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micro-and
mesozooplankton
communities in the
Baltic**

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Micro- and mesozooplankton community response to increasing CO₂ levels in the Baltic Sea: insights from a large-scale mesocosm experiment

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Abstract

Community approaches investigating ocean acidification (OA) effects suggest a high tolerance of micro- and mesozooplankton to carbonate chemistry changes expected to occur within this century. Plankton communities in the coastal areas of the Baltic Sea frequently experience pH variations partly exceeding projections for the near future both on a diurnal and seasonal basis, thus some level of tolerance/adaptation may be expected. We conducted a large-scale mesocosm CO₂ enrichment experiment (~ 55 m³) enclosing the natural plankton community in Tvärminne/Storfjärden for eight weeks during June–August 2012 and studied community and species/taxon response of microzooplankton (ciliates) and mesozooplankton to CO₂ elevations expected for this century. Besides the response to *f*CO₂ and associated changes in carbonate chemistry speciation, we also considered temperature and chlorophyll *a* variations in our analyses. Shannon diversity of microzooplankton significantly decreased with *f*CO₂ and temperature with a greater dominance of smaller species. Small sized ciliates (*Myrionecta rubra*, *Balanion comatum*, *Strombidium* cf. *epidemum*, *Strobilidium* sp.) showed significant relations with one or more of the factors. The phototrophic *Myrionecta rubra* seemed to directly benefit from higher CO₂ concentrations and showed increased abundance in the pre-bloom phase. With respect to mesozooplankton, we neither detected significant effects for total abundance nor for Shannon diversity. The cladocera *Bosmina* occurred at distinctly higher abundance (more than twice as high compared to the control mesocosms) for a short time period during the second half of the experiment in three of the CO₂-enriched mesocosms except for the highest CO₂ level. The ratio of *Bosmina* with empty to embryo/resting egg bearing brood chambers, however, was significantly affected by all three factors. An indirect CO₂ effect via increased food availability stimulating *Bosmina* reproduction is suggested, but too low sampling frequency of this highly flexible organism probably entailed proving a significant relation with *f*CO₂. Filter-feeding cladocerans effectively transfer microbial loop carbon to higher trophic levels. Thus, under increasing OA in cladoceran dominated

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gas emissions (Riebesell et al., 2009). Until now, most attempts to test for sensitivities of marine organisms to OA were conducted as single species experiments under controlled (optimal) laboratory conditions. Such an approach can not account for community interactions in natural environments, and thus application of results to natural environments is limited. Laboratory experiments suggest calcifying organisms to be most vulnerable to OA because the formation and preservation of calcareous structures is hindered (Riebesell et al., 2000; Hoegh-Guldberg et al., 2007; Lischka et al., 2011). Non-calcareous micro- and mesozooplankton is generally considered quite robust to elevated CO_2 concentrations. Effects on the microzooplankton level seem to be of more indirect nature through changes in primary production, phytoplankton community composition and stoichiometry (Suffrian et al., 2008; Feng et al., 2009; Rossoll et al., 2012). Mesozooplankton is often dominated by copepods (Longhurst, 1985) which are relatively insensitive to $f\text{CO}_2/\text{pH}$ changes expected for this century and direct negative effects usually do not occur unless exposed to much higher $f\text{CO}_2$ levels projected only much later (Kurihara et al., 2004; IPCC, 2013). More recent evidence suggests, however, that nauplii stages may be the weak point in copepod's life cycles (Cripps et al., 2014). As for the microzooplankton, studies on copepods and cladocerans suggest CO_2 effects may be more indirectly mediated to the zooplankton level through CO_2 induced changes in the biochemical and/or stoichiometric composition of their food (Urabe et al., 2003; Rossoll et al., 2012).

Holistic approaches studying CO_2 effects on entire natural plankton communities including zooplankton are still rare. In a preceding similar mesocosm experiment, Aberle et al. (2013) and Niehoff et al. (2013) found no effects on Arctic micro- and mesozooplankton communities, neither with respect to abundance of single species or total numbers nor with respects change in community diversity. In terms of ciliates, these communities were dominated by large-sized forms ($> 30 \mu\text{m}$), in terms of mesozooplankton by copepods and cirripedia larvae. Among microzooplankton, ciliates and heterotrophic dinoflagellates dominate in summer in Tvärminne/Storfjärden, among mesozooplankton rotifers, copepods and cladocera (Kivi, 1986; Viitasalo, 1992; Koski et al., 1999).

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The amount of carbon transferred to higher trophic levels depends on the mesozooplankton species composition (Hansen et al., 1994). In Storfjärden, during late summer and autumn, the microbial loop is of particular importance when filter-feeding cladocerans mediate carbon transfer to higher trophic levels including fish (Koski et al., 1999, and references therein).

As part of the KOSMOS Tvärminne mesocosm experiment, we examined CO₂ effects on the enclosed micro- and mesozooplankton community. Between June and August 2012, an fCO₂ gradient was set up in approximately six 55 m³ mesocosms covering fCO₂ projections for this century or beyond (IPCC, 2013). Abundance and community composition was followed through enumeration of regularly taken water- and net samples. Per definition, micro- and mesozooplankton include heterotrophic proto- and/or metazoa ranging between 0.02–0.2 mm (20–200 μm) and 0.2–20 mm (200–20,000 μm) in size, respectively. In this study, we do not follow this classification strictly. The category “microzooplankton” (MiZP) comprises ciliates only, including some species that can be facultative autotrophs or obligate phototrophs (for instance *Myrionecta rubra*), whereas all metazoa independent of their body size were assigned to the category “mesozooplankton” (MZP). Temperature can have a general effect on MiZP abundance and community composition and governs the dynamics of crustacean species (for instance affects productivity of cladocerans) in late summer in our study area (Nanazato and Yasuno, 1985; Koski et al., 1999; Rose et al., 2009; Aberle et al., 2013). To consider possible impact of temperature variation and/or CO₂ driven chlorophyll *a* differences (Schulz et al., 2013), in addition to fCO₂, we also included temperature and chlorophyll *a* as explanatory variables in our statistical analyses.

2 Methods

To study the effect of elevated fCO₂ on a natural plankton community in the Baltic Sea, nine KOSMOS offshore pelagic mesocosms (Kiel Off-Shore Mesocosms for future Ocean Simulation) were deployed and moored on 12 June 2012 until the middle

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of August in the Tvärminne/Storfjärden archipelago area at the south-west coast of Finland at 59°51.5' N and 23°15.5' E. The water depth at the mooring site was approximately 30 m. The mesocosm bags extended down to 17 m and were closed with 2 m long sediment traps at the bottom of the bags to enclose an isolated water body with its natural plankton community. After deployment, the mesocosm bags were initially kept open and submerged ~ 0.5 m below the surface to allow for a free exchange of the water and plankton community in the bags with the surrounding water masses. Organisms > 3 mm such as fish and cnidaria were excluded by 3 mm nets at the top and bottom openings of the bags during the first five days. These nets were removed on t_{-7} (i.e. seven days before the first CO₂ addition on t_0), the sediment traps were attached to the bottom, and the top ends of the mesocosm bags pulled up to 1.5 m above the surface to isolate the enclosed pelagic community from the Baltic Sea. The final volumes of the mesocosms ranged between 53.1 and 55.1 m³ (Paul et al., 2015). The nine mesocosms were enriched with different amounts of CO₂ saturated seawater to set up an initial gradient of f CO₂ from 240 μatm (ambient, control mesocosms) up to ~ 1650 μatm. Three mesocosms (M2, M4, M9) were lost during the course of the experiment due to leakage. f CO₂ values in the six remaining mesocosms averaged over the sampling period (t_1 – t_{43}) were 365 μatm (M1 control), 368 μatm (M5, control), 497 μatm (M7), 821 μatm (M6), 1007 μatm (M3) and 1231 μatm (M8). CTD profiles and samples for dissolved inorganic nutrients (silicate, phosphate, nitrate, nitrite, ammonium) and carbonate chemistry system parameters (DIC, TA, pH₇) were either taken daily or every second day. For more technical details about the experimental set-up, the CO₂ manipulations, and sampling procedures for various analyses see Paul et al. (2015). Sampling days were enumerated consecutively with t_{-3} indicating three days before CO₂ manipulation, t_0 as the day of the first CO₂ manipulation, and t_{1+x} as the days following the first CO₂ manipulation.

2.1 Microzooplankton sampling

Water samples for the enumeration of ciliates were taken every second day with a depth-integrating sampler (0–17 m), IWS (HYDRO-BIOS, Kiel, Germany), between 09:00 and 12:00 a.m. from six mesocosms. After careful mixing, 250 ml of seawater were filled into brown-glass bottles and preserved in acidic Lugol's iodine (1 % final concentration). 50 ml of the sample were transferred to Utermöhl sedimentation chambers. After 24 h settling time, ciliates were counted with a Zeiss Axiovert 100 inverted microscope at 200× magnification Utermöhl (1958). At high cell numbers (> 400 cells), half the bottom plate area was counted. If less than 400 cells were found in the first half of the bottom plate area, the entire chamber was counted. Rare species were counted on the whole bottom plate. Ciliates were identified to the lowest possible taxonomic level (genus/species) according to Setälä et al. (2009) and Telesh et al. (2009). 138 samples were analyzed in total. Abundances were calculated as cells L⁻¹.

