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Mesozooplankton community development at elevated CO₂ concentrations: results from a mesocosm experiment in an Arctic fjord

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Abstract

The increasing CO₂ concentration in the atmosphere caused by burning fossil fuels leads to increasing pCO₂ and decreasing pH in the world oceans. These changes may have severe consequences for marine biota, especially in cold-water ecosystems due to higher solubility of CO₂. However, studies on the response of mesozooplankton communities to elevated pCO₂ are yet lacking. In order to test whether abundance and taxonomic composition change with pCO₂, we have sampled nine mesocosms, which were deployed in Kongsfjorden, an Arctic fjord at Svalbard, and were adjusted to eight CO₂ concentrations, initially ranging from 185 μatm to 1420 μatm. Samples were taken weekly over a six-week period with an Apstein net (55 μm mesh size) in all mesocosms and the surrounding fjord. In addition, sediment trap samples, taken every second day in the mesocosms, were analyzed to account for losses due to vertical migration and mortality. The taxonomic analysis revealed that meroplanktonic larvae (cirripeds, polychaetes, bivalves, gastropod, and decapods) dominated in the mesocosms while copepods (*Calanus* spp., *Oithona similis*, *Acartia longiremis* and *Microsetella norvegica*) were found in lower abundances. In the fjord copepods prevailed for most of our study. With time, abundance and taxonomic composition developed similarly in all mesocosms; the pCO₂ had no significant effect on the overall community structure. However, single taxa responded to elevated CO₂ concentrations. The ratio of cirripedia nauplii to cypris larvae, the next developmental stage, in the sediment traps averaged over the entire experiment increased with pCO₂ and this suggests that increased pCO₂ may have delayed their development. Also, the number of bivalves, averaged over the experimental period, decreased significantly with increasing pCO₂. The nature of the CO₂ effect, either direct or indirect, remains open and needs to be addressed in future.

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1 Introduction

The increasing CO₂ concentration in the atmosphere caused by burning fossil fuels leads to increasing CO₂ concentrations in the world oceans at a rate yet unprecedented in the earth history. Since preindustrial times, atmospheric CO₂ concentrations increased from about 280 to 380 μatm, and future scenarios predict up to 1000 μatm by the end of this century (IPCC, 2007). When CO₂ dissolves, it reacts with water and the hydrogen ion concentration increases. Thus the oceans do not only accumulate carbon but also become more acidic. Accordingly, the pH in surface seawaters today has decreased by 0.1 unit from preindustrial values of approx 8.2, and is projected to further decrease by approximately 0.5 units if the increase in CO₂ proceeds (Caldeira and Wickett, 2003; Feely et al., 2005). Such changes are expected to have severe consequences for marine biota and may alter the ecosystem functioning (e.g. Riebesell et al., 2009). As the solubility of CO₂ increases with decreasing temperature, polar waters are particularly subject to ocean acidification (OA).

At elevated CO₂ levels, pelagic primary production may increase due to lower costs of carbon fixation, the stoichiometry of the algae may change and carbon overconsumption may lead to increased exudation of transparent extracellular particles. This will, in turn, influence the microbial loop and carbon fluxes (reviewed by Riebesell and Tortell, 2011). OA directly affects calcifying planktonic organisms such as coccolithophora, foraminifera, echinodermata, bivalvia and pteropoda as the carbonate ion concentration will decrease with decreasing pH and increasing pCO₂ and this will effect the formation of calcareous structures and the energy budget (e.g. Lischka et al., 2011, Talmage et al., 2011; Yu et al., 2011). The direct effect of CO₂ on non-calcifying zooplankton organisms is less studied. Calanoid copepods, which often dominate marine zooplankton communities (e.g. Longhurst, 1985; Fransz et al., 1991), seem to respond only at fairly high CO₂ concentrations. Egg production, hatching success and/or survival rates of nauplii, copepodites and adults decreased significantly only at concentrations higher than 5000 μatm while they remained high at lower CO₂ levels

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(*Acartia* spp. Kurihara et al., 2004; Kurihara and Ishimatsu, 2008; *Calanus* spp., Mayor et al., 2007, 2012; several epi- and meso/bathypelagic species, Watanabe et al., 2006). Eggs of the Antarctic krill *Euphausia superba*, in contrast, did not hatch at 2000 μatm (Kawaguchi et al., 2011), suggesting that this species is more sensitive to CO_2 than copepods for reasons, which yet remain to be solved (Mayor et al., 2012). Also, non-calcifying meroplanktonic larvae of some benthic species, which at times occur in high abundances and can even outnumber the holoplankton (e.g. Fransz et al., 1991; Fetzer et al., 2002; Walkusz et al., 2009), were shown to be sensitive to $p\text{CO}_2$, e.g. barnacle nauplii by Findlay et al. (2009, 2010).

In contrast to single species studies in the laboratory, mesocosm experiments are particularly suitable for studying the impact of ocean acidification on pelagic community dynamics (e.g. Delille et al., 2005; Paulino et al., 2008). Up to date, there have been mesocosm experiments studying the impact of $p\text{CO}_2$ on plankton communities in the outdoor facilities at Espegrend, Bergen, Norway. Studies from high latitudes, however, are lacking although cold-water ecosystems are likely to be severely effected by climate change. Moreover, the focus of the studies in Bergen was on bacteria, phytoplankton and microzooplankton communities (reviewed by Riebesell et al., 2008) while to our knowledge there is only one outdoor-mesocosm experiment on mesozooplankton, which studied the response of a single species, i.e. *Calanus finmarchicus* (Carotenuto et al., 2008). In the present mesocosm experiment, which is part of the European Project on Ocean Acidification (EPOCA), the response of the pelagic community including all organisms < 3 mm to elevated CO_2 concentrations was investigated in June/July 2010 in a high latitude glacial fjord, Kongsfjorden, Svalbard (see publications within this issue). Our study aims at the mesozooplankton and focuses at detecting whether abundance and taxonomic composition change with $p\text{CO}_2$. We sampled nine mesocosms, which were initially adjusted to eight CO_2 concentrations ranging from 185 μatm to 1420 μatm (for exact $p\text{CO}_2$ see Bellerby et al., 2012) over six weeks. Our data indicate that within this period, CO_2 had no significant effect on the

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structure of the mesozooplankton community but single taxa did respond to elevated CO₂ concentrations.

2 Methods

The present study focusing on the zooplankton community development was part of the EPOCA CO₂ enrichment mesocosm experiment conducted in Kongsfjorden (78°56'2" N und 11°53'6" E) in Ny-Ålesund, Svalbard in June/July 2010. Kongsfjorden, a glacial fjord at the West coast of Spitsbergen, is influenced by the inflow of warm Atlantic water from the West Spitsbergen current, by Arctic water and by freshwater run-off from the surrounding glaciers (for hydrographical details see Svendsen et al., 2002).

2.1 Experimental design

To study the effect of CO₂ on the dynamics in the pelagic system, nine KOSMOS (Kiel Off-Shore Mesocosms for future Ocean Simulation) offshore mesocosms of 15 m length below sea surface and approx. 47 m³ volume were deployed in the fjord at a water depth of ~ 40 m. Two m above the bottom, a sediment trap was installed inside each mesocosm. The mesocosms were designed by the GEOMAR, Kiel, Germany and details are described in Czerny et al. (2012b); Schulz et al. (2012) and Riebesell et al. (2012).

