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Effect of increased pCO_2 on the planktonic metabolic balance during a mesocosm experiment in an Arctic fjord

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Abstract. The effect of ocean acidification on the balance between gross community production (GCP) and community respiration (CR) (i.e., net community production, NCP) of plankton communities was investigated in summer 2010 in Kongsfjorden, west of Svalbard. Surface water, which was characterized by low concentrations of dissolved inorganic nutrients and chlorophyll *a* (a proxy of phytoplankton biomass), was enclosed in nine mesocosms and subjected to eight pCO_2 levels (two replicated controls and seven enhanced pCO_2 treatments) for one month. Nutrients were added to all mesocosms on day 13 of the experiment, and thereafter increase of chlorophyll *a* was provoked in all mesocosms. No clear trend in response to increasing pCO_2 was found in the daily values of NCP, CR, and GCP. For further analysis, these parameters were cumulated for the following three periods: phase 1 – end of CO_2 manipulation until nutrient addition ($t4$ to $t13$); phase 2 – nutrient addition until the second chlorophyll *a* minimum ($t14$ to $t21$); phase 3 – the second chlorophyll *a* minimum until the end of this study ($t22$ to $t28$). A significant response was detected as a decrease of NCP with increasing pCO_2 during phase 3. CR was relatively stable throughout the experiment in all mesocosms. As a result, the cumulative GCP significantly decreased with increasing pCO_2 during phase 3. After the nutrient addition, the ratios of cumulative NCP to cumulative consumption of NO_3 and PO_4 showed a significant decrease during phase 3 with increasing pCO_2. The results suggest that elevated pCO_2 influenced cumulative NCP and stoichiometric C and nutrient coupling of the plankton community in a high-latitude fjord only for a limited period. However provided that there were some differences or weak correlations between NCP data based on different methods in the same experiment, this conclusion should be taken with caution.

1 Introduction

The balance between photosynthetic carbon production and consumption of organic carbon in the ocean's surface layer is of importance in understanding the ocean's role in the global carbon cycle. Marine phytoplankton play an important role in the carbon cycle, being responsible for about half of the global primary production (Field et al., 1998). A large portion of organic carbon produced by photosynthesis is remineralized by respiration (del Giorgio and Duarte, 2002). Heterotrophic prokaryotes (hereafter "bacteria") can consume a significant fraction of primary production in pelagic systems (Cole et al., 1988; Ducklow and Carlson, 1992). Mineral nutrients (e.g., N, P) can be a limiting factor of growth or organic carbon production by phytoplankton and bacteria.

Because of the stoichiometric constraint on an organism's elemental composition, changes in the stoichiometric coupling between organic carbon and mineral nutrients in the lower part of the pelagic food web in response to environmental change may have consequences for the carbon cycle and/or the nutrient cycle in the ocean (Thingstad et al., 2008).

The increasing concentration of carbon dioxide (CO_2) in the atmosphere leads to an increase of the partial pressure of CO_2 (pCO_2) in seawater, and related changes in the chemistry of the carbonate system, such as a reduced pH (Orr, 2011). These changes could lead to changes in carbon production and consumption (Riebesell and Tortell, 2011) and, therefore, to changes in oxygen production and consumption. Net community production (NCP) is defined as the balance between gross community production (GCP) and community respiration (CR). NCP thus describes the net metabolism of the ecosystem. A positive NCP indicates that more organic carbon is produced than respired, so-called net autotrophy, while negative NCP indicates respiration exceeds primary production, net heterotrophy.

The effects of increasing pCO_2 on production and respiration of pelagic plankton have been studied on single-species in laboratory cultures up to semi-natural communities in field mesocosms (reviewed by Riebesell and Tortell, 2011). Primary production measured by ^{14}C fixation or production of particulate organic carbon (POC) at elevated pCO_2 is enhanced (Hein and Sand-Jensen, 1997; Riebesell et al, 2000; Zondervan et al., 2001; Schippers et al., 2004; Leonardos and Geider, 2005; Egge et al., 2009; Borchard et al., 2011), decreased (Sciandra et al., 2003), or shows no significant difference compared to the control (Tortell et al., 2002; Delille et al., 2005). It thus has been shown that increasing pCO_2 mostly enhances primary production. Measurements of primary production based on ^{14}C fixation or POC production are relatively numerous, but few studies have examined the metabolic balance (i.e., NCP, CR, and GCP) of planktonic communities based on changes of dissolved oxygen (DO) concentration at different pCO_2 levels. The oxygen-based NCP measurement has shown a significant decrease in NCP of *Emiliania huxleyi* at elevated pCO_2 in a N-limited chemostat culture (Sciandra et al., 2003), and insignificant changes in NCP of semi-natural plankton community at different pCO_2 levels in mesocosm experiments (Delille et al., 2005; Egge et al., 2009).

The objective of the present study was to investigate the effect of ocean acidification on the balance between GCP and CR (i.e., NCP) of a plankton community in a northern high-latitude fjord. The Arctic Ocean is particularly affected by ocean acidification: undersaturation for aragonite already occurs seasonally and will spread the whole surface of the Arctic Ocean in 2100 (Steinacher et al., 2009). In summer 2010, a multidisciplinary experiment was conducted for about one month using free-floating mesocosms deployed at Ny-Ålesund, Spitsbergen, as part of the EPOCA (European Project on Ocean Acidification) project. Seven enhanced pCO_2 treatments plus two replicated controls (no CO_2 enrichment) were established for post-bloom plankton community at the start of the experiment. Nutrients were added to all mesocosms in the middle of the experiment in order to stimulate phytoplankton growth. A series of chemical, biogeochemical, biological, and physiological parameters were measured during this experiment. We have analyzed NCP, CR, and GCP based on changing concentrations of dissolved oxygen in incubation bottles together with other related chemical and biological parameters. We also compare NCP estimated by different methods based on dissolved oxygen (this study), stable carbon isotope (de Kluijver et al., 2012), and total carbon (Silyakova et al., 2012).