2.2 Mesozooplankton sampling

Mesozooplankton samples from six mesocosms were taken with an Apstein net of 17 cm diameter and 100 µm mesh size. Zooplankton were sampled between 08:00 and 11:00 am by towing the net vertically from 17 m depth to the mesocosm surface. In total, at eleven sampling days, vertical net hauls were done from the mesocosms: prior to the CO₂ addition (t_{-3} , t_{-2} , t_{-1}), at the day of the first CO₂ addition (t_0), and after the first CO₂ addition (t_3 , t_{10} , t_{17} , t_{24} , t_{31} , t_{38} , t_{45}). After collection, the samples were brought back to the lab in the Tvärminne zoological station (University of Helsinki) and preserved in 70 % ethanol. Zooplankton abundance was calculated assuming 100 % filtering efficiency of the net. The samples were divided with a Folsom plankton splitter (1 : 2, 1 : 4, 1 : 8, 1 : 16, 1 : 32) and the aliquots of the samples were counted. Organisms were counted and determined under a stereo microscope (WILD M3B) to the lowest taxonomical level possible. Abundant species/taxa (> 30 individuals in an aliquot) were only counted from subsamples, while less abundant species/taxa

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were counted from the whole sample. Juvenile bivalves did not distribute equally in the Folsom splitter due to their relatively large mass and were therefore counted from the whole sample. Copepods (*Acartia* spp., *Eurytemora* spp., *Temora* spp.) were identified according to different stages (adult females, adult males, copepodite stages CI–CV).

Copepod nauplii were counted but not determined to species level. The counting of the cladoceran species (*Bosmina* spp., *Evadne* spp., *Podon* spp.) was distinguished according to organisms with empty or filled brood chambers, respectively (i.e. organisms that had empty brood chambers or bore embryos/resting eggs, respectively, in their brood chambers) and categorized as 'empty' or 'filled'. For data analyses, the ratio between the number of organisms with 'empty' to 'filled' individuals was calculated for each mesocosm and sampling day, i.e. a small ratio stands for a higher proportion of reproducing organisms in the population in a particular mesocosm at a particular sampling day. A total of 66 samples were analyzed. Abundances were calculated as individuals m^{-3} .

2.3 Data analysis and statistics

To assure equally spaced data, some sampling days were excluded from statistical analyses. For the microzooplankton data this applied to t_{-3} , t_0 , t_2 and t_4 , and for the mesozooplankton this applied to t_{-3} , t_{-2} , t_{-1} and t_0 . However, for demonstration purpose only, the data of these sampling days were included in the figures.

As explanatory variables, fCO_2 , temperature and chlorophyll *a* were used to test for effects on different response variables (see below). Collinearity was checked prior to analyses. To account for the change in fCO_2 over time due to ingassing/outgassing as well as temperature and chlorophyll *a* changes over time, all explanatory variables were used as continuous variable for each *t* day included in the analyses. All analyses were carried out with R using the package nlme, mgcv, Hmisc and MASS. All plots were done in ggplot (R Development Core Team, 2012).

The Shannon index (*H*) was calculated as a measure of diversity in each of the mesocosms and to estimate changes in the relative contribution of single species/groups

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in the whole micro-/mesozooplankton community over time and in response to different abiotic parameters such as the $f\text{CO}_2$ levels. When all considered species/groups contribute equally to the community in terms of their abundances, H calculated on the natural logarithm becomes 2.3. The more a community is dominated by single species/group, the smaller the Shannon index gets. Calculations of H were performed in the vegan package of the R environment (Oksanen et al., 2012).

For the *microzooplankton*, 14 species/groups were included to calculate H : *Balanion comatum*, *Strombidium* cf. *epidemum*, *Mesodinium* sp., *Myrionecta rubra* ($\leq 10 \mu\text{m}$), *M. rubra* (11–20 μm), *M. rubra* ($> 20 \mu\text{m}$), *Rimostrombidium* sp., *Spathidium* sp., *Strobilidium* sp. ($< 20 \mu\text{m}$), *Strobilidium* sp. ($> 20 \mu\text{m}$), *Strombidium* sp., Tintinnids, cysts (*Strobilidium* sp., unidentified cysts), and ciliates sp. (*Euplotes* sp., *Lacrymaria* sp., *Strobilidium* sp., unidentified ciliates).

For the *meosozooplankton*, 17 species or taxonomic groups were included in the calculation of H : copepodite stages and larval stages of *Balanus* sp. (nauplii and cypris larvae) were summarized on the genus level (*Copepoda*: *Acartia* sp., *Eurytemora* sp., *Temora* sp., Harpacticoida sp., copepod nauplii; *Cladocera*: *Bosmina* sp., *Daphnia* sp., *Evadne* sp., *Podon* sp.; *Rotifera*: *Asplanchna* sp., *Keratella* sp., *Synchaeta* sp., Rotifera sp.; larvae of *Balanus* sp., juvenile bivalves, juvenile gastropods, and larvae of polychaets).

2.3.1 Microzooplankton

Statistical analyses were done on total cell numbers, the Shannon index H as well as the abundance of particular groups that showed distinct differences such as small size-class *Myrionecta rubra*, *Balanion comatum*, *Strombidium* cf. *epidemum*, and small *Strobilidium* sp. Linear mixed effects modelling (LME) was applied on a Gaussian distribution to determine the effect of CO_2 , temperature and chlorophyll a . Actually, count data should be modelled on a Poisson distribution, but model selection (s.b.) yielded in convergence problems in R for Poisson distribution. Therefore, we used a Gaussian distribution, which can also be applied on count data (Zuur et al., 2009). If preced-

t_{38} and t_{45} , and for temperature, and chlorophyll *a* on t_{38} and t_{45} . Missing observations for t_{24} and t_{38} were estimated by building the mean of values measured at t_{23}/t_{25} and respectively t_{37}/t_{39} . t_{45} was the last sampling day and hence it was not possible to estimate a mean from the preceding and following day. Therefore missing values for t_{45} were estimated from a polynomial fit curve applied on phase III values (Paul et al., 2015).

3 Results

3.1 Microzooplankton

3.1.1 Microzooplankton total abundance

Total abundance of microzooplankton at experiment start (t_0) varied between 78 120 cells L⁻¹ (M5) and 52 360 cells L⁻¹ (M3) and more or less continually decreased from the beginning over time until t_{17} when a plateau was reached with low cell numbers between 7080 (M8) and 10 940 (M3) until t_{33} . During the last five sampling days (t_{35} – t_{43}), total cell numbers were more variable again with some small ups and downs and reached minimum values between 900 cells L⁻¹ (M6) and 3580 cells L⁻¹ (M8) on the last sampling day (Fig. 1).

3.1.2 Abundance of *Myrionecta rubra*

Myrionecta rubra was (by far) the most dominant ciliate species during the entire period (Fig. 2a). *M. rubra* occurred in three different size classes ($\leq 10 \mu\text{m}$, $11\text{--}20 \mu\text{m}$, $> 20 \mu\text{m}$) of which organisms of the smallest size range made up the highest numbers. On t_0 cell numbers of *M. rubra* of the smallest size class varied between 26 720 cells L⁻¹ and 44 520 cells L⁻¹. Cell numbers stayed relatively high until t_{11}/t_{13} (16 600–37 400 cells L⁻¹) when they strongly declined to values below 10,000 cells L⁻¹ on t_{17}

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and further decreased with some fluctuations until the end of the experiment to reach final values of between 130 cells L⁻¹ and 1740 cells L⁻¹ among all mesocosms. Some striking difference, however, occurred between t_{25} – t_{35} when abundance in the three highest CO₂ mesocosms was higher compared to the two controls and the lowest CO₂ enriched mesocosm (mean: 4518 cells L⁻¹ (SD 1082) and mean: 3459 cells L⁻¹ (SD 383), respectively). *M. rubra* of the medium size class also had maximum numbers on t_0 ranging from 17 600 cells L⁻¹ to 25 680 cells L⁻¹. From the experiment start, numbers more or less continually decreased and reached minimum values of between 480 cells L⁻¹ and 0 cells L⁻¹ from t_{19} on. The largest *M. rubra* occurred only rarely but as in the other two size classes, highest numbers were found during the first few sampling days varying between 2680–5800 cells L⁻¹ on t_0 and reaching very low numbers already on t_7/t_9 (1080–280 cells L⁻¹). After t_{19} , *M. rubra* > 20 µm occurred only exceptionally.

