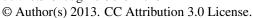
Biogeosciences, 10, 5619-5626, 2013 www.biogeosciences.net/10/5619/2013/ doi:10.5194/bg-10-5619-2013







## Preface

# "Arctic ocean acidification: pelagic ecosystem and biogeochemical responses during a mesocosm study"

U. Riebesell<sup>1</sup>, J.-P. Gattuso<sup>2,3</sup>, T. F. Thingstad<sup>4</sup>, and J. J. Middelburg<sup>5</sup>

Correspondence to: U. Riebesell (uriebesell@geomar.de)

The growing evidence of potential biological impacts of ocean acidification affirms that this global change phenomenon may pose a serious threat to marine organisms and ecosystems. Whilst ocean acidification will occur everywhere, it will happen more rapidly in some regions than in others. Due to the high CO<sub>2</sub> solubility in the cold surface waters of high-latitude seas, these areas are expected to experience the strongest changes in seawater chemistry due to ocean acidification. This will be most pronounced in the Arctic Ocean. If atmospheric pCO<sub>2</sub> levels continue to rise at current rates, about 10% of the Arctic surface waters will be corrosive for aragonite by 2018 (Steinacher et al., 2009). By 2050 one-half of the Arctic Ocean will be sub-saturated with respect to aragonite. By the end of this century corrosive conditions are projected to have spread over the entire Arctic Ocean (Steinacher et al., 2009). In view of these rapid changes in seawater chemistry, marine organisms and ecosystems in the Arctic are considered particularly vulnerable to ocean acidification. With this in mind, the European Project on Ocean Acidification (EPOCA) chose the Arctic Ocean as one of its focal areas of research.

With the majority of studies conducted in the laboratory and most of them investigating the responses of single species, we presently know little about how organism responses scale up to the community and ecosystem level and what the consequences are for marine food webs and biogeochemical cycles. To help close this critical gap in our knowledge on ocean acidification impacts, EPOCA put an emphasis on community-level experimentation. This, in combination with EPOCA's focus on Artic waters, paved the way for a multidisciplinary mesocosm CO<sub>2</sub> perturbation experiment off the northwest coast of Svalbard in 2010. With a total of 35 participants from 9 EPOCA partner institutes and 4 non-EPOCA partners, this was the project's largest joint activity (Fig. 1).

Nine units of the Kiel Off-Shore Mesocosms for Ocean Simulations (KOSMOS) were deployed in Kongsfjorden about 1.5 nautical miles north-west of the Ny-Ålesund research base on 31 May. Each unit enclosed ca. 50 m<sup>3</sup> in a 17 m-long, 2 m in diameter polyurethane bag (Fig. 1; see Riebesell et al., 2013 and Schulz et al., 2013 for details on the experimental design). The plankton community at the start of the experiment was characteristic for a post-bloom situation and a retention-type food web with high bacterial production, high abundance of mixotrophic phytoplankton, and comparatively low mesozooplankton grazing. After closing the mesocosms and completing the CO<sub>2</sub> manipulation, the enclosed plankton community passed through three distinct phases, each characterized by a peak in phytoplankton biomass dominated by different species assemblages: phase 1 - end of  $CO_2$  manipulation until nutrient addition (t4 to t13); phase 2 – inorganic nutrient addition until the second chlorophyll a minimum (t13 to t21); phase 3 – the second chlorophyll a minimum until the end of this study (t21 to t30).

In total over 50 parameters were measured daily during the experimental period. This unique and comprehensive data set, available at Pangaea doi:10.1594/PANGAEA.769833, lends itself for in-depth analyses and well-grounded interpretations of the observed trends, both in terms of the unperturbed plankton community succession and

<sup>&</sup>lt;sup>1</sup>GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

<sup>&</sup>lt;sup>2</sup>INSU-CNRS, Laboratoire d'Océanographie de Villefranche, Villefranche sur Mer, France

<sup>&</sup>lt;sup>3</sup>Université Pierre et Marie Curie-Paris 6, Observatoire Océanologie de Villefranche, Villefranche sur Mer, France

<sup>&</sup>lt;sup>4</sup>Department of Biology, University of Bergen, Bergen, Norway

