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Mesozooplankton community development at elevated CO_2 concentrations: results from a mesocosm experiment in an Arctic fjord

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Abstract. The increasing CO_2 concentration in the atmosphere caused by burning fossil fuels leads to increasing pCO_2 and decreasing pH in the world ocean. These changes may have severe consequences for marine biota, especially in cold-water ecosystems due to higher solubility of CO_2. However, studies on the response of mesozooplankton communities to elevated CO_2 are still lacking. In order to test whether abundance and taxonomic composition change with pCO_2, we have sampled nine mesocosms, which were deployed in Kongsfjorden, an Arctic fjord at Svalbard, and were adjusted to eight CO_2 concentrations, initially ranging from 185 µatm to 1420 µatm. Vertical net hauls were taken weekly over about one month 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 analysed to account for losses due to vertical migration and mortality. The taxonomic analysis revealed that meroplanktonic larvae (Cirripedia, Polychaeta, Bivalvia, Gastropoda, and Decapoda) 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 and the pCO_2 had no significant effect on the overall community structure. Also, we did not find significant relationships between the pCO_2 level and the abundance of single taxa. Changes in heterogeneous communities are, however, difficult to detect, and the exposure to elevated pCO_2 was relatively short. We therefore suggest that future mesocosm experiments should be run for longer periods.

1 Introduction

The increasing CO_2 concentration in the atmosphere caused by burning fossil fuels leads to increasing CO_2 concentrations in the world ocean at a rate unprecedented in the earth history. Since preindustrial times, atmospheric CO_2 concentrations have increased from about 280 to 380 µatm, and future scenarios predict up to 1000 µatm by the end of this century (IPCC, 2007). When atmospheric CO_2 dissolves in seawater, it reacts with water to form carbonic acid (H_2CO_3). Carbonic acid dissociates immediately to bicarbonate ($[HCO_3^-]$) and hydrogen ions ($[H^+]$). In a second, pH-dependent reaction, bicarbonate ions dissociate to carbonate $[CO3^{-2}]$ and $[H^+]$. Thus, with increasing pCO_2 the seawater pH decreases and free carbonate ions protonate and form bicarbonate. This process is referred to as ocean acidification (OA) as the oceans not only accumulate carbon but also become more acidic. Accordingly, the pH in surface seawaters today has decreased by 0.1 units from preindustrial values of approx 8.2. A modelling study by Caldeira and Wicket (2003), who used the atmospheric pCO_2 as observed from 1975 to 2000 and CO_2 emissions from the IPCC's business-as-usual IS92a scenario, suggests that the pH may drop by approximately 0.5 units by the end of this century and reach a maximum decrease of 0.77 at around the year 2300. 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 CO_2 increases with decreasing temperatures, polar waters are particularly subject to ocean acidification (Orr et al., 2005).

At elevated CO_2 levels, pelagic primary production may increase due to lower costs of carbon fixation, the stoichiometry and the biochemical composition of some algal species may change (*Emiliania huxleyi*, Leonardos and Geider, 2005; Borchard et al., 2011, *Thalassiosira pseudonana*, Rossoll et al., 2012) and carbon overconsumption may lead to increased exudation of transparent extracellular particles (Engel, 2002). 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 coccolithophores, Foraminifera, Pteropoda and larvae of Echinodermata and Bivalvia as the carbonate ion concentration will decrease and this will affect the formation of calcareous structures and the energy budget (e.g. Lischka et al., 2011; Talmage and Goebler, 2010; Yu et al., 2011). The direct effect of CO_2 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 to fairly high CO_2 concentrations. Egg production, hatching success and/or survival rates of nauplii, copepodites and adults decreased significantly only at concentrations > 5000 ppm while they remained high at lower CO_2 levels (*Acartia* spp., Kurihara et al., 2004; Kurihara and Ishimatsu, 2008; *Calanus* spp., Mayor et al., 2007, 2012; *C. glacialis*, Weydmann et al., 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 ppm (Kawaguchi et al., 2011), suggesting that this species is more sensitive to CO_2 than copepods for reasons that still remain to be solved (Mayor et al., 2012). In shelf seas and coastal areas, meroplanktonic larvae occur in seasonally high abundances (e.g. Fransz et al., 1991; Fetzer et al., 2002; Walkusz et al., 2009). Among these, non-calcifying larvae of some benthic species were also shown to be sensitive to $p\mathrm{CO_2}$, e.g. barnacle nauplii (Findlay et al., 2009, 2010). Beside direct effects, increased $p\mathrm{CO_2}$ may also alter trophic interactions. Rossoll et al. (2012) have shown that the food quality, i.e. the content of polyunsaturated fatty acids in diatoms fed to *Acartia tonsa*, was altered by increasing $p\mathrm{CO_2}$, which in turn reduced the reproductive success of the copepods. Similarly, laboratory experiments by Urabe et al. (2003) indicate that lower growth rates of the pelagic freshwater species *Daphnia pulicaria* (Branchiopoda) at high $p\mathrm{CO_2}$ were due to altered algal C : P ratios.

Laboratory studies, both on direct and indirect effects, are especially suitable to tackle physiological thresholds and mechanisms but cannot target the question how mesozooplankton organisms respond in their natural environment. Mesocosm experiments, in contrast, are considered an important tool for studying the impact of ocean acidification on pelagic community dynamics under near-natural conditions (e.g. Delille et al., 2005; Paulino et al., 2008). Up to date, there has been one large mesocosm experiment within the Pelagic Ecosystem CO_2 Enrichment study (PeECE III;

reviewed by Riebesell et al., 2008) studying the impact of $p\mathrm{CO_2}$ at the outdoor facilities at Espegrend, Bergen, Norway. Studies from high latitudes, however, are lacking. Moreover, the focus of the study in Bergen was on bacteria, phytoplankton and microzooplankton communities (see references in Riebesell et al., 2008). Only Carotenuto et al. (2007) studied a mesozooplankton species, i.e. *Calanus finmarchicus*, and they suggested that the quality of its algal food was altered by increasing $p\mathrm{CO_2}$, which in turn affected nauplii recruitment.

In the present mesocosm experiment, which is part of the European Project on Ocean Acidification (EPOCA), the response of different tropic levels to elevated CO_2 concentrations was investigated in June/July 2010 in a high latitude glacial fjord, Kongsfjorden, Svalbard (see publications within this issue). Within this framework our study focuses on determining the abundance and taxonomic composition of the mesozooplankton at different $p\mathrm{CO_2}$ levels. Direct and indirect effects of high CO_2 concentrations on single pelagic species, which provoke lower growth (e.g. Yu et al., 2011), recruitment (Carotenuto et al., 2007) and reproductive rates (Rossoll et al., 2012) as well as higher mortality (Findlay et al., 2009, 2010), may ultimately change the community dynamics (Doney et al., 2009) with possibly severe consequences for the food web (Fabry et al., 2008). At present, however, it is not known whether species-specific effects found in laboratory experiments will also occur in natural pelagic environments and, if they do, whether they are strong enough to change the community structure. Therefore, we sampled nine mesocosms, which were initially adjusted to eight CO_2 concentrations ranging from 185 µatm to 1420 µatm (Bellerby et al., 2012) to determine the abundance and taxonomic composition of mesozooplankton and monitor their development at different CO_2 concentrations. As sampling frequency and net size were limited, we focus here on the dominating groups in the community.

