Biogeosciences Discuss., 9, 13031–13051, 2012
www.biogeosciences-discuss.net/9/13031/2012/
doi:10.5194/bgd-9-13031-2012

Biogeosciences Discussions

High tolerance of protozooplankton to ocean acidification in an Arctic coastal plankton community

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Received: 31 July 2012 – Accepted: 3 August 2012 – Published: 20 September 2012

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Impacts of ocean acidification (OA) on marine biota have been observed in a wide range of marine systems. We used a mesocosm approach to study the response of a high Arctic coastal protozooplankton (PZP in the following) community during the post-bloom period in the Kongsfjorden (Svalbard) to direct and indirect effects of high pCO_2/low pH. We found almost no direct effects of OA on PZP composition and diversity. Both, the relative shares of ciliates and heterotrophic dinoflagellates as well as the taxonomic composition of protozoans remained unaffected by changes in pCO_2/pH. The different pCO_2 treatments did not have any effect on food availability and phytoplankton composition and thus no indirect effects e.g. on the total carrying capacity and phenology of PZP could be observed. Our data points at a high tolerance of this Arctic PZP community to changes in pCO_2/pH. Future studies on the impact of OA on plankton communities should include PZP in order to test whether the observed low sensitivity of protozoans to OA is typical for coastal communities where changes in seawater pH occur frequently.

1 Introduction

Since the beginning of the industrial revolution, the oceans have absorbed ca. 30 % of anthropogenic CO_2 (Sabine et al., 2004) and oceans thus serve as one of the largest sinks for anthropogenic CO_2 which in turn affects the marine carbonate system. The on-going increase in atmospheric pCO_2 results in decreasing seawater pH and carbonate ion (CO_3^{2-}) and increasing bicarbonate (HCO_3^-) and CO_2 concentrations. Especially the predicted drop in pH, in the following referred to as "ocean acidification (OA)", is considered to affect a variety of biological and biogeochemical processes in the oceans with potentially far-reaching consequences on the community and ecosystem level (Riebesell et al., 2007). In general, open ocean plankton communities are considered more vulnerable to OA since the pH in coastal environments fluctuates more

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strongly with frequent variations by up to 1 or more pH units (Hinga, 2002). Therefore, one of the central questions of the present study was whether arctic coastal plankton communities are negatively affected directly or indirectly by high pCO_2/low pH and thus are susceptible to ocean acidification.

Protozooplankton (here ciliates and heterotrophic dinoflagellates) are considered as major phytoplankton consumers worldwide (Calbet and Landry, 2004; Sherr and Sherr, 2007) and there is strong evidence that heterotrophic protists play a pivotal role in suppressing phytoplankton blooms in temperate (Johansson et al., 2004; Aberle et al., 2007) and cold waters (Levinsen and Nielsen, 2002; Seuthe et al., 2011). Protozooplankton usually show a rapid numerical response to changes in food availability and the occurrence of specific protozoa in the plankton can be directly linked to specific prey items (Loeder et al., 2011).

Changes in pCO_2 are known to affect consumers indirectly via changes in e.g. phytoplankton community structure, size classes and/or stoichiometry (Suffrian et al., 2008; Feng et al., 2009; Rossoll et al., 2012). On the other hand, protists are known for a direct pH sensitivity (Hinga, 2002; Pedersen, 2003) and a drop in seawater pH as a result of increasing pCO_2 could thus directly affect the physiology of both autotrophic and heterotrophic protists by changing e.g. intracellular pH, membrane potentials and enzyme activities (Nielsen et al., 2010 and citations therein).

In the present study we hypothesized that:

1. Direct effects of high pCO_2 on heterotrophic protists will alter PZP community composition and diversity.

2. Indirect effects of high pCO_2 by changes in phytoplankton composition or stoichiometry will alter the carrying capacity and phenology of PZP.

To investigate the impact of OA on a natural Arctic plankton community, a mesocosm experiment was conducted in Kongsfjorden, Svalbard, over a period of about one month in June/July 2010. In the fjord the initiation of the phytoplankton spring bloom starts already under ice cover, culminating between April and early June after

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ice break-up (Eilertsen et al., 1989; Seuthe et al., 2011). After the spring bloom, phytoplankton remains moderately high during late spring and summer (Hop et al., 2002). Protozooplankton is under-investigated in the Kongsfjorden so far but there is profound evidence that ciliates and heterotrophic dinoflagellates play an important role as trophic intermediaries in Arctic plankton communities (Seuthe et al., 2011). On the one hand PZP is strongly bottom-up controlled since its development can be directly linked to food availability. But at times when mesozooplankton abundance is high, top-down control e.g. by copepods or meroplanktonic larvae plays a crucial role in suppressing PZP abundance considerably (Levinsen and Nielsen, 2002).

The present work aimed at elucidating the role of PZP in a high-latitude plankton community in the light of OA and to draw implications on how direct and indirect effects of OA on heterotrophic protists might alter Arctic coastal ecosystems.