<sup>&</sup>lt;sup>5</sup>Faculty of Geosciences, Utrecht University, Utrecht, the Netherlands





Fig. 1. Top – KOSMOS mesocosms depkoyed in Kongsfjord, Svalbard. Bottom – participants of the mesocosmistudy (from left to right - front row: Eva Leu, Ulf Riebesell<sub>m</sub>Rui Zhang<sub>tl</sub>Anna de Klajiyer, Chiaki Motegi, Michael Meyerhöfer, Signe Koch-Klavsen, Sarah Romac, Andrea Ludwig, Corinna Borchard, Richard Bellerby; back<sub>M</sub>ow: John Stephens, Tauneo Tanaka, Kai Schulz, Jan Czarny, Nicole Händel, Matthias Fischer, Martin Sperling, Anja Engel, Judith Piontek, Tor Einag de Lange<sub>k</sub> Merel Colkenteur, Tim Boxhammer, Anna Silyakova, Michael Sswat, Jozef Nissimov, Françes Hopkins, Kerstin Nachtigall, Susan Kimmance, Corina Brussaard, Jean-Pierre Gattuso, Anna Noordeloos, Sebastian Krug, Lucie Bittner, Harry Witte)

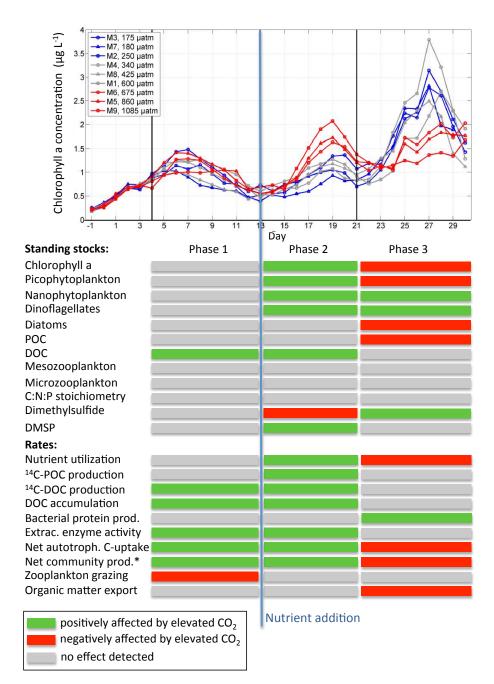
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biogeochemical cycling as well as their modifications in response to ocean acidification. Integrating the broad spectrum of observations allows for a synoptic view of pelagic ecosystem sensitivities to ocean change in Arctic waters. Here we summarize some of the major results of this study (see also Box 1):

#### Autotrophic standing stocks, composition, and activities:

1. Autotrophic biomass was similar in all CO<sub>2</sub> treatments during phase 1 prior to nutrient addition, was higher at elevated *p*CO<sub>2</sub> during phase 2 after nutrient addition, and lower at elevated *p*CO<sub>2</sub> during phase 3 (Schulz et al., 2013).

- m e y h N a K B ... y
- 2. The rate of nutrient utilization after nutrient addition was higher at elevated  $pCO_2$  (Schulz et al., 2013).
- 3.  $^{14}$ C fixation was higher at elevated  $pCO_2$ ; for POC production this trend was significant after nutrient addition, for DOC production it was significant both before and after nutrient addition (Engel et al., 2013). DOC accumulation during phases 1 and 2 correlated positively with  $pCO_2$  (Czerny et al., 2013).
- 4. Following nutrient addition, elevated *p*CO<sub>2</sub> stimulated picoeukaryotic photoautotrophs and to a lesser degree nanophytoplankton, leading to stronger nutrient drawdown in the high CO<sub>2</sub> treatments during phase 2; as a result of this, growth and biomass of the diatom community developing during phase 3 was negatively correlated with *p*CO<sub>2</sub> (Brussaard et al., 2013; Schulz et al., 2013).



