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Dynamics of dimethylsulphoniopropionate and dimethylsulphide under different CO_2 concentrations during a mesocosm experiment

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Abstract

We investigated the potential impact of seawater acidification on the concentrations of dimethylsulfide (DMS) and dimethylsulfoniopropionate (DMSP), and the activity of the enzyme DMSP-lyase during a pelagic ecosystem CO_2 enrichment experiment (PeECE III) in spring 2005. Natural phytoplankton blooms were studied for 24 days under present, double and triple partial pressures of CO_2 (pCO_2; pH=8.3, 8.0, 7.8) in triplicate 25 m^3 enclosures. The results indicate similar DMSP concentrations and DMSP-lyase activity patterns for all treatments. Hence, DMSP and DLA do not seem to have been affected by the CO_2 treatment. In contrast, DMS concentrations showed small but statistically significant differences in the temporal development of the "present" versus the high CO_2 treatments. The "present" enclosures had higher DMS concentrations during the first 10 days, after which the levels decreased earlier and more rapidly than in the other treatments. Integrated over the whole study period, DMS concentrations were not significantly different from those of the double and triple pCO_2 treatments. Pigment and flow-cytometric data indicate that phytoplanktonic populations were generally similar between the treatments, suggesting a certain resilience of the marine ecosystem under study to the induced pH changes, which is reflected in DMSP and DLA. However, there were significant differences in bacterial community structure and the abundance of one group of viruses. The amount of DMS accumulated per total DMSP or chlorophyll-*a* differed significantly between the present and future scenarios, suggesting that the pathways for DMS production or bacterial DMS consumption were affected by seawater pH.

1 Introduction

Dimethylsulphide (DMS) is a volatile sulfur compound produced from the algal secondary metabolite dimethylsulfoniopropionate (DMSP) by complex biotic interactions in marine ecosystems (Stefels et al., 2007). DMS is the main natural source of sul-

fate aerosol to the atmosphere and the major route by which sulfur is recycled from the ocean to the continents. The particulate atmospheric oxidation products of DMS can act as cloud condensation nuclei and thereby affect the radiative properties of the atmosphere by reflecting solar radiation (Charlson et al., 1987).

The physiological roles of algal DMS and DMSP are not fully understood. DMSP is a compatible solute with multifunctional properties that is synthesized by marine phytoplankton for osmoregulation and cellular cryoprotection (Stefels, 2000). DMSP and its cleavage products DMS and acrylate have been suggested to serve as antioxidants under light or nutrient stress (Sunda et al., 2002), and to act as a chemosensory and chemotactic compound (Nevitt, 1995; Zimmer-Faust et al., 1996; Wolfe, 2000; Steinke et al., 2006). Both DMS and DMSP may also play a role in chemical defense mechanisms (Wolfe et al.,1997; Strom et al., 2003).

The production of DMSP is strongly dependent on the species composition of the marine ecosystem under investigation. Some phytoplankton groups, such as the haptophytes, are prolific producers of DMSP with high DMSP/cell ratios (Keller et al., 1989). The haptophyte coccolithophore *Emiliania huxleyi* also contains DMSP-lyase isozymes (Steinke et al., 1998) and is able to enzymatically cleave DMSP to DMS. Other haptophytes such as *Phaeocystis* and dinophytes also produce high concentrations of DMSP but many other algal taxa are poor DMSP-producers (Liss et al., 1994). Intracellular DMSP is released to the water during cell lysis caused by grazing (Dacey and Wakeham, 1986), or due to natural mortality and after viral infection (Malin et al., 1998). Once in solution, DMSP can be utilized by many bacteria as a sulfur, carbon or energy source via catabolic demethylation to 3-methylmercaptopropionate and 3-mercaptopropionate (Kiene and Linn, 2000; Howard et al., 2006). Bacteria and algae have also been shown to enzymatically cleave DMSP to DMS and acrylate (Kiene, 1993; Ledyard and Dacey, 1996; Stefels and Dijkhuizen, 1996; Steinke and Kirst, 1996) and novel evidence suggests DMSP-dependent DMS-production without the release of acrylate (Todd et al., 2007). DMS can be used as a metabolite by bacteria (Vila-Costa et al., 2006), photochemically degraded at the sea surface (Brimblecombe and Shooter, 1986; Kieber

et al., 1996), or transferred to the atmosphere (Liss and Slater, 1974). Since several biological components of the marine microbial food-web add to the physico-chemical processes that are involved in the production and consumption of DMSP and DMS, the concentrations of both may be affected by changes in environmental conditions. Thus, DMS could serve as a sensitive indicator to human-induced climate change.