2 Materials and methods

2.1 Experimental setup and sampling

The mesocosm experiment was conducted in Kongsfjorden, northern Spitsbergen (78°56.2′ N, 11°53.6′ E), in June and July 2010 as part of the EPOCA Svalbard experiment (see Czerny et al., 2012; Riebesell et al., 2012; Schulz et al., 2012 for details). In Kongsfjorden, the spring phytoplankton bloom occurs in April, which results in low concentration of dissolved inorganic nutrients (Rokkan Iversen and Seuthe, 2011; Hodal et al., 2012). Nine Kiel off-shore mesocosms (KOSMOS: thermoplastic polyurethane 0.5 to 1 mm thick, 17 m long, and 2 m in diameter, approximately 50 m^3 volume) were deployed on 31 May 2010 (t–7). The site of the mesocosm mooring was ice-free during the experiment except for a few occasions when ice floats needed to be pushed out from the site (Riebesell et al., 2012). All mesocosms were filled with nutrient-poor, post-bloom, and sieved (3 mm mesh) fjord water. The CO_2 manipulation was carried out between 6 and 11 June ($t-1$ to $t4$), establishing seven enhanced pCO_2 treatments and two replicated controls (no pCO_2 treatment). pH and approximate pCO_2 levels in all mesocosms on $t8/9$ and $t26/27$ are shown in Table 1 (see also Bellerby et al., 2012). While pH and pCO_2 changed in all mesocosms because of air/sea gas exchange and biological carbon uptake to different degrees, the gradients of pH and pCO_2 between the treatments remained until the end of the experiment (Bellerby et al., 2012; Schulz et al., 2012; Silyakova et al., 2012). To induce the development of a phytoplankton bloom, 5 µM of nitrate (NO_3), 0.31 µM of phosphate (PO_4), and 2.5 µM of silicate (Si) were added early in the morning on 20 June ($t13$) (i.e., before the routine sampling) to all mesocosms. The nutrient concentrations were chosen to simulate an upwelling event (Schulz et al., 2012). The additions of CO_2 ($t-1$ to $t4$) and inorganic nutrients ($t13$) were performed in the upper 13 m of the mesocosms using the dispersal device in order to assure an even distribution in the water column (Riebesell et al., 2012; Schulz et al., 2012).

Table 1. Average pH_T and approximate pCO_2 levels (µatm) on $t8/9$ and $t26/27$ during the experiment (Bellerby et al., 2012).

	$t8/9$		$t26/27$	
Mesocosm	pH_T	pCO_2	pH_T	pCO_2
3*	8.32	185	8.36	165
7*	8.31	185	8.37	160
2	8.18	270	8.25	220
4	8.05	375	8.15	290
8	7.96	480	8.07	365
1	7.81	685	7.94	500
6	7.74	820	7.90	555
5	7.64	1050	7.80	715
9	7.51	1420	7.73	855

* Mesocosms 3 and 7 received no pCO_2 manipulation (i.e., control).

Depth-integrated water samples (0–12 m) were collected in each mesocosm using Hydro-Bios integrated water samplers (5 L volume). Samples for nutrients and chlorophyll *a* (Chl *a*) were collected in the morning (09:00–11:00), whereas those for measurement of community metabolism were collected in the afternoon (13:00–15:00). Such a separate sampling program was used because of logistical constraints. The experiment ended on 7 July ($t30$). Sampling for NCP and CR determination ended on 5 July ($t28$).

2.2 Net community production, community respiration, and gross community production

Water samples from each mesocosm were distributed into 12 biological oxygen demand (BOD) bottles (60 mL) by overflowing by 4–5 times the bottle volume, as soon as the water samples were brought back to shore. Four bottles were immediately fixed with Winkler reagents to determine the initial concentration of dissolved oxygen (DO), and served as a control. Then, two quadruple sets of bottles served for determination of NCP and CR. Prior to filling, the BOD bottles had been washed with HCl (5 %) and rinsed thoroughly with Milli-Q water.

Meroplankton larvae (*Cirripedia nauplii*) were abundant (1×10^4–2×10^4 individuals m^{-3}) in the mesocosms between $t-2$ and $t11$ (Niehoff et al., 2012), and several individuals of this species and mesozooplankton were sometimes distributed in quadruple sets of BOD bottles (Tanaka et al., unpublished). The heterogeneous inclusion of large organisms can to an extent contribute to the variation in concentration of DO between replicated samples during the first half of the experiment. However since we wanted to minimize the perturbation, water samples collected from the mesocosms were poured into BOD bottles without any pre-treatment.

NCP and CR were measured every 2 and every 4 days, respectively, between $t-1$ and $t7$ and between $t12$ and $t28$. That is, the incubations of both NCP and CR bottles and that of NCP bottles alone were done alternatively during the experiment. BOD bottles for NCP measurement were incubated for 24 h at a mooring site, which was located about 300 m from the mesocosms. The BOD bottles were incubated at 4 m depth, at which the irradiance corresponded to the average irradiance of the water column sampled in the mesocosms (0 to 12 m). As the summer season progressed, the mooring site sometimes became influenced by the plume of a nearby stream. Therefore, the mooring was moved closer (about 100 m) to the mesocosms on 13 June ($t6$). For the CR measurement, dark BOD bottles were incubated at the in situ mooring site until 18 June ($t11$), and clear BOD bottles were incubated in a dark laboratory incubator from 19 June ($t12$) onwards due to logistical constraints. The temperature in the laboratory incubator was adjusted to the mean water temperature in the top 12 m on the day of sampling (2 to 4 °C). Preliminary measurements of CR with Kongsfjorden samples did not detect a statistically significant decrease in DO during the first 24 h of incubation in the dark. The CR samples were therefore incubated for 48 h. Upon completion of the incubation, the bottles were fixed with Winkler reagents as described by Knap et al. (1996).