2   Methods

This present study was part of the EPOCA CO_2 enrichment mesocosm experiment conducted in Kongsfjorden ($78°56.2'$ N and $11°53.6'$ E) in Ny-Ålesund, Svalbard, in June/July 2010. Kongsfjorden, a glacial fjord on 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 CO_2 on the dynamics in the pelagic system, nine KOSMOS (**K**iel **O**ff-**S**hore **M**esocosms for future **O**cean **S**imulation) offshore mesocosms of 15 m water

depth and approx. $47\,m^3$ volume were deployed in Kongsfjorden at a bottom depth of $\sim 40\,m$ and were enriched with different CO_2 concentrations. Two metres above the bottom, a sediment trap was installed inside each mesocosm, covering the entire mesocosm area ($3.14\,m^2$) to minimise material losses (Czerny et al., 2012b). The mesocosms were designed by the GEOMAR, Kiel, Germany, and technical details are described in Riebesell et al. (2012), Czerny et al. (2012a) and Schulz et al. (2013). The day of sampling after the first injection of CO_2 into the mesocosms was defined as the beginning of the CO_2 experiment (t_0), and $t_{>0}$ indicates the number of days of exposure to manipulated CO_2 conditions (Riebesell et al., 2012). Samples taken prior to the manipulation (for mesozooplankton t_{-2} in the water column and t_{-1} in the sediment traps) reflect the initial status of the pelagic community.

When the enclosure 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, Chaetognatha and adult pteropods, which are low in abundance and patchily distributed, from the zooplankton community. Pteropods are important in Arctic waters, and laboratory experiments have shown that their shells dissolve at elevated pCO_2 (Lischka et al., 2011). To study their response to elevated pCO_2 at near-natural conditions, 190 live *Limacina helicina*, sampled from the fjord, were added to each mesocosm (Schulz et al., 2013). The pteropods, however, did not survive for long, and after one week most snails had vanished from the water column in the mesocosms.

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 salt additions (Schulz et al., 2013). 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 ($+5\,\mu mol\,kg^{-1}$), phosphate ($+0.3\,\mu mol\,kg^{-1}$) and silicate ($+2.5\,\mu mol\,kg^{-1}$) were added to each mesocosm on t_{13} (Schulz et al., 2013).

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). Starting at t_{-1} after the sampling routine, this water (70–$320\,L$) was injected stepwise over four days until the target CO_2 concentrations were reached at t_2; some fine-tuning was conducted on 11 June (t_4; Riebesell et al., 2012). Two mesocosms served as controls and were not manipulated; here filtered seawater was injected to initiate the same perturbation as in the CO_2 manipulated mesocosms. Initial CO_2 levels at t_8, when mixing with the dead water volume below the sediment traps was completed, were 185 (mesocosm M3 and M7), 270 (M2), 375 (M4), 480 (M8), 685 (M1), 820 (M6), 1050 (M5) and

1420 (M9) μatm; the ambient concentration in the fjord at that time was $145\,\mu atm$, which indicates post-bloom conditions (Bellerby et al., 2012). Due to gas exchange and biological processes, the CO_2 concentration decreased continuously over the entire experimental period in all mesocosms (pCO_2 at t_{30} was $165\,\mu atm$ in M3, $160\,\mu atm$ in M7, $220\,\mu atm$ in M2, $290\,\mu atm$ in M4, $365\,\mu atm$ in M8, $500\,\mu atm$ in M1, $555\,\mu atm$ in M6, $715\,\mu atm$ in M5 and $855\,\mu atm$ in M9) (Czerny et al., 2012a; Bellerby et al., 2012). The gradient from low to high CO_2 levels, however, remained throughout the experiment (Bellerby et al., 2012).

CTD casts were taken daily between 02:00 and 04:00 p.m. to monitor the development of temperature, salinity and pH in the mesocosms and the fjord (Schulz et al., 2013). Temperature increased from 2 to $6\,°C$ in all mesocosms, following the temperature development in the surrounding fjord water (Schulz et al., 2013). Salinity was ~ 33.5 when the mesocosms were closed. After the salt addition the salinity was ~ 34 and remained stable throughout the experiment (Schulz et al., 2013). Depth-integrated water samples were taken also daily between 09:00 and 11:00 a.m. using an Integrating Water Sampler (Hydro-Bios, Kiel, Germany) to determine CO_2 concentration from total alkalinity 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 bloom events which occurred simultaneously in all nine mesocosms: the first in phase 1 (t_4–t_{13} from the end of the CO_2 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., 2013).

2.2 Zooplankton sampling

In order not to re-suspend material that had settled in the sediment traps, sampling of the water column was restricted to $12\,m$ depth. Zooplankton were sampled between 09:00 a.m. and 02:00 p.m. in approximately weekly intervals by vertical net tows with an Apstein net of $17\,cm$ diameter and $55\,\mu m$ mesh size in the mesocosms and in the fjord. Sampling days were t_{-2} prior to CO_2 manipulation, t_2 after the CO_2 manipulations were completed, 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 hexamethylenetetramine. Under a dissecting microscope, the organisms were sorted and determined to the lowest taxonomical level, if possible to species and/or developmental stage (*Calanus* spp.). In the fjord, zooplankton abundances were relatively low, and thus all organisms were sorted and counted in each sample. In the mesocosms, the abundance of mesozooplankton organisms was considerably

higher for most of the experimental period, and therefore the samples were subdivided with a plankton splitter (Hydro-Bios) usually to 1/8 (44 of the 53 mesocosm samples) and at maximum to 1/32 (2 of the 53 mesocosm samples). Abundant species ($n > 50$ in an aliquot) were sorted only from one subsample, while less abundant species were sorted from at least two subsamples. Comparing the subsamples indicates that the numbers of organisms, even of rare species, did not differ much among the subsamples. Abundances were calculated in terms of individuals m^{-3}. Eggs and larvae $< 55\,\mu m$, e.g. trochophore larvae, were not sampled quantitatively with the Apstein net and are not further considered.

The sediment traps were emptied every second day using a vacuum system, and then the major part of a sample was analysed for total particulate carbon and nitrogen content (Czerny et al., 2012a). For the determination of mesozooplankton abundance and community composition, 20–30 ml subsamples from the traps (in total 153) were completely analysed 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 analysed at the Kings Bay Marine Laboratory within 24 h after collection. Thereafter, they were preserved in 4 % formalin buffered with hexamethylenetetramine and analysed later at the Alfred Wegener Institute (Bremerhaven, Germany).

The Shannon index (H) was calculated as an index for the biodiversity in each mesocosm, as it represents the occurrence of a group and its relative contribution to the community. The ten groups included in the calculation were larvae of Cirripedia, Polychaeta, Bivalvia, Gastropoda and Euphausiacea, copepod nauplii, *Calanus*, *Acartia*, *Oithona* and *Microsetella*; the developmental stages of Cirripedia and Copepoda were not distinguished. When all groups in the respective data set are equally common, the Shannon index is $l_n(10$ *groups*), i.e. 2.3; lower values indicate that single groups dominate the community. Linear mixed effect models were then fitted to the Shannon indices of the water column and sediment trap samples, respectively, to determine the dependence of diversity H on time and on CO_2 as a linear response combined with two nutrient conditions (t_{-2}, t_2 and t_{11} representative of phase 1 and t_{18}, t_{24} and t_{30} representative of phase 2 and 3; Schulz et al., 2013). In addition, random effects were modelled by CO_2, grouping the data by mesocosm (i.e. CO_2 concentration). Computations were performed with the programme R (R development core team, 2011), using lmer (maximum likelihood method) from package lme4 (Bates et al., 2012); H was computed in the vegan package (Oksanen et al., 2012).