When the bags of the mesocosms were lowered into the fjord on 31 May (t_{-7}), the upper and lower openings were covered with 3 mm mesh, excluding fishes and large mesozooplankton e.g. cnidaria, chaetognathes, adult pteropods and large copepods, from the zooplankton community. After two days during which the water in the mesocosms was allowed to exchange with the surrounding fjord water, the mesocosms were closed (t_{-5} ; 2 June). To calculate the exact volume of each mesocosm (Czerny et al., 2012b), salt was added (t_{-4} and t_4) and salinity was measured prior to and after the

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salt additions (Schulz et al., 2012). One major goal of the experiment was to study phytoplankton dynamics, but the natural nutrient concentration and phytoplankton abundance were low due to post bloom conditions in the fjord. To initiate a bloom, nitrate ($5 \mu\text{mol kg}^{-1}$), phosphate ($0.3 \mu\text{mol kg}^{-1}$) and silicate ($2.5 \mu\text{mol kg}^{-1}$) were added to each mesocosms on t_{13} (Schulz et al., 2012).

To adjust the water in the mesocosms to the respective CO_2 concentrations, ambient seawater was aerated with pure CO_2 (Riebesell et al., 2012). This water was injected stepwise over six days (t_{-1} to t_4) into the mesocosms until the target CO_2 concentrations were reached. Initial CO_2 levels at t_8 , when mixing with the dead water volume below the sediment traps was completed (Riebesell et al., 2012), were $185 \mu\text{atm}$ in mesocosm (M)3 and M7, $270 \mu\text{atm}$ in M2, $375 \mu\text{atm}$ in M4, $480 \mu\text{atm}$ in M8, $685 \mu\text{atm}$ in M1, $820 \mu\text{atm}$ in M6, $1050 \mu\text{atm}$ in M5 and $1420 \mu\text{atm}$ in M9; the ambient concentration in the fjord at that time was $145 \mu\text{atm}$, which indicates post-bloom conditions (Bellerby et al., 2012). Due to gas exchange and biological processes, the CO_2 concentration decreased continuously over time in all mesocosms (to $165 \mu\text{atm}$ in M3, $160 \mu\text{atm}$ in M7, $220 \mu\text{atm}$ in M2, μatm 290 in M4, μatm 365 in M8, μatm 500 in M1, μatm 555 in M6, μatm 715 in M5 and μatm 855 in M9) (Czerny et al., 2012a). The gradient from low to high CO_2 levels, however, remained throughout the six weeks of the experiment (Bellerby et al., 2012). Approximately 200 live pteropods (*Limacina helicina*) sampled from the fjord were added to study the effect of CO_2 on their biology. The pteropods, however, did not survive for long and after one week, most snails had vanished from the water column in the mesocosms.

CTD casts were taken daily to monitor the development of temperature, salinity and pH in the mesocosms and the fjord. Temperature increased from 2 to 6°C in all mesocosms, following the temperature development in the surrounding fjord water (Schulz et al., 2012). Salinity was ~ 33.5 when the mesocosm were closed. After the salt addition the salinity was ~ 34 and remained stable throughout the experiment (Schulz et al., 2012). Depth integrated water samples were taken using an Integrating Water Sampler (HydroBios, Kiel, Germany) to determine CO_2 concentration from total alkalinity

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and total dissolved carbon measurements (Bellerby et al., 2012). Chlorophyll *a* concentrations, among other parameters, were measured from the same water samples (Riebesell et al., 2012). The chlorophyll *a* concentrations indicate three simultaneous bloom events in all nine mesocosms, the first in phase 1 (t_4 – t_{13} from the end of the CO₂ manipulation until nutrient addition), the second in phase 2 (t_{13} to t_{21} from nutrient addition until the second chlorophyll minimum) and in phase 3 (t_{22} to t_{30} , from the second chlorophyll minimum until the end of the experiment; Riebesell et al., 2012; Schulz et al., 2012).

2.2 Sampling

In order not to re-suspend material, which had settled in the sediment traps, sampling of the water column was restricted to 12 m depth. Zooplankton was sampled approximately weekly by vertical net tows with an Apstein net of 17 cm diameter and 55 μ m mesh size. Sampling days were t_{-2} prior to CO₂ manipulation, t_{-2} in between CO₂ manipulations, t_{-11} during phase 1, t_{18} during phase 2, t_{24} during phase 3 and t_{30} at the end of the experiment. The samples were brought to the Kings Bay Marine Laboratory and then preserved in 4% formalin buffered with hexamethylenetetramin. Under a dissecting microscope, the organisms were sorted and determined to the lowest taxonomical level, if possible to species and developmental stage. When the numbers of zooplankton organisms were high, the samples were subdivided using a Folsom plankton splitter, and abundances in terms of individuals m^{-3} were calculated from these subsamples. Eggs and larvae $< 55 \mu$ m, e.g. early trochophora larvae, were not sampled quantitatively with the Apstein net and are thus not further considered.

The sediment traps were emptied every second day using a vacuum pump system except for t_{10} when samples were taken after 24 h (Riebesell et al., 2012). Twenty to thirty ml subsamples of the material from the traps were analyzed for mesozooplankton abundance and community composition to account for dead zooplankton and species and developmental stages, respectively, which tend to migrate to deeper water layers. During the first three weeks of the experiment, the non-preserved sub-samples were

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analyzed at the Kings Bay Marine Laboratory within 24 h after collection. During the last three weeks, they were preserved in 4 % formalin buffered with hexamethylenetetramin and analyzed later at the Alfred Wegener Institute (Bremerhaven, Germany).

2.3 Statistical analyses

5 To test the effect of $p\text{CO}_2$ on the abundance of specific taxa, linear regressions have been performed using Graph Pad Prism (Version 4.0c). To compare the mesozooplankton communities developing in the different mesocosms routines from multivariate statistics (Primer Version 5 software) were used to calculate Bray-Curtis similarities. Non-metric multidimensional scaling two-dimensional plots (nMDS) were produced to
10 indicate the similarity of the samples from both, the water column and the sediment traps of all nine mesocosms. For the analyses, abundance data were square root transformed. The accuracy of the two-dimensional representation in nMDS is indicated by the “stress” value (Kruskall’s stress formula). Stress levels of < 0.1 indicate good representation of the data, values between 0.1 and 0.2 provide a potentially useful 2-
15 dimensional picture and stress levels > 0.2 exhibit an increasing risk of arbitrary data placement. For all theoretical aspects of the analyses see Clarke and Gorley (2006) and Clarke and Warwick (2001).

3 Results

3.1 Total zooplankton abundance

20 The initial total zooplankton abundance differed among the mesocosms ranging from 9286 ind. m^{-3} in M8 and 27 858 ind. m^{-3} in M1 (Fig. 1a). During the entire experiment, the total abundance changed only slightly and with no apparent trend, neither with time nor with CO_2 concentration. The zooplankton abundance in the fjord was very low (Fig. 2a) except for t_2 .

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The sediment traps, which were only deployed in the mesocosms but not in the fjord, collected on average 352 503 (SD 67 202) organisms mesocosm⁻¹ over the entire experiment, which equals 11 016 ind. d⁻¹ mesocosm⁻¹. Most of the individuals were vivid in the unpreserved samples and completely intact in the preserved samples indicating that they did not sink after death but rather swam into the traps. There was no relation between the number of zooplankton organisms in the traps and the CO₂ concentration (linear regression, $p > 0.05$), however, the number of organisms changed with time in all mesocosms (Fig. 1b). From t_{-2} to t_{10} the average number decreased from 24 089 (SD 5650) to 10 832 (SD 3763) ind. 48 h⁻¹. From t_{12} to t_{16} it increased to the overall maximum of 70 674 (SD 36 602) ind. 48 h⁻¹. Thereafter it decreased again to 11 072 (SD 7303) ind. 48 h⁻¹ at t_{24} . During the last week of the experiment, the average number of organisms in the traps varied between 10 096 (SD 2001) and 22 630 (SD 9259) ind. 48 h⁻¹.