DO concentrations were determined with an automated Winkler titration method using a potentiometric end-point detection (Titrando888). Reagents and standardizations were similar to those described by Knap (1996). Rates of NCP and CR were determined by linear regression of DO against time (slope ± standard error: µmol O_2 L^{-1} d^{-1}). GCP was calculated as the difference between NCP and CR. The combined uncertainty of GCP (SE_{GCP}) was calculated using the standard error of NCP (SE_{NCP}) and CR (SE_{CR}) according to

$$SE_{GCP} = \sqrt{SE_{NCP}{}^2 + SE_{CR}{}^2}. \quad (1)$$

The cumulative values of NCP, CR, and GCP were calculated for different periods, which were defined based on the timing of manipulations and the temporal changes of phytoplankton biomass (see Riebesell et al., 2012): (1) phase 1 – end of CO_2 manipulation until nutrient addition ($t4$ to $t13$); (2) phase 2 – nutrient addition until the second Chl *a* minimum ($t14$ to $t21$); (3) phase 3 – the second Chl *a* minimum until the end of this study ($t22$ to $t28$); (4) phase 2 + 3 ($t14$ to $t28$); and (5) whole period ($t4$ to $t28$). Because NCP and CR were measured every 2 and 4 days, respectively during most of the experimental period, the data on the days when the measurement was not done were estimated by the linear interpolation. The cumulative values were then summed up for the corresponding period.

2.3 Statistical analysis

Linear regression was used to analyze the significance of responses of NCP, CR, GCP, and ratios of cumulative NCP to cumulative consumption of NO_3 and PO_4 to increased pCO_2 levels. When pCO_2-dependent NCP, CR, and GCP were analyzed on a certain day, the pCO_2 values measured on that

Table 2. Initial condition in the nine mesocosms. Data on $t0$ are shown as a reference (Schulz et al., 2012). DIN (dissolved inorganic nitrogen) is the sum of NO_3, NO_2, and NH_4.

Parameter	Temperature (°C)[1]	NO_3 (µmol -N L^{-1})	NO_2 (µmol -N L^{-1})	NH_4 (µmol -N L^{-1})	PO_4 (µmol -P L^{-1})	Si (µmol -Si L^{-1})	DIN: PO_4	DIN: Si	Si: PO_4	Chl *a* ($\mu g\,L^{-1}$)[2]
Mean ± SD ($n = 9$)	2.9 ± 0.1	0.02 ± 0.01	0.00 ± 0.00	0.59 ± 0.05	0.05 ± 0.01	0.13 ± 0.02	11.3 ± 1.4	4.7 ± 0.9	2.5 ± 0.6	0.21 ± 0.02

[1] The data on temperature were based on the mean of 0–12 m in each mesocosm (Schulz et al., 2012).
[2] The data on Chl *a* are based on the HPLC method (Schulz et al., 2012).

day were used. For the regression analysis of the cumulative parameters, the mean pCO_2 during the corresponding period was used. All statistical analyses were performed with R (R Development Core Team, 2008).

3 Results

The Arctic coastal water used to fill the mesocosms had low concentrations of dissolved inorganic nutrients and Chl *a*. The concentrations of NO_3 and PO_4 but not NH_4 were close to the detection limit of the conventional nutrient analysis, and the mean Chl *a* concentration determined by the high-performance liquid chromatography method was 0.21 $\mu g\,L^{-1}$ on $t0$ (Table 2; Schulz et al., 2012). The mean ratios of dissolved inorganic nitrogen (DIN: sum of NH_4, NO_3, and NO_2) to PO_4, DIN to Si, and Si to PO_4 were 11.3, 4.7, and 2.5, respectively, in all mesocosms (Table 2; Schulz et al., 2012). The water temperature was homogeneous in the water column of the mesocosms at the beginning, and increased gradually, especially in the upper 5 to 10 m, until the end of the experiment (~ 2.7 to $\sim 5.5\,°C$), while it was always similar in all mesocosms (coefficient of variation: 0 to 6 %; see Schulz et al., 2012).

The concentrations of dissolved inorganic nutrients remained low in all mesocosms until the nutrient addition performed on $t13$ (Schulz et al., 2012). After the addition of nutrients, the net consumption rate of NO_3 and PO_4 was statistically higher in higher pCO_2 mesocosms from $t17$ to $t22$, while the cumulative nutrient consumption became similar in all mesocosms toward the end of the experiment (Schulz et al., 2012). The concentration of Chl *a* ranged from 0.1 to 2.6 $\mu g\,L^{-1}$ ($t0$ to $t30$) and increased during the experiment (Fig. 1, see also Schulz et al., 2012). Peaks of Chl *a* were observed three times in all mesocosms: once before the nutrient addition ($t8$, range: 0.5–0.9 $\mu g\,L^{-1}$) and twice after the nutrient addition ($t19$ and $t28$, range: 0.3–1.0 $\mu g\,L^{-1}$ and 0.6–1.8 $\mu g\,L^{-1}$, respectively). The first Chl *a* peak during phase 1 was largely dominated by haptophytes, while, after the nutrient enrichment, the second was due to prasinophytes, dinoflagellates, and cryptophytes, and the third was due to haptophytes, prasinophytes, dinoflagellates, and chlorophytes (Schulz et al., 2012). Top-down control on nanophytoplankton by microzooplankton grazing and viral lysis was important especially during phase 1 (Brussaard et al., 2012). The Chl *a* concentration at elevated pCO_2 was statistically higher during phase 2, but lower during phase 3 (Schulz et al., 2012).