**Box 1. Upper panel**: Chlorophyll a concentration ( $\mu$ g L<sup>-1</sup>) in the nine mesocosms over time. Colours and symbols represent the different CO<sub>2</sub> treatments; blue – low pCO<sub>2</sub> (175–250  $\mu$ atm), grey – intermediate pCO<sub>2</sub> (340–600  $\mu$ atm), red – high pCO<sub>2</sub> (675–1085  $\mu$ atm). **Bottom panel**: effects of elevated CO<sub>2</sub> on measured standing stocks and rates; phase 1 – end of CO<sub>2</sub> manipulation until nutrient addition (t4 to t13); phase 2 – inorganic nutrient addition until the second chlorophyll a minimum (t13 to t21); phase 3 – the second chlorophyll a minimum until the end of this study (t21 to t30). \* Net community production estimated from carbonate chemistry measurements.

- 5. Growth of dinoflagellates, developing during phase 2 and into phase 3, was positively affected by elevated *p*CO<sub>2</sub> (Schulz et al., 2013; Leu et al., 2013).
- 6. CO<sub>2</sub>-related changes in phytoplankton taxonomic composition during phases 2 and 3 were mirrored in the

fatty acid composition of suspended matter: the contribution of poly-unsaturated fatty acids (PUFA) correlated positively with  $pCO_2$  (Leu et al., 2013); an exception to this is 20:5n3 eicosapentaenoic acid (EPA), an important diatom marker, which was negatively correlated with  $pCO_2$  during phase 3 (Leu et al., 2013).

7. No indications were found for a generally detrimental effect of ocean acidification on the planktonic food quality in terms of essential fatty acids (Leu et al., 2013).

#### Microbial heterotrophic diversity and activities

- The bacterial community attached to particles was more diverse at high compared to medium and low pCO<sub>2</sub> (Sperling et al., 2013).
- The maximum apparent diversity of bacterioplankton differed significantly between CO<sub>2</sub> treatments; the relative abundance of *Bacteroidetes* correlated negatively with pCO<sub>2</sub> at the end of the experiment; in general bacterial diversity, taxonomic richness and community structure were influenced primarily by variation in primary production (Zhang et al., 2013).
- 3. Fifteen rare bacterial taxa correlated significantly with the *p*CO<sub>2</sub> treatment, most of which increased in abundance with higher CO<sub>2</sub> (Roy et al., 2013).
- 4. Time-integrated primary production and bacterial protein production were positively correlated, suggesting that higher amounts of phytoplankton-derived organic matter were assimilated by heterotrophic bacteria at increased primary production (Piontek et al., 2013).
- 5. Extracellular enzyme activity of  $\beta$ -glucosidase and leucine-aminopeptidase increased with increasing  $pCO_2$  (Piontek et al., 2013).
- 6. Higher rates of viral lysis at elevated pCO<sub>2</sub> led to lower bacterial abundances in phase 3 (Brussaard et al., 2013). Bacterial protein production (BPP) was higher in high CO<sub>2</sub> treatments during phase 3 despite lower total bacterial cell numbers (Piontek et al., 2012).
- 7. No CO<sub>2</sub> effect was observed for bacterial respiration, carbon demand, and growth efficiency (Motegi et al., 2013).

#### Zooplankton abundance and composition

- Meroplanktonic larvae (cirripedia, polychaeta, bivalvia, gastropoda, and decapoda) dominated the mesozooplankton community while copepods (*Calanus* spp., *Oithona similis*, *Acartia longiremis* and *Microsetella* norvegica) were found in lower abundances (Niehoff et al., 2013).
- 2. Mesozooplankton abundance and taxonomic composition developed similarly in all mesocosms with no  $p\text{CO}_2$  effect on the abundance of single taxa and the overall community structure (Niehoff et al., 2013).

3. Microzooplankton composition and diversity was similar in all CO<sub>2</sub> treatments, indicating that neither direct *p*CO<sub>2</sub>/pH effects nor indirect effects through changes in food composition impacted microzooplankton carrying capacity and phenology (Aberle et al., 2013).