2 Methods

In summer 2010 nine polyethylene mesocosms ($\sim 50\,m^3$, 17 m long) were deployed at 78°56.2′ N, 11°53.6′ E in Kongsfjorden, Svalbard from 28 May 2010 until 7 July 2010. The mesocosms were moored and each mesocosm was filled with nutrient-poor, post-bloom seawater from the fjord passed through a net of 3 mm mesh-size during filling. CO_2-enriched seawater was injected into the mesocosms to achieve a gradient in pCO_2 levels ranging between 175 and 1085 µatm corresponding to a pH range between 8.34 and 7.63 respectively (from ambient post bloom conditions to 21st century predictions). Three different levels were defined: low pCO_2 level: 175–250 µatm, intermediate pCO_2 level: 340–600 µatm and high pCO_2 level: 675–1085 µatm where the pCO_2 values given are calculated as the mean pCO_2 from Day 8–27. On Day 13, nutrients where added to all pCO_2 treatments to ensure a sufficient nutrient supply for bloom development. The added nutrient concentrations were ~ 5 µM nitrate, ~ 0.3 µM phosphate and ~ 2.5 µM silicate. A detailed description of the mesocosm design, the deployment logistics, the methodology of CO_2-enrichment and the maintenance of

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the mesocosms throughout the duration of the experiment is given in Riebesell et al. (2012).

2.1 Protozooplankton sampling and identification

Seawater samples for PZP enumeration were taken once a week by a depth-integrating water sampler (depth integration: 0–12 m water depth). 250 ml of seawater were transferred to brown-glass bottles and fixed with acidic Lugol's iodine (2 % final concentration). 100 ml of each sample were transferred to sedimentation chambers and PZP was counted by the inverted microscope method (Utermöhl 1958) at a 200× magnification with a Zeiss Axiovert 135. The whole area of the bottom plate was counted for each sample in order to guarantee comparability of the counting method both at periods of high and low PZP abundance. PZP was identified to the lowest possible taxonomic level (species or genus level) according to Kahl (1932), Foissner et al. (1991, 1992, 1994, 1995), Strüder-Kypke et al. (2002), Tomas (1996) and Scott (2005). For biovolume calculations geometric proxies were used according to Hillebrand et al. (1999) and carbon biomass was calculated using the conversion factors given in Putt and Stoecker (1989). Diversity was measured by the Shannon-Wiener function (H'; $\log_e$) (Shannon and Weaver, 1963).

2.2 Phytoplankton sampling and identification

100 ml water sample from a depth-integrating water sampler (depth integration: 0–12 m water depth) were filled in brown-glass bottles and fixed with alkaline Lugol's iodine (1 % final concentration). The counting was performed after Utermöhl (1958) with an inverted microscope (Zeiss Axiovert, 100). Cells bigger than 12 µm were counted on the half bottom area at 200 fold magnification and cells less than 12 µm (~ 5–12 µm) on two to four stripes at 400 fold magnification. The settling volume was 25 ml. For identification Tomas (1996), Hoppenrath et al. (2009) and Kraberg et al. (2010) were

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used. The biovolumes were calculated after Olenina et al. (2006) and for transformation to carbon the equations of Menden-Deuer and Lessard (2000) were used.

2.3 Chlorophyll measurements

250–500 ml of seawater was sampled and filtered onto GF/F for chlorophyll *a* analysis. Filters were stored frozen for at least 24 h and homogenized in 90 % acetone with glass beads (2 and 4 mm) in a cell mill thereafter. After centrifugation at 5000 rpm chlorophyll *a* concentrations were determined in the supernatant on a fluorometer (TURNER, 10-AU) according to Welschmeyer (1994).

2.4 Statistical analysis

To test for significant effects of pCO_2 on PZP diversity, a regression analysis was conducted. As independent factor pCO_2 and as dependent factor H' were chosen using STATISTICA 6.0. Diversity was calculated using PRIMER 5.2 (© 2001 Primer-E Ltd.).

3 Results

3.1 Chlorophyll *a*, phytoplankton biomass and composition

The phytoplankton standing stock started with fairly low values at the beginning of the experiment showing initial chlorophyll *a* concentrations between 0.26 (pCO_2 1085) and 0.36 µg l^{-1} (pCO_2 180) (Fig. 1). In general, a three-phase bloom development occurred at all pCO_2 levels: the 1st phase before nutrient addition (before Day 13), the 2nd phase after nutrient addition until the second chlorophyll minimum (Day 13–21) and the 3rd phase until the end of the experiment (after Day 21). Each phase was characterized by an increase in phytoplankton biomass and a subsequent decline in chlorophyll *a* right after the bloom. Chlorophyll *a* reached maximum peak heights during the 3rd phase of bloom development while highest chlorophyll *a* concentrations occurred at low (pCO_2:

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175–250; Fig. 1a–c) and intermediate pCO_2 levels (pCO_2: 340–600; Fig. 1d–f) and reduced chlorophyll *a* peaks were observed at high pCO_2 levels (pCO_2: 675–1085; Fig. 1g–i).

During the 1st phase of bloom development the phytoplankton (PP) community was dominated by crysophytes and nanoflagellates (3–8 µm) at all pCO_2 levels (Fig. 2). During the 2nd phase, a moderate bloom of prasinophytes (~ 5 µm) occurred showing slightly higher peak heights at intermediate and high pCO_2 levels (pCO_2: 425–1085; Fig. 2d–i) (see also Brussaard et al. (2012) for details. The 3rd phase was dominated by autotrophic dinoflagellates (mainly *Heterocapsa rotundata*) which showed a higher biomass at intermediate and high pCO_2 levels (pCO_2: 425–1085; Fig. 2e–i). Diatoms were of minor importance occurring only at low biomass at the end of the experiment.

