

Metabolic balance of a plankton community in a pelagic water

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Metabolic balance of a plankton community in a pelagic water of a northern high latitude fjord in response to increased $p\text{CO}_2$

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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.

5 Surface water, which was characterized by low concentrations of dissolved inorganic nutrients and chlorophyll, was enclosed in 9 mesocosms and subjected to 8 $p\text{CO}_2$ levels (2 replicated controls and 7 enhanced $p\text{CO}_2$ treatments) for one month. Nutrients were added to all mesocosms on day 13 of the experiment, and thereafter increase of chlorophyll (index of phytoplankton biomass) was provoked in all mesocosms. No
10 clear trend in response to increasing $p\text{CO}_2$ 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 (t_4 to t_{13}); phase 2: nutrient addition until the second chlorophyll minimum (t_{14} to t_{21}); phase 3: the second chlorophyll minimum until the end of this study (t_{22} to t_{28}). Significant response was
15 detected as a decrease of NCP with increasing $p\text{CO}_2$ during phase 3. CR was relatively stable throughout the experiment in all mesocosms. As a result, the cumulative GCP significantly decreased with increasing $p\text{CO}_2$ during phase 3. After the nutrient addition, the ratios of cumulative NCP to cumulative consumption of NO_3 and PO_4 showed significant decrease during phase 3 with increasing $p\text{CO}_2$. The results suggest that
20 elevated $p\text{CO}_2$ 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.

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1 Introduction

The balance between photosynthetic carbon production and consumption of organic carbon in the ocean's surface layer is of an 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 organisms' 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 ($p\text{CO}_2$) 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 $p\text{CO}_2$ 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

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measured by ^{14}C fixation or production of particulate organic carbon (POC) at elevated $p\text{CO}_2$ 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 that increasing $p\text{CO}_2$ mostly enhances primary production. Measurement 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 $p\text{CO}_2$ levels. The oxygen-based NCP measurement has shown a significant decrease in NCP of *Emiliana huxleyi* at elevated $p\text{CO}_2$ in a N-limited chemostat culture (Sciandra et al., 2003), and insignificant changes in NCP of semi-natural plankton community at different $p\text{CO}_2$ 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. 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.

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). Briefly, nine Kiel off-shore mesocosms (KOSMOS) were deployed on 31 May 2010 ($t - 7$), and all mesocosms were filled with nutrient-poor, post-bloom, and sieved (3 mm mesh) fjord water. The CO₂ manipulation was carried out between 6 and 11 June ($t - 1$ to t_4), establishing 7 enhanced $p\text{CO}_2$ treatments and 2 replicated controls (no $p\text{CO}_2$ treatment). pH and approximate $p\text{CO}_2$ levels in all mesocosms on $t_8/9$ and $t_{26}/27$ are shown in Table 1 (see also Bellerby et al., this volume). To induce the development of a phytoplankton bloom, 5 μM of nitrate (NO₃), 0.3 μM of phosphate (PO₄), and 2.5 μM of silicate (Si) were added early in the morning on 20 June (t_{13}) (i.e. before the routine sampling) to all mesocosms.

Depth-integrated water samples (0–12 m) were collected in each mesocosm using Hydrobios 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). The experiment ended on 7 July (t_{30}). Sampling for NCP and CR determination ended on 5 July (t_{28}).

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. Then, two quadruple sets of bottles served for determination of

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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 ($1 \times 10^4 - 2 \times 10^4$ 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 data). 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 day and every 4 day, respectively, between $t - 1$ and $t7$ and between $t12$ and $t28$. BOD bottles for NCP measurement were incubated for 24 h at a mooring site which was located about 300 m from the mesocosms. The incubation was 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 ($t6$). The dark BOD bottles used for the determination of CR measurement were incubated at the in situ mooring site until 18 June ($t11$) and in a laboratory incubator from 19 June ($t12$) due to logistic constraints. The incubation temperature was adjusted to the mean water temperature in the top 12 m on the day of sampling (2–4 °C). Preliminary measurements of CR with Kongsfjorden samples did not detect statistically significant change in DO during 24 h incubations 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 (Titrand888). 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 \pm standard error: $\mu\text{mol O}_2 l^{-1} d^{-1}$).

