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Effects of CO$_2$ on particle size distribution and phytoplankton abundance during a mesocosm bloom experiment (PeECE II)

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Abstract

The influence of seawater CO_2 concentration on the size distribution of suspended particles (2–60 μm) and on phytoplankton abundance was investigated during a mesocosm experiment at the large scale facility (LFS) in Bergen, Norway, in the frame of the
5 Pelagic Ecosystem CO_2 Enrichment study (PeECE II). In nine outdoor enclosures the partial pressure of CO_2 in seawater was modified by an aeration system to simulate past (~190 parts per million by volume (ppmV) CO_2), present day (~370 ppmV CO_2) and future (~700 ppmV CO_2) CO_2 conditions in triplicates. Due to initial addition of inorganic nutrients, phytoplankton blooms developed in all mesocosms and were mon-
10 itored over a period of 19 days. Seawater samples were collected daily for analysing the abundance of suspended particles and phytoplankton with the Coulter Counter and Flow Cytometry, respectively. During the bloom period, the abundance of small particles (<4 μm) significantly increased at past, and decreased at future CO_2 levels. At that time, the total surface to total volume ratio of suspended particles was significantly
15 related to DIC concentration in all mesocosms. Significant changes with respect to the CO_2 treatment were also observed in the phytoplankton community structure. While some populations such as diatoms seemed to be insensitive to the CO_2 treatment, others like *Micromonas* spp. increased with CO_2, or showed maximum abundance at present day CO_2 (i.e. *Emiliania huxleyi*). The strongest response to CO_2 was observed
20 in the abundance of small autotrophic nano-plankton that strongly increased during the bloom in the past CO_2 mesocosms. Together, changes in particle size distribution and phytoplankton community indicate a complex interplay between the ability of the cell to physiologically respond to changes in CO_2 and size selection. Size of cells is of general importance for a variety of processes in seawater such as diffusion-limited uptake
25 of substrates, resource allocation, preditor-prey interactions, and gravitational settling. The observed changes in particle size distribution are therefore discussed with respect to biogeochemical cycling and ecosystem functioning.

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1 Introduction

The increase in atmospheric CO_2 since the beginning of industrialisation, associated risks of ocean acidification, and the potential consequences for marine carbon cycling and global climate have recently gathered attention beyond purely scientific interest. Prior to the industrial burning of fossil fuels, CO_2 concentration varied between 180 and 280 ppmV, with the lower values observed during glacial times. Since the middle of the 18th century, the atmospheric concentration of CO_2 (pCO_2) has increased rapidly from 280 ppmV to 366 ppmV in 1998, and several future scenarios predict a further increase to 750 ppmV in 2100 (IPCC scenario IS92a) (Houghton et al., 2001). The seawater carbonate chemistry has responded noticeably, with a decrease from preindustrial surface ocean pH of 8.25 down to 8.08 presently. Modelling studies predict a further reduction of pH by 0.7 up to the year 2300, which would be more than experienced by marine life for the last 300 000 years (Caldeira and Wickett, 2003).

Although CO_2 plays a fundamental role for organic matter production in the ocean, as it is a substrate in algal photosynthesis, the direct effects of changes in CO_2 availability on organism performance, and their possible transfer to the ecosystem level are still poorly understood. Only recently, studies showed that marine autotrophic communities such as seagrasses (Zimmerman et al., 1997), macroalgae (Gao et al., 1993), diatoms (Riebesell et al., 1993; Chen and Durbin, 1994), coccolithophores (Riebesell et al., 2000; Delille et al., 2005; Engel et al., 2005), and cyanobacteria (Qiu and Gao, 2002; Barcelos e Ramos et al., 2007; Hutchins et al., 2007) exhibit higher rates of production under CO_2 enrichment. It has also been shown that phytoplankton assemblages can experience marked shifts in composition under elevated pCO_2 conditions (Boyd and Doney, 2002; Tortell et al., 2002).

The previous, rather minor scientific interest in direct effects of CO_2 on marine ecosystems largely resulted from the assumption that CO_2 is a non-limiting substrate for primary production in seawater. Although CO_2 concentrations are only in order 8–22 μmol L^{-1} (Goerike and Fry, 1994), the total reservoir of dissolved inorganic car-

bon is about ~2000 μmol/l. Thus, CO_2 is continuously supplied from the pool of bicarbonate and carbonate. Riebesell et al. (1993) showed that marine phytoplankton may indeed be limited by ambient CO_2 availability and that they respond to increased CO_2 concentration with increased growth rates. These results were somewhat contra-
5   dictory to theoretical considerations that for most phytoplankton cells the supply with CO_2 by diffusion is much larger than the cell's need for carbon (Wolf-Gladrow et al., 1999). Seemingly, it is the inefficiency of the CO_2/O_2 fixing enzyme Ribulose-1,5 bisphosphate-carboxylase/oxygenase (RubisCo), with a half-saturation constant (Km) of 20–70 μmol L^{-1} (Badger et al., 1998), that can cause a rate limitation of primary pro-
10 duction in marine phytoplankton. However, measurements of primary production of various phytoplankton species yielded much lower Km values, indicating an enhanced CO_2 concentration at the site of carboxylation (Raven and Johnson, 1991; Rost et al., 2003; Giordano et al., 2005). Species with a low Km value have a high affinity to CO_2 and/or HCO_3^- and nearly saturate primary production at present day values, while at
15 the same time minimizing energy loss due to photorespiration. An increase of CO_2 in these species must be anticipated to have no effect on primary production. In contrast, for species with high Km, such as the coccolithophore *Emiliania huxleyi*, an enhancement of carboxylation can be expected, if CO_2 concentration increase from low values (6–8 μmol L^{-1}), as estimated for the last glacial maximum to high concentration as
20 expected for the future ocean (~22 μmol/l) (Rost and Riebesell, 2004). Thus, under conditions where CO_2 concentration regulates growth (no co-limitation), species with high CO_2 affinity perform better and might out-compete those with lower affinity. The Km value for CO_2 depends, among others, on the capability of the phytoplankton cell to express carbon concentrating mechanisms (CCMs), which include the enzymatically
25 enhanced uptake of CO_2 and/ or HCO_3^- and/ or conversion of HCO_3^- to CO_2 (Raven and Johnson, 1991; Giordano et al., 2005). CCM operation has been observed in many marine microalgae, and we can expect selective advantages for those species that most efficiently apply CCM to enhance carbon acquisition and cell growth. However, like any enzymatically driven process, CCMs require energy and substrates, in

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particular nitrogen, phosphate (ATP) and micronutrients for the synthesis and activation of involved enzymes, such as carbonic anhydrase (Young and Beardall, 2005; Beardall et al., 2005). Thus, the ability to express CCM under natural conditions may be restrained by nutrient and light availability.

