



## Results of laboratory and field experiments of the direct effect of increasing CO<sub>2</sub> on net primary production of macroalgal species in brackish-water ecosystems

Liina Pajusalu<sup>\*</sup>, Georg Martin, Arno Põllumäe, and Tiina Paalme

Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia

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**Abstract.** Studies on the effects of increasing acidification on marine communities have been previously mostly carried out in truly marine areas whereas brackish-water ecosystems such as the Baltic Sea have been less studied. The current study analyses how acidification induced by elevated atmospheric carbon dioxide affects the photosynthetic net production of different macroalgal species in the brackish Baltic Sea. Research methods include sets of laboratory and field experiments carried out in shallow coastal brackish waters. The aim of the laboratory experiments was to develop the necessary techniques and experience for the mesocosm experiments. Laboratory experiments were carried out using specimens of the red alga *Furcellaria lumbricalis* collected from Kakumäe Bay. The mesocosm experiments were conducted in Kõiguste Bay during the field season of 2011. Separate mesocosms were operated in each set with different CO<sub>2</sub> concentrations and a control treatment in natural conditions. Field experiments were carried out with three species representing three different morphological and ecological groups: *Ulva intestinalis*, a fast-growing green alga; *Fucus vesiculosus*, a perennial brown alga with a slow metabolism; and *Furcellaria lumbricalis*, a perennial red alga. Photosynthetic activity was used as the response variable. In the laboratory decreasing pH increased the net primary production of *F. lumbricalis* with the lowest net primary production values measured at pH 8.0 and the highest at pH 6.5. Results of the field experiments indicated that increased CO<sub>2</sub> levels in seawater favoured photosynthetic activity of the macroalgae *U. intestinalis* and *F. lumbricalis*, but *F. vesiculosus* showed no response to elevated CO<sub>2</sub>. Elevated CO<sub>2</sub> levels are suggested to favour the production of fast-growing filamentous species, which thus may indirectly enhance the effect of eutrophication in the shallow coastal brackish waters.

**Key words:** carbon dioxide, Baltic Sea, marine acidification, *Furcellaria lumbricalis*, *Ulva intestinalis*, *Fucus vesiculosus*, net primary production.

### INTRODUCTION

Evidence on a continuous increase in atmospheric CO<sub>2</sub> is not under discussion any more. Studies show that atmospheric CO<sub>2</sub> has increased from 280 to 370  $\mu\text{atm}$  during the last 200 years, which has caused a decrease of 0.08 pH units in the ocean surface water during the same period (Khesghi, 1995). Scenario modelling suggests that there could be a continuous drop of 0.5 units in pH by the year 2100 (Caldeira and Wickett, 2003; Raven et al., 2005). Estimates suggest that ocean acidification in

the Baltic Sea may cause a  $\leq 3$  times increase in acidity (reduction of 0.2–0.4 pH units) by the year 2100 (Havenhand, 2012).

Ocean acidification is still a developing research subject and there is a need to develop experimental techniques and approaches, as well as to collect in situ field data. So far perturbation experiments are one of the key approaches used to investigate the biological response to elevated partial pressure of carbon dioxide ( $p(\text{CO}_2)$ ) (Gattuso and Lavigne, 2009). The whole topic is complicated due to the fact that experiments to determine the biological effects of increased CO<sub>2</sub> on marine organisms are not straightforward because of the

<sup>\*</sup> Corresponding author, [liina.pajusalu@ut.ee](mailto:liina.pajusalu@ut.ee)

complicated chemical processes in seawater associated with pH alteration. The carbon speciation in seawater has changed, which has strong implications for photosynthesis, respiration, and calcification (Hurd et al., 2009). The effect of changes in  $p(\text{CO}_2)$  could potentially have a strong effect especially on organisms inhabiting coastal shallow-water systems. In these ecosystems marine macroalgae play the most important role in the carbon cycle (Gao et al., 1999). Shifts in seawater pH may be significant in shallow areas with high plant densities when water movement is restricted (Semesi et al., 2009). Periods of high pH will occur when photosynthetic production is high and carbon dioxide is removed, causing a decrease in total inorganic carbon availability and an increase in the pH of the surrounding water (Middelboe and Hansen, 2007; Semesi et al., 2009). However, the effect of continuous elevated CO<sub>2</sub> background forcing is not known and we are aiming at studying the response to such elevated stress factors.

