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In situ production of charophyte communities under reduced light conditions in a brackish-water ecosystem

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Abstract. There is a lot of circumstantial evidence that light conditions affect the growth and distribution of charophyte communities. In general, limited light availability causes plants to reduce their growth and ultimately disappear from the area. We experimentally evaluated how reduced water transparency affected the photosynthetic production of a charophyte community dominated by *Chara aspera* and *C. canescens* in a brackish-water ecosystem of Haapsalu Bay in June–July 2009. Plastic shades were used to manipulate light conditions in the experimental plots. Two types of nets were used so that plants received either 25% or 50% of the natural irradiance relative to the control community (100%). The results clearly demonstrated that light limitation significantly reduced the net photosynthetic production of charophytes, but a considerable effect was observed within the first 24 h only. What is more significant, the charophyte community recovered its photosynthetic production within two weeks of the experiment in spite of the constant reduction of light down to 25% of the natural irradiance. This suggests that charophytes are able to adapt to a low light environment and recover their photosynthetic performance within a short period even under stressful brackish-water conditions.

Key words: macroalgae, charophytes, photosynthetic production, net photosynthesis, experiment, light conditions.

INTRODUCTION

Charophyte communities are an important element in shallow enclosed fresh- and brackish-water ecosystems (Mathieson and Nienhuis, 1991; van den Berg et al., 1998; Pełechaty et al., 2006). They provide shelter and habitat for numerous species including epiphytic microalgae, filamentous macroalgae, as well as various crustacean and insect species (Lindén et al., 2003; Schmieder et al., 2006; Torn et al., 2010). Besides, charophytes are an important component in the food web as part of the diet of benthic invertebrates (Kotta et al., 2004, 2013), waterfowl (Noordhuis et al., 2002; Schmieder et al., 2006), and fish and fish larvae (de Winton et al., 2002; Dugdale et al., 2006).

Declining distribution and diversity of charophytes have been observed in many regions worldwide including the brackish Baltic Sea (Blindow, 2000, 2001; Schubert and Blindow 2003; Munsterhjelm, 2005). Eutrophication is assumed to be the most important threat to charophytes causing their decline (e.g. Blindow, 1992; Auderset Joye et al., 2002). The main effect associated with eutrophication is the bloom of ephemeral planktonic algae, which leads to increased sedimentation, water turbidity and, as a result, reduced light availability. The shortage of light may reduce the photosynthetic production and growth of charophytes down to the level where their sustainable development becomes impossible (Blindow et al., 2002; Johnsen and Sosik, 2004; Hautier et al., 2009; Dickey et al., 2011).

On the other hand, charophytes often prefer soft bottom habitats where even moderate wind may cause sediment resuspension and sedimentation of particles on the plant surface. In such habitats underwater light climate is naturally very variable (Schneider et al., 2006 and references therein). Thus, charophytes are adapted to periodic stress of low light intensities. Nevertheless, the interactive effect of elevated eutrophication and weather variables may result in poorer light conditions than expected from their separate effects (Blindow et al., 2003; Kling et al., 2003).

So far, the studies concerning photosynthesis of charophytes are mainly based on laboratory experiments with either detached pieces or single individuals (e.g. Blindow et al., 2003; Marquardt and Schubert, 2009). Very few have been carried out in the natural environments, especially in brackish bodies of water. As compared to their freshwater counterparts, charophytes are often naturally stressed at elevated salinity and therefore are expected to respond differently to changes in light conditions (e.g. Blindow et al., 2003). The existing data on in situ primary production of charophytes related to light limitation are scarce and hardly comparable because of difference in methodologies and the environmental conditions among habitats (Kufel and Kufel, 2002).

Light is a key limiting factor for photosynthetic production in aquatic environments (Kurtz et al., 2003; Asaeda et al., 2004, Binzer et al., 2006; Zhang et al., 2010). Earlier experimental studies carried out at the community level have also shown that canopy density and canopy structure significantly affect the photosynthetic production of marine macroalgae (Middelboe et al., 2006). This suggests that macroalgal communities are largely light-limited and such light limitation increases with canopy height and/or community biomass (Pärnoja et al., 2013). Altough the photosynthetic production of marine macroalgae at the community level has been increasingly studied (Middelboe and Binzer, 2004; Middelboe et al., 2006; Pärnoja et al., 2013), to the best of our knowledge, there is only a single study on charophyte communities (Libbert and Walter, 1985).

