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Discussions

Net community production and stoichiometry of nutrient consumption in a pelagic ecosystem of a northern high latitude fjord: mesocosm CO_2 perturbation study

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Abstract

Net community production (NCP) and ratios of carbon to nutrient consumption were studied during a large-scale mesocosm experiment on ocean acidification in Kongsfjorden, West Spitsbergen, during June–July 2010. Nutrient-deplete fjord water with natural phyto- and bacteriaplankton assemblages, enclosed in nine mesocosms of ~50 m^3 volume, was exposed to $p\mathrm{CO_2}$ levels ranging from 185 to 1420 µatm on initial state. Mean values of $p\mathrm{CO_2}$ levels during experiment ranged from 175 to 1085 µatm in different mesocosms. Phytoplankton growth was stimulated by nutrient addition. In this study NCP is estimated as a cumulative change in dissolved inorganic carbon concentrations. Stoichiometric couping between inorganic carbon and nutrient is shown as a ratio of a cumulative NCP to a cumulative change in inorganic nutrients. Three peaks of chlorophyll *a* concentration occurred during the experiment. Accordingly the experiment was divided in three phases. Overall cumulative NCP was similar in all mesocosms by the final day of experiment. However, NCP varied among phases, showing variable response to CO_2 perturbation. Carbon to nitrogen (C : N) and carbon to phosphorus (C : P) uptake ratios were estimated only for the period after nutrient addition (post-nutrient period). For the total post-nutrient period ratios were close to Redfield proportions, however varied from it in different phases. The response of C : N and C : P uptake ratios to CO_2 perturbation was different for three phases of the experiment, reflecting variable NCP and dependence on changing microbial community. Through the variable NCP, C : N and C : P uptake ratios for 31 days of the experiment we show a flexibility of biogeochemical response establishing a strong microbial loop in Kongsfjorden under different CO_2 scenarios.

1 Introduction

The Arctic Ocean is a key player in the global cycling of carbon (e.g. Bates et al., 2009), and the Arctic shelves are currently amongst the most productive areas in the world oceans (Wassmann, 2011). Over the past several decades, the Arctic Ocean has experienced significant changes due to a combination of both natural and anthropogenic factors (e.g. Christensen et al., 2007 and references therein). These changes include warming (e.g. ACIA, 2005; Loeng, 2005; Trenberth et al., 2007), declining sea-ice (e.g. Stroeve et al., 2007), freshening (McPhee et al., 2009 and reference therein) and increasing surface carbon dioxide (CO_2) concentrations (Cai et al., 2010) with concomitant ocean acidification (Bellerby et al., 2005; Olafsson et al., 2009; Yamamoto-Kawai et al., 2009, 2011).

The largest ocean acidification signal in the world oceans is projected to occur in Arctic surface waters (Steinacher et al., 2009). Undersaturation with respect to aragonite is found already in the surface waters of the Canada basin (Yamamoto-Kawai, 2009). Model studies show that the Arctic Ocean may become entirely undersaturated with respect to aragonite already by 2050 (Andersson et al., 2010). Experiments performed on different marine ecosystems with different CO_2 gradients (and thus pH and saturation states gradients) indicate potentially deleterious effects of ocean acidification on marine calcifying organisms (e.g. coccolithophores; Riebesell et al., 2000; Orr et al., 2005; Ridgewell et al., 2009), and on organisms at higher trophic levels (e.g. Comeau et al., 2009; Lischka et al., 2011; Frommel et al., 2011).

Increasing inorganic carbon concentrations have also been shown to promote primary production and carbon assimilation in marine phytoplankton (Hein and Sand-Jensen, 1997; Engel et al., 2008; Tortell et al., 2008). Increasing carbon uptake could cause a shift towards ecosystems with higher carbon-to-nutrient utilization ratios (Riebesell et al., 2008; Bellerby et al., 2008). Model studies show that by consuming more carbon in the surface layer, marine phytoplankton may potentially reduce atmospheric pCO_2 globally by 20 % (Schneider et al., 2004). However, the ecosystem of the Arctic Ocean is dynamic in terms of production and respiration of organic matter. Therefore pelagic system will not necessarily act as sink of atmospheric CO_2 (Borges et al., 2005; Thomas et al., 2005).

Despite the hypothesis that Arctic marine ecosystem may experience the greatest changes under ocean acidification (e.g. Merico et al., 2006), no mesocosm studies testing that hypothesis have, to the best of our knowledge, been conducted in the northern high latitudes. This paper presents results from the first large-scale mesocosm experiment on ocean acidification conducted in the Arctic. Here we present the net community production (NCP) estimated from a net biological uptake of inorganic carbon and the stoichiometry of inorganic carbon to nutrient consumption in an ecosystem of a high latitude fjord under a range of $p\mathrm{CO_2}$ levels from 175 to 1085 µatm. The effect of $\mathrm{CO_2}$ perturbation on NCP and stoichiometry of element utilization varied through the course of the experiment, thus our results emphasize the variability in the coupling between autotrophic and heterotrophic processes.

2 Material and methods

2.1 Study area

The experiment took place in Kongsfjorden (78°56.2′ N, 11°53.6′ E, Fig. 1), West Spitsbergen, Svalbard archipelago. The fjord is 26 km long and its width varies from 4 to 10 km. The water in Kongsfjorden is characterized by a mixture of Arctic water masses (which are transported by the coastal current flowing from the Barents Sea over the West Spitsbergen Shelf), Atlantic water masses (West Spitsbergen current), and freshwater input from calving and melting glaciers as well as precipitation (Svendsen, 2002; Hop et al., 2006). In winter the hydrography is dominated by Arctic water masses and in summer it is under Atlantic dominance (Svendsen, 2002). The dominant water mass may determine the structure of the microbial community, thus influencing the biogeochemical cycling in the fjord. Heterotrophic bacteria, picoplankton and nanoflagellates contribute to ecosystem structure and functioning in all seasons. Therefore, in nutrient-limited post-bloom conditions, there is an efficient microbial loop (Rokkan Iversen and

Seuthe, 2011) that provides inorganic nutrients to phytoplankton and bacteria through rapid organic matter remineralization.

