**Biogeosciences
Discussions**

Enhanced carbon overconsumption in response to increasing temperatures during a mesocosm experiment

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Abstract

Increasing concentrations of atmospheric carbon dioxide are projected to lead to an increase in sea surface temperatures, potentially impacting marine ecosystems and biogeochemical cycling. Here we conducted an indoor mesocosm experiment with a natural plankton community taken from the Baltic Sea in summer. We induced a plankton bloom via nutrient addition and followed the dynamics of the different carbon and nitrogen pools for a period of one month at temperatures ranging from 9.5 °C to 17.5 °C, representing a range of ±4 °C relative to ambient temperature. The uptake of dissolved inorganic carbon (DIC) and the net build-up of both particulate (POC) and dissolved organic carbon (DOC) were all enhanced at higher temperatures and almost doubled over a temperature gradient of 8 °C. Furthermore, elemental ratios of carbon and nitrogen (C:N) in both particulate and dissolved organic matter increased in response to higher temperatures, both reaching very high C:N ratios of > 30 at +4 °C. Altogether, these observations suggest a pronounced increase in excess carbon fixation in response to elevated temperatures. Most of these findings are contrary to results from similar experiments conducted with plankton populations sampled in spring, revealing large uncertainties in our knowledge of temperature sensitivities of key processes in marine carbon cycling. Since a major difference to previous mesocosm experiments was the dominant phytoplankton species, we hypothesize that species composition might play an important role in the response of biogeochemical cycling to increasing temperatures.

1 Introduction

Climate change is expected to affect marine ecosystems and biogeochemical cycling in the oceans in a variety of ways (Riebesell et al., 2009; IPCC, 2007a). Since the beginning of the 20th century, global average sea surface temperatures have already increased by 0.6 °C. Recent climate projections suggest an increase in global surface

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air temperatures by about 1.1 to 6.4 °C by the end of this century (relative to 1980–1999), thereby also leading to a further warming of the upper ocean (IPCC, 2007b). This will affect marine ecosystems indirectly, as thermal stratification of the water column becomes stronger, leading to changes in the availability of nutrients and light. It

5 is also likely that sea surface warming will have pronounced direct effects on pelagic ecosystems and marine carbon cycling, as temperature is a major environmental factor controlling the rates of biological processes (Brown et al., 2004). Experimental evidence suggests a clear relationship between temperature and phytoplankton growth (Eppley, 1972).

10 A number of studies have already investigated the effects of increasing temperatures on the ecosystem level. Common observations were a decrease in body size of planktonic organisms (Moran et al., 2010; Daufresne et al., 2009), effects on timing of the bloom (Sommer and Lengfellner, 2008; Lassen et al., 2010), coupling of phytoplankton and bacterial processes (Hoppe et al., 2008) as well as changes in food web dynamics,

15 i.e., a shift from autotrophic to more heterotrophic states of the respective ecosystems (Muren et al., 2005; O'Connor et al., 2009). In some of these experiments a lower overall biomass was found in response to warming (O'Connor et al., 2009; Lassen et al., 2010).

However, most of these studies did not explicitly monitor biogeochemical dynamics.

20 A recent mesocosm study with a natural plankton community investigated possible impacts of warming on biogeochemical cycling under spring bloom conditions (Wohlers et al., 2009). The results suggested an acceleration of respiratory carbon consumption over autotrophic production and an associated decrease in carbon drawdown at elevated temperatures. Furthermore, they found that warming shifted the partitioning

25 of organic matter between the particulate and dissolved phase, with a higher fraction building up as dissolved material. This observation is also supported by another similar mesocosm experiment (Kim et al., 2011). Yet, little is known whether these observed temperature sensitivities are a general pattern in marine ecosystems, or if the response of key processes in carbon cycling to sea surface warming depends on the

phytoplankton assemblage. In both of the above mesocosm experiments, the dominant phytoplankton species was the diatom *Skeletonema costatum*. In this study, we investigated the effect of temperature changes on marine carbon cycling in a natural plankton community in summer and discuss differences to previous experiments.

2   Material and methods

2.1   Experimental setup

The indoor mesocosm study was carried out between 16 June and 16 July 2010 at the Helmholtz Centre for Ocean Research Kiel (GEOMAR) in Kiel, Germany. Nine mesocosms with a volume of 1400 l each were set up in triplicates in three temperature controlled climate chambers, and filled simultaneously with unfiltered seawater from approximately 6 m depth in Kiel Fjord (Western Baltic Sea). Thus, the water in the mesocosms contained a natural summer plankton community representative for this region at that time.

Mesozooplankton (copepods of the species *Acartia clausi*) was added from net catches (64 µm mesh size) with densities of ~ 10 individuals l^{-1}. Since *Acartia clausi* is the dominant mesozooplankton species ($> 90\%$) during most years in this region and the density of 10 $ind^{-1} l^{-1}$ is a reasonable number for this region and time of year (Behrends, 1996), we believe that our added mesozooplankton provides an adequate representation of field conditions.

To investigate the effects of temperature on a summer bloom situation, the temperature in the three climate chambers was adjusted to 9.5 °C, 13.5 °C and 17.5 °C (in the following referred to as "low", "intermediate" and "high" temperature, respectively). The intermediate temperature level of 13.5 °C corresponded to the temperature of near-surface water (~ 5 m depth) in the Kiel Fjord at the start of the experiment. The other temperature regimes were equivalent to in situ +4 °C and in situ −4 °C, thereby establishing an overall temperature gradient of 8 °C. Previous mesocosm experiments had

only considered a temperature gradient in the direction of warming. In our experimental setup a temperature gradient towards both cooling and warming was established, in order to ensure that the observed effects are truly associated to the absolute temperature and are not merely a stress response to a temperature change in either direction.

Light supply during the experiment was provided by a computer-controlled system, generating a light curve with a light/dark cycle of $\sim 17/7$ h. It contained full-spectrum light tubes (12×80 W per mesocosm; 10×4000 K and 2×9000 K color temperature) covering the full range of photosynthetically active radiation (PAR: 400–700 nm). The daily light dose was calculated for the respective latitude and day of the year following Brock (1981), resulting in a maximum irradiance intensity of ~ 690 W m^{-2} and an integrated daily light supply of ~ 1100 W h m^{-2}.

Measured concentrations of dissolved inorganic nutrients in the mesocosms on day t1 amounted to ~ 0.1 µmol l^{-1} phosphate (PO_4^{3-}), ~ 1.5 µmol l^{-1} nitrate (NO_3^-), ~ 0.4 µmol l^{-1} ammonium (NH_4) and ~ 12.2 µmol l^{-1} silicate ($Si(OH)_4$). In order to initiate a phytoplankton bloom, inorganic nutrients were added to the mesocosms in Redfield stoichiometry on day t1, with concentrations of 16.0 µmol l^{-1} NO_3^- and 1.0 µmol l^{-1} (PO_4^{3-}). While these nutrient concentrations are not typical of summer conditions in the field, such nutrient pulses can regularly occur in summer in this region and induce summer plankton blooms, e.g., through wind-induced convective events (Carstensen et al., 2004). In our mesocosm experiment this nutrient addition was necessary to induce a plankton bloom with the processes and dynamics we intended to study in a time frame of weeks.