So far research into water-column and benthic processes associated with changes in  $p(\text{CO}_2)$  has focused mostly on calcifying organisms (Connell and Russell, 2010; Fernand et al., 2011). There is evidence that a change in  $p(\text{CO}_2)$  and the accompanying acidification can influence the physiological functions of all algae, both calcareous and non-calcareous. However, there are very few studies showing the impact of elevated CO<sub>2</sub> on calcareous and non-calcareous macroalgae (Hurd et al., 2009). Even though some recent studies have found the effects of anticipated levels of acidification on calcareous temperate algae (e.g. Martin and Gattuso, 2009), only a few have studied the effects of elevated CO<sub>2</sub> and temperature on non-calcareous species. Connell and Russell (2010) for example investigated these effects on the kelp *Ecklonia radiata*. In this study we used as a test species *Fucus vesiculosus*, which is a canopy-forming species like kelps.

Some macroalgal studies have shown a negative effect of acidification on particular species, while other species show positive or no response to increasing CO<sub>2</sub> (e.g. Israel et al., 1999; Israel and Hophy, 2002; Connell and Russell, 2010; Porzio et al., 2011). There is evidence that seagrasses seem to be favoured by elevated CO<sub>2</sub> levels (Palacios and Zimmerman, 2007; Hall-Spencer et al., 2008; Eklöf et al., 2012).

So far most acidification studies have focused on the open-ocean systems and very little has been done in the shelf and coastal sea environments (Fernand et al., 2011). In the Baltic Sea there is not much scientific evidence of changing pH in the seawater in the open parts but significant effects of acidification have been reported from several coastal areas affected by direct freshwater runoff (e.g. Urho et al., 1990). The number of studies dealing with the effect of acidification on the Baltic Sea biota is very limited.

The aims of the current study were (1) to investigate the short-term variability of  $p(\text{CO}_2)$  and pH in natural conditions and (2) to examine the direct effect of increasing CO<sub>2</sub> on the photosynthetic net primary production of coastal macroalgae in shallow brackish waters.

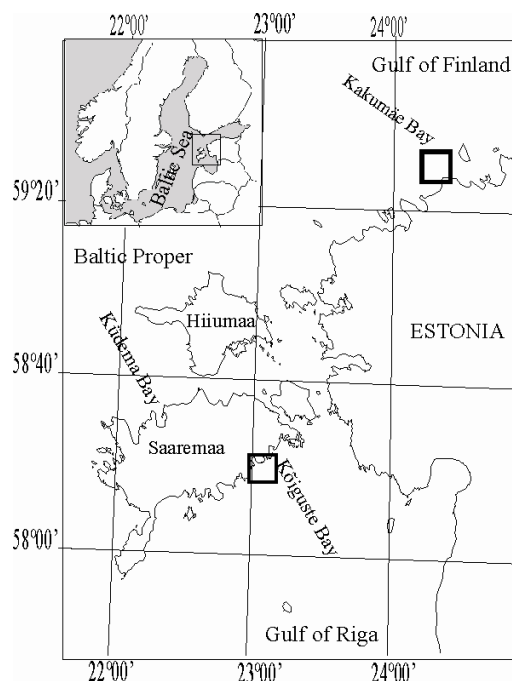
## MATERIAL AND METHODS

The current study was carried out in two stages. The first set of experiments were carried out in the laboratory conditions. The aim of the laboratory experiments was to develop the necessary techniques and experience for the following field experiments.

### Laboratory experiments

Laboratory experiments were carried out using the laboratory facilities of the Estonian Marine Institute, University of Tartu. The experiments were conducted using specimens of the red alga *Furcellaria lumbricalis* collected from Kakumäe Bay (at 3.8 m depth) (Fig. 1) on 28.04.2011. During sampling salinity was ~5.3 and water temperature 7.5 °C.