To elucidate whether the abundance of specific groups decreases with the CO_2 level, we have calculated Spearman rank correlation coefficients (r_s), which measure the strength of association between two ranked variables (pCO_2 level and abundance at different sampling dates). This test does not depend on normal distribution and does not require a linear relationship between the parameters. We tested for significance of the relationship using the program GraphPad Prism (version 4.0 for Mac).

3 Results

3.1 Total zooplankton abundance

The initial total zooplankton abundance at t_{-2} in the water column of the mesocosms ranged from 9290 ind. m^{-3} in M4 (later adjusted to 480 µatm) to 27 860 ind. m^{-3} in M1 (later adjusted to 685 µatm). During the entire experiment, the total abundance changed slightly in all mesocosms (Fig. 1a) but with no apparent trend, neither with time nor with CO_2 concentration. Only in M2 (270 µatm), the Spearman rank correlation indicated a significant decrease of total abundance with time (r_s: -0.886, $p = 0.03$). No significant relationships between the CO_2 levels and the total zooplankton abundance were found on any sampling day (Spearman rank tests, $p > 0.05$). The zooplankton abundance in the fjord was low (Fig. 2a) except for t_2.

The sediment traps, which were only deployed in the mesocosms but not in the fjord, collected between approx. 277 000 (M8, 480 µatm) and 505 000 (M2, 270 µatm) organisms over 32 days of sampling, which equals 8600 and 15 800 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. The number of organisms found in the traps changed with time in all mesocosms (Fig. 1b). From t_{-1} to t_3, the numbers of organisms ranged between approx. 14 600 and 35 400 ind. h^{-1}, while from t_5 to t_{12} fewer organisms were found (5600 and 18 900 ind. 48 h^{-1}). At t_{14}, in all mesocosms more than 17,000 organisms were collected with a maximum of 33 800 ind. 48 h^{-1} in M1 (685 µatm). At t_{16}, overall the highest numbers were recorded in the traps, ranging from 41 500 (M9, 1420 µatm) to 160 900 ind. 48 h^{-1} (M2, 270 µatm). At t_{18}, the number of organisms had decreased to 28 800 (M8, 480 µatm) and a maximum of 46 900 (M6, 820 µatm) ind. 48 h^{-1}. Until the end of the experiment, the numbers varied between 5800 and 43 400 ind. 48 h^{-1}. The relationship between the CO_2 level and the total number of organisms found in the traps was not significant on any sampling day (Spearman rank tests, $p > 0.05$), except for t_{16} ($r = 0.695$, $p = 0.043$).

3.2 Community composition

In total, ten groups contributed regularly to the communities in the mesocosms, i.e. larvae of cirripedes, polychaetes, bivalves, gastropods and euphausiids as well as copepod nauplii and the copepod genera *Calanus*, *Acartia*, *Oithona* and *Microsetella* (including both adults and copepodite stages). Cirripedia and copepods dominated the community over the
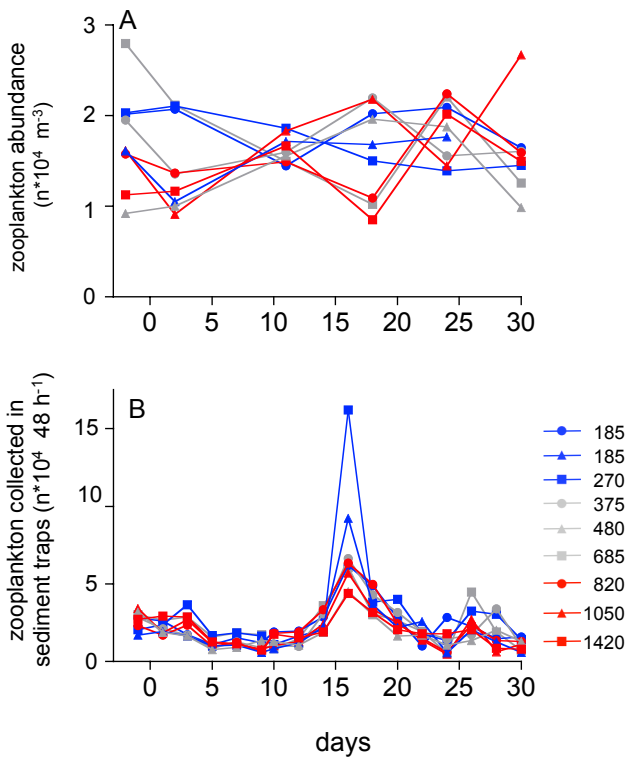
Fig. 1. Total mesozooplankton abundance in the water column **(A)** and in the sediment traps **(B)** of nine mesocosms with different CO_2 levels. The numbers in the legend present initial CO_2 concentrations (µatm) after the CO_2 manipulation was completed.

Fig. 2. Development of the mesozooplankton in Kongsfjorden. Presented are total abundance **(A)**, community composition **(B)** and abundance and taxonomic composition of the copepod population **(C)**. The copepod data include both copepodites and adults; copepod nauplii are presented as a different group. Please, note that the scales are different.

experimental period while bivalve larvae and calyptopis larvae of *Thysanoessa raschii* (Euphausiacea) were frequently found but usually in low numbers (< 5 % of the zooplankton abundance). Gastropod larvae (*Limacina helicina*) were only found toward the end of the mesocosm experiment, mainly at t_{24} and t_{30}. Polychaete larvae were always present, and their contribution to the community changed considerably with time. Chaetognatha, Cnidaria and Amphipoda (*Themisto* sp.) and Pteropoda (juvenile and adult *Limacina helicina*) were very rare (≪ 1 % of the zooplankton abundance). We believe that these groups were not sampled quantitatively, and therefore they are not considered in the analysis of community development. The community in the fjord (Fig. 2b) was completely different from those enclosed in the mesocosms. In the fjord, copepods were always the most abundant taxon, except for t_2 when Cirripedia were found in high numbers.

The changes of the relative contribution of the ten taxa to the community (Figs. 3 and 4) are reflected in the Shannon index (H). H values were low (< 0.4) in the water column when the mesocosms were closed and increased towards maximum values (> 1.1) in all mesocosms at t_{18} (Fig. 5a), indicating that the groups contributed more evenly to the community. In the sediment traps, H values were highest at the beginning of our study (> 1, except for M1, 650 µatm) and
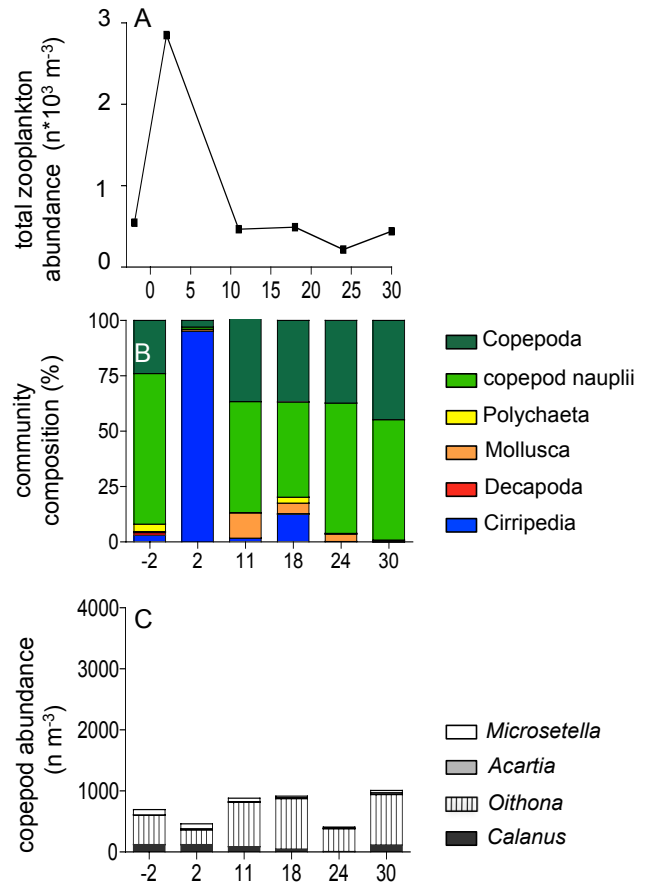
decreased within the first two weeks of exposure to different CO_2 levels to lower values (Fig. 5b). Overall lowest values were found at t_{16}, when H was < 0.6 in all mesocosms, likely reflecting that the relative contribution of cypris larvae had increased considerably. Thereafter, H increased again in all mesocosms and values at t_{30} ranged between 0.6 and 1.25.

