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CO_2 increases ^{14}C-primary production in an Arctic plankton community

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Abstract

Responses to ocean acidification in plankton communities were studied during a CO_2-enrichment experiment in the Arctic Ocean, accomplished from June to July 2010 in Kongsfjorden, Svalbard (78°56, 2′ N, 11°53, 6′ E). Enclosed in 9 mesocosms (volume: 43.9–47.6 m^3), plankton was exposed to CO_2 concentrations, ranging from glacial to projected mid-next-century levels. Fertilization with inorganic nutrients at day 13 of the experiment supported the accumulation of phytoplankton biomass, as indicated by two periods of high Chl *a* concentration.

This study tested for CO_2 sensitivities in primary production (PP) of particulate organic carbon (PP_{POC}) and of dissolved organic carbon (PP_{DOC}). Therefore, ^{14}C-bottle incubations (24 h) of mesocosm samples were performed at 1 m depth receiving about 60 % of incoming radiation. PP for all mesocosms averaged 8.06 ± 3.64 µmol C l^{-1} d^{-1} and was slightly higher than in the outside fjord system. Comparison between mesocosms revealed significantly higher PP_{POC} at elevated compared to low pCO_2 after nutrient addition. PP_{DOC} was significantly higher in CO_2 enriched mesocosms before as well as after nutrient addition, suggesting that CO_2 had a direct influence on DOC production. DOC concentrations inside the mesocosms increased before nutrient addition and more in high CO_2 mesocosms. After addition of nutrients, however, further DOC accumulation was negligible and not significantly different between treatments, indicating rapid utilization of freshly produced DOC. Bacterial biomass production (BP) was coupled to PP in all treatments, indicating that 3.5 ± 1.9 % of PP, or 21.6 ± 12.5 % of PP_{DOC} provided sufficient carbon for synthesis of bacterial biomass. The response of ^{14}C-based PP rates to CO_2 enrichment was at odds with O_2-based net community production (NCP) rates that were also determined during this study, albeit at lower light level. We conclude that the enhanced release of labile DOC during autotrophic production at high CO_2 exceedingly stimulated activities of heterotrophic microorganisms. As a consequence, increased PP induced less NCP, as suggested earlier for carbon limited microbial systems in the Arctic.

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1 Introduction

The Arctic Ocean is predicted to be among the most affected marine ecosystems with respect to consequences of anthropogenic emissions of carbon dioxide (CO_2), such as ocean acidification and warming (Anisimov et al., 2007; Steinacher et al., 2009). The Kongsfjord is situated at the west coast of Spitsbergen as part of the Arctic archipelagos Svalbard. The Kongsfjord is a relatively well-studied system, compared to other areas in the Arctic, as several research stations are located in the village of Ny Ålesund. A review by Hop et al. (2002) provides a compilation of current knowledge obtained for this pristine ecosystem. A total of 148 taxa have been reported for the phytoplankton community at Kongsfjorden and showed the numerical dominance of diatoms and dinoflagellates (Eilertsen et al., 1989; Hasle and Heimdal, 1998; Keck et al., 1999; Wiktor, 1999). Primary production (PP) in Kongsfjord was determined during several field studies, focusing mainly on the spring period (Piwosz et al., 2009; Rokkan and Seuthe, 2010; Hodal et al., 2011) when availability of nutrients and light after the polar night support a substantial fraction of the annual PP (Sakshaug, 2004).

Primary production is based on CO_2 as the main substrate, and since the CO_2-binding enzyme RuBisCO has a low affinity for its substrate (Badger et al., 1998), an increase in seawater pCO_2 was hypothesized to stimulate phytoplankton PP (Riebesell et al., 2000; Schippers et al., 2004; Rost et al., 2008). The impact of increased pCO_2 on PP has been investigated theoretically as well as experimentally. Some authors report small, if any, effects (Clark and Flynn, 2000; Tortell et al., 2002), whereas others document a clear increase in PP with increasing pCO_2 (Hein and Sand-Jensen, 1997; Schippers et al., 2004; Riebesell et al., 2007). The effect of seawater carbonate chemistry on photosynthesis thereby depends strongly on the presence and characteristics of cellular CO_2-concentrating mechanisms (CCMs; Rost et al., 2003; Giordano et al., 2005). Phytoplankton species that are able to enhance their CO_2 supply by CCMs (Raven, 1991) may exhibit no or minimal sensitivity to CO_2 enrichment (Raven and Johnson, 1991; Rost et al., 2003; Giordano et al., 2005). Others, such as the

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coccolithophore *Emiliania huxleyi*, respond to CO_2 enrichment with an increase in PP (Rost and Riebesell, 2004). This suggests that the efficiency and regulation of CCMs differ among phytoplankton functional groups and species. Moreover, the capability of the phytoplankton cell to express a CCM relies on the availability of energy and nutrients (Young and Beardall, 2005; Beardall et al., 2005), and may thus be restrained under sub-optimal conditions. Changes in CO_2 availability might therefore affect competition and succession of phytoplankton species (Burkhardt et al., 2001; Rost et al., 2003; Tortell et al., 2002).

Effects of elevated pCO_2 on phytoplankton PP are of major interest for understanding global biogeochemical cycles, since PP mediates the transformation of CO_2 into organic carbon with variable stoichiometric relationships to other major elements, for example phosphorus (P) and nitrogen (N). If CO_2 assimilation is decoupled from other major elements, changes in the stoichiometric composition of organic material and altered biogeochemical pathways through the microbial food web are potential consequences. A particular increase in C assimilation during PP relative to the uptake of N and P and compared to Redfield stoichiometry of 106C:16N:1P is referred to as *carbon overconsumption* (Toggweiler, 1993). This imbalance in carbon and nutrient assimilation has been related to nutrient limitation of the cell (Wood and van Valen, 1990; Engel et al., 2002; Schartau et al., 2007) and also to enhanced CO_2 concentration (Engel, 2002; Riebesell et al., 2007; Kim et al., 2011; Borchard and Engel, 2012). Carbon overconsumption is often accompanied by a release of dissolved organic carbon (DOC) from the cell, either by passive (leakage) or active processes (exsudation) (Fogg, 1966; Bjørnsen, 1988; Engel et al., 2004a, b; López-Sandoval et al., 2011). The extracellular release of DOC is a normal function of algal cells (Fogg, 1966) and represents with ~3–40 % (percentage of extracellular release, PER) a significant fraction of PP (Myklestad, 1977; Mague et al., 1980; Baines and Pace, 1991). Factors influencing PP, such as light and temperature, were shown to also affect primary production of DOC (PP_{DOC}) (Zlotnik and Dubinsky, 1989; Baines and Pace, 1991; Engel et al., 2011).

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PP_{DOC} is the major source of labile and semi-labile DOC in the ocean, and drives the microbial loop (Azam et al., 1983), whereby DOC is either transferred to higher trophic levels, or respired back to CO_2 (Ducklow et al., 1986). Microbial mineralization thus represents an important loss for DOC globally (Williams, 2000; Hansell et al., 2009). Under a "malfunctioning" of the microbial loop, DOC accumulates (Thingstad et al., 1997) and may be subject to abiotic aggregation into gel particles, known as transparent exopolymer particles (TEP) (Alldredge et al., 1995). TEP formation thereby represents a repartitioning of dissolved organic carbon into particles without loss of mass (Engel et al., 2004b). An increase in TEP-C may raise C : N or C : P ratios in particulate organic matter, potentially providing an enhanced sinking flux of carbon to depth (Schneider et al., 2004).

In Arctic ecosystems, heterotrophic microbes are often limited by the amount of labile DOC (Kirchman et al., 2009) and co-limited by nutrients (Cuevas et al., 2011). An increased input of labile DOC (glucose) was rapidly consumed by bacteria and other osmotrophs during an earlier mesocosm experiment at Svalbard, resulting in enhanced competition for inorganic nutrients between phyto- and bacterioplankton, and in an overall reduction of autotrophic productivity of the system (Thingstad et al., 2008). A hypothesis that came out of the Thingstad et al. (2008)-study was that stimulation of the microbial loop in Arctic waters by increased PP_{DOC} under high pCO_2 may result in a counterintuitive carbon cycling, i.e. "more organic carbon gives less organic carbon", and not necessarily enhance carbon export.

In order to address potential consequences of the ongoing seawater pCO_2 increase in pelagic ecosystems in the Arctic, a mesocosm study was conducted in the framework of the European Project on Ocean Acidification (EPOCA). Here, we report on sensitivities in primary production (PP) to increasing pCO_2, for both the production of POC and of DOC, using ^{14}C-bottle incubations (24 h) of mesocosm samples at the 60 % light level. PP was compared to changes in the concentration of DOC and to the secondary production of bacterial biomass in order to infer the fate of PP produced at different pCO_2 in this Arctic ecosystem.

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2 Material and methods

2.1 Sampling and incubation

The mesocosm experiment was conducted in Kongsfjorden, Northern Spitsbergen (78°56, 2′ N, 11°53, 6′ E) from June to July 2010 as a part of the European Project on Ocean Acidification (EPOCA). Detailed information about the set-up of the experiment, the CO_2-perturbation of seawater within the mesocosms and sampling procedures is given elsewhere in this issue (Schulz et al., 2012; Czerny et al., 2012; Bellerby et al., 2012; Silyakova et al., 2012). Briefly, nine mesocosms were deployed close to the coast of Spitsbergen near Ny-Ålesund on 28 May 2010 (day 10). All mesocosms enclosed nutrient-poor, post-bloom fjord water. The CO_2 manipulation was carried out between 3 and 6 June (day 1 to day 4) by the addition of different quantities of pre-filtered (55 µm) CO_2-enriched natural water from the fjord (Fig. 1). Two untreated mesocosms served as controls, while 7 mesocosms were manipulated to establish elevated pCO_2 in a range of ~170–1100 µatm. Ten days after CO_2 enrichment, nutrients were added to yield concentrations of 5 µmol l^{-1} NO_3, 0.32 µmol l^{-1} PO_4, and 2.5 µmol l^{-1} Si to induce the development of a phytoplankton bloom.