GCP ranged from -0.5 ± 1.0 to 11.2 ± 2.3 µmol $O_2\,L^{-1}\,d^{-1}$ between $t-1$ and $t28$ (Fig. 1). Note that negative values were not statistically different from 0 (F-test, $P > 0.05$). The lowest and the highest GCPs were mostly observed, respectively, before the nutrient addition and towards the end of the experiment ($t24$ or $t28$). There were a few exceptions: the smallest GCP was observed after the nutrient addition ($t16$) in M6, and the highest value was observed before the nutrient addition ($t12$) in M9. After the nutrient addition, while GCP showed two peaks in M1 and a reduction in M9, it increased towards the end of the experiment in the other mesocosms. Linear regression analysis detected a significant decrease of GCP as a function of increasing pCO_2 on $t24$ (-0.008 ± 0.002 µmol $O_2\,L^{-1}\,d^{-1}\,\mu atm^{-1}$, $P < 0.05$).

The extent of temporal variation of CR (-5.6 to 0.25 µmol $O_2\,L^{-1}\,d^{-1}$) was about half of that of GCP during the experiment (Fig. 1). The positive CR measured in M2 on $t7$ was not statistically different from zero (F-test, $P = 0.89$). The highest CR was observed before the nutrient addition in M1, M2, M3, M4, and M7, and after the nutrient addition in M5, M6, M8, and M9. Linear regression analysis detected no significant relationship between CR and pCO_2 levels on any day (F-test, $P > 0.05$).

NCP was mostly close to zero or positive during the experiment (Fig. 1). Statistically significant negative NCP values were detected seven times (M2 and M8 on $t-1$, M7 on $t7$, M5 and M7 on $t12$, M6 on $t16$, and M6 on $t24$). Similar to GCP, the smallest and the highest NCP in each mesocosm were mostly observed before the nutrient addition and towards the end of the experiment ($t26$ or $t28$), respectively. There were a few exceptions: the lowest NCP was observed after the nutrient addition ($t16$) in M6, and the highest was observed before the nutrient addition ($t12$) in M9. NCP in all mesocosms but M9 tended to increase

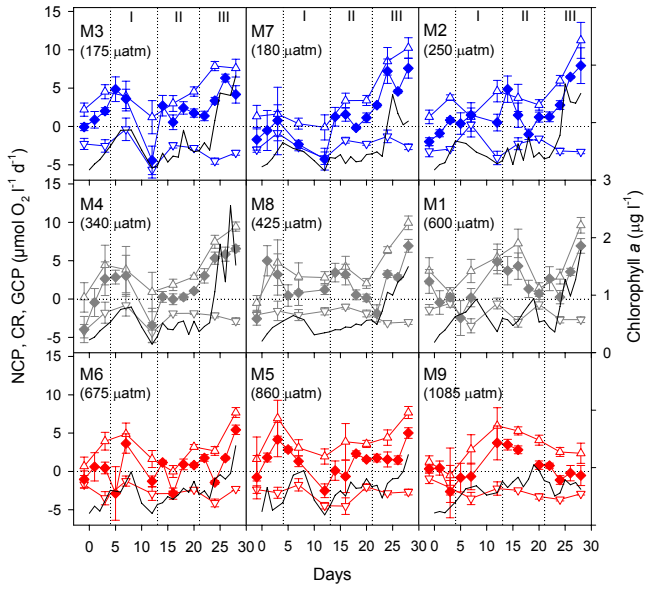

Fig. 1. Temporal changes of gross community production (GCP: open upside triangle), net community production (NCP: filled diamond), and community respiration (CR: open downside triangle) based on changes of dissolved oxygen during incubation. Values are mean ± standard error (µmol O_2 L^{-1} d^{-1}). The color code is as follows: blue for low pCO_2 treatments (M3, M7, and M2), grey for intermediate pCO_2 treatments (M4, M8, and M1) and red for high pCO_2 treatments (M6, M5, and M9). Black solid lines are HPLC-based chlorophyll *a* concentration (µg L^{-1}: Schulz et al., 2012). Vertical dotted lines separate phases 1, 2, and 3 during the experiment (see also the text). pCO_2 values (µatm) denote the mean during the experiment (Bellerby et al., 2012).

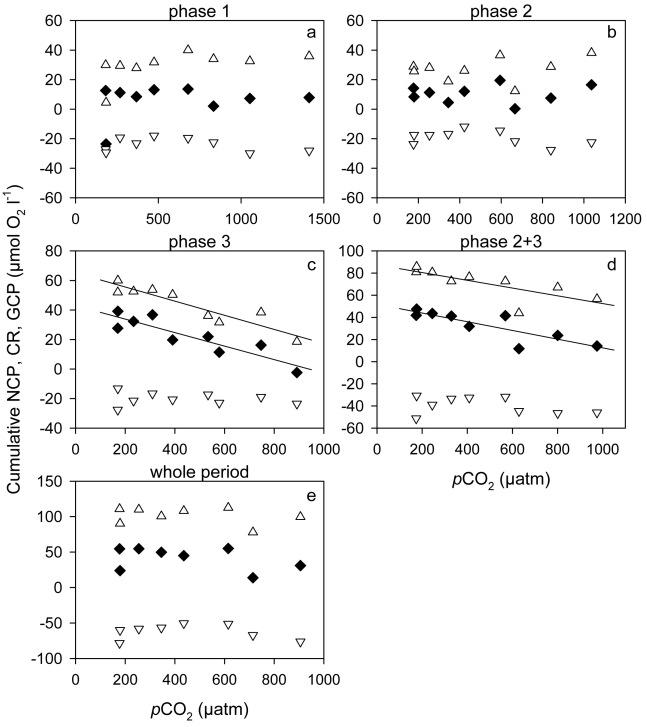

Fig. 2. Relationship between cumulative GCP (open upside triangle), NCP (filled diamond), and CR (open downside triangle) (µmol O_2 L^{-1}) vs. the mean pCO_2 (µatm) during **(a)** phase 1 (end of CO_2 manipulation until nutrient addition: $t4$ to $t13$), **(b)** phase 2 (nutrient addition until the second chlorophyll minimum: $t14$ to $t21$), **(c)** phase 3 (the second chlorophyll minimum until the end of this study: $t22$ to $t28$), **(d)** phase 2 + 3 (after nutrient addition: $t14$ to $t28$), and **(e)** the whole period ($t4$ to $t28$). The lines indicate statistically significant relationship (F-test, $P < 0.05$).