Based on the above, our goal was to determine the primary production of a charophyte community under manipulated in situ light conditions. We hypothesized that (a) the community would have higher responses under more severe light limitation and (b) the recovery of charophyte photosynthetic performance would be faster under less severe disturbances.

MATERIAL AND METHODS

The study was conducted in the shallow semi-enclosed Haapsalu Bay, the Baltic Sea (Fig. 1). The bay is situated in the Väinameri area, which is a low-water region between continental Estonia and its western islands. The surface area of Haapsalu Bay is only 50 km^2. The bottom sediments are sands, gravels, and clays of various structure. The bay is relatively shallow, with a maximum depth of less than 5 m and an average depth of 2 m. Extensive soft-bottom shallows and relative isolation from waves make Haapsalu Bay an ideal habitat for charophytes. Well-developed charophyte communities are observed from the seashore at depths to 1 m, but single plants may occur down to 3 m depth (Kotta et al., 2008 and references therein).

The light reduction experiment was conducted at 0.7–1 m depth (58.96 N, 23.55 E). The main sediment types in the experimental area were sand and silt. The salinity varied within 5–6. The study site was fully covered by a well-developed community of *Chara aspera* C. L. Willdenow and *Chara canescens* J. L. A. Loiseleur-Deslongschamps. The charophytes were partly covered by the filamentous epiphytes *Cladophora glomerata* (Linnaeus) Kützing and *Pilayella littoralis* (L.) Kjellmann. The canopy height was about 15–20 cm. There was no spatial difference in community composition, height and cover of charophyte canopy within the study area.

The experiment was performed from the late June to the early July 2009 and lasted two weeks. Plastic shades were used to manipulate light conditions in the

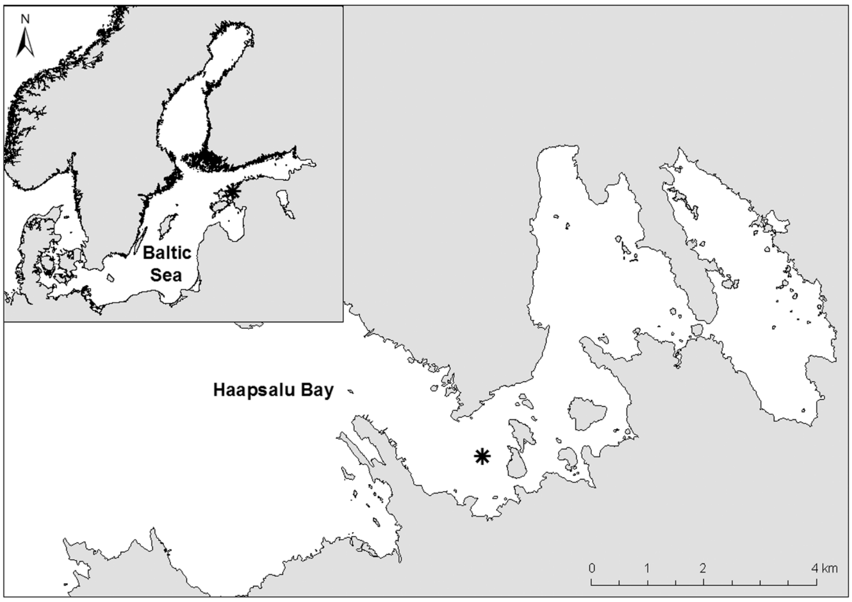

Fig. 1. Location of the study area in Haapsalu Bay.

experimental plots. Light exclusion shades were constructed using 1.2 m × 1.2 m wooden frames affixed with a plastic net. Two types of net were used so that plants received either 25% or 50% of the natural irradiance relative to the control community (100%). Experimental plots were randomly chosen within the community of *C. aspera* and *C. canescens*. Metal posts were driven into the sediment and frames were fixed on them at a depth of 0.5 m above the bottom sediments. Three replicate plots were used for each light treatment (25%, 50%, and 100%). Experimental plots were shaded during the whole two-week experimental period. The photosynthetic production of charophyte plots was measured on the 2nd and the 14th day of the experiment.

In order to determine the species composition and biomass of the charophyte community, a rectangular frame with a size of 0.2 m × 0.2 m was used to collect quantitative samples. For the estimation of the initial biomass of the charophyte community three frame samples were taken adjacent to the experimental plots during the 2nd day of the experiment. Additionally, one sample was taken from all experimental plots at the end of the experiment. The samples were stored in a deep freezer at –20 °C with a subsequent sorting and determination of algal species in a laboratory using a stereomicroscope. The dry weight of each species was obtained after drying the material at 60 °C to constant weight (HELCOM, 2014).