Sampling of seawater from the mesocosms was conducted with a depth-integrated water sampler (Hydro-Bios). The sampler is equipped with a motor and continuously collects water (5 l volume) while being lowered from surface to 12 m depth. Samples were collected in the morning (9 a.m.–11 a.m.).

2.2 Chlorophyll *a*

Concentration of Chlorophyll *a* (Chl *a*) in the mesocosms and in the fjord was determined from 500 ml seawater filtered onto glass fibre filters (Whatman GF/F 25 mm, pre-combusted 450° C for 5 h) by low vacuum filtration (< 200 mbar) and stored frozen at −20° C. Chl *a* was determined fluorometrically according to Welschmeyer (1994) using a Turner fluorometer 10-AU (Turner BioSystems, CA, USA). Changes in Chl *a*

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concentration (range: ~1–3 µg l^{-1}) during the study indicated the development of one smaller phytoplankton bloom before addition of nutrients to the mesocosms on day 13, as well as two bloom peaks after nutrient addition (Fig. 1). For more information see Schulz et al. (2012).

2.3 ^{14}C primary production

Primary production was determined by the ^{14}C method, according to Steemann Nielsen (1952) and Gargas (1975). Polycarbonate bottles (NUNC Easyflask, 75 cm^2) were filled with 260 ml pre-filtered (mesh size 200 µm) sample and spiked with approximately 8 µCi $NaH^{14}CO_3^-$ (Perkin Elmer, Norway). Standardization of added activity was made by removing an aliquot of 200 µl from the incubation bottle and transferring it to a 5 ml scintillation vial with 200 µl of 2M NaOH. Triplicate light incubations, and one dark incubation were made for each of the 9 mesocosms and for the fjord every other day of the experiment on days 1, 2, 5, 7, 10, 12, 14, 16, 18, 20, 22, 24, 26, and 28. Samples were incubated for 24 h in situ at 1 m depth close to the Marine Lab. Dark uptake was measured in black taped bottles. Incubations were stopped by filtration of a 50 or 100 ml sub-sample onto 0.4 µm polycarbonate filters (Nuclepore). Primary production of DOC (PP_{DOC}) was determined from the filtrate, while particulate material on the filter was used to determine primary production of POC (PP_{POC}). All filters were rinsed with 10 ml sterile filtered (<0.2 µm) seawater, and then acidified with 250 µl 2N HCl in order to remove inorganic carbon (Descy et al., 2002). Filters were transferred into 5 ml scintillation vials, 200 µl of 2N NaOH, and 4 ml scintillation cocktail (Ultima Gold AB) were added and samples were counted in a Liquid Scintillation Analyser (Packard Tri Carb, model 1900 A) the next day.

For determination of PP_{DOC}, 4 ml of filtrate was transferred to 20 ml scintillation vials, acidified (100 µl 1N HCl) and left open in the fume hood in order to remove inorganic carbon. Then, 800 µl of 2M NaOH and 15 ml scintillation cocktail were added before counting on the next day.

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Calculations of PP were done according to Gargas (1975). Implemented concentrations of total inorganic carbon for the different mesocosms and the fjord are given in Silyakova et al. (2012).

2.4 Light and temperature during the incubations

At the incubation site light conditions were determined regularly in the afternoon (between 3 and 4 p.m.) throughout the experiment from day 1 onwards by the use of a lightmeter (LiCor 250A) equipped with a LI-COR Quantum Sensor (above incubations in air) and a LI-COR Underwater Quantum Sensor (at incubation site in water). From d7 onwards, additional light and temperature measurements were accomplished at 1 m depth next to the incubations with the same instrument used in the mesocosms (Schulz et al., 2012).

2.5 Dissolved organic carbon (DOC)

Samples for dissolved organic carbon (DOC) were collected in combusted glass ampoules after filtration through combusted GF/F filters. 20 ml samples were acidified with 100 µl of 85 % phosphoric acid and stored at 4° C in the dark until analysis. DOC samples were analysed using the high-temperature combustion method (TOC -VCSH, Shimadzu) (Qian and Mopper, 1996). A multi-point calibration curve was constituted for each day of measurement using potassium hydrogen phthalate standard, which was prepared in MilliQ water. Additionally, two reference seawater standards (Hansell laboratory, RSMAS, University of Miami) were used to determine the instrument blank. Each sample was measured in quadruplets.

2.6 Bacterial secondary production

Bacterial production (BP) was estimated from the uptake of ^{14}C-leucine during < 24 h incubations in 2 ml vials at 2° C in the dark. Duplicate incubations revealed an analytical error ≤10 %. Rates of ^{14}C-leucine incorporation were converted into BP applying a

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conversion factor of 1.5 kg C mol^{-1} leucine (Ducklow et al., 1999). For more information see Piontek et al. (2012).

2.7 Data treatment

PP measurements were determined after 24 h of incubation. Data assignment was made to the day of sampling. Missing values were calculated by linear interpolation between measurements.

Differences in data as revealed by statistical tests (t-test, ANOVA, Kolmogorov-Smirnov test) were accepted as significant for $p < 0.05$. Average values for total concentrations are given by their arithmetic mean, averages for ratios by their geometric mean.

For identifying differences between the pCO_2 treatments, absolute deviations ($AD_{(xi)}$) were calculated by subtracting from each observation (X_i) the arithmetic mean of all observations ($\overline{x}$) at a specific time-point (t).

$$AD_{(x)} = X_i - \overline{x} \quad (1)$$

Mean deviations (MD) were calculated for each mesocosm and for the fjord according to:

$$MD = \frac{1}{N} \sum_{1}^{N} AD_x \quad (2)$$

With N being the number of observation and expressed as a relative value (%).

Calculations, statistical tests and illustration of the data were performed with the software packages Microsoft Office Excel 2010 and Sigma Plot 12.0 (Systat).

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3 Results

3.1 Light and temperature conditions

Seawater temperature increased during the mesocosm study from 2.0° C at the beginning of June to 5.2° C at the end of the study. No temperature differences were observed among the nine mesocosms, and between the mesocosms and the fjord. At the site and depth of ^{14}C-incubations, temperature was on average 1–1.5° C higher than at the location of mesocosm deployment.

Photosynthetically active radiation (PAR), for practical reasons defined as radiation in the wavelength range 400–700 nm, ranged between 130 and 800 µmol photons m^{-2} s^{-1} at 1 m depth, representing cloudy and clear sky, respectively. PAR at the incubation site (1 m) was not significantly different from the 1 m depth horizon in the mesocosms (p = 0.09) and corresponded to approximately 60 % of surface light for most time (range: 45–85 %) (Fig. 2).

3.2 Primary production of organic carbon

Primary production ($PP = PP_{POC} + PP_{DOC}$) during the full time of the experiment (d5–d28) averaged 8.06 ± 3.64 µmol C l^{-1} d^{-1} in all mesocosm samples and was slightly higher than in the fjord samples with 6.49 ± 2.54 µmol C l^{-1} d^{-1} (Table 1). PP varied significantly between mesocosm samples (ANOVA; $p < 0.001$), with highest rates observed in the high CO_2/low pH mesocosm (M9), and lowest rates in the low CO_2/high pH mesocosm (M7).

PP in the mesocosms, as well as in the fjord samples, was not significantly related to chlorophyll *a* (Chl *a*) concentration (Fig. 3). Yet, [PP] : [Chl *a*] (µmol C d^{-1}: µg Chl *a*) ratios were significantly different between mesocosms (ANOVA, $p < 0.05$), yielding highest time-averaged [PP] : [Chl *a*] ratios (range: 9.5–11.0 µmol C $µg^{-1}$ Chl *a* d^{-1}) for the high CO_2 mesocosms (M9, M5, M6) as well as for the medium CO_2 mesocosm M8 (Table 1). Lowest time-averaged [PP] : [Chl *a*] ratios were determined for

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the low CO_2 mesocosm M7 and for the medium CO_2 mesocosm M4 (range: 4.2–4.6 µmol C µg^{-1} Chl *a* d^{-1}). In all other mesocosms and the fjord, [PP] : [Chl *a*] ranged between 6.5 and 8.7 µmol C µg^{-1} Chl *a* d^{-1}. PP in all samples was also not directly related to PAR measured at the incubation site (1 m depth).

We observed that PP at the first day of incubation (day 1), i.e. after first salt addition but before pCO_2 perturbation, was not equal among the samples collected from the mesocosms. While mesocosms 1–3 had a similarly high primary production of POC (PP_{POC}) in range of 4.1–6.1 µmol C l^{-1} d^{-1}, comparable to PP_{POC} observed in the fjord sample, mesocosm 4–9 clearly showed lower productivity. This difference in the initial conditions between mesocosms disappeared during the following days and was already absent at day 2 (Table 2). Time-averaged PP_{POC} in mesocosm samples ranged from 3.45 ± 1.69 µmol C l^{-1} d^{-1} (M7) to 9.41 ± 3.51 µmol C l^{-1} d^{-1} (M9) and encompassed PP_{POC} observed in the fjord (5.76 ± 2.52 µmol C l^{-1} d^{-1}; Table 1). The rate of primary production of DOC (PP_{DOC}) in the mesocosms ranged from 0.85 ± 0.39 µmol C l^{-1} d^{-1} (M7) to 1.77 ± 0.78 µmol C l^{-1} d^{-1} (M9), compared to 0.79 ± 0.38 µmol C l^{-1} d^{-1} for the fjord system.