Throughout the experiment, the water in the mesocosms was gently mixed by attached propellers. This way, settling of particulate organic matter onto the bottom of the mesocosms was minimized as far as possible and a homogenous water body was maintained, allowing discrete water samples to be representative of the whole mesocosm. Therefore, this mixing should not be confused with convective mixing in the real ocean, as the mesocosms in our experiment were intended to mimic a water parcel in the surface ocean that would not mix with water from the deeper ocean.

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After the addition of nutrients on 17 June (t1) the development and decline of the plankton bloom were followed over 30 days with samples being taken three times a week from intermediate depth with a silicon tube.

2.2 Measurements

Temperature, salinity and pH were measured with a WTW conductivity/pH probe (calibrated with NBS buffer). Samples for dissolved inorganic nitrate, nitrite, ammonium, phosphate and silicate were prefiltered through 0.2 µm cellulose acetate filters and measured with an autoanalyzer (AA II) (Hansen and Koroleff, 2007).

Dissolved inorganic carbon (DIC) was measured spectrophotometrically on an autoanalyzer (Stoll et al., 2001). Samples were sterile filtered (0.2 µm) and stored in borosilicate bottles, sealed with butyl/PTFE septa at temperatures below 10 °C until analysis.

For the determination of particulate organic carbon and nitrogen (POC and PON), samples were filtered onto precombusted (5 h at 450 °C) glassfibre filters (Whatman, GF/F, 0.7 µm nominal poresize) and frozen (at −20 °C) until analysis. POC filters were fumed overnight with hydrochloric acid (37 %) in order to remove particulate inorganic carbon (PIC) and dried at 60 °C for approximately 12 h. Afterwards they were analyzed on a Eurovector EuroEA-3000 elemental analyzer (Sharp, 1974).

Samples for dissolved organic carbon and total dissolved nitrogen (DOC and TDN) were filtered through precombusted GF/F filters, with the filtrate being collected in acid-washed (HCl, 10%) and precombusted (12 h at 250 °C) glass vials and frozen (at −20 °C) until analysis. Prior to measurements, the pH was adjusted to pH=2 with HCl (p.a.) and automatically purged with synthetic air in the DOC analyzer to remove inorganic carbon. The analysis was carried out by catalytic high-temperature combustion on a Shimadzu TOC-V analyzer with a total nitrogen module (TNM-1). The accuracy of the analysis was confirmed with deep-sea reference water samples provided by the University of Miami. The accuracy with respect to deep-sea water was within 5 % relative error and detection limits were 5 µmol l^{-1} for DOC and 1 µmol l^{-1} for TDN. Procedural blanks did not yield detectable amounts of DOC and TDN. Dissolved organic

nitrogen (DON) was calculated as the difference between TDN and the sum of all dissolved inorganic nitrogen species (nitrate, nitrite, and ammonium).

2.3 Calculations

Calculation of additional carbonate system variables (such as p_{CO_2}) from measured DIC and pH were carried out with the program CO2SYS (Lewis and Wallace, 1998), using the dissociation constants for carbonic acid as refitted by Dickson and Millero (1987). The pH values used for these calculations were measured on the NBS scale. The salinity of our seawater was ∼ 13 and thus did not allow the use of certified reference buffers for calibration on the total scale. While we are aware that this might create electrode-specific uncertainties in measured pH, it would not change the observed dynamics of calculated p_{CO_2} over the course of the experiment, i.e., significantly lower minimum values at higher temperatures.

Air-water gas exchange of CO_2 between mesocosms and atmosphere was estimated following the stagnant boundary layer model of Smith (1985), with molecular diffusivity calculated as described in Jähne et al. (1987) and a chemical enhancement factor derived from pH as in Kuss et al. (2004). However, this approach has originally been developed for field conditions and not specifically for the application to conditions like in our experimental setup, with constant mechanical mixing of the water column and a wind speed close to zero. Consequently, gas exchange is strongly underestimated, when wind speed is set to zero in the calculations and mixing of the mesocosms is not accounted for. Therefore we adjusted the wind speed in the calculation for stagnant layer thickness in order to account for constant mixing of the water column in the mesocosms. Without gas exchange, the amount of total carbon (DIC+POC+DOC) should not increase, as biological processes only lead to shifts between the different pools. Therefore any change in total carbon concentrations is attributable to gas exchange, assuming no loss of carbon, e.g., through sinking. To account for the observed increase in total carbon, wind speed was adjusted to a value of $6\,\mathrm{m\,s^{-1}}$ in our calculations, yielding the best fit to the observed net carbon uptake in the mesocosms

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at different temperatures. Consequently, our estimates of air-sea CO_2 exchange are different from previous studies (Delille et al., 2005; Wohlers et al., 2009) that did not apply the modifications described above. Without these modifications it was impossible to balance the carbon budget in our experiment.

Nutrient concentrations for day t0 are estimated from data of day t1, since sampling and measurements only started on day t1, immediately prior to nutrient addition. These measurements revealed already slight differences between temperature treatments, which were probably caused by different biological activities at different temperatures. Concentrations of NO_3^- on day t1 ranged from ~ 0.7 to $2.6\,\mu mol\,l^{-1}$ between warm and cold mesocosms. Since nutrient uptake was slowest in the colder mesocosms, we assumed the initial nutrient concentrations in all mesocosms on day t0 to correspond to the concentrations in the low temperature treatment as the best approximation possible. For day t1 the presented nutrient data was calculated as the sum of measured values and nutrient addition ($16.0\,\mu mol\,NO_3\,l^{-1}$) for the respective mesocosms.

2.4 Statistical analysis

The influence of temperature on response variables was tested for statistical significance by means of a one-factorial analysis of variance (ANOVA), since the various data subsets were normally distributed. Normality was tested with Shapiro-Wilk's test and accepted if the p-value of this test was larger 0.05. Statistical analysis was performed using Statistica version 8 (STATSOFT). A statistically significant effect of temperature was assumed, if the p-value was < 0.05 (see Table 1). Homogeneity of variances was tested using Levene's test and was accepted if the p-value was > 0.05.

Furthermore, the data for maximum drawdown of DIC, maximum build-up of POC and DOC, and maximum ratios of POC:PON and DOC:DON were analyzed with a linear regression model. We chose this approach as it provides valuable quantitative information for biogeochemical modeling.