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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: (1) phase 1: end of CO_2 manipulation until nutrient addition (t_4 to t_{13}), (2) phase 2: nutrient addition until the second chlorophyll minimum (t_{14} to t_{21}), (3) phase 3: the second chlorophyll minimum until the end of this study (t_{22} to t_{28}), (4) phase 2+3 (t_{14} to t_{28}), and (5) whole period (t_4 to t_{28}). 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 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

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0.21 $\mu\text{g l}^{-1}$ on t_0 (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 similar in all mesocosms (coefficient of variation: 0 to 6 %), and increased gradually during the experiment (2.7 to 5.5 °C; Schulz et al., 2012).

Nutrient concentrations remained low in all mesocosms until the nutrient addition on t_{13} (Schulz et al., 2012). After the addition of nutrients, the cumulative nutrient consumption of NO_3 and PO_4 was higher in higher $p\text{CO}_2$ mesocosms from t_{17} to t_{22} , and 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 $\mu\text{g l}^{-1}$ (t_0 to t_{30}) and increased during the experiment (Riebesell et al., 2012). Peaks of Chl-*a* were observed 3 times in all mesocosms, once before the nutrient addition (t_8 , range: 0.5–0.9 $\mu\text{g l}^{-1}$) and twice after the nutrient addition (t_{19} and t_{28} , range: 0.3–1.0 $\mu\text{g l}^{-1}$ and 0.6–1.8 $\mu\text{g l}^{-1}$, respectively). The Chl-*a* concentration was higher at elevated $p\text{CO}_2$ at the second peak, whereas it was lower at elevated $p\text{CO}_2$ levels at the third peak.

GCP ranged from -0.5 ± 1.0 to $11.2 \pm 2.3 \mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$ between $t - 1$ and t_{28} (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 (t_{24} or t_{28}). There were a few exceptions: the smallest GCP was observed after the nutrient addition (t_{16}) in M6, and the highest value was observed before the nutrient addition (t_{12}) 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 $p\text{CO}_2$ on t_{24} ($-0.008 \pm 0.002 \mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1} \mu\text{atm}^{-1}$, $P < 0.05$).

The extent of temporal variation of CR (-5.6 to $0.25 \mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$) was about half of that of GCP during the experiment (Fig. 1). The positive CR measured in M2 on t_7 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

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in M5, M6, M8, and M9. Linear regression analysis detected no significant relationship between CR and $p\text{CO}_2$ 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 7 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 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 $p\text{CO}_2$ level. Linear regression analysis detected a significant decrease of NCP with increase of $p\text{CO}_2$ level on $t24$ and $t26$ (slope \pm se: -0.008 ± 0.003 and $-0.008 \pm 0.001 \mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1} \mu\text{atm}^{-1}$ 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 used as the control. Provided that the periods during which the cumulative values were calculated are different between phase 1 (10 days) and phase 2+3 (15 days), the proportion of the cumulative NCP and GCP after the nutrient addition compared to the whole period tended to be higher (53% to 85% and 56% to 95%, respectively). The cumulative CR after the nutrient addition corresponded to 51% to 66% of the whole period.

A linear regression describes the $p\text{CO}_2$ dependent decrease of cumulative NCP during phase 3 (slope \pm se: $-0.05 \pm 0.01 \mu\text{mol O}_2 \text{ l}^{-1} \mu\text{atm}^{-1}$, $n = 9$, F-test, $P = 0.001$) and during phase 2+3 (slope \pm se: $-0.04 \pm 0.01 \mu\text{mol O}_2 \text{ l}^{-1} \mu\text{atm}^{-1}$, $n = 9$, F-test, $P = 0.005$). The cumulative NCP slightly increased with increasing $p\text{CO}_2$ during phases 1 and 2, although the regression slope was not significant ($P > 0.05$). The relationship between cumulative NCP and $p\text{CO}_2$ during the whole period was statistically negative

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(F-test, $P = 0.02$) only when the data from M7 was not included in the analysis. The relationship between CR and $p\text{CO}_2$ was always insignificant (F-test, $P > 0.05$). The cumulative GCP significantly decreased with increasing $p\text{CO}_2$ during phase 3 (slope \pm se: $-0.05 \pm 0.01 \mu\text{mol O}_2 \text{ l}^{-1} \mu\text{atm}^{-1}$, $n = 9$, F-test, $P < 0.001$) and during phase 2+3 (slope \pm se: $-0.04 \pm 0.01 \mu\text{mol O}_2 \text{ l}^{-1} \mu\text{atm}^{-1}$, $n = 9$, F-test, $P = 0.019$).