PP_{POC} as well as PP_{DOC} increased with increasing phytoplankton biomass after nutrient addition on day 13 (Tables 2, 3). Response of PP_{POC} to nutrient addition was clearly faster in the high pCO_2 mesocosms; i.e. between day 12 and day 16 PP_{POC} increased by 74 % in the high CO_2 mesocosms (M5, M6, M9), by 48 % in the medium (M4,M8,M1) and by only 21 % in the low CO_2 mesocosms (M2, M3, M7).

Based on ^{14}C-primary production rates, the cumulative production of POC and DOC was calculated from the sum of daily production rates (Fig. 4a, b). Values for days when measurements were not taken were calculated by linear interpolation between adjacent data points. For the total period of the experiment (day 5–day 28), a cumulative PP_{POC} between 84 and 174µmol C l^{-1} was obtained for the three lowest, between 94–203 µmol C l^{-1} for the three medium, and between 196–222 µmol C l^{-1} for the three highest pCO_2 mesocosms. For comparison, cumulative PP_{POC} in the fjord was 138 µmol C l^{-1} and therewith in the range of data observed in mesocosms at

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similar low pCO_2 levels. Cumulative PP_{POC} of the autotrophic community clearly increased with CO_2 concentration ($p < 0.01$), while the variability between mesocosms decreased. Hence, highest variability of cumulative POC production was observed at the lower end of the pCO_2 range (Fig. 4a). The difference in cumulative PP_{POC} between low and high CO_2 treatments covered a relatively broad range, i.e. 29 µmol C l^{-1} comparing M3 and M5, or 138 µmol C l^{-1} comparing M7 and M9, equivalent to an CO_2 induced increase by 10–60 %.

The cumulative production (day 5–day 28) of DOC was estimated in a similar way and ranged between 19 and 36 µmol C l^{-1} in the low, 20–34 µmol C l^{-1} in the medium, and 32–40 µmol C l^{-1} in the high pCO_2 mesocosms (Fig. 4b). Cumulative PP_{DOC} in the fjord, was estimated to be 19 µmol C l^{-1}, and thus at the lower end of values observed in the mesocosms. Similar to cumulative PP_{POC}, cumulative PP_{DOC} increased significantly with CO_2 concentration ($p < 0.05$). Maximum difference in potential cumulative PP_{DOC} was observed between M9 (high pCO_2) and M7 (low pCO_2) with 21 µmol C l^{-1}, equivalent to an increase by about 50 %. However, variability of cumulative PP_{DOC} was high at the lower pCO_2 range also; i.e. the low pCO_2 mesocosm M3 yielded about 11 % higher cumulative PP_{DOC} than the high CO_2 treatments M5 and M6.

PP_{DOC} increased after nutrient addition, following the general course of PP (Table 1). The percentage of extracellular organic carbon release (PER); calculated as $PER\ (\%) = PP_{DOC}/(PP_{DOC} + PP_{POC}) \times 100$, decreased immediately after nutrient addition in all mesocosms (Fig. 5). Until day 12, PER ranged between 21 and 23 %. After nutrient addition, PER was 17.7 ± 6 % in the three low pCO_2 mesocosms (M2, M3, M7,) and decreased with increasing pCO_2 to 13.8 ± 4.7 % in the three high CO_2 mesocosms (M5, M6, M9) (t-test, $p < 0.05$). Thus, under nutrient replete conditions cells at higher pCO_2 exuded relatively less organic carbon than cells at low pCO_2. This, in turn, suggests that an even higher proportion of PP was used for PP_{POC} after nutrient addition in the high CO_2 mesocosms. However, due to absolute higher PP, the total amount of DOC released by autotrophs was still higher at high CO_2 despite of lower PER.

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In the fjord, PER was 14 ± 8 % until day 12, and also decreased – not impacted by nutrient addition – to 11 % by day 14. Thus, nutrient addition was not the sole factor potentially responsible for the PER decrease after day 12. Another factor that has often been reported to increase exudation of organic carbon is light (Zlotnik and Dubinsky, 1989). During this study, we also observed a moderate increase in PER with light intensity (Fig. 6, $p < 0.05$). Following this argument, light was likely not responsible for the reduction of PER observed on day 14, because PAR at that day was 325 ± 164 µmol photons m^{-2} s^{-1} and rather above than below the PAR of previous days. Temperature has also been suggested to affect exudation, yielding higher PER at higher temperatures (Zlotnik and Dubinsky, 1989; Moran et al., 2006; Engel et al., 2011). However, since temperature increased in the course of the mesocosms study, this also would rather favor than suppress PER. We do not known if the decrease in PER in fjord and in mesocosms samples around day 14 were related, or just coincided. Therefore, we cannot exclude a potential co-effect on PER besides nutrient availability.

In order to better understand the variability of data obtained during this mesocosm experiment, mean deviations (MD) for PP_{POC} and PP_{DOC} were calculated according to Eq. (2); i.e. the arithmetic mean of all deviations of one mesocosm and of the fjord with respect to the average of all mesocosms. Three time intervals were considered, i.e. total period of CO_2 treatment (day 5–day 28), before nutrient addition (day 5–day 12) and after nutrient addition (day 14–day 28). The MD-values indicate how much each CO_2-treatment and the fjord deviated from the average development of all mesocosms.

For PP_{POC}, the three highest CO_2 mesocosms showed positive MD during all periods (Fig. 7a–c). This was most pronounced for the period after nutrient addition, when MD of PP_{POC} in M9 was 55 % higher than average. Again, relatively large differences were observed among the low CO_2 mesocosms, where MD-PP_{POC} ranged from −46 % to +5 %. For the total period, a significant positive relationship was observed between MD-PP_{POC} and average pCO_2 ($p < 0.05$) (Fig. 7a). This relationship was not seen during the time before nutrient addition, but clearly observed thereafter ($p < 0.05$) (Fig. 7b, c).

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For PP_{DOC}, the relationships of MD to average pCO_2 during the respective periods were significant before as well as after nutrient addition (Fig. 8a–c). Largest negative values for MD-PP_{DOC} were observed for the period after nutrient addition for the fjord (172 µatm pCO_2; −57 %) and for M7 (175 µatm pCO_2; −57 %). Largest positive values for MD-PP_{DOC} again were determined in samples of M9 (974 µatm pCO_2; +52 %).

3.3 DOC concentration

Considerable day-to-day variations of DOC concentrations of up to 30 % were observed on some days in all mesocosms and in the fjord samples. These variations may partly be attributed to contamination of samples during sample collection and transport as well as during instrument deployment inside the mesocosms. We assume that this methodological error occurred randomly and was not discriminating between CO_2 treatments. Thus, although the absolute concentration of DOC may have been defective on individual days, averaged and time-averaged differences in DOC concentration between treatments should be reliable. Concentrations of DOC determined during this study were lower than the annual range of 100–244 µmol C l^{-1} determined for the Kongsfjord by Iversen and Seuthe (2011), but comparable to data received for the Arctic Ocean by Cuevas et al. (2011), i.e. 61–84 µmol l^{-1}, and by Myklestad and Boersheim (2007), i.e. 87 ± 16 µmol C l^{-1}.

Average DOC concentration in the mesocosm at day 1 was 76 ± 3 µmol C l^{-1}, and slightly higher than observed in the fjord at that day (71 µmol C l^{-1}). DOC concentration increased significantly between day 4 and day 13 in all mesocosms, yielding a rate of 1.64 ± 5.4 µmol C l^{-1} d^{-1} ($p < 0.01$) (Fig. 9), equivalent to 15 ± 5.4 µmol C l^{-1} for this period. DOC accumulation before nutrient addition was thus comparable to cumulative PP_{DOC} (range day 12: 8–13 µmol C l^{-1}). For the period after nutrient addition, no further accumulation of DOC was observed, and values averaged 91 ± 7 µmol C l^{-1}. The absence of DOC accumulation during the bloom periods was in contrast to the

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potential production of DOC by PP_{DOC}, which was estimated for that period to amount 11–27 µmol C l^{-1}.

In order to identify treatment related differences, we calculated mean deviations of DOC concentration (MD-DOC) in the mesocosms. We did not include fjord samples in this analysis, because temporal variations of DOC concentration in the fjord may have been due to processes other than biological activity, such as glacial melting and terrestrial melt-water run-off. The latter was at times indicated in the area of mesocosm deployment by a brownish color of surface water.

For the mesocosms, a positive correlation between MD-DOC and average pCO_2 was observed only for the period before nutrient addition ($p < 0.05$) (Fig. 10), and in accordance with increasing PP_{DOC} at higher pCO_2 observed during this period (Fig. 6b). After nutrient addition, no significant differences in MD-DOC between mesocosms were observed, despite CO_2-related differences in carbon exudation.

3.4 Primary vs. bacterial production

Primary produced organic compounds directly fuel the heterotrophic food web, amongst which bacteria are the main consumers. Bacterial production (BP) during this study ranged between 0.04 and 0.54 µmol C l^{-1} d^{-1} in the mesocosms, and between 0.10 and 0.84 µmol C l^{-1} d^{-1} in the fjord sample. Detailed information is given in Piontek et al. (2012). BP was directly related to PP considering the entire duration of the experiment (day 5–day 28) and all mesocosms ($n = 108$, $r^2 = 0.28$, $p < 0.001$) (Fig. 11). For the total period, the ratio of BP to PP in all mesocosms was 3.5 ± 1.9 %, and lower than in the fjord at the same time (6.5 ± 4.0 %). BP:PP did not differ significantly between mesocosms, nor over time (ANOVA; $p > 0.1$), and no significant influence of nutrient addition at day 13 was determined either (t-test; $p > 0.1$). However, lowest ratios were observed at highest pCO_2 (Fig. 12b).