2.2 Experimental set up

Nine mesocosm bags two m in diameter and 17 m long were deployed in Kongsfjorden in late May of 2010 (for details see Riebesell et al., 2012). Briefly, bags attached to hard floating frames, were made of TPU (thermoplastic polyurethane), which transmits ~ 95 % of the incoming solar radiation. The mesocosms enclosed ~ 45 m^3 of fjord water with its natural phyto- ans bacteriaplankton assemblages. After closing the mesocosms at the bottom, there was no exchange with the ambient fjord water. The bottom plate was made of polycarbonate. A hood made of transparent PVC (polyvinyl chloride) plastic was mounted on the top of the floating rafts to minimize precipitation and birds' excrement input into the systems.

The experiment lasted 31 days, from 7 June (day $t0$) to 7 July (day $t30$). A CO_2 addition was implemented in four steps (Schulz et al., 2012). Filtered seawater, enriched with CO_2 was injected into the mesocosms and evenly distributed throughout the water column. Exchange of CO_2-enriched water with unperturbed water in a "dead" volume underneath the sediment traps caused an initial decline in $p\text{CO}_2$ levels until day $t8$. At this stage, $p\text{CO}_2$ in the mesocosms covered a range from 185 to 1420 µatm (Bellerby et al., 2012). Table 1 shows mean $p\text{CO}_2$ and pH values in seven perturbed (M1, M2, M4, M5, M6, M8, M9) and two control mesocosms (M3, M7) for different periods of the experiment that followed peaks of biomass growth: Phase I ($t4$–$t13$), Phase II ($t14$–$t21$), Phase III ($t22$–$t27$), post-nutrient period $t14$–$t27$, and total period of the experiment $t8$–$t27$.

Nutrients were added to mesocosms on experimental day $t13$ to stimulate a phytoplankton bloom. Water samples were collected daily using a 5 l depth-integrated sampler lowered down to 12 m. A detailed description of the experimental set up can be found in Riebesell et al. (2012), Czerny et al. (2012) and Schulz et al. (2012).

2.3 Data

To estimate net community production (NCP) and the stoichiometric rates of carbon to nutrient utilization, we used measurements of total inorganic carbon concentration (CT), determined by coulometry; total alkalinity (AT), determined by Gran titration (Gran, 1952; Bellerby et al., 2012); inorganic nutrient concentrations (phosphate – PO_4^{3-}, nitrate – NO_3^-, nitrite – NO_2^-, ammonium – NH_4^+) (Schulz et al., 2012); air/sea gas exchange ($CO_{2(ex.)}$) (estimated by measured loss of N_2O added to the mesocosms as a deliberate tracer) (Czerny et al., 2012). We also show temporal evolution of chlorophyll *a* concentration, measured fluorometrically according to Welschmeyer (1994) and Schulz et al. (2012).

2.4 Net community production derived from changes in CT concentration

To estimate the net effect of CT utilization by phytoplankton during photosynthesis and CT release due to bacterial degradation of organic matter, we calculated NCP with the method previously employed in the PeECE mesocosm studies (Delille et al., 2005; Bellerby et al., 2008).

For each mole of NO_3^-, NO_2^- and PO_4^{3-} consumed through biosynthesis, alkalinity increases by 1 mol (Redfield et al., 1963). Additionally, each mole of consumed NH_4^+ decreases alkalinity by 1 mol (Wolf-Gladrow et al., 2007). Therefore AT was corrected to cumulative changes in inorganic nutrient concentrations (Eq. 1).

$$AT_{corrected} = AT_{measured} - \Delta NO_3^- - \Delta PO_4^{3-} - \Delta NO_2^- + \Delta NH_4^+ \quad (1)$$

The change in CT concentration was corrected for the air/sea gas exchange (Eq. 2).

$$CT_{corrected} = CT_{measured} - CO_{2(ex.)} \quad (2)$$

Corrected AT and CT concentrations were normalized to salinity to account for evaporation from the first day of each phase (Eqs. 3 and 4) (Schulz et al., 2012).

$$\mathrm{AT}_{\mathrm{norm.}}(x_n) = \mathrm{AT}_{\mathrm{corrected}}(x_n) \cdot \frac{S(x_n)}{S(x_1)} \tag{3}$$

$$\mathrm{CT}_{\mathrm{norm.}}(x_n) = \mathrm{CT}_{\mathrm{corrected}}(x_n) \cdot \frac{S(x_n)}{S(x_1)} \tag{4}$$

where S is salinity, x_n and x_1 are corresponding to day n and day 1 respectively, of the time period for which AT and CT are normalized.

The net community calcification NCC was estimated as cumulative change in $\mathrm{AT}_{\mathrm{norm.}}$ (Eq. 5).

$$\mathrm{NCC} = -0.5 \cdot \frac{\Delta \mathrm{AT}_{\mathrm{norm.}}}{\Delta t} \tag{5}$$

Calcification was insignificant during the experiment, therefore calculated NCC expresses the precision of AT measurements, which was $< 2\,\mu\mathrm{mol\,kg^{-1}}$ (Bellerby et al., 2012).

Net community production is computed as a cumulative change in $\mathrm{CT}_{\mathrm{norm.}}$, accounting for cumulative change in $\mathrm{AT}_{\mathrm{norm.}}$ (Eq. 6).

$$\mathrm{NCP} = -\frac{\Delta \mathrm{CT}_{\mathrm{norm.}}}{\Delta t} + 0.5 \cdot \frac{\Delta \mathrm{AT}_{\mathrm{norm.}}}{\Delta t} \tag{6}$$

2.5 Statistical analysis

To test the difference in NCP between $\mathrm{CO_2}$ scenarios, values of a cumulative NCP calculated for every time period, were plotted against mean $p\mathrm{CO_2}$ values for $t8$–$t27$ period. Additionally we plotted the ratio of values of a cumulative NCP to a cumulative difference in nitrogen and phosphate, calculated for every time period, against mean $p\mathrm{CO}_2$ values for $t8$–$t27$ period to test the difference in C : N and C : P utilization ratios among $p\mathrm{CO}_2$ scenarios. Linear regression analysis (F-test) was applied to identify the effect of $p\mathrm{CO}_2$ treatment on NCP, C : N and C : P utilization ratios. Regression coefficients, slopes, R^2 and p-values derived from this analysis are shown in Table 2.