3.1.3 Abundance of other species/genera/groups

Other dominant groups/species that contributed to the total cell numbers of microzooplankton were *Mesodinium* sp., *Balanion comatum*, *Strombidium* cf. *epidemum*, *Rimostrombidium* sp., *Strobilidium* sp. (< 20 µm and > 20 µm), *Strombidium* sp., Tintinnids, *Spathidium* sp., cysts, and ciliates that could not be identified (Fig. 2b and c). Among those, *Strombidium* cf. *epidemum* was most dominant and showed three peaks, around t_9/t_{11} , t_{23} , and t_{37} . Peak values ranged between 1160 cells L⁻¹ and 4000 cells L⁻¹ on t_9/t_{11} and showed some distinct difference between control and CO₂ enriched mesocosm (mean: 1250 cells L⁻¹ (SD 180) and mean: 2205 cells L⁻¹ (SD 851), respectively). On t_{23} peak values ranged between 2300 cells L⁻¹ and 3840 cells L⁻¹, and between 1980 cells L⁻¹ and 6,740 cells L⁻¹ on t_{37} . *Balanion comatum*, *Rimostrombidium* sp., *Strobilidium* sp. (< 20 µm), *Spathidium* sp., and tintinnids were of some importance during the first days of the experiment showing peaks in cell numbers of 1760 cells L⁻¹ on t_7 , 1680 cells L⁻¹ on t_0 , 3640 cells L⁻¹ on t_{11} , 1760 cells L⁻¹ on t_0 , and 1080

cells L⁻¹ on t_0 , respectively. Peak abundance of *Balanion comatum* diverged with CO₂ concentration with higher mean cell numbers in the control and lowest enriched mesocosm compared to the three high CO₂ mesocosms (mean: 1680 cells L⁻¹ (SD 139) and mean: 880 cells L⁻¹ (SD 223), respectively). Likewise, small *Strobilidium* sp. developed some CO₂ related difference with mean abundance of 1360 cells L⁻¹ (SD 170) and 2400 cells L⁻¹ (SD 872) in the two controls and the CO₂ enriched mesocosms, respectively. Later in the experiment, these species/groups were not of importance anymore. *Mesodinium* sp. and *Strobilidium* sp. > 20 μm occurred always in relatively low cell numbers (< 550 cells L⁻¹ and < 700 cells L⁻¹, respectively). From t_0 onwards, cysts and unidentifiable ciliates never accounted for more than 700 cells L⁻¹ and 850 cells L⁻¹, respectively.

3.1.4 Percent contribution of numerically dominant species/genera/groups to total cell numbers

Figure 3b and c show the percent contribution of dominant species/genera/groups to the total cell numbers over time for each of the mesocosms. For better clarity, *Myrionecta rubra* size classes, *Strobilidium* sp. size classes together with *Rimostrombidium* sp., *Strombidium* spp. and cysts together with ciliates sp. were combined. *M. rubra* dominated the microzooplankton community in all mesocosms most of the time. During the first days of the experiment, *M. rubra* contributed ~ 90 % to the total cell numbers in all mesocosms and stayed above 50 % until t_{21} . Minimum contributions occurred on t_{37} when *M. rubra* had a share of only 6–24 %. After t_{37} , *M. rubra* proportions ranged between 18 and 67 %. The second most important group was *Strombidium* sp. and among this *Strombidium* cf. *epidemum*. *Strombidium* sp. had highest shares during the second half of the experiment. It started with relatively low contributions during the first days of the experiment and increased depending on the mesocosm from t_{19}/t_{21} on to proportions of 17–36 %. Maximum contributions varied between 58 and 69 % during t_{35} – t_{39} . All remaining groups usually had contributions below 15 %.

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The Shannon diversity index H ranged from 0.58–1.66 over the whole period of time (Fig. 4). In general, it showed a slightly increasing trend varying between 1.04 and 1.23 on t_{-3} and, respectively 1.30 and 1.66 on t_{43} . Overall, H showed a non-monotonic relationship with a slightly increasing trend at lower $f\text{CO}_2$ and a decreasing trend the more the $f\text{CO}_2$ increased, and as well as a decreasing trend with temperature.

3.1.5 Statistical analyses microzooplankton

GAMM's determined significant effects for total abundance, small size class *Myrionecta rubra*, *Balanion comatum*, *Strombidium cf. epidemum*, *Strobilidium* sp., and the Shannon index H in response to one or more of the included explanatory variables. Detailed statistical results are shown in Table 1. Model validation showed some residual pattern in all cases, but most of the obtained p values are highly significant and are therefore reasonably trustworthy (Zuur et al., 2009). Only with respect to *Balanion comatum*, p values should be seen with some caution as they are not highly significant.

3.2 Mesozooplankton

3.2.1 Mesozooplankton total abundance

Total abundance of mesozooplankton caught in the net samples on t_{-2} varied between 4841 ind. m^{-3} in M1 and 31471 ind. m^{-3} in M8 (Fig. 5). During the course of the experiment abundances increased in all mesocosms continuously until peak abundances were reached between t_{24} and t_{31} . M7, M6, and M3 (497–1007 μatm) had highest peak values ranging between 130 276 ind. m^{-3} and 162 082 ind. m^{-3} , whereas abundance in M1 and M8 were somewhat lower with 111 980 ind. m^{-3} and 90 975 ind. m^{-3} , respectively. In M5, no abundance peak occurred but zooplankton developed a plateau between t_{24} until t_{38} of around 70–74 000 ind. m^{-3} . Towards the end of the experiment, zooplankton total abundance returned to about the initial values (29 325–44 824 ind. m^{-3} in M8 and M1, respectively).

3.2.2 Community composition

The mesozooplankton community was dominated by five taxonomic groups, i.e. cladocera (*Bosmina* sp., *Daphnia* sp., *Evadne* sp., *Podon* sp.), copepoda (*Acartia* sp., *Eurytemora* sp., *Temora* sp., copepod nauplii, Harpacticoida, Cyclopoida, Copepoda sp.), crustacea (*Balanus* sp., including nauplii and cyprid larvae), mollusca (juvenile Bivalvia and Gastropoda) and rotifera (*Asplanchna* sp., *Keratella* sp., *Synchaeta* sp., *Rotifera* sp.). The group 'others' comprises larvae of Bryozoans (cyphonautes), juvenile Polychaeta, and unidentifiable organisms (Fig. 6). Among these groups, cladocerans and copepods dominated the zooplankton community during the entire experimental period. Cladocerans contributed usually between 50 and 95 % to the total abundance. Low abundances of cladocerans occurred only at the beginning (t_{-2} , t_{-1}) and on t_{17} when they only had a share of between 8 and 28 % of the whole community. Copepods had a relatively low share early in the experiment and at the end (~10–20 %), but half way through the experiment copepods constituted 74–84 % (t_{17}) of the whole community. Rotifera were a major part of the zooplankton only during the first days of the experiment with about 11 % to 42 % between t_{-1} and t_3 , later on they almost disappeared in all mesocosms (<1 %) except for M8 where on t_{45} 2 % of the whole community were rotifera. Among the group mollusca, gastropods always had a smaller share than bivalves with usually below 2 % contribution to the total abundance of this group, only in a few cases (M1 and M5 on t_{10} and t_{24}) gastropods had a share of 5 % and at the last day in M8 of 14 % of the mollusca group. Juvenile bivalves mainly occurred from the start until day t_{10} and had maximum contributions of 17–45 % to the total zooplankton community between t_{-2} and t_0 . By day t_{10} their abundances decreased to 7–0.6 % of the total community. The group 'crustacea' comprises mainly larvae of *Balanus* sp. (nauplii and cyprids). Only very rarely a mysid was found and specimen of this order were also included in the group crustacea. The main occurrence of 'crustacea' was from t_{-1} until t_{10} contributing between 10 and 2 % to the total zooplankton community

cosms. At the beginning and towards the end of the study, most of *Acartia* sp. were in the copepodite stage CI–CV. Adult females and males occurred during the whole period of time and had maximum proportions half way through the experiment (t_{17} , t_{24}) when the share of copepodite stages was negligible. During this time, reproduction took place indicated by the following increase in copepodite stages during the second half of the study. The stage distribution of *Temora* sp. was similar to *Acartia* sp. with a peak of copepodite stages CI–CV during the first and the last sampling days. Most of the time, however, adult females and males dominated and overall *Temora* sp. was not of great importance in the copepod community.