If we assume that bacteria preferentially consumed dissolved organic compounds, a much higher ratio of BP : PP_{DOC} would be expected, ranging on average between 20 %

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and 50 % in the mesocosms (Fig. 12a). Again, fjord water outside the mesocosms showed higher ratios.

4 Discussion

During this mesocosm study, different methods have been applied to investigate the sensitivity of plankton productivity to CO_2 perturbation, including the O_2-method with bottle incubations at 4 m depth outside the mesocosms (Tanaka et al., 2012), changes in DIC concentration inside the mesocosms (Silyakova et al., 2012) and uptake of ^{13}C-labelled DIC (de Kluijver et al., 2012). This study used the classical Steeman-Nielsen ^{14}C-tracer approach (Steeman-Nielsen, 1952) to determine carbon incorporation into particulate and dissolved organic matter in bottle incubations outside of the mesocosms at 1 m depth and over a period of 24 h. The incubation period was chosen for two reasons. First, we expected an overall low productivity of the Arctic phytoplankton community at low temperatures, low biomass density, and low nutrient concentrations at the start of the experiment. Under these conditions, short-term incubations of only a few hours may underestimate PP because carbon assimilation by algal cells may be too low to discriminate against ^{14}C adsorption as determined in blank dark incubation. Another reason was to cover the daily photoperiod for the cells. Since the experiment was conducted at high latitude (78°56′ N) and around the time of summer solstice, light availability was high (>100 µmol photons m^{-2} s^{-1}) even during midnight (Schulz et al., 2012), and supported autotrophic production over a 24 h period. Other studies in the Svalbard area therefore also used 24 h incubations for measurements of PP when working with the ^{14}C-tracer (Iversen and Seuthe, 2011; Hodal et al., 2011).

The ^{14}C-tracer approach has the advantage of being highly sensitive, and thus ideally suited for fieldwork, when there is low photosynthetic activity. One drawback of this method, however, is that PP rates determined this way cannot be attributed precisely to either net or gross primary production (Peterson, 1980; Dring and Jewson, 1982). Short-term incubations are expected to provide gross rates of C-fixation, whereas

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longer incubations tend to measure net photosynthesis. This, however, strongly depends on the productivity and activity of the microbial community included. Release of freshly assimilated carbon into the pool of DOM has a time scale of several hours, because of equilibration of the tracer with the DOC pool and because metabolic processes of organic carbon exudation follow those of carbon fixation inside the cell.

During this study, incubations were performed at 1 m incubation depth, receiving about 60 % incoming PAR during most time of the study. For comparison, O_2 incubations were performed at 4 m depth, equivalent to 20 % PAR, whereas productivity estimates directly in the mesocosms obtained from DIC changes (Silyakova et al., 2012) or ^{13}C-incorporation (de Kluijver et al., 2012) yielded integrated values over a 12 m-water column that received 100–17 % of incoming light, with a median value of 23 % (see Fig. 2). Hence, ^{14}C-primary production rates were obtained at a relatively high light level. This level was chosen to ensure that cells would not become light limited in the course of the study. Moreover, one question to be addressed was the release of DOC by algal cells. Carbon exudation in marine phytoplankton has been reported to increase with light availability (Zlotnik and Dubinsky, 1989), and during this study we also observed the tendency of increasing PER with increasing light.

PP values obtained at 1 m depth exceeded O_2-gross community production (GCP) determined at 4 m depth by a factor of about 2, and O_2- and ΔDIC-based net community production (NCP) by a factor of 3–4. These discrepancies may be largely due to the different amount of light that cells received during the various incubations, and are comparable to differences observed for polar phytoplankton along comparable depth and light gradients, respectively (Yun et al., 2012).

However, for some periods, and particularly towards the end of the experiment, a qualitative difference between PP and NCP was observed, as NCP seemed to decrease with CO_2 (Tanaka et al., 2012), while PP clearly increased. This resulted in an apparent anti-correlation of cumulative PP as calculated from ^{14}C-data and cumulative NCP derived from O_2-consumption when considering the full period of the experiment (d4–d28) (Fig. 13). We will provide potential explanations for this observation below.

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4.1 Temporal development of primary production

The experiment started at a time when the natural autotrophic community in the Kongsfjord experienced low nutrient concentrations (Schulz et al., 2012). Until the day of nutrient addition (day 13) absolute rates of PP_{POC} and PP_{DOC} in the mesocosms were similar to rates determined in the fjord. During this time, CO_2-related differences were identified for PP_{DOC} but not for PP_{POC}. Higher exudation of $DO^{14}C$ at higher pCO_2 was in good accordance with higher accumulation of DOC.

Addition of nutrients initiated the bloom-development of phytoplankton in the mesocosms that exhibited two distinct bloom phases; a first bloom phase (day 14–day 22) with faster growth and higher abundance of phytoplankton biomass in the high CO_2 mesocosms, and a second bloom phase after day 23 with lower biomass of the autotrophic community in the higher CO_2 mesocosms and higher biomass in the lower CO_2 mesocosms (Brussaard et al., 2012; Schulz et al., 2012). The immediate response of the autotrophic community to nutrient addition was thus more pronounced in the high CO_2 mesocosms, leading to significantly higher PP_{POC}. Towards the end of the first bloom phase (i.e. day 22), nutrient concentration clearly differed between the mesocosms, yielding about 60 % higher concentrations of nitrate and phosphate at low compared to high pCO_2. Thus, during the second bloom phase PP was clearly co-impacted by lower nutrient availability in the high CO_2 mesocosms.

For PP_{POC}, our finding of increased primary production rates at high seawater pCO_2 agrees well with the ^{14}C-PP results of Egge et al. (2009) obtained during an earlier mesocosm study, as well as with laboratory studies showing PP-enhancement by CO_2 for a variety of phytoplankton species and at different light and temperature conditions (Hein and Sand-Jensen, 1997; Schippers et al., 2004; Rost et al., 2008). Moreover, the range of PP_{POC} rates determined during this study (Tables 1, 3) compares well to other measurements at the same site; Hodal et al. (2011) determined PP_{POC} rates from 4-8 µmol C l^{-1} d^{-1} for a phytoplankton community with about 1 µg Chl a l^{-1} incubated directly beneath the surface (0 m) in May in 2002.

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Variability of PP_{POC} and PP_{DOC} during this study was more pronounced at the lower CO_2 range, while rates were rather similar in the high pCO_2 range (600–1400 µatm). This finding may be related to the Michaelis-Menten type relationship between photosynthesis rate and CO_2 concentration, and to differences in the CO_2 affinity (K_m-value) between phytoplankton species (Reinfelder, 2011). Due to the higher sensitivity of photosynthesis to changes in CO_2 at the lower concentration range, the natural variability in species composition and physiology of phytoplankton likely translated into larger differences of primary production rates among the low CO_2 mesocosms compared to the high and potentially saturating CO_2 treatments.

4.2 Counterintuitive carbon cycling induced by CO_2

Interestingly, estimates of NCP gained by bottle incubations and the O_2-technique did not show an increase with CO_2 concentration during this experiment (Tanaka et al., 2012), as well as during the earlier CO_2-mesocosm study of Egge et al. (2009). During this study, estimates of carbon uptake due to PP and due to NCP were even anti-correlated (Fig. 13), suggesting that carbon and oxygen cycling in the surface ocean may be differently affected by CO_2. It has to be emphasized that the ^{14}C-technique determines something in excess of net carbon assimilation into POC and DOC. Even under high heterotrophic activities ^{14}C-primary production rates cannot become negative, as organic matter respiration by heterotrophic organisms cannot be accounted for. This, however, is included in NCP measurement based on O_2 or DIC.

Discrepancies between PP and NCP, as well as between PP and organic matter accumulation during this study were primarily observed after the addition of nutrients. Under nutrient replete conditions, two processes of counter-intuitive carbon cycling were observed: (a) high PP_{DOC} was not mirrored in high DOC concentration, and (b) NCP decreased with pCO_2 – as derived from O_2-measurements (Tanaka et al., 2012), and from DIC measurements (phase III, Silyakova et al., 2012) – whereas PP_{POC} clearly increased. How can these discrepancies be explained?

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4.2.1 (a) More PP_{DOC} – less DOC accumulation

During this study, heterotrophic activity was closely coupled to PP, as derived from bacterial production and from hydrolytic enzyme activities (Fig. 11; see also Piontek et al., 2012). Prior to the experiment, bacterial growth was limited by the availability of labile organic carbon and co-limited by nitrogen (Piontek et al., 2012). It can therefore be assumed that bacteria directly responded to the release of labile organic carbon by phytoplankton. Nutrient addition at day 13 not only provided substrate for autotrophic cells but also fueled the growing community of heterotrophic bacteria. Thus, after day 13, enhanced PP_{DOC} was likely counteracted by the growing community of heterotrophic bacteria, resulting in little accumulation of DOC.

After nutrient addition, values of PER decreased in all mesocosms. Nutrient limitation has been shown earlier to increase PER in marine phytoplankton (Myklestad, 1977; Obernosterer and Herndl, 1995; López-Sandoval et al., 2011). A reduction of PER in response to the elimination of nutrient limitation as observed during this study supports the idea of exudation being a discharge mechanisms for excess photosynthates (Wood and van Valen, 1990; Schartau et al., 2007). Nevertheless, as PP was higher at high CO_2, the absolute rate of PP_{DOC} was still higher in the high CO_2-mesocosm samples. The observation that PP_{DOC} increased with pCO_2 after nutrient addition, but DOC concentration did not, suggests that DOC was consumed to a larger extent at high pCO_2.