To calculate C : N and C : P utilization ratios we plotted cumulative NCP against a cumulative difference in nitrogen and phosphate uptakes for every period in every mesocosm. Linear regression analysis (F-test) was applied to estimate a ratio of carbon to nitrogen and phosphate consumption. Regression coefficients, R^2, and p-values derived from this analysis are shown in Table 3 for C : N uptake ratio and in Table 4 for C : P uptake ratio. Analyses were performed with a Statistics toolbox in Matlab.

3 Results

3.1 Net community production

The initial $p\mathrm{CO}_2$ of the ambient water in the fjord was ∼ 170 µatm, corresponding to a pH of ∼ 8.3 (Bellerby et al., 2012). Concentrations of nitrate and phosphate in the water were close to detection limit at the beginning of the experiment (0.11 $\mu\mathrm{mol\,kg}^{-1}$ for nitrate, 0.13 $\mu\mathrm{mol\,kg}^{-1}$ for phosphate). Concentration of ammonia was 0.7 $\mu\mathrm{mol\,kg}^{-1}$ (Schulz et al., 2012). Additionally, there were 5.5 $\mu\mathrm{mol\,kg}^{-1}$ of dissolved organic nitrogen, 0.20 $\mu\mathrm{mol\,kg}^{-1}$ of dissolved organic phosphorus (Schulz et al., 2012) and 75.0 $\mu\mathrm{mol\,kg}^{-1}$ of dissolved organic carbon (Engel et al., 2012). Reduced $p\mathrm{CO}_2$ and inorganic nutrient concentrations, and increased concentrations of organic carbon, nitrogen and phosphorus indicated a post-bloom situation in the fjord at the start of the experiment.

The concentration of chlorophyll *a* increased three times during the course of experiment in the form of three bloom events (Fig. 2). Peak concentrations were observed on days $t6$, $t19$ and $t27$ (Riebesell et al., 2012). According to observed peaks, the results of the experiment are presented for three phases: Phase I from *t*4 to *t*13; Phase II from *t*14 to *t*21; Phase III from *t*22 to *t*27. The CO_2 added between *t*1 and *t*4 was found to have equilibrated with the water in the dead volume below the sediment traps by *t*8. Therefore we discuss the NCP of Phase I only from *t*8 to *t*13 (Fig. 3a and b). Additionally we show some results for the total period of the experiment *t*8–*t*27, and for the post-nutrient period *t*14–*t*27.

Our approach implies evaluating the net utilization of total carbon (CT) accounting for the net change in total alkalinity and CO_2 gas exchange through the air/water interface. Net community production (NCP) is the result of community production and respiration. We observed NCP variability among three phases of the experiment and between the nine CO_2 scenarios. Overall cumulative NCP, calculated for the period *t*8–*t*27 showed similar values in all mesocosms – $\sim 50 \pm 5\,\mu\mathrm{mol\,kg^{-1}}$ (Fig. 3a). However in the different phases NCP varied among different $p\mathrm{CO_2}$ scenarios (Figs. 3b and 4). In Phase I NCP was positive in mesocosms with high and intermediate CO_2 levels (cumulative NCP on *t*13 in high $\sim 6.1 \pm 1.5\,\mu\mathrm{mol\,kg^{-1}}$ and intermediate $\sim 2.8 \pm 1.4\,\mu\mathrm{mol\,kg^{-1}}$; Fig. 4), indicative for an autotrophic system. Cumulative NCP in mesocosms with low CO_2 treatment was close to zero by *t*13, indicating that autotrophic and heterotrophic processes were evenly active ($\sim -0.2 \pm 0.9\,\mu\mathrm{mol\,kg^{-1}}$). In Phase II all mesocosms were autotrophic and had positive values of NCP. The highest mean cumulative NCP by *t*21 was in mesocosms with high CO_2 treatment – $\sim 13.9 \pm 4.3\,\mu\mathrm{mol\,kg^{-1}}$. In mesocosms with intermediate and low CO_2 treatments mean cumulative NCP was lower: in intermediate – $\sim 10.3 \pm 3.9\,\mu\mathrm{mol\,kg^{-1}}$, in low – $\sim 8.9 \pm 0.9\,\mu\mathrm{mol\,kg^{-1}}$.

In Phase III all mesocosms were autotrophic with the highest cumulative NCP rates during the experiment. The highest NCP in Phase III was in mesocosms with low ($34.4 \pm 1.7\,\mu\mathrm{mol\,kg^{-1}}$) and intermediate CO_2 levels ($31.4 \pm 6.2\,\mu\mathrm{mol\,kg^{-1}}$). In mesocosms with high CO_2 level cumulative NCP was only $\sim 19.2 \pm 3.2\,\mu\mathrm{mol\,kg^{-1}}$.

Regression analysis (F-test) of a cumulative NCP calculated for different time periods against mean $p\mathrm{CO_2}$ values calculated for *t*8–*t*27 periods showed a positive response of NCP to $p\mathrm{CO_2}$ in Phase I ($p = 0.000$) and in Phase II ($p = 0.076$) (Table 2, Fig. 5). A negative response of NCP to pCO_2 was observed in Phase III ($p = 0.000$) and for the total period $t8$–$t27$ ($p = 0.094$).

3.2 Stoichiometry of carbon-to-nutrients consumption

Since the concentrations of inorganic nutrients in Phase I (prior nutrients addition) were low, we evaluated the stoichiometry of carbon uptake (in this study shown as NCP) to inorganic nitrogen uptake (presented as sum of nitrate, nitrite and ammonium) (hereafter C : N uptake ratio) and inorganic phosphate uptake (hereafter C : P uptake ratio) only for Phase II, Phase III (Figs. 6 and 7) and additionally for the post nutrient period $t14$–$t27$.