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3 Results

3.1 Bloom development and community composition

The development of the phytoplankton bloom was characterized by a rapid decline in dissolved inorganic nutrients (Fig. 1), the drawdown of dissolved inorganic carbon and the build-up of particulate organic matter (Fig. 3). At the beginning of the experiment, the phytoplankton community was composed of $\sim 54\%$ diatoms and $\sim 46\%$ cryptophytes in terms of biomass. After nutrient addition and with the onset of the bloom, diatoms became strongly dominant ($> 99\%$ of biomass) in all mesocosms, in particular the species *Dactyliosolen fragilissimus*. Other functional groups (e.g., dinoflagellates) remained at very low abundances throughout the bloom ($< 1\%$) and are thus likely negligible for the overall dynamics of the plankton bloom.

Copepod abundance remained approximately at initial levels of $\sim 10\,\mathrm{ind^{-1}\,l^{-1}}$ during the phytoplankton bloom in the first half of the experiment and was not affected by temperature (not shown).

3.2 Nutrient consumption

Calculated initial concentrations (on day t0) of NO_3^- and PO_4^{3-} in the mesocosms were 2.6 and $0.2\,\mathrm{\mu mol\,l^{-1}}$, respectively. Initial levels of silicate were $12.3\,\mathrm{\mu mol\,l^{-1}}$. With the addition of $16.0\,\mathrm{\mu mol\,l^{-1}}$ and $1.0\,\mathrm{\mu mol\,l^{-1}}$, the total amount of available nutrients added up to $18.6\,\mathrm{\mu mol\,l^{-1}}$ (NO_3^-) and $1.2\,\mathrm{\mu mol\,l^{-1}}$ (PO_4^{3-}). Following the addition of nitrate and phosphate on day t1, inorganic nutrients were consumed very rapidly and were depleted in all mesocosms a few days after nutrient addition (Fig. 1). While both NO_3^- and PO_4^{3-} and were already exhausted on day t5, the consumption of silicate was slightly slower, with exhaustion on day t7. The depletion of silicate is in line with analysis of phytoplankton species composition, suggesting diatoms to constitute a major fraction of phytoplankton biomass.

Nutrient concentrations on day t2 of the experiment were significantly lower in the mesocosms at higher temperatures ($p < 0.001$, Table 1), thus indicating a faster consumption with increasing temperatures. After reaching exhaustion on day t5, concentrations of NO_3^- stayed below $1.0\,\mu mol\,l^{-1}$ and those of PO_4^{3-} below $0.1\,\mu mol\,l^{-1}$ for the rest of the experiment. Ammonium concentrations were almost constant and not affected by temperature, with concentrations in all mesocosms fluctuating between ~ 0.2 and $0.6\,\mu mol\,l^{-1}$ throughout the experiment (not shown).

3.3 Nitrogen

After addition of inorganic nutrients, particulate organic nitrogen (PON) built up in all mesocosms from initial concentrations of $\sim 4.4\,\mu mol\,N\,l^{-1}$ to maximum concentrations of ~ 20.2, 17.9 and $15.2\,\mu mol\,N\,l^{-1}$ around day t5 at low, intermediate and high temperatures, respectively (Fig. 2a). Maximum build-up of PON was significantly lower at higher temperatures ($p < 0.001$, Table 1). After the peak of the bloom PON decreased in all mesocosms until the end of the experiment, reaching concentrations of ~ 8.0, 9.9 and $12.2\,\mu mol\,N\,l^{-1}$ at low, intermediate and high temperatures, respectively. Thus, PON concentrations at the end of the experiment were significantly higher at high temperatures ($p < 0.005$, Table 1).

Concentrations of dissolved organic nitrogen (DON) increased constantly throughout the experiment, reaching final concentrations of $\sim 18.7\,\mu mol\,N\,l^{-1}$ averaged over all mesocosms. An effect of temperature on the accumulation of DON could not be observed (Fig. 2b).

The total amount of nitrogen (PON + DON + DIN) decreased in all mesocosms over the course of the experiment (Fig. 2c). Initial concentrations were $\sim 25.4\,\mu mol\,N\,l^{-1}$ and maximum concentrations occurred one day after nutrient addition (day t2) with ~ 40.5, 38.3 and $37.7\,\mu mol\,N\,l^{-1}$ in the mesocosms at low, intermediate and high temperatures, respectively. During the bloom phase, total nitrogen decreased in all mesocosms (until t14 to t16). Afterwards, total nitrogen fluctuated strongly, reaching final concentrations (day t30) of ~ 27.2, 29.3 and $32.3\,\mu mol\,N\,l^{-1}$ at low, intermediate and high

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temperatures, respectively. Thus, total nitrogen at the end of the experiment was significantly higher at high temperatures ($p < 0.001$, Table 1), though this difference was significant only during the last few days of the experiment (Fig. 2c).

3.4 Carbon

3.4.1 DIC uptake

The consumption of inorganic nutrients was accompanied by photosynthetic uptake of dissolved inorganic carbon (DIC). Temporal dynamics of DIC concentrations showed a clear response to temperature, with average concentrations in the replicate mesocosms decreasing from initial levels of $\sim 1860\,\mu\mathrm{mol\,l^{-1}}$ on day t0 to a minimum of ~ 1590, 1475 and $1310\,\mu\mathrm{mol\,l^{-1}}$ until day t12 at low, intermediate and high temperatures, respectively (Fig. 3a). Minimum concentrations of DIC were significantly lower at higher temperatures ($p < 0.0005$). After the peak of the bloom, i.e., from day t12 onwards, concentrations of DIC in the mesocosms increased again for the rest of the experiment, reaching approximately initial concentrations on day t30.

When correcting for air-water gas exchange, the maximum uptake of DIC reached $\sim 380\,\mu\mathrm{mol\,C\,l^{-1}}$ on average at low, $520\,\mu\mathrm{mol\,C\,l^{-1}}$ at intermediate, and $700\,\mu\mathrm{mol\,C\,l^{-1}}$ at high temperatures (Fig. 4a). Accordingly, the biologically mediated drawdown of DIC was significantly enhanced at higher temperatures (Fig. 3d, $p < 0.0001$, Table 1), corresponding to an increase of maximum DIC consumption of $\sim 40\,\mu\mathrm{mol\,C\,l^{-1}\,^{\circ}C^{-1}}$. Accordingly, the rate of net DIC consumption during the bloom phase increased with higher temperatures, accelerating from an average of $\sim 32\,\mu\mathrm{mol\,C\,l^{-1}\,d^{-1}}$ in the cool mesocosms, to $44\,\mu\mathrm{mol\,C\,l^{-1}\,d^{-1}}$ at intermediate, and $56\,\mu\mathrm{mol\,C\,l^{-1}\,d^{-1}}$ at high temperatures. This corresponds to a Q_{10} value of ~ 2.0 for net DIC uptake.