4. Zooplankton grazing decreased with increasing  $pCO_2$  during phase 1 (de Kluijver et al., 2013).

#### Community structure, production, and respiration

- 1. The planktonic community developed from a postbloom retention-type system at the start of the experiment to a new production system after nutrient addition; the nutrient-induced increase in primary production and phytoplankton biomass was initially dominated by picoand nanophytoplankton (phase 2) before it shifted towards microphytoplankton, predominantly diatoms and dinoflagellates (phase 3) (Schulz et al., 2013; Brussaard et al., 2013).
- Elevated pCO<sub>2</sub> enhanced net autotrophic community carbon uptake during phases 1 and 2; the opposite trend was observed during phase 3 (Czerny et al., 2013; de Kluijver et al., 2013).
- 3. Net community production obtained from carbonate chemistry measurements increased with increasing *p*CO<sub>2</sub> during phases 1 and 2 and decreased with *p*CO<sub>2</sub> during phase 3 (Silyakova et al., 2013).
- Significantly lower gross and net community production at elevated pCO<sub>2</sub> during phase 3 was also obtained from changes in dissolved oxygen during incubations (Tanaka et al., 2013).
- Community respiration remained relatively constant throughout the experimental period, with no significant differences between CO<sub>2</sub> treatments (Tanaka et al., 2013).

#### Biogeochemical processes and production of trace gases

- 1. Following inorganic nutrient addition, the carbon to nutrient uptake ratios were lower than Redfield proportions during phase 2 and higher than Redfield during phase 3, with no detectable effect of *p*CO<sub>2</sub> on uptake stoichiometry (Silyakova et al., 2013); for the total postnutrient period (phases 2 and 3) ratios were close to Redfield proportions.
- 2.  $pCO_2$  had no significant effect on the elemental composition of particulate organic matter (Czerny et al., 2013).
- 3. Budget calculations revealed that  ${\rm CO}_2$ -stimulated carbon consumption resulted in higher accumulation of

dissolved organic carbon in high compared to low  $pCO_2$  treatments (Czerny et al., 2013).

- 4. Export of fresh organic matter increased with increasing pCO<sub>2</sub> before nutrient addition (de Kluijver et al., 2013), but overall carbon export decreased with increasing pCO<sub>2</sub> during the export event thereafter (Czerny et al., 2013).
- 5. Concentrations of dimethylsulfide (DMS) were reduced by 35 % at intermediate and by 60 % at high  $pCO_2$  levels relative to ambient  $pCO_2$ ; in contrast, concentrations of dimethylsulphoniopropionate (DMSP), the precursor of DMS, were elevated by 30 % and 50 % at intermediate and high  $pCO_2$ , respectively. Elevated DMSP production at high  $pCO_2$  correlates positively with higher dinoflagellate biomass (Archer et al., 2013).
- 6. The response of halocarbons to pCO<sub>2</sub> was subtle or undetectable: despite strong significant correlations with biological parameters, iodomethane (CH<sub>3</sub>I) dynamics were unaffected by pCO<sub>2</sub>. In contrast, a significant positive response to pCO<sub>2</sub> was obtained for diiodomethane (CH<sub>2</sub>I<sub>2</sub>) with respect to concentration, the rate of net production and the sea-to-air flux; there was no clear effect of pCO<sub>2</sub> on bromocarbon concentrations or dynamics (Hopkins et al., 2013).

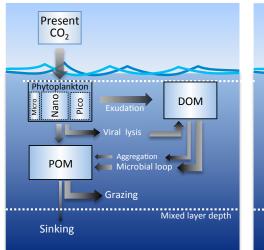
Taken together, these results indicate a considerable resilience of the enclosed plankton communities to ocean acidification, but also some notable sensitivities which - if representative for plankton communities in high latitudes – point towards substantial restructuring of pelagic ecosystems and biogeochemical cycling under future ocean conditions. Distinctly different responses thereby occurred before and after nutrient addition (Box 1). In the absence of inorganic nutrients CO<sub>2</sub>-stimulated photosynthetic carbon fixation did not translate into phytoplankton biomass production, but resulted in increased DOC exudation at elevated CO<sub>2</sub> (Fig. 2, upper panel). At this stage excess DOC accumulating in high CO<sub>2</sub> treatments did not stimulate the microbial loop, indicating limitation of bacterial growth by inorganic nutrients. Viral lysis and microzooplankton grazing were the dominant loss processes for phytoplankton biomass, with the latter correlating negatively with  $pCO_2$ . Sinking of particulate organic matter was of minor importance during this phase. Due to the lack of data on transparent exopolymeric particles (TEP) it is unclear to what extent rising DOC concentrations led to increased TEP formation, which may have contributed to the observed higher particle sinking of fresh organic matter at elevated CO<sub>2</sub>. The latter response to elevated CO<sub>2</sub>, i.e. increased DOC release followed by enhanced TEP formation and particle sinking, was in fact described in Arrigo (2007) based on observations reported in Riebesell et al. (2007) and Bellerby et al. (2008).