Ocean acidification is one of the effects of increased anthropogenic CO_2. In the past 200 years, the oceans have absorbed approximately half of the CO_2 emitted by human activities such as fossil fuel burning and cement manufacturing (Sabine et al., 2004). This uptake of CO_2 has led to changes in the chemical equilibrium of the seawater and to a reduction of the pH of the ocean surface waters by 0.1 units. If emissions were to continue according to present trends, ocean surface pH could decrease by 0.3–0.5 units by the end of the 21st century. This is equivalent to a three fold increase of the concentration of H^+ ions in the surface ocean (Caldeira and Wickett, 2005). The impacts of ocean acidification on marine organisms and ecosystems are still poorly understood. Laboratory experiments and field studies indicate that acidification will adversely affect calcification (Royal Society, 2005; Kleypas et al., 2006), a process by which marine organisms fabricate shells and plates from calcium and carbonate ions. Coccolithophorids, such as *E. huxleyi*, are one of the phytoplanktonic groups expected to be strongly affected by ocean acidification (Riebesell et al., 2000). *E. huxleyi* is abundant in temperate oceans and is a prolific producer of DMS (Keller et al., 1989; Holligan et al., 1993; Malin et al., 1993). It is possible that the intracellular production of DMSP or its direct conversion to DMS by *E. huxleyi* DMSP-lyases is affected by ocean acidification. Additionally, as mentioned above, oceanic DMS production is a result of complex interactions within the marine food-web. Consequently, ocean acidification may affect DMS concentrations and fluxes by altering one or more of the various pathways or impacting some of the species involved. Ocean acidification may therefore affect the feedback of DMS on climate via aerosol formation, as described by the CLAW-hypothesis (Charlson et al., 1987). Previous studies (Avgoustidi et al., 2007[1])

[1] Avgoustidi, V., Joint, I., Nightingale, P. D., Steinke, M. Turner, S. M., and Liss, P. S.:

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showed reduced DMS concentrations under high CO_2 in both field and laboratory studies. If these results can be extrapolated to the globe, reduced DMS emissions could lead to a significant positive feedback on global warming.

Here, we present the concentrations of DMS, DMSP and DMSP-lyase activities (DLA) during a mesocosm study in a Norwegian Fjord in May and June 2005. Our goal was to investigate differences in DMS dynamics under elevated CO_2 and to address factors that may result in altered DMS dynamics. Furthermore, we investigate the relevance of our results with respect to global climate change and its impact on global DMS fluxes.

2 Materials and methods

2.1 General experimental set-up

The experiment was conducted at the Norwegian National Mesocosm Center at the Espeland Marine Biological Station, University of Bergen (Norway) in May and June 2005. The set-up consisted of 9 polyethylene enclosures (ca. 25 m^3, 9.5 m water depth) moored to a raft in the Raunefjord (60.3° N, 5.2° E): 3 bags with present day pCO_2, hereafter referred to as "present" (P, 350 ppmv partial pressure of CO_2), 3 bags with double pCO_2, referred to as "future" treatments (F, 700 ppmv) and 3 bags with triple pCO_2, referred to as "far future" treatments (FF, 1050 ppmv). These bags were simultaneously filled with unfiltered fjord water pumped from a depth of 12 m. Fresh water (0.6 m^3) was mixed into the upper 5 m of the mesocosm bags to stratify the water column. The future and far future bags were aerated with CO_2 enriched air, until the water pCO_2 reached the target values (day 0), the present bags were aerated with ambient air. To allow biological processes to alter water pCO_2, no further adjustments were carried out after day 1. All mesocosm bags were covered with transparent hoods of ethylene tetrafluorethylene foil (Foiltec, Bremen, Germany), which allowed transmission of

Dimethyl sulphide production in a double-CO_2 world, in preparation, 2007.

95% of incoming light intensity for the complete solar spectrum. The headspaces underneath the hoods were kept at target pCO_2 by flushing them with CO_2-enriched air (23–35 L min^{-1}). A phytoplankton bloom was triggered via the addition of nutrients on day 0 (16 May 2005; 0.7 μmol L^{-1} PO_4, 15 μmol L^{-1} NO_3) and the bloom was studied over a period of 24 days. Throughout the study period, the upper 5m of the water column were gently mixed by means of an airlift system. Further details of the set-up and procedures can be found in (Engel et al., 2005; Schulz et al., 2007[2]).

2.2 Sampling for sulfur compounds

Samples from all nine mesocosms were taken daily at 10:30 h, simultaneous with other measurements conducted during PeECE III. Bubble-free sampling was carried out with nine 5 L polyethylene aspirators. Prior to sampling, all aspirators were thoroughly rinsed first with natural fjord water and then with water from the respective mesocosms. The mouths of the aspirators were covered with a 200 μm mesh in order to exclude mesozooplankton grazers and taps were left open to release air during sampling. The aspirators were then inverted and slowly immersed through the water surface to a depth of approximately 0.3 m. A minimum of 3 L of water was sampled before closing the taps, slowly turning over and capping off the aspirators and transporting them to a cold-room where the samples were stored at in situ water temperature (9–11.5°C) and in dim light. Sub-samples were taken using Teflon tubing and gas-tight syringes (20 mL) after slowly rotating the aspirators to re-suspend particulate matter.