3.2 Protozooplankton biomass

The experiment started with fairly high PZP biomass at all pCO_2 levels ranging between a minimum of 15 µg C l^{-1} (pCO_2 600) and a maximum of 54 µg C l^{-1} (pCO_2 675) (Fig. 1a–i). While the PZP biomass in the low (pCO_2: 175–250; Fig. 1a–c) and the high pCO_2 levels (pCO_2: 675–1085; Fig. 1g–i) decreased during the 1st phase of the experiment until Day 13, biomass in the intermediate pCO_2 level (pCO_2: 340–600; Fig. 1d–f) increased from Day 0 to Day 7, followed by a decline until Day 13. During the 2nd and the 3rd phase, an increase in PZP biomass was observed at all pCO_2 levels reaching highest biomass peaks of 46 µg C l^{-1} (pCO_2 175, Fig. 1a) and 50 µg C l^{-1} (pCO_2 250, Fig. 1c) at low pCO_2 levels.

3.3 Protozooplankton composition and diversity

Heterotrophic dinoflagellates dominated the PZP community throughout the experiment, independent of pCO_2 level, while ciliates contributed to lower proportions to the PZP biomass (Fig. 2a–i). The taxonomic composition of the PZP community showed almost identical patterns at all pCO_2 levels (see Table A1 for details). In general,

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small-sized (< 30 µm) ciliates and dinoflagellates played only a minor role while large-sized (> 30 µm) ciliates and dinoflagellates showed a higher PZP biomass. Small-sized ciliates comprised of the choreotrichid *Lohmaniella oviformis* and strombidiids (*Strombidium* sp.), while small-sized dinoflagellates comprised of *Gymnodinium cf. arcticum*, *Katodinium cf. glaucum* and *Protoperidinium brevipes*. Large-sized ciliates where mainly represented by *Strombidium capitatum* and large-sized dinoflagellates by *Gyrodinium cf. fusiforme*. The dinoflagellate *Protoperidinium pellucidum* and *Protoperidinium ovatum* and the ciliates *Laboea strobila*, *Strobilidium spiralis, Strombidium cf. conicum, Rimostrombidium* sp. and *Myrionecta rubra* occurred only sporadically. Protozooplankton diversity (H') ranged between 1.64 (pCO_2 175) and 1.79 (pCO_2 340) and no correlation was found between H' and pCO_2.

3.4 Protozooplankton succession

During the 1st phase of bloom development, biomass response of PZP at the different pCO_2 levels was quite heterogeneous. The strongest positive biomass response to increasing chlorophyll *a* concentrations during the 1st phase was observed for the dinoflagellate *Gymnodinium cf. arcticum* (Fig. 3a). Most protozoans showed a distinct biomass increase during the 2nd or the 3rd phase of bloom development at all pCO_2 levels (Fig. 3). While the biomass of the ciliates *Lohmaniella oviformis*, *Rimostrombidium* sp. and *Strombidium cf. conicum* peaked already during the 2nd phase of bloom development at all pCO_2 levels (Fig. 3c–e), other protozoans e.g. *Katodinium cf. glaucum* showed increasing biomass until the 3rd phase. Overall responses of single protozoans to increasing phytoplankton availability showed similar patterns at all pCO_2 levels and no trend in peak biomass maxima of protozoans in relation to the different pCO_2 levels was observed. However, some species e.g. *Strombidium cf. conicum* and *Katodinium cf. glaucum* showed a steeper growth increase at intermediate and higher pCO_2 levels (Fig. 3e–f).

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4 Discussion

The initial PZP biomass of 15–54 µg C l^{-1} in our mesocosm study in Kongsfjorden in late May 2012 was high compared to studies from the same season and location where PZP biomass ranged between 2 and 13 µg C l^{-1} (Seuthe et al., 2011; Hodal et al., 2012). However, our data is in line with post-bloom PZP biomass reported for other coastal Arctic regions e.g. Disko Bay, West Greenland (Levinsen et al., 2000; Hansen et al., 2003). In good agreement to Hodal et al. (2012), small-sized ciliates and dinoflagellates were of minor importance while large-sized ciliates and dinoflagellates dominated the PZP. Furthermore, the taxonomic composition of the PZP community we found in 2012 was similar to that of the post-bloom period in Kongsfjorden in 2006 (Seuthe et al., 2011).

4.1 Direct effects of high pCO_2 on heterotrophic protists will alter protozooplankton community composition and diversity

Previous studies on the impact of OA on PZP communities showed no clear trend (Suffrian et al., 2008; Rose et al., 2009). In order to understand the causes and consequences of future CO_2 and pH conditions it is essential to consider all components of the plankton, from protists to metazoans, and to compare among sites with different degrees of natural pH fluctuations (Nielsen et al., 2012).

