



Ocean acidification affects growth but not nutritional quality of the seaweed *Fucus vesiculosus* (Phaeophyceae, Fucales)



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ABSTRACT

Understanding the ecological implications of global climate change requires investigations of not only the direct effects of environmental change on species performance but also indirect effects that arise from altered species interactions. We performed CO₂ perturbation experiments to investigate the effects of ocean acidification on the trophic interaction between the brown seaweed *Fucus vesiculosus* and the herbivorous isopod *Idotea baltica*. We predicted faster growth of *F. vesiculosus* at elevated CO₂-concentrations and higher carbon content of the algal tissue. We expected that *I. baltica* has different consumption rates on algae that have been grown at different CO₂ levels and that the isopods remove surplus carbon metabolically by enhanced respiration. Surprisingly, growth of *F. vesiculosus* as well as the C:N-ratio of the algal tissue were reduced at high CO₂-levels. The changes in the elemental composition had no effect on the consumption rates and the respiration of the herbivores. An additional experiment showed that consumption of *F. vesiculosus* by the isopod *Idotea emarginata* was independent of ocean acidification and temperature. Our results could not reveal any effects of ocean acidification on the *per capita* strength of the trophic interaction between *F. vesiculosus* and its consumers. However, reduced growth of the algae at high CO₂-concentrations might reduce the capability of the seaweed to compensate losses due to intense herbivory.

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1. Introduction

Ocean acidification has substantial effects on the performance of a great variety of marine organisms (Chan and Conolly, 2013; Harvey et al., 2013; Kroeker et al., 2010, 2013; Widdicombe and Spicer, 2008). Negative effects of ocean acidification arise from enhanced dissolution of carbonate shell structures in calcifying organisms as well as from impaired extra-cellular acid–base regulation in marine animals (Hall-Spencer et al., 2008; Pörtner et al., 2004). In autotrophic organisms the predicted shift in the seawater carbonate chemistry can facilitate the acquisition of inorganic carbon for photosynthesis (Hurd et al., 2009) allowing for the allocation of more energy into somatic processes. Accordingly, elevated growth has been observed in non-calcifying seaweeds and seagrasses under conditions of ocean acidification (Zimmermann et al., 1997; Zou, 2005). However, the responses of non-calcifying seaweeds to ocean acidification are inconsistent and may vary between closely related species or even within species among different developmental stages (Olischläger et al., 2012; Swanson and Fox, 2007). Additionally, subtle interactions of ocean acidification with other environmental variables, such as temperature, complicate the prediction of effects of ocean acidification on seaweeds (Martin and Gattuso, 2009; Sarker et al., 2013).

Recent studies have predominantly addressed the direct effects of ocean acidification on marine species. However, indirect effects of ocean acidification, which are mediated through altered species interactions, have received much less attention (Falkenberg et al., 2013a,b; Poore et al., 2013). Indirect effects can modify single species responses, and are thus crucial for a comprehensive understanding of the implications of global climate change for the structure and functioning of marine ecosystems (Alsterberg et al., 2013). Ocean acidification may affect the outcome of species interactions through “density effects” (sensu Kordas et al., 2011), i.e. when interacting species respond differentially in terms of abundance to altered environmental conditions (Connell and Russell, 2010). Ocean acidification can also affect the *per capita* strength of an interaction (“*per capita* effects” sensu Kordas et al., 2011) if, for example, a consumer changes its food consumption in response to environmentally induced changes in prey palatability (Falkenberg et al., 2013b; Poore et al., 2013). Additionally, feeding rates and selectivity of consumers themselves may respond to ocean acidification. Assuming that food uptake of ectotherms scales with metabolic processes and given the profound effects of ocean acidification on various metabolic processes (Widdicombe and Spicer, 2008), consumption rates are likely influenced by ocean acidification either directly or indirectly through altered metabolic rates. Moreover, considering the complex interactive effects of ocean acidification and other environmental variables on biological processes (Harvey et al., 2013) feeding rates of herbivores will probably not only scale with pCO₂ but also depend on variations in other factors.

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Many marine benthic herbivores are sensitive to variations in the palatability of their algal food. The palatability of a seaweed is determined by structural (e.g., tissue toughness) and chemical (e.g., elemental composition, defense chemicals) tissue characteristics which can vary in response to changing environmental conditions (Hemmi and Jormalainen, 2002; Long et al., 2013). Compared to animal tissue, algal tissue has a higher carbon content and relatively low contents of nitrogen and phosphorous. Thus, algae are a stoichiometrically imbalanced food for herbivores. Elevated carbon supply can shift the stoichiometry of marine primary producers towards higher C:N and C:P ratios, thereby further decreasing the nutritional quality for herbivores (Urabe et al., 2003; van de Waal et al., 2010). Herbivores can compensate for low levels of essential nutrients in their food by increasing consumption (Lincoln et al., 1986). Surplus carbon can then be removed metabolically, e.g. through enhanced respiration (Darchambeau et al., 2003). Elevated consumption of carbon enriched algal tissue is, thus, a possible mechanism for how ocean acidification might affect the *per capita* interaction strength between marine herbivores and seaweeds. In addition to the elemental composition chemical herbivore deterrents, such as phlorotannins, are important determinants of seaweed palatability (Poore, 1994). However, the sensitivity for chemical defenses varies among grazer species (Pavia and Toth, 2000) and the effects of ocean acidification on the phlorotannin content of seaweeds are inconsistent (Olischläger et al., 2012; Swanson and Fox, 2007). Accordingly, the effects of ocean acidification on the nutritional quality of seaweeds and, thus, on the interaction between seaweeds and their consumers are largely unpredictable.