2.3 Quantification of sulfur compounds

Particulate DMSP ($DMSP_p$):

Slow syringe filtration was used to filter 5 to 20 mL of sample through 25 mm glass-fibre filters (Whatman GF/F). The filtrate was directly injected into a purge vessel for

[2] Schulz, K., Riebesell, U., et al.: Build up and decline of organic matter during PeECE III, Biogeosci. Discuss., 2007.

the analysis of DMS (see below). Thereafter, the filters were folded and placed into glass vials containing NaOH, using 3 mL of 500 mmol L^{-1} NaOH in 4 mL screw-capped vials (days 1 to 4) or 13 mL of 500 mmol L^{-1} NaOH in 20 mL crimp-sealed vials (days 5 to 24). The alkaline hydrolysis of DMSP resulted in equimolar quantities of DMS. Vials were sealed immediately with Teflon-coated septa, stored in the dark and transported to our laboratory at the University of East Anglia (UEA). The headspace analysis of DMS resulting from $DMSP_p$ cleavage commenced with a 24 h incubation of the vials at a standard temperature of 30°C before manual injection of 50 to 200 μL of headspace for quantitative analysis of DMS using gas chromatography and flame-photometric detection (Shimadzu GC-2010 with 30 m×0.53 mm CP-Sil 5CB capillary column). DMS standards for calibration were prepared using commercial DMSP standard (Centre for Analysis, Spectroscopy and Synthesis (CASS), University of Groningen Laboratories, The Netherlands) added to vials containing 3 or 13 mL NaOH at a final concentration of 0.3 to 3 μmol DMS L^{-1}. The detection limit for a 20 ml sample was about 2 nmol L^{-1} DMSP. The analytical error was less than 12%, as estimated from a comparison of replicate samples (n=16).

DMS: After filtration for $DMSP_p$, 5 to 18 mL of the filtrate was used for DMS analysis. The analytical volumes for the DMS measurements were adjusted during the course of the experiment to accommodate changes in concentration. DMS measurements were conducted within 2 h of sampling using the gas chromatographic system described above, in combination with a purge-and-trap system for cryogenic enrichment of DMS at −150°C (details in Turner et al. 1990). Calibrations were carried out every 3 – 4 days with DMSP stock solution equivalent to 0.3 to 24.3 nmol L^{-1} and addition of NaOH to more than 500 mmol L^{-1}. The detection limit of the above described gas chromatographic system was less than 0.3 nmol L^{-1} DMS. The analytical error was 6%, as estimated from replicate calibration standards (n=69).

Dissolved DMSP ($DMSP_d$): After purging the water sample for DMS analysis was completed, 4 to 13 mL of purged, de-gassed sample was transferred into 20 mL vials and brought to a volume of 13 mL with MilliQ water for analysis of $DMSP_d$. Samples

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were adjusted to 500 mmol L^{-1} NaOH by adding 684 μL of 10 mol L^{-1} NaOH. Vials were immediately capped with Teflon-coated crimp seals and stored in the dark prior to analysis. Samples were incubated at 30°C for 24 h before manual injection of 200 μL of headspace for the analysis of DMS using the gas chromatographic system described above. DMS concentrations were quantified via the addition of DMSP standard to 13 mL 500 mmol L^{-1} NaOH at a final concentration of 6 to 60 nmol L^{-1}. Detection limit in 13 mL of sample was about 1.3 nmol L^{-1} $DMSP_d$.

Total DMSP ($DMSP_t$): Because of concerns about potential filtration artifacts (Kiene and Slezak, 2006) we also considered total DMSP ($DMSP_t$) concentrations for our analyses. $DMSP_t$ was calculated as the sum of $DMSP_d$ and $DMSP_p$ concentrations.

DMSP- lyase activity (DLA): Measurements of DMSP-lyase activity were conducted using headspace measurements of DMS using the methods described in (Steinke et al., 2000; Steinke et al., 2007). In brief, 250 to 300 mL of seawater was filtered through polycarbonate filters of 47 mm diameter and 2 μm pore size (Whatman Nuclepore). The filters were folded twice and placed into cryo-vials before snap-freezing in liquid nitrogen and storage at −80°C. DLA samples were transported on dry ice to our laboratory at UEA. The DMSP-lyase was extracted using sonication on ice with a 3 mm sonotrode (5 bursts of 5 s at 5 W) into 1.8 mL of 0.3 mol L^{-1} sterile BTP buffer (1,3-bis[tris(hydroxymethyl)methylamino]propane) that was amended with 0.5 mol L^{-1} NaCl at pH 8.2. Assays were conducted with 100 to 295 μL of the crude extract and linear production of DMS was quantified at 30°C for 15–45 min after the addition of buffer and 5 μL of 1.2 mol L^{-1} DMSP stock (t=0) that was adjusted to pH 6.2 with NaOH to a total volume of 300 μL (final DMSP concentration was 20 mmol L^{-1} and final pH was 8.2).

2.4 Additional measurements

Chlorophyll-*a* (chl-*a*) and diagnostic pigment distributions were determined using HPLC analysis methods. CHEMTAX (Mackey et al., 1996) was used to derive the fraction of chl-*a* attributable to the dominant phytoplankton groups, based on the pigment distri-

bution and the pigment ratios of phytoplankton taxa present in situ. Counts of *Emiliania huxleyi* cells and other phyto-, bacterio- and virioplankton were conducted using flow cytometric methods (Becton-Dickinson, FACSCalibur). Flow cytometry has a size cut-off of approximately 30 μm and was used to count smaller organisms. The partial pressure of CO_2 was quantified using a Neil system shower equilibrator pCO_2 instrument (as described in Wanninkhof and Thoning, 1993).