The cumulative consumption of NO_3 and PO_4 with increasing $p\text{CO}_2$, 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 $t28$ (phases 2 and 3), the cumulative consumption of NO_3 and PO_4 was respectively similar between 9 mesocosms ($5.3\text{--}5.5 \mu\text{mol N l}^{-1}$, $0.32\text{--}0.38 \mu\text{mol P l}^{-1}$), 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, 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 6.5 and 1 to 94, respectively, during phase 2 and -2.7 to 18 and -39 to 326, respectively, during phase 3 (Fig. 3). The negative ratios were due to the negative cumulative NCP in M9 during phase 3. The $p\text{CO}_2$ dependent decrease in ratio of cumulative NCP to cumulative consumption of NO_3 and PO_4 was detected during phase 3 (slope \pm se: $-0.02 \pm 0.01 \mu\text{mol C } \mu\text{mol N}^{-1} \mu\text{atm}^{-1}$, $n=9$, F-test, $P = 0.005$; slope \pm se: $-0.32 \pm 0.08 \mu\text{mol C } \mu\text{mol P}^{-1} \mu\text{atm}^{-1}$, $n = 9$, F-test, $P = 0.007$, respectively) and during phase 2+3 (slope \pm se: $-0.007 \pm 0.001 \mu\text{mol C } \mu\text{mol N}^{-1} \mu\text{atm}^{-1}$, $n = 9$, F-test, $P = 0.005$; slope \pm se: $-0.11 \pm 0.03 \mu\text{mol C } \mu\text{mol P}^{-1} \mu\text{atm}^{-1}$, $n = 9$, F-test, $P = 0.012$, respectively).

4 Discussion

This experiment was set up as a gradient of $p\text{CO}_2$ levels with a range of 185 to $1420 \mu\text{atm}$ on $t8/9$ (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 nutrient enrichment was performed during a period of increasing sea-water temperature in all mesocosms (total increase: 3.6 to 3.9°C). 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 $p\text{CO}_2$ set up at the start of the experiment, overridden with a gradual increase of water temperature throughout the experiment and a nutrient enrichment on *t*13 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 $p\text{CO}_2$ after nutrient addition during the period of the second chlorophyll 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 $p\text{CO}_2$. As a result, the cumulative gross community production (the difference between NCP and CR) significantly decreased with increasing $p\text{CO}_2$ level during phase 3. While the nutrient addition on *t*13 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 $p\text{CO}_2$ during phase 3, suggesting alterations of the stoichiometric C : N and C : P uptake by the plankton community in response to increasing $p\text{CO}_2$.

In this experiment NCP was determined based on three different methods: temporal changes of total carbon (C_T) concentration (hereafter, C_T -NCP) (Silyakova et al., 2012),

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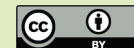
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net ^{13}C -POC production (hereafter, ^{13}C -NCP) (de Kluijver et al., 2012), and net oxygen production in incubation bottles (hereafter, O_2 -NCP) (this study). Conceptually these methods are considered to measure the process of NCP, however there are some differences in practice (see 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 highly correlated ($r = 0.785\text{--}0.976$, $P < 0.05$) 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 using ^{14}C measured 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 $p\text{CO}_2$ were somewhat different between the three measurements: (1) insignificant responses of O_2 -NCP with increasing $p\text{CO}_2$ 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 $p\text{CO}_2$ during 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 $p\text{CO}_2$ tended to be positive but was statistically insignificant. Moreover the ratio of cumulative O_2 -NCP to NO_3 and PO_4 with increasing $p\text{CO}_2$ was significant during phase 3 but the ratio of

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cumulative C_T -NCP to NO_3 and PO_4 was insignificant with increasing pCO_2 (Fig. 3; Silyakova et al., 2012).