On the community level, theoretical considerations suggest that phytoplankton respond to changes in substrate availability by variation of organism size (Irwin et al., 2006). In general, small cells have a higher surface to volume ratio and can faster satisfy the demand for substrates that are transported into the cell by diffusion. Accordingly, if we assume that diffusion was a significant process for CO_2-uptake by the cell, we would expect smaller cells to have a selective advantage over larger cells. Hence, changes in size spectrum of natural phytoplankton communities in response to changes in CO_2 concentration could potentially indicate the relevance of diffusive transport processes.

To the best of our knowledge, no studies have addressed direct effects of CO_2 concentration on the size distribution of particles during phytoplankton blooms so far, or have dealt with the selective advantage of cell size variation versus physiological performance with respect to carbon uptake. Here, we investigate the effect of CO_2 availability on the size frequency distribution of marine phytoplankton under conditions mimicking a phytoplankton bloom during a mesocosm experiment.

2 Material and methods

2.1 Set-up of the mesocosm experiment

The study was conducted in the framework of the Pelagic Ecosystem CO_2 Enrichment Study (PeECE II) in spring 2003 at the Large Scale Facility in Bergen, Norway. Nine outdoor mesocosms ($\sim$20 m^3, 9.5 m depth) were filled with unfiltered, nutrient-poor, post-bloom fjord water, which was pumped from 2 m depth adjacent to the raft and aerated with CO_2/air mixtures in order to achieve 3 different CO_2 levels (190 ppmV,

370 ppmV and 700 ppmV) in triplicates. The general set-up of the mesocosm study has been described in Engel et al. (2005) and Delille et al. (2005) for a similar experiment (PeECE I) and in Grossart et al. (2006) for the 2003 experiment (PeECE II). Nutrients were added initially to obtain concentrations in the seawater of 8.6 μmol L^{-1} nitrate, 0.38 μmol L^{-1} phosphate and 12 μmol L^{-1} phosphate silicate (Carbonel and Chou, personal communication). Daily samples were taken from each mesocosm using 4 m long Polyethylene tubes (10 cm diameter) integrating the upper water column and transferred to 20 L carboys. Immediately after sampling the carboy were brought to the lab and subsamples were taken for various analyses. Intrusion of higher salinity water was observed for mesocosm 9 at day 9. Therefore, data from this mesocosm after day 9 were disregarded.

2.2 Carbonate chemistry

Samples for total alkalinity (TA) and total dissolved inorganic carbon (DIC) were poisoned with HgCl$_2$ on collection, stored in bottles with ground glass stoppers and filtered through GF/F filters prior to analysis. TA was measured using the classical Gran potentiometric titration method (Gran, 1952). The reproducibility of measurements was usually within 4 μmol kg$^-$1. Dissolved inorganic carbon (DIC) was measured by coulometric titration (Johnson et al., 1987) with a precision of 2 μmol kg^{-1}. Other CO$_2$ system variables (pH, CO$_3^{2-}$, HCO$_3^-$) were calculated using the CO$_2$ SYS program (Lewis and Wallace, 1998).

The pCO$_2$ in seawater was measured by means of an equilibrator (Frankignoulle et al., 2001) coupled to an infrared analyzer (Li-Cor 6262). The system was calibrated routinely with air standards with nominal mixing ratios of 0 and 375 ppmV of CO$_2$ (Air Liquide Belgium). Temperature at the inlet of the pump and in the equilibrator was measured simultaneously with two Li-Cor thermosensors. For each measurement of CO$_2$, samples for TA were taken. The pCO$_2$ was corrected for temperature changes using the dissociation constants of Roy et al. (1993) and TA measurement.

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2.3 Particulate organic matter

Total particulate carbon (TPC) and particulate organic nitrogen (PON) were determined by elemental analysis from 1 L (day 0–12) or 0.5 L (day 13–19) samples filtered gently (200 mbar) through precombusted (24 h, 500°C) glass fibre filters (GF/F, Whatman). For determination of POC, filters were fumed for 2 h with saturated HCl to remove all particulate inorganic carbon, and dried for 2 h at 50°C. TPC, POC, and PON were subsequently measured on an Europa Scientific ANCA SL 20–20 mass spectrometer.

2.3.1 Solid particles

Concentration and size distribution of solid particles were determined with a Beckmann Coulter Counter (Coulter Multisizer III), according to Sheldon and Parsons (1978). Three replicate samples of 2000 μL volume were measured daily for each mesocosm using the 120 μm orifice tube. Particles between 2 and 60 μm equivalent spherical diameters (ESD) were binned into 256 size classes.

2.3.2 Chlorophyll-*a*

Concentration of Chl-*a* was determined fluorometrically from 100 mL samples filtered onto dublicate 0.45 μm cellulose nitrate filters and extracted in 90% Acetone overnight. Chl-*a* concentration was measured using a Turner Design fluorometer (model 10-AU) and a standard solution of pure Chl-*a* for calibration.

2.3.3 Flow cytometry

Phytoplankton counts were performed with a FACSCalibur flow-cytometer (Becton Dickinson) equipped with an air-cooled laser providing 15 mW at 488 nm and with a standard filter set-up. The cells were analysed from fresh prefiltered (30 μm mesh) samples at high flow rate ($\sim$60 μ l min^{-1}). Autotrophic groups were discriminated on

the basis of their right angle light scatter (RALS) and chlorophyll fluorescence. List-mode files were analysed using WinMDI.

2.4 Statistical treatment of data

Average values are given by the statistical mean ($\bar{x}$) and its standard deviation (SD). Mean values were compared by means of a t-test. Significance of the correlation coefficient (r^2) against H_o: $\rho=0$ was tested by a Student-test according to Sachs (1974):

$$\hat{t} = \frac{r\sqrt{n-2}}{\sqrt{1-r^2}}, \tag{1}$$

with n = numbers of observations and the degree of freedom, $df=n-2$. H_o ($r^2=0$) is rejected for $\hat{t} \geq \hat{t}_{n-2}; p$. The influence of the CO_2-treatment on biological or chemical variables was determined by means of the analysis of variance (ANOVA) or covariance (ANCOVA). The effect of the CO_2-treatment on a linear relationship between two biological or chemical variables was tested by comparing the slope (b) of the linear regression ($F(x)=b(x)+a$), as calculated for each treatment separately, with a t-test (Sachs, 1974) with $dF=n_1+n_2-4$. Significance level of each test was $p<0.05$.