The brown seaweed *Fucus vesiculosus* is an important component of rocky shore ecosystems in the temperate North Atlantic. The species forms dense inter- and shallow subtidal canopies and provides extensive habitat and food for a great variety of species (Wikström and Kautsky, 2007). Additionally, floating sporophytes of *F. vesiculosus* in coastal waters serve as dispersal vector for the seaweed itself and for numerous associated rafting organisms (Vandendriessche et al., 2006). An important consumer of *F. vesiculosus* is the herbivorous isopod *Idotea baltica* which uses the alga not only as food but also as habitat, shelter from predators and as a dispersal vector (Franke et al., 1999; Vesakoski et al., 2008). Recent studies on trophic interactions between *I. baltica* and *F. vesiculosus* showed that the palatability of the seaweed changes with environmental conditions (e.g. eutrophication) and that the isopods are sensitive to variations in the nutritional quality of the alga (Hemmi and Jormalainen, 2002; Honkanen et al., 2002). We used *F. vesiculosus* and its consumer *I. baltica* as a model system to study potential effects of ocean acidification on the trophic interaction between seaweeds and herbivores. We conducted CO₂ perturbation experiments to test the following hypotheses: (1) Ocean acidification enhances growth of *F. vesiculosus*. (2) Elevated CO₂ levels increase the C:N and C:P ratios of *F. vesiculosus* tissue. (3) *I. baltica* displays different consumption rates on algae that have been grown at different CO₂ levels. (4) *I. baltica* shows elevated respiration rates when fed with *F. vesiculosus* that has been grown at elevated CO₂ levels than on algae grown under ambient CO₂ conditions. Additionally, we tested (5) the effects of ocean acidification on the consumption rates of herbivores for *F. vesiculosus* and (6) whether ocean acidification interacts with temperature in its effect on the consumption rate of the herbivore. For the latter experiments we used the isopod *Idotea emarginata* as consumer, which is a common rafter on floating *F. vesiculosus* in the North Sea (Franke et al., 1999; Gutow and Franke, 2003).

2. Material and methods

To allow for sufficient replication the first experiment on *F. vesiculosus* and *I. baltica* was performed in two consecutive sets of sub-experiments due to logistical constraints. The first sub-experiment was started in late winter (February 2010) and the second in early spring (March 2010).

2.1. Cultivation of algae

F. vesiculosus was collected on the island of Helgoland in the German Bight, North Sea (54°10'39" N, 7°53'45" E). Non-reproductive apical thallus tips (length: >2 cm; wet weight (WW): 0.15–0.18 g) without visible epiphytes were haphazardly cut off from thalli growing on a sheltered rocky harbor jetty. The tips were transferred into 10 L glass bottles (43 cm height; 20 cm diameter) which were filled with sterile filtered (0.02 µm) North Sea water and subjected to one of two CO₂ treatments: 280 µatm (i.e. pre-industrial atmospheric CO₂ level; Feely et al., 2004) and 700 µatm (i.e. predicted atmospheric CO₂ levels by the end of the 21st century; Caldeira and Wickett, 2005), respectively. The CO₂ partial pressure (pCO₂) of the seawater was adjusted by continuous incubation with CO₂-enriched artificial air (80% nitrogen, 20% oxygen; gas-mixer: HTK Hamburg GmbH, Germany) through air stones at a continuous gas supply rate of about 0.2 L min⁻¹ bottle⁻¹. Probably due to the metabolic activity of the algae and potentially associated micro-organisms (the cultures were non-axenic) the actual pCO₂ of the seawater medium deviated from the target values (Table 1). Accordingly, the two treatments are hereafter referred to as low and high pCO₂, respectively. Each bottle received 16 algal tips. Six replicate bottles were set up for each CO₂ concentration. The bottles were covered with glass lids to reduce evaporation.

The algae were transferred in two steps from the cold winter conditions in the field to the experimental temperature of 10 °C. After three days at 5 °C, the replicate bottles with the tips were transferred to a culture room of 10 °C where each sub-experiment ran for four weeks at a light/dark rhythm of L:D = 16:8 h. The glass bottles were illuminated with cool-white fluorescent tubes (Osram, L36W/954; Munich, Germany) with a light intensity of 70 µmol photons m⁻² s⁻² at the bottom of the bottles and 100 µmol photons m⁻² s⁻² at their surface (LI-185B with a LI-190SB quantum sensor, LI-COR® Biosciences, Lincoln, USA). In the field, *F. vesiculosus* experiences light intensities of up to 500 µmol photons m⁻² s⁻² while severe light-limitation of the species occurs below the light-compensation point of about 20 µmol photons m⁻² s⁻² (Weinberger et al., 2011). No additional nutrients were added to the seawater. The total biomass (WW) of all algal pieces in each bottle was measured five times during the culturing period and divided by the number of algal tips per bottle to calculate the average biomass of the algal tips. The average growth rate (mg_{WW} d⁻¹) of the tips was calculated from the slope of linear biomass increase (see Section 2.).