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 and 3, O_2 -NCP was measured every second day, while C_T -NCP and ^{13}C -NCP were measured every day (except on t_{26} and t_{28} 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 and that 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 (see also Engel et al., 2012). However, unless the irradiance was significantly different between the mesocosm site and the mooring site only during phase 2, it is difficult to explain why the 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. 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. While the photosynthetic quotient was assumed to be 1, it generally varies in a range of 1.2 to 1.8 (Laws, 1991). It is possible that the photosynthetic quotient is a function of the nutrient concentration (Williams et al., 1979). In addition, an application of a

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constant photosynthetic quotient to all $p\text{CO}_2$ 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 $p\text{CO}_2$ remains to be clarified. A significant increase of C_T -NCP and an insignificant response of O_2 -NCP with increasing $p\text{CO}_2$ have been reported from a $p\text{CO}_2$ 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 $p\text{CO}_2$ and concludes that natural phytoplankton assemblages consistently show a relatively modest increase in carbon fixation at elevated $p\text{CO}_2$ (Hendriks et al., 2010). Yoshimura et al. (2010) reported that increasing $p\text{CO}_2$ 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 chlorophyll and POC, but phytoplankton growth or production were not measured. Their results may hint at reduced NCP with increasing $p\text{CO}_2$. In the present study, even though phase 3 seems relatively short (one-third of whole experimental period), the cumulative NCP based on all three measurements showed significantly negative effect of increasing $p\text{CO}_2$ for pelagic plankton communities (Fig. 2; de Kluijver et al., 2012; Silyakova et al., 2012).

The cumulative consumption of NO_3 and PO_4 was higher at the higher levels of $p\text{CO}_2$ during phase 2 and at the lower $p\text{CO}_2$ levels during phase 3. This is in contrast with the findings of Riebesell et al. (2007) who reported higher NO_3 consumption at lower $p\text{CO}_2$ 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 $p\text{CO}_2$ levels and about 6 at the higher $p\text{CO}_2$ levels at the end of the experiment (Schulz et al.,

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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 $p\text{CO}_2$ treatments from t_{20} onward in the same experiment (Schulz et al., 2012). The mechanism(s) that caused these stoichiometric changes remains to be elucidated.

5 Yet it is evident that increasing $p\text{CO}_2$ 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 balance (NCP, CR, and GCP) of planktonic communities based on changes of DO concentration at different $p\text{CO}_2$ levels showed insignificant response of NCP during phases 1 and 2 and a significant decrease of NCP as a function of increasing $p\text{CO}_2$ during phase 3. CR was relatively stable throughout the experiment in all mesocosms. As a result, the cumulative GCP significantly decreased with increasing $p\text{CO}_2$ 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 $p\text{CO}_2$. The results suggest that elevated $p\text{CO}_2$ 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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Table 1. Average pH_T and approximate $p\text{CO}_2$ levels (μatm) on $t8/9$ and $t26/27$ during the experiment (Bellerby et al., 2012).

Mesocosm	$t8/9$		$t26/27$	
	pH_T	$p\text{CO}_2$	pH_T	$p\text{CO}_2$
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

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Table 2. Initial condition in the nine mesocosms. Data on t_0 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)	NO_3 ($\mu\text{mol-N l}^{-1}$)	NO_2 ($\mu\text{mol-N l}^{-1}$)	NH_4 ($\mu\text{mol-N l}^{-1}$)	PO_4 ($\mu\text{mol-P l}^{-1}$)	Si ($\mu\text{mol-Si l}^{-1}$)	DIN: PO_4	DIN: Si	Si: PO_4	Chl- <i>a</i> ($\mu\text{g l}^{-1}$)
Mean \pm 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

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

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Table 3. Correlation analysis of NCP measured with four 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 (t_8 to t_{13}), phase 2 (t_{14} to t_{21}), phase 3 (t_{22} to t_{27}), phase 2+3 (t_{14} to t_{22}), and the whole period (t_8 to t_{27}). When NCP was not measured every day, the data were linearly interpolated before cumulation. Significant coefficients of correlation were 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**