Samples with seawater in plastic bags were transported in 2–3 hours to the laboratory. In the laboratory, specimens were acclimated in 54-litre aquariums for 14 days (28.04–11.05.2011) before incubation experiments were carried out with manipulated pH for 9 days



**Fig. 1.** Location of the study area. The squares mark the experimental sites.

(12.05–20.05.2011). Throughout the acclimation period the salinity, light, oxygen, and nutrients in the aquariums were kept under similar experimental conditions. However, macroalgae were acclimated at pH ~8 and the temperature was enhanced every second day degree by degree until 15°C. The pH sensors were connected to a multi-channel pH controller, which automatically streamed CO<sub>2</sub> through the inlets into the aquarium according to the predetermined pH, namely, 6.5, 7.0, and control ~8.0. During the experiments the environmental conditions in the aquariums were kept similar to those in the natural environment (constant salinity, light, nutrients, oxygen, and temperature). The salinity was kept at the natural level of ~5.0, water temperature at 15°C; the steady temperature was acquired through an active temperature controller. The light–dark cycle was 12:12 h and during the light cycle the photosynthetically active radiation (PAR) was ~200 μmol m<sup>-2</sup> s<sup>-1</sup>. The photosynthetic response of the plants was measured every day by the oxygen method (Paalme, 2005).

### Field experiments

The set of mesocosm experiments were carried out in Kõiguste Bay (58°37.104N, 22°98.007E) (Fig. 1) during the field season of 2011 (two experimental periods: 05.07–08.07.2011 and 19.07–22.07.2011). In both cases the macroalgal material was acclimated on the first day and the net primary production measurements were conducted during the next three days. Kõiguste Bay is situated in the northern part of the Gulf of Riga and is considered to be a sea area with high natural background nutrient concentrations (Suursaar, 1995).

The field experiments were carried out with three species common in the adjacent sea area representing three different morphological and ecological groups: *Ulva intestinalis*, a filamentous, fast-growing green alga; *Fucus vesiculosus*, a perennial brown alga with slow metabolism; and *Furcellaria lumbricalis*, a perennial red alga. Specimens of macroalgae were collected by SCUBA diving from the sea area adjacent to the mesocosm incubation sites. Macroalgae were incubated in short-term experiments with manipulated CO<sub>2</sub> concentrations. Two open plastic bag mesocosms with an approximate volume of 400 L with an elevated CO<sub>2</sub> level were set up. The gas was slowly added directly into the mesocosm water. The amount of the added CO<sub>2</sub> was not actively controlled, and the concentrations fluctuated during the whole experimentation period, but always exceeded the average natural level. However, the actual  $p(\text{CO}_2)$  was always measured before incubations. All three species were kept under the same conditions, but due to different incubation

schedules, the measured CO<sub>2</sub> concentrations may vary. Algae kept outside of the mesocosms were used as controls. The concentrations of CO<sub>2</sub> were measured with a CO<sub>2</sub> automatic data logger (CONTROSTM DETECT 2.0). The pH (on the total scale) of each treatment was measured with a pH-meter (HACH sensION).

The photosynthetic activity response of the macroalgae was measured every day by the oxygen method. For this procedure about 0.1 g (dry weight, DW) of algal material was incubated in 600-mL glass bottles filled with seawater from inside the mesocosm study site and incubated horizontally on special transparent trays hanging at 1-m depth. Three replicates were used per treatment. Bottles without algae served as controls. The DW of the algal material was determined after drying at 60°C for 48 h. The hourly net primary production (NP) rates (given as mg O<sub>2</sub> g DW<sup>-1</sup> h<sup>-1</sup>) were calculated from the differences in oxygen concentrations, measured over the incubation period (ca 1 h) (Paalme, 2005). The dissolved oxygen concentrations were measured with an oxygen meter (Marvet Junior, MJ2000). The irradiance at the incubation depths was measured as photosynthetically active radiation (PAR) using a light meter LI-COR 250. Measurements were carried out between 10 am and 4 pm.