Protists play a major role in the global carbon cycle by fixing inorganic carbon and the interplay between auto- and heterotrophic protists is crucial since up to 60–75 % of phytoplankton production in coastal and open oceans is consumed by protozoans (Landry and Calbet, 2004). Protozooplankton thus acts as a trophic link between phytoplankton and mesozooplankton and contributes substantially to the cycling of bulk organic matter and nutrients (Irigoien et al., 2005; Calbet and Saiz, 2005). However, only few studies have addressed the impact of OA on PZP communities so far although there is indication for pH sensitivity of heterotrophic protists at elevated pH (pH of ~8.0 to 9.5) (Hinga, 1992; Pedersen and Hansen, 2003). Experimental studies off the coast of

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Norway (Suffrian et al., 2008) and in the open North Atlantic Ocean (Rose et al., 2009) found no direct effects of a high pCO_2/low pH on protozoans. This is in line with our observation, since no direct effects on PZP composition and diversity was observed; neither the relative shares of ciliates and heterotrophic dinoflagellates were affected nor did a low pH induce changes in taxonomic composition. However, Nielsen et al. (2012) showed that a reduced pH ($\sim$6.3) can alter the performance of autotrophs (reduced abundance and photosynthetic rate) and protozoa (reduced abundance). For coccolithophores such direct effects are assumed to be related to changes in the intra-cellular pH which in turn alters enzymatic reactions and growth rates (Nimer et al., 1994; Suffrian et al., 2011). In our study, the changes in pCO_2 and pH were within the range expected for the 21st century and thus not as extreme as in the scenario simulated by Nielsen et al. (2012). But similar to their study, we found a high tolerance of protozoans towards moderate changes in pH which might be a typical pattern of coastal plankton since seawater pH in coastal regions shows significant natural fluctuations (Hansen, 2002). So, even today coastal protists is temporarily experience high pCO_2/low pH as predicted for the next century, but the question remains whether communities that are permanently subjected to a high CO_2 world will display the same level of pH tolerance.

4.2 Indirect effects of high pCO_2 by changes in phytoplankton composition or stoichiometry will alter the carrying capacity and phenology of PZP

Elevated pCO_2 is known to affect autotrophic processes directly (Riebesell and Tortell, 2011), while PZP is considered to be predominantly indirectly affected by high pCO_2 from changes in phytoplankton community structure, size classes, and/or stoichiometry (Suffrian et al., 2008; Rose et al., 2009).

Our initial expectation was that the different pCO_2 levels would induce general shifts in phytoplankton composition which in turn could affect the carrying capacity and phenology of PZP. Phytoplankton composition in our mesocosms showed some clear CO_2-dependent trends, e.g. a positive CO_2 effect on dinoflagellates while prasinophytes and haptophytes profited at low CO_2 levels during phase 3 of the experiment (Schulz et

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al., 2012). However, these changes in phytoplankton community composition did neither alter the carrying capacity nor the phenology of PZP. This might be related to the fact that changes in community composition happened only on short time scales and responses were usually not maintained over a longer period of bloom development (Brussaard et al., 2012). Phytoplankton usually comprises a multitude of species and thus, short-term, pCO_2-induced alterations in algal diets of consumers can often be mitigated (Urabe and Waki, 2009). Further, as pointed out by Suffrian et al. (2008), the distinct effects of elevated CO_2 on single plankton species observed in laboratory studies are not comparable to those obtained in experiments simulating close-to natural conditions since such complex systems seem to have a higher buffering capacity to changes in pCO_2. This is in line with observations of Rose et al. (2009) where no relationship between the PZP community composition and elevated CO_2 could be observed, but only when the factor temperature was not additionally manipulated.

In the mesocosms, nanophytoplankton (e.g. nanoflagellates and crysophytes) played a major role during the 1st phase of bloom development and, apart from microzooplankton grazing, viral lysis enforced the nanophytoplankton bloom to decline (Brussaard et al., 2012). The rapid decline in nanophytoplankton induced by viruses corresponds well with the steep biomass decline of ciliates and dinoflagellates during the 1st phase of bloom development which points at a food shortage of protozoa. This is also confirmed by the moderate grazing rates observed for PZP during the nanophytoplankton bloom at all pCO_2 levels (Brussaard et al., 2012).

During the 2nd and the 3rd phase of bloom development, increases in PZP biomass were observed at all pCO_2 levels. This corresponds well to the high nanophytoplankton biomass (mainly prasinophytes, autotrophic dinoflagellates and haptophytes; see Schulz et al., 2012 for details) during the second half of the experiment (phase 2 and 3). In addition, high PZP grazing rates on pico- and nanophytoplankton were observed during the phases after nutrient addition from Day 13 on (Brussaard et al., 2012). But despite a continuously high pico- and nanophytoplankton availability and an increasing biomass of autotrophic dinoflagellates (mainly *H. rotundata*), PZP showed a rapid

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decline during the 3rd phase of bloom development. This phenomenon is most likely not bottom-up regulated but related to an enhanced top-down control of PZP by mesozooplankton. In our study the mesozooplankton comprised of cirripedia and copepod nauplii initially and shifted towards a community dominated by polychaete larvae and copepodites (mainly *Calanus* spp.) from Day 18 onwards at all pCO_2 levels (Niehoff et al., 2012). Cirripedia larvae, which dominated the mesozooplankton clearly during the 1st phase of bloom development are characterized by a herbivorous feeding mode in contrast to other meroplanktonic larvae such as e.g. copepod nauplii (Turner et al., 2001). This might explain the high initial PZP biomass in the mesocosms when predation pressure by omnivorous mesozooplankton was still low. Subsequently, polychaete larvae and *Calanus* copepodites, effective grazers of PZP (Turner et al., 2001), became highly abundant thus pointing at a suppression of PZP by mesozooplankton. As a result, a distinct bloom formation of autotrophic dinoflagellates (mainly *H. rotundata*) occurred although the genus *Heterocapsa* is considered as a good prey item for zooplankton (Kamiyama and Masuyama, 2005).