Table 1

Carbonate system of the seawater medium in which apical tips of *Fucus vesiculosus* and individuals of *Idotea emarginata* were cultured. Algae were cultured at low and high pCO₂ (incubated at 280 and 700 µatm, respectively) in two consecutive sub-experiments. Isopods were cultured at combinations of two different pCO₂ (incubated at 280 and 1200 µatm, respectively) and two temperatures (10 and 15 °C). Data are mean ± SD.

<i>Fucus vesiculosus</i>	1st sub-experiment		2nd sub-experiment	
	Low pCO ₂	High pCO ₂	Low pCO ₂	High pCO ₂
pH (NBS-scale)	8.32 ± 0.09	7.99 ± 0.06	8.29 ± 0.06	7.94 ± 0.06
Salinity	31.9 ± 0.1	32.7 ± 0.1	31.8 ± 0.1	32.1 ± 0.2
Total alkalinity	2415 ± 17	2436 ± 55	2448 ± 51	2464 ± 23
pCO ₂ (µatm)	282 ± 71	656 ± 101	305 ± 53	754 ± 118
CO ₂	13 ± 3	29 ± 4	14 ± 2	34 ± 5
CO ₃ ⁻	184 ± 29	99 ± 13	176 ± 19	89 ± 11
HCO ₃ ²⁻	1965 ± 75	2294 ± 53	2019 ± 82	2247 ± 35
<i>Idotea emarginata</i>	10 °C		15 °C	
	Low pCO ₂	High pCO ₂	Low pCO ₂	High pCO ₂
pH (total scale)	7.86 ± 0.05	7.51 ± 0.06	7.88 ± 0.05	7.47 ± 0.09
Salinity	33.3 ± 0.2	33.4 ± 0.2	33.3 ± 0.1	33.5 ± 0.2
Total alkalinity	2442 ± 42	2454 ± 50	2403 ± 87	2450 ± 64
pCO ₂ (µatm)	383 ± 53	1021 ± 189	456 ± 73	1368 ± 309
CO ₂	17 ± 2	45 ± 8	17 ± 3	52 ± 12
CO ₃ ⁻	151 ± 16	70 ± 9	153 ± 18	67 ± 13
HCO ₃ ²⁻	2072 ± 42	2283 ± 59	2025 ± 83	2286 ± 64

To avoid accumulation of metabolites and nutrient depletion, the medium was exchanged every 2–3 days throughout the entire experimental period. Before seawater exchange, freshly filtered North Sea water (salinity: 31–32) was incubated at the respective target pCO₂ for at least 24 h before it was used in the experiments. The pH (NBS scale) (WTW720 WTW-GmbH, Weilheim, Germany, equipped with an ILine-electrode, SI-analytics GmbH, Mainz, Germany) and the salinity (WTW-LF 197-S, WTW-GmbH, Weilheim, Germany) of the seawater were measured once a week before the medium was exchanged. Before seawater exchange a 250 mL seawater sample from each replicate bottle was collected in brown borosilicate flasks for determination of total alkalinity. The total alkalinity of the seawater was determined in subsamples of 25 mL by potentiometric titration (Gran, 1952) using a computer controlled automated titration system (TitroLine® alpha plus; equipped with a SCHOTT® Instruments ILine IL-MICRO-pH-A-DIN pH electrode, SI Analytics GmbH, Mainz, Germany) and the software package Titrisoft 2.60 (SI Analytics GmbH, Mainz, Germany). The components of the seawater carbonate system were calculated from pH, total alkalinity and salinity with the MS Excel-AddIn CO2sys (Lewis and Wallace, 1998) using the equilibrium constants for the dissociation of carbonic acid in seawater from Mehrbach et al. (1973) refit by Dickson and Millero (1987) and by Dickson (1990) for KSO₄.

2.2.1. Elemental composition of algal tissue

For the feeding assays (described in the next section), the proximal 2 cm of the tips, which had been produced in the field, were cut off so that the isopods received only the distal sections which were grown at the respective pCO₂. The distal section of one algal tip from each bottle (i.e., six replicates per pCO₂ and sub-experiment) was cut longitudinally in two halves. One half was offered to an isopod in the feeding assay. The other half was further divided into three equal longitudinal sections which were stored at –30 °C for later determination of the C, N and P contents.

For the determination of the C and N contents, the algal fragments were dried at 60 °C for 24 h and stored for ~1 week in an exsiccator. Before further processing, the tissue was again lyophilized, pulverized in liquid nitrogen and weighed to the nearest 0.01 mg. C and N contents (% DW) were determined in subsamples of 0.01–0.02 mg (Carlo Erba NA-1500 elemental analyzer) against an acetanilide standard. The total P content of the pieces was determined after Grasshoff et al. (1983) from 0.01 to 0.02 g_{ww} of algal material after drying (60 °C for 24 h) and grinding in a mortar. The elemental ratios were expressed as molar ratios.

2.2. Herbivore food consumption

I. baltica were taken from cultures where the isopods were kept in a continuously aerated non-flow-through seawater system at 10 °C and a light/dark rhythm of L:D = 12:12 h. The natural North Sea water was exchanged twice a week. Brown algae (*Ascophyllum nodosum* and *F. vesiculosus*) were offered as food.