3 Results

3.1 Bloom development

Following the development of the phytoplankton bloom, Chl-a increased exponentially in each of the mesocosms until a maximum value was reached between day 9 and day 13 of the experiment (Fig. 1a). The peak of the Chl-a concentration coincided with the depletion of nutrients, which was observed for nitrate between day 11 and 12 for all mesocosms (Carbonell and Chou, personal communication). Thereafter, Chl-a concentration declined until the end of the experiment. The bloom can be divided

into a pre-bloom phase that covers the first week of the experiment, a bloom phase during the second week, and a post-bloom phase towards the end of the experiment. Small, inevitable variations during the initialisation introduced variability between all mesocosms. This leads to one to three days deviations regarding the timing of the maximum Chl-a concentration and the onset of decline phase within the CO_2 treat-ments. For later reference we defined more narrow windows for the three phases of the experiment that can clearly be differentiated in all mesocosms; the pre-bloom: days 1–3, the bloom peak: of Chl-a max ±1 day, and the post bloom: day 18–21.

With respect to the CO_2-treatment no significant difference in Chl a concentration or the timing of the maximum concentration were observed. Nutrient draw-down was not significantly different between the CO_2 treatments at any time of the experiments (Carbonel and Chou, personal communication) either.

Particulate organic nitrogen (PON) concentration was initially $2.4\pm0.5\,\mu$mol L^{-1} and increased to maximum values of $7.1\pm1\,\mu$mol L^{-1} on day 9 of the bloom (Fig. 1b). PON concentration was remarkably similar in all mesocosms and no significant effects of the CO_2 treatment on PON concentration was determined (ANOVA).

Particulate organic carbon (POC) concentration started with $15\pm3.0\,\mu$mol L^{-1} and increased throughout the study in all mesocosms to final values of 23–$34\,\mu$mol L^{-1} (Fig. 1c). Like for PON, POC concentration was not related to CO_2 concentration either (ANOVA). Maximum molar [POC]:[PON] ratios were observed during the post-bloom phase with 8.6 ± 0.8, 10 ± 1.0 and 9.7 ± 1.3 for the past, present and future CO_2 scenario, respectively (average ±1 standard deviation calculated from three mesocosms). No significant CO_2 effect on the C:N ratios of POM was determined (ANOVA).

3.2 Particles abundance and size distribution

More than 95% of all particles between 2 and $60\,\mu$m equivalent spherical diameter (ESD) were detected with the Coulter Counter in the size range between 2 and $10\,\mu$m ESD. Larger particles were counted randomly, with number counts that fall into the range of uncertainty (variability) of one treatment, represented by three mesocosms

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(replicates). Total abundance of Coulter Counter particles (CCP) measured shortly after initialisation in all mesocosms, was indifferent between treatments, yielding an average of $7750\pm560\,\text{N mL}^{-1}$. The CCP abundance increased exponentially during the bloom until maximum concentrations were reached between day 11 and day 15 (day 9 for M9) (Fig. 2). Maximum CCP abundances, as averaged separately for the three CO_2 treatments, were $4300\pm500\,\text{N mL}^{-1}$ for the past, and 5260 ± 9500, and $4250\pm1160\,\text{N mL}^{-1}$ for the present and future CO_2 treatment, respectively. The net specific growth rate (μ_t) for CCP during the phase of exponential growth was calculated for each mesocosm: $\mu_t=[\ln(C_i)-\ln(C_{i-1})]/[t_i-t_{i-1}]$, with $\ln(C_i)$ and $\ln(C_{i-1})$ being the natural logarithms of CCP concentrations at two consecutive days. Maximum values for μ_t ranged between $0.30\,\text{d}^{-1}$ (M1) and $0.68\,\text{d}^{-1}$ (M7). No significant effects of the CO_2 treatment on the parameter (μ_t) or on the maximum values for μ were identified.

The size frequency distributions, or size spectra, of CCP, changed over time in all mesocosms (Fig. 3). Size spectra were not significantly different for the three treatments during the pre-bloom phase (ANOVA), but developed differently during growth of the phytoplankton community. Given the present day CO_2 treatment as a reference, we find two distinct maxima in the size spectra, one around $2\,\mu\text{m}$ ESD and another close to $5\,\mu\text{m}$ ESD. Compared to the present day CO_2 treatment, there was a lack of the larger population in the past CO_2 treatment, whereas a drastic reduction of particles abundance was observed at small size ($<4\,\mu\text{m}$) in the future CO_2 treatment (Fig. 3). These distinct differences persisted during the post-bloom phase, but with an increase in variability within the individual treatments.

Differences in size distribution were reflected in significant differences of the median particle size of CCP between the CO_2 treatments over the course of the experiment (ANOVA, $p<0.001$, t-test$_{future-present}$ $p<0.005$, t-test$_{present-past}$ $p<0.001$; Fig. 4). The highest value for median particle size of CCP was observed on day 7 in the future CO_2 treatment with $4.23\pm0.11\,\mu\text{m}$ ESD. The maximum value for median size in the present day CO_2 treatment was observed at day 7 also, but with slightly smaller value of $4.12\pm0.10\,\mu\text{m}$ ESD. Clearly smaller particles were observed in the mesocosms of

the past CO_2 treatment, yielding a maximum median size of 3.70±0.05 μm ESD at day 5. The temporal development of the median size of particles followed similar dynamics irrespectively of the CO_2 concentration; i.e. the median size increased at the beginning of the experiment, had a maximum value during mid or late pre-bloom, a declining phase during the peak of the bloom, and varied only little during the post-bloom phase.

However, median sizes in past CO_2 treatment deviated from the present day or future CO_2 already on day 4. Moreover, the maximum value of median sizes was observed on day 5 in past CO_2 treatment and thus two days earlier than in the other two treatments. This indicated that the absolute value of median size as well as the timing of the saddle point was affected by the CO_2-treatment.

Effects of the CO_2 treatment on particles size were also reflected in the ratio of the total surface to total volume (TS:TV), calculated as

$$TS : TV = \sum_i^{ii} \left\{ \pi(ESD_i)^2 \times n_i \right\} / \sum_i^{ii} \left\{ 1/6\pi(ESD_i)^3 \times n_i \right\} \qquad (2)$$

with ESD_i being the smallest (2 μm) and ESD_{ii} the largest (60 μm) size class observed.

During the 7-day period of the bloom of the phytoplankton community, TS:TV ratios were significantly related to DIC concentration of seawater ($p < 0.001$) and decreased with increasing DIC (Fig. 5).