after the nutrient addition towards the end of the experiment. The temporal variation of NCP in each mesocosm during the experiment tended to decrease with increasing pCO_2 level. Linear regression analysis detected a significant decrease of NCP with increase of pCO_2 level on $t24$ and $t26$ (slope ± se: -0.008 ± 0.003 and -0.008 ± 0.001 µmol O_2 L^{-1} d^{-1} µatm^{-1}, respectively on $t24$ and $t26$, F-test, $P < 0.05$ for both cases).

The cumulative NCP revealed that it was negative in only one mesocosm (M7) before the nutrient addition (phase 1) (Fig. 2). It should be noted that M3 and M7 were treated as the control in the same way with regard to the CO_2 perturbation (i.e., no CO_2 enrichment). During phase 3, only the cumulative NCP in M9 was negative. The proportion of the cumulative NCP during the whole period was highest during phase 3 in all mesocosms except M9. The cumulative CR in all mesocosms tended to be similar between different phases. The proportion of the cumulative GCP was highest during phase 3 in all mesocosms except M1, 6, and 9.

A linear regression describes the pCO_2-dependent decrease of cumulative NCP during phase 3 (slope ± se: -0.05 ± 0.01 µmol O_2 L^{-1} µatm^{-1}, $n = 9$, F-test, $P = 0.001$) and during phase 2 + 3 (slope ± se: -0.04 ± 0.01 µmol O_2 L^{-1} µatm^{-1}, $n = 9$, F-test, $P = 0.005$). The cumulative NCP slightly increased with increasing pCO_2 during phases 1 and 2, although the regression slope was not significant ($P > 0.05$). The relationship between cumulative NCP and pCO_2 during the whole period was statistically negative (F-test, $P = 0.02$) only when the data from M7 were not included in the analysis. The relationship between CR and pCO_2 was always insignificant (F-test, $P > 0.05$). The cumulative GCP significantly decreased with increasing pCO_2 during phase 3 (slope ± se: -0.05 ± 0.01 µmol O_2 L^{-1} µatm^{-1}, $n = 9$, F-test, $P < 0.001$) and during phase 2 + 3 (slope ± se: -0.04 ± 0.01 µmol O_2 L^{-1} µatm^{-1}, $n = 9$, F-test, $P = 0.019$).

The net consumption rate of NO_3 and PO_4 with increasing pCO_2, both significantly increased during phase 2 and decreased during phase 3 (F-test, $P < 0.05$; Schulz et al., 2012). During the period between $t14$ and $t28$ (phase 2 + 3), the cumulative consumption of NO_3 and PO_4 was respectively similar between nine mesocosms

(5.3–5.5 µmol N L^{-1}, 0.32–0.38 µmol P L^{-1}), and thus the ratios of cumulative consumption of NO_3 to PO_4 were similar in all mesocosms (range: 14–17, $n = 9$; Schulz et al., 2012), which is close to Redfield ratio of 16. Assuming a photosynthetic quotient of 1.25 (Williams, et al., 1979), the ratios of cumulative NCP to cumulative consumption of NO_3 and PO_4 (i.e., C:N and C:P ratios) in all mesocosms were 0.1 to 5.2 and 1 to 76, respectively, during phase 2 and −1.6 to 12 and −24 to 210, respectively, during phase 3 (Fig. 3). The negative ratios were due to the negative cumulative NCP in M9 during phase 3. The pCO_2-dependent decrease in ratio of cumulative NCP to cumulative consumption of NO_3 and PO_4 was detected during phase 3 (slope ± se: -0.014 ± 0.003 µmol C µmol N^{-1} µatm^{-1}, $n = 9$, F-test, $P = 0.003$; slope ± se: -0.22 ± 0.05 µmol C µmol P^{-1} µatm^{-1}, $n = 9$, F-test, $P = 0.003$, respectively) and during phase $2 + 3$ (slope ± se: -0.005 ± 0.001 µmol C µmol N^{-1} µatm^{-1}, $n = 9$, F-test, $P = 0.011$; slope ± se: -0.07 ± 0.02 µmol C µmol P^{-1} µatm^{-1}, $n = 9$, F-test, $P = 0.019$, respectively).