The photosynthetic production of the charophyte community was measured in a transparent chamber. The surface area of the chamber was 0.08 m^2 and its volume was 29 L. The chamber was placed on the sediment of the experimental plot. During incubations the circulation of water between the chamber and the environment was eliminated. All manipulations were done on foot and utmost care was taken to avoid resuspended sediment to be transported into experimental chambers. Oxygen concentration in the chamber was measured every second using a calibrated Optode type oxygen sensor (Aanderaa Instruments) connected to a data logger (Optode data recorder by Alec Electronics). The sensor also provided water temperature data. Photosynthetically active irradiance (PAR) just above the charophyte meadow was also measured every second using a calibrated spherical quantum sensor connected to a data logger (Optode data recorder by Alec Electronics). Changes in dissolved oxygen were used as a proxy of photosynthetic production. The changes had to remain constant for at least 10 min in order to be considered as valid measurements. Each incubation lasted 30 min. During each experimental day three incubations were carried out within each experimental plot to cover differences in daily light regimes. The measurements were performed simultaneously in control and experimental chambers. The photosynthetic production of algal communities was expressed as the mean change of dissolved oxygen during incubation per time unit and dry weight of algae. These incubation means were used in the further statistical analysis.

In order to assess the relative contribution of experimental light manipulation and temporal variability in natural light conditions to the variability of photosynthetic production of the charophyte community, the Boosted Regression Trees (BRT) modelling was used. The BRT model iteratively develops a large ensemble of small regression trees constructed from random subsets of data. Each successive tree predicts the residuals from the previous tree to gradually boost the predictive performance of the overall model. The BRT modelling has no need for prior data transformation or elimination of outliers and can fit complex nonlinear relationships. What is most important in the ecological perspective, it automatically handles the interaction effects between predictors (Elith et al., 2008).

In addition, one-way ANOVA was used to seek the effect of experimental light manipulation on the photosynthetic production of the charophyte communities. Fisher's Least Significant Difference post-hoc test was used to analyse the statistical significance of predicted differences among light treatment levels (25% and 50% of the natural irradiance or control).

RESULTS

The dry biomass of the charophyte community varied between 60 and 116 g m^{-2} in the experimental plots. The most abundant species was *C. aspera*, which contributed on average 75% of the community's biomass. It was followed by *C. canescens* with a share of 23%. The epiphytic *C. glomerata* and *P. littoralis* constituted only about 1% of the community's biomass. The biomasses of other species, the chlorophytes *Monostroma balticum* (Areschoug) Wittrock and *Ulva intestinalis* L. and the vascular plants *Myriophyllum spicatum* L., *Najas marina* L., and *Zannichellia palustris* L. were below 0.01 g m^{-2}.

During incubations the values of natural irradiance varied between 225 and 1410 µmol m^{-2} s^{-1}, depending on the time and day of the experiment. Due to varying weather conditions charophytes received less light on the 14th day compared to the 2nd day of the experiment. The values of maximum and minimum irradiance on the 14th day of the experiment were 72.9% and 21.5% of the 2nd day values, respectively.

The BRT model described a total of 81% of the photosynthetic production of the charophyte community. BRT analysis showed that the experimental light manipulation contributed 90% of the observed variability of photosynthetic production whereas diel and daily differences in the natural light level accounted only for 10% of the observed variability (Fig. 2).

Similarly, ANOVA results showed that the experimental light manipulation significantly affected the photosynthetic production of the charophyte community (Table 1, Fig. 3) whereas temporal variability in the ambient light conditions was statistically nonsignificant (Table 2, post-hoc test on differences in the photosynthetic production of control treatments between the 2nd and the 14th day of the experiment $p = 0.48$). The ANOVA tests also showed that light reduction significantly decreased the net photosynthetic production of charophytes. Statistical differences were observed during the 2nd day of the experiment with a reduced photosynthetic production. The differences occurred at all levels of light reduction treatments compared to the control values (see the results of a post-hoc Fisher's LSD test in Table 2 and Fig. 3).