3.2.4 Cladocera

Four species of cladocera were found in the mesocosms: *Bosmina* sp., *Podon* sp., *Evadne* sp. and *Daphnia* sp. *Daphnia* sp. occurred only rarely in very low abundances (<0.5% contribution to total cladocera, abundance range: 2.6–12.8 ind. m⁻³). *Evadne* sp. had maximum abundances on t_3/t_{10} ranging between 184 ind. m⁻³ and 3893 ind. m⁻³, respectively, and contributed up to 38% to this group during the first days of the experiment but decreased noticeably in importance later. *Podon* sp. dominated among the cladocerans at the beginning of the experiment accounting for more than 80% of the total abundance until day t_{10} (max. numbers: 43 688–15 272 ind. m⁻³) when *Bosmina* sp. started to increase in abundance. By day t_{17} *Bosmina* clearly dominated among cladocerans reaching more than a 90% share until termination of the experiment (Fig. 8a and b). Peak abundance of *Bosmina* sp. occurred at different time points in the different mesocosms and was distinctly higher at 497 μ atm (M7, 138 394 ind. m⁻³, t_{31}), 821 μ atm (M6, 114 169 ind. m⁻³, t_{38}), and 1007 μ atm (M3, 127 080 ind. m⁻³, t_{24}) as compared to the two controls (M1, 72 020 ind. m⁻³, t_{24} and M5, 58 107 ind. m⁻³, t_{38} , respectively) and the mesocosm with the highest $f\text{CO}_2$ concentration of 1231 μ atm (M8, 63 182 ind. m⁻³, t_{31}).

of the Gulf of Finland varied between 10–50 000 cells L⁻¹ in 1988 and 1990, respectively, and hence are in the same range as in our study, and also consisted of the same typical species/groups (Setälä and Kivi, 2003).

4.1.1 Changes in microzooplankton species diversity

5 Previous studies on sensitivities of MiZP communities towards ocean acidification are inconsistent. For example Rose et al. (2009) report on significant changes in MiZP abundance and community composition in the open North Atlantic Ocean between their single factor (only temperature) and two factor (temperature and CO₂) experiments and conclude that a combination of direct and indirect (bottom-up) effects were responsible for observed changes. Mesocosm studies off the coast of Norway and in the Arctic revealed no effect of different CO₂ concentrations on the MiZP community neither with respect to abundance nor community composition (Suffrian et al., 2008; Nielsen et al., 2010; Aberle et al., 2013). In the latter study, positive effects on the autotrophic biomass with higher and lower CO₂ concentrations were found for dinoflagellates and respectively prasinophytes and haptophytes but these effects did not translate to the MiZP level (Schulz et al., 2013). While we found no significant relation between microzooplankton total abundance and *f*CO₂ concentration, total abundance was significantly affected by temperature and the microzooplankton community seemed to change with respect to species diversity *H* towards a higher dominance of single species with increasing temperature and *f*CO₂, respectively. Most likely, small species/genus are responsible for this change in diversity. During the first days of the experiment (*t*₅, *t*_{5–t₉}, and *t*_{7–t₁₃}, respectively) small species such as *Balanion comatum*, *Strombidium* cf. *epidemum*, and *Strobilidium* sp. (< 20 μm) show some distinct differences in abundance between the three higher and lower *f*CO₂ mesocosms. While *B. comatum* occurs at higher abundance in the control mesocosms and the lowest CO₂ enrichment level (M7, 497 μatm), *S. cf. epidemum* and *Strobilidium* sp. have higher abundances in the three high CO₂ mesocosms. Later in the experiment, between *t*₁₉ and *t*₃₁, the small size class

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Myrionecta rubra for example occurred in much higher numbers in the mesocosms with the three highest $f\text{CO}_2$ concentrations. For the mentioned species, significant relations were determined for all factors included in our analyses, except for *Balanion comatum* that showed no significant response to chlorophyll *a* and *Strombidium cf. epidemum* that only showed a significant relation with chlorophyll *a*. Rose et al. (2009) also report on increased dominance of smaller taxa (mostly *Lohmaniella* sp. among ciliates) during the course of their experiment, but dependent on a combination of different factors, i.e. temperature, CO_2 and changes in the top-down control. Finally, they conclude on a more general effect of temperature on MiZP abundance and community composition. A relationship between temperature and Shannon diversity *H* on ciliate communities and on heterotrophic ciliates, respectively, was also shown by Setälä and Kivi (2003) and Aberle et al. (2007). In contrast to our present study, Aberle et al. found *H* to increase with higher temperature and it was larger ciliates (mostly *Strombidium* species) that caused the community shift.

4.1.2 May *Myrionecta rubra* benefit from OA?

For the present study, a positive CO_2 effect on community chlorophyll *a* is described with significantly higher concentrations between day t_{21} and t_{39} (phase II and III) attributed for up to 90 % to picophytoplankton ($\leq 2 \mu\text{m}$). The relative contribution of the 2–20 μm size fraction to total chlorophyll *a* was estimated as about 20 % (Paul et al., 2015). This period of increased chlorophyll *a* concentrations under high CO_2 also coincides well with increased abundances of the probably predominantly photoautotrophic ciliate *Myrionecta rubra* ($\leq 10 \mu\text{m}$) in the high CO_2 mesocosms. Blooms of *M. rubra* can cause red tides and are characterized by high uptake rates of inorganic nutrients and they can contribute significantly to chlorophyll *a* values and primary production in estuaries, fjords and upwelling areas. *M. rubra* robs plastids from cryptophytes. In the absence of cryptophytes, they sustain a larger cell volume but exposure to cryptophytes stimulates incorporation and cell division of *M. rubra* resulting in a decreased average cell but increased population size (hence biomass) (Lindholm, 1985; Gustafson Jr

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et al., 2000, and references therein). Cryptophytes were among the main contributors to total chlorophyll *a* in particular during phase I and showed a significant negative effect of CO₂ during the first phase of the experiment (Paul et al., 2015). Moreover, small picophytoplankton of approx. 2.9 μm cell diameter most likely representing cryptophytes had highest abundances during phases II and III and showed a distinct negative correlation with *f*CO₂ (Crawfurd et al., 2015). Cryptophyte biomass decreased from *t*₃ to *t*₁₇ as did the total abundance of *M. rubra*, but whereas the 11–20 μm size class of *M. rubra* almost disappeared by that time or even earlier for the ≥ 20 μm size class, the small size-class cells remained and developed a distinct difference in abundance between the higher and lower CO₂ mesocosms. Growth and photosynthetic performance of *M. rubra* is ultimately dependent on the availability of cryptophytes, but the ciliate can sustain long periods without feeding by functioning as a phototroph and has the ability to control cryptophyte plastids' division and synthesize chlorophyll (Johnson and Stoecker, 2005; Johnson et al., 2006). Photosynthetic performance of *M. rubra* may have been stimulated by elevated CO₂ concentrations and thus this ciliate may be “co-responsible” for the CO₂ driven total chlorophyll *a* differences observed during phases II and III. Consequently, higher cell numbers of small sized *M. rubra* may be a combination of indirect and direct CO₂ effects through 1) availability of cryptophytes in phase I, II and III maybe being partly responsible for the negative CO₂ effect on cryptophyte biomass and abundances reported by Crawfurd et al. (2015) and Paul et al. (2015), and 2) through a CO₂-mediated higher photosynthetic rate of *M. rubra* supporting its own growth. We have no (strong) support, however, that the negative CO₂ effect on cryptophyte abundance during phase I is related to higher grazing pressure of *M. rubra* resulting in an abundance increase. A certain affinity of *Mesodinium rubrum* (synonymous *Myrionecta rubra*) to low pH is supported by a microcosm study with a coastal plankton community that revealed clearly higher abundance at the lowest pH level (6.0) Nielsen et al. (2010). During this phase, *M. rubra* abundances showed much variability between sampling days. Some higher abundances in the small and medium size class *M. rubra* especially in M6 and M8 between *t*₂ and *t*₁₁, however, may point

in this direction. During phase II and III, however, *M. rubra* may have benefitted from CO₂ stimulated photosynthetic activities and controlled cryptophyte abundances, and hence, decreased cryptophyte numbers would represent an indirect CO₂ effect through *M. rubra* (Crawfurd et al., 2015).

4.2 Mesozooplankton

The MZP community enclosed in the mesocosms reflected fairly well the natural succession of MZP in Tvärminne/Storfjärden where rotifers, cladocerans and calanoid copepods comprise the major zooplankton taxa. Usually rotifers numerically dominate in spring/early summer (*Synchaeta* sp.) and reach a second peak in mid-summer/autumn (*Keratella* sp.). The calanoid copepods *Acartia bifilosa* and *Eurytemora affinis* show two abundance peaks, in mid-June and mid-September, respectively, and *Temora longicornis* occurs only at low numbers year-round. Cladocerans peak in summer (August/September) with *Bosmina longispina maritima* clearly dominating among *Podon* spp. and *Evadne nordmanni*. Highest MZP biomass is build up in summer (August/September) (Kivi, 1986; Viitasalo, 1992; Koski et al., 1999). The species composition in the mesocosms resembled well natural conditions and were dominated by the most common and successful genus/species known for the Gulf of Finland and the Tvärminne region such as *Acartia bifilosa*, *Eurytemora affinis*, *Bosmina longispina maritima*. Due to the rather late start of our mesocosm experiment after the spring phytoplankton bloom, the usual peak of *Synchaeta* sp. in spring/early summer – also one of the most successful species (i.e. *Synchaeta baltica*) – was barely visible during the first days, later rotifers still occurred until termination but were not of great importance anymore (Viitasalo, 1992).