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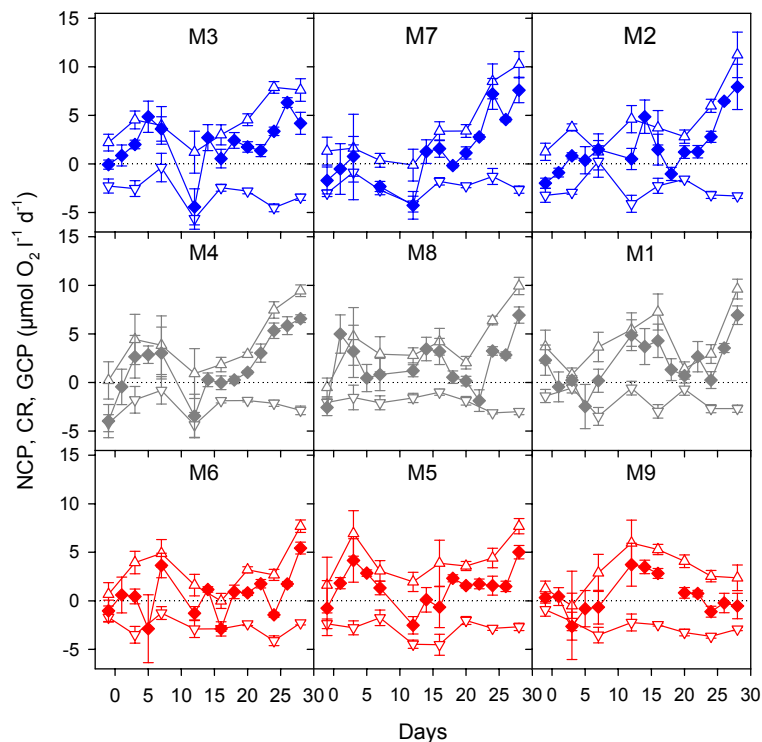


Fig. 1. Temporal changes of gross community production (open upside triangle), net community production (filled diamond), and community respiration (open downside triangle) based on changes of dissolved oxygen during incubation. Values are mean \pm standard error ($\mu\text{mol O}_2 \text{l}^{-1} \text{d}^{-1}$). The color code is as follows: blue for low $p\text{CO}_2$ treatments (M3, M7, and M2), grey for intermediate $p\text{CO}_2$ treatments (M4, M8, and M1) and red for high $p\text{CO}_2$ treatments (M6, M5, and M9).

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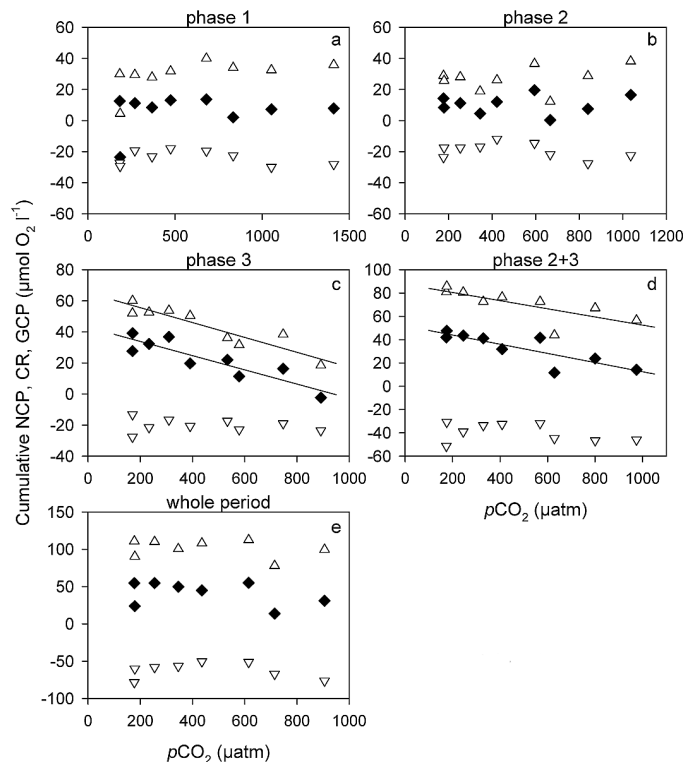


Fig. 2. Relationship between cumulative GCP (open upside triangle), NCP (filled diamond), and CR (open downside triangle) ($\mu\text{mol O}_2 \text{l}^{-1}$) vs. the mean $p\text{CO}_2$ (μatm) during phase 1 (end of CO_2 manipulation until nutrient addition: t_4 to t_{13}) (a), phase 2 (nutrient addition until the second chlorophyll minimum: t_{14} to t_{21}) (b), phase 3 (the second chlorophyll minimum until the end of this study: t_{22} to t_{28}) (c), phase 2+3 (after nutrient addition: t_{14} to t_{28}) (d), and the whole period (t_4 to t_{28}) (e). The lines indicate statistically significant relationship (F-test, $P < 0.05$).