Furthermore, the role of PZP in improving the food quality for higher trophic levels by buffering nutritional imbalances at the interface between primary production and consumption ("trophic upgrading") has been stressed (Malzahn et al., 2010). Thus, with decreasing food quality of phytoplankton, heterotrophic components in the plankton become more important as food source for mesozooplankton. This is most conspicuous during the decay of a bloom when nutrients become limiting and e.g. copepods switch from autotrophic to PZP diets (Loeder et al., 2012). There is indication that such a switch from autotrophic to heterotrophic diets occurred during the 2nd phase of bloom development where an increase in copepods' egg production was observed (Niehoff et al., 2012) in concert with a biomass peak of PZP. This finding is further supported by the high proportions of PUFA and DHA (Leu et al., 2012) during the 2nd bloom phase since these fatty acid markers give indication for a strong degree of carnivory (El-Sabaawi et al., 2009). Concurrently with the decline in egg production rates, biomass of PZP as well as the relative shares of PUFA and DHA decreased.

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Acknowledgements. This work is a contribution to the "European Project on Ocean Acidification" (EPOCA) which received funding from the European Community's Seventh Framework Programme (FP7/2007–2013) under grant agreement no. 211384. We gratefully acknowledge the logistical support of Greenpeace International for its assistance with the transport of the mesocosm facility from Kiel to Ny-Ålesund and back to Kiel. We also thank the captains and crews of M/V ESPERANZA of Greenpeace and R/V *Viking Explorer* of the University Centre in Svalbard (UNIS) for assistance during mesocosm transport and during deployment and recovery in Kongsfjorden. We thank the staff of the French-German Arctic Research Base at Ny-Ålesund, in particular Marcus Schumacher, for on-site logistical support. Arne Malzahn is thanked for fruitful comments on earlier versions of the manuscript.

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Table A1. Taxonomic composition of protozooplankton (biomass in µg C l^{-1}) over the course of the mesocosm experiment (white rows: dinoflagellates; bright grey rows: ciliates) in the different pCO_2 treatments.

Taxa	175pCO_2 (Day of the experiment)						180pCO_2 (Day of the experiment)						250pCO_2 (Day of the experiment)					
	0	7	13	19	25	29	0	7	13	19	25	29	0	7	13	19	25	29
Gyrodinium cf. fusiforme	21.50	13.52	5.99	8.45	22.81	3.95	21.12	15.13	3.92	7.45	8.52	1.34	21.27	16.20	5.15	10.90	18.28	6.45
Gymnodinium cf. arcticum	3.93	4.21	1.53	2.62	5.34	3.98	4.38	3.02	2.67	3.24	2.62	1.13	6.23	4.58	1.39	1.98	6.98	1.60
Katodinium cf. glaucum	0.44	0.40	0.54	0.89	3.09	2.95	0.24	0.10	0.97	1.38	2.46	0.68	0.30	0.37	0.52	0.73	2.73	0.61
Protoperidinium cf. pellucidum	0.62	0.62	0.00	0.00	3.10	0.31	0.31	1.24	0.93	0.93	0.31	2.17	0.31	0.00	0.00	0.00	5.58	1.71
Protoperidinium cf. brevipes	0.18	0.00	0.09	0.00	0.35	0.18	0.00	0.22	0.00	0.35	0.44	0.66	0.09	0.09	0.09	0.00	0.44	0.20
Protoperidinium cf. ovatum	0.75	0.86	0.43	0.43	4.28	4.38	0.86	1.28	1.92	0.00	2.57	0.86	0.32	1.92	0.21	0.86	3.42	5.13
Strombidium cf. conicum	0.00	0.04	1.99	0.40	0.51	0.47	0.25	0.40	1.91	0.61	0.43	0.04	0.05	0.14	2.38	0.47	0.79	0.07
Strombidium capitatum	0.00	0.00	6.79	5.66	2.26	0.00	6.04	1.51	1.51	10.94	0.00	0.00	7.55	1.89	6.41	1.13	4.53	0.00
Cyst *Strombidium capitatum*	1.65	0.47	0.24	0.47	1.88	0.71	5.65	0.24	0.24	0.00	0.24	0.71	2.24	2.12	1.41	0.00	2.35	0.24
Strombidium spp.	1.61	0.23	0.29	0.29	0.06	0.04	1.94	0.42	0.34	0.50	0.00	0.00	1.97	0.92	0.87	0.37	0.09	0.00
Rimostrombidium sp.	0.61	0.26	0.69	0.87	0.17	0.09	0.00	0.26	0.09	0.78	0.00	0.26	0.30	0.69	0.52	2.60	0.26	0.17
Lohmaniella oviformis	0.20	0.10	0.01	0.77	0.60	0.00	0.14	0.16	0.57	1.25	0.00	0.01	0.02	0.09	0.05	0.58	0.15	0.34
Myrionecta rubra	0.72	0.36	0.36	0.00	0.00	0.00	2.29	0.36	0.00	0.00	0.00	0.24	0.30	0.96	0.24	0.00	0.00	0.00
Strobilidium spiralis	1.11	0.00	0.00	0.64	1.27	1.11	0.32	0.48	1.11	0.48	0.32	0.16	0.40	0.16	0.32	0.00	1.91	0.08
Laboea strobila	1.05	0.79	0.79	1.31	0.53	0.79	2.36	1.71	2.89	2.36	0.53	0.53	0.00	0.53	1.84	1.84	2.63	1.05