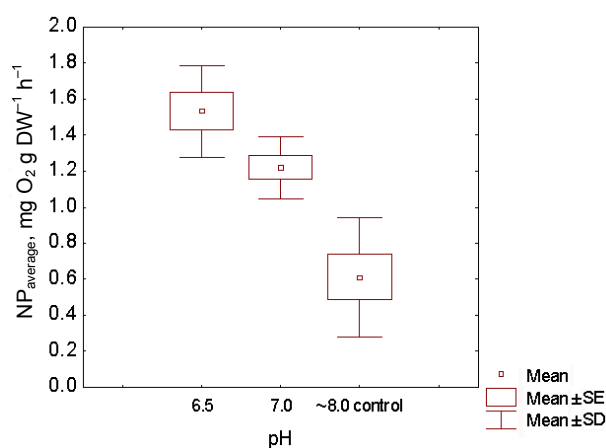
Seawater samples were taken from the experimental site three times per day and frozen immediately for further laboratory analyses. Concentrations of nutrients (TN, TP, P-PO<sub>4</sub>, Si-SiO<sub>4</sub>, N-NO<sub>x</sub>) were measured in laboratory with continuous flow automated wet chemistry analyser Skalar SAN<sup>plus</sup> using the methods EVS-EN ISO 11905-1:2003, EVS-EN ISO 15681-2:2005, EVS-EN ISO 16264:2004, EVS-EN ISO 13395:1999. Then the mean nutrient concentration values ( $n=3$ ) were calculated. Temperature, pH, salinity, and oxygen were measured parallel to net primary production measurements in the mesocosms and in natural conditions during both experimental periods.

The results of laboratory experiments were statistically analysed using one-way ANOVA: pH as independent variable with three levels and net primary production as dependent variable. Analysis of covariance (ANCOVA) was used to evaluate separate and interactive effects of CO<sub>2</sub>, PAR (covariates), and species (categorical predictor) on the NP rate in the mesocosm experiments. We used square transformed CO<sub>2</sub> and PAR values as covariates to meet the assumption of homogeneity of variances (Cochran's test). Effects were considered to be statistically significant if the  $p$ -value was <0.05. When significant differences among main factors or their interactions were found, Bonferroni tests were used as post hoc comparisons to contrast specific means.

## RESULTS

### Laboratory incubation

The results of the laboratory experiments demonstrated the suitability of the chosen method. *Furcellaria lumbricalis* showed a significant response to the changes in the pH level measured as the increase in net primary production rates with increased acidification. Two tested pH levels gave in response a significantly higher net primary production rate compared to the control (Fig. 2). According to the Bonferroni post-hoc test significant differences ( $p < 0.01$ ) between the *F. lumbricalis* photosynthetic net production rates and three different pH levels were found.



**Fig. 2.** Net photosynthetic rates (mean values,  $n = 3$ ) at different pH levels obtained in the laboratory experiments (salinity  $\sim 5.0$ , water temperature  $15^{\circ}\text{C}$ ; and PAR  $\sim 200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) of the red alga *Furcellaria lumbricalis*.

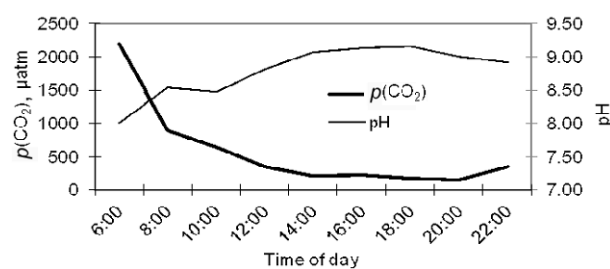
### Field experiments

#### Environmental variables

There was a large diurnal variability in the environmental parameters such as pH and partial pressure of CO<sub>2</sub> in natural conditions (Fig. 3). The diurnal difference in the pH measured was as high as 1.2 pH units. The lowest  $p(\text{CO}_2)$  (and respectively the highest pH) values were registered in the afternoon. The environmental conditions were similar within the two different experimental periods (Table 1).