3 Results

3.1 DMS

Figure 1 shows DMS concentrations for the 3 triplicates of each treatment (Fig. 1a–c) and the mean DMS concentrations for the 3 treatments (Fig. 1d). At the beginning of the experiment, DMS concentrations were low in all replicates due to the low concentrations of DMS in the original fjord water and possible loss of DMS during the aeration procedure. After day 0, DMS concentrations increased in all treatments, with the "present" bags accumulating slightly more DMS than the F and FF treatments. On day 10 the maximum in DMS concentration was reached in P, with an average value of 29.5 nmol L^{-1}. This peak was followed by an abrupt, steep decline, which was measured consistently in all P triplicates. In the averages of the F and FF treatments, DMS concentrations reached a plateau between day 10 and day 12, with maximum average concentrations of 27.4 nmol L^{-1} (F) and 25.3 nmol L^{-1} (FF). The slope of the DMS decline was rather gentle in the future and far future treatments. A two-way analysis of variance with log transformed data for the 3 treatments shows that the temporal development of DMS between the 3 treatments was significantly different (Fig. 1d; $F = 8.157$, $df = 2$, $\sigma < 0.001$). The time integrated averages of DMS (days 0–18) show that over the whole duration of the experiment, 25% more DMS was produced in FF and 14% more DMS in F than in P. In contrast to the findings by Wingenter et al. (2007), we did not find our difference to be statistically significant (One-way ANOVA, $F = 1.799$,

$df = 2$, $\sigma = 0.244$). Air concentrations of DMS were in phase with our observed water measurements (Sinha et al., 2007; Wingenter et al., 2007).

3.2 DMSP$_p$, DMSP$_d$, DMSP$_t$

The differences in DMS concentrations between present and enhanced pCO_2 treatments are not reflected in the particulate DMSP concentrations (Fig. 2a). This was also true for the dissolved fraction (Fig. 2b) and for total DMSP (Fig. 2c). As all replicates showed very similar concentration patterns, we only show the mean concentrations for each treatment. At the beginning of the experiment, DMSP$_p$ concentrations were below 50 nmol L^{-1} in all treatments. After day 4, DMSP$_p$ rapidly increased in all treatments, and were maximal on day 10 in P (366 nmol L^{-1}) and F (370 nmol L^{-1}) and on day 12 in FF (415 nmol L^{-1}). Thereafter, DMSP$_p$ declined in all treatments. DMSP$_d$ concentrations remained constant at around 20 nmol L^{-1} until day 8 of the experiment, when it increased for all treatments. DMSP$_d$ concentrations peaked on day 12 in P (86 nmol L^{-1}), on day 14 in F (72 nmol L^{-1}) and on day 13 in FF (96 nmol L^{-1}), whereafter DMSP$_d$ decreased in all treatments. DMSP$_t$ concentrations increased steadily after day 4 and reached a first peak on day 10, with average DMSP$_t$ concentrations of 374 nmol L^{-1} in P, 405 nmol L^{-1} in F and 410 nmol L^{-1} in FF. DMSP$_t$ concentrations in P and F declined after day 10 in a similar fashion. In contrast, DMSP$_t$ concentrations showed a brief increase in the FF treatments, reaching a maximal average concentration of 493 nmol L^{-1} on day 13 before declining.

3.3 DMSP-lyase activity

The measured DMSP-lyase activity (DLA) is comprised of the activity of DMSP-lyase from algae and attached bacteria and has been analyzed without replication for each treatment (Fig. 2d). Due to our choice of filter (pore size of 2 μm), the potential contribution of many non-attached bacteria to DMSP-lyase activity was not included. We

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show data from mesocosm bags 2 (FF), 5 (F), and 8 (P), because most other measured parameters from collaborating groups are available for these bags. DLA peaked on day 6 for the present (4354 nmol $L^{-1}h^{-1}$), and on day 8 for F and FF treatments with values of 5116 and 3801 nmol $L^{-1}h^{-1}$, respectively. After day 8, DLA decreased gradually in all treatments, until a minimum in activity was reached in all bags on day 15. After day 18, DLA increased rapidly in all treatments and reached a second maximum on day 20, with 4952 nmol $L^{-1}h^{-1}$ for P, 2590 nmol $L^{-1}h^{-1}$ for F and 3849 nmol $L^{-1}h^{-1}$ for FF treatments.

3.4 Ecosystem composition

All bags showed similar chl-*a* concentrations (Fig. 3a), with chl-*a* being slightly lower in P than in F and FF. The maximum of average chl-*a* occurred on day 10 in all treatments. A succession of different phytoplankton taxa occurred during the course of the experiment (Riebesell et al., 2007). Between days 6 and 10, when most of the DMS was accumulated, the bloom was dominated by diatoms and haptophytes, including lithed *E. huxleyi* cells (Fig. 3b). During the whole study period, prasinophytes contributed up to 20% to total chl-*a*. Towards the end of the bloom, after day 18, dinoflagellate and *Synechococcus* species contributed significantly to total chlorophyll (Riebesell et al., 2007). A similar succession of species was observed in all treatments.