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3.4.2 POC build-up

The drawdown of DIC was reflected in a concomitant build-up of particulate organic carbon (POC), which peaked between days t9 and t12 in the different mesocosms (Fig. 3b). Starting from initial levels of $\sim$ 25–30 μmol C l^{-1}, POC concentrations rapidly increased and reached a maximum build-up of POC of $\sim$ 210 μmol C l^{-1} at low, 325 μmol C l^{-1} at intermediate, and 410 μmol C l^{-1} at high temperatures. This corresponds to a linear increase of maximum POC build-up with temperature of 26 μmol C l^{-1} °C^{-1}. Thus, similar to DIC uptake, the build up of POC was significantly higher at higher temperatures (Fig. 3e, $p < 0.0005$, Table 1). Accordingly, the rate of POC build-up during the bloom phase showed a clear response to higher temperatures, amounting to $\sim$ 22, 27 and 39 μmol C l^{-1} d^{-1} at low, intermediate and high temperatures, respectively. This corresponds to a Q_{10} value of $\sim$ 2.0 for net POC build-up.

After the peak of the bloom, POC concentrations in the water column decreased again. However, in contrast to DIC concentrations POC did not reach initial levels, but remained at concentrations much higher than at the beginning of the experiment.

3.4.3 DOC accumulation

Along with the decrease in DIC and build-up of POC, a substantial increase in dissolved organic carbon (DOC) was observed over the course of the experiment in all mesocosms (Fig. 3c). Starting from initial concentrations of $\sim$ 290 μmol C l^{-1}, DOC concentrations increased steadily over the course of the experiment, with maximum accumulation of DOC amounting to $\sim$ 160 μmol C l^{-1} at low, 240 μmol C l^{-1} at intermediate, and 290 μmol C l^{-1} at high temperatures. Thus, maximum build-up of DOC was significantly higher at elevated temperatures (Fig. 3f, $p < 0.005$, Table 1), corresponding to a linear increase of maximum DOC accumulation of 16 μmol C l^{-1} °C^{-1}. The rate of net DOC accumulation showed a positive relationship with temperature as well, increasing from an average of 3.8 μmol C l^{-1} d^{-1} at low, to 6.0 μmol C l^{-1} d^{-1} at intermediate, and

8.6 μmol C l^{-1} d^{-1} at high temperatures. This increase corresponds to a Q_{10} value of ~ 2.7 for the net build-up of DOC.

3.4.4 Carbon budget

After the peak of the bloom, the amount of total organic carbon (TOC), i.e., the sum of particulate and dissolved organic carbon decreased relatively slowly and remained at levels much higher than initial concentrations until the end of the experiment (Fig. 4a). The decrease in POC was closely balanced by the increase in DOC, resulting in almost constant levels of TOC in the mesocosms at all temperatures. However, TOC concentrations after the bloom remained elevated at higher temperatures. On the last day of the experiment (t30), TOC concentrations were significantly higher at higher temperatures ($p < 0.0005$, Table 1), amounting to ~ 490, 660 and 780 μmol C l^{-1} at low, intermediate and high temperature, respectively.

In contrast to TOC, an increase of DIC concentrations began in all mesocosms with the decline of the bloom, with DIC approaching initial levels again at the end of the experiment (Fig. 3a). The phytoplankton bloom and the associated uptake of DIC were accompanied by a sharp decrease in the partial pressure of carbon dioxide (p_{CO_2}) in the water. Early levels of p_{CO_2} (day t2) were between ~ 360 and 430 μatm in all mesocosms, and thus near equilibrium with the atmosphere. Through biological uptake of DIC during the phytoplankton bloom, p_{CO_2} dropped to minimum values of ~ 78 μatm at low, 45 μatm at intermediate, and 24 μatm at high temperatures in the relatively weakly buffered low-salinity Baltic Sea water (Fig. 4c). Minimum levels of p_{CO_2} (day t12) were significantly lower at higher temperatures ($p < 0.0005$, Table 1).

This gradient between p_{CO_2} in water and air led to a flux of CO_2 from the atmosphere into the water in all mesocosms. This CO_2 flux was stronger in the mesocosms at higher temperatures, where more inorganic carbon had been taken up and converted to organic carbon and consequently higher air-water p_{CO_2} gradients were reached. This fact is also reflected in the total amount of carbon (i.e., the sum of organic and inorganic

carbon) in the mesocosms at the end of the experiment. Concentrations of total carbon on day t30 amounted to $\sim$ 2380, 2500 and 2600 µmol C l^{-1} at low, intermediate and high temperatures, respectively, and where thus significantly elevated at higher temperatures (Fig. 4b, $p < 0.001$, Table 1). Furthermore, there is a positive effect of temperature on gas transfer velocity, enabling higher rates of gas exchange at higher temperatures ($\sim$ 25 % higher at 17.5 °C than at 9.5 °C).

Our estimates of cumulative DIC increase due to air-water gas exchange range from $\sim$ 240 µmol C l^{-1} at low, to $\sim$ 320 µmol C l^{-1} at intermediate, and $\sim$ 380 µmol C l^{-1} at high temperatures over the course of the whole experiment, showing a significant effect of temperature ($p < 0.01$, Table 1).

3.5 Stoichiometry

3.5.1 Drawdown of carbon and nitrogen

While the same amount of NO_3^- was consumed in the mesocosms at all temperatures ($\sim$ 18.3 µmol l^{-1}), the decrease in DIC concentrations and the calculated uptake of DIC (corrected for gas exchange) showed a significant increase with temperature (see Sect. 3.3.1). Accordingly, the ratio of maximum DIC uptake to the maximum consumption of NO_3^- increased from $\sim$ 20.8 at low, over 29.0 at intermediate, to 38.5 at high temperatures. This trend of increasing consumption of carbon over nitrogen at higher temperatures is reflected in the elemental ratios of particulate and dissolved organic matter (POM and DOM). Differential build-up and removal of particulate and dissolved organic matter led to temporal variations in the respective elemental ratios.

3.5.2 C:N of POM

The molar ratio of carbon to nitrogen (C:N) of particulate organic matter was $\sim$ 6.1 in all mesocosms at the beginning of the experiment and thereby close to the Redfield value of 6.6. From day t4 on, POC:PON started to increase in all mesocosms, and showed

a positive correlation with temperature (Fig. 5a). The maximum ratio of POC:PON was significantly enhanced at higher temperatures and reached 15.9 at low, 29.0 at intermediate, and 33.7 at high temperatures (Fig. 5b; $p < 0.0005$). After the decline of the bloom, POC:PON began to decrease again, however not back to initial values.

3.5.3 C:N of DOM

The elemental ratios of dissolved organic matter already deviated significantly from Redfield stoichiometry at the beginning of the experiment, with an average molar DOC:DON ratio of 16.1 over all mesocosms. C:N ratios of DOM were steadily increasing before, during and after the phytoplankton bloom over the entire course of the experiment, showing clear differences between temperature treatments (Fig. 5c). The maximum ratio of DOC:DON was significantly affected by temperature and reached 25.6 at low, 28.1 at intermediate, and 30.8 at high temperatures (Fig. 5d; $p < 0.005$).