The average (± SD) biomass of the isopods used in the no-choice feeding assays was 0.25 ± 0.05 g_{ww} for the first sub-experiment and 0.44 ± 0.07 g_{ww} for the second sub-experiment. The isopods were maintained individually in plastic cups (volume: 100 mL) with 60 mL of ambient, filtered (0.02 µm) seawater. The feeding assays were conducted at summer conditions of 15 °C and a light/dark rhythm of 12:12 h to stimulate the feeding activity of the isopods. Prior to the feeding assay the isopods were starved for 24 h to remove all gut content. Subsequently (still prior to the start of the assay), the isopods were fed for two days distal sections of the tips of *F. vesiculosus* that were grown at low and high pCO₂, respectively. During these two days, the algal food was renewed daily.

For the feeding assays, the remaining half of the longitudinally cut distal sections of the algal tips (see previous section) was weighed (WW) and offered to each of six replicate isopods for 24 h for the

determination of the ingestion rate. The initial biomass of the algal pieces ranged from 0.10 to 0.18 g_{ww}. Six similarly treated algal pieces (one from each bottle) were weighed and maintained individually under the same conditions for 24 h without grazer as control for autogenic weight change. At the end of the feeding assay the isopods and the remaining algal pieces were weighed. The daily (the experiments ran for 24 h) consumption rates of the isopods were calculated as $C = W_i * (C_f / C_i) - W_f$ (Cronin and Hay, 1996) and related to the biomass of the grazer. W_i and W_f are the initial and the final WW of the algal tissue, respectively, and C_i and C_f are the equivalent WW of the control pieces.

2.3. Herbivore respiration

After the feeding assays, the isopods were kept individually in 60 mL glass cups for another day feeding on *F. vesiculosus* from the same CO₂-treatment used during the feeding assay. Prior to the determination of the respiration rates, the isopods were kept for 12 h without food for defecation. Oxygen consumption rates of the isopods were determined by the Winkler method (Grasshoff et al., 1983). Filtered (0.2 µm) seawater was adjusted overnight to the experimental temperature of 15 °C and filled into incubation bottles (0.608 ± 0.007 L). Each respiration chamber was equipped with a 1 cm² piece of gauze for the isopods to cling to. After the isopods had been respiring in the incubation bottles for 6–7 h, sub-samples of the seawater were transferred into Winkler flasks (50–60 mL) and fixed for the quantification of dissolved oxygen following the procedures described by Grasshoff et al. (1983). Four bottles were run as controls without isopods. Dissolved oxygen in each sub-sample was measured in triplicates. At the end of the experiments the isopods were weighed, dried at 60 °C for 24 h and combusted at 500 °C for 12 h for the determination of dry weight (DW) and ash free dry weight (AFDW).

2.4. Effects of temperature and CO₂ on herbivore food consumption

I. emarginata were taken from laboratory cultures that were run under the same conditions as described above for *I. baltica*. Male *I. emarginata* were kept individually in 400 mL glass beakers in one out of four possible combinations of two pCO₂ (280 and 1200 µatm) and two temperatures (10 and 15 °C) (Table 1). The isopods received freshly collected pieces of *F. vesiculosus* which were exchanged every day. The experiments were conducted in temperature controlled rooms at a light–dark regime of L:D = 16:8. The carbonate chemistry of the seawater was adjusted following the same procedures as described above for the incubation of *F. vesiculosus*. Again, the actual seawater carbonate chemistry deviated from the desired target conditions probably due to the animals' metabolism (Table 1). Therefore, the treatments will be referred to as low and high pCO₂, respectively. The seawater was exchanged every day and the seawater carbonate chemistry was documented every 2–3 days again following the same procedures as described above for the incubation of *F. vesiculosus*, with the exception that the seawater pH was expressed on the total scale. The total pH was determined from subsamples of the 250 mL seawater samples. The electromotive force of the seawater and of Tris-buffer seawater standards (Oceanic Carbon Dioxide Control, Scripps Institution of Oceanography, San Diego, CA, USA) was measured at 25 °C. The total pH (pH_t) was calculated as follows:

$$\text{pH } t = \text{pH}(S) + \frac{E(s) - E(x)}{RT \ln 10 / F}$$

with pH(S) = pH of the seawater standard, E(s) and E(x) being the electromotive force of the seawater standard and the seawater sample, respectively, R = gas constant, T = temperature (K), and F = Faraday constant (Dickson et al., 2007).

After 12 days of culturing, ten replicate isopods (biomass: 0.056–0.601 g_{ww}) were used from each of the four pCO₂-temperature combinations

for feeding assays. The isopods received freshly collected pieces of *F. vesiculosus* which were weighed (WW) prior to and at the end of the 24 h feeding period. The initial biomass of the algal pieces offered to the isopods ranged from 0.133 to 0.274 g. For each treatment, ten control pieces (WW range: 0.129–0.284 g) each were kept under the same conditions without grazers to determine the autogenic weight change of the algal pieces. The WW of the isopods was also measured at the end of the feeding period and the consumption rates were calculated using the equation by Cronin and Hay (1996) and related to the body mass of the isopods.