Total population densities known for mesozooplankton in the Tvärminne area more or less coincide with abundances found in the mesocosms and range from median values between ~ 22 000–~ 40 000 ind. m⁻³ with occasional peak abundance for *Acartia bifilosa* and *Bosmina* sp. of up to 45 000 and 82 000 ind. m⁻³, respectively. Average peak abundance of *Acartia bifilosa* and *Bosmina* sp., respectively, during a period from

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1967–1984 was $\sim 10\,000$ ind. m^{-3} and respectively $\sim 20\,000$ ind. m^{-3} (Viitasalo et al., 1995; Viitasalo, 1992). Between t_{24} and t_{31} , however, some exceptional high numbers ($> 150\,000$ ind. m^{-3}) occurred in the mesocosms mainly attributed to extremely high occurrence of *Bosmina* sp.. Even higher densities exceeding $1\,000\,000$ ind. m^{-3} during blooms of blue-green algae are known for *B. fatalis* in an eutrophic lake in Japan (Hanazato and Yasuno, 1987). The MZP community in the surrounding water did not entirely correspond with the mesocosms over the course of the experiment. Whereas the dominance of particular species corresponded quite well until t_3 , it diverged progressively after t_{10} when in the surrounding water the occurrence of colonies of blue-green algae (*Aphanizomenon*) and rotifera were higher than in the mesocosms, and the abundance of copepods and cladocerans comparatively lower (S. Lischka, pers. obs., 2012). Most likely, this is a result of isolation of the mesocosm bags from surrounding water mass exchange and incoming plankton communities and selective advantage of single species in the mesocosms.

4.2.1 Copepods

Up to date, there are only very few large CO_2 enrichment mesocosm studies with an as far as possible holistic plankton community approach (Riebesell et al., 2008, 2013b). Therefore, this study is still one of the first to follow MZP community development subjected to ocean acidification scenarios projected for this century in a close-to natural whole plankton community. Previous study using the same mesocosm set-up investigated effects on an Arctic MZP community and found no significant difference neither in total abundance or abundance of single taxa nor in species diversity. This Arctic MZP community was dominated by meroplanktonic larvae and copepods played a minor role, and thus differed in species type composition compared to the Baltic community enclosed in our mesocosms (Niehoff et al., 2013; Riebesell et al., 2013a). In general, on the mesozooplankton level, calcifiers seem to be more sensitive to CO_2 increases than crustaceans (Kurihara, 2008; Kroeker et al., 2013), i.e. copepods which dominate

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zooplankton communities in boreal and higher latitude regions. While copepods are thought to be rather robust against ocean acidification with negative effects occurring usually not until $p\text{CO}_2$ levels far beyond projections for end of this century (Kurihara et al., 2004; Mayor et al., 2007; Weydmann et al., 2012; McConville et al., 2013; Almén et al., 2015), more recent studies give evidence that copepods' sensitivity may be highly stage dependent and thus so far mostly underestimated due to the fact that most studies done to-date considered only adult stage copepods. Mortality of the nauplii stage *Acartia tonsa* for example increased threefold already at CO_2 concentrations expected for the end of this century (Cripps et al., 2014). These authors highlight the importance of a holistic life-stage approach in order to provide meaningful data for climate change projections.

Copepods comprised one of the two dominant taxonomic groups in the present study and the mesocosm approach allowed to investigate CO_2 effects on the succession of all different life stages from eggs to reproducing adults. The CO_2 scenario chosen in the present study covered the range projected for this century (IPCC, 2013). Over this range, we found no distinct abundance differences for neither of the species. The permanent occurrence of adult males and females together with copepodite stages and nauplii suggest more or less continuous reproduction. Concurrent lab experiments investigating the effect of CO_2 on reproductive success of *Eurytemora affinis* are in agreement with the observations from the mesocosms (Almén et al., 2015, this issue). Incubated *Acartia bifilosa* showed $f\text{CO}_2$ unaffected egg production, but slight negative effects on egg hatching and development were found and adult females were smaller in the two highest CO_2 mesocosms (Vehmaa et al., 2015, this issue). Our results are also in line with Niehoff et al. (2013) who do not describe any apparent CO_2 effect on an Arctic MZP community including copepods. Therefore, results from our study are completely in line with earlier studies describing copepods rather robust against CO_2 changes at least in the range projected for the end of this century. Copepods in the study region naturally experience $f\text{CO}_2$, pH and also temperature fluctuations of more than 0.5 pH units and 5°C temperature during daily vertical migrations which is more

than the predicted climate change for the year 2100. I.e. these copepods are probably well adapted to short-term physico-chemical changes (Lewis et al., 2013; Almén et al., 2014).

4.2.2 Mollusks

Mollusks enclosed in the mesocosms comprised for more than 90 % of juvenile bivalves of the species *Macoma balthica* and occurred during the first ten days of the experiment. Calcifiers are among the most vulnerable organisms to ocean acidification, and within this investigation bivalve larvae were therefore subjected to a more detailed study on their occurrence and length distribution over time. The main findings from this study suggest reduced settling rates and a developmental delay with increasing $f\text{CO}_2$. For more details see Jansson et al. (2015, this issue).

4.2.3 Cladocera – OA effect on *Bosmina* spp. through increased food availability?

Most conspicuous differences found in mesozooplankton abundance are due to the cladoceran *Bosmina* sp. between t_{24} and t_{31} . In three of the four CO_2 enriched mesocosms (497 μatm , 821 μatm , 1007 μatm) peak numbers were twice or even more than twice as high compared to the control and the highest CO_2 mesocosms, though a significant relation with $f\text{CO}_2$ could not be proved. Nevertheless, this striking difference may possibly point to an indirect CO_2 effect through higher food availability under high CO_2 .

In the inner parts of the Baltic proper, the endemic *Bosmina longispina maritima* is most abundant among the genus *Bosmina*. Its life cycle includes many parthenogenetic generations in the summer, sexual reproduction occurs only during late summer and autumn from which fertilized resting eggs result that overwinter in the sediment and develop in spring (Kankaala and Wulff, 1981, and references therein). Cladocerans are highly reproductive at times of favourable environmental conditions. The lifespan

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of *Bosmina* spp. varies between 20–25 days, age of first reproduction is between 4–7 days (food dependent), they can bear several developmental stages in the brood pouch of the mother and at favourable conditions, populations can increase twofold within 5–10 days (Purasjoki, 1958; Kankaala and Wulff, 1981; Hanazato and Yasuno, 1987; Biswas et al., 2014). Population dynamics of *Bosmina longirostris* are highly food-sensitive with food concentrations having a significant effect on growth, net reproductive rate and rate of population increase. For example at high food concentration more broods occur and more eggs are produced (Kankaala and Wulff, 1981; Urabe, 1991), whereat not only food quantity but also quality influences life time and together were shown to shorten it to up to 10 days. (Hanazato and Yasuno, 1987). *Bosmina* is also very quick in taking advantage of favourable environmental conditions and has a high plasticity to customize its life cycle and growth patterns. For example, to avoid predation they can allocate energy to somatic growth instead of early reproduction to attain larger size and escape prey size spectrum of copepods (Kankaala, 1983; Jankowski, 2004). Cladocerans are opportunistic feeders that graze on nano- and microplankton, bacteria (including cyanobacteria), and detritus (Purasjoki, 1958; Nanazato and Yasuno, 1985; Work and Havens, 2003; Kluijver et al., 2012). *Bosmina* tolerates low pH in acidic lakes well (Uimonen-Simola and Tolonen, 1987) and has two modes of feeding: small-particle filtering and large-particle grasping (DeMott, 1982a, b; Bleiwas and Stokes, 1985).