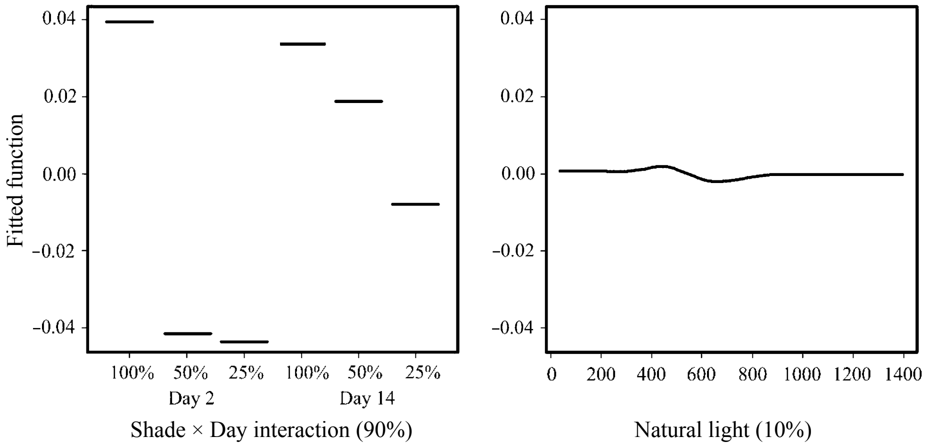

Fig. 2. Partial dependence plots showing the effect of the ambient light condition and experimental light manipulation on the photosynthetic production of the charophyte community. The contribution of each variable to the model is shown in brackets.

Table 1. Results of one-way ANOVA on the effects of light availability on the photosynthetic production of charophytes. Statistically significant effects are presented in bold

		Sum of squares	Mean square	F	Significance
Day 2	Intercept	0.0156	0.0156	1.9518	0.1717
	Light	**0.1214**	**0.0607**	**7.5985**	**0.0019**
Day 14	Intercept	0.0124	0.0124	1.2180	0.2777
	Light	0.0137	0.0068	0.6706	0.5182

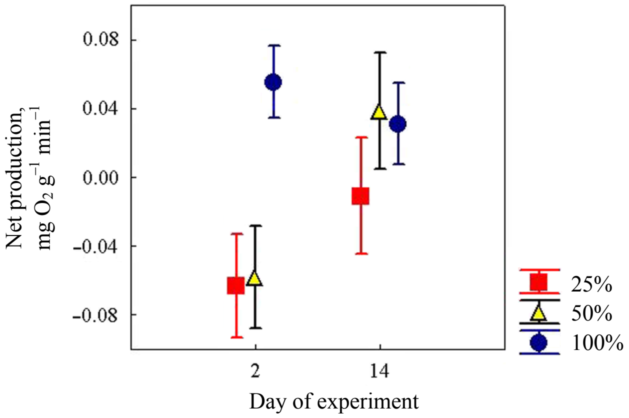

Fig. 3. Mean net photosynthetic production of the charophyte community (±SE) under different light regimes on different days of the experiment. The percentage refers to the amount of natural irradiance penetrated to the charophyte community.

Table 2. The results of the Fisher's Least Significant Difference post-hoc test about the effects of light reduction on the photosynthetic production of the charophyte community. Statistically significant differences between different light levels are presented in bold. The percentage refers to the amount of natural irradiance penetrated to the charophyte community

		25%		50%		100%	
		Day 2	Day 14	Day 2	Day 14	Day 2	Day 14
25%	Day 2		0.2893	0.9117	**0.0271**	**0.0034**	**0.0183**
	Day 14	0.2893		0.2974	0.2756	0.0932	0.2847
50%	Day 2	0.9117	0.2974		0.0546	**0.0049**	**0.0252**
	Day 14	**0.0271**	0.2756	0.0546		0.6655	0.8492
100%	Day 2	**0.0034**	0.0932	**0.0047**	0.6655		0.4828
	Day 14	**0.0183**	0.2847	**0.0252**	0.8492	0.4828	

By the 14th day of the experiment, statistical differences in the photosynthetic production of the charophyte community between the different levels of light reduction treatment and control values had disappeared (Table 2, Fig. 3). The lack of statistical differences indicated a quick recovery of charophyte communities under constant reduction of light.