3.3 Phytoplankton community composition

Total abundance of autotrophic cells as determined by Flow Cytometry in the size range 1.5–30 μm was 6300±1700 N mL^{-1} initially and increased throughout the experiment in all mesocosms (Fig. 3a–c). Maximum average phytoplankton abundance was 36 000±1500 N ml^{-1}, 38 500±9450 N ml^{-1} and 34 500±3930 N ml^{-1} for the past, present day and for the future CO_2 treatments, respectively. During the course of the experiment, total abundance of phytoplankton cells differed significantly between the treatments (ANOVA, $p < 0.005$), with the future CO_2 treatment having the lowest autotrophic cell abundance (t-test, $p < 0.001$). Comparing the total abundance of phytoplankton (covering the size range 1.5–30 μm) with total CCP abundance in the size

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range 2–60 μm revealed a similar temporal development (Fig. 3a–c). However, the Flow Cytometry data showed systematically higher total phytoplankton abundance during the pre-bloom and bloom phase up to day 10 of the experiment. This can be attributed to the lower size detection limit of the Flow Cytometer. After day 10, the num-
5 ber of CCP increased over the number of phytoplankton, indicating the transition from a small-celled autotrophic community to a mixed community including heterotrophic organisms and detritus particles. In general, the relative contribution of autotrophic cells to total particles was highest in the past CO_2 treatment and similar in the present day and the future CO_2 treatment.
10   The species composition of phytoplankton, as determined by Flow Cytometry, indicate that the phytoplankton community was initially similar in all enclosures and was dominated, in terms of numbers, by the phytoflagellate *Micromonas* spp. (Fig. 6). Other major phytoplankton species included diatoms, specifically *Nitzschia* spp., the coccolithophore *Emiliania huxleyi*, and the nanoflagellate *Phaeocystis* spp. During the bloom,
15 the relative abundance of phytoplankton species developed significantly differently in the CO_2 treatments (ANOVA, $p<0.05$). In the past CO_2 treatment, populations of small unidentified autotrophic cells grew rapidly and dominated the community structure during the bloom to a large extend. The *E. huxleyi* population was most prominent in the present, and, although to a smaller degree, in the future CO_2 treatment. The *E. hux-*
20 *leyi* population was determined by the Coulter Counter in the size range 4–8 μm and identified in the future and present day mesocosms by clear peaks. Because no significant differences between the future and present day CO_2 treatment were observed for the median particle size in this 4–8 μm size window, we can assume that the size of the *E. huxleyi* population itself did not vary significantly with CO_2. Diatoms contributed
25 between 4 to 12% to total phytoplankton abundance with the higher values observed during the pre-bloom phase. Within the group of diatoms, a smaller size population of *Nitzschia* was differentiated from a group of larger diatoms. For both diatom groups, no significant differences terms of absolute and relative abundance between the CO_2 treatment were observed (ANOVA, $p>0.05$). During the post-bloom phase the aver-

age phytoplankton composition of the future and present CO_2 treatment converged to those observed for the past treatment during the bloom and no significant CO_2 related differences were determined.

4 Discussion

The aim of this study was to test the hypothesis that CO_2 concentration can affect particle, respectively cell size distribution, during the course of a phytoplankton bloom. Our results revealed that the size distribution of suspended particles in the range 2–60 μm ESD differed significantly between the three CO_2 treatments during the bloom phase itself, when biological processes were dominated by autotrophic growth. There were several indications for particles tending to be smaller at lower CO_2 concentration and larger at higher CO_2 concentration relative to the present day concentration, i.e. in the median sizes of suspended particle, in the ratios of total surface: total volume, and in the spectral distribution of particle size. Changes in CO_2 also led to significant structural effects on the autotrophic community, as indicated by the different abundance of phytoplankton groups using Flow Cytometry. Thereby, the major phytoplankton populations were affected differently. While some populations such as diatoms seemed to be insensitive to the CO_2 treatment, others increased in abundance with CO_2, or were most abundant at present day CO_2.

4.1 CO_2 effects on size distribution of suspended particles

Causes for changes in the size distribution of autotrophic cells can be manifold. In general, metabolic processes, such as growth, nutrient and light acquisition, or respiration, are related to organism size (Peters, 1983). Grazers often select their prey according to size, and the settling rate of most types of marine particles increases with size. For marine phytoplankton, metabolic scaling has previously been shown for some processes such as nutrient uptake, photosynthesis and growth (Finkel et al., 2004). For

others, such as respiration, the existence of size dependence has been questioned (Falkowski and Owens, 1978). Moreover, the relative surface area can be of greater importance than cell diameter, mass or volume with respect to processes such as nutrient uptake, because it is the surface that interferes with the outer medium containing the substrate reservoir. The relative surface area of a phytoplankton cell increases with decreasing size, but also with increasing eccentricity of the cells. Small or elongated phytoplankton species should be better competitors for resources, in particular when these limit biomass production (Grover, 1989). Therefore, small-sized phytoplankton cells are likely to dominate under oligotrophic conditions, whereas elevated nutrient concentration induce growth of larger cells (Irwin et al., 2006).

During this study, significant effects of the CO_2 treatment on particle size distribution were most obvious during the time of the bloom when autotrophic cells dominated particle abundance. This indicates a bottom-up effect of CO_2 on size on the phytoplankton community level. Particle size during this study, however, was derived from volume and expressed as equivalent spherical size without any additional information on the shape of the cells. Information gained from the Flow-Cytometer and from microscopy nevertheless revealed that most species in the size range 1.5–30 μm were indeed rather spherical, with the exception of *Nitzschia* spp. Although the distal length of *Nitzschia* spp. is relatively large, their proximal size is small and thus the volume is small. However, abundance of *Nitzschia* spp. was not significantly different between the CO_2 treatments. Hence, eccentricity of cells did not bias the observation of a general decrease in cell size with increasing CO_2 during this study.

During the bloom phase, the observed differences in particle size spectra and median particle size were related to differences in phytoplankton community composition. *Micromonas* spp. and *E. huxleyi*, for example were more abundant in the present day and future than in the past CO_2 treatment. In the latter, smaller autotrophic nanoplankton clearly dominated the bloom by number. Size variations within individual species were presumably not related to the CO_2-treatment. However, at least for *E. huxleyi* potential changes in the protoplast size may have been masked by simultaneous changes

in coccosphere size due to potential effect of CO_2 on calcification (Riebesell et al., 2000). During a similar mesocosm study (PeECE I), when the phytoplankton community was clearly dominated by *E. huxleyi*, Engel et al. (2005) observed that the sizes and weights of coccospheres were largest at low CO_2. During PeECE I, no significant differences in the phytoplankton community were observed with respect to the CO_2 treatment. One reason for the different outcome of PeECE I and II with respect to CO_2 influence on phytoplankton community composition may be that nutrients in the 2005-experiment were added in a $NO_3:PO_4$ ratio of 30 and without any additional supply of silicate in order to favour the blooming of *E. huxleyi*. In the present study N:P:Si were added in "Redfield-ratio" in order to allow for a mixed assemblage of diatoms, coccolithophores and other autotrophic species.