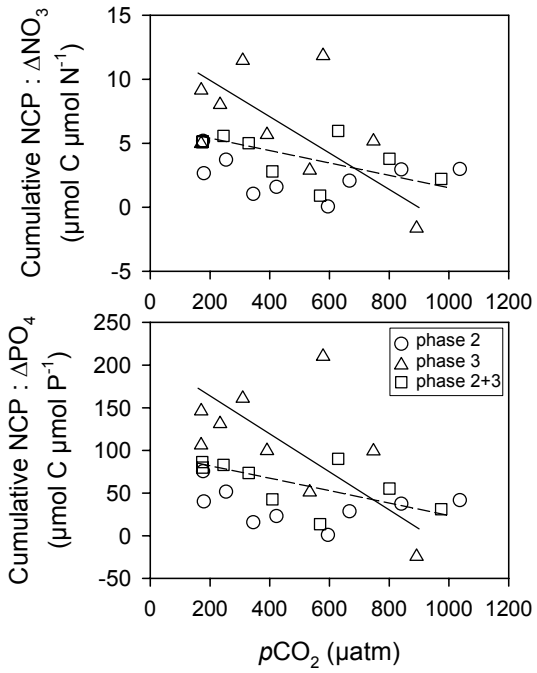

Fig. 3. Relationships between ratios of NCP (µmol C L^{-1} d^{-1}) to cumulative consumption of NO_3 (µmol N L^{-1}) and PO_4 (µmol P L^{-1}) vs. the mean pCO_2 (µatm) during phase 2 (nutrient addition until the second chlorophyll minimum: $t14$ to $t21$) (circle), phase 3 (the second chlorophyll minimum until the end of this study: $t22$ to $t28$) (triangle), and phase $2 + 3$ (after nutrient addition: $t14$ to $t28$) (square). NCP values based on changes of dissolved oxygen concentration were converted to carbon unit under an assumption of photosynthetic quotient of 1.25 (Williams et al., 1979). The solid and dotted lines indicate statistically significant relationship during phase 3 and phase $2 + 3$, respectively (F-test, $P < 0.05$).

4 Discussion

This experiment was set up as a gradient of pCO_2 levels with a range of 185 to 1420 µatm on $t8/9$ (Table 1; Bellerby et al., 2012). The water used to fill the mesocosms had low concentrations of NO_3, PO_4, Si, and Chl a, and the nutrient stoichiometry suggests a depletion of dissolved inorganic nitrogen and Si compared to PO_4 (Table 2; Schulz et al., 2012). The water temperature increased gradually, especially in the upper 5 to 10 m, in all mesocosms during the experiment (2.7 to 5.5 °C; Schulz et al., 2012). The growth rate of planktonic organisms is sensitive to increasing water temperature (Eppley, 1972; Rose and Caron, 2007; Kirchman et al., 2009). Significant effects of temperature and/or nutrient supply on microbial metabolism are observed in cold waters (e.g., Pomeroy et al., 1991), but CR remained relatively stable in our study. Since our experimental design did not include a control mesocosm with regard to water temperature and nutrients, it is not possible to separate the effect of temperature and availability of nutrients from that of ocean acidification on the responses of NCP, CR, and GCP values reported in the present study. In other words, the responses of the metabolic balance in each mesocosm can be regarded as an effect of a given pCO_2 set up at the start of the experiment, overridden with a gradual increase of water temperature throughout the experiment and a nutrient enrichment on $t13$ to all mesocosms.

The cumulative net community production of the post-bloom plankton community in a high-latitude fjord estimated using the oxygen technique significantly decreased with increasing pCO_2 after nutrient addition during the period of the second Chl a minimum until the end of this study (phase 3). Community respiration was relatively stable throughout the experiment in all mesocosms, with no consistent pattern found in response to changes in pCO_2. As a result, the cumulative gross community production (the difference between NCP and CR) significantly decreased with increasing pCO_2 level during phase 3. While the nutrient addition on $t13$ induced an increase of phytoplankton biomass in all mesocosms, the ratio of cumulative NCP to cumulative consumption of NO_3 and PO_4 significantly decreased with increasing pCO_2 during phase 3, suggesting alterations of the stoichiometric C:N and C:P uptake by the plankton community in response to increasing pCO_2.

In this experiment NCP of whole plankton community was determined based on three different methods: temporal changes of total carbon (C_T) concentration (hereafter, C_T-NCP) (Czerny et al., 2012; Silyakova et al., 2012), net ^{13}C-POC production (hereafter, ^{13}C-NCP) (de Kluijver et al., 2012), and net oxygen production in incubation bottles (hereafter, O_2-NCP) (this study). Conceptually, these methods are considered to measure the process of NCP. However, there are some differences in practice (see Czerny et al., 2012;

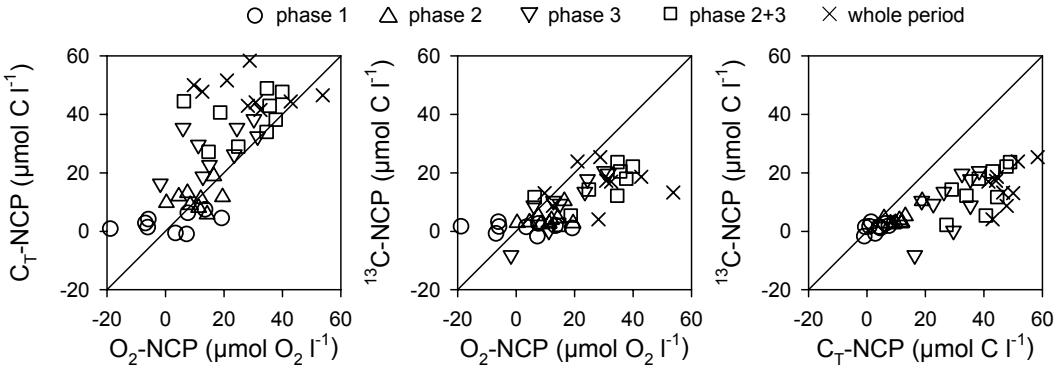

Fig. 4. Comparison of NCP measured with three different methods: temporal changes of total carbon concentration (hereafter, C_T-NCP) (Silyakova et al., 2012), net ^{13}C-POC production (hereafter, ^{13}C-NCP) (de Kluijver et al., 2012), and net oxygen production in incubation bottles (hereafter, O_2-NCP) (this study). The data were cumulated for each period: phase 1 ($t8$ to $t13$; circle), phase 2 ($t14$ to $t21$; upward triangle), phase 3 ($t22$ to $t27$; downward triangle), phase $2+3$ ($t14$ to $t22$; square), and the whole period ($t8$ to $t27$; cross). When NCP was not measured every day, the data were linearly interpolated before cumulation. See also Table 3. The solid lines indicate the 1 : 1 relationship.

de Kluijver et al., 2012; Silyakova et al., 2012). C_T-NCP is based on daily measurements of C_T in integrated samples (no incubation) and on a correction for gas exchange. ^{13}C-NCP is a measure of mesocosm-scale accumulation of ^{13}C-POC in the water column and sediment material, and also does not require incubation (addition of ^{13}C-bicarbonate to the mesocosms on $t-4$). O_2-NCP is based on changes in the concentration of DO during 24 h incubation of the integrated samples at a fixed depth outside the mesocosms.