Until t_{18} , the major part of the material from the sediment trap samples consisted of zooplankton organisms, their exuvia and eggs as well as their fecal pellets. Beginning with t_{20} , long chained diatoms appeared. It was not possible to quantify their mass, however, their amount as observed during sorting increased rapidly within 6 days and remained high in the last week of the experiment. Consequently, the first peak in zooplankton organisms matches the peak in organic carbon export while the major part of the carbon collected towards the end of our study can be attributed to the diatoms (Fig. 1c).

3.2 Community composition

In the mesocosms, meroplanktonic larvae, including that of cirripedia, polychaeta, and mollusca, were the major component of the zooplankton community both in the water column and in the sediment traps (approximately 60–90 %) while holoplanktonic organisms, mainly copepods, contributed only approximately 10 to 40 % (Figs. 3 and 4). In all mesocosms, also calyptopis larvae of *Thysanoessa raschkii* (decapoda) were found

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but usually in low numbers (< 5%). Chaetognatha, cnidaria and amphipoda (*Themisto* sp.) and pteropods (*Limacina helicina*) were rare (< 1% of the zooplankton abundance) and are therefore not considered in the analysis of community development. In the fjord (Fig. 2b), the community was completely different as compared to the community enclosed in the mesocosms. Here, copepods were always the most abundant taxon, except for t_2 when cirripedia were found in high numbers.

The Bray-Curtis similarity analyses, based on square root transformed abundance data, indicate that the community composition did not differ significantly among the different CO₂ treatments, neither in the water column (stress 0.05, Fig. 5a) nor in the sediment traps (stress 0.11; Fig. 5b). The sampling dates, however, were separated indicating that the mesozooplankton community composition changed significantly with time. The separation is more distinct in the water column than in the sediment trap samples, which can be attributed to the larger number of samples from the traps as these data reflect the continuous temporal development better than the weekly sampling.

3.3 Cirripedia

Cirripedia dominated the zooplankton community in the water column of the mesocosms over the first two weeks of the experiment (Fig. 3) and in the sediment traps over the entire experiment (Fig. 4). At the beginning of the experiment almost all individuals were in the nauplius stage (approx. 5000–20 000 ind. m⁻³) while cypris larvae, the next developmental stage, were rare (Fig. 6a and b). With time, the number of nauplii decreased and cypris larvae increased in abundance (maximum of 3000 ind. m⁻³). Interestingly, the cypris larvae abundance was low in the water column as compared to the nauplius abundance (Fig. 6a and b) but the larvae reached high abundances in the sediment traps (Fig. 6d), indicating that this stage migrated towards deeper water.

There were no significant relations to the CO₂ levels in abundance of both, nauplii and cypris larvae, neither in the water column nor in the sediment trap samples. In the sediment trap samples of the high CO₂ mesocosms, however, relatively more nauplii were found than cypris larvae and the ratio of nauplii to cypris larvae (averaged

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over time) was significantly related to CO₂ concentration ($p = 0.0116$, $r^2 = 0.58$, Fig. 7) which suggests that development of the nauplius to the cypris stage was influenced by CO₂ concentration.

3.4 Polychaete larvae

5 At the beginning of the experiment (t_{-2}) before the mesocosms were treated with CO₂, polychaete larvae of $> 500 \mu\text{m}$ length were found in all mesocosms, except for M4, and they reached relatively high abundances of up to 882 ind. m^{-3} (M1). At this time, they were also found in the fjord (184 ind. m^{-3}). Two weeks later (t_{11}), larvae were found
10 in only four mesocosms (M1, M7, M8, M9) with a maximum abundance of 29 ind. m^{-3} (M9); in the fjord no larvae were encountered. Within the following weeks, the number of polychaete larvae increased in all mesocosms but overall abundances remained low (maximum of 59 ind. m^{-3} ; M1). Consistent with the development in the water column, the sediment traps collected up to 12 500 individuals from t_{-1} to t_5 and much less until end of the experiment from t_6 to t_{30} (total of 714 to 2927 individuals mesocosm⁻¹,
15 corresponding to an average of 28 to 112 individuals mesocosm⁻¹ day⁻¹). Neither the larval abundance in the water column nor in the sediment trap samples correlated with the CO₂ concentration (linear regression, $p > 0.05$).

Small polychaete larvae of 300–500 μm length appeared at t_{11} , two days before nutrient addition in all mesocosms except for M1 and M8. Their number increased considerably during the following week to maximum abundances between 6024 (M5) and 10 667 (M4) ind. m⁻³. Thus, for the second half of the experiment, the polychaete larvae contributed significant proportions to the zooplankton communities in the mesocosms (Fig. 2). A correlation of their abundance to the CO₂ concentration was not found, neither in day of appearance nor in maximum and averaged abundances (linear regres-
20 sions, $p > 0.05$). The sediment trap samples rarely collected small polychaete larvae, and in the fjord, this larval type was only found on t_{18} with comparable low abundance of 110 ind. m⁻³.
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3.5 Molluscs

The abundance of bivalve larvae was as low compared to the other taxa (Fig. 2). At the beginning of our experiment 0–44 ind. m⁻³ were found and the larval abundance increased within the first two weeks in all mesocosms indicating that a new generation developed from eggs. Maximum abundance was 455 ind. m⁻³ (M6) on t_{24} in the mesocosms and 522 ind. m⁻³ on t_{11} in the fjord. The maximum abundances did not correlate with the CO₂ concentration ($p > 0.05$, linear regression) but when averaged over time, the bivalve larvae abundance decreased significantly with $p\text{CO}_2$ (linear regression, $p = 0.012$, $r^2 = 0.62$, Fig. 8).

In contrast to the water column, bivalve larvae contributed a significant portion to the zooplankton from the sediment trap samples from t_{-1} to t_7 (Fig. 3). During this time, between 10 200 (M3) and 32 200 (M1) larvae were collected, corresponding to an average of 1133 and 3568 ind. day⁻¹. From t_7 until the end of the experiment, the number of bivalves decreased, and on average between 93 and 1070 ind. d⁻¹ were collected by the traps. In contrast to the water column, there was no significant correlation between the number of bivalves collected in the sediment traps, neither in total amount of organisms nor in mean sinking rates per day (linear regressions, $p < 0.05$).

Also, gastropod larvae were rare in the water column. Their maximum abundance ranged between 15 (M7) to 191 (M4) ind. m⁻³ and again, there was no correlation of their abundance with the CO₂ concentration. In the fjord, maximum abundance was also low with 29 ind. m⁻³ and hardly any gastropod larvae were found in the sediment traps. The adults of the pteropod *Limacina helicina* did not appear in the water column samples and were rarely found intact in the sediment trap samples. Observations by divers indicate that many had migrated into the water body below the sediment traps. In the water column above the traps, quite a few must have died within a few days as shell fragments were frequently observed in the sediment trap samples. A few days after adult *L. helicina* were added, their eggs appeared in samples from all mesocosm, indicating that the pteropods had spawned. Over the experiment between 49 739 (M9)

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and 152 133 (M6) eggs were collected by the traps. Both, the total number and the day of appearance of the eggs were not related to the CO₂ concentration.