2.5. Statistical analysis

Growth of *F. vesiculosus* over the culturing period was analyzed by linear regression. The growth rate ($\text{mg}_{\text{WW}} \text{d}^{-1}$) of an average algal piece was estimated for each bottle from the slope of the specific linear regression line. Growth rates and elemental ratios (C:N, C:P, N:P) of *F. vesiculosus* as well as consumption and respiration rates of *I. baltica* were tested for treatment effects using 2-factorial ANOVA with the two factors “pCO₂” (two factor levels) and “sub-experiment” (two factor levels). Consumption rates of *I. emarginata* were tested for treatment effects using two-factorial ANOVA with the two factors “pCO₂” (two factor levels) and “temperature” (two factor levels). Prior to ANOVA the data were tested for homogeneity of variances using Levene’s test. In case of heteroscedasticity, the data were ln-transformed. All statistical analyses were performed with the software STATISTICA 7.1 (StatSoft Inc., Tulsa, USA).

3. Results

3.1. Algal growth

The algal tips grew linearly in both CO₂-treatments. The linear regression model explained 87–95% of the variation. The growth rate of *F. vesiculosus*, calculated over the whole experimental period, was significantly higher at low pCO₂ than at high pCO₂ ($F_{1,20} = 11.17$, $p < 0.01$; Fig. 1). At low pCO₂, the average (\pm SEM) growth rate of the algal tips was $14.4 \pm 0.5 \text{ g}_{\text{WW}} \text{d}^{-1}$ and $13.0 \pm 1.5 \text{ g}_{\text{WW}} \text{d}^{-1}$ in the first and in the second sub-experiment, respectively. At the high pCO₂, the average growth rate was $10.4 \pm 0.5 \text{ g}_{\text{WW}} \text{d}^{-1}$ in the first and $11.0 \pm 0.6 \text{ g}_{\text{WW}} \text{d}^{-1}$ in the second sub-experiment. The algal tips had similar growth rates in the first and in the second sub-experiment ($F_{1,20} = 0.24$, $p = 0.63$). There was no interactive effect of pCO₂ and the timing of the sub-experiment on the growth of *F. vesiculosus* ($F_{1,20} = 1.19$, $p = 0.29$). Accordingly, the data from the two sub-experiments were combined in Fig. 1.

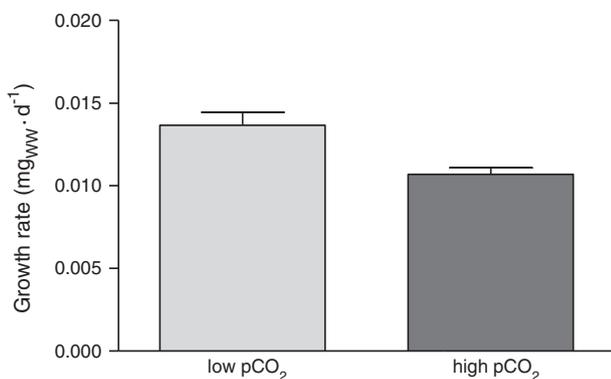


Fig. 1. *Fucus vesiculosus*: growth rates of apical thallus tips at low and high pCO₂ (incubated at 280 and 700 μatm , respectively). The growth rates were similar in the two consecutive sub-experiments and the data were, therefore, combined in the figure. Growth was significantly reduced at high pCO₂. Data are mean \pm SEM ($n = 12$).

3.2. Elemental composition of algal tissue

The C:N ratio of *F. vesiculosus* was significantly reduced by the high pCO₂ ($F_{1,20} = 4.59$, $p = 0.04$; Fig. 2). At the low pCO₂ the C:N ratio ranged from 16.8 to 35.9 while at the high pCO₂ the ratio varied between 18.2 and 28.1. The C:N ratio of the algae did not differ between the two sub-experiments ($F_{1,20} = 2.67$, $p = 0.12$). pCO₂ and the timing of the sub-experiment had no interactive effect on the C:N ratio of the algae ($F_{1,20} = 0.05$, $p = 0.83$).

The C:P ratio of *F. vesiculosus* was not affected by the pCO₂ ($F_{1,20} < 0.01$, $p = 0.98$) and ranged between 304.0 and 1808.5 (Fig. 2). The C:P ratio did not vary between the two sub-experiments ($F_{1,20} = 3.28$, $p = 0.09$). For the C:P ratio the two main factors did not interact ($F_{1,20} = 0.02$, $p = 0.90$).

The N:P ratio of *F. vesiculosus* was also independent of the pCO₂ ($F_{1,20} = 0.43$, $p = 0.52$) and did not vary between the two sub-experiments ($F_{1,20} = 4.08$, $p = 0.06$; Fig. 2). Again, the two main factors did not interact ($F_{1,30} = 0.04$, $p = 0.84$). The N:P ratio of the algae ranged between 12.0 and 69.4.

The average molar C:N:P ratios of *F. vesiculosus* were 669:29:1 and 696:24:1 for the low and the high pCO₂-treatment, respectively, in the first sub-experiment, and 1007:25:1 and 991:21:1 for the low and the high pCO₂-treatment, respectively, in the second sub-experiment (Fig. 2). Since the ratios were similar between the two sub-experiments the data were combined in Fig. 2.