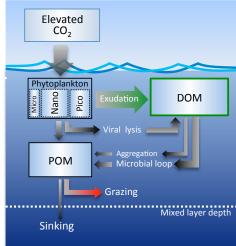
Following nutrient addition (phase 2), growth of phytoplankton was stimulated by elevated CO<sub>2</sub> in the pico- and

nanoplankton size fractions, leading to enhanced nutrient uptake and higher biomass build-up in these groups (Box 1, Fig. 2, lower panel). DOC production and accumulation continued to be higher under elevated CO<sub>2</sub> during phase 2. Contrary to the previous phase, under nutrient-replete conditions the microbial loop now responded to the CO<sub>2</sub>-stimulated DOC production with higher turn-over under elevated CO<sub>2</sub>. CO<sub>2</sub> stimulation of the microbial loop may also partly explain the higher grazing rates, predominantly by microzooplankton, in high CO<sub>2</sub> treatments (Box 1, Fig. 2, lower panel). In the microphytoplankton size range growth of dinoflagellates, which started to increase during phase 2, was also stimulated by elevated CO2. CO2-enhanced nutrient utilization by pico- and nanophytoplankton occurred at the expense of diatoms (Fig. 3), which increased in biomass only during phase 3. The impact of a CO<sub>2</sub>-induced stimulation of pico- and nanophytoplankton growth at the expense of diatoms on biogeochemical cycling was visible in sedimentation fluxes, which were lower at elevated  $pCO_2$ . With more of the available nutrients utilized by pico- and nanoplankton and channelled into the microbial loop, less of the primary produced organic matter is available for transfer to higher trophic levels (Fig. 3). While this can be expected to also impact growth and reproduction of mesozooplankton, this study was too short to resolve this kind of indirect response, particularly because the difference in diatom production occurred towards the end of the study. In summary, under nutrient-replete conditions, the combination of CO<sub>2</sub>-stimulated growth in the pico- and nanoplankton size range, CO<sub>2</sub>-stimulated DOC production, enhanced microbial degradation, and reduced diatom production resulted in a reduced strength of the biological pump at the expense of heterotrophic consumption in a retention-type food web (Fig. 2, lower panel).

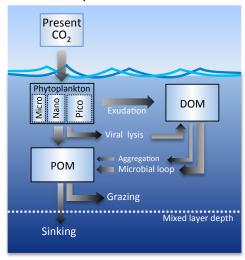
In the seasonal succession of pelagic systems nutrientreplete conditions supporting export production are typically followed by nutrient-limiting conditions favouring a retention-type community. Due to the risk of sea ice formation in the study area early in the year, our mesocosm experiment only started after the winter/spring bloom had terminated and inorganic nutrients were exhausted. Because nutrients were added only half way through the experiment, the community succession induced in the mesocosms was therefore in reverse order. To what extent this has influenced the observed responses is presently unclear. Obviously, future experiments of this kind should avoid employing nutrient additions at times when the plankton community is not naturally expecting inorganic nutrient supply. Notwithstanding the reversed order of nutrient-limited versus nutrient-replete conditions, our results demonstrate that the impacts of elevated CO<sub>2</sub> on pelagic systems are strongly modified by nutrient availability. The effect sizes for the different phases during the seasonal succession and their relative contributions to the annual primary production and organic matter turn-over will ultimately determine the net impact on an annual basis.