3.5 Relationships between DMS, $DMSP_t$, chlorophyll-*a* and *E. huxleyi*

We used Spearman rank correlation to study temporal correlation between DMS, $DMSP_t$, chl-*a* and *E. huxleyi* abundances. As a general trend, DMS, $DMSP_t$ and chl-*a* tended to be more closely correlated in F and FF than in P. $DMSP_t$ and chl-*a* were temporally correlated in all 3 treatments and over the whole duration of the experiment (n =16; P: r_s = 0.84, F: r_s = 0.92, FF: r_s = 0.86). DMS and chl-*a* were temporally correlated in all treatments (n = 16; P: r_s = 0.82, F: r_s = 0.91, FF: r_s = 0.89), as were DMS and $DMSP_t$ (n = 19; P: r_s = 0.80, F: r_s = 0.98, FF: r_s = 0.94). The lower corre-

lations in P in the latter two cases are due to the step decline of DMS concentrations in P after day 10. DMS and *E. huxleyi* numbers were well correlated in P (r_s = 0.79) and slightly less in F (r_s = 0.63) and FF (r_s = 0.61). Hence, rather than concluding that DMS concentrations of F and FF stayed elevated for a longer time, one may argue that DMS concentrations in P decreased earlier than in F and FF.

Figure 4 shows the ratios of DMS, $DMSP_t$ and chl-*a* against time. This figure both visualizes and summarizes the above described relationships. Constant parts in the graphs imply strong linear correlation and monotonously increasing/decreasing parts of the graphs imply temporal correlation, i.e. high Spearman values. Figure 4a shows the ratio of DMS to $DMSP_t$. Until day 10, all 3 curves follow a very similar trend. From day 10–16 there is a phase lag between the peaks of DMS and $DMSP_t$, manifested in the split up between the F, FF and P curves. Figure 4b shows the ratio of $DMSP_t$ to chl-*a*. During the whole experiment, there were no significant differences between treatments. This similar temporal development indicates that there were no major shifts in ecosystem composition that affected DMSP production and could have resulted in the differences in DMS concentrations between the 3 treatments. The seemingly large deviations after day 18 are due to low concentrations both in $DMSP_t$ and in chl-*a*. Due to the analytical uncertainty in measurements of both DMSP and chl-*a*, this type of analysis does not provide detailed insight into the role of small fluctuations in ecosystem composition or slight changes in cell quota or DMS exudation rates, which potentially could have an effect on DMS production. The ratio between DMS and chl-*a* showed significant differences between the treatments (Fig. 4c). Up to day 10 of the experiment DMS and chl-*a* concentrations co-varied for all 3 treatments. After day 10 and until day 18, significantly more DMS per chl-*a* was accumulated in the perturbed treatments, comparable to what was observed for the DMS and $DMSP_t$. As in the case of DMS and chl-*a*, DMS and *E. huxleyi* cell numbers were well in phase for the unperturbed P bags and showed a lag of 1–2 days between peaks in *E. huxleyi* numbers and peaks in DMS for the F and FF treatments (data not shown).

4 Discussion

Several previous mesocosm studies conducted at the same facility in Bergen report DMSP, DMS and chl-*a* concentrations under present CO_2 (Levasseur et al., 1996; Williams and Egge, 1998; Wilson et al., 1998; Steinke et al., 2007). The DMSP and DMS concentrations we found are within the range of concentrations found in previous mesocosm studies, but concentrations vary with respect to the boundary conditions of the experiments, i.e. they depend on the organisms dominating the bloom and the manipulations under which the system was investigated. The species composition reported from this experiment is typical for waters in the investigated region and the time of the year. However, temperature and light intensities were unusually low for May, which could have influenced the bloom development and species succession.

In contrast to a previous CO_2 enrichment study (Engel et al., 2005) conducted under very similar experimental conditions, neither HPLC pigment analyses nor flow cytometry detected significant phytoplankton species shifts between treatments. The ecosystem composition, bacterial and phytoplankton abundances and productivity, grazing rates and total grazer abundance and reproduction were not significantly affected by CO_2 induced effects (Riebesell et al., 2007; Egge et al., 2007[3]; Larsen et al., 2007[4]; Suffrian et al., 2007[5]; Carotenuto et al., 2007[6]). This finding suggests that the system under study was surprisingly resilient to abrupt and large pH changes.

[3]Egge, J.: Primary production at elevated nutrient and pCO_2 levels, to be submitted, Biogeosci. Discuss., 2007.

[4]Larsen, A.: Marine viral populations at elevated nutrient and pCO_2 levels, Biogeosci. Discuss., 2007.

[5] Suffrian, K., Simonelli, P., Antia, A., Putzeys, S., Carotenuto Y. and Nejstgaard J.: Phytoplankton-zooplankton grazing and growth interactions during the PeECE III mesocsom study (2005), to be submitted, Biogeosci. Discuss., 2007.

[6]Carotenuto, Y.: Feeding and reproduction of the copepod *Calanus finmarchicus* in nutrient-induced phytoplankton blooms under different CO_2 regimes: the Pelagic Ecosystem CO_2 Enrichment III (PeECE III) Mesocosm Experiment, Biogeosci. Discuss., 2007.