4.2.2 (b) Anti-correlation of PP and NCP

Higher PP_{POC} in the high CO_2 mesocosms translated into higher phytoplankton biomass directly after nutrient addition and before re-depletion of DIP and DIN. This is in accordance with our expectation, as the utilization of photosynthetic products for biomass synthesis by heterotrophic as well as by autotrophic cells depends on the availability of nitrogen and phosphorus. Data on cell abundance as determined by Flow

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Cytometry suggests that particularly fast-growing pico-autotrophic cells benefitted from nutrient addition at high pCO_2 (Brussard et al., 2012).

However, with regard to the entire study period, the maximum yield of phytoplankton biomass in the low CO_2 mesocosms exceeded the maximum biomass yield in the high CO_2 treatments, despite higher PP_{POC} in the latter. This apparent difference between autotrophic POC production and accumulation may be explained by either one, or a combination of following processes at high CO_2: (i) enhanced settling loss of phytoplankton biomass from the water column, (ii) enhanced solubilization and remineralisation of phytoplankton cells, or (iii) increased nutrient competition between auto- and heterotrophic microorganisms. (i): it has been suggested that under nutrient limiting conditions phytoplankton produce more exopolymer carbohydrates at high CO_2 (Engel, 2002; Borchard and Engel, 2012). Since exopolymer carbohydrates are important agents in coagulation processes and enhance aggregate formation, a higher export of organic matter may be inferred. However, higher export fluxes and therewith a higher loss of organic matter from the water column in the high CO_2 bags were not directly observed during this study (Czerny et al., 2012); (ii): recent studies suggest that bacterial processes such as organic matter solubilisation and hydrolysis by extracellular enzymes are enhanced by ocean acidification (Grossart et al., 2006; Piontek et al., 2010; Yamada and Suzumura, 2010; Endres et al., 2012). Higher activities of hydrolytic enzymes were observed at reduced pH also during side-experiments of this study (Piontek et al., 2012), and may have resulted in faster degradation of organic matter, including autotrophic biomass; (iii): it is well known that the release of organic substrates from phytoplankton fuels the microbial food web (Azam and Hodson, 1977; Azam et al., 1983). The higher production and release of DOC at high CO_2 likely enhanced the utilization of organic carbon, oxygen and nutrients by marine bacteria also during this study. The higher demand for nitrogen and phosphorus in marine bacteria, potentially exacerbated competition between phyto- and bacterioplankton for inorganic nutrients, and curtailed autotrophic growth. During this study, nutrient consumption directly after nutrient addition was faster in the high CO_2 mesocosms. Although more

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autotrophic biomass, as indicated from Chl *a*, was observed at higher pCO_2 initially, a much stronger phytoplankton bloom developed later during the experiment at low pCO_2 (Schulz et al., 2012). As a consequence the peak ratios of [Chl *a*] : [PON] achieved during this study were lower at high pCO_2 than at medium and low pCO_2 (data Schulz et al., 2012). This supports the idea that a higher amount of nutrients were partitioned into the heterotrophic food web.

Neither can we fully rule-out nor clearly demonstrate one of the above-mentioned processes.

However, in principle all three processes act into the direction of reduced autotrophic and increased heterotrophic production. Direct effects of lowered pH, i.e. higher activities of hydrolytic enzymes, as well as direct effects of high pCO_2, i.e. enhanced release of DOC, both stimulate the microbial loop. As a result, NCP may decrease at high pCO_2 while the microbial loop system benefits from the increased supply of labile organic carbon, and competition between phyto- and bacterioplankton for inorganic nutrients increases. Such a counterintuitive cycling of carbon, i.e. higher autotrophic carbon fixation leads to less net production of the whole community has been hypothesized for Arctic systems previously (Thingstad et al., 2008).

The Arctic Ocean at present is a net sink for atmospheric CO_2 on an annual scale (Arrigo et al., 2011), and an increase in primary production and biological CO_2 drawdown associated to the ongoing sea-ice loss have been predicted (Arrigo et al., 2008). This study reveals that primary production may increase in the wake of ocean acidification. However, the heterotrophic microbial community has a strong potential to diminish air-sea carbon fluxes and need to be considered when estimating the response of the Arctic Ocean to future environmental changes.

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Table 1. Time averaged (day 5–day 28) rates (µmol C l^{-1} d^{-1}) of total primary production (PP), primary POC production (PP_{POC}), and primary DOC production (PP_{DOC}), based on ^{14}C bottle incubations, as well as ratios of PP normalized to chlorophyll a concentration (µmol C $µg^{-1}$ Chl *a* d^{-1}). Averages (avg.) and standard deviations (SD) were calculated from $n = 12$ observations for each mesocosm and for the fjord, respectively.

		Mesocosms									
		1	2	3	4	5	6	7	8	9	fjord
PP	avg	7.36	7.29	8.65	4.60	9.49	9.83	4.23	10.09	11.02	6.49
	SD	3.29	1.82	2.50	1.69	3.20	3.15	1.90	4.26	3.69	2.54
PP_{POC}	avg	6.24	6.15	7.17	3.83	8.17	8.54	3.45	8.67	9.41	5.76
	SD	3.17	1.84	2.33	1.68	2.92	3.09	1.69	4.25	3.51	2.52
PP_{DOC}	avg	1.22	1.25	1.62	0.85	1.44	1.41	0.85	1.55	1.77	0.79
	SD	0.44	0.35	0.75	0.45	0.67	0.49	0.39	0.47	0.78	0.38
[PP] : [Chl *a*]	avg	6.59	7.08	8.32	4.30	8.95	9.30	3.87	9.29	10.31	6.00
	SD	3.35	2.12	2.89	2.02	3.88	4.06	2.05	4.75	4.70	2.53

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Table 2. Production rates (µmol l^{-1} d^{-1}) of particulate organic carbon (POC), based on ^{14}C bottle incubations. Averages (avg) and standard deviations (SD) were calculated from on triplicate measurements of 24 h incubations.

		Mesocosm									
Sampling (d)		1	2	3	4	5	6	7	8	9	Fjord
−1	avg	4.07	5.95	6.08	1.09	1.59	1.55	0.29	1.45	1.27	6.53
	SD	1.14	0.61	0.45	0.04	0.04	0.52	0.01	0.07	0.35	2.38
2	avg	1.91	2.05	2.05	0.32	2.04	1.82	0.92	2.15	2.01	2.54
	SD	0.01	0.17	0.37	0.02	0.02	0.02	0.06	0.34	0.09	0.27
5	avg	1.52	3.75	4.31	3.13	4.64	3.86	2.00	3.25	2.61	1.16
	SD	0.34	0.47	0.33	0.11	0.37	0.17	0.44	0.04	0.72	2.00
7	avg	5.67	4.58	4.95	4.33	3.95	4.78	1.72	3.60	4.65	5.04
	SD	0.15	0.37	0.72	0.30	0.12	0.19	0.29	0.18	0.48	0.36
10	avg	7.87	7.89	7.47	3.14	9.34	9.22	3.76	6.45	9.77	10.08
	SD	0.58	1.00	1.04	0.30	0.82	1.34	0.26	2.51	0.59	0.45
12	avg	5.93	6.65	4.67	2.15	5.18	5.39	2.75	5.75	7.42	6.48
	SD	2.73	0.50	0.32	0.04	0.47	0.11	0.11	0.70	0.14	0.25
14	avg	3.30	5.52	4.98	4.86	4.64	5.08	1.48	5.15	6.22	4.69
	SD	0.61	0.30	0.59	0.49	0.23	0.54	0.25	0.57	0.44	0.35
16	avg	8.18	7.46	7.13	4.80	9.74	8.88	2.50	7.50	12.84	3.23
	SD	0.58	0.19	0.64	0.39	1.88	0.73	0.39	1.05	2.15	0.48
18	avg	6.80	6.37	10.32	5.01	11.53	8.81	6.65	10.03	9.85	5.41
	SD	0.58	0.46	0.19	0.25	0.44	7.64	0.32	3.04	8.58	0.71
20	avg	2.39	3.16	7.34	2.03	9.94	11.54	6.11	8.41	14.34	5.78
	SD	0.63	0.74	2.04	0.39	3.12	0.74	0.32	0.34	0.92	0.25
22	avg	3.05	5.12	7.39	3.97	6.98	9.79	4.52	10.55	10.23	3.57
	SD	0.58	0.67	1.42	0.55	1.06	2.36	1.86	3.84	2.18	0.61
24	avg	9.61	8.05	10.95	7.82	11.79	10.55	3.18	14.92	11.24	6.69
	SD	1.56	1.64	1.49	1.62	1.68	0.38	0.59	0.73	0.30	0.34
26	avg	9.04	9.31	10.39	2.10	10.97	13.60	4.48	16.49	11.89	8.23
	SD	1.32	0.95	0.39	0.60	1.05	0.65	0.40	1.73	0.24	0.66
28	avg	11.56	5.94	6.17	2.60	9.43	11.04	2.25	12.05	11.92	8.85
	SD	0.55	0.86	0.25	0.22	1.22	0.28	0.27	2.03	1.77	0.30

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Table 3. Production rates (µmol C l^{-1} d^{-1}) of dissolved organic carbon (DOC), based on ^{14}C bottle incubations. Averages (avg) and standard deviations (SD) were calculated from on triplicate measurements of 24 h incubations.