3.6 Copepods

Copepods were dominated by *Calanus* spp., *Acartia longiremis* (both Calanoida), *Oithona similis* (Cyclopoida) and *Microsetella norvegica* (Harpacticoida). *Pseudocalanus* spp. were only rarely found throughout the study period in both, the mesocosms and the fjord.

At the beginning of our study, most of the copepods were in a nauplius stage and among the copepodites and adults, *Oithona similis* dominated the community in the water column of the mesocosm followed by *Microsetella norvegica* while *Calanus* spp. were rare (Fig. 9). With time, the nauplius abundance decreased in the mesocosms while the abundance of copepodites and adult copepods increased (Fig. 2), especially that of *O. similis* and *Calanus* spp. Also, we found increasing numbers of *Acartia longiremis* while the abundance of *M. norvegica* remained low. The contribution of copepods, including nauplii and older stages, to the sediment trap samples was low over the entire study period (Fig. 3), and in accordance with the development of the copepod population in the water column, first nauplii and later copepodites/adults dominated. In the sediment trap samples (Fig. 10), relatively few *O. similis* were found, while *Calanus* spp. was quite abundant, especially between t_{14} and t_{28} . Again, there was no significant relation of copepod abundance – neither of the total abundance nor of the abundance of the different groups – to the CO₂ concentration (linear regressions, $p > 0.05$).

4 Discussion

This mesocosm experiment is the first, which studies the effect of CO₂ enrichment on an Arctic mesozooplankton community. The initial CO₂ concentrations, ranging from 185 µatm to 1420 µatm, cover the range from glacial p CO₂ to what has been projected

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to occur in the atmosphere in the next 100 to 200 years (e.g. Caldeira & Wicket, 2005; Feely et al., 2009; IPCC, 2007). We have to be aware, however, that the CO₂ concentration in the mesocosms decreased with time due to outgassing and CO₂ uptake by algae (Czerny et al., 2012a). The mesozooplankton sampled at a given time thus does not mirror a community, which has developed at a certain pH or CO₂ level but at continuously decreasing CO₂ concentration and increasing pH. In contrast to other pelagic compartments, such as viruses, bacteria and phytoplankton and most microzooplankton, the response time of the mesozooplankton to changing environmental conditions is often 24h and longer. For example, changes in food quality and quantity are mirrored in egg production rates, enzyme activities and biochemical composition of calanoid copepods after at least one day in boreal species and up several days to weeks in Arctic species (e.g. Jonasdottir, 1989; Niehoff, 2004; Graeve et al., 2004; Kreibich et al., 2011). Thus, differences in growth rates as determined via the abundance of consecutive developmental stages, which would ultimately result in different communities, are visible after longer intervals. It is therefore not meaningful to relate abundances of certain taxa and developmental stages to the actual CO₂ concentrations on a particular day. Composition and temporal development of the mesozooplankton community were similar in all nine mesocosms, and statistically no differences were found among the communities at different CO₂ treatments.

The effect of CO₂ on zooplankton can either be direct, especially in calcifying organisms (e.g. Kurihara and Shirayama, 2004; Kurihara, 2008; Dupont et al., et al 2008; Lischka et al., 2011), or indirectly by alterations of the base of the pelagic food web, i.e. the phytoplankton community and its biochemical composition and, thus, its nutritional value (e.g. Tortell et al., 2002; Nielsen et al., 2010; Urabe et al., 2003; Rossoll et al., 2012). In our mesocosms study, the phytoplankton community indeed changed with *p*CO₂. The diatom biomass, which had increased towards the end of the experiment, was highest in the low and intermediate *p*CO₂ levels, while the abundance of autotrophic dinoflagellates increased with *p*CO₂ (Brussard et al., 2012; Leu et al., 2012; Schulz et al., 2012). The heterotrophic dinoflagellate and microzooplankton community,

on the other hand, did not respond significantly to elevated CO₂ concentrations (Aberle et al., 2012). This suggests that the changes in primary producers did not immediately propagate to higher trophic levels. However, de Kluijver et al. (2012) found that grazing rates of *Calanus* spp. and cirripedia nauplii decreased with increasing pCO₂. It is thus possible that the mesozooplankton grazers can compensate changes in their food regime for a limited time, e.g. copepods by using internal energy stores (Graeve et al., 1994 and references therein), and that the experimental period of six weeks was too short to result in significant differences in community structures. However, even though the mesozooplankton community did not change as a whole, some taxa actually did respond to elevated CO₂ concentrations.

The mesocosms were closed during mass occurrence of barnacle nauplii (Cirripedia), which is a common phenomenon in spring in coastal areas including Kongsfjorden (Willis et al., 2006; Walkusz et al., 2009). In Kongsfjorden, *Semibalanus balanoides* is highly abundant (Jørgensen and Gulliksen, 2001) and together with *Balanus crenatus* it is a major competitor for space in encrusting species in Subarctic and Arctic ecosystems (Barnes and Kuklinski, 2004). Cirripedia larvae pass through six nauplius stages and one non-feeding cypris stage. The nauplii remain in the water column only for a short period until they molt to cypris larvae, which settle on hard substrate. Accordingly barnacle nauplii were extremely abundant in the fjord only at t₂ (28 522 ind. m⁻³) and thereafter cirripedia almost completely vanished from the water column. In the mesocosms, the cirripedia were trapped and were thus found throughout the entire study. Interestingly, their abundances were already high at t₋₂, while their abundance in the fjord at that time was low. It is thus possible that the barnacles were especially attracted by the conditions, e.g. low turbidity, within the bags. Also, compared to a previous study from Kongsfjorden (Walkusz et al., 2009; 3870 nauplii m⁻³) the initial cirripedia abundances were high in the mesocosms, ranging from 5200 to 20 500 nauplii m⁻³. We believe that, besides the favorable conditions the mesocosms may have provided, the sampling depth of only 12 m can partly explain our exceptionally high numbers of barnacle larvae. Tapia et al. (2010) show that, close to the coast

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of Southern California, the nauplii of several barnacle species were concentrated in the upper 10m. If the cirripedia in our study also exhibited such vertical distribution pattern, we have indeed sampled the layer of highest abundance while other studies integrated from the surface down to at least 25 m (Walkusz et al., 2009). However, also Basedow et al. (2010) found high numbers ($30\ 500\ \text{m}^{-3}$) at the Polar Front in northwestern Barents Sea, and thus very high abundances of barnacle nauplii do not seem unusual. With time, the number of nauplii decreased in all mesocosms while the number of cypris larvae increased indicating that the development of the cirripedia proceeded in the mesocosms. The cypris larvae in our study were quite abundant in the sediment traps, suggesting that they preferred deeper water and this matches the deeper vertical distribution of cypris larvae as described by Tapia et al. (2010).