In both the water column and the sediment traps, the CO_2 level had no significant influence on H as the linear mixed model fits revealed that a fixed effect of CO_2 is not significant for the time dependency of H (ANOVA, $p = 0.11$ for data from the water column; $p = 0.46$ for data from the sediment traps, Fig. 5).

3.3 Cirripedia

Cirripedia dominated the zooplankton community in the water column (Fig. 3) of the mesocosms over the first two weeks of the experiment and in the sediment traps (Fig. 4) over the entire experiment. At the beginning of the
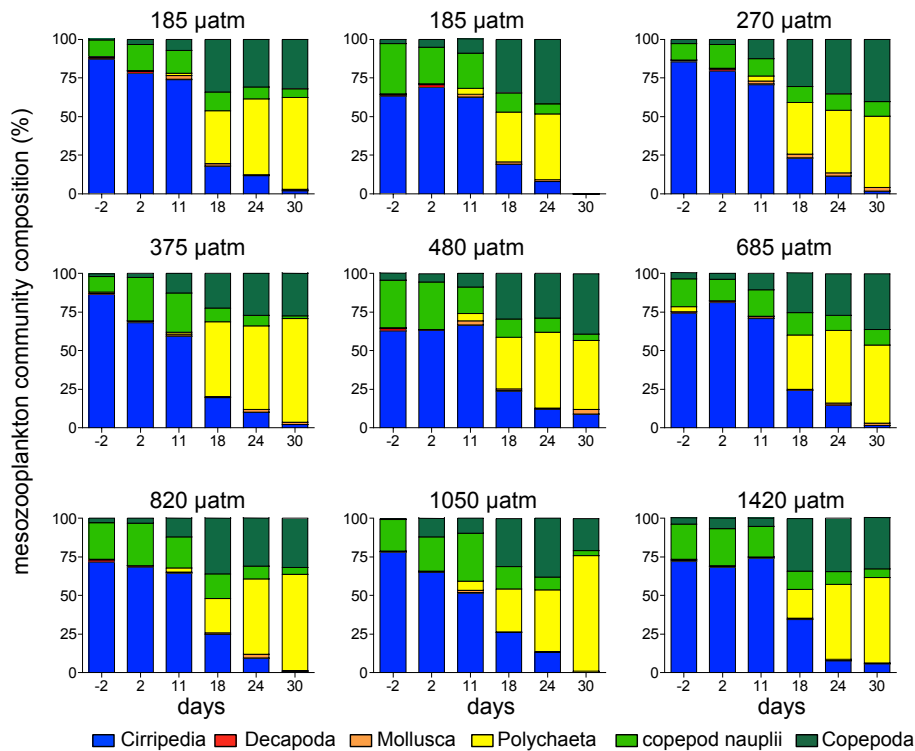
Fig. 3. Mesozooplankton community composition (%) in the water column of nine mesocosms: numbers on top of the panels present the initial CO_2 concentration in each mesocosm after the CO_2 manipulation was completed. At t_{30}, no samples were taken in M7 (185 µatm) and no data are available. Please, note that "Copepoda" includes both copepodites and adults; copepod nauplii are presented as a different group.

experiment, almost all individuals were in the nauplius stage (approx. 5000–20 000 ind. m^{-3}) while cypris larvae, the last developmental stage, which settles on hard substrate, were rare (Fig. 6a and b). With time, the number of nauplii decreased and cypris larvae increased in abundance (maximum of approx. 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 were frequent in the sediment traps (Fig. 6d), indicating that this stage migrated towards deeper water. Significant relationships between the number of Cirripedia and the pCO$_2$ level were not found on any sampling day (Spearman rank tests, $p > 0.05$), except for cypris larvae at t_{16}, when their abundance decreased with increasing pCO$_2$ in the sediment traps.

3.4 Polychaetes

At the beginning of the experiment (t_{-2}) before the mesocosms were treated with CO_2, polychaete larvae of > 500 µm length were found in all mesocosms except for M4 (375 µatm) and they reached relatively high abundances of up to 882 ind. m^{-3} (M1, 685 µatm). At this time, they were also found in the fjord (184 ind. m^{-3}). Two weeks later (t_{11}), larvae were found in the four mesocosms adjusted to 185, 480, 685 and 1420 µatm with a maximum abundance of

29 ind. m^{-3} (M9, 1420); 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, 685 µatm). 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 by end of the experiment from t_6 to t_{30} (total of 715 to 2930 ind. mesocosm^{-1}, corresponding to an average of 28 to 112 ind. mesocosm^{-1} d^{-1}).