4 Discussion

4.1 Budgets of carbon and nitrogen

4.1.1 Air-water gas exchange

Without external sources or sinks, the amount of total carbon (DIC + POC + DOC) in the mesocosms would be constant, as biological processes do not influence the overall mass balance of carbon, but only shift matter between the different pools. If at all, one would expect a loss of total carbon in such an experiment, e.g., through wall growth or sinking of organic matter to the bottom of the mesocosms. However, we observed a strong increase of total carbon in the mesocosms, with clearly elevated concentrations at higher temperatures at the end of the experiment (Fig. 4b). Accordingly, this increase in total carbon could only be attributable to an external input of carbon into the mesocosms, which was only possible through continuous and rapid air-water gas

exchange of CO_2 in our experiment. Due to the rapid decrease in p_{CO_2} associated with DIC uptake (Fig. 4c), a considerable air-water flux of CO_2 started with the onset of the bloom and prevailed for the rest of the experiment (see Sect. 3.4.4 and Fig. 4a). High rates of gas exchange were facilitated through continuous mixing of the water column

5 by propellers attached to the mesocosms. Thereby, the boundary layer that is exchanging gas with the atmosphere was constantly renewed and rapid air-water gas exchange was facilitated even at virtually zero wind speed. Since more DIC was consumed and converted to organic matter during the bloom phase at higher temperatures, the air-water difference in p_{CO_2} and the magnitude of gas exchange were also enhanced at

10 higher temperatures. The positive effect of temperature on gas transfer velocity additionally facilitated gas exchange at higher temperatures. Consequently, temperature affected carbon uptake by the water column in two ways: directly, by enhancing the gas transfer velocity and indirectly by enhancing biological carbon drawdown and the associated effect on p_{CO_2}.

15 **4.1.2   Loss of organic matter**

The delay between rapidly decreasing seawater p_{CO_2} levels and the increase in total carbon in the mesocosms suggests that air-water CO_2 flux was possibly balanced by the loss of organic matter to a certain extent during this bloom phase (until day t14). These considerations are supported by the temporal development of total nitro-

20 gen (PON + DON + DIN), which decreased in all mesocosms by $\sim 8.4\,\mu mol\,N\,l^{-1}$ over the course of the experiment, most pronounced during the bloom phase until day t14 (Fig. 2c).

   In mesocosm experiments, organic matter can potentially get lost through wall growth or sinking of organic matter to the bottom of the mesocosms. Based on repeated in-

25 spections we could not observe considerable growth of algae on our mesocosm walls. Furthermore, using a similar experimental setup, Sommer et al. (2007) concluded that it takes a few weeks until the development of wall growth plays a significant role. On the other hand, the sedimentation of particles to the bottom of the mesocosms can never

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be ruled out completely. Previous studies have shown, that sinking of organic matter can lead to a considerable loss of biomass from the surface layer in mesocosm experiments (Keller et al., 1999; Wohlers et al., 2009). Since high concentrations of POC and PON were reached very rapidly in our experiment, it is possible that some of this newly produced biomass has sunken to the bottom of the mesocosms. Although mixing of the water column by the propeller should minimize particle settling, this can obviously never be excluded entirely. However, our experimental design minimized the loss terms for organic matter as far as possible and our results do not indicate a relevant influence of this loss on biogeochemical dynamics and its temperature sensitivity.

4.2 Carbon overconsumption and temperature

4.2.1 Dynamics of DIC and particulate organic matter

Our results suggest a positive effect of temperature not only on the relative consumption of DIC over nutrients, but also on the build-up and elemental ratios of POM for the plankton community in our experiment. Especially after nutrient depletion, strong differences in POC dynamics occurred between the different temperature treatments (Fig. 3b), revealing a clear effect of temperature on the POC:PON ratio (Fig. 5a,c).

The main mechanism responsible for the higher uptake of DIC at higher temperatures in our experiment was the higher relative consumption of carbon over nitrogen and its associated conversion to biomass. Excess uptake of DIC over inorganic nitrogen, a phenomenon called carbon overconsumption (Toggweiler, 1993), has been observed in previous experiments and field studies. Some earlier studies, which found enhanced drawdown of carbon over nitrogen, did not find changes in POC:PON like in our experiment (Banse, 1994; Riebesell et al., 2007). Instead, a common assumption was, that the excess carbon is exuded by phytoplankton mainly in the form of DOC (Kähler and Koeve, 2001). However, in agreement with our study, an increasing number of studies have reported a decoupling of carbon and nitrogen dynamics in phytoplankton blooms and an associated increase of the POC:PON ratio (Wetz and

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Wheeler, 2003; Biddanda and Benner, 1997; Engel et al., 2002). Generally, elemental stoichiometry of phytoplankton and POM can vary widely, depending on nutrient status and environmental conditions (Geider and La Roche, 2002; Finkel et al., 2010). An increasing cellular quota of carbon to nitrogen in phytoplankton has been found for
5 different species under nutrient limitation (Harrison et al., 1977; Goldman, 1992) and there is also evidence for an influence of temperature on intracellular C:N ratios, at least for some species (Thompson et al., 1992; Berges et al., 2002). Hence, this mechanism might have contributed to the high C:N ratios of POM in our experiment. Since an increase in POC:PON is usually observed after nutrient exhaustion, carbon over-
10 consumption is commonly assumed to be associated with nutrient stress (Biddanda and Benner, 1997; Wetz and Wheeler, 2003). This is in line with the observations in our experiment: While PON reached its highest levels at the same time as nutrients were exhausted (day t5), minimum levels of DIC and maximum concentrations of POC occurred much later (between day t9 and t11). Furthermore, the major differences in
15 drawdown of DIC and build-up of POC and DOC among the different temperature treatments occurred after nutrient depletion. These observations further support the major role of excess carbon fixation for biogeochemical dynamics and its response to increasing temperatures in our experiment.

Engel et al. (2002) also observed an increase in POC:PON, which they concluded
20 to be attributable to excess carbon fixation. However, they found a significant portion of excess carbon fixation to be channeled into the pool of transparent extracellular particles (TEP). Since we observed a massive build-up of POC and an associated strong increase in POC:PON, it is likely that at least part of these dynamics are attributable to the accumulation of carbon-rich (and nitrogen-poor) extracellular organic
25 matter. This consideration is also supported by the strong build-up of dissolved organic matter in our experiment, as previous studies have shown that a considerable fraction of excess POC can be associated with TEP that form from dissolved polysaccharides (Engel et al., 2004). The transformation of DOC into extracellular POC via aggregation of TEP has been shown before in experimental studies (Mopper et al., 1995) and the

underlying mechanisms have already been investigated and discussed further (Passow, 2002). Furthermore, it is unlikely that the increase in POC:PON is entirely attributable to changes in the elemental composition of phytoplankton. Intracellular C:N ratios of diatoms are usually < 10 (Thompson et al., 1992; Goldman, 1992) and do not exceed a value of 15 even under nutrient starvation (Harrison et al., 1977). Thus, we believe that the accumulation of carbon-enriched extracellular particles is the most likely explanation for the strong decoupling of POC and PON in our experiment.