C : N and C : P uptake ratios in period $t14$–$t27$ were close to Redfield values, and ratios varied among pCO_2 treatments. A mean C : N uptake ratio in mesocosms with low CO_2 level was ~ 8.9, while it was ~ 8.7 in intermediate CO_2 level and ~ 6.6 in high CO_2 level (Table 3). Thus the negative trend of C : N uptake ratio with increasing pCO_2 was pronounced in $t14$–$t27$ period (Fig. 8a). Similar to C : N uptake ratio, C : P uptake ratio was close to Redfield, and varied amongst CO_2 treatments. Mean C : P uptake ratio was ~ 136.3 in mesocosms with low pCO_2 level, ~ 127.3 in mesocosms with intermediate pCO_2 level and ~ 93.0 in mesocosms with high CO_2 level (Table 4). A negative response of C : P uptake ratio to CO_2 treatment was observed in the post nutrient period $t14$–$t27$ (Fig. 8b).

Values of C : N uptake ratio in Phase II were similar and lower than Redfield ratio (6.6) in all mesocosms (Fig. 6a–c). C : N uptake ratio was on average 4.01 in mesocosms with low, 4.0 in mesocosms with intermediate and 4.2 in mesocosms with high CO_2 treatment (Table 3). C : P uptake ratio was two times lower than Redfield value (106) in Phase II (Fig. 7a–c). Mean C : P uptake ratio in Phase II did not show a clear response to CO_2 treatment, and was 62.0 in mesocosms with low, 54.6 in mesocosms with intermediate and 55.3 in mesocosms with high CO_2 treatment (Table 4, Fig. 8b).

In contrast to Phase II C : N uptake ratio in Phase III was slightly higher than the Redfield value (Fig. 6d–f). The mean C : N uptake ratio was 8.8 in mesocosms with low and intermediate CO_2 treatments, but only 6.7 in mesocosms with high CO_2 treatment (Table 3). Thus the C : N uptake ratio had a slight negative trend with increasing pCO_2 (Table 2). In Phase III C : P uptake ratio was higher than Redfield (Fig. 7d–f) and showed a negative response to CO_2 perturbation (Fig. 8b). C : P uptake ratio decreased from 136.0 in low, to 127.0 in intermediate and 93.0 in high CO_2 treatment (Table 4).

3.3 Summary

Cumulative NCP was similar in all CO_2 scenarios by *t*27, but varied among CO_2 scenarios in different experimental phases. For the major part of experiment the pelagic system in the mesocosms was autotrophic, but in Phase I mesocosms with low CO_2 levels were close to heterotrophic. The highest cumulative NCP rates were observed in Phase III. The cumulative NCP was increasing with higher CO_2 in Phases I and II. The mean cumulative NCP was decreasing with higher CO_2 in Phase III, which caused negative response of NCP to CO_2 in total experimental period *t*8–*t*27.

C : N and C : P uptake ratios were lower than Redfield in Phase II, higher than Redfield in Phase III, and close to Redfield in post-nutrient *t*14–*t*27 period. The mean C : N and C : P uptake ratios were decreasing with higher CO_2 treatment in post-nutrient *t*14–*t*27 period. In Phase II the mean C : N and C : P uptake ratios were slightly increasing with higher CO_2. In Phase III, C : N and C : P uptake ratios were decreasing with higher CO_2.

4 Discussion

The overall effect of CO_2 treatment on net community production and net stoichiometry of nutrient and CT utilization during the experiment on ocean acidification in the high northern latitude fjord was not clear. A distinct succession in phytoplankton groups occurred over the experimental period (Schulz et al., 2012; Brussaard et al., 2012). The rates of net community production and net stoichiometry varied over the experimental period and most likely reflected the specific sensitivities of the dominant phytoplankton groups to CO_2 perturbation.

The experiment in Kongsfjorden started after the spring phytoplankton bloom. Dissolved organic nutrients and carbon were the substrate for a recycling system in the fjord. Due to an efficient microbial loop, inorganic nutrients and CT were resupplied to the water column by heterotrophs. In Phase I, concentrations of mineral nutrients were low, suggesting a tight coupling between the release of nutrients from organic matter and their rapid utilization in primary production. Therefore, the first chlorophyll *a* peak occurring in Phase I was most likely fueled by a phosphate remineralized from organic matter and most importantly ammonium as N-source, remaining after the spring bloom. Peaks of phytoplankton growth similar to the one observed in Phase I have been described as common events in the fjord during the summer (Hop et al., 2006). In Phase I after $t8$ the concentration of chlorophyll *a* was already declining, which was probably caused by grazing (Niehoff et al., 2012) or viral infection (Brussaard et al., 2012). However, we observed net autotrophy in the mesocosms with high CO_2 treatment, while mesocosms with intermediate and low CO_2 treatment were net heterotrophic. Production rates, which were higher than respiration rates in mesocosms with high CO_2 treatment, were stimulated by CO_2 perturbation (Engel et al., 2012).

Nutrient addition on $t13$ stimulated biomass growth in all mesocosms from $t15$ peaking at $t19$. In Phase II that followed nutrient addition, we observed net autotrophy in all mesocosms. NCP was increasing with higher CO_2 treatment. Nutrients were consumed at higher rates with increasing CO_2 (Schulz et al., 2012). Both increased NCP and nutrient uptake rates in mesocosms with higher CO_2 treatment resulted in similar C : N and C : P ratios among pCO_2 treatments. Nevertheless, stoichiometric uptake ratios were lower than Redfield in Phase II. This may be the result of luxury consumption of inorganic nutrient that followed nutrient addition on $t13$. It is also possible that through the microbial loop N and P were utilized, but CT was released to the system due to organic carbon respiration (Thingstad et al., 2008). This result shows that along with variable elemental stoichiometry (e.g. Sterner and Elser 2002) net uptake stoichiometry of carbon and nutrients during photosynthetic fixation and bacterial respiration varies in time and regionally.