Small polychaete larvae of 300–500 µm length appeared at t_{11}, two days before nutrient addition, in all mesocosms except for M1 (685 µatm) and M4 (480 µatm). Their number increased considerably during the following week to maximum abundances between approx. 6000 (M5, 1050 µatm) and 10 700 (M4, 375 µatm) ind. m^{-3}. Thus, for the second half of the experiment, the polychaete larvae contributed high proportions to the zooplankton communities in the mesocosms (Fig. 3). The sediment traps rarely collected small polychaete larvae, and in the fjord this larval type was only found on t_{18} with a comparably low abundance of 110 ind. m^{-3}. Neither in the water column nor in the sediment traps, there were significant relationships between the number of polychaetes and the pCO$_2$ level on any sampling day (Spearman rank tests, $p > 0.05$).
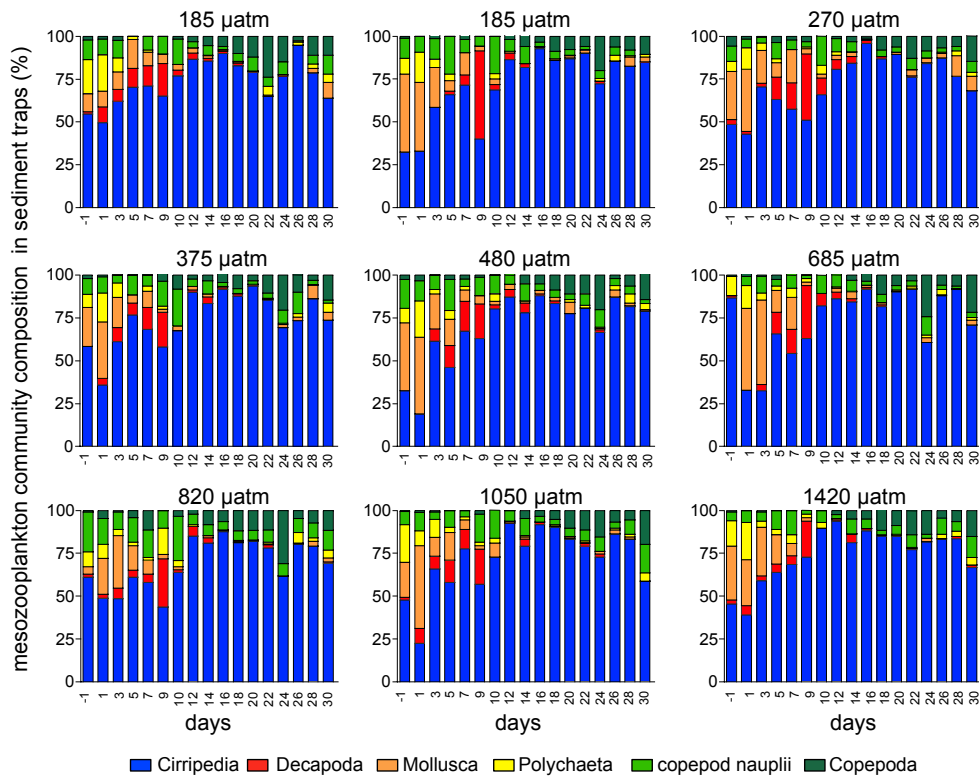
Fig. 4. Mesozooplankton community composition (%) in the sediment traps of the mesocosms: numbers on top of the panels present the initial CO_2 concentration in each mesocosm after the CO_2 manipulation was completed. Please, note that "Copepoda" includes copepodites and adults; copepod nauplii are presented as a different group.

Fig. 5. Shannon indices (H) calculated for samples from the water column (**A**) and the sediment traps (**B**). The numbers in the legend present initial CO_2 concentrations (µmol) after the CO_2 manipulation was completed. Linear mixed effects models (dotted lines) were fitted to determine the dependence of diversity H on time and on CO_2 as a linear response combined with two nutrient conditions (t_{-2}, t_2 and t_{11} representative of phase 1 and t_{18}, t_{24} and t_{30} representative of phase 2 and 3).

3.5 Molluscs

The abundance of bivalve larvae (Fig. 7a) was low as compared to the other taxa. At the beginning of our experiment, only 0–44 ind. m^{-3} were found but 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, 820 µatm) on t_{24} in the mesocosms (Fig. 7a) and 522 ind. m^{-3} on t_{11} in the fjord. Relationships of bivalve larval abundance and CO_2 level were not significant except for on t_2, immediately after the CO_2 manipulation (Spearman $r = -0.725$, $p = 0.03$), and t_{18}, the first sampling after nutrients had been added at t_{13} (Spearman $r = -0.815$, $p = 0.01$). It has to be, however, noted that the bivalve larvae abundance on three to five sampling dates exceeded 100 ind. m^{-3} in mesocosms of initial CO_2 concentrations between 185 and 480 µatm. At initial pCO_2 of 685, 820 and 1050 µatm, abundances > 100 ind. m^{-3} were only found once, and in M9 (1420 µatm) bivalve abundance never exceeded 88 ind. m^{-3} (Fig. 7a).

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. 4). During this time, between approx. 10 200 (M3, 185 µatm) and 32 200 (M1, 685 µatm) larvae were collected, corresponding to an average
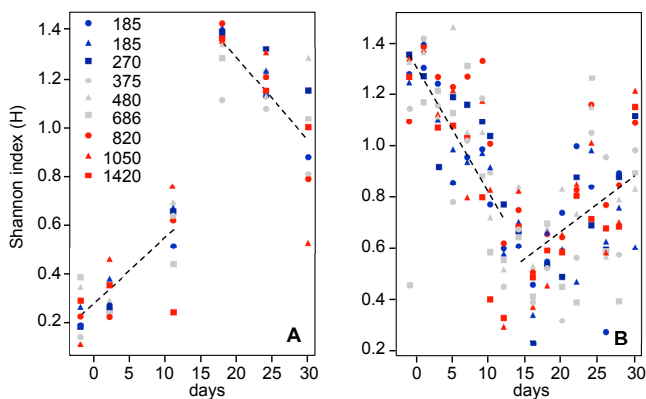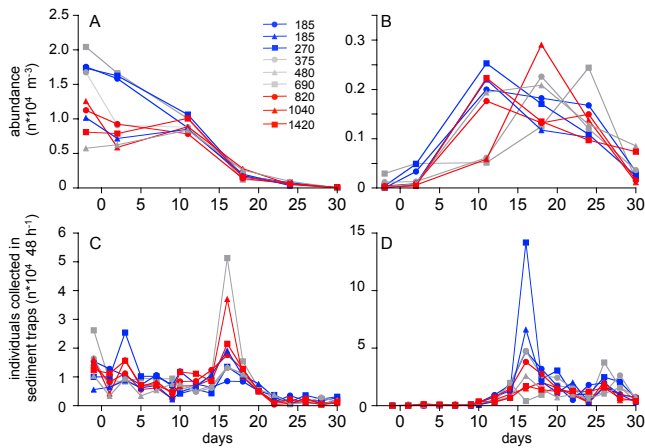
Fig. 6. Development of the Cirripedia abundance in the mesocosms. **(A)** (nauplii) and **(B)** (cypris larvae) present data from the water column; **(C)** (nauplii) and **(D)** (cypris larvae) present data from the sediment trap samples. The numbers given in the legend present initial CO_2 concentrations (µatm) in the mesocosms after the CO_2 manipulation was completed. Please note that the scales are different.

Fig. 7. Abundances of larvae of bivalves **(A)** and gastropods **(B)** on the different sampling days in the water column in relation to initial CO_2 concentrations (µatm) in the mesocosms after the CO_2 manipulation was completed. Please note that the scales of **(A)** and **(B)** are different.

of 1100 and 3600 ind. d^{-1}. From t_7 until the end of the experiment, the number of bivalves decreased, and on average between 90 and 1070 ind. d^{-1} were collected in the traps. Significant relationships between the number of bivalves collected by the traps and the pCO_2 level were only found on t_9, t_{28} and t_{30} (t_9: Spearman $r = -0.698$, $p = 0.043$, t_{28}: $r = -0.719$, $p = 0.037$; t_{30}: $r = -0.689$, $p = 0.043$), indicating that there was no trend of higher numbers of bivalves with increasing pCO_2.

Gastropod larvae did not appear in the water column before t_{11} (270 and 480 µatm, Fig. 7b) and reached maximum abundances between 15 (M7, 185 µatm) and 191 (M4, 375 µatm) ind. m^{-3} toward the end of our experiment (t_{24} and t_{30}). In the fjord, maximum abundance was also low with 29 ind. m^{-3}, and hardly any gastropod larvae were found in the sediment traps. Adults of the pteropod *Limacina helicina* did not appear in the water column and were rarely found intact in the sediment traps. Observations by divers indicate that some had migrated through the small space between the sediment traps and the bags into the water body below the 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 mesocosms, indicating that the pteropods had spawned, and over the experiment between 49 750 (M9, 1420 µatm) and 152 150 (M6, 820 µatm) eggs were collected by the traps.