3.3. Herbivore food consumption

The consumption rates did not differ between isopods that were feeding on algae from different CO₂ treatments ($F_{1,20} = 0.01$, $p = 0.91$). However, *I. baltica* consumed more algal tissue in the first than in the second sub-experiment ($F_{1,20} = 11.45$, $p < 0.01$; Fig. 3). The consumption rates varied between 0.02 and 0.34 $\text{g}_{\text{WW}} \cdot \text{g}_{\text{WW}}^{-1} \text{d}^{-1}$ in the first sub-experiment and between 0.04 and 0.31 $\text{g}_{\text{WW}} \cdot \text{g}_{\text{WW}}^{-1} \text{d}^{-1}$ in the second sub-experiment. The pCO₂ and the timing of the sub-experiment did not interactively affect the consumption rate of *I. baltica* ($F_{1,20} = 1.58$, $p = 0.22$).

3.4. Herbivore respiration

The oxygen consumption of *I. baltica* varied between 0.92 and 3.92 $\text{mg O}_2 \text{ g}_{\text{AFDW}}^{-1} \text{ h}^{-1}$. Isopods feeding on *F. vesiculosus* from different pCO₂-treatments had similar respiration rates ($F_{1,20} = 0.56$, $p = 0.46$; Fig. 4). The isopods also had similar respiration rates in both sub-experiments ($F_{1,20} = 0.40$, $p = 0.54$). In the first sub-experiment the respiration rate was slightly higher in isopods that had been feeding

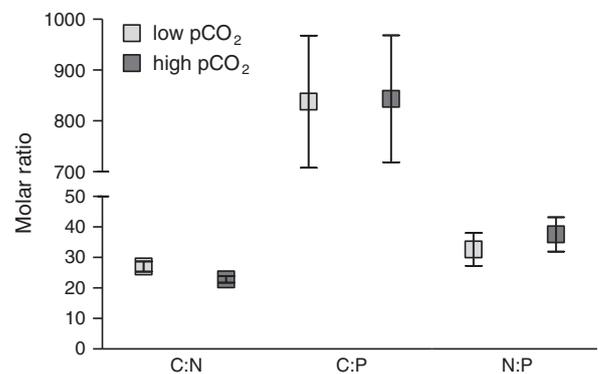


Fig. 2. *Fucus vesiculosus*: molar ratios of C:N, C:P and N:P of apical thallus tips cultured at low or high pCO₂ (incubated at 280 and 700 μatm , respectively). Elemental ratios were similar in the two consecutive sub-experiments and the data were, therefore, combined in the figure. The C:N ratio was significantly reduced at high pCO₂. Data are mean \pm SEM ($n = 12$).

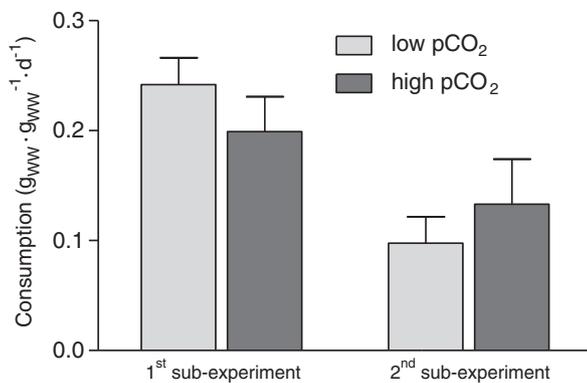


Fig. 3. *Idotea baltica*: consumption rates of the isopods on *Fucus vesiculosus* that had been growing at either low or high pCO₂ (incubated at 280 and 700 μatm, respectively) in two consecutive sub-experiments. Consumption rates were significantly higher in the first sub-experiment. Data are mean ± SEM (n = 6).

on algae from the low pCO₂ while in the second sub-experiment the isopods consumed more oxygen when feeding on algae from the high CO₂ treatment resulting in an interactive effect of the two main factors on the respiration rate of the isopods ($F_{1,20} = 5.23$, $p = 0.03$).

3.5. Effects of temperature and CO₂ on herbivore food consumption

I. emarginata that had been maintained at low and high pCO₂, respectively, had similar feeding rates on *F. vesiculosus* ($F_{1,36} = 2.86$, $p = 0.10$; Fig. 5). Similarly, temperature had no effect on the feeding rates of the isopods ($F_{1,36} = 2.43$, $p = 0.13$). CO₂ and temperature did not interactively affect the feeding rates of *I. emarginata* ($F_{1,36} = 3.98$, $p = 0.05$). The average (± SEM) consumption rate of *I. emarginata* was $0.14 \pm 0.02 \text{ g g}^{-1} \text{ d}^{-1}$.

4. Discussion

Elevated CO₂ levels lowered the C:N ratio of *F. vesiculosus*. However, the changes in the elemental composition had no effect on the nutritional quality of the algae for the herbivorous isopod *I. baltica*. The isopods had similar consumption rates on algae that had been grown at different pCO₂. Moreover, the consumption rate of the isopod *I. emarginata* on *F. vesiculosus* was largely independent of pCO₂ and temperature. Hence, the results of our CO₂ perturbation experiments gave no indication for changes in the *per capita* strength of the interaction between *F. vesiculosus* and its isopod consumers. However, growth of *F. vesiculosus* was reduced at elevated CO₂ levels. This might lead to

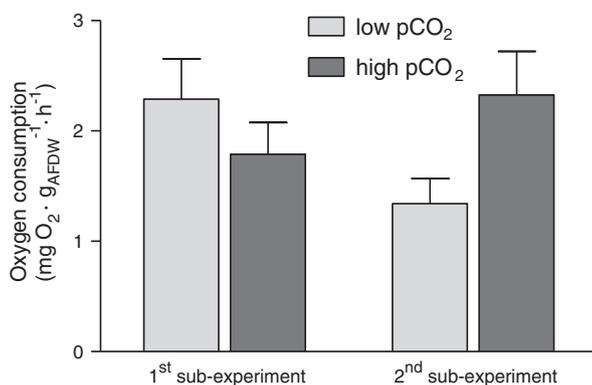


Fig. 4. *Idotea baltica*: respiration rates of isopods that had been feeding on *Fucus vesiculosus* grown at either low or high pCO₂ (incubated at 280 and 700 μatm, respectively) in two consecutive sub-experiments. pCO₂ and the timing of the sub-experiments had a significant interactive effect on the oxygen consumption of the isopods. Data are mean ± SEM (n = 6).