The above mentioned population increase of *Bosmina* in the mesocosms coincides with significant CO₂ mediated differences during phase III in chlorophyll *a*, chlorophytes and particulate organic matter during the respective days and probably represented favourable food conditions for this species enhancing asexual reproduction in particular in the elevated CO₂ mesocosms (Paul et al., 2015). Only M8, the mesocosm with the highest CO₂ concentration, diverged from this trend. The stoichiometry of food organisms can affect growth in cladocerans, for example, growth of *Daphnia pulex* was reduced due to reduced C : P ratios of high CO₂ cultivated food algae (Urabe et al., 2003). In the present study the average C : P ratio of particulate organic matter did not vary with fCO₂, however this can only be seen as an estimate for the food that was

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effectively ingested by *Bosmina* (Paul et al., 2015). Peak abundance in all mesocosms occurred only on one sampling day, i.e. did not stay high for a longer period but was low at the preceding sampling day and had dropped already at the following sampling day. Most likely, the drop in population size that occurred earlier than to be expected from *Bosmina*'s lifespan of around 20 days was due to high mortality and/or change to sexual reproduction producing resting eggs. Therefore, a possible explanation why *Bosmina* in M8 did not follow the trend observed in the other CO₂-elevated mesocosms may be that due to the rather low possible sampling frequency (every seven days) the actual abundance peak was missed (Riebesell et al., 2013a). Reason for mortality could be in response to the overall drop in available food during phases II and III and/or stress response due to extreme densities or reproductive rates of *Bosmina* itself. It is known, that *Bosmina* sp. can die earlier when they have higher reproductive rates and switch to sexual reproduction producing resting eggs, respectively, at too high population densities (so called "crowding phenomenon") (Purasjoki, 1958; Acharya et al., 2005). In Kankaala (1983), *Bosmina* started sexual reproduction at around 4500 ind. m⁻³ which is about 1–2 orders of magnitude less than observed peak numbers in the mesocosms. The significant results we found for the ratio of *Bosmina* with empty and full brood chambers strongly suggest that organisms in the high CO₂ mesocosms had higher reproductive activities during the time of actual peak abundance. In particular, *Bosmina* in M8 and M3 (two highest CO₂ levels) had continuously low brood chamber ratios (i.e. large proportion of actively reproducing organisms in the population) from t_{10} onwards (with the ratio in M8 mostly even lower than in M3). This supports our assumption that we missed to sample the abundance peak of *Bosmina* in M8 possibly obstructing to prove a significant indirect f CO₂ effect on *Bosmina* abundance through increased food availability.

5 Conclusions

Our study gives evidence for direct and/or indirect CO₂ effects on the micro- and mesozooplankton community. For the MiZP community composition we determined significant changes with a shift towards smaller species/genus with increasing CO₂ levels.

5 The phototrophic ciliate *Myrionecta rubra*, as well as *Balanion comatum*, *Strombidium* cf. *epidemum*, *Strobilidium* sp. and the short-lived cladocera *Bosmina* seemed to benefit from increased CO₂ concentrations, the first one probably directly, the others rather indirectly. Although our results show no direct significant relation with abundance, we assume *Bosmina* growth and reproduction was stimulated from increased food availability at elevated CO₂ mostly during phases II and III (higher post-bloom chlorophyll *a* and particulate organic matter). This may point to an indirect CO₂ effect that was masked as a consequence of too low sampling frequency not allowing to adequately capture the population dynamics of this short-lived and highly adjustable genus. For the study region, microbial loop has been shown to be of particular importance during late summer and autumn when most of the secondary production including fish is fueled by carbon channeled from the microbial loop to crustacean zooplankton. Filter-feeding cladocerans directly feed on bacteria and flagellates and effectively transfer carbon from the microbial loop to higher trophic levels. Contrary, in copepod dominated communities, the carbon transfer from microbial loop is comparatively low because an intermediate trophic level is needed (heterotrophic flagellates, ciliates) (Koski et al., 10 1999, and references therein). Therefore, we conclude, under increasing ocean acidification in cladoceran dominated MZP communities, the importance of trophic transfer from the microbial loop to higher trophic levels becomes more efficient.

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Table 1. Statistics summary table of retained fixed effects of the GLM's and GAMM's. Significant p values are indicated in bold (Temp: temperature).

	Explanatory variable	DF	t	p -value	Model
Microzooplankton					
MiZP total abundance	Temp	1	-3.506	0.0007	GAMM
<i>Myrionecta rubra</i> , $\leq 10 \mu\text{m}$	Temp	1	2.376	0.019	GAMM
<i>Myrionecta rubra</i> , $\leq 10 \mu\text{m}$	$f\text{CO}_2 \cdot \text{Temp}$	1	-2.298	0.024	GAMM
<i>Myrionecta rubra</i> , $\leq 10 \mu\text{m}$	$f\text{CO}_2 \cdot \text{Chl } a$	1	2.936	0.004	GAMM
<i>Balanion comatum</i>	Temp	1	2.320	0.022	GAMM
<i>Balanion comatum</i>	$f\text{CO}_2$	1	-2.210	0.030	GAMM
<i>Strombidium cf. epidemum</i>	Chl a	1	-3.229	0.002	GAMM
<i>Strombidium sp.</i> , $< 20 \mu\text{m}$	Temp	1	2.811	0.006	GAMM
<i>Strombidium sp.</i> , $< 20 \mu\text{m}$	Chl a	1	-4.603	<0.00001	GAMM
<i>Strombidium sp.</i> , $< 20 \mu\text{m}$	$f\text{CO}_2 \cdot \text{Temp}$	1	-3.600	0.0005	GAMM
<i>Strombidium sp.</i> , $< 20 \mu\text{m}$	$f\text{CO}_2 \cdot \text{Chl } a$	1	3.926	0.0002	GAMM
Shannon index H	Temp	1	3.652	0.0004	GAMM
Shannon index H	$f\text{CO}_2$	1	2.824	0.006	GAMM
Shannon index H	$f\text{CO}_2 \cdot \text{Temp}$	1	-3.454	0.0008	GAMM
Mesozooplankton					
MZP total abundance	Temp	31	-1.155	0.257	GLM
MZP total abundance	$f\text{CO}_2$	31	-0.025	0.980	GLM
MZP total abundance	Chl a	31	0.550	0.586	GLM
MZP total abundance	$f\text{CO}_2 \cdot \text{Temp}$	31	0.947	0.351	GLM
MZP total abundance	$f\text{CO}_2 \cdot \text{Chl } a$	31	-1.081	0.288	GLM
<i>Bosmina sp.</i>	Chlor a	1	0.76	0.453	GAMM
<i>Bosmina sp.</i> ratio empty/full brood chambers	Temp	1	-3.572	0.001	GAMM
<i>Bosmina sp.</i> ratio empty/full brood chambers	$f\text{CO}_2$	1	-2.684	0.011	GAMM
<i>Bosmina sp.</i> ratio empty/full brood chambers	Chl a	1	-3.980	0.0004	GAMM
<i>Bosmina sp.</i> ratio empty/full brood chambers	$f\text{CO}_2 \cdot \text{Chl } a$	1	2.738	0.01	GAMM
Shannon index H	Chl a	1	-0.555	0.582	GAMM

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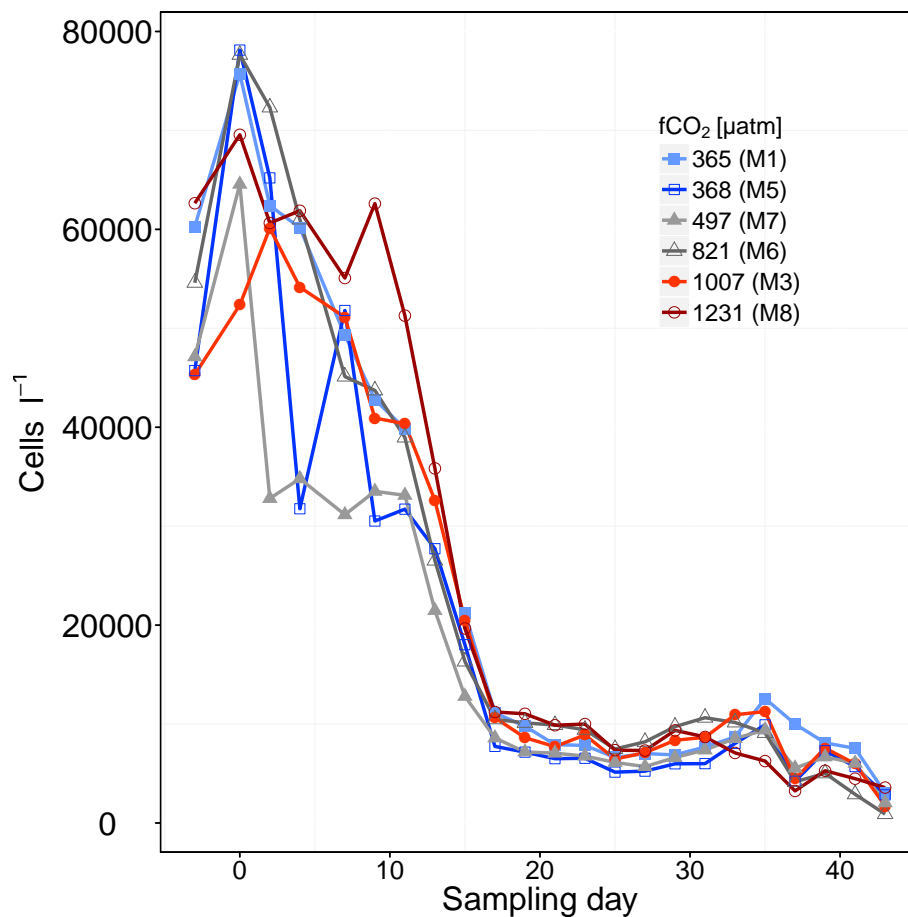


Figure 1. Total abundance of microzooplankton during the course of the experiment. Note there is one missing value in M1 on t_{13} .