		Mesocosm									
Sampling (d)		1	2	3	4	5	6	7	8	9	Fjord
−1	avg	1.76	1.99	1.25	0.42	1.03	0.32	0.87	1.06	0.38	0.95
	SD	0.60	0.20	0.49	0.05	0.84	0.45	0.42	0.05	0.23	0.23
2	avg	0.22	0.49	0.05	0.27	0.39	0.34	0.48	0.77	0.52	0.48
	SD	0.05	0.21	0.03	0.14	0.00	0.11	0.07	0.51	0.02	0.08
5	avg	1.39	0.93	1.71	1.53	1.56	0.93	0.87	1.77	1.39	1.32
	SD	0.15	0.81	0.42	0.23	0.06	0.85	0.57	0.29	0.13	0.24
7	avg	2.03	1.76	2.32	1.13	1.20	1.96	1.33	1.91	1.97	1.45
	SD	1.82	0.11	0.68	0.98	1.10	0.35	0.46	0.17	0.29	0.09
10	avg	1.18	1.02	0.89	0.72	1.61	1.65	0.92	1.26	1.21	1.16
	SD	0.34	0.22	0.35	0.27	1.40	0.33	0.34	1.06	0.34	1.10
12	avg	1.04	1.00	0.91	0.14	0.97	1.11	0.48	0.96	1.23	0.73
	SD	0.82	0.18	0.26	0.12	0.15	0.40	0.15	0.12	0.14	0.07
14	avg	0.44	0.89	0.38	0.93	0.67	0.65	0.29	0.92	0.90	0.60
	SD	0.13	0.31	0.33	0.32	0.38	0.41	0.26	0.42	0.25	0.02
16	avg	1.32	1.10	1.09	0.75	1.58	1.33	0.17	0.84	1.59	0.52
	SD	0.35	0.51	0.29	0.55	0.52	0.17	0.13	0.33	0.55	0.49
18	avg	1.41	1.93	2.03	1.15	3.23	2.12	1.14	2.11	3.76	0.46
	SD	0.13	0.06	0.57	0.28	0.37	0.96	0.35	0.68	0.72	0.33
20	avg	0.88	1.26	2.84	1.23	1.23	1.85	1.11	1.59	2.03	0.23
	SD	0.76	0.83	1.32	0.43	1.23	0.24	0.09	0.16	0.55	0.23
22	avg	0.77	1.14	1.70	0.98	0.96	1.79	0.75	1.77	2.33	0.58
	SD	0.41	0.15	0.13	0.17	0.83	0.54	0.26	0.45	0.48	0.38
24	avg	1.76	1.99	1.25	0.42	1.03	0.32	0.87	1.06	0.38	0.95
	SD	0.60	0.20	0.49	0.05	0.84	0.45	0.42	0.05	0.23	0.23
26	avg	0.22	0.49	0.05	0.27	0.39	0.34	0.48	0.77	0.52	0.48
	SD	0.05	0.21	0.03	0.14	0.00	0.11	0.07	0.51	0.02	0.08
28	avg	1.39	0.93	1.71	1.53	1.56	0.93	0.87	1.77	1.39	1.32
	SD	0.15	0.81	0.42	0.23	0.06	0.85	0.57	0.29	0.13	0.24

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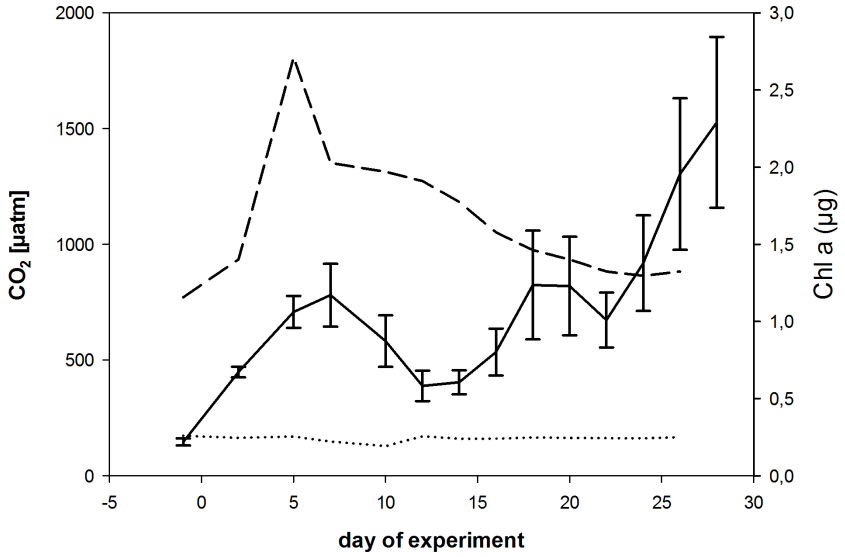

Fig. 1. Development of maximum (dash line) and minimum (dotted line) pCO_2 (µatm) in the course of the Svalbard mesocosm experiment, and biomass changes of the phytoplankton community in the mesocosm as indicated by average (±1 SD) chlorophyll *a* (Chl *a*) concentration (solid line and error bars).

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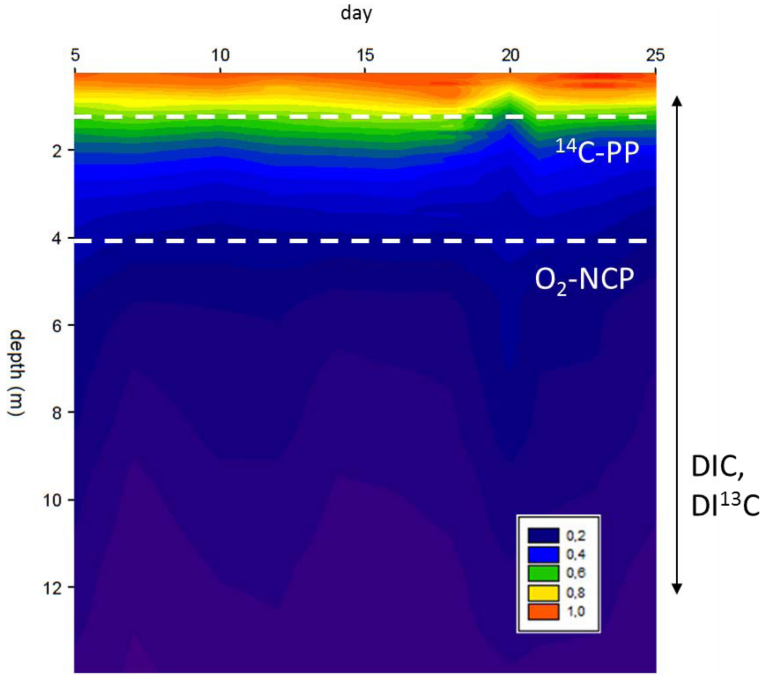

Fig. 2. Fraction of surface light received at different depths in the mesocosms in the course of the study as exemplified for M1. For comparison, bottle incubations were performed at 1 m depth (^{14}C-incubations) and at 4 m depth (O_2, Tanaka et al., 2012), while changes in DIC concentration were calculated from depth integrated water sampling (0–12 m; Silyakova et al., 2012).

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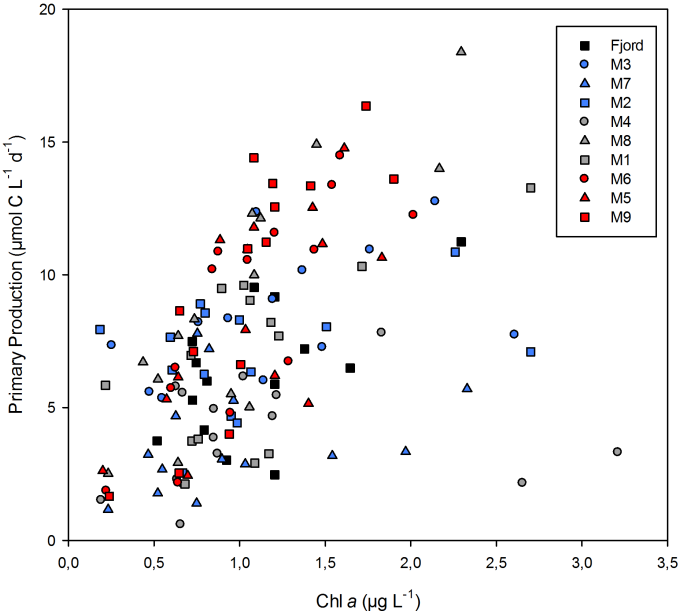

Fig. 3. Total primary production (PP_{POC} + PP_{DOC}), as determined for each of the nine mesocosms and for the fjord during the mesocosm study, was not related to Chl *a* concentration. Red symbols: high pCO_2 mesocosms (M5, M6, M9), grey symbols: medium pCO_2 mescosms (M1, M4, M8), blue symbols: low pCO_2 mesocosms (M2, M3, M7), black symbols: fjord.