#### Field incubation experiments

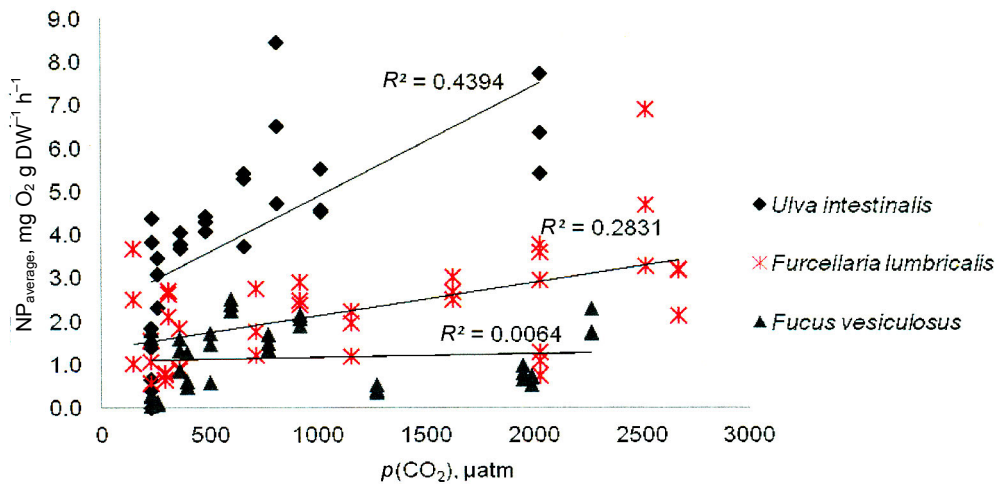
The response of macroalgal photosynthesis to elevated  $p(\text{CO}_2)$  in seawater was species specific. Two out of three tested species responded to the increase in  $p(\text{CO}_2)$  in both incubation experiments. The highest response was observed for the green alga *Ulva intestinalis*. The red alga *Furcellaria lumbricalis* showed a response with lower absolute net production values while the response of the brown alga *Fucus vesiculosus* was not significant at the tested  $p(\text{CO}_2)$  levels (Fig. 4). At 2 and 4 times as



**Fig. 3.** Natural fluctuation of seawater pH values and  $p(\text{CO}_2)$  levels outside mesocosms (control treatment) at 0.5 m depth (incubation period 21–22.07.11). The measurements were carried out a few metres from the shore in shallow water with high macroalgal densities and restricted water movement.

**Table 1.** Environmental variables: salinity, daily maximum of photosynthetically active radiation (PAR), daily minimum and maximum of water temperature, mean values ( $n = 3$ ) of the concentrations of total nitrogen (TN), total phosphorus (TP), phosphates (P-PO<sub>4</sub>), silicates (Si-SiO<sub>4</sub>), and nitrites+nitrates (N-NO<sub>x</sub>) in the water measured in natural conditions during two experimental periods

Date	Salinity	PAR (max), $\mu\text{mol m}^{-2} \text{s}^{-1}$	Water temperature, $^{\circ}\text{C}$		Concentration, $\mu\text{mol L}^{-1}$				
			Min	Max	TN	TP	P-PO <sub>4</sub>	Si-SiO <sub>4</sub>	N-NO <sub>x</sub>
6.07.2011	4.9	1000	21.0	22.6	29.0	0.70	0.21	5.58	<0.30
7.07.2011	5.0	1000	20.9	23.8	31.7	0.82	0.25	5.55	<0.30
8.07.2011	4.8	1100	23.7	24.1	36.8	0.97	0.22	6.35	<0.30
20.07.2011	5.3	600	20.6	22.3	32.4	1.04	0.32	4.92	<0.30
21.07.2011	5.2	900	19.6	24.7	33.3	0.93	<0.13	4.49	<0.30
22.07.2011	5.3	800	21.4	24.6	31.5	0.88	<0.13	4.16	<0.30



**Fig. 4.** Net primary production rates of the three tested macroalgae *Ulva intestinalis*, *Fucus vesiculosus*, and *Furcellaria lumbricalis* (incubation periods 06–08.07.2011 and 20–22.07.2011) at different  $\text{CO}_2$  concentrations. All three species were kept under the same conditions, but due to different incubation schedules, the measured  $\text{CO}_2$  concentrations may vary. During the two experimental periods the salinity, photosynthetically active radiation (PAR), oxygen, water temperature, and nutrient concentrations were similar.

high  $p(\text{CO}_2)$  levels as the natural, background level the net primary production of *Ulva* was respectively 0.5 and 2 times higher than control. A similar response pattern was observed for *Furcellaria*.