4.1 DMSP and DMS

The resilience of the system is well reflected in the canon of marine biogenic sulphur compounds. There were no differences in $DMSP_p$, $DMSP_d$, $DMSP_t$ or DLA and only small differences in the temporal development of DMS. These differences in DMS concentrations may be due to several factors, as discussed below:

A difference in ecosystem composition is one of the most plausible explanations for the differences in the temporal development of DMS. However, cell counts, HPLC pigment analysis (Riebesell et al., 2007) and flow cytometry data (Larsen et al., 2007[4]) show rather similar population patterns for all the treatments. Even though we could exclude major shifts in ecosystem composition to account for the differences in DMS, the effect of smaller shifts in species succession could not be studied in our measurements. Additionally, changes in algal physiology leading to altered exudation rates or changes in DMSP cell quota were not studied. Haptophytes such as *E. huxleyi* are high DMS producers and are expected to be affected by ocean acidification (Riebesell, 2004). Furthermore, haptophytes dominated the phytoplankton bloom in this experiment and are thus likely to have been important players in the production of DMSP and DMS during this experiment. Observed differences in *E. huxleyi* cell numbers (see Fig. 3b) could partly account for the differences in DMS concentrations between the treatments. Flow cytometry determines the number of lithed *E. huxleyi* cells. Changes in the fraction of unlithed or "naked" *E. huxleyi* could account for changes in DMS, as the DMS yield from DMSP could differ between naked and lithed cells. However, the fraction of unlithed cells is expected to be small and constant (A. Paulino, personal communication).

Grazing has been shown to play a crucial role in the production of DMS from phytoplanktonic DMSP (Wolfe and Steinke, 1996). In this experiment, there were no significant differences in the feeding, growth and reproduction parameters for copepods and in growth and grazing parameters for microzooplankton (Suffrian et al., 2007[5]). The only exception was a significant difference in the number of mollusc veliger larvae.

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However, the biomass of these larvae was relatively low and other zooplankton dominated the feeding in the mesocosm bags, so that this difference is unlikely to explain the difference in DMS production.

During the course of the experiment a statistically significant difference in the community structure of free-living bacteria (0.2–5.0 μm) was detected for the three different treatments (Allgaier et al., 2007[7]). Denaturing Gradient Gel Electrophoresis (DGGE) band pattern analysis showed that while the populations of the present and future treatments were similar to the fjord population, the free-living bacterial communities of the far future treatments diverged much more from the original population. Despite these clear differences in bacterial community structure, the DMS concentration patterns of FF and F were very similar. Currently, there is no quantitative evidence for an effect of pCO_2 on bacteria that degrade DMS or DMSP, but such an effect could lead to different DMSP or DMS consumption rates or to a different microbial DMS yield from DMSP, resulting in differences in DMS concentration patterns. The community structure of attached bacteria (>5.0 μm) did not exhibit statistical differences between the treatments.

R. Thyrhaug (personal communication, 2007) found a significant CO_2 effect on the abundance of a group of viruses identified by flow cytometry. During days 15–22, this group of viruses was ca. 40% more abundant in the present treatments than in F and ca. 66% more abundant in F than FF. The flow cytometric signature of this virus resembles signatures of several previously isolated viruses infecting nanoeukaryotes. Species in this group can produce DMSP (Keller et al., 1989) and viral infection can lead to significant production of DMS (Malin et al., 1998) and are likely to have played an important role in terminating the bloom during this experiment.

Taken together, processes related to bacterial and viral activities may explain part of the difference in amount and temporal structure of DMS that we observed.

[7] Allgaier, M., Riebesell, U., and Grossart, H. P.: Coupling of heterotrophic bacteria to phytoplankton bloom development at different pCO_2 levels: a mesocosm study, to be submitted, Biogeosci. Discuss., 2007.

4.2 DLA

In general, DLA was higher than previous measurements in *E. huxleyi* dominated waters in the North Atlantic and North Sea (Steinke et al., 2002a; Steinke et al. 2002b) and in a mesocosm experiment in 2003 (Steinke et al., 2007). No clear difference between the CO_2 treatments was observed. Coccolithophores such as *E. huxleyi* contain the enzyme DMSP-lyase and they were dominating the bloom during days 1–10. Hence, we speculate that a significant part of the measured DLA during days 1–10 is due to coccolithophorid or other planktonic DMSP. At the end of the bloom (day 18 to day 22), a dinoflagellate bloom occurred in the mesocosms (Riebesell et al., 2007). Some dinoflagellates contain high amounts of $DMSP_p$ per cell and can show high DMSP-lyase activity. The beginning of their bloom coincided well with the second increase in DLA after day 18. We speculate that a significant amount of the DMSP-lyase activity detected in this phase of the bloom may be due to dinoflagellates. It is likely that phytoplanktonic DMSP-lyase contributed to DMS production, but we cannot yet assess the importance of algal DLA for overall DMS accumulation in this study.