When settled, some barnacle species such as *Chthamalus stellatus* inhabiting the sediment close to a volcanic vent may survive pH minima by closing their rostral plates (Hall-Spenser et al., 2008). However, mortality rates and reproductive success of *Semibalanus balanoides* were reduced at high $p\text{CO}_2$ ($922\ \mu\text{atm}$) as compared to natural $p\text{CO}_2$ ($380\ \mu\text{atm}$, Findlay et al., 2009). Also the nauplii have been shown to respond to elevated $p\text{CO}_2$ ($1000\ \mu\text{atm}$) with a 15 % lower survival rate than at control conditions (Findlay et al., 2010). We, in contrast, did not find an increase in mortality in high-level CO_2 mesocosms. Also, the carbon and nitrogen content of the nauplii ($4.6 \pm 3.1\ \mu\text{g C}$ and $1.1 \pm 0.5\ \mu\text{g N ind.}^{-1}$) and cypris larvae ($13.6 \pm 14.1\ \mu\text{g C}$ and $2.6 \pm 1.8\ \mu\text{g N ind.}^{-1}$), which were however only measured at the beginning of the experiment and at t_{11} , did not differ significantly among individuals from the different mesocosms (Niehoff, unpublished data). This indicates that – at least within the first two weeks of the experiment – the body mass of the barnacle larvae was unaffected by increased $p\text{CO}_2$. However, the relation of cirripedia nauplii and cypris larvae found in the sediment traps averaged over the entire experiment increased with the initial CO_2 concentration and this suggests that CO_2 could delay the development of cirripedia nauplii. De Kluijver et al. (2012), studying trophic interactions by means of stable isotope analyses, found that cirripedia grazing rates decreased with increasing CO_2 and they conclude that food

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quality was the major reason. Considering the results from the laboratory experiment (Findlay et al., 2010), we cannot, however, rule out a negative direct effect of CO₂ on the barnacle nauplii.

Besides cirripedia, polychaete larvae contributed considerably to the mesozooplankton communities but only towards the end of our experiment. During the first two weeks, it was mainly larger and, thus, older larvae while after t_{11} , small, early polychaete larvae appeared. As there were no adults entrapped in the mesocosms we believe that these larvae developed from eggs or trochophora larvae, which were not counted in our samples. In Kongfjorden, a large variety of benthic species is found (Wlodarska-Kowalczyk and Pearson, 2004) and small-bodied polychaetes such as *Chone paucibranchiata*, *Levinsenia gracilis*, *Aricidea* spp. and *Chaetozone setosa* often dominate the infauna (Kendall et al., 2003). Polychaete larvae, especially during their early development, are extremely difficult to distinguish. We, thus, cannot attribute the mass occurrence of the early polychaete larvae to any specific species. We do, however, believe that due to the synchrony of their occurrence and their uniform morphology, all small larvae belonged to one single species. The morphology of the older stages was heterogeneous and these larvae therefore very likely represented different species.

Both, the decrease in older larval stages and the increase in young stages were not related to the CO₂ concentration in the mesocosms or to the development of the phytoplankton, measured in terms of chlorophyll *a* (Schulz et al., 2012) suggesting that life cycle events rather than external factors, i.e. CO₂ and food supply, have caused the changes in the polychaete larvae abundance. Like other meroplanktonic organisms, polychaete larvae may reach high abundances in spring and summer due to pulsed reproduction (Mileikovsky, 1970 and references therein; Hickel, 1975; Frasz et al., 1991; Schlüter and Rachor, 2001). In the fjord, however, polychaete larvae were rare and it is thus possible that the entrapment within the mesocosms has favoured their development. To our knowledge there is yet no study on the impact of elevated $p\text{CO}_2$ on polychaete larvae. Studies on settled stages of *Nereis virens* indicate that this species indeed tolerates a pH as low as 6.5 (Batten and Bamber, 1996; Widdicombe

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and Needham, 2007). Also field studies in environments with naturally low pH such as volcanic CO₂ vents show that many polychaete species survive and grow even at extremely low pH (Cigliano et al., 2011; Kroeker et al., 2011).

Laboratory experiments have shown diverging results of high CO₂ concentrations on calcification. Shells of bivalves and gastropods, which were exposed to high CO₂ concentrations, were fragile and perforated (e.g. review by Kurihara, 2008; Lischka et al., 2011). Other studies (e.g. Wood et al., 2008; Ries et al., 2009), in contrast, have shown that some echinoderm, mollusc, coral and crustacean species either maintain or increase calcification at $p\text{CO}_2 < 1000 \mu\text{atm}$. However, the energetic costs for growth may increase and, therefore, calcifying organisms may be especially threatened when food is limited (e.g. Michaelidis et al., 2005; Wood et al., 2008). In our study, bivalve and gastropod larvae represented the calcifying fraction of the mesozooplankton, echinoderm larvae were not present and decapod larvae (i.e. *Thysanoessa raschkii*) were too scarce to reveal reliable information. Gastropod larvae did not show any response to $p\text{CO}_2$, but their numbers were overall low and thus possible effects of CO₂ may have not been detected. In contrast, the abundance of bivalve larvae as averaged over the entire experiment decreased with increasing $p\text{CO}_2$, and in the mesocosm with the highest $p\text{CO}_2$ (initially 1420 μatm , M9), their abundance never exceeded 88 larvae m^{-3} . The total number of bivalve larvae collected in the sediment traps, however, did not relate to the CO₂ concentration indicating that an increase in $p\text{CO}_2$ did not result in increased mortality. When the mesocosms were closed, the bivalve abundance was overall low (maximum of 44 larvae m^{-3}) and with time it increased in all mesocosms. Thus, our data suggest (i) that the larvae developed in the mesocosms from eggs or larvae $< 55 \mu\text{m}$, which were not captured and counted, respectively, in our samples and (ii) that their development was negatively influenced by elevated CO₂ concentrations. Whether the negative effects were due to hampered calcification and increasing energy demands (e.g. Gazeau et al., 2007; Ries et al., 2009) or due to shifts in the food regime (Brussard et al., 2012) cannot be clarified. Moreover, as in polychaetes, we did not determine the larvae to species level. In Kongsfjorden, several bivalve species are

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abundant (Włodarska-Koiczuk and Pearson, 2004) and all could have contributed to the larval population. To clarify whether and how elevated CO₂ may affect the different species needs to be studied in future.

Copepods often dominate zooplankton communities in all world oceans and play a major role in the trophic structure of pelagic ecosystems (e.g. Longhurst, 1985; Runge, 1988). In different species, mostly from boreal areas, egg production and hatching rate were reduced only at CO₂ concentrations > 5000 µatm and thus at values which greatly exceed what has been predicted for the future oceans (Mayor et al., 2007; Kurihara et al., 2004; Kurihara and Ishimatsu, 2008). In accordance to that, the copepod population developed similarly in all mesocosms with no apparent response to the CO₂ conditions. At the beginning (t_{-2}) the number of nauplii exceeded by far that of copepodite stages CI – CV and adults suggesting recent in situ reproductive activity. With time, the nauplii developed to copepodites and adults as their number increased in all mesocosms.

It is very likely that deeper sampling and using larger nets and mesh sizes, respectively, i.e. Nansen nets or WP2 nets and meshes > 150 µm as are usually used for collecting the larger mesozooplankton organisms (see Benfield and Wiebe, 2001, for review), would have yielded in larger numbers of larger, and thus, older copepod development stages as well as in greater species richness. Our Apstein net equipped with 55 µm meshes, however, was well designed for sampling in the mesocosms; larger nets were not suitable due to the diameter of the mesocosms of 2 m and the limited volume of the enclosed water. The copepod species, i.e. *Oithona similis*, *Calanus* spp. *Acartia longiremis* and *Microsetella norvegica*, we found in the upper 12 m water column are typical for Kongsfjorden (e.g. Weslawski et al., 1991). Also typical for this time of the year, *O. similis* was the most abundant copepod species (Walkucsz et al., 2004; Lischka and Hagen, 2005). In the genus *Calanus*, three species co-occur, i.e. *C. hyperboreus*, *C. glacialis* and *C. finmarchicus* which can be distinguished mainly by size (Kwasniewski et al., 2003). Prosome length measurements indicate that mostly *C. glacialis* were captured in the mesocosms; only few individuals were of the size of *C. finmarchicus* and *C. hyperboreus*, respectively (Niehoff, unpublished

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data). Other species frequently found in Kongsfjorden (Walkucsz et al., 2004; Lischka and Hagen, 2005), were absent (*Metridia longa*) or rare (*Pseudocalanus minutus*). *M. longa* as a mesopelagic species is unlikely to be located in the upper water column (e.g. Kosobokova and Hirche, 2000), and although *P. minutus* does inhabit the epipelagial, Lischka and Hagen (2005) found this species mostly below 50 m depth.