The decline of phytoplankton production after *t*19 was probably caused by viral infection (Brussaard et al., 2012). The decline was the end of Phase II. On *t*22 chlorophyll *a* concentration increased for the third time during the experiment, peaking on *t*27 (Schulz et al., 2012). Although the majority of inorganic nutrients were consumed during Phase II, we observed the highest rates of NCP in Phase III after *t*22. C : N and C : P uptake ratios were higher than Redfield in Phase III, because of high NCP rates and low nutrients concentrations towards the end of experiment.

Despite variable NCP response to CO_2 treatment in different phases, cumulative carbon uptake was similar in all mesocosms by the last day of the experiment. C : N and C : P uptake ratios during the post-nutrient period (Phase II + Phase III) were close to Redfieldian, and decreased from low to high $p\mathrm{CO}_2$ levels.

Overall trends of net community production estimated in this study are in good agreement with a temporal evolution of chlorophyll *a* (Schulz et al., 2012). Net community production estimated from CT uptake, and its negative response to $p\mathrm{CO}_2$ treatment in Phase III are consistent with NCP estimated by oxygen consumption and release (Tanaka et al., 2012), and with NCP estimated by net ^{13}C-POC production (de Kluijver et al., 2012). Despite the similarity, the results should be taken with caution, because in low and intermediate CO_2 treatments the bloom was peaking on *t*27 with the following decline. In high CO_2 treatment, however, the bloom was still developing on *t*27, allowing for different carbon-to-nutrient coupling and, hence, different NCP than it was in low and intermediate CO_2 treatments. Engel et al. (2012) observed higher production and release of dissolved organic carbon in mesocosms with high CO_2 treatment. Thus there was a stimulated bacterial growth, which was leading the system of high CO_2 mesocosms to a heterotrophic state. Thus, NCP dynamics in Phase III was based on biogeochemical conditions resulted from Phase II.

5 Conclusions

We studied net community production and the stoichiometry of carbon and nutrient consumption during a mesocosm experiment to test the effect of CO_2 perturbation on the marine pelagic ecosystem in a high latitude Arctic fjord. This study emphasizes the importance to account for the presence of a strong microbial loop in the Arctic waters, which leads to a high plasticity in production and stoichiometry of uptake ratios. Thus the observed NCP, C : N and C : P uptake ratios varied between different phases of the experiment indicating species-specific responses to $p\mathrm{CO}_2$ treatment. Overall cumulative net community production, however, was similar in all mesocosms by the last day of experiment. Mean C : N and C : P uptake ratios in the post nutrient period were close to Redfield ratio although were different from it when considering different phases. Biogeochemical conditions established in the fjord in the beginning of the experiment played an important role in the community response to experimental treatment. Similarly to that, biogeochemical conditions resulted in a community response in a certain phase, affected the community response in the following phase. This observation may lead to a conclusion, that microbial community is adapting to a treatment to a certain degree, affecting following bloom stages.

The evidence of a strong microbial loop in the Arctic Ocean in this study strengthens the recommendation to implement the microbial loop into regional biogeochemical models for more reliable projections of the future of a polar marine ecosystem and its feedback to a changing climate and ocean acidification.

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Table 1. Mean values of pCO_2 and pH (total scale) levels in mesocosms for every phase, post-nutrients period $t14$–$t27$ and the overall period $t8$–$t27$. pCO_2 and pH are calculated from total carbon and total alkalinity using CO_2SYS program (Lewis and Wallace, 1998). The dissociation constants are: for carbonic acid (Dickson and Millero, 1987), boric acid (Dickson, 1990a) and sulphuric acid (Dickson, 1990b) and the CO_2 solubility coefficient from Weiss (1974).

	Phase I		Phase II		Phase III		$t14$–$t27$		$t8$–$t27$	
	pH T	pCO_2 (µatm)	pH T	pCO_2 (µatm)	pH T	pCO_2 (µatm)	pH T	pCO_2 (µatm)	pH T	pCO_2 (µatm)
M3	8.33	185	8.34	176	8.35	170	8.34	174	8.34	177
M7	8.32	187	8.33	179	8.35	170	8.34	175	8.33	179
M2	8.18	270	8.2	253	8.24	233	8.22	245	8.21	252
M4	8.06	375	8.09	344	8.13	309	8.1	329	8.09	342
M8	7.96	480	8.01	422	8.04	389	8.02	409	8.01	426
M1	7.82	690	7.87	594	7.92	533	7.89	568	7.87	598
M6	7.74	820	7.82	665	7.89	578	7.85	629	7.82	676
M5	7.64	1050	7.73	838	7.78	746	7.75	800	7.72	861
M9	7.52	1420	7.64	1033	7.71	891	7.67	974	7.63	1084

Table 2. Dependence of NCP, C : N and C : P uptake ratios on pCO_2 (F-test).

Variable	Period	intercept	slope	R^2	p
NCP	$t8$–$t13$ Phase I	−1496	0.009	0.856	0.000
	$t14$–$t21$ Phase II	7393	0.007	0.382	0.076
	$t22$–$t27$ Phase III	40 288	−0.023	0.899	0.000
	$t8$–$t27$ Overall	52 473	−0.01	0.348	0.094
C : N ratio	$t14$–$t27$ after nutrients addition	10 606	−0.003	0.710	0.004
	$t14$–$t21$ Phase II	3475	0.001	0.052	0.557
	$t22$–$t27$ Phase III	16 486	0.005	0.185	0.248
C : P ratio	$t14$–$t27$ after nutrients addition	164 998	−0.046	0.685	0.006
	$t14$–$t21$ Phase II	51 232	0.007	0.059	0.528
	$t22$–$t27$ Phase III	188 289	0.369	0.650	0.009

Table 3. Dependence of NCP on N consumption (C : N uptake ratio, F-test).

