	0
<i>Potamogeton pectinatus</i>	A	0.016 \pm 0.009	0.068 \pm 0.024	0	0.021 \pm 0.007	0.136 \pm 0.032	0.036 \pm 0.012
<i>Furcellaria lumbricalis</i>	R	0	0.003 \pm 0.002	0.014 \pm 0.006	0.003 \pm 0.002	0.006 \pm 0.003	0
<i>Myriophyllum spicatum</i>	A	0	0	0	0	0.003 \pm 0.002	0
<i>Zannichellia palustris</i>	A	0	0	0	0	0	0
<i>Chorda filum</i>	P	0	0.001 \pm 0.000	0	0.001 \pm 0.000	0	0

The code of plant taxonomic groups is as follows: R = Rhodophyta; P = Phaeophyceae; C = Chlorophyta; A = Angiospermae.

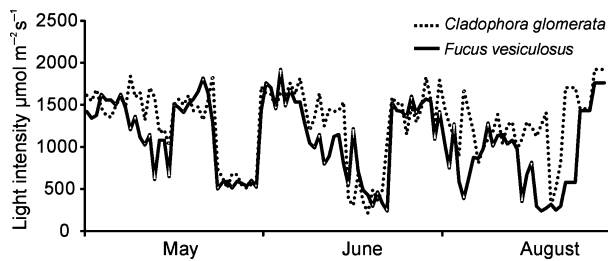


Fig. 4. The variation of light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$) during photosynthetic production measurements of *Cladophora glomerata* and *Fucus vesiculosus* in May, June and August.

Table 2. RM factorial ANOVA analysis on the separate and combined effects of the studied factors and interactions on net photosynthesis.

Source	Numerator df	Denominator df	F	Significance
Intercept	1	86.682	13.6	<0.001
1: Community	1	38.381	55.8	<0.001
2: Organization	1	59.754	34	<0.001
3: Month	2	114.266	17.6	<0.001
1 × 2	1	38.686	12.7	0.001
1 × 3	2	81.952	24.3	<0.001
2 × 3	2	98.784	6.37	0.003
1 × 2 × 3	2	83.129	5	0.009
4: Light	1	110.03	3.75	0.055
5: Temperature	1	86.31	8.28	0.005
4 × 5	1	95.245	3.69	0.058

Factors and levels were as follows: months (levels: May, June, August), organizational level (levels: individual, community), community (levels: *Fucus vesiculosus*, *Cladophora glomerata*). Covariates: (light, temperature).

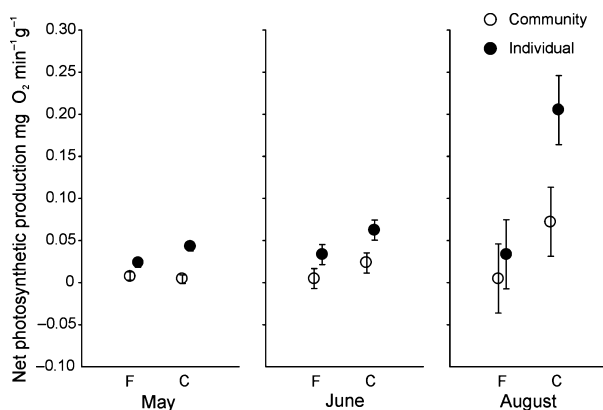


Fig. 5. The net photosynthetic production of macroalgae at individual and community levels in different months (means \pm SE). F = *Fucus* community; C = *Cladophora* community.

levelled off at higher biomasses (Fig. 7). The GPP showed similar responses to increased light intensities as compared with the NPP.

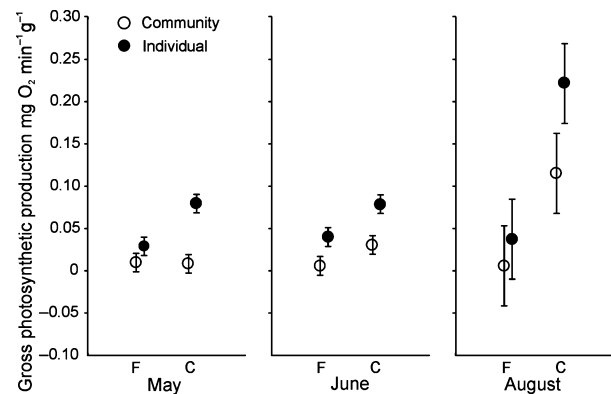


Fig. 6. The gross photosynthetic production of macroalgae at individual and community levels in different months (means \pm SE).