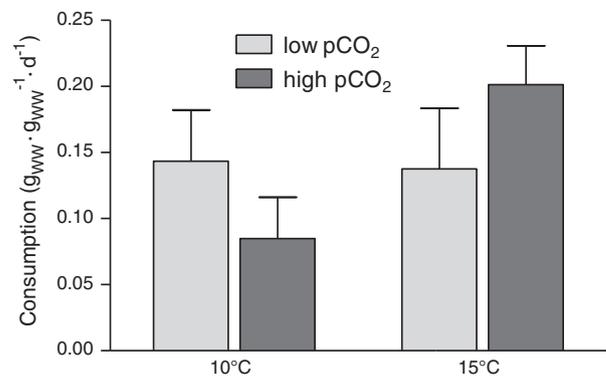


Fig. 5. *Idotea emarginata*: consumption rates of isopods that had been cultured for twelve days at combinations of high and low pCO₂ (incubated at 280 and 1200 μatm, respectively) and two temperatures (10 and 15 °C) on *Fucus vesiculosus*. Data are mean ± SEM (n = 10).

density effects if populations of consumers or competitors of the seaweed remain unaffected or benefit from ocean acidification.

4.1. Growth of *F. vesiculosus*

Non-calcifying autotrophic organisms are expected to benefit from enhanced CO₂ supply for photosynthesis and, in fact, examples exist for marine algae and seagrasses that grow faster at elevated pCO₂ (Olischläger and Wiencke, 2013; Olischläger et al., 2013; Sarker et al., 2013; Swanson and Fox, 2007; Zimmermann et al., 1997). Accordingly, non-calcifying seaweeds are suggested to largely benefit from the changes in seawater carbonate chemistry (Kroeker et al., 2010, 2013) although the reactions of seaweeds to ocean acidification are variable (Olischläger et al., 2012; Swanson and Fox, 2007). The low sensitivity of many seaweed species to elevated CO₂ availability has been explained by the existence of an enzymatic carbon concentrating mechanism (CCM) that allows for the acquisition of carbon from the vast pool of bicarbonate in seawater which is virtually unlimited under current conditions and even more so under enhanced levels of ocean acidification (Israel and Hophy, 2002; Raven et al., 2011). In addition to the CCM, seaweeds of the genus *Fucus* possess an internal organic carbon pool which makes the algae even more independent of external CO₂ fluctuations (Kawamitsu and Boyer, 1999). In clear contradiction to our hypothesis, growth of *F. vesiculosus* was reduced by about 10 to 15% at elevated CO₂ levels. Negative effects of ocean acidification on growth have been observed in other seaweed species as well. For example, growth of the red alga *Porphyra linearis* was inhibited at seawater pH < 8.0 (Israel et al., 1999) possibly due to the pH sensitivity of the specific CCM of *Porphyra* species (Moulin et al., 2011). Similarly, growth of the kelp *Saccharina latissima* was substantially lower at a high pCO₂ of 1300 μatm than at ambient CO₂ levels (Swanson and Fox, 2007). The authors suggested that *S. latissima* was negatively affected by ocean acidification because the CCM of this species allows for optimal photosynthesis at high seawater pH (Axelsson et al., 2000). Growth of marine algae does not only depend on the availability of CO₂ but also on other environmental variables such as nutrients (Xu et al., 2010) and irradiance levels (Sarker et al., 2013). Interactive effects of CO₂ and other parameters might influence the responses and, thus, complicate the prediction of implications of ocean acidification for seaweeds.

4.2. Nutritional quality of *F. vesiculosus*

Xu et al. (2010) showed that carbon utilization of the red alga *Gracilaria lemaneiformis* was enhanced at high pCO₂ while nitrogen uptake decreased. Poore et al. (2013) did not detect effects of ocean acidification on the elemental composition of the brown alga *Sargassum linearifolium*. However, the herbivorous amphipod *Peramphithoe parmerong* consumed more *S. linearifolium* at elevated pCO₂ when the