ANCOVA results show that the rate of net primary production was dependent on species and was interactively affected by the increase of  $p(\text{CO}_2)$  and the amount of PAR (Table 2).

According to the Bonferroni post-hoc test significant differences ( $p < 0.01$ ) between the photosynthetic net production rates of all estimated algal species (i.e. *Ulva intestinalis*, *Furcellaria lumbricalis*, and *Fucus vesiculosus*) were found.

**Table 2.** Results of ANCOVA analysis on the separate and interactive effects of  $\text{CO}_2$ , PAR, and species on the net primary production rate in mesocosm experiments. Significant effects are indicated in bold

Source	DF	MS	F	p
Intercept	1	<b>97.719</b>	<b>53.674</b>	<b>&lt;0.001</b>
Species	2	<b>22.386</b>	<b>12.296</b>	<b>&lt;0.001</b>
PAR <sup>2</sup>	1	0.613	0.337	0.563
CO <sub>2</sub> <sup>2</sup>	1	3.176	1.744	0.189
Species × PAR <sup>2</sup>	2	0.700	0.385	0.682
Species × CO <sub>2</sub> <sup>2</sup>	2	2.202	1.210	0.302
PAR <sup>2</sup> × CO <sub>2</sub> <sup>2</sup>	1	<b>8.015</b>	<b>4.402</b>	<b>0.038</b>
Species × PAR <sup>2</sup> × CO <sub>2</sub> <sup>2</sup>	2	1.845	1.013	0.366
Error	105	1.820		

## DISCUSSION

The present study showed that elevated  $\text{CO}_2$  levels in seawater may have a positive effect on the photosynthetic activity of macroalgae, at least on short-term basis. However, this effect was highly species specific.

In the laboratory experiments the macroalga *Furcellaria lumbricalis* showed the highest net primary production at the lowest pH values (pH 6.5) compared to the natural level of pH. Björk et al. (2004) and Semesi et al. (2009) also found that macroalgae show decreased photosynthesis with increasing pH levels. As our experimental setup was based on controlling seawater pH during the experiment by adding  $\text{CO}_2$ , the positive effect on net primary production of *Furcellaria* was probably due to the increased concentration of  $\text{CO}_2$  in the water.

The response to changes in the  $\text{CO}_2$  concentration was species specific, reflecting the morphology and life strategy of the species. The measured net primary production rates corresponded to those reported in the literature (Wallentinus, 1978; Schramm et al., 1988; Paalme and Kukk, 2003). The bladderwrack *F. vesiculosus*, a perennial brown alga with slow metabolism, showed no response to elevated  $\text{CO}_2$  levels at least on short-term basis. Our measurement results indicate that elevated  $\text{CO}_2$  levels in seawater will stimulate the growth of fast-growing filamentous species of macroalgae. Mass occurrence of filamentous macroalgae is

considered to be one of the main effects of eutrophication in shallow coastal areas of the Baltic Sea. Thus, an increase in the CO<sub>2</sub> level in seawater may indirectly enhance eutrophication effects in the shallow coastal brackish waters because of contributing to accelerated growth of filamentous ephemeral macroalgae. However, this statement needs further verification.

There is evidence in the literature that the effects of elevated CO<sub>2</sub> concentrations on seaweeds largely depend on the degree of carbon limitation present in the natural system (Zou and Gao, 2010). Our results showed that at the natural level of  $p(\text{CO}_2)$  the net primary production rate was lower. This may lead to the conclusion that the natural content of CO<sub>2</sub> in seawater limits the photosynthetic activity of macroalgae in shallow coastal waters.

The CO<sub>2</sub> system, including parameters such as pH and  $p(\text{CO}_2)$ , has large seasonal and inter-annual variability in the Baltic Sea. These parameters are affected by different processes, such as air–sea gas exchange, physical mixing, and biological processes (Wesslander, 2011).