4.2 CO_2 effects on phytoplankton community composition

Recent investigations on CO_2 acquisition in marine phytoplankton species demonstrated that many phytoplankton groups including diatom species such as *Skeletonema costatum* efficiently apply one or several carbon concentrating mechanisms (CCM) (Rost et al., 2003). CCMs can be understood as a physiological regulation of CO_2 acquisition to maintain high photosynthetic rates even at reduced CO_2 concentration. Goldman (1999) observed no reduction in cell growth of large diatom species until CO_2 concentrations fell as low as $4\,\mu$mol L^{-1}, indicating that growth of these species was not depending on the diffusional uptake of CO_2, but supported by CCMs. During this study the abundance of diatoms was not significantly different between the CO_2 treatments, supporting the idea that diatoms can indeed regulate their C-uptake and are insensitive to changes in CO_2 concentrations over a relatively wide range. Abundance of *E. huxleyi*, in contrast, was significantly reduced in the past CO_2 treatment. This is in accordance with our expectations, since *E. huxleyi* has been shown to have a low affinity to CO_2 (Rost et al., 2003). Abundance of *Micromonas* spp. increased with increasing CO_2, indicating that this species does not apply CCM efficiently, either. However, the strongest response to CO_2 concentration was observed in the group of small

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autotrophs that grew abundantly in the past CO$_2$ treatment, but little in the future CO$_2$ treatment. Changes in the abundance of these small cells were mainly responsible for the changes in size spectra compared to the present day treatment.

Interestingly, it was this group of small-celled algae that numerically dominated phytoplankton community at low CO$_2$, and not diatoms, which we expected to be good competitors based on their high CO$_2$ affinity and physiological capability. Because we did not determine CCM operations in phytoplankton during this study, we can only speculate about possible explanations for the observed CO$_2$-effects on phytoplankton abundance and size distribution. First, CCMs in diatoms, or other species, may have been co-limited by phosphate or light availability (Young and Beardall, 2005; Beardall et al., 2005) and were not efficient enough to give a competitive advantage. Phosphate concentrations during this study decreased strongly within the first week, while at the same time NO$_X$:PO$_4^{3-}$ ratios increased up to 28 (Carbonel and Chou, personal communication), indicating high phosphorus demand of phyto- and bacterioplankton cells. To prevent depletion, PO$_4^{3-}$ was added again to all mesocosms on day 8. By this time differences in the particle size spectra had already evolved (Fig. 4). Thus, we cannot exclude that P limitation may have affected CCM of algal species and was co-limiting active C-uptake in the past CO$_2$ mesocosms. If P were the potentially limiting nutritious element, we would expect that species allocating PO$_4^{3-}$ efficiently for reproduction have an advantage over those species, which additionally need to allocate PO$_4^{3-}$ for CCM operation. Under these circumstances, reduction of cell size would be beneficial to circumvent both P- and CO$_2$ limitation and may help to explain the observed relationship between size and DIC availability during this study. We may then speculate that future effects of elevated CO$_2$ concentration increase on the size spectrum of phytoplankton communities may especially occur in oceanic regions, where P is limiting phytoplankton production.

Another hypothesis would be that CCM only acted as a surplus to carbon acquisition and equally well in all phytoplankton species observed in the past CO$_2$ treatment. Cassar et al. (2004) estimated that 50% of carbon uptake in a natural diatom population

was comprised by HCO_3^- uptake, the remaining 50% by CO_2. Reduction of cell size may therefore be pivotal to enhance the fraction of CO_2 taken up by diffusion, and to accelerate growth rates of small cells. Certainly, more investigations are needed to elucidate the interplay between size and physiological regulation of carbon uptake dur-
5 ing natural phytoplankton blooms, and the impact on carbon acquisition and species selection in the future ocean.

During the post-bloom phase, species composition was quite similar in all CO_2 treatments indicating that factors other than CO_2, possibly grazing, were influencing species distribution at this time.

10 ## 4.3 Potential consequences for carbon cycling

Particle size distribution and phytoplankton species composition were rather similar in the present day and the future CO_2 treatment, and clearly different from the past CO_2 treatment. This is in accordance with the non-linear relationship between CO_2 concentration and primary production, indicating that the selective pressure towards a larger
15 relative surface area, i.e. cell size reduction, for species relying on CO_2 uptake, whatsoever, increase with decreasing CO_2. As mentioned above, we do not have information about potential enhancement of carbon uptake due to CCM operations in phytoplankton during this study. In order to estimate potential differences in carbon acquisition within the three CO_2 treatments due to the observed differences in cell size, we can
20 only estimate the treatment effect on the diffusive supply of CO_2. To estimate the spectral distribution of CO_2 supply during the bloom phase in the mesocosms, we calculated theoretical rates of CO_2 supply to the cell according to the simplified model of Riebesell et al. (1993) (Fig. 7); see also Gavis and Ferguson (1975) and Wolf-Gladrow and Riebesell (1997) for further information. In alteration to Riebesell et al. (1993) CO_2-
25 supply rates were calculated for each size class from 2 μm ESD to 60 μm ESD using the average observed CO_2 concentrations during the "bloom-period", i.e. 22.34, 14.28 and 8.49 μmol kg^{-1} for the future, present day and past CO_2 treatment, respectively.