5 Conclusions

The mesocosm communities differed considerably from that in the fjord, and thus our results cannot fully reflect the natural situation, even at control conditions (M3 and M7). However, the communities in the different mesocosms can be very well compared among each other as their initial compositions were similar and the abundant taxa survived and developed under the experimental conditions. Our experiment has shown that the mesozooplankton did not respond significantly to elevated CO₂ concentration on the community level within the six weeks of our study. However, specific taxa, i.e. cirripedia and bivalvia, have been affected by the experimental treatment and it appears that their development and growth was hampered by high pCO₂. This suggests that if elevated CO₂ concentrations have persisted, also the community structure in the mesocosms might have changed significantly. The nature of the CO₂ effect, either direct or indirect, remains open and needs to be addressed in future studies.

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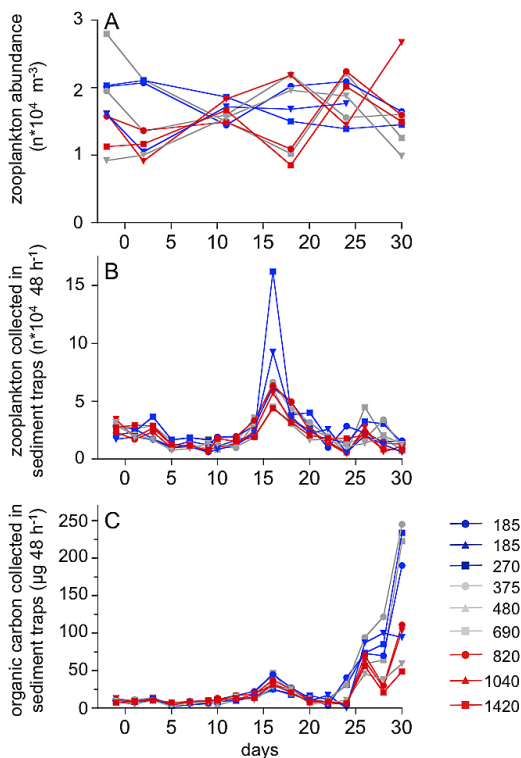


Fig. 1. Total mesozooplankton abundance and carbon flux in nine mesocosms with different CO₂ concentrations. **(A)** Abundance in the water column of the mesocosms, **(B)** total number of organisms collected by the sediment traps, **(C)** total organic carbon collected by sediment traps. The numbers given in the legend present initial CO₂ concentrations (µatm) in the mesocosms. Regarding sediment trap data **(B, C)** note that the sampling interval at t_{10} was 24 h and thus the data were projected to n individuals collected in 48 h. At t_{30} , no sample was taken in the water column of M7 **(A)**.

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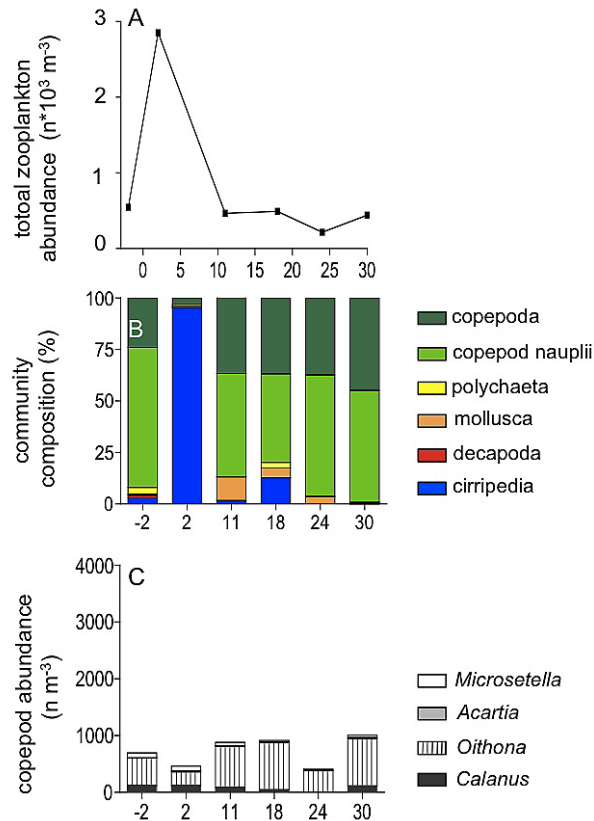


Fig. 2. Development of the mesozooplankton in Kongsfjorden. **(A)** Total abundance, **(B)** community composition (note that “copepoda” includes copepodite stages and adults), **(C)** copepod abundance and taxonomic composition.

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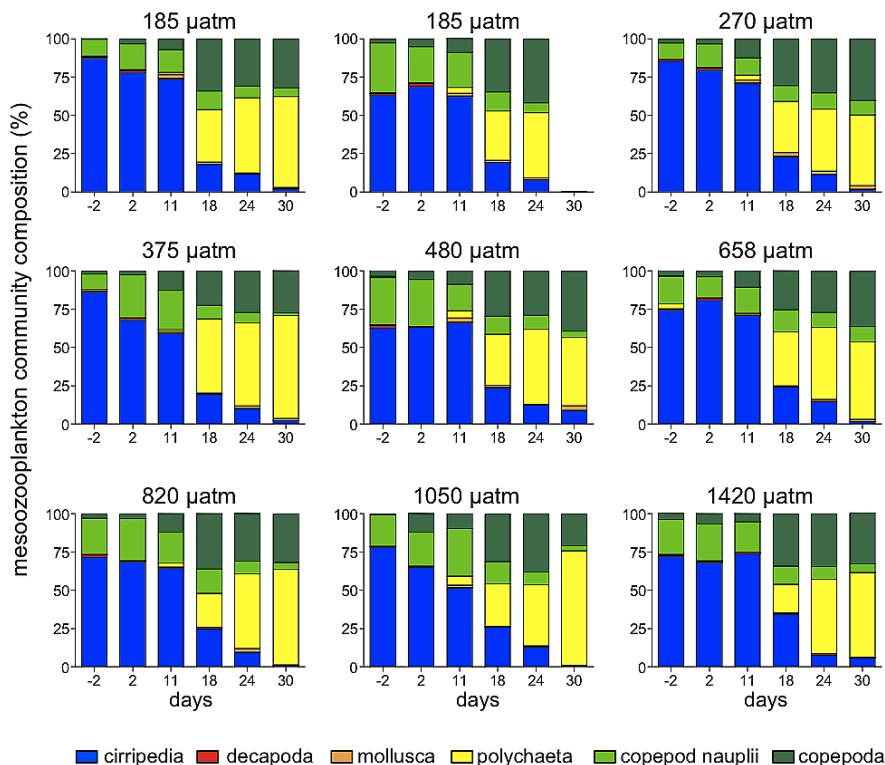


Fig. 3. Mesozooplankton community composition in the water column of nine mesocosms, numbers on top of the panels present initial CO₂ concentration in each mesocosm. Note that “copepoda” includes copepodite stages and adults. At t_{30} , no sample was taken in M7.