3.6 Copepods

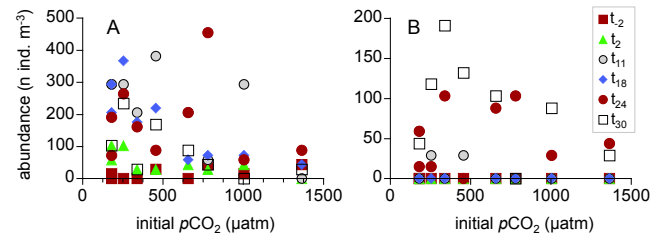Copepods were dominated by *Calanus* spp., *Acartia longiremis* (both Calanoida), *Oithona similis* (Cyclopoida) and *Microsetella norvegica* (Harpacticoida). *Pseudocalanus* spp. were only rarely found throughout the study period in both the mesocosms and the fjord.

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. 8). With time, the nauplius abundance decreased in the mesocosms while the abundance of copepodites and adult copepods increased, 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. 4), 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, relatively few *O. similis* were found, while *Calanus* spp. was quite abundant, especially between t_{14} and t_{28} (Fig. 9). As in the other taxa, there was no consistent trend of abundance in relation to pCO_2 in any of the copepod species (Spearman rank tests, $p > 0.05$).

Calanus spp. was determined to nauplius (N) and copepodite (C) stages as an example for development within a taxon, and our data indicate that these copepods continued to grow and moult in all mesocosms (Fig. 9). When the mesocosms were closed (t_{-2}), most *Calanus* nauplii were NIII and NIV in all mesocosms. At t_2 the relative contribution of NIII had decreased, and mostly NIV and NV were found. At t_{11}, NV was most abundant, and at t_{18} CI was the most dominant stage. CII contributed proportions of $> 25\%$ at t_{24}, and at the last sampling date CIII was found in all mesocosms (25–51 %). Older stages, especially females ($< 2\%$), were always rare. However, beginning with t_{18}, the relative contribution of NI/II increased in all mesocosms, suggesting that some reproducing females were present.
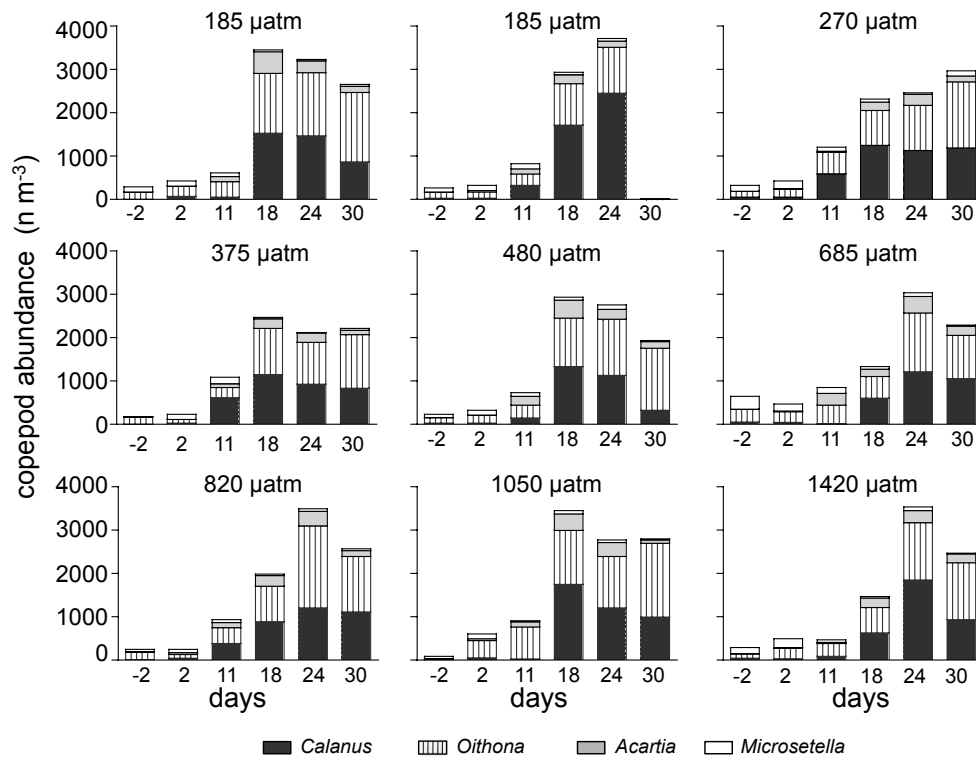
Fig. 8. Copepod abundance and taxonomic composition (genera) in the water column of the mesocosms; the data presented here include copepodites and adults of the respective genus; numbers on top of the panels present the initial CO_2 concentration in each mesocosm after the CO_2 manipulation was completed. At t_{30}, no samples were taken in M7 (185 µatm) and no data are available.

4 Discussion

This mesocosm experiment is the first that describes the development of a mesozooplankton community at elevated $p\mathrm{CO_2}$. The initial CO_2 concentrations, ranging from 185 µatm to 1420 µatm, cover the range from glacial $p\mathrm{CO_2}$ to what has been projected to occur in the atmosphere in the next 100 to 200 yr (e.g. Caldeira and Wicket, 2003; Feely et al., 2009; IPCC, 2007). We have to be aware, however, that the CO_2 concentration in the mesocosms decreased with time due to outgassing and CO_2 uptake by algae (Czerny et al., 2012a). The mesozooplankton present at a given time thus do not mirror a community that has developed at a certain pH or CO_2 level but at continuously decreasing CO_2 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 24 h 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 to several days to weeks in Arctic species (e.g. Jonasdottir, 1989; Niehoff, 2004; Graeve et al., 1994; Kreibich et al., 2011). Thus, differences in growth and development as determined via the abundance of consec-

utive 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 CO_2 concentrations on a particular day.