Cumulative O_2-NCP was generally similar to cumulative C_T-NCP and higher than cumulative ^{13}C-NCP (Fig. 4). Cumulative O_2-NCP positively correlated with both cumulative C_T- and ^{13}C-NCP during phases 3 and $2+3$ ($P < 0.05$) (Table 3). However, the correlation between O_2-NCP and the other NCPs was low during the other phases. Cumulative C_T- and ^{13}C-NCP always showed the same trend and were highly correlated ($r = 0.785$–0.976, $P < 0.05$) except during phase 1 (Table 3), while cumulative ^{13}C-NCP tended to be smaller than cumulative C_T-NCP (Fig. 4). Production rate of POC and DOC for the < 200 µm community measured using ^{14}C in the same experiment, which is somewhat between net and gross primary production, was always higher than these three NCPs (see Engel et al., 2012). Hence, the responses of cumulative NCP with increasing pCO_2 were somewhat different between the three measurements: (1) insignificant responses of O_2-NCP with increasing pCO_2 during phases 1 and 2, but significant positive responses of C_T-NCP during phase 1 and ^{13}C-NCP during phase 2; (2) insignificant responses of O_2-NCP with increasing pCO_2 during the whole period, but significant negative response of ^{13}C-NCP (Fig. 2; de Kluijver et al., 2012; Silyakova et al., 2012). The cumulative O_2-NCP during phases 1 and 2 in response to increasing pCO_2 tended to be positive but was statistically insignificant. Moreover the ratio of cumulative O_2-NCP to NO_3 and PO_4 with increasing pCO_2 was significant during phase 3, but the ratio of cumulative C_T-NCP to NO_3 and PO_4 was insignificant with increasing pCO_2 (Fig. 3; Silyakova et al., 2012).

Table 3. Correlation analysis of NCP measured with three different methods: temporal changes of total carbon concentration (C_T-NCP) (Silyakova et al., 2012), net ^{13}C-POC production (^{13}C-NCP) (de Kluijver et al., 2012), and net oxygen production in incubation bottles (O_2-NCP) (this study). The data were cumulated for each period: phase 1 ($t8$ to $t13$), phase 2 ($t14$ to $t21$), phase 3 ($t22$ to $t27$), phase $2+3$ ($t14$ to $t22$), and the whole period ($t8$ to $t27$). When NCP was not measured every day, the data were linearly interpolated before cumulation. Significant coefficients of correlation are shown in bold with * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$) ($n = 9$ for all cases). See also Fig. 4.

Period	Parameter	C_T-based	^{13}C-based
phase 1	O_2-based	0.369	−0.086
phase 2		−0.108	0.377
phase 3		**0.927*****	**0.913*****
phase $2+3$		**0.792***	**0.751***
whole period		0.113	0.128
phase 1	C_T-based	–	0.553
phase 2			**0.785***
phase 3			**0.937*****
phase $2+3$			**0.976*****
whole period			**0.838****