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A conversion factor (ak) of 400 was assumed, accounting for the $HCO_3^--CO_2$ equilibrium at the observed pH- and temperature range. The half-saturation constant (Km) was fixed to $10 \, \mu mol \, kg^{-1}$, assuming that this is a representative value for a mixed phytoplankton community of diatoms, coccolithophores and *Phaeocystis* spp. However, varying Km from 0.5 to 20 had only little effect on the estimates for CO_2 fluxes (<0.1%) in our model. To calculate the maximum CO_{2-} supply rate ($V_{max}=\mu_{max}\times Q_c$), the maximum growth rate of cells (μ_{max}, d^{-1}) was calculated with a parameterization that scales with cell volume (V, μm^3): $\mu_{max}=a(V)^b$; with $a=5.37$, $b=-0.25$ after Irwin et al. (2006); the carbon cell quota (Qc; $pg \, C$) was calculated using $Q_c=d(V)^e$, with $d=0.436$, $e=0.863$ after Verity et al. (1993). The results of these calculations show that the spectral distributions of total diffusive CO_2-supply during the time of the bloom were different in the three CO_2 treatments (Fig. 8). With the exception of the very the low size range (<4 μm) the estimated total CO_2-supply at all size classes was higher in the present day and future CO_2 treatment than in the past. Only at particle sizes <4 μm, the higher abundance of particles in the past CO_2 treatment could partially compensate for the lower supply rates per cell. Integration over the size range 2–60 μm ESD yielded similar values for potential CO_2-supply for the future and present day CO_2 treatment with $100 \, \mu mol \, h^{-1} \, kg^{-1}$, and a much lower value for the past CO_2 treatment with $46 \, \mu mol \, h^{-1} \, kg^{-1}$. It has to be emphasized that these rates address only the aspect of diffusive flux of CO_2 to the cells. Averaged rates of primary production during this experiment yielded much lower values (Egge et al., 2007[1]). Nevertheless, our calculations indicate that the total supply of cells with CO_2 was lowest in the past treatment despite the strong increase in the abundance of small cells, whereas the present day and future CO_2 treatment may have been equally productive despite the lower abundance of particles and autotrophic cells in the latter. A potentially higher CO_2-supply

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[1]Egge, J. K., Thingstad, T. F., Engel, A., and Riebesell, U.: Primary production during nutrient-induced blooms at elevated CO_2 concentrations, Biogeosciences Discuss., submitted, 2007.

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of cells in the future and present day CO_2 treatment is in accordance with earlier observations obtained during PeECE I, showing that the ΔDIC:Δ cell ratio increased with CO_2 concentration (Engel et al., 2005).

It is interesting to note that neither the potential differences in CO_2 supply nor the structural differences in the size spectra and in the phytoplankton community composition were reflected in the standing stocks of POC and PON. One might argue that PON production was rather related to the supply of inorganic nitrogen than to the availability of carbon, as inorganic nitrogen became exhausted in all mesocosms during the bloom development. Then, however the smaller cells in the past CO_2 treatment should have contributed to PON in a higher proportion. In fact, Verity et al. (1993) showed that the scaling exponent for the increase of nitrogen and carbon with cell volume is less than 1, and thus the volume of cells increases faster with size than the concentration of elemental components. Moreover, the scaling exponent for nitrogen is lower than for carbon leading to an increase of C:N ratios with cell size. However, estimates for the carbon and nitrogen content of cells vary even for cultures of the same species (Montagnes et al., 1994) and may not be representative for particles encountered during this study.

Assuming that CO_2-supply rates were potentially higher in the present day and future CO_2-treatments, and assuming that a higher supply with CO_2 resulted in higher carbon uptake rates, the fate of this excessive carbon remains unclear. Dellile et al. (2005) and Engel et al. (2005) suggested that carbon exudation and formation of extracellular organic particles, such as transparent exopolymer particles (TEP), as well as subsequent differential aggregation and settlement of organic matter may represent a potential pathway for a CO_2 depended sink for carbon. In fact, Engel et al. (2004) observed higher per cell production of TEP at high CO_2 during PeECE I. TEP concentrations determined during PeECE II also indicate higher production with increasing CO_2 (data not shown). Coccolithophores as well as diatoms are known to produce copious amounts of TEP (Passow, 2002; Engel et al., 2004). A species shift towards these phytoplankton groups may therefore also contribute to higher TEP production at present day and

future CO_2 concentrations.

4.4 Potential consequence for ecosystem functioning

Structural changes in the size distribution of particles were observed during this meso-com experiments, together with changes in the composition of the phytoplankton community. Phytoplankton species responded to changes in CO_2 in way that cannot be explained with a single general scaling law (Enquist et al., 1998; Belgrano and Brown, 2002). Rather, our observed CO_2 response suggests a complex interplay between a variety of scaling effects: 1) Pico- and small nanoplankton cells with a large surface-to-volume ratio are efficient in taking up resources, of which only a small fraction is needed for enzymes involved in C-fixation. These cells have a potential advantage under low substrate and low CO_2 conditions but are susceptible to grazing by small protozoans and micro-zooplankton; 2) Large phytoplankton cells have a small surface-to-volume ratio and are less competitive in terms of resource uptake, but they can allocate more luxury resources that may allow them to better compensate environmental changes (e.g. better acclimation to varying environmental factors). Their larger size can moreover be advantageous to escape micro-zooplankton grazing; 3) Intermediate-sized nano-phytoplankton have to find a balance between resources needed purely for growth, those that enhance physiological acclimation, and those resources that support predation defence. Thus, intermediate-sized nano-phytoplankton have no obvious advantage when it comes to escape grazing pressure, but also with respect to resource uptake. Instead, they rely on a fine balance (trade-off). However, exceptions may be given for species growing in chains, colonies or filaments, such as *Phaeocystis* and diazotrophic cyanobacteria.

Due to the structural change of the phytoplankton community, effects of CO_2 can potentially be transferred to higher trophic levels. During this experiment, CO_2-sensitivity was found within a size spectrum that is rather narrow compared to the total phytoplankton size range (i.e. $1–5\times10^3\,\mu m$). Nevertheless, the sensitive size range overlapped with those inherent to the microbial food web of pico- and nano-plankton. The

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microbial food web comprises a tight linkage between trophic interactions and DOM utilisation (Azam et al., 1983). Therefore, CO_2 related changes in the size distribution of phytoplankton involved in the microbial food web can be anticipated to also affect DOM quality and grazing response of micro-zooplankton.

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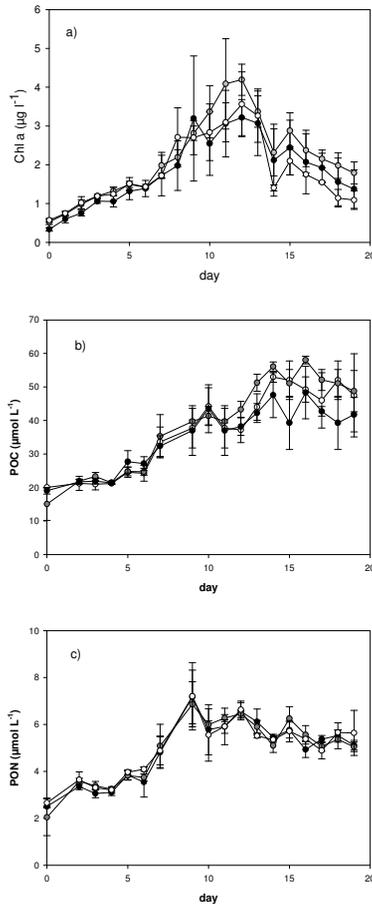
Fig. 1. Temporal development of Chl-*a*, **(a)**, POC, **(b)**, and PON, **(c)**, concentrations as averaged for the three mesocosms in the future, present and past CO$_2$ treatment, respectively. Error bars denote ±1 SD. Open circles: past, grey circles: present, and solid circles: future treatment.