Usually, Bongo, Nansen or WP2 nets, often equipped with meshes > 150 µm, are used for collecting mesozooplankton (see Wiebe and Benfield, 2003, for review). In mesocosm experiments, however, it is a major problem that sampling zooplankton by net hauls alters their abundance. Therefore, in our study the sum of all net hauls was kept to less than one-sixth of the total cross-sectional area of the enclosure bags (Riebesell et al., 2012); thus, sampling frequency and plankton net size were limited. As also other groups collected mesozooplankton (see de Kluijver et al., 2012; Leu et al., 2013; D. O. Hessen, unpublished data), it was not possible to take replicates for the determination of mesozooplankton abundance and species composition. Unfortunately, due to limited time and manpower, we also did not take replicate samples in the fjord or at the end of the experiment, which would have helped to estimate sampling accuracy. Rare groups, i.e. Chaetognatha, Cnidaria, Amphipoda and juvenile and adult pteropods (< 1 % of the mesozooplankton abundance), were thus not well represented by our sampling routine and were not considered in our analyses.
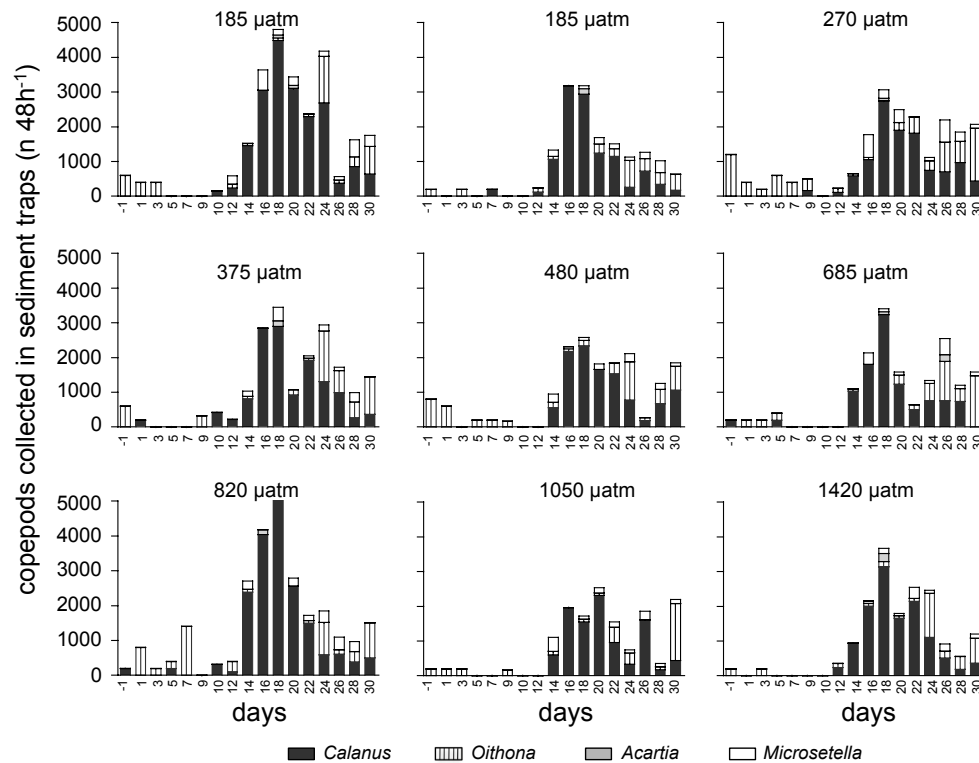
Fig. 9. Copepod abundance and taxonomic composition (genera) in the sediment traps of the mesocosms; data presented here include copepodites and adults of the respective genus; numbers on top of the panels present the initial CO_2 concentration in each mesocosm after the CO_2 manipulation was completed.

The groups we did include were represented well in our samples, even if the numbers of individuals, e.g. bivalve and gastropod larvae, were low. Cirripedia, bivalve and polychaete larva, copepod nauplii, *Calanus*, *Acartia*, *Oithona* and *Microsetella* were all present in more than 80 % of the samples from the water column (total of 59). Euphausiid larvae were found in 66 % and gastropod larvae were present in 39 % of the samples. Accordingly, usually either eight or nine groups were found in a sample. We therefore believe that the taxonomic composition, including only frequently found groups, does reflect the dominating taxa of the mesozooplankton community in the mesocosms despite the limitations in sampling procedure.

If and to which extent zooplankton exhibit diel vertical migration (DVM) patterns under midnight sun is under debate (e.g. Dale and Kaartvedt, 2000; Blachowiak-Samolyk et al., 2006). In our study, DVM would have resulted in quickly decreasing abundances of specific taxa in the water column while – at the same time – these organisms would have been found in large numbers in the sediment traps. This was not the case in any of the taxa, and we therefore believe that DVM was not a major issue in our study. We did, however, find indications for ontogenetic migration in Cirripedia. While the Cirripedia nauplii were abundant in the water column, the cypris larvae were frequent in the sediment traps,

suggesting that they preferred deeper water. This matches the deeper vertical distribution of cypris larvae of several barnacle species close to the coast of southern California, while the nauplii were concentrated in the upper 10 m (Tapia et al., 2010).

An important aspect of this kind of work is whether the communities, which have been enclosed in different mesocosms, had differed already at the start of an experiment; i.e. if, by chance, the abundances of the total mesozooplankton or of certain groups were related to the target CO_2 concentration already prior to the manipulations, an effect of pCO_2 cannot be studied. In our study the initial abundances at t_{-2} of none of the groups analysed were related to the target pCO_2, and none of the mesocosms was characterized by particularly low or high abundances throughout our experiment. This indicates that the mesozooplankton community was randomly enclosed and, thus, that the initial conditions allowed for studying the effect of pCO_2.

The zooplankton abundance as determined from the Apstein net hauls varied at maximum by a factor of three among sampling days and mesocosms, respectively. Moreover, different life history traits and seasonal development in the mesozooplankton groups, which in addition often relate to external factors such as food supply, complicate the analyses of the development of the community. Effects of elevated
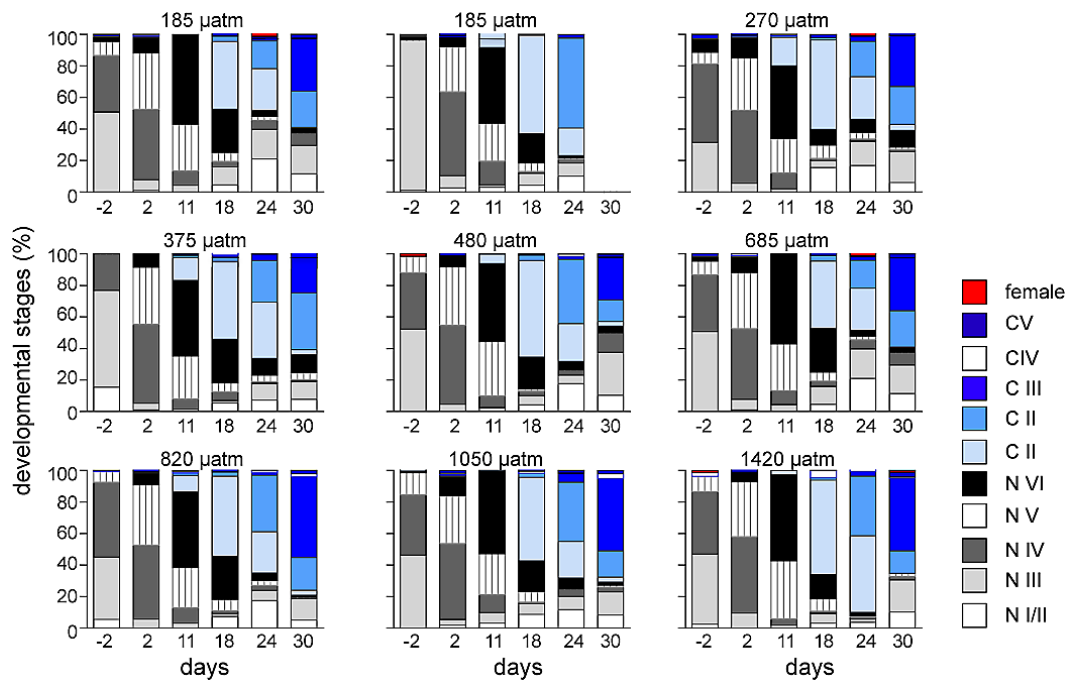
Fig. 10. Developmental stage distribution of *Calanus* spp. in the water column of the mesocosms: C = copepodite stage; N = nauplius stage; numbers on top of the panels present the initial CO_2 concentration in each mesocosm after the CO_2 manipulation was completed.

pCO_2 on abundances would thus have had to be severe in order to being detected during our study. If, for example, the mortality of specific groups had increased dramatically due to elevated CO_2 concentrations, lower abundances would have been found in the corresponding mesocosm(s) and higher numbers would have been found in the sediment traps, respectively. It would also have been possible that the development of specific groups changed due to alterations of the base of the food web (Fabry et al., 2008). We did, however, not find clear effects within our 30-day study period, and composition and temporal development of the mesozooplankton community were similar in all nine mesocosms.