We speculate that these differences were due to (1) less frequent measurement of O_2-NCP, (2) less representative measurement of O_2-NCP, and/or (3) possible modification of C and O_2 coupling of the plankton community. Since the cumulative calculation was based on only three data points during phase 1 (Fig. 1), the less frequent measurement could contribute to a relatively large uncertainty for the cumulative O_2-NCP. It should be noted that the correlation between C_T-NCP and ^{13}C-NCP was insignificant during phase 1 (Table 3). During phases $2+3$, O_2-NCP was measured every second day, while C_T-NCP and ^{13}C-NCP were measured every day (except on $t26$ and $t28$ for ^{13}C-NCP). Unless skewed increases of NCP happened on daily scale, it is difficult to explain why a similar response was detected for all three NCP datasets during phase 3 but the response of O_2-NCP was different from the others only during phase 2 (marginally positive for C_T-NCP during phase 2, $P = 0.08$). As mentioned above, there were some important differences in measurement and incubation of samples between the three methods. O_2-NCP was measured by incubating the integrated samples for 24 h at a fixed depth at the mooring site. Although we chose the incubation depth of 4 m at which the irradiance corresponded to the average irradiance of the water column sampled in the mesocosms (0 to 12 m), the mooring site was occasionally influenced by the plume of a nearby stream, resulting in reduced water transparency and irradiance. In the mesocosms, photosynthetically active radiation at 14.5 m and 4.2 m depth varied in a range of 2–15 % and 10–30 %, respectively, in comparison to the surface layer (0.1 to 0.2 m), which was likely because of temporal changes of phytoplankton biomass (Schulz et al., 2012). Gao et al. (2012) recently reported that the growth rate of three species of diatoms subjected to elevated pCO_2 is inversely related to light at irradiance levels above 22 to 36 % of surface irradiance in the South China Sea, and the threshold of photoinhibition occurs at lower irradiance in elevated pCO_2 compared to the ambient pCO_2. This demonstrates the confounding effects of the synergistic and antagonistic interactions of pCO_2 and irradiance conditions on the response of phytoplankton (e.g., Boyd et al., 2010). In this study, irradiance was not measured at the mooring site during the experiment, preventing the comparison of the light condition between the mesocosm site and the mooring site. It has been reported that long incubation (24 h for NCP and 48 h for CR in this study) in bottles can result in important changes in the abundance, activity, and composition of the community, leading in turn to significant changes in the planktonic metabolism (Pomeroy et al., 1994; Calvo-Díaz et al., 2011). However, unless the irradiance was significantly different between the mesocosm site and the mooring site and/or the artifact of bottle incubation was only significant during phase 2, it is difficult to explain why a similar response was detected for all three NCP datasets during phase 3 but only the response of O_2-NCP was different from the others during phase 2. Interestingly, Schulz et al. (2012) report that numerous parameters of standing stock and phytoplankton composition positively or negatively correlated with increasing pCO_2, and pCO_2-related differences in phytoplankton pigment composition, phytoplankton carbon biomass, and organic matter became increasingly significant as the experiment progressed. While the photosynthetic quotient was assumed to be 1.25 in this study, it generally varies in a range of 1.2 to 1.8 (Laws, 1991). A study in the Canadian high Arctic reports an apparent photosynthetic quotient in the range of 1.3 to 1.8 (Platt et al., 1987). Assuming a photosynthetic quotient of 1.8, the ratios of cumulative NCP to cumulative consumption of NO_3 and PO_4 (i.e., C:N and C:P ratios) in all mesocosms would be proportionally reduced (C:N $= 0.05$ to 3.6 and C:P $= 1$ to 52 during phase 2 and C:N $= -1.1$ to 8.2 and C:P $= -17$ to 146 during phase 3) but the significant relationships would remain unchanged (data not shown). It is possible that the photosynthetic quotient is a function of the nutrient concentration (Williams et al., 1979). In addition, an application of a constant photosynthetic quotient to all pCO_2 treatments may add further uncertainty to the comparison of O_2-NCP with the carbon-based NCP, although to our knowledge change of photosynthetic quotient in response to increasing pCO_2 remains to be clarified. A significant increase of C_T-NCP and an insignificant response of O_2-NCP with increasing pCO_2 have been reported from a pCO_2-manipulated mesocosm experiment performed using relatively temperate coastal water in Norway (60.6° N, 5.2° E) (Riebesell et al., 2007; Bellerby et al., 2008; Egge et al., 2009).

Ocean acidification leads to both negative and positive effects on biological processes (reviewed by Hendriks et al., 2010; Kroeker et al., 2010; Liu et al., 2010). A meta-analysis suggests that photosynthetic organisms show higher growth rates with increasing pCO_2 and concludes that natural phytoplankton assemblages consistently show a relatively modest increase in carbon fixation at elevated pCO_2 (Hendriks et al., 2010). Yoshimura et al. (2010) reported that increasing pCO_2 treatment resulted in a significantly smaller accumulation of dissolved organic carbon with a reduced contribution of fucoxanthin-containing phytoplankton such as diatoms in the phytoplankton community in a CO_2-manipulated experiment in the Sea of Okhotsk. They did not find any significant effect on Chl *a* and POC, although phytoplankton growth or production was not measured. Their results may hint at reduced NCP with increasing pCO_2. In the present study, even though phase 3 seems relatively short (one-third of the whole experimental period), the cumulative NCP based on all three measurements showed significantly negative effect of increasing pCO_2 for pelagic plankton communities (Fig. 2; de Kluijver et al., 2012; Silyakova et al., 2012).

The net consumption rate of NO_3 and PO_4 was higher at the higher levels of pCO_2 during phase 2 and at the lower pCO_2 levels during phase 3 (Schulz et al., 2012). During phase 2, a statistically significant, positive correlation with increasing pCO_2 was found for the concentrations of DOC, POC, PON, and POP, but not for any stoichiometric ratio

(Schulz et al., 2012). The higher consumption rate of NO_3 at higher pCO_2 levels observed in the same study (Schulz et al., 2012) is in contrast with the findings of Riebesell et al. (2007) who reported higher NO_3 consumption at lower pCO_2 levels at the beginning of the experiment. While the cumulative consumption of NO_3 was similar between the mesocosms during phase 2+3 in the present study, the ratio of POC to PON in the mesocosm water column was about 8 at the lower pCO_2 levels and about 6 at the higher pCO_2 levels at the end of the experiment (Schulz et al., 2012). This trend was amplified in the ratio of POC to PON in the sediment materials of mesocosms (Czerny et al., 2012). The abundance of diatoms increased faster in the lower pCO_2 treatments from $t20$ onward in the same experiment (Aberle et al., 2012; Schulz et al., 2012), and higher amounts of diatom-derived material were collected in the sediment traps of the lower pCO_2 mesocosms (Czerny et al., 2012). The mechanism(s) that caused these stoichiometric responses remains to be elucidated. Yet it is evident that increasing pCO_2 resulted in alteration of stoichiometric coupling of C and nutrients in the present study, which may change the nutritional value for higher trophic levels.

In conclusion, the metabolic parameters (NCP, CR, and GCP) of planktonic communities based on changes of DO concentration at different pCO_2 levels showed insignificant response of NCP during phases 1 and 2 and a significant decrease of NCP as a function of increasing pCO_2 during phase 3. CR was relatively stable throughout the experiment in all mesocosms. As a result, the cumulative GCP significantly decreased with increasing pCO_2 only during phase 3. Similarly, the ratios of cumulative NCP to cumulative consumption of NO_3 and PO_4 showed insignificant response during phase 2 but significant decrease during phase 3 with increasing pCO_2. The results suggest that elevated pCO_2 influenced cumulative NCP and stoichiometric C and nutrient coupling of the plankton community in a high-latitude fjord only for a limited period. Since there were some differences or weak correlations between O_2-NCP vs. C_T-NCP and ^{13}C-NCP during phases 1 and 2, this conclusion should be taken with caution.

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