Macroalgae themselves modify the pH of seawater, especially in dense macroalgal communities in shallow coastal areas (Hurd et al., 2009; Semesi et al., 2009). Our short-term experiments revealed a large amplitude of natural variability of the daily pH in shallow coastal conditions. The diurnal variation in the pH was ~1.2 units in shallow coastal areas. We found that in the early morning  $p(\text{CO}_2)$  values were extremely high in natural conditions ( $p(\text{CO}_2)$  ~2300 µatm). When algae photosynthesize, the removal of CO<sub>2</sub> in assimilation by RUBISCO usually occurs faster than CO<sub>2</sub> can be resupplied from the atmosphere, so there is a reequilibration among the inorganic species, which yields a decrease in HCO<sub>3</sub><sup>-</sup> and an increase in CO<sub>3</sub><sup>2-</sup> and pH (Hurd et al., 2009). Our results indicated that when inorganic carbon was assimilated in the net primary production, the  $p(\text{CO}_2)$  declined to ~150 µatm in natural conditions.

## CONCLUSIONS

1. Increased CO<sub>2</sub> levels in seawater may increase the photosynthetic activity of macroalgae in shallow coastal brackish-water ecosystems under summer conditions.
2. The natural content of CO<sub>2</sub> in seawater most likely limits the photosynthetic activity of macroalgae, especially in dense macrophyte stands.
3. By accelerating the growth of fast-growing filamentous macroalgae an increase of CO<sub>2</sub> levels in seawater may enhance indirectly eutrophication effects in shallow coastal brackish-water ecosystems.

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## Labori- ja välikatsete tulemused: kasvava CO<sub>2</sub> kontsentratsiooni mõju makrovetikate neto-primaarproduksioonile riimveelistes tingimustes

Liina Pajusalu, Georg Martin, Arno Põllumäe ja Tiina Paalme

Käesoleva ajani on hapestumise mõju uuritud peamiselt avaookeanis, vähem on teadustöid, mis käsitlevad madala rannikumere ökosüsteeme. Uurimise eesmärgiks oli välja selgitada, kuidas CO<sub>2</sub> emissioonist põhjustatud merevee happesuse suurenemine mõjutab Läänemere põhjakoosluste kolme võtmeliigi – niitja rohevetika *Ulva intestinalis*, agariku *Furcellaria lumbricalis* ja põisadru *Fucus vesiculosus* – fotosünteesilist aktiivsust riimveelistes tingimustes. Uurimisala merevee süsinikdioksiidisüsteemi iseloomustamiseks mõõdeti looduslikes tingimustes kaht parameetrit: pH ja süsiniku partsiaalrõhk  $p(\text{CO}_2)$  µatm. Esimesed katsed, mille peamiseks eesmärgiks oli arendada meetodeid ja leida välikatse jaoks tehnilisi lahendusi, viidi läbi laboritingimustes. Laborikatse andmed näitasid, et CO<sub>2</sub> sisalduse tõusust tingitud pH taseme langus mõjutab positiivselt makrovetika *F. lumbricalis* neto-primaarproduksiooni. Kõige kõrgem neto-primaarproduksioon mõõdeti kõige madalama pH juures (pH 6,5) ja kõige madalam tulemus mõõdeti kontrolltingimustes, kus oli kõige kõrgem pH (pH 8,0) tase. Välikatse tulemused näitasid, et CO<sub>2</sub> sisalduse suurenemine merevees mõjutab positiivselt katsetes kasutatud makrovetikate – niitja rohevetika *U. intestinalis* ja agariku *F. lumbricalis* – neto-primaarproduksiooni ning ei avalda mõju põisadrule *F. vesiculosus*. Analüüsitud makrovetikatest oli niitja rohevetika *U. intestinalis* neto-primaarproduksioon märkimisväärselt kõrgem kui teistel testitud vetikalikiidel. CO<sub>2</sub> sisalduse tõus merevees võib süvendada (kaudselt) eutrofeerumisnähtusi Läänemeres, kuna see kiirendab üheaastaste niitjate vetikate kasvu. Tulemused näitasid, et ööpäevased  $p(\text{CO}_2)$  kontsentratsioonid ja pH varieeruvad madala rannikumere tingimustes väga laias vahemikus.