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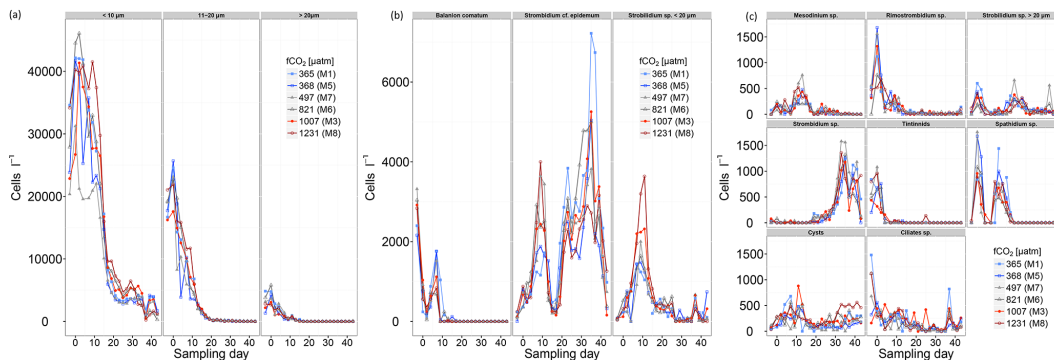


Figure 2. (a) Abundance of different size classes of *Myrionecta rubra*. (b) Abundance of other microzooplankton species/genera/groups. (c) Abundance of other microzooplankton species/genera/groups. Note there is one missing value in M1 on t_{13} in each of the subfigures.

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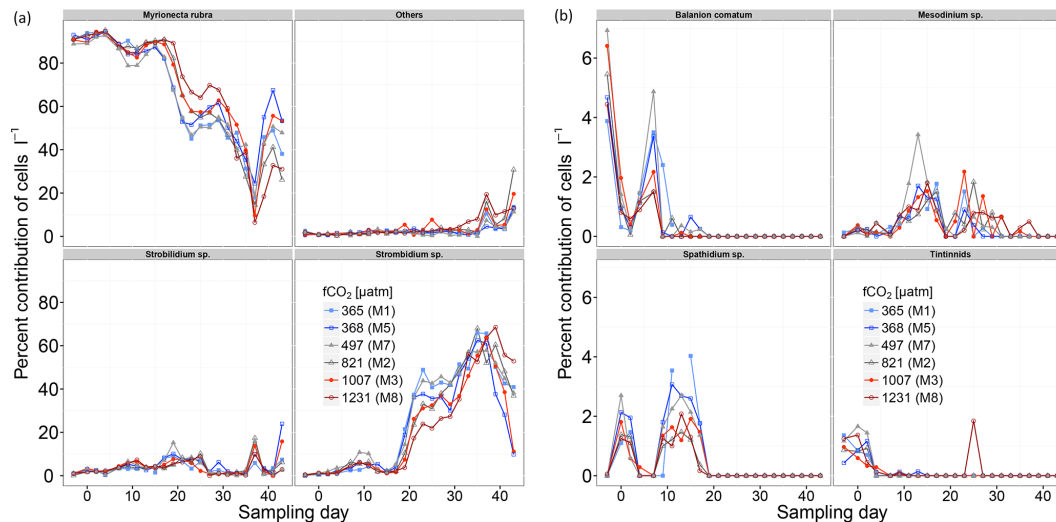


Figure 3. Percent contribution of major taxonomic species/genera/groups to the microzooplankton community. Note there is one missing value in M1 on t_{13} .

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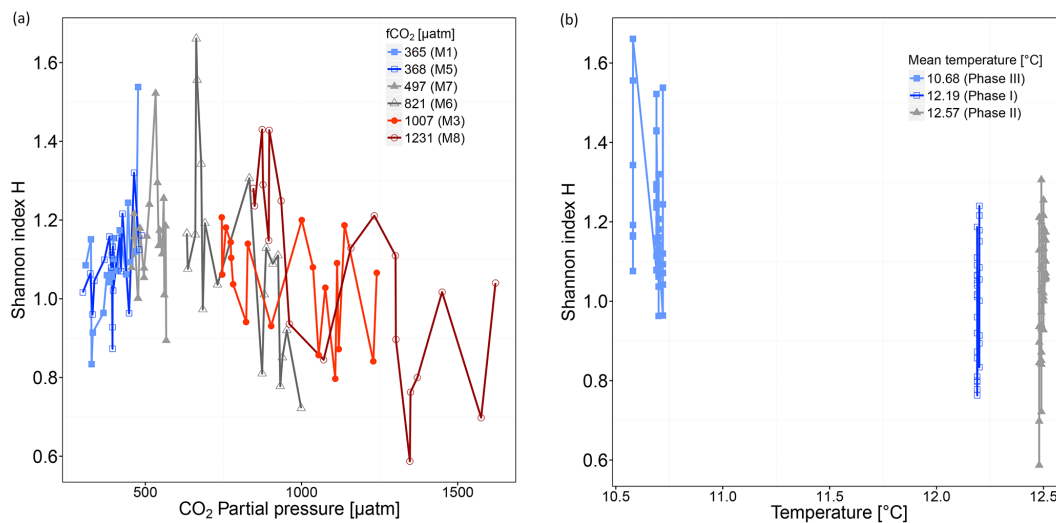


Figure 4. (a) Microzooplankton, Shannon diversity index H in relation to the daily change of $f\text{CO}_2$. Symbols and colours identify the mean $f\text{CO}_2$ for each mesocosm. (b) Microzooplankton, Shannon diversity index H . For better visibility, H is plotted against the mean phase (I, II, III) temperature of each mesocosm. Symbols and colours identify mean phase temperature across all mesocosms.

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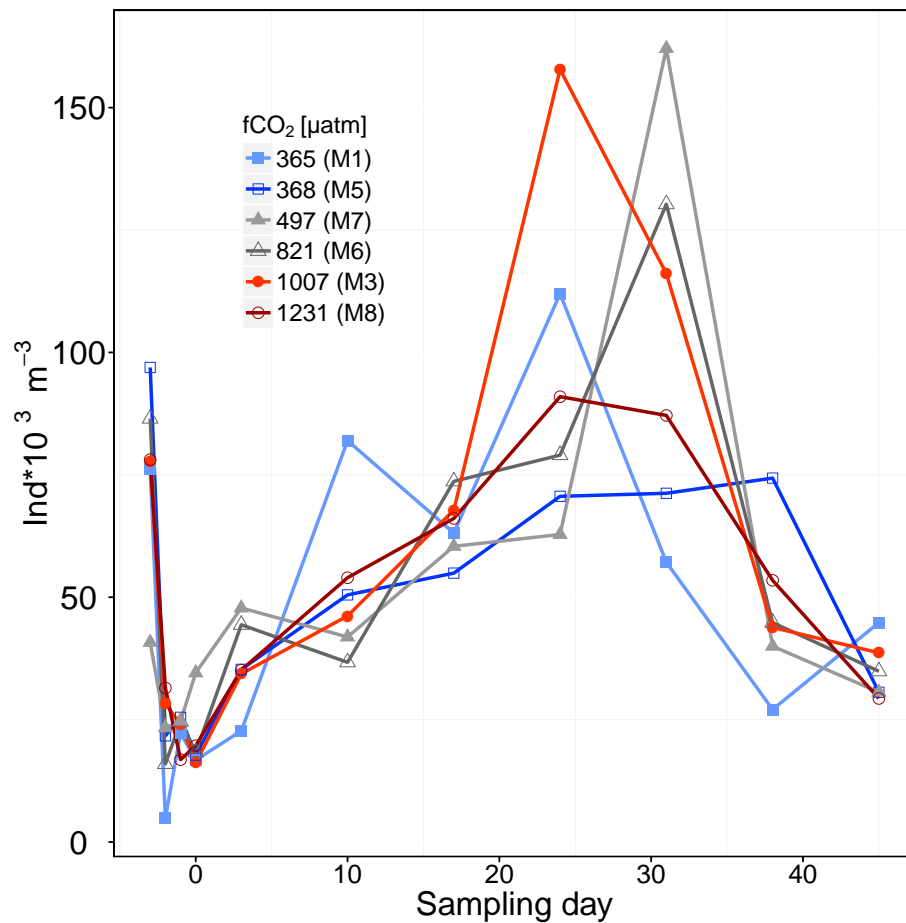


Figure 5. Mesozooplankton total abundance.