Table 3. RM factorial ANOVA analysis on the separate and combined effects of the studied factors and interactions on gross photosynthesis.

Source	Numerator df	Denominator df	F	Significance
Intercept	1	71.401	7.71	0.007
1: Community	1	39.278	95.28	<0.001
2: Organization	1	61.801	35.35	<0.001
3: Month	2	114.522	12.16	<0.001
1 × 2	1	39.717	12.71	0.001
1 × 3	2	83.390	19.78	<0.001
2 × 3	2	99.593	1.63	0.202
1 × 2 × 3	2	84.391	1.15	0.322
4: Light	1	100.857	2.31	0.132
5: Temperature	1	71.043	3.37	0.071
4 × 5	1	82.978	2.33	0.131

Factors and levels were as follows: months (levels: May, June, August), organizational level (levels: individual, community), community (levels: *Fucus vesiculosus*, *Cladophora glomerata*). Covariates: (light, temperature).

Table 4. Summary table of the linear regression analysis on the separate and combined effects of macroalgal biomass and light on the ratio of individual photosynthetic production to community photosynthetic production ($F_{3,36} = 3.66$, $P < 0.021$, $R^2 = 0.23$).

	Regression coefficients	Standard error of coefficients	t	P
Intercept	-1.029	1.745	-0.590	0.559
1: Macroalgal biomass	0.029	0.015	1.895	0.066
2: Light	0.004	0.001	2.900	0.006
1 × 2	<0.001	<0.001	-1.574	0.124

Discussion

We predicted that photosynthetic production is higher at the individual than the community level. The results of

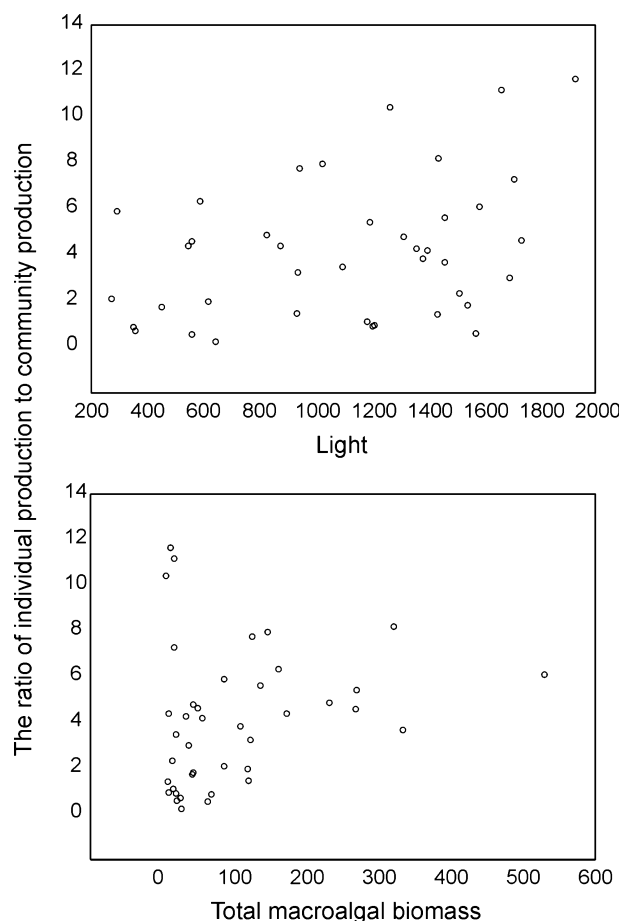


Fig. 7. Relationships between light, total macroalgal biomass and the ratio of individual photosynthetic production to community photosynthetic production.

our experiment agreed with this hypothesis and showed significantly larger individual level photosynthetic production compared with community level photosynthetic production. Likewise, our results confirm that photosynthetic rates were much more variable for individual thalli than communities of the same algae (Binzer & Middelboe 2005; Middelboe *et al.* 2006; Sand-Jensen *et al.* 2007).

At low light intensities a large difference between individual and community photosynthetic production is not expected, as light is not sufficient to induce a positive net photosynthetic production. With increasing light intensities the difference in algal photosynthetic production between community and individual levels is expected to increase due to the greater effect of shading at the community level. The observed relationship was linear and the values of community photosynthetic production did not level off even at high light intensities around 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. This suggests that light saturation

and light inhibition were never observed and the observed macroalgal communities were always light-limited.