	Phase II ($n = 8$)			Phase III ($n = 6$)			$t14$–$t27$ ($n = 14$)		
CO_2 level	R^2	p	intercept	R^2	p	intercept	R^2	p	intercept
Low (M3, M2, M7)	0.878	0.001	4005	0.941	0.001	16 813	0.927	0.000	8889
Intermediate (M1, M4, M8)	0.949	0.000	4023	0.954	0.001	17 893	0.918	0.000	8743
High (M5, M6, M9)	0.926	0.000	4164	0.787	0.018	14 722	0.913	0.000	6580

Table 4. Dependence of NCP on P consumption (C : P uptake ratio, F-test).

	Phase II ($n = 8$)			Phase III ($n = 6$)			$t14$–$t27$ ($n = 14$)		
CO_2 level	R^2	p	intercept	R^2	p	intercept	R^2	p	intercept
Low (M3, M2, M7)	0.875	0.001	62 001	0.902	0.004	276 242	0.892	0.000	136 325
Intermediate (M1, M4, M8)	0.902	0.000	54 616	0.879	0.006	290 583	0.859	0.000	127 303
High (M5, M6, M9)	0.857	0.001	55 317	0.760	0.024	458 313	0.824	0.000	92 866

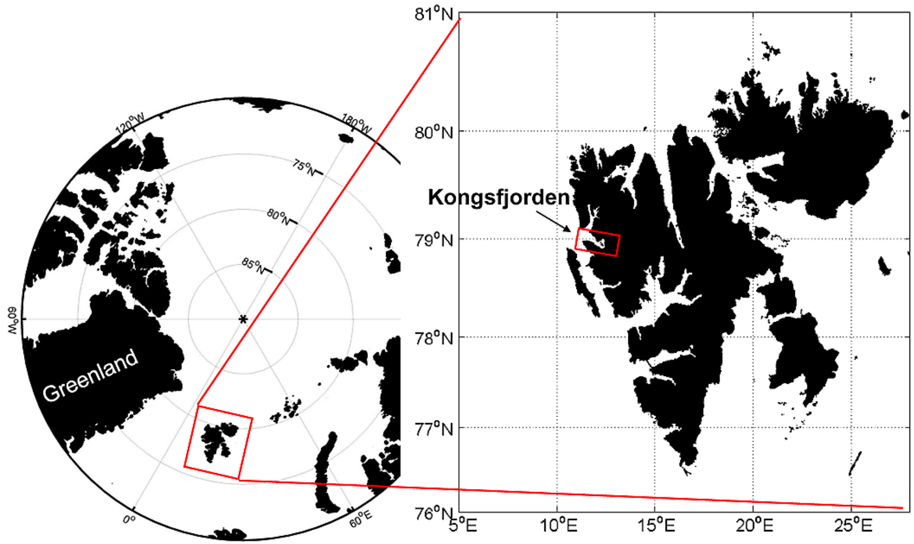

Fig. 1. Map of the Arctic Ocean with the Svalbard archipelago highlighted in red, and enlarged map of the latter with a red square indicating the location of Kongsfjorden.

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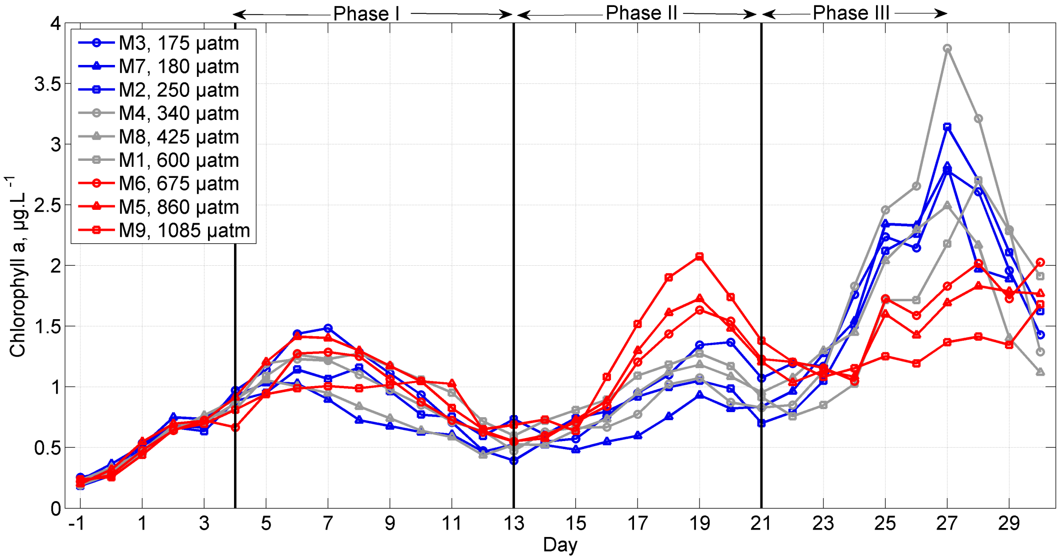

Fig. 2. Temporal evolution of chlorophyll *a* concentrations in different mesocosms. Vertical lines on *t*4, *t*13 and *t*22 show the start and the end of each experimental phase. Blue colour of the lines indicates low $p\mathrm{CO_2}$ level, grey – intermediate $p\mathrm{CO_2}$ level and red – high $p\mathrm{CO_2}$ level. Numbers in a legend next to every line with symbol are the rounded $p\mathrm{CO_2}$ levels for *t*8–*t*27 period.