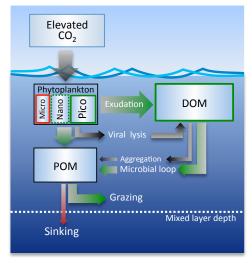
## **Nutrient limiting conditions**





### Nutrient replete conditions



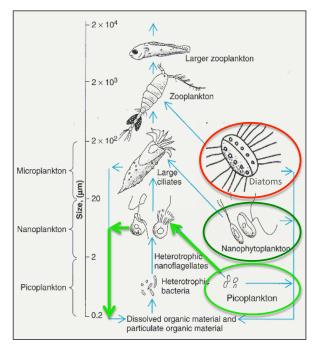


**Fig. 2.** Sketch of carbon pools and fluxes at present day (**left panels**) and elevated CO<sub>2</sub> levels (**right panels**) under nutrient-limiting (**upper panels**) and nutrient-replete conditions (**lower panels**). The sizes of the boxes represent pool sizes, the thickness of the arrows represent the magnitude of the fluxes between pools; green arrows indicate fluxes stimulated by elevated CO<sub>2</sub>, red arrows fluxes which are reduced at elevated CO<sub>2</sub>. POM, particulate organic matter, DOM, dissolved organic matter. With a depth of 17 m, the water body enclosed in the mesocosms was entirely in the euphotic zone. Note that some of the fluxes were not measured directly but calculated or inferred from other measured parameters. Modified from Arrigo (2007) according to the outcome of this study.

While it is too early to conclude what the net impact will be, it is obvious from these results that substantial changes in ecosystem dynamics and biogeochemical cycling will occur in a future high CO<sub>2</sub> Arctic Ocean.

The results of this study demonstrate the high potential of community-level field experimentation to better understand the complex interactions triggered by both direct and indirect responses to environmental changes. They emphasize the importance of accurately replicating the environmental conditions and covering the natural community succession. In this context, the mesocosm methodology provides an ideal platform for a systemic approach, integrating across scientific

disciplines and thus providing a holistic view of the sensitivities of marine biota to ocean change. The use of a mobile experimental platform, such as the KOSMOS system, opens up the opportunity to test for impacts of ocean changes on ecosystems and in regions deemed most vulnerable to environmental perturbations. Future studies using this or similar approaches in other oceanographic settings and covering different periods of the seasonal plankton succession are urgently needed to evaluate the representativeness of the findings obtained in the EPOCA 2010 mesocosm study off Svalbard.



outcompeted at high CO<sub>2</sub>

moderately stimulated at high  ${\rm CO_2}$ 

strongly stimulated at high CO<sub>2</sub>

**Fig. 3.** Sketch of plankton groups and size classes represented in the mesocosms; blue arrows indicate trophic linkages; green circles and arrows indicate groups and processes stimulated by elevated CO<sub>2</sub>, red circle indicates diatoms being negatively impacted through CO<sub>2</sub>-stimulated effects in the smaller size classes (graph copyright 2001 by Benjamin Cummings).

Acknowledgements. The design, construction and field testing of the KOSMOS mesocosms was made possible through financial support of the GEOMAR and the integrated project SOPRAN (Surface Ocean PRocesses in the ANthropocene) funded by the German Ministry for Education and Research (BMBF). GEOMAR and SOPRAN provided the KOSMOS facility for the Svalbard 2010 experiment, organized the logistics leading up to and during the experiment. GEOMAR was responsible for deploying the mesocosms, running the experiment and coordinating all scientific aspects before, during and after the experiment. The scientific work is a contribution to the "European Project on Ocean Acidification" (EPOCA) which received funding from the European Community's Seventh Framework Programme (FP7/2007-2013) under grant agreement no. 211384. Additional financial support was provided by IPEV, the French Polar Institute. Several participants of this study received funding from the European Community's Seventh Framework Programme under grant agreement no 228224, MESOAQUA. We gratefully acknowledge the logistical support of Greenpeace International for its assistance with the transport of the mesocosm facility from Kiel to Ny-Ålesund and back to Kiel. We also thank the captains and crews of M/V ESPERANZA of Greenpeace and R/V Viking Explorer of the University Centre in Svalbard (UNIS) for assistance during mesocosm transport and during deployment and recovery in Kongsfjord. All participants thank the staff of the French-German Arctic Research Base (AWIPEV) at Ny-Ålesund, in particular Marcus Schumacher, for on-site logistical support and Anne-Marin Nisumaa for efficiently managing the data.

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