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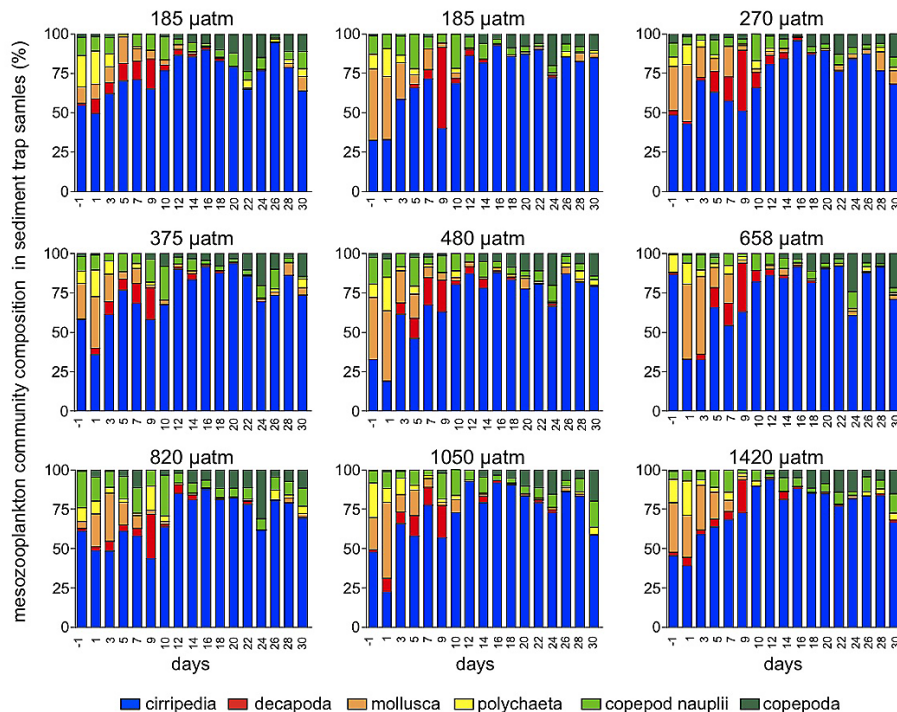


Fig. 4. Mesozooplankton composition in the sediment traps of the mesocosms, numbers on top of the panels present initial CO₂ concentration in each mesocosm, note that “copepoda” includes copepodite stages and adults.

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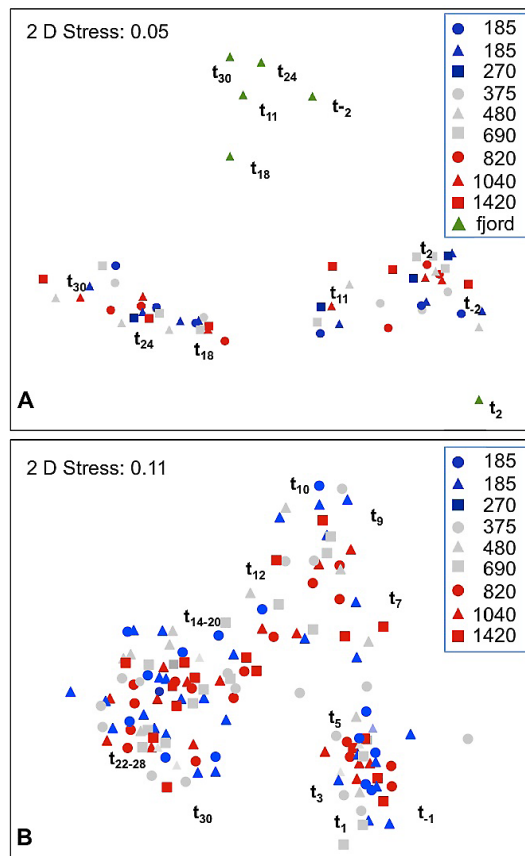


Fig. 5. Multi-dimensional scaling plots (Bray-Curtis similarities) of square root transformed abundance data including all species which contributed > 1 % to the mesozooplankton community; **(A)** presents the results from all water column samples, **(B)** the results from all sediment trap samples. t_{-2} – t_{30} indicate the position of the respective sampling dates.

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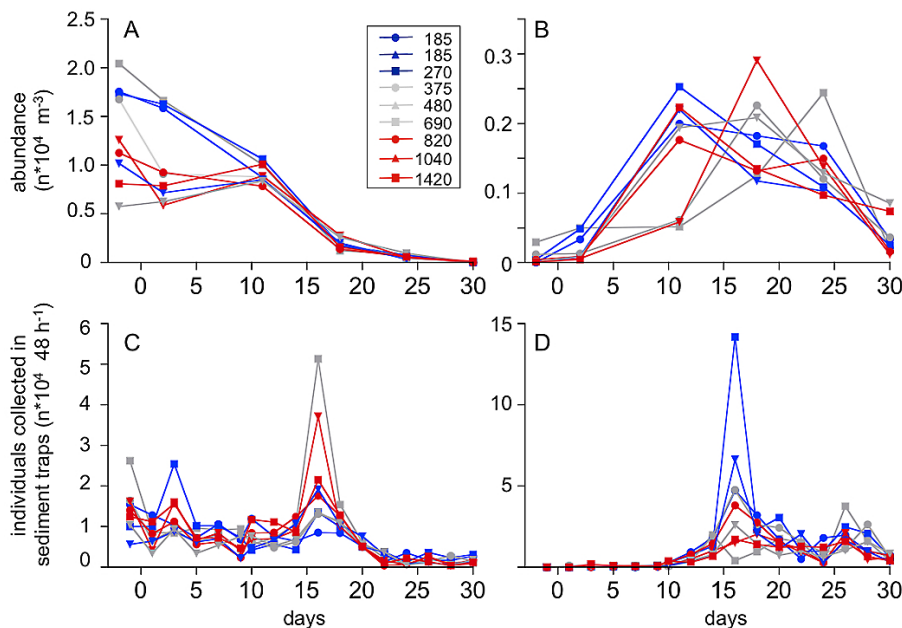


Fig. 6. Development of the cirripedia abundance in the mesocosms. **(A)** (Nauplii) and **(B)** (cypris larvae) present data from the water column, **(C)** (nauplii) and **(D)** (cypris larvae) present data from the sediment trap samples. The numbers given in the legend present initial CO₂ concentrations (μatm) in the mesocosms. Regarding sediment trap data **(C, D)** note that the sampling interval at t_{10} was 24 h and thus the data were projected to n individuals collected in 48 h. At t_{30} , no sample was taken in the water column of M7.

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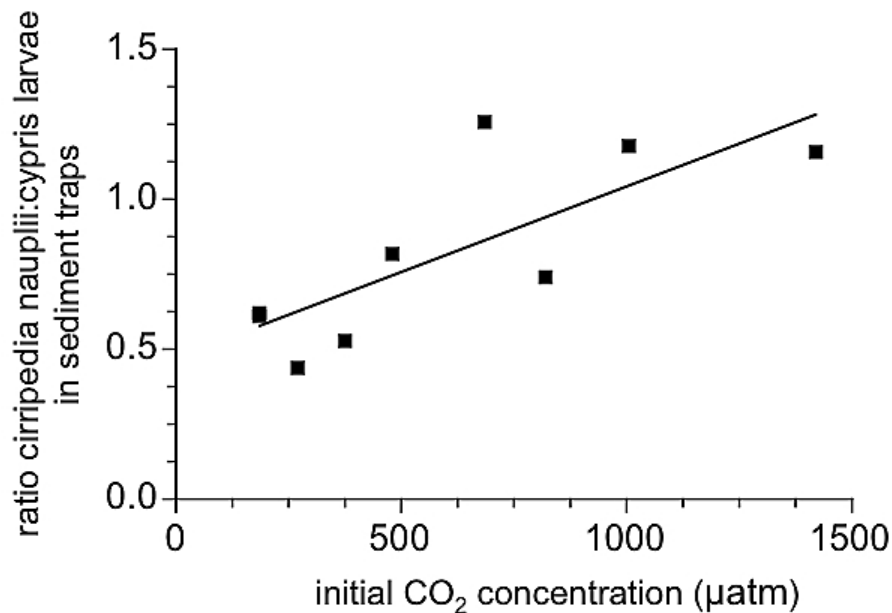


Fig. 7. Ratio of cirripedia nauplii to cypris larvae (averaged over the entire experimental period) in the sediment trap samples in relation to the initial $p\text{CO}_2$, linear regression.