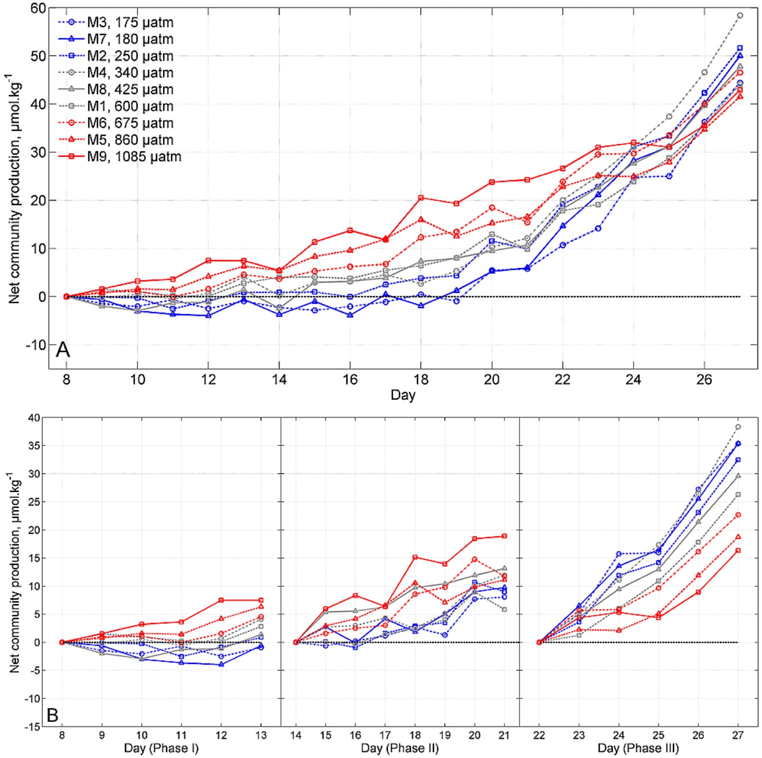

Fig. 3. (A) Cumulative net community production for the total period of the experiment; **(B)** cumulative net community production in every phase of the experiment. Horizontal dashed line on both figures shows the border between heterotrophic (below 0) and autotrophic (above 0) systems. Line colors and numbers in a legend are as described for Fig. 2.

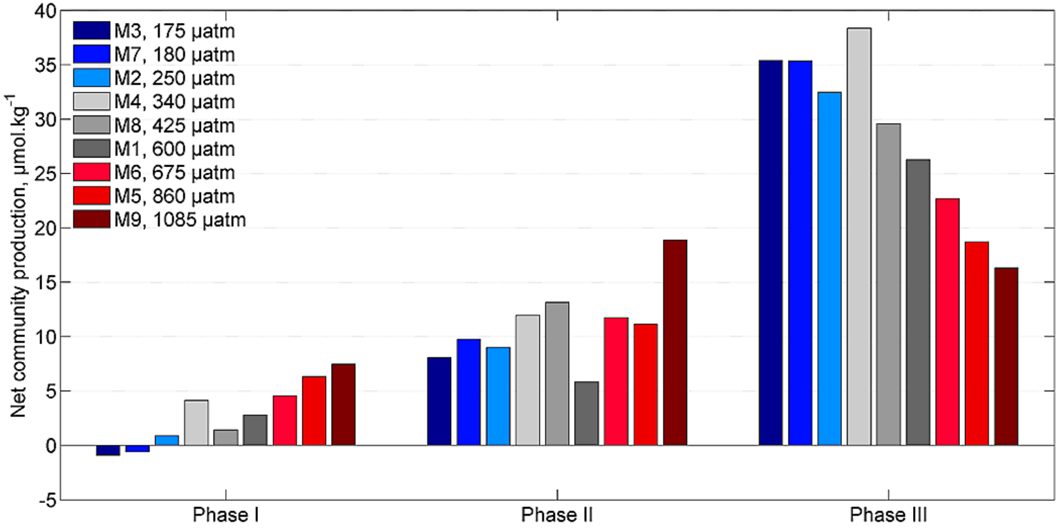

Fig. 4. Cumulative net community production on the last day of every experimental phase for 9 mesocosms.

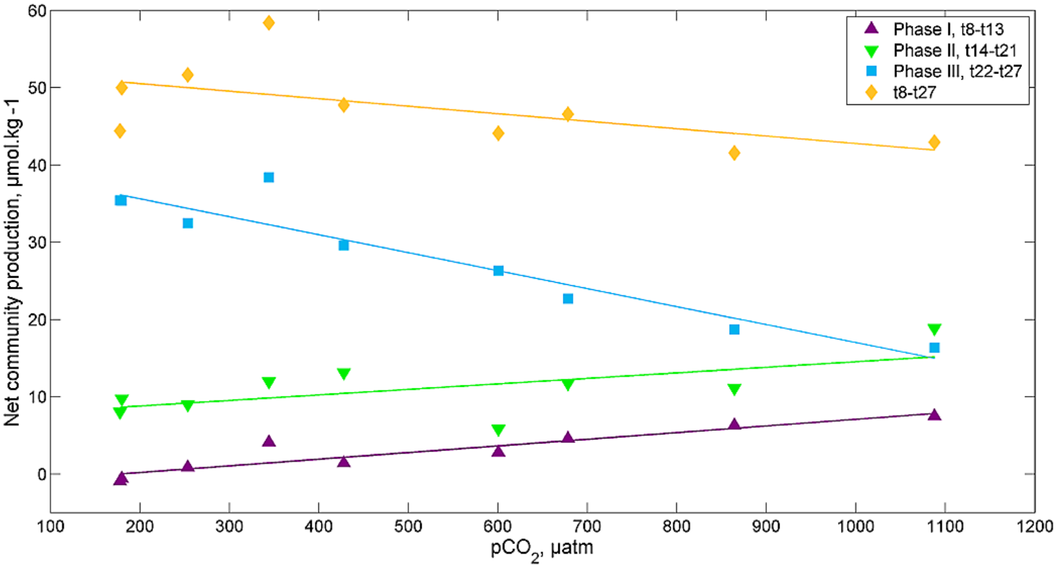

Fig. 5. Linear regressions for the cumulative net community production calculated for different time periods against mean $p\mathrm{CO}_2$ levels for $t8$–$t27$ period.