4.3 DMS and ocean acidification

The implications of our findings for the future global ocean and climate are still unclear. Firstly, the changes in pCO_2 studied here have been triggered abruptly from present values on day 0 to double and triple concentrations on day 2, without allowing the systems under study to fully acclimate or adapt. Future ocean acidification will proceed at a much slower rate and this temporal scale difference could potentially alleviate the consequences of ocean acidification. Secondly, blooms of the magnitude we observed in this mesocosm study are rare in the open ocean. $DMSP_t$ concentrations of 300–500 nmol L^{-1} and DMS concentrations of 40 nmol L^{-1} are untypical in the open ocean, where the 95 percentile of all measured DMS concentration is below 5 nmol L^{-1} (Kettle and Andreae, 2000). As the regions where DMS fluxes are most important are remote regions such as the Southern Ocean where chlorophyll is significanty lower, we cannot

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extrapolate our results to global scales at this point. Thirdly, mesocosms do not seem to respond in a consistent way to manipulations such as in CO_2 enrichment studies. We cannot confirm the finding of previous studies (Avgoustidi et al., 2007[1]) that DMS accumulation was significantly reduced under simulated seawater acidification. However, DMS concentrations varied between treatments in both studies. In particular, DMS proved to be one of the very few measured parameters that had a clear response to the CO_2 perturbation in this study.

5 Summary and conclusion

We studied DMS, $DMSP_p$ and $DMSP_d$ dynamics under 3 different pCO_2 conditions during a mesocosm experiment in Norway. There were no statistically significant differences in the temporal development of $DMSP_t$, $DMSP_p$ and $DMSP_d$ concentrations and in DLA, which hints at a certain resilience of the studied system to changes in pCO_2. However, we found differences in the temporal development of DMS concentrations. While DMS stayed elevated in the treatments with elevated pCO_2, we observed a steep decline in DMS concentration in the treatment with present pCO_2. As the ratio of DMS to DMSP varied strongly between treatments, but DMSP per chl-*a* did not, we hypothesize that the observed differences result from differences in DMS production or degradation mechanisms rather than from large shifts in community structure. Observed differences in bacterial community structure and viral abundances may play a role, but other mechanisms such as differences in exudation rates etc. cannot be excluded.

It is too early to draw conclusions regarding the importance of ocean acidification on the global sulphur cycle. This is only the third report that we are aware of that addresses changes in DMS dynamics under future CO_2 scenarios. As some marine trace gases appear to be sensitive to CO_2 enrichments (Wingenter et al., 2007) there is a need for further studies on the impact of ocean acidification on the production of climate-relevant gases such as DMS. Future studies should be conducted under open

ocean conditions using for example free-floating mesocosms, should focus on rate measurements as well as concentrations, and must include estimations of bacterial DMSP consumption rates in combination with detailed analyses of the cellular DMSP quota of algal taxa present in the investigated habitat. Only then will it be possible to separate physiological processes from the effect of trophic interactions on DMS dynamics and to assess possible implications for DMS fluxes under future climate change. Improving the understanding of DMS production and consumption under future pCO_2 will not only extend our understanding of the effects of ocean acidification on marine ecosystems but will also decrease the uncertainty in future model predictions of the number density of cloud condensation nuclei and the feedback of climate change on DMS.

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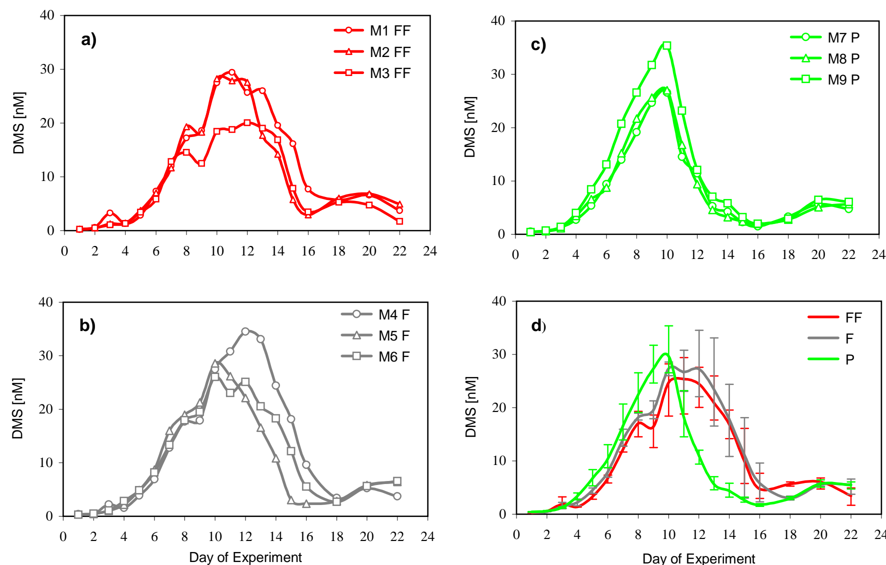

Fig. 1. DMS concentrations in nmol L^{-1} for the 3 replicates of each treatment **(a)** FF (Mesocosms M1-M3) **(b)** F (Mesocosms M4-M6) **(c)** P (Mesocosms M7-M9) and **(d)** averages for all 3 treatments with range bars indicating the spread of the data. Green lines show present (P), grey lines future (F) and red lines depict far future (FF) treatments with pCO_2 of 375 ppmv, 750 ppmv and 1150 ppmv, respectively.