An effect of temperature on the magnitude of POC production and POC:PON resulting from carbon overconsumption as observed in our experiment has, to the best of our knowledge, not been reported so far. Nor did previous mesocosm experiments (Wohlers et al., 2009) find an effect of temperature on POC:PON. It is also notable, that POC:PON reached very high absolute values in comparison to previous studies (between 16 and 34 at temperatures ranging from 9.5 to 17.5 °C). This suggests relatively high levels of carbon overconsumption, which increase with temperature.

Furthermore, results from single-species culture experiments indicate that TEP production is highly variable between phytoplankton species and that it is a function of temperature (Claquin et al., 2008). Accordingly, species-specific differences in TEP production could also contribute to the observed differences in carbon dynamics between our and earlier mesocosm experiments.

4.2.2 Dynamics of dissolved organic matter

Another remarkable observation in our experiment was the substantial build-up of DOC and its clear relationship with temperature. While the dynamics of DON did not show any response to temperature (Fig. 2b), the accumulation of DOC was clearly enhanced at higher temperatures (Fig. 3c,f), with the maximum build-up of DOC being enhanced by +47 % and +79 % at intermediate and high temperatures, respectively, compared to low temperatures.

Net accumulation of DOC usually occurs when biological production and loss processes are temporarily decoupled, which often happens in phytoplankton blooms

(Carlson, 2002). A large portion of up to 50 % of primary production can be channeled into the DOC pool (Hansell et al., 2009). The release of DOC by phytoplankton is generally assumed to increase with the onset of nutrient limitation (Biddanda and Benner, 1997). However, only few studies on the influence of temperature on DOC production exist and the results from single-species experiments are controversial. While Verity et al. (1981) could not observe an effect of temperature on dissolved primary production after acclimatization, Zlotnik and Dubinsky (1989) found clearly higher DOC excretion with increasing temperatures. However, they used different phytoplankton species in their studies. More recent findings from short-term warming experiments with natural plankton communities support the latter study, suggesting an increase of dissolved primary production at elevated temperatures (Moran et al., 2006). This is in line with the observed effect of temperature on net DOC accumulation in our experiment and other recent mesocosm studies (Wohlers et al., 2009; Engel et al., 2011; Kim et al., 2011). Thus, our results strongly support the assumption that phytoplankton exudation of DOM is temperature sensitive.

The ratio of DOC:DON was also increasing with temperature in our experiment, suggesting enhanced exudation of DOC over DON by phytoplankton at higher temperatures (Fig. 5d). Since a temperature effect on autotrophic production is also mirrored in the response of POC and POC:PON to higher temperatures, enhanced release of carbon-enriched DOM by phytoplankton due to carbon overconsumption is the most likely explanation for the observed dynamics of DOC accumulation and the DOC:DON ratio.

The net accumulation of DOC throughout the experiment (Fig. 3c) and the relative constancy of TOC after the peak of the bloom (Fig. 4b) did not indicate any substantial decrease of organic matter through microbial consumption. As bacterial production has not been measured in our experiment, it is not possible to make statements about gross rates. Thus, there is a possibility that microbial consumption of organic matter occurred, and that it was approximately balanced by production. On the other hand, inhibition of microbial degradation of DOC might also explain our finding. This has been

observed before, e.g., due to high resistance of fresh DOC to microbial decomposition (Fry et al., 1996), or nutrient limitation by bacteria, leading to inefficient bacterial decomposition (Thingstad et al., 1997). Further factors like the molecular weight and chemical composition of DOM play a crucial role in its availability for bacterial degradation, although there are still huge gaps in our understanding of these aspects (Dittmar and Paeng, 2009).

4.3 Why is the response to temperature changes so different from previous experiments?

Temperature is a key factor in controlling ecological processes through its effect on metabolic rates (Brown et al., 2004). Our study revealed a strong effect of temperature on the dynamics of particulate organic matter, which was not observed in previous experiments. Most comparable studies investigating effects of temperature on marine ecosystems report negative impacts of increasing temperatures, e.g., on production of biomass derived from cell counts (O'Connor et al., 2009; Lassen et al., 2010; Muren et al., 2005), as well as on the build-up of measured POC (Wohlers et al., 2009; Kim et al., 2011). In contrast, both the magnitude and the rate of POC build-up were considerably elevated at higher temperatures in our experiment. Maximum build-up of POC increased by +52 % and +96 % at intermediate and high, compared to low temperatures, respectively. The calculated Q_{10} value of ~ 2.0 for the rate of POC build-up in our experiment lies at the upper end of estimates for the temperature dependence of autotrophic processes like phytoplankton growth and photosynthesis ($1 < Q_{10} < 2$), which are also limited by light and nutrients (Eppley, 1972). The net build-up of DOC, which likely originates from exudation by phytoplankton, revealed an even higher effect of temperature ($Q_{10} \sim 2.7$). This tendency of enhanced DOC accumulation at elevated temperatures (Fig. 3f) is in line with results from previous mesocosm studies (Wohlers et al., 2009; Kim et al., 2011). Our results suggest that these high Q_{10} values are mainly attributable to the temperature sensitivity of carbon overconsumption by phytoplankton

and could hence be interpreted as net Q_{10} factors for processes related to excess carbon fixation.

The previously reported shift from autotrophy to heterotrophy in response to warming (Wohlers et al., 2009; O'Connor et al., 2009; Muren et al., 2005) and an associated decrease in overall biomass could not be observed in our experiment. Wohlers et al. (2009) found a lower consumption of DIC at elevated temperatures (decrease of up to -31% when increasing temperature by 2–6 °C), which they attributed mainly to a stronger effect of warming on respiratory consumption relative to autotrophic production. Such an effect could not be observed in our experiment, where the net drawdown of DIC was strongly enhanced at higher temperatures ($+43\%$ and $+97\%$, Fig. 4a). Possibly, the temperature effect on carbon overconsumption and DOC exudation prevented a substantial imbalance between production and consumption of organic matter towards the latter in our experiment.

Altogether, our results revealed a fundamentally different response of carbon cycling to sea surface warming. Consequently, the question is why our results are so different to the ones of previous studies.