DISCUSSION

Our experiment showed that a reduced light availability diminished the photosynthetic production of the charophyte community. We expected higher and more significant responses under more severe light limitation; however, this expectation did not hold true. The observed light limitation was short-term only, and within two weeks of constant shade the charophyte community had recovered in its photosynthetic production. We also expected that the responses of charophyte photosynthetic performance would be faster under less severe disturbances, but again the expectation did not hold true. Nevertheless, on the 14th day the charophyte community exposed to 25% of the natural irradiance had a much lower photosynthetic production than the control; however, owing to the large variability of the 25% light reduction treatment, differences between the control and the treatment were not statistically significant. This suggests that charophytes are able to adapt to a low light environment and recover their photosynthetic performance within a short period; moreover, the extent of recovery is largely not related to the severity of light stress. Earlier studies suggest that the mechanism optimizing the photosynthetic efficiency of charophytes under impoverished light conditions is most probably related to an increased production of photosynthetic pigments and chloroplasts leading to an enhanced efficiency of photosynthetic activity, which helps plants to recover when light becomes limiting (e.g. Andrews et al., 1984; Küster et al., 2000; Asaeda et al., 2004; Copertino et al., 2006; Marquardt and

Schubert, 2009). Nevertheless, our study also suggests that charophyte communities experiencing light reduction more than 50% of natural values are expected to be highly variable in their photosynthetic performance and therefore vulnerable to further disturbances.

Charophytes have been also previously reported to be relatively resilient to adverse environmental conditions (Schwarz et al., 1999; Küster et al., 2000, 2004). Specifically, following the experimentally induced massive sedimentation, the growth of charophytes remained unchanged for ten days (Henricson et al., 2006). Nevertheless, disturbance longer than that significantly decreased their growth and ultimately resulted in their death (Henricson et al., 2006). Thus, charophytes seem to recover easier from constant light reduction than sedimentation. Another study about the effect of encrustation on the photosynthetic performance of charophytes demonstrated negligible differences in the photosynthesis–irradiance curve among unencrusted and heavily encrusted plants (Marquardt and Schubert, 2009). Such results also indicate that charophytes efficiently adjust to the changing light conditions and confirm their short-term acclimation ability under adverse light conditions. According to the earlier investigations (Küster et al., 2004), the optimal irradiance for the vegetative growth of *C. canescens* ranges from 35 to 380 µmol m^{-2} s^{-1}. Taking this into account, the charophyte community under study at 25% of the natural irradiance actually experienced adverse light conditions.

Nevertheless, numerous studies have suggested a direct dependence of charophytes on light availability (e.g. Libbert and Walter, 1985; Blindow, 2000; Schneider et al., 2006), although differences between species are large (Küster et al., 2004; Sorrell et al., 2012). Several authors proposed that a reduction of water transparency and associated light limitation under elevated eutrophication are a primary factor leading to the decline of charophytes (e.g. Kufel and Kufel, 2002; Schubert and Blindow, 2003; Langangen, 2007). Such evidence, however, is largely circumstantial. Our experiment showed that when light became less available, the photosynthetic production of charophytes significantly dropped. However, within a short period of time charophytes were able to increase their photosynthetic performance to the pre-disturbance level, demonstrating thus their adaptation potential to a broad range of reduced light conditions. Thereby, it may reasonable to suggest that although moderate light limitation has profound effects, it need not be a prime reason for the observed charophyte decline in many water bodies. Instead, an elevated eutrophication may induce a bloom of filamentous macroalgae and aquatic vascular plants and the blooming macrophytes may ultimately outcompete charophytes (van den Berg et al., 1998). It is also reasonable to assume that charophytes are exposed to the combination of stresses that may lead to their decrease. Specifically, under constant light reduction charophytes are expected to grow more quickly towards the surface layer where light is more plentiful. This in turn results in tall but weak plants (Andrews et al., 1984; Henricson et al., 2006). Such plants are very sensitive to any environmental disturbances, including increased sedimentation, ice scrape, and wave action (Henricson et al., 2006; Kovtun et al., 2011) and therefore a notable loss of biomass is likely.

It can be concluded that the photosynthetic production of a charophyte community is significantly influenced by light availability, but under constant reduction of light the community is able to largely recover its photosynthetic performance. Thus, the experiment points out that charophytes are able to quickly adapt to a broad range of changing environmental conditions. Although our experiment did not reveal the point where the recovery of charophytes seems impossible, it is plausible that such light conditions are naturally not observed in the studied charophyte habitat even under severe eutrophication or climate change conditions. It is also reasonable to assume that a decline of charophytes documented in many areas of the Baltic Sea is not directly related to water transparency, but is a result of interspecific competition, morphological changes, and/or a critical combination of other threats.

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