We also predicted that elevated algal biomasses increase light limitation as shown by larger differences in individual and community level photosynthetic production. The data did not fully agree with the hypothesis. Instead, the light limitation (i.e. assessed by a ratio of individual to community level photosynthetic production) seemed to be variable at low macroalgal biomasses and displayed uniformly high values at biomasses above 100 g m^{-2} . This suggests that dense macroalgal communities are characterized by near-constant light limitation of photosynthesis regardless of light intensities. This lack of a continuous relationship with macroalgal biomass and light limitation may arise from the morphology of macroalgae. Macroalgae are generally able to become saturated at lower irradiances than terrestrial plants because their non-rigid structure can ensure an even distribution of light among the photosynthetic tissue (Sand-Jensen & Krause-Jensen 1997; Beyschlag & Ryel 1998; Binzer & Sand-Jensen 2002). As the algae are in continuous motion, small changes in biomass might not affect light limitation in the canopy (Hurd 2000). Besides, the different parts of macroalgal thalli have variable capabilities to utilize irradiance depending on their absorption abilities, potential to carry out photosynthesis and capacity to distribute irradiance (Binzer & Middelboe 2005).

Finally, we predicted that owing to higher structural and species diversity, the *Fucus vesiculosus* community would have a more stable community photosynthetic production than the *Cladophora glomerata* community. The results of our experiment agreed with this hypothesis. Within a diverse community of *F. vesiculosus*, different species complement each other spatially and temporally and thus such a functional redundancy in the community has a positive and stabilizing effect on production (Middelboe *et al.* 2006; Sand-Jensen *et al.* 2007). In fact variable or high abundance of species can ensure stable and predictable community metabolism, because different species complement one another in utilizing all of the available light (Middelboe *et al.* 2006). Moreover, as compared with the light environment above algae, the natural variability in light intensity within the algal canopy is not large and therefore low variability in community photosynthetic parameters and production capacity is expected (Sand-Jensen *et al.* 2007). In addition, the perennial *F. vesiculosus* plants are relatively resistant to physical disturbances, independent of the direct resource acquisition and therefore vary less in their occurrence and biomass seasonally, as compared with *C. glomerata* (Pedersen & Borum 1996; Kiirikki & Lehvo 1997). On the other hand, the filamentous *C. glomerata* may occasionally bloom and have a high productivity (Littler & Littler 1984) but even

small physical disturbances may severely damage the photosynthetic tissues of the algae and result in a large decrease in the community photosynthetic production.

Reduced salinity is known to decrease the photosynthetic production of macrophytes (Pregnall & Rudy 1985; Koch & Lawrence 1987; Phooprong *et al.* 2007). As our measurements were conducted at a low salinity level (Kotta *et al.* 2008; Lauringson *et al.* 2009), the observed differences in the macroalgal photosynthetic production between individual and community levels are expected to be even larger in fully marine conditions. This is also confirmed when comparing our estimates with the published data on the macroalgal photosynthetic production. Although different studies report in different units, the photosynthetic production values are much lower in our study than those measured under fully marine conditions (Middelboe & Binzer 2004; Binzer & Middelboe 2005; Middelboe *et al.* 2006).

To conclude, the observed relationships give clear evidence that in shallow water, where light should be plentiful, macroalgal communities are nevertheless strongly light-limited. Although the photosynthetic production estimates at individual level are traditionally extrapolated to the community level, such estimates largely overestimate reality and give a false impression of potential photosynthetic production of macroalgae. In addition, this study adds to the knowledge of how the canopy-forming algae provide not only biodiversity (Kotta *et al.* 2000; Råberg & Kautsky 2007; Wikström & Kautsky 2007) but also stable photosynthetic production (i.e. food and habitat resource) through the large range of hydrographic conditions.

Acknowledgements

Funding for this research was provided by Institutional Research Funding IUT02-20 of the Estonian Research Council, the Estonian Science Foundation grants 7813 and 8254, the Central Baltic Interreg IVa Programme HISPARES, the projects 'The status of marine biodiversity and its potential futures in the Estonian coastal sea' no. 3.2.0801.11-0029 and 'EstKliima' no. 3.2.0802.11-0043 of the Environmental Protection and Technology Programme of the European Regional Fund and Archimedes Foundation (Estonia, DoRa programme 8).

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