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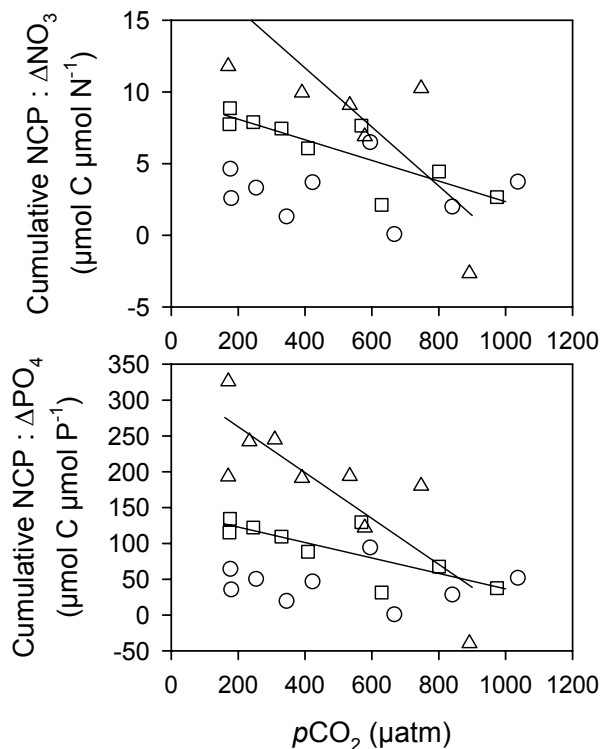


Fig. 3. Relationships between ratios of NCP ($\mu\text{mol C l}^{-1} \text{d}^{-1}$) to cumulative consumption of NO_3 ($\mu\text{mol N l}^{-1}$) and PO_4 ($\mu\text{mol P l}^{-1}$) vs. the mean $p\text{CO}_2$ (μatm) during phase 2 (nutrient addition until the second chlorophyll minimum: t_{14} to t_{21}) (circle), phase 3 (the second chlorophyll minimum until the end of this study: t_{22} to t_{28}) (triangle), and phase 2+3 (after nutrient addition: t_{14} to t_{28}) (square). NCP values based on changes of dissolved oxygen concentration were converted to carbon unit under an assumption of photosynthetic quotient of 1. The lines indicate statistically significant relationship (F-test, $P < 0.05$).

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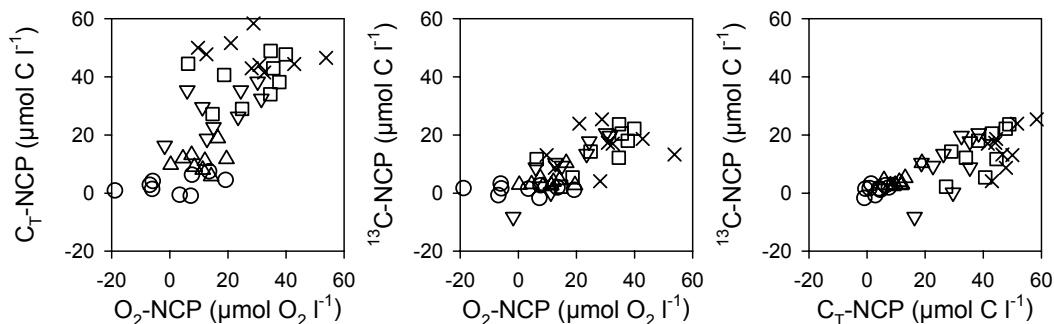


Fig. 4. Comparison of NCP measured with four different methods: temporal changes of total carbon concentration (hereafter, C_T -NCP) (Silyakova et al., 2012), net ^{13}C -POC production (hereafter, ^{13}C -NCP) (de Kluijver et al., 2012), and net oxygen production in incubation bottles (hereafter, O_2 -NCP) (this study). The data were cumulated for each period: phase 1 (t_8 to t_{13} ; circle), phase 2 (t_{14} to t_{21} ; upward triangle), phase 3 (t_{22} to t_{27} ; downward triangle), phase 2+3 (t_{14} to t_{22} ; square), and the whole period (t_8 to t_{27} ; cross). When NCP was not measured every day, the data were linearly interpolated before cumulation. See also Table 3.

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