Taxa	340pCO_2 (Day of the experiment)						425pCO_2 (Day of the experiment)						600pCO_2 (Day of the experiment)					
	0	7	13	19	25	29	0	7	13	19	25	29	0	7	13	19	25	29
Gyrodinium cf. fusiforme	9.94	13.05	2.15	7.37	7.37	2.99	18.20	16.59	3.99	5.53	5.22	0.42	6.14	18.66	6.68	8.45	9.37	1.46
Gymnodinium cf. arcticum	1.61	4.87	0.54	2.62	5.05	3.02	3.78	7.02	1.73	2.99	4.68	0.73	0.83	4.77	2.40	4.03	10.09	0.66
Katodinium cf. glaucum	0.25	0.65	0.25	1.20	1.96	1.86	0.62	2.02	0.65	1.15	2.71	0.56	0.03	0.78	0.80	1.77	3.37	0.34
Protoperidinium cf. pellucidum	0.16	0.00	0.00	0.93	0.62	0.93	0.31	1.86	0.31	0.62	0.00	1.55	0.62	0.00	0.93	0.00	2.48	1.40
Protoperidinium cf. brevipes	0.00	0.22	0.00	0.40	0.31	0.18	0.00	0.44	0.18	0.18	0.22	0.22	0.18	0.09	0.04	0.09	0.00	0.09
Protoperidinium cf. ovatum	0.53	0.86	0.64	0.00	2.57	4.06	1.71	0.00	0.64	1.92	1.28	0.96	0.21	0.86	0.64	1.92	0.00	1.50
Strombidium cf. conicum	0.00	1.05	0.43	0.29	0.25	0.33	0.18	1.30	1.59	0.65	0.43	0.22	0.00	1.26	1.23	0.54	0.22	0.00
Strombidium capitatum	5.28	7.92	3.02	3.02	0.00	0.38	2.64	4.53	1.13	4.90	3.77	0.00	5.09	8.30	2.26	1.13	0.00	0.00
Cyst *Strombidium capitatum*	2.47	1.06	0.00	0.71	0.47	0.71	1.65	2.35	0.94	0.47	0.00	0.47	1.18	0.24	0.47	0.00	0.00	0.24
Strombidium spp.	0.16	2.25	0.06	0.23	0.02	0.03	2.90	4.35	0.20	0.47	0.11	0.00	0.00	1.30	0.32	0.31	0.17	0.00
Rimostrombidium sp.	0.22	1.13	0.35	1.47	0.09	0.09	0.00	0.69	0.43	0.43	0.09	0.00	0.13	0.43	0.35	4.60	0.00	0.13
Lohmaniella oviformis	0.01	0.11	0.06	0.91	0.89	0.41	0.11	0.07	0.10	1.27	0.24	0.23	0.02	0.11	0.16	1.38	0.65	0.18
Myrionecta rubra	1.39	1.08	0.72	0.00	0.00	0.00	2.05	0.00	0.00	0.00	0.00	0.00	0.24	0.96	0.36	6.39	0.00	0.00
Strobilidium spiralis	0.64	0.80	0.00	1.27	0.64	0.00	0.16	0.32	0.96	0.00	0.32	0.16	0.00	0.16	0.48	0.48	0.48	0.08
Laboea strobila	0.79	0.79	0.53	0.79	0.26	0.26	2.89	0.00	0.53	3.41	0.53	0.00	0.00	0.26	0.53	1.84	0.00	0.39