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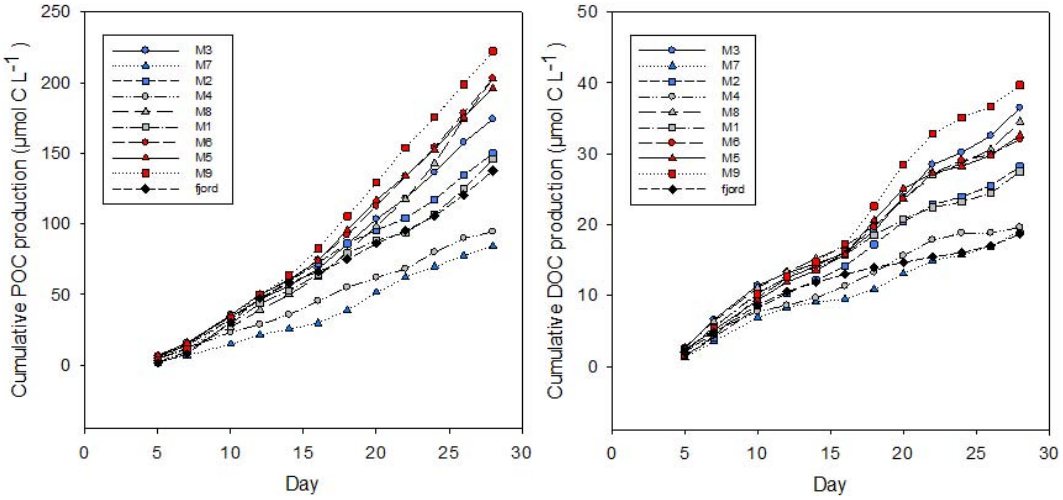

Fig. 4. Cumulative primary production of POC **(a)** and of DOC **(b)** as determined from ^{14}C-bottle incubations. Red symbols: high pCO_2 mesocosms (M5, M6, M9), grey symbols: medium pCO_2 mescosms (M1, M4, M8), blue symbols: low pCO_2 mesocosms (M2, M3, M7), black symbols: fjord.

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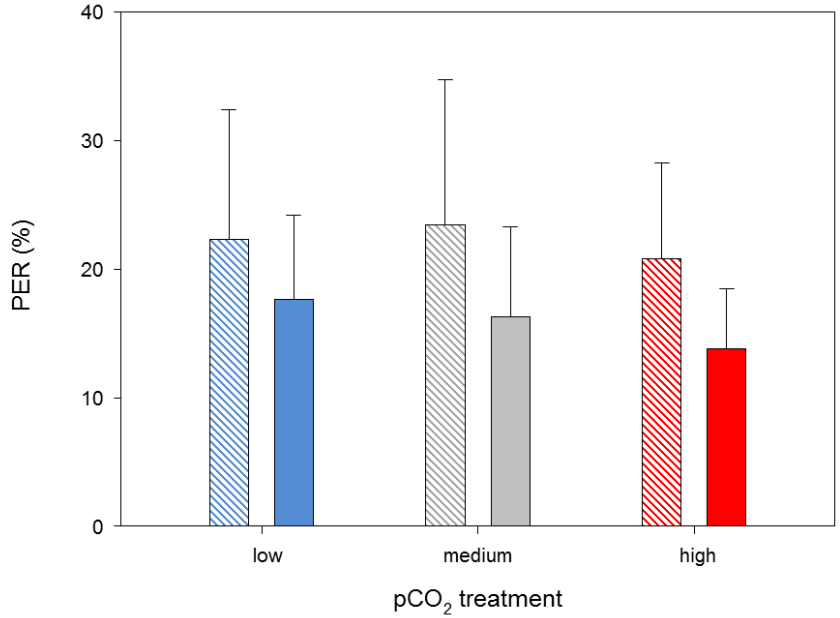

Fig. 5. Exudation of DOC calculated as percentage of extracellular release (PER) and averaged for grouped treatments (low, medium, high pCO_2) for the time before nutrient addition (hatched bars, day 5–day 12, $n = 12$), and after nutrient addition (solid bars, day 14–day 28; $n = 21$). For color information see Fig. 3. PER was not significantly different before nutrient addition, but decreased thereafter with increasing pCO_2 (t-test, $p < 0.05$).

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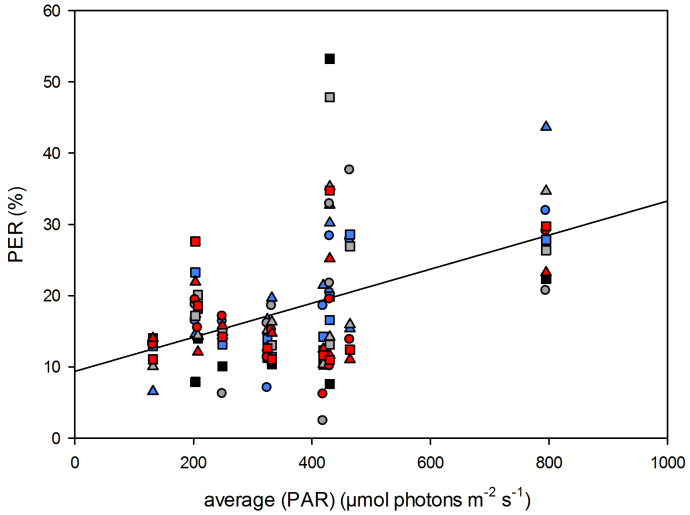

Fig. 6. PER during the total period of observation (day 5–day 28) increased with average PAR received during the 24 h bottle incubations. For color information see Fig. 3.

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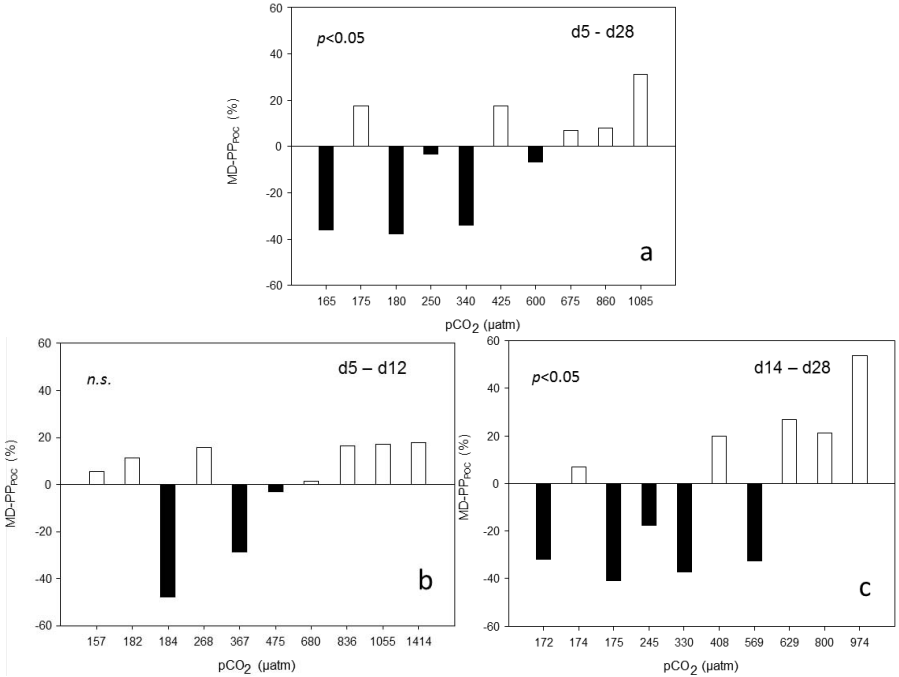

Fig. 7. Mean deviations of PP_{POC} (MD-PP_{POC}, %) for the nine mesocosms and for the fjord (left bar) calculated for **(a)**: the total period of observation (day 5–day 28; $n = 12$), **(b)**: the period before nutrient addition (day 5–day 12; $n = 4$), and **(c)**: the period after nutrient addition (day 14–day 28; $n = 8$). Significance of relation between MD-PP_{POC} and average pCO_2 at the time of observation was calculated by linear regression.

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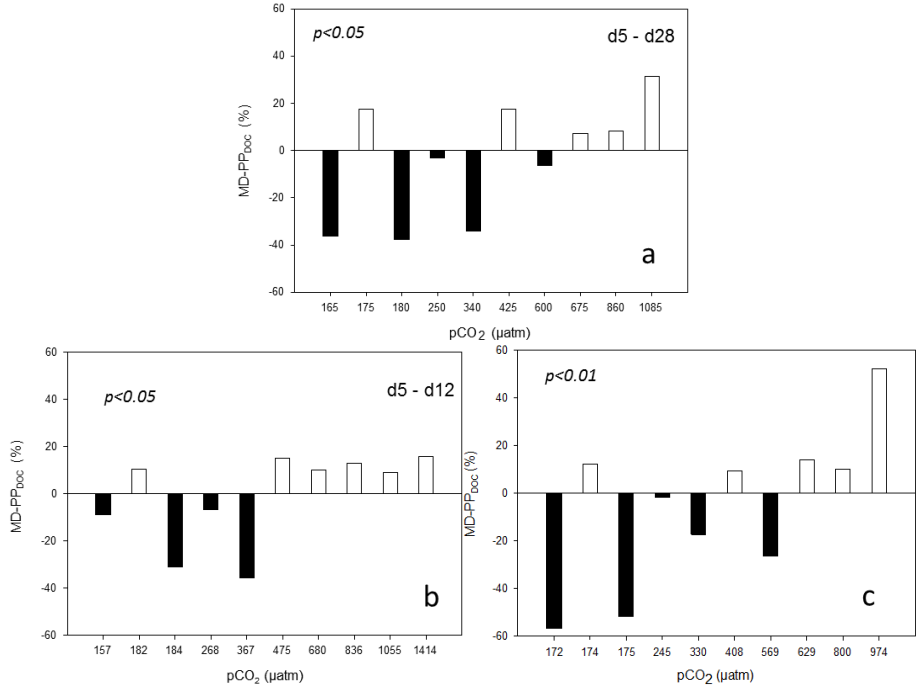

Fig. 8. Mean deviations of PP_{DOC} (MD-PP_{DOC}, %) for the nine mesocosms and for the fjord calculated (left bar) for **(a)**: the total period of observation (day 5–day 28; $n = 12$), **(b)**: the period before nutrient addition (day 5–day 12; $n = 4$), and **(c)**: the period after nutrient addition (day 14–day 28; $n = 8$). Significance of relationship between MD-PP_{DOC} and average pCO_2 at the time of observation was calculated by linear regression.