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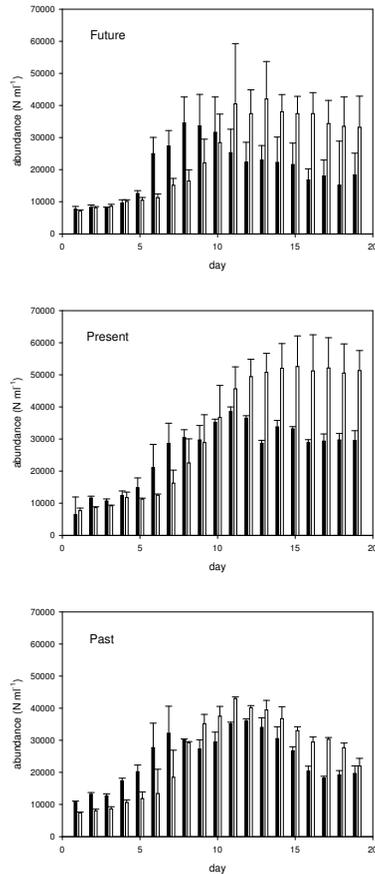
Fig. 2. Temporal changes in the average total abundance of autotrophic cells (solid bars) and total particles (open bars) as determined by Flow Cytometry and Coulter Counter, respectively, averaged for the future, present and past CO$_2$ treatment, respectively. Error bars denote ±1 SD.

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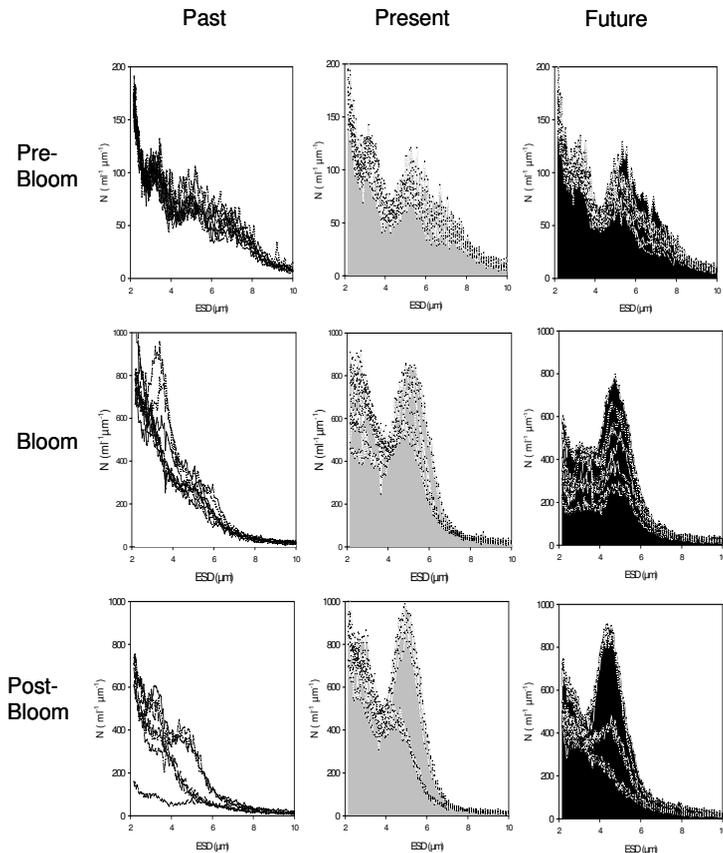
Fig. 3. Spectral distribution of Coulter Counter particles in the size range 2–10 μm during the pre-bloom, bloom and post-bloom phases of the experiments for the three different CO$_2$ treatments. Figures show the spectral distributions of the three mesocosms of each treatment during days 1–3 in the pre-bloom, and days 18–20 in the post-bloom phase. For the bloom phase, the time span includes the day of Chl-*a* maximum for each mesocosm and ±1 day.
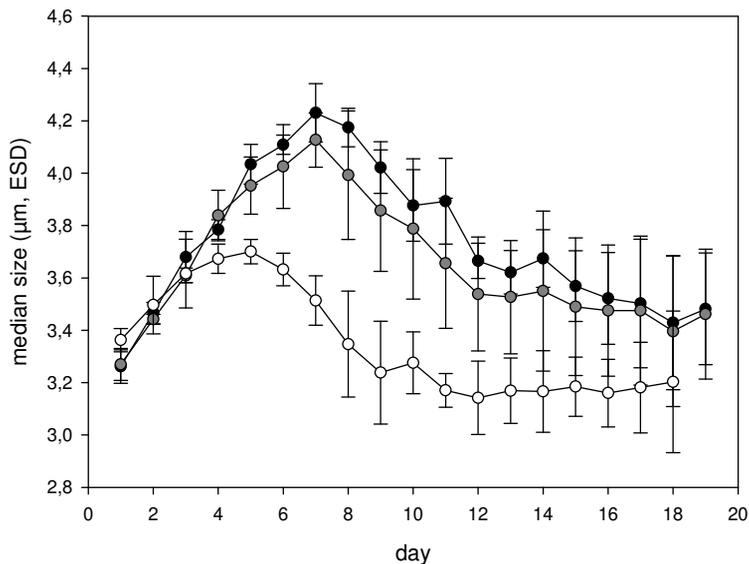
Fig. 4. Median size of Coulter Counter particles in the size range 2–60 μm ESD, averaged for three mesocosms per CO$_2$ treatment over the course of the experiment. Open circles: past, grey circles: present, and solid circles: future treatment. Error bars denote ±1 SD.