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DMSP and DMS dynamics under different CO_2 conditions

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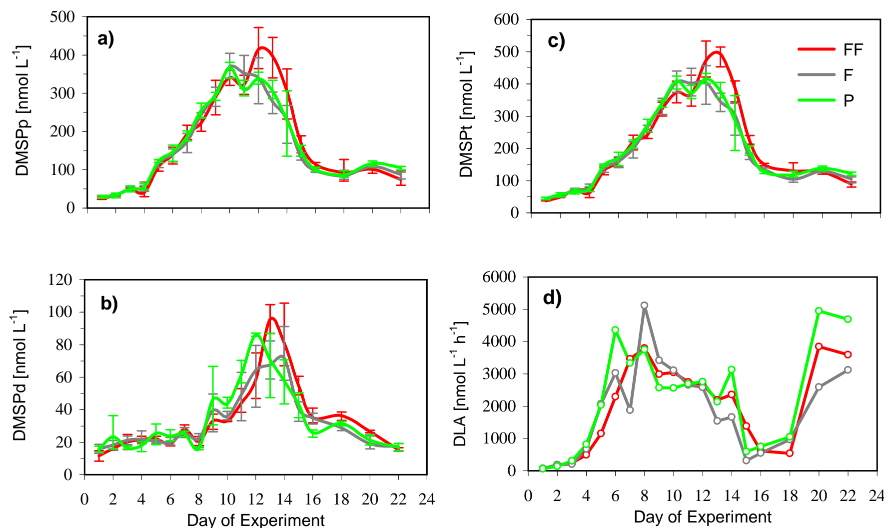

Fig. 2. Average **(a)** $DMSP_p$ in $nmol\,L^{-1}$, **(b)** $DMSP_d$ in $nmol\,L^{-1}$, **(c)** $DMSP_t$ in $nmol\,L^{-1}$ **(d)** DMSP-lyase activity (DLA) for selected bags 2 (P), 5 (F) and 8 (FF). Green lines show present (P), grey lines future (F) and red lines depict far future (FF) treatments with pCO_2 of 375 ppmv, 750 ppmv and 1150 ppmv, respectively. The values shown are average values for 3 replicate bags. Vertical bars indicate the range of the data.

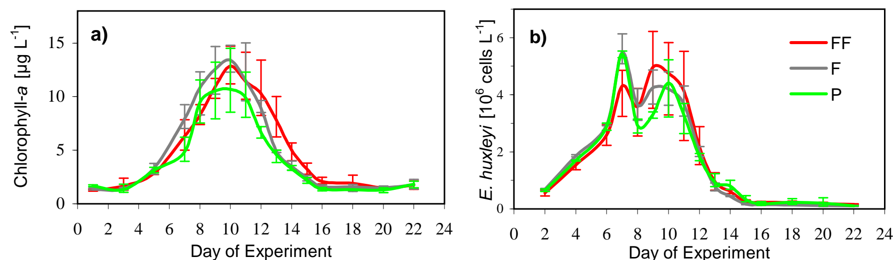

Fig. 3. **(a)** Chl-*a* in μg L^{-1} and **(b)** *E. huxleyi* abundance in 10^6 cells L^{-1} plotted as a function of time. Green lines show present (P), grey lines future (F) and red lines depict far future (FF) treatments with pCO_2 of 375 ppmv, 750 ppmv and 1150 ppmv, respectively. The values shown are average values for 3 replicate bags. Vertical bars indicate the range of the data.

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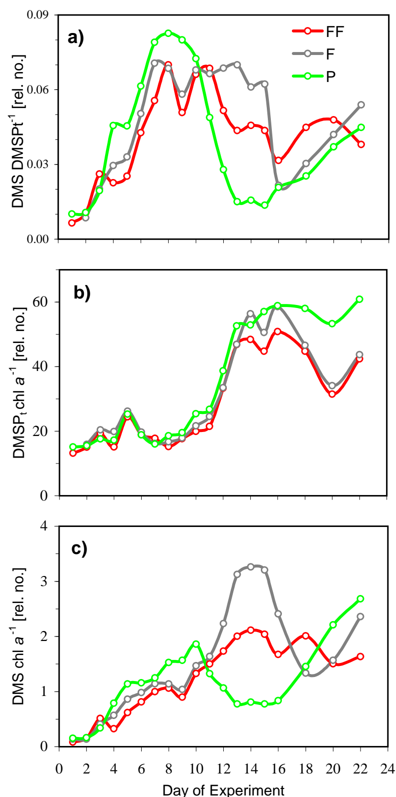

Fig. 4. Ratios of mean **(a)** DMS to $DMSP_t$ **(b)** $DMSP_t$ to chl-*a* in (nmol $^{-1}$ μg^{-1}) and **(c)** DMS to chl-*a* in (nmol $^{-1}$ μg^{-1}) for the present (P, green lines), future (F, grey lines) and far future (FF, red lines) treatments.