Taxa	675 pCO_2 (Day of the experiment)						860 pCO_2 (Day of the experiment)						1085pCO_2 (Day of the experiment)					
	0	7	13	19	25	29	0	7	13	19	25	29	0	7	13	19	25	29
Gyrodinium cf. fusiforme	20.43	16.74	3.07	6.45	7.37	2.23	17.47	10.37	3.76	6.68	6.76	1.11	19.20	11.90	5.53	5.68	3.46	0.38
Gymnodinium cf. arcticum	4.70	5.61	1.46	3.36	3.24	3.61	2.55	4.28	1.61	3.29	4.81	2.81	4.38	4.01	3.14	5.74	3.14	1.39
Katodinium cf. glaucum	0.44	0.40	0.80	2.63	2.70	1.51	0.30	0.62	0.75	2.53	2.11	0.90	0.46	0.84	0.59	2.35	2.15	0.70
Protoperidinium cf. pellucidum	0.31	0.00	0.31	0.00	1.55	3.41	0.16	0.00	0.00	0.31	0.93	2.17	0.31	0.31	0.00	0.00	2.17	1.40
Protoperidinium cf. brevipes	0.09	0.22	0.26	0.22	0.40	0.18	0.09	0.22	0.09	0.35	0.09	0.11	0.00	0.26	0.22	0.31	0.31	0.11
Protoperidinium cf. ovatum	1.92	0.86	1.07	1.71	1.50	1.28	1.60	1.50	2.99	0.00	0.64	1.60	1.92	1.92	1.92	2.14	1.50	0.00
Strombidium cf. conicum	0.47	0.43	0.76	0.72	0.00	0.00	0.13	0.25	1.16	0.14	0.25	0.18	0.33	0.61	1.55	0.40	0.40	0.13
Strombidium capitatum	11.32	5.28	1.51	1.51	0.00	0.38	9.62	3.40	1.13	0.00	0.00	0.19	5.66	3.02	1.51	5.66	1.13	0.00
Cyst *Strombidium capitatum*	6.83	1.18	0.47	1.88	1.41	0.00	2.47	1.65	0.94	0.00	0.00	0.71	4.24	0.47	0.24	0.24	1.88	0.00
Strombidium spp.	3.23	1.42	0.07	0.06	0.00	0.00	0.42	1.21	0.06	0.03	0.01	0.00	2.46	2.51	0.23	0.19	0.29	0.01
Rimostrombidium sp.	0.00	0.35	0.17	1.21	0.43	0.09	0.22	0.69	0.00	0.43	0.35	0.43	0.00	0.35	0.52	0.82	2.17	0.13
Lohmaniella oviformis	0.19	0.16	0.06	0.27	0.00	0.61	0.09	0.22	0.11	0.96	0.70	0.28	0.15	0.14	0.47	0.96	1.11	0.03
Myrionecta rubra	1.33	0.24	0.36	0.00	0.00	0.00	4.40	0.24	0.24	0.00	0.00	0.00	1.45	0.00	0.00	0.00	0.36	0.00
Strobilidium spiralis	0.80	0.80	0.80	2.87	1.43	0.64	0.08	0.80	0.32	2.23	1.75	0.40	0.48	0.32	0.80	0.96	4.62	0.40
Laboea strobila	1.84	0.79	0.00	3.68	1.58	0.00	0.13	1.84	0.53	2.36	0.00	1.58	2.89	1.05	0.53	0.53	1.31	0.00

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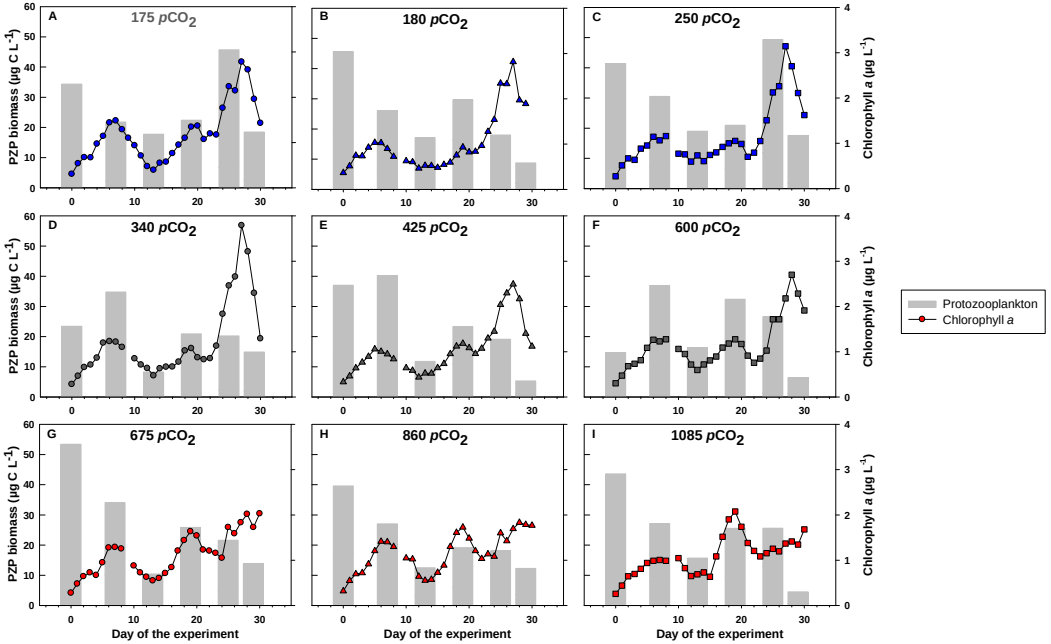

Fig. 1. Protozooplankton (PZP) biomass ($\mu g\,C\,l^{-1}$) and chlorophyll *a* concentrations ($\mu g\,C\,l^{-1}$) in the different pCO_2 treatments (blue lines: pCO_2 of 175 **(A)**, 180 **(B)** and 250 **(C)**; grey lines: pCO_2 of 340 **(D)**, 425 **(E)** and 600 **(F)**; red lines: pCO_2 of 675 **(G)**, 860 **(H)** and 1085 **(I)**).