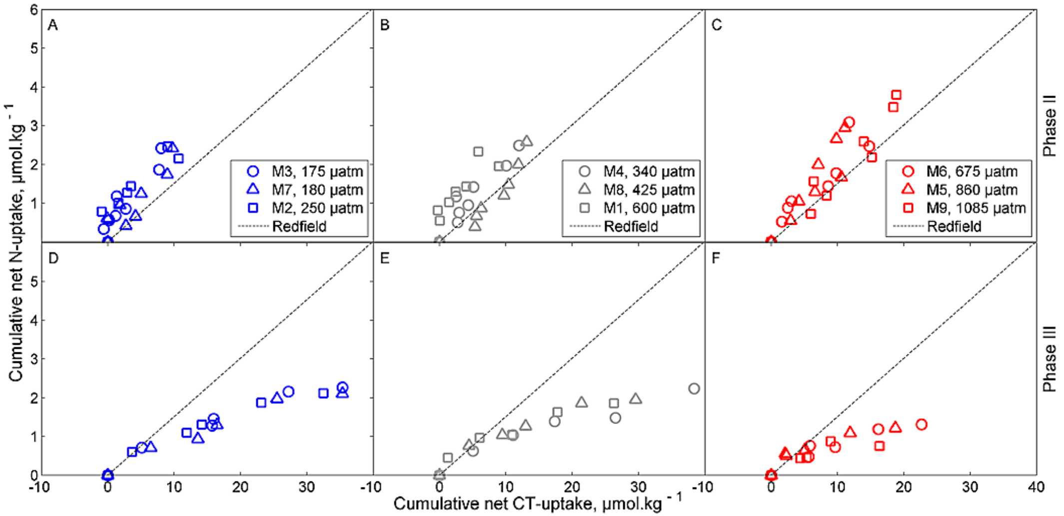

Fig. 6. Ratios of cumulative net community production to a cumulative change in inorganic nitrogen uptake. **(A, B, C)** show ratios in low, intermediate and high $p\text{CO}_2$ mesocosms respectively during Phase II. **(D, E, F)** show ratios in Phase III. Dashed black line is the Redfield C : N elemental ratio.

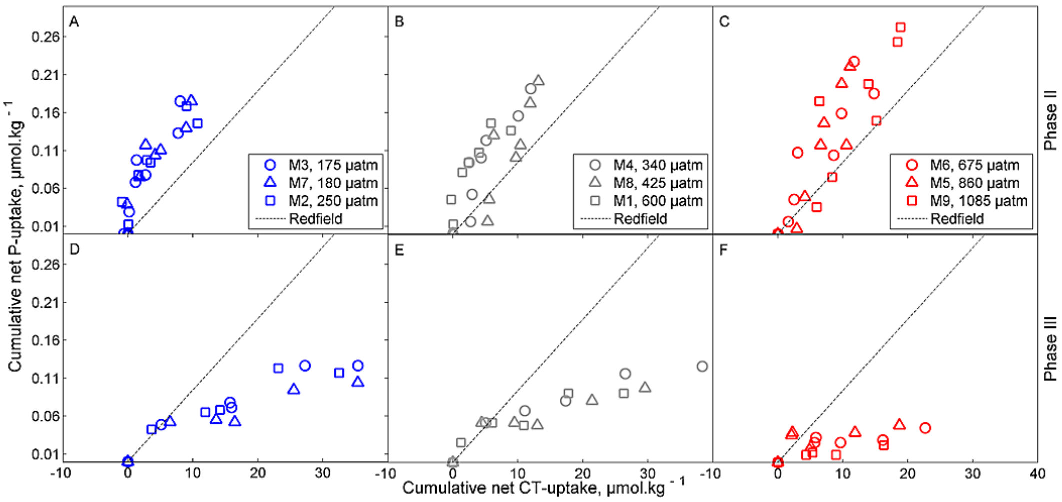

Fig. 7. Ratios of cumulative net community production to a cumulative change in inorganic phosphate uptake. **(A, B, C)** show ratios in low, intermediate and high pCO_2 mesocosms respectively during Phase II. **(D, E, F)** show ratios in Phase III. Dashed black line is the Redfield C : P elemental ratio.

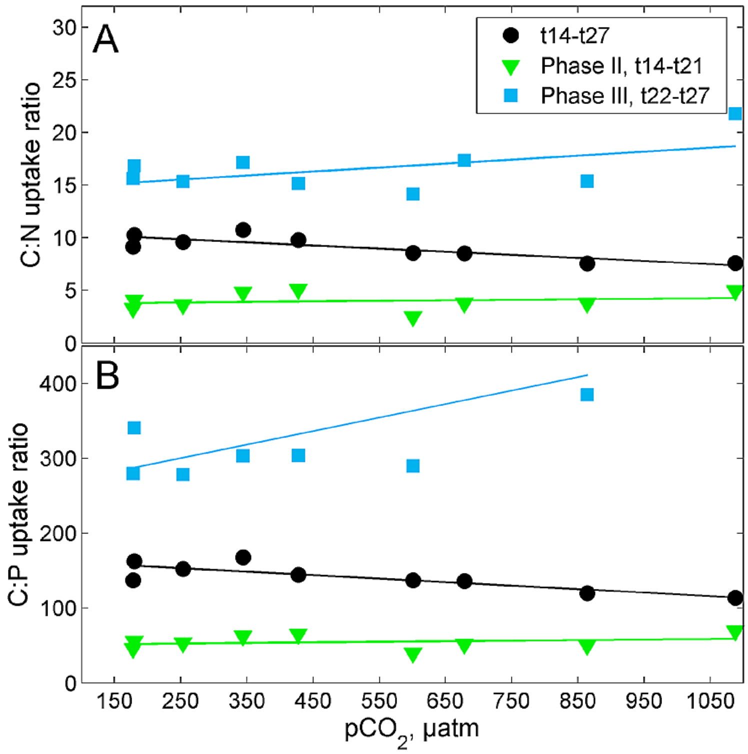

Fig. 8. Linear regressions of the mean C : N uptake ratio **(A)** and the mean C : P uptake ratio **(B)** estimated for different periods of the experiment against the mean $p\text{CO}_2$ levels for $t8$–$t27$ period.