algae were simultaneously exposed to elevated temperatures indicating interactive effects of ocean acidification and warming on the palatability of the algae (Poore et al., 2013). In our experiments, high pCO₂ led to a decreased C:N ratio of *F. vesiculosus*. However, consumption rates of *I. baltica* were independent of the algal treatment, indicating that the altered elemental composition did not change the nutritional quality of *F. vesiculosus* for the herbivores. In field based mesocosm experiments in an Australian kelp forest ocean acidification led to an elevated nitrogen content in small turf algae (Falkenberg et al., 2013b). Falkenberg et al. (2013a) suggested that a more efficient photosynthesis at high pCO₂ might allow algae to re-allocate nitrogen to other metabolic processes resulting in a higher tissue N-content. In contrast to our results the elevated nitrogen content of the turf algae stimulated the consumption by the herbivorous gastropod *Austrocochlea concamerata* (Falkenberg et al., 2013b). Our results indicate that ocean acidification alone is not able to change the nutritional quality of *F. vesiculosus* for *I. baltica*. However, the two-factorial (ocean acidification and temperature) experiment by Poore et al. (2013) as well as the study by Falkenberg et al. (2013b), which was conducted under variable field conditions, indicate that interactions between ocean acidification and other environmental parameters are able to influence the palatability of seaweeds in ways that changes the *per capita* interaction strength between algae and their consumers. A similar interaction of ocean acidification with other environmental factors became evident from the interactive effect of pCO₂ and the timing of the sub-experiments on the respiration rate of *I. baltica*. The two consecutive sub-experiments were conducted under identical conditions. Accordingly, the environmental factor, which interacted with the pCO₂, could not be identified from our experimental approach but might have been associated with seasonal processes occurring in *F. vesiculosus* between the two field sampling campaigns.

4.3. Food consumption of *I. emarginata*

Many crustaceans are expected to be largely insensitive to ocean acidification (Kroeker et al., 2010, 2013; Whiteley, 2011). Nevertheless, examples exist of the effects of ocean acidification on the performance of marine crustaceans. Growth and survival of the amphipod *Gammarus locusta* were not affected by ocean acidification (Hauton et al., 2009). However, the authors could show responses of the amphipods to elevated pCO₂ in terms of gene expression. Poore et al. (2013) showed that growth and survival of the amphipod *P. parmerong* were negatively affected by ocean acidification and high seawater temperatures, but the temperature effects were more pronounced than the CO₂ effects. Food consumption of *P. parmerong* was independent of pCO₂. Similarly, Falkenberg et al. (2013b) excluded direct effects of ocean acidification on the consumption rates of herbivorous gastropods. In agreement with the results from these previous studies, food consumption did not vary with pCO₂ in *I. emarginata*, the other isopod species used in our study. These results indicate that possible negative effects of ocean acidification on small herbivorous crustaceans, such as enhanced amphipod mortality observed by Poore et al. (2013), are probably not related to processes that could be compensated by enhanced food consumption.

Temperature also did not affect the consumption rate of *I. emarginata*. Metabolic theory predicts that food assimilation in ectotherms increases with temperature to meet enhanced metabolic demands. However, previous studies indicate that other factors such as body size and food availability are better determinants of consumption rates of marine herbivores than temperature (Hillebrand et al., 2009; Saiz and Calbet, 2011). Accordingly, clear evidence for a positive correlation between temperature and feeding rates is still lacking for small benthic marine herbivores. Feeding rates of the amphipod *Ampithoe longimana* varied stronger at elevated temperatures but did not show a clear increase (O'Connor, 2009). Similarly, food consumption of *P. parmerong* was independent of temperature (Poore et al., 2013). Solely the medium

sized herbivorous gastropod *Tegula* spp. showed enhanced feeding rates on seaweeds at elevated temperatures (Yee and Murray, 2004).

The interactive effect of ocean acidification and temperature on the consumption rate of *I. emarginata* was close to significant. At low pCO₂, feeding rates of the isopods were similar at both temperatures. At high pCO₂, however, elevated temperatures apparently stimulated (though not significantly) the food uptake indicating that elevated CO₂ concentrations may increase the temperature sensitivity of the isopods. This would be in agreement with the findings by Walther et al. (2009), who observed that ocean acidification can affect the thermal tolerance of a marine crustacean. Together these results indicate that in interaction with rising seawater temperature ocean acidification may be able to affect not only metabolic processes of single individuals but also complex consumer–prey interactions.

4.4. Conclusion

In our experiments ocean acidification did not clearly affect the *per capita* interaction strength between the seaweed *F. vesiculosus* and the herbivores *I. baltica* and *I. emarginata*. Interactive effects with other environmental variables remain to be tested for this algae–grazer system. Reduced growth of *F. vesiculosus* under conditions of ocean acidification might reduce the capacity of the seaweed to compensate for intense herbivory, potentially resulting in smaller standing biomass of this species.

In our experiments the thallus pieces of *F. vesiculosus* were permanently submerged in the culture medium. In the North Sea, however, *F. vesiculosus* lives in the intertidal and might thus benefit from regular tidal emergence as other intertidal species do (Madsen and Maberly, 1990). Accordingly, permanent submergence might make intertidal algae more susceptible to ocean acidification. In the field *F. vesiculosus* frequently becomes detached from the substratum, for example after storm events, and floats at the sea surface where the algae do not experience regular tidal emergence. Ocean acidification will, thus, have implications for the growth of floating *F. vesiculosus*. Associated herbivores continuously graze upon floating algae thereby accelerating the decomposition of algal rafts (Rothäusler et al., 2009; Vandendriessche et al., 2007). Raft decomposition can be partly compensated by algal growth. However, if algal growth is reduced by ocean acidification while the consumption of herbivores remains unaffected, the decomposition of algal rafts might be accelerated under future conditions. This could have implications for the dispersal of *F. vesiculosus* and for species that rely on algal rafting, for example for connectivity of coastal populations.

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