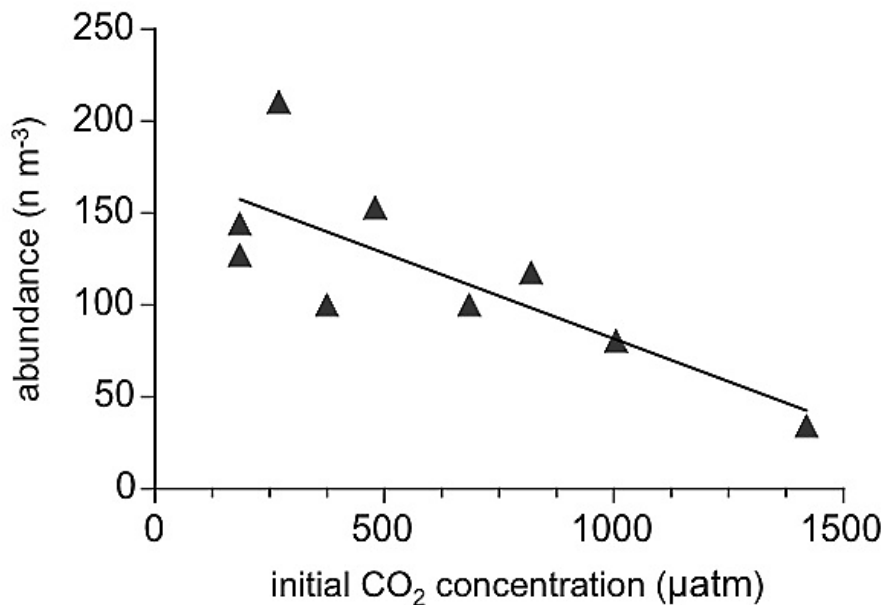


Fig. 8. Abundance of bivalve larvae (averaged over the entire experimental period) in the water column in relation to the initial $p\text{CO}_2$.

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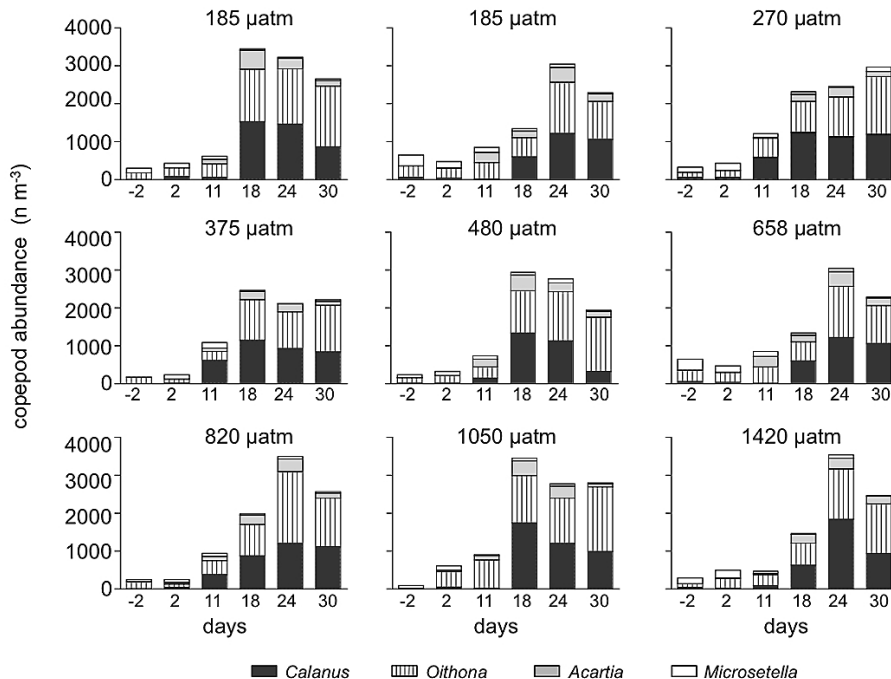


Fig. 9. Copepod abundance and taxonomic composition (genera) in the water column of the mesocosms; the data presented here include copepodites and adults of the respective genus; numbers on top of the panels present initial CO₂ concentrations in each mesocosm. At t_{30} , no sample was taken in M7.

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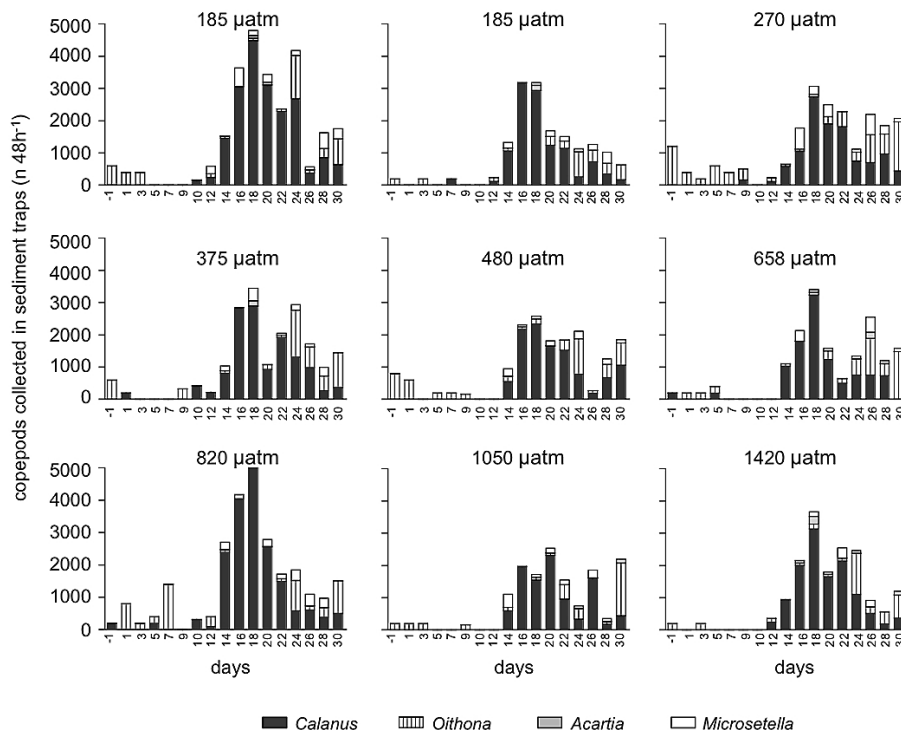


Fig. 10. Copepod abundance and taxonomic composition (genera) in the sediment traps of the mesocosms; data presented here include copepodites and adults of the respective genus; numbers on top of the panels present initial CO₂ concentration in each mesocosms. Note that the sampling interval at t_{10} was 24 h and thus the data were projected to n individuals collected in 48 h.

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