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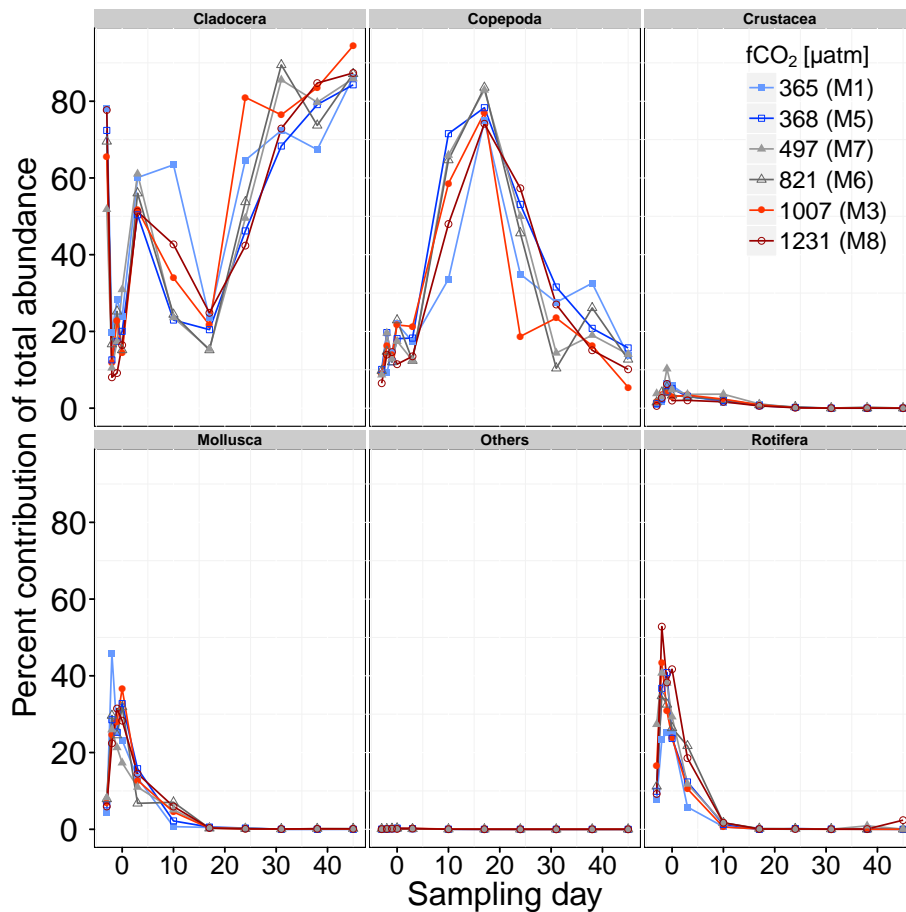


Figure 6. Percent contribution of mesozooplankton main taxonomic groups.

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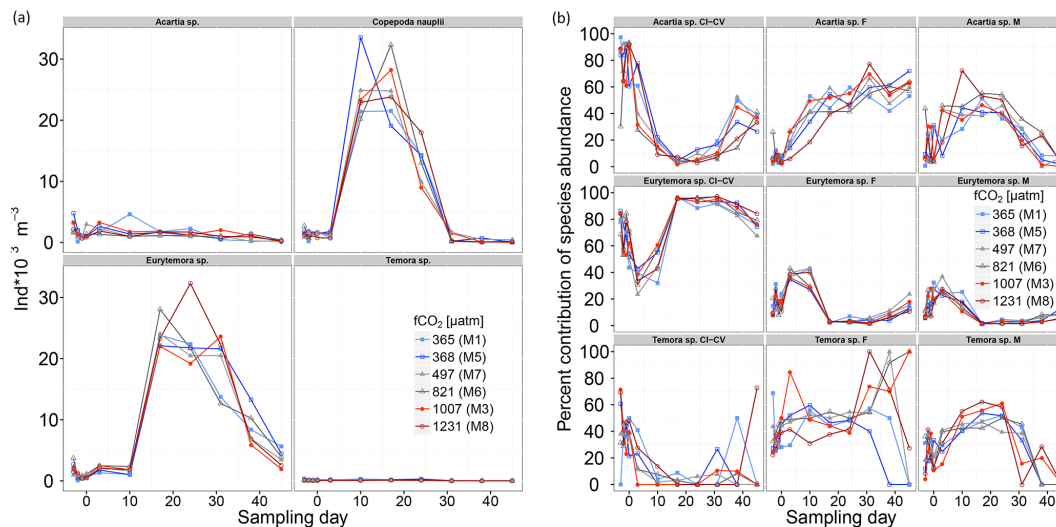


Figure 7. (a) Abundance of the dominant copepods species *Acartia* sp., *Eurytemora* sp., *Temora* sp., and copepod nauplii. (b) Percent contribution of different stages of dominant copepods. CI–V: copepodite stages, F: females, M: males.

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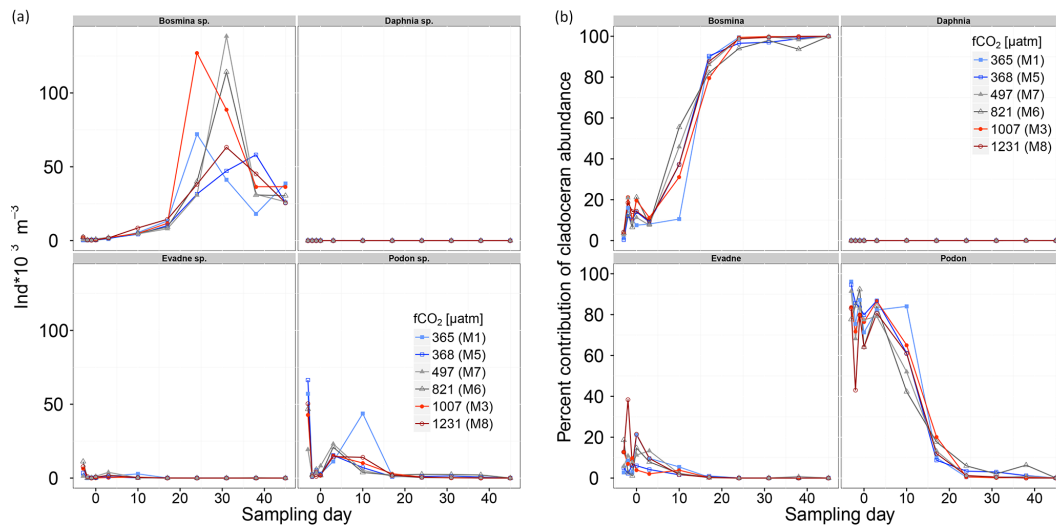


Figure 8. (a) Abundance of cladoceran species. (b) Percent contribution of different cladoceran species to the total abundance of cladocera.

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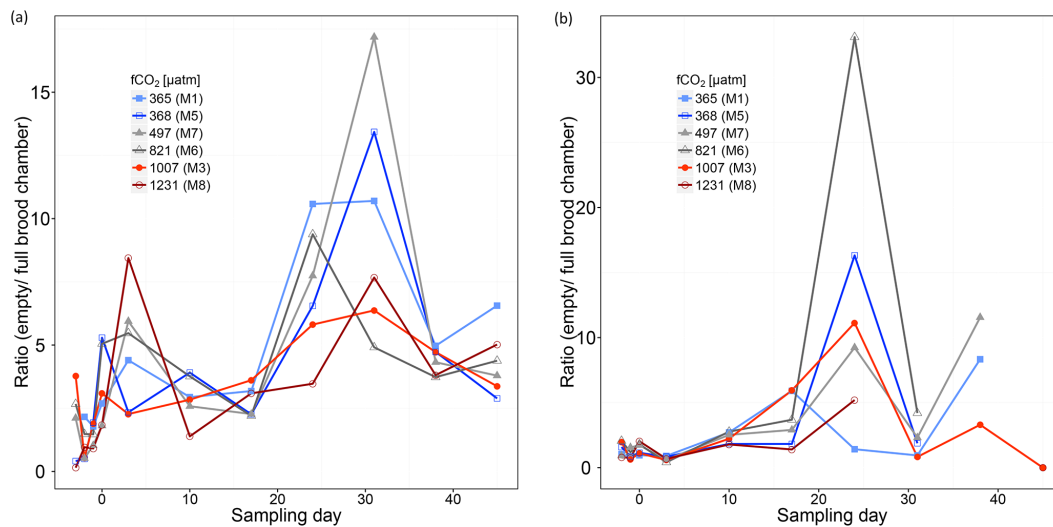


Figure 9. (a) Ratio of *Bosmina* with empty to full brood chambers. Note: Figure shows all data, but statistics were done on data from t_3 – t_{45} only to assure equally spaced data. (b) Ratio of *Podon* with empty to full brood chamber. Note 1: Ratio on t_3 was huge and therefore values not shown here to obtain reasonable scaled y-axis. Note 2: occurrence of missing values means no individuals with full brood chambers were present, hence, no ratio could be calculated.

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