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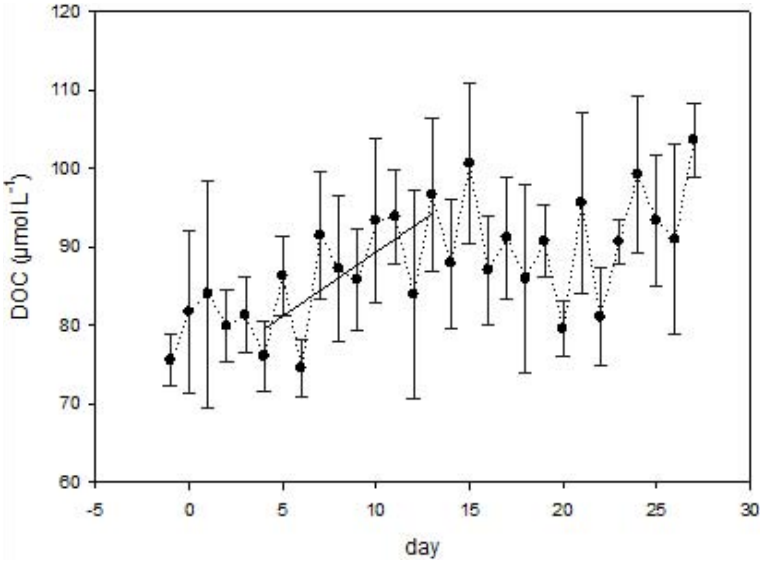

Fig. 9. Average concentration of dissolved organic carbon (DOC) in the course of the mesocosm experiment as determined from depth-integrated samples of the nine mesocosms. Error bars give ±1 SD. Between day 4 and day 13 (nutrient addition), DOC increased significantly over time ($r^2 = 0.45$, $n = 10$, $p = 0.01$), whereas no significant increase of DOC concentration was observed afterwards.

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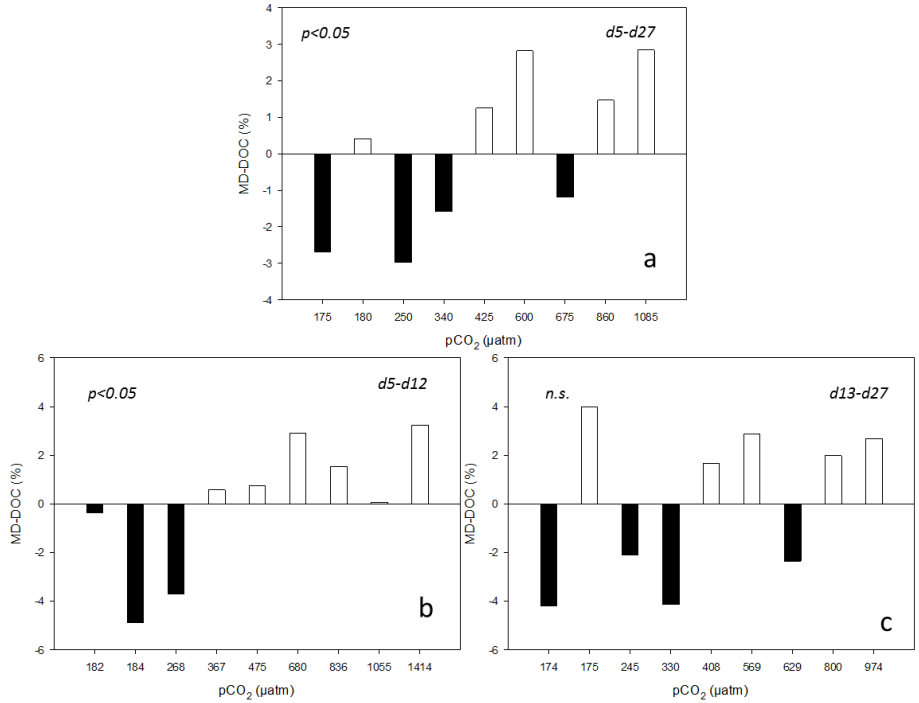

Fig. 10. Mean deviations of DOC concentrations (MD_{DOC}, %) for the nine mesocosms, for **(a)**: the total period of observation (day 4–day 27; $n = 24$), **(b)**: the period before nutrient addition (day 4–day 13; $n = 10$), and **(c)**: the period after nutrient addition (day 14–day 27; $n = 14$). Significance of relation between MD_{DOC} and average pCO_2 at the time of observation was calculated by linear regression. Fjord samples were not included.

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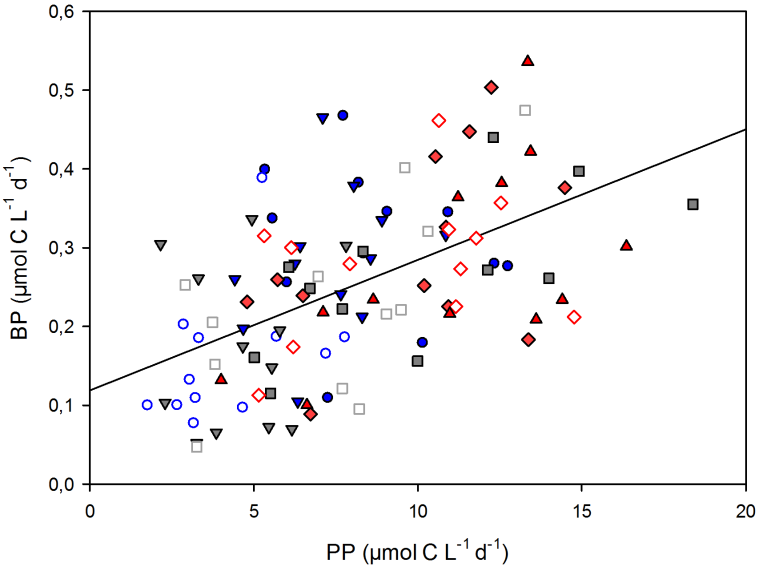

Fig. 11. Relationship between bacterial biomass production (BP) and primary production (PP) in the mesocosm samples was highly significant ($p < 0.001$, $n = 108$) for the total period of the experiment (day 4–day 28).

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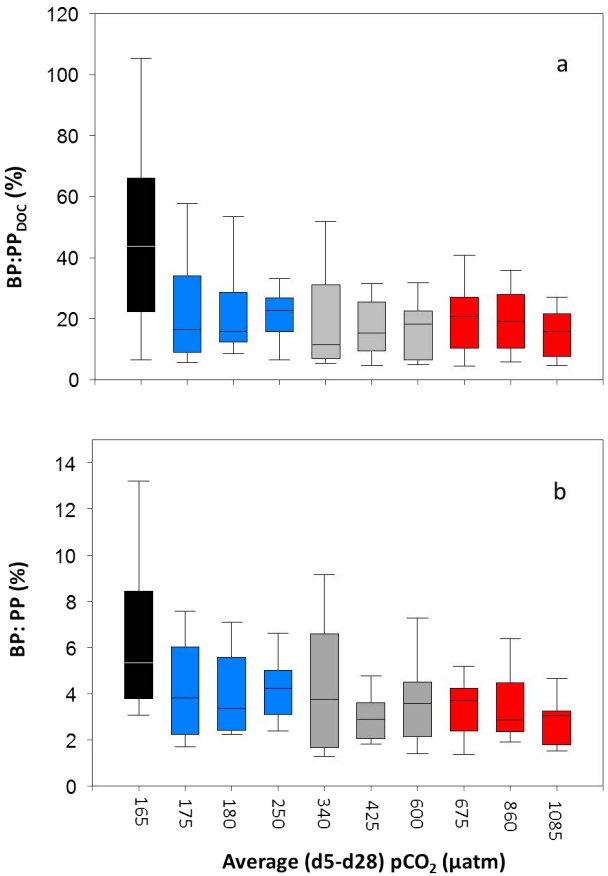

Fig. 12. Box-and-whisker plots of the ratio of bacterial biomass production (BP) to primary production (PP = PP_{POC} + PP_{DOC}) and to autotrophic DOC production (PP_{DOC}) as derived from dark and light bottle incubations.

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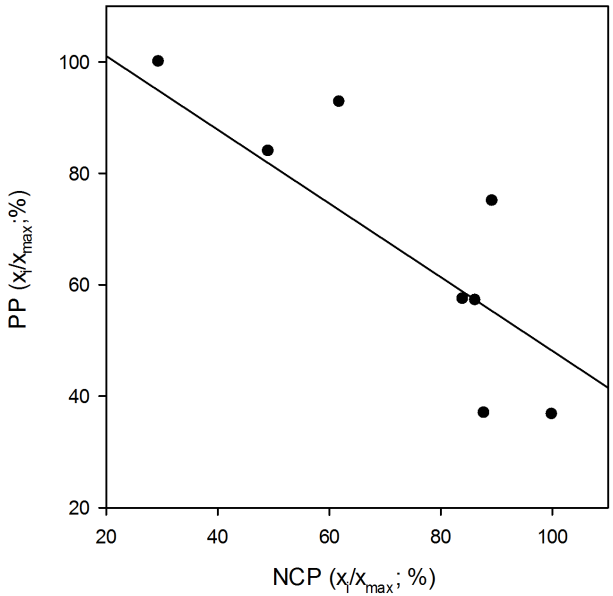

Fig. 13. Anti-correlation between primary production (PP) as determined by ^{14}C-bottle-incubations and net community production (NCP) as derived from O_2-bottle incubations. Shown are cumulative values for each mesocosm over the total duration of the experiment (day 5–day 28) and normalized (%) to the maximum cumulative value observed.

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