One possible explanation for the different temperature sensitivity of biogeochemical dynamics might be the taxonomic composition of the phytoplankton assemblage prior to the bloom and especially the dominant species. At the beginning of our experiment (day t0) it consisted of $\sim 53\%$ diatoms and 47% cryptophytes in terms of biomass. After nutrient addition diatoms dominated the phytoplankton bloom ($> 99\%$), which is in line with previous mesocosm experiments (Kim et al., 2011; Wohlers et al., 2009). However, the prevailing diatom species was different than in those studies. While *Skeletonema costatum* dominated in the two earlier experiments, *Dactyliosolen fragilissimus* was the dominant species in our experiment, constituting 80–99 % of phytoplankton biomass. It has been shown in a number of studies that different diatom species can have different cellular composition and produce different amounts of extracellular carbohydrates. (Wetz and Wheeler, 2007, 2003; Goldman, 1992; Myklestad, 1974). Furthermore, differences in the response to changing temperatures among diatom species

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have been observed. While reports on possible temperature effects on the cellular composition of diatoms are contradictory (Montagnes and Franklin, 2001), the release of DOC (Zlotnik and Dubinsky, 1989) and production of TEP (Claquin et al., 2008) seem to increase with temperature.

Although no study on the physiology of *Dactyliosolen fragilissimus* and the mechanisms related to carbon overconsumption exists to the best of our knowledge, we hypothesize that physiological properties of this dominant phytoplankton species (e.g., carbon fixation, exudation of DOM and TEP, intracellular C:N) could be decisive for the response of the whole ecosystem and may thus explain the different response to temperature changes compared to previous experiments. This is supported by the fact that the bloom was strongly dominated by this single species and other mechanisms such as grazing dynamics appear to be of minor importance in our experiment and do not seem to deviate substantially from earlier studies.

The abundance of the copepod *Acartia clausi* was rather low and very similar at all temperatures during the bloom phase ($\sim$ 10 individuals l^{-1}) when the major differences in carbon and nitrogen cycling occurred, and should thus not explain differences between our temperature treatments. Furthermore, assuming typical values for grazing rates (0.1–0.5 μmol C ind^{-1} d^{-1}) and body mass (3–5 μg C ind^{-1}) of *Acartia clausi* (Fileman et al., 2010), we estimate that copepod grazing effects are far too small in our experiment to explain the observed differences in POC and DOC concentrations.

The overall higher temperatures in our experiment might also have contributed to the differences to previous experiments. Higher temperatures and associated higher levels of metabolic rates might have revealed temperature effects on processes like carbon overconsumption that could not be found in previous experiments at lower temperatures, where these processes might have been inhibited or temperature-driven differences were to small to be detected. Furthermore, the present study had higher light levels compared to previous experiments, as it was intended to mimic the summer conditions in the field at the time of the experiment. This may have additionally favored excess carbon fixation of phytoplankton, since exudation of DOC has been observed to

increase with irradiance (Verity, 1981; Zlotnik and Dubinsky, 1989). Possibly, these different boundary conditions contributed additionally to the response of biogeochemical element cycling to temperature in our experiment.

5   Conclusions

The balance between build-up and decline of organic matter in the surface ocean plays a major role in marine biogeochemical cycling, as it strongly affects the uptake and sequestration of carbon and other elements to the deep ocean. The present study revealed large uncertainties in our knowledge of temperature sensitivities of key processes in marine carbon cycling.

Our results show that increasing temperatures can have previously not considered effects on the build-up of organic matter and uptake of carbon dioxide by marine ecosystems. The response of some processes was contrary to previous experiments, suggesting that temperature effects on biogeochemical cycling are potentially depending on the composition of the phytoplankton assemblage. Especially processes like carbon overconsumption and exudation of DOM seem to be highly temperature sensitive and might play an important role in the ecosystem response to sea surface warming. This might not only alter the balance between production and consumption of organic matter, but also the partitioning between particulate and dissolved organic matter.

Thus, our findings also imply further challenges for ecosystem modeling and climate change projections. Only little attention has been paid to the effects of increasing temperatures on biological processes in global warming simulations. Current representations of temperature sensitivity in marine ecosystem models differ greatly among models. Consequently, it is currently not possible to forecast how the effect of future sea surface warming on marine carbon cycling will look like on a global scale (Taucher and Oschlies, 2011). Furthermore, our study clearly shows that increasing sea surface temperatures might have substantial impacts on marine ecosystems and that we do not even know the direction in which some key physiological and ecosystem processes

will respond under future warming. We therefore conclude that temperature effects on these processes require further research, both in experimental and modeling studies, in order to improve our understanding of possible impacts of sea surface warming on marine biogeochemical cycling.

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Table 1. F and p-values of an ANOVA, together with respective day, for various biogeochemical variables (df = 2 for all).