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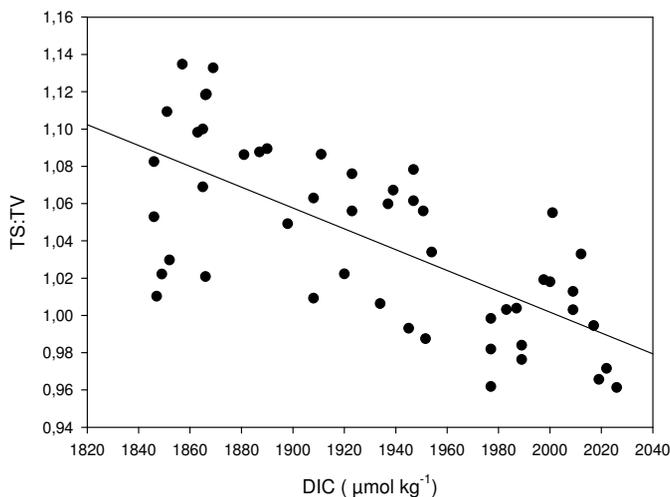
Fig. 5. The total surface (TS) to total volume (TV) ratio of particles determined with the Coulter Counter in the size range 2–60 μm ESD was significantly related to the concentration of DIC in the seawater (p<0.001). Data: bloom phase of each mesocosm; n=50.
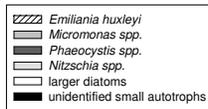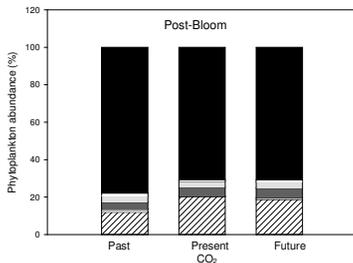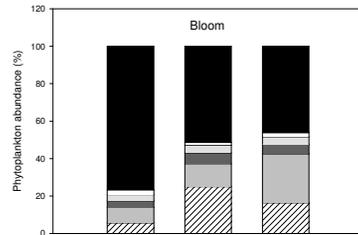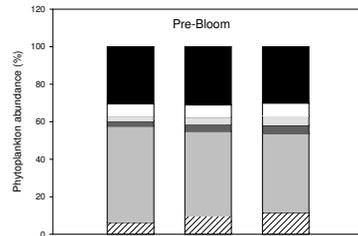
Fig. 6. Relative composition of the phytoplankton community in the size range 1.5–30 μm during the different phases of the experiment and separated for the three CO$_2$ treatments. Data are averages of three mesocosms per treatment calculated for days 1–3 in the pre-bloom, and days 18–20 in the post-bloom phase. For the bloom phase, averages were calculated from the data of the day of Chl-*a* maximum for each mesocosm and ±1 day. Species: 1. *Micromonas* spp., 2. *E. huxleyi*, 3. unidentified small autotrophs, 4. "large" diatoms, 5. *Phaeocystis* spp., 6. *Nitzschia* spp.
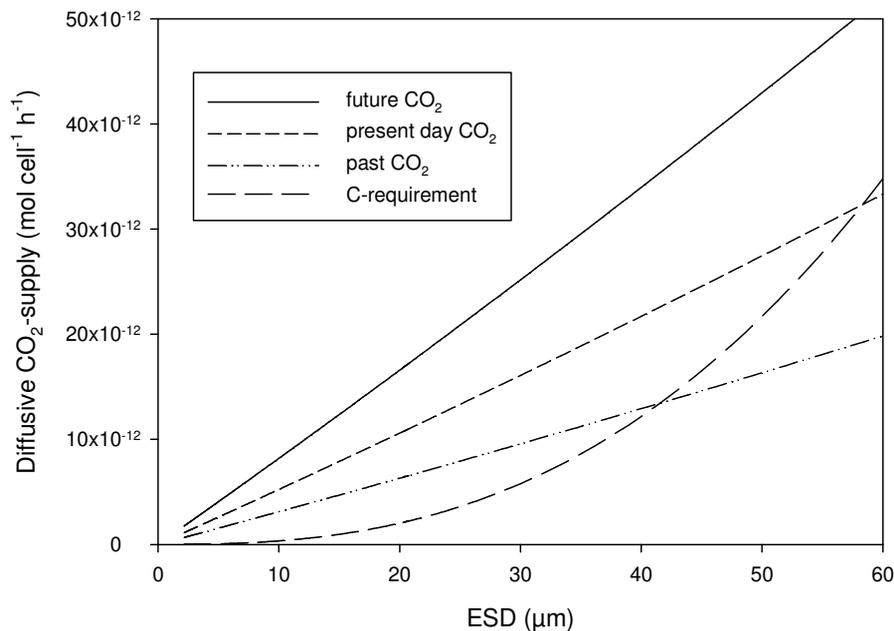
Fig. 7. Theoretical rates for the diffusive CO$_2$-supply to the cell during the peak of the bloom for the different CO$_2$ treatments as a function of cells size. The dashed line indicates the theoretical carbon requirement for maintaining maximum cell quota at a growth rate of $1\,\mathrm{d}^{-1}$. Further information is given in the text.

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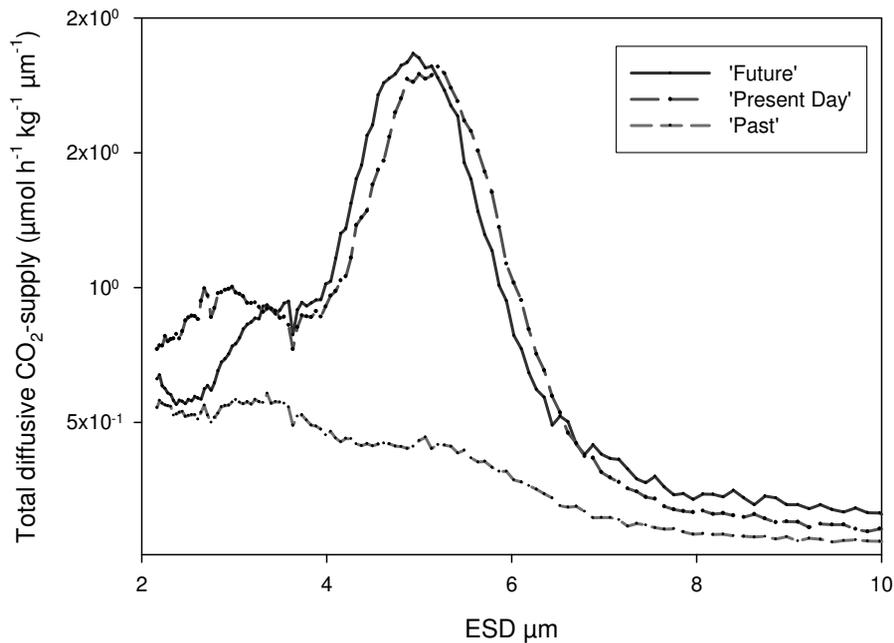
Fig. 8. Spectral distribution (2–10 μm) of total diffusive CO$_2$ supply calculated for the peak of the bloom in the three different CO$_2$ treatments.