The effect of CO_2 on zooplankton can either be direct, especially in calcifying organisms, (e.g. Kurihara and Shirayama, 2004; Kurihara, 2008; Dupont et al., 2008; Lischka et al., 2011) or indirect by changes in 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 mesocosm study, the phytoplankton community indeed changed with pCO_2. The diatom biomass, which had increased towards the end of the experiment, was highest at low and intermediate pCO_2 levels, while the abundance of autotrophic dinoflagellates increased with pCO_2 (Brussaard et al., 2013; Leu et al., 2013; Schulz et al., 2013). The heterotrophic dinoflagellate and microzooplankton community, on the other hand, did not respond significantly to elevated CO_2 concentrations (Aberle et al., 2013). This suggests that the changes in primary producers did not immediately propagate to higher trophic lev-

els. However, de Kluijver et al. (2012) found that grazing rates of *Calanus* spp. and Cirripedia nauplii decreased with increasing pCO_2. 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 about one month was too short to result in significant differences in community structure.

The mesocosms were closed during mass occurrence of barnacle nauplii (Cirripedia), which is a common phenomenon in spring in coastal areas including Kongsfjorden (e.g. Willis et al., 2006; Walkusz et al., 2009; Basedow et al., 2010). 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 moult to cypris larvae, which settle on hard substrate. Accordingly, barnacle nauplii were extremely abundant in the fjord only at t_2 (approx. 28 500 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, here 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. 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. 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-Spencer et al., 2008). However, mortality rates and reproductive success of *Semibalanus balanoides* were reduced at high pCO_2 (922 µatm) as compared to natural pCO_2 (380 µatm, Findlay et al., 2009). Also the nauplii have been shown to respond to elevated pCO_2 (1000 µatm) with a 15 % lower survival rate than at control conditions (Findlay et al., 2010). In our study, we were not able to show a similar effect on Cirripedia nauplii. However, the variability due to sampling may have masked such effect.

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 trochophore larvae, which were not counted in our samples. In Kongsfjorden, a large variety of benthic species is found (Wlodarska-Kowlczuk 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 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 CO_2 concentration in the mesocosms or to the development of the phytoplankton, measured in terms of chlorophyll *a* (Schulz et al., 2013). This suggests that life cycle events rather than external factors, i.e. CO_2 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; Fransz 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 pCO_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 and Needham, 2007). Also field studies in environments with naturally low pH such as volcanic CO_2 vents show that many polychaete species survive and grow even at extremely low pH (Cigliano et al., 2010; Kroeker et al., 2011).

Laboratory experiments have shown diverging results of high CO_2 concentrations on calcification. Shells of bivalves and gastropods, which were exposed to high CO_2 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 $pCO_2 < 1000$ µatm. 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 community; echinoderm larvae were not present. Gastropod larvae were found at the end of our experiment (t_{24} and t_{30}), and we assume that these have developed from the eggs spawned by *Limacina helicina*, which were added to the mesocosms. The larval abundance was low, and thus possible effects of CO_2 may not have been detected. Bivalve larvae, in contrast, were found throughout our study, although in relatively small numbers. When the mesocosms were closed, the bivalve abundance was overall low (maximum of 44 larvae m^{-3}) and increased with time in all mesocosms indicating that these larvae had developed in the mesocosms from eggs or small larvae, respectively, which were not counted. Overall, higher abundances were found in the mesocosms with low pCO_2 as compared to elevated pCO_2, and their abundance never exceeded 88 larvae m^{-3} in the mesocosm with the highest pCO_2 (initially 1420 µatm, M9). This suggests that the bivalve larval development may have been negatively influenced by elevated CO_2 concentrations. The data set is, however, limited and does not allow for elaborate statistics due to lacking replicates. Moreover, as in polychaetes, we did not determine the larvae to species level. In Kongsfjorden, several bivalve species are abundant (Wlodarska-Koiczuk and Pearson, 2004) and all could have contributed to the larval population. Future studies are thus essential to determine whether and how elevated CO_2 may affect different species and whether negative effects are 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 (Brussaard et al., 2013).

Copepods often dominate zooplankton communities in the world ocean 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 CO_2 concentrations > 5000 µatm and thus at values which greatly exceed what has been predicted for the future oceans (Kurihara et al., 2004; Mayor et al., 2007; Weydmann et al., 2012). In accordance with that, the copepod population developed similarly in all mesocosms with no apparent response to the CO_2 conditions. At the beginning (t_{-2}) the number of nauplii exceeded 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.

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 species (Lischka and Hagen, 2005; Walkucsz et al., 2009). 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; Daase et al., 2011). Prosome length measurements of nauplii and copepodites suggest that both *C. finmarchicus* and *C. glacialis* were captured in the mesocosms; only few individuals were of the size of *C. hyperboreus*, respectively (B. Niehoff and T. Schmithüsen, unpublished data, 2012). Other species frequently found in Kongsfjorden (Lischka and Hagen, 2005; Walkucsz et al., 2009) 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 epipelagic zone, Lischka and Hagen (2005) found this species mostly below 50 m depth.

The effect of elevated $p\text{CO}_2$ on the development of copepods has previously been studied in laboratory experiments with *Acartia tsuensis* (Kurihara and Ishimatsu, 2008), a fast-growing tropical species (e.g. Takahasi and Ohno, 1996). In this species, length, survival, development and reproductive rates did not differ between individuals kept at control conditions and at $p\text{CO}_2 > 2000$ (Kurihara and Ishimatsu, 2008). Also our study at high latitudes did not point to an effect of elevated $p\text{CO}_2$ on *Calanus* spp. When the mesocosms were closed, the nauplii were mostly in NIII/NIV. Within the experimental period of 30 days, the population in all mesocosms, i.e. at all CO_2 concentrations, developed to CII/CIII and there was no indication of lower abundances of later copepodite stages in mesocosms with elevated $p\text{CO}_2$.

5   Conclusions

Information on the mesozooplankton species composition and abundance is vital for understanding and quantifying the processes in the mesocosms. In our study, the mesozooplankton contributed considerably to the carbon pool (Czerny et al., 2012a), and as grazers they were an important component of the trophic structure (de Kluijver et al., 2012). The mesocosm communities differed considerably from those in the fjord, and thus our results do not fully reflect the natural situation, even under control conditions (M3 and M7, both 185 µatm). The communities in the different mesocosms, on the other hand, 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. Within our study the mesozooplankton did not respond

significantly to elevated CO_2 concentrations, and our data suggest that only bivalve larvae may have been affected by high $p\text{CO}_2$. It has to be kept in mind, however, that detecting effects in such heterogeneous communities is difficult, especially when replicate sampling for abundance is not possible. Also, the time span of exposure to elevated $p\text{CO}_2$ (30 days) may have been too short to detect any changes in the mesozooplankton community or even just individual species in the high Arctic fjord. Future mesocosm studies on mesozooplankton should therefore, although logistically challenging, be run over longer periods and/or at lower latitudes where the life cycles of dominant species are often shorter than in the Arctic. Long-term effects on survival, growth and development and, in the end, on the structure of the community are potentially more easily detected. In order to elucidate the immediate response of the zooplankton species to elevated $p\text{CO}_2$ at near-natural conditions, additional measurements of eco-physiological parameters (e.g. respiration, grazing and reproductive rates and enzyme activities) should also be included in future mesocosm experiments.

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