	F	p
NO_3, t2	58.238	0.000118
PON, t5	44.075	0.000259
PON, t30	18.188	0.002839
TN, t30	34.07	0.0005
DIC, t12	38.53	0.00037
POC, t12	14.21	0.0052
DOC, t30	15.31	0.00439
TOC, t30	34.9	0.000496
p_{CO_2}, t12	40.79	0.000321
Total carbon, t30	30.06	0.000747
DIC from gas exchange	12.62	0.00708
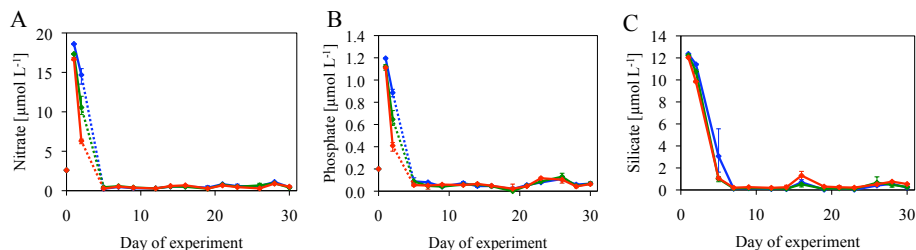
Fig. 1. Temporal development of **(A)** nitrate, **(B)** phosphate, and **(C)** silicate in the mesocosms at low (blue), intermediate (green) and high (red) temperature. Vertical lines denote range of replicates within each temperature treatment.
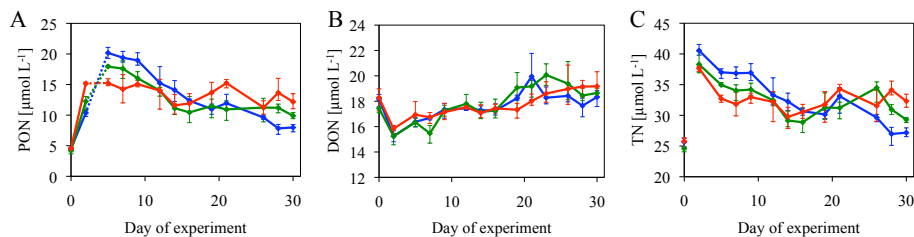
Fig. 2. Temporal development of **(A)** PON, **(B)** DON and **(C)** total nitrogen. Style and color-coding follow that of Fig. 1.
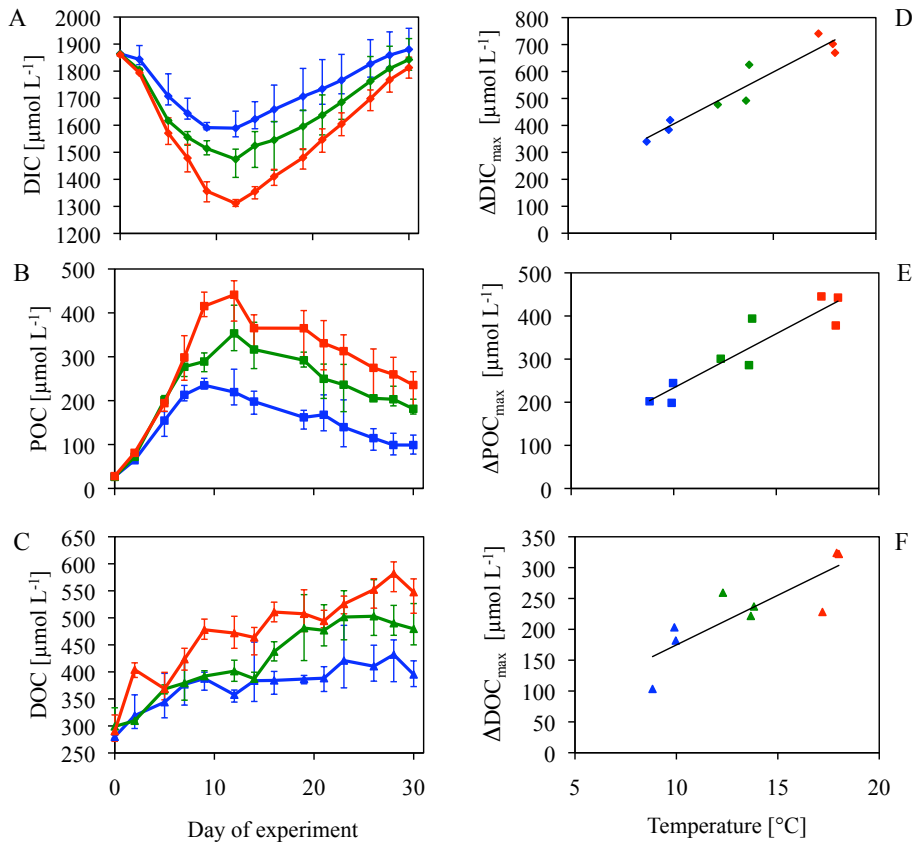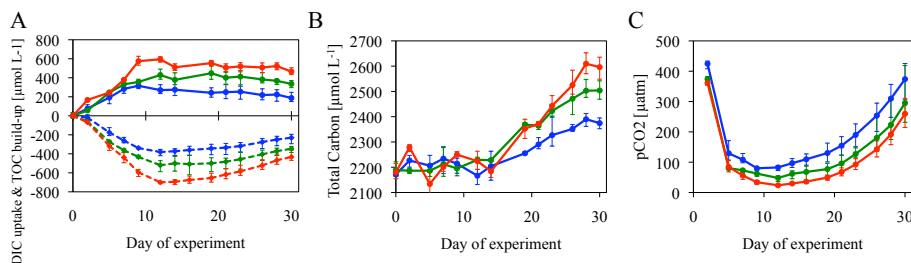
Fig. 3. Temporal development of **(A)** measured DIC, **(B)** POC and **(C)** DOC. Style and color-coding follow that of Fig. 1. **(D)** Maximum uptake of DIC including correction for gas exchange, **(E)** maximum build-up of POC and **(F)** DOC as a function of temperature. Color-coding as in Fig. 1. Solid lines denote linear regressions ($n = 9$; ΔDIC_{max}: $R^2 = 0.92$, $p < 0.0001$; POC_{max}: $R^2 = 0.85$, $p < 0.0005$; ΔDOC_{max}: $R^2 = 0.71$, $p < 0.005$).

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Interactive Discussion

Fig. 4. Temporal development of **(A)** DIC uptake, corrected for air-water gas exchange (dashed) and TOC build-up (solid), **(B)** measured total carbon concentrations and **(C)** pCO_2 (water) in the mesocosms. Style and color-coding follow that of Fig. 1.

Full Screen / Esc

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Interactive Discussion
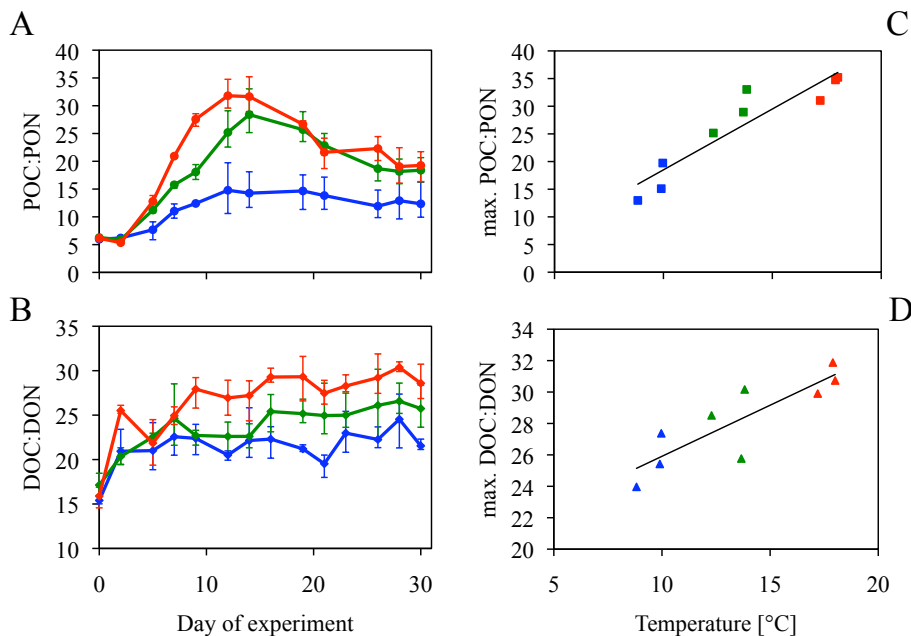
Fig. 5. Temporal development of C:N in **(A)** particulate and **(B)** dissolved organic matter. Maximum C:N of **(C)** particulate and **(D)** dissolved organic matter as a function of temperature. Style and color-coding follow that of Fig. 3. Solid lines denote linear regressions ($n = 9$; POC:PON$_{max}$: $R^2 = 0.86$, $p < 0.0005$; DOC:DON$_{max}$: $R^2 = 0.73$, $p < 0.005$).