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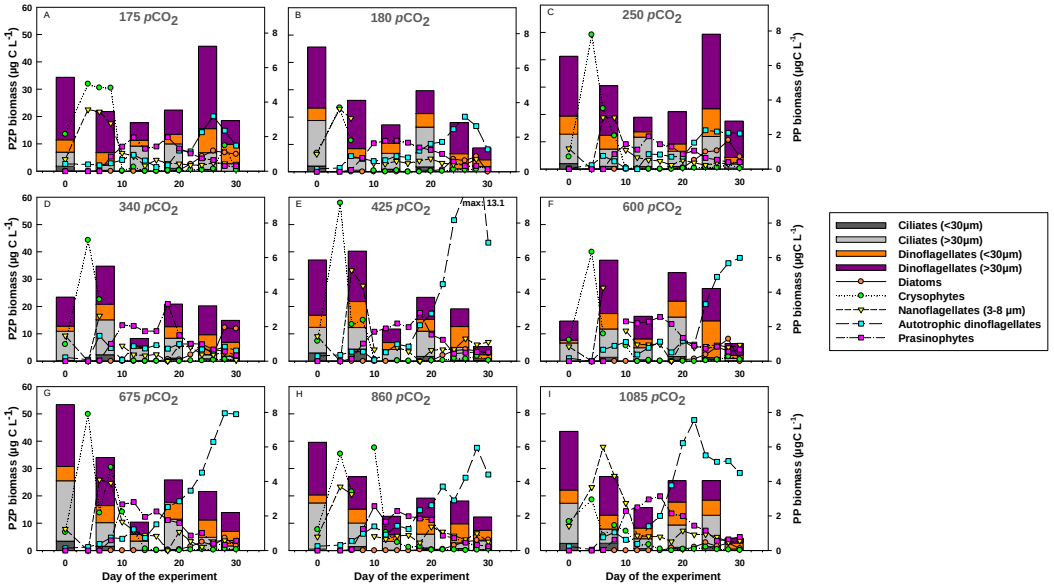

Fig. 2. Protozooplankton (PZP) biomass ($\mu g\,C\,l^{-1}$) (dark grey: ciliates < 30µm; bright grey: ciliates > 30µm; orange: dinoflagellates < 30µm; purple: dinoflagellates > 30µm) and phytoplankton (PP) biomass ($\mu g\,C\,l^{-1}$) of different taxonomic groups (orange circles: Diatoms; green circles: Crysophytes; yellow triangles: Flagellates (3–8 µm); blue circles: autotrophic dinoflagellates (mainly *Heterocapsa rotundata*) and pink squares: Prasinophytes) in the different pCO_2 treatments (pCO_2 of 175 **(A)**, 180 **(B)**, 250 **(C)**, 340 **(D)**, 425 **(E)**, 600 **(F)**, 675 **(G)**, 860 **(H)** and 1085 **(I)**).

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Tolerance of protozooplankton to ocean acidification

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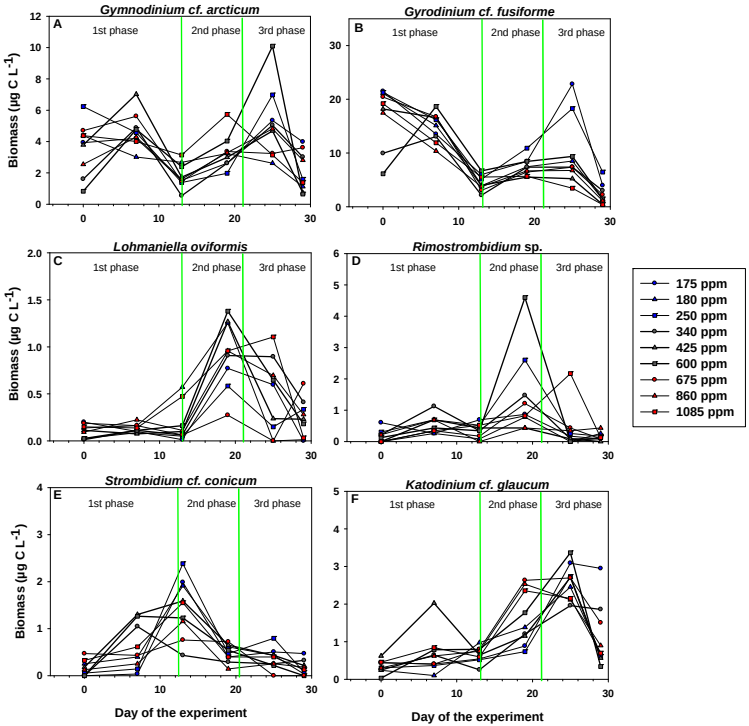

Fig. 3. Temporal succession of specific protozooplankton species: *Gymnodinium cf. arcticum* **(A)**, *Gyrodinium cf. fusiforme* **(B)**, *Lohmaniella oviformis* **(C)**, *Rimostrombidium* sp. **(D)**, *Strombidium cf. conicum* **(E)** and *Katodinium cf. glaucum* **(F)** in the different pCO_2 treatments (blue lines: pCO_2 of 175, 180 and 250; grey lines: pCO_2 of 340, 425 and 600; red lines: pCO_2 of 675, 860 and 1085). Note the different scaling on the y-axes. Vertical green lines depict the three phases of bloom development.

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