Deep-Sea Research II 127 (2016) 75–92

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Effects of acute ocean acidification on spatially-diverse polar pelagic foodwebs: Insights from on-deck microcosms

G.A. Tarling [a,*], V.L. Peck [a], P. Ward [a], N.S. Ensor [a,b], E. Achterberg [c,d], E. Tynan [c], A.J. Poulton [e], E. Mitchell [f], M.V. Zubkov [e]

[a] British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Rd, Cambridge CB3 0ET, UK
[b] Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen AB11 9DB, UK
[c] Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton SO14 3ZH, UK
[d] GEOMAR Helmholtz Centre for Ocean Research, Kiel, 24148 Kiel, Germany
[e] National Oceanography Centre, Waterfront Campus, European Way, Southampton SO14 3ZH, UK
[f] Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, Argyll PA37 1QA, UK

ARTICLE INFO

Available online 16 February 2016

Keywords:
Arctic
Southern Ocean
Copepod
Phytoplankton
Dinoflagellates
Bacteria
Nannoplankton
Transparent exopolymeric particles
PCO_2

ABSTRACT

The polar oceans are experiencing some of the largest levels of ocean acidification (OA) resulting from the uptake of anthropogenic carbon dioxide (CO_2). Our understanding of the impacts this is having on polar marine communities is mainly derived from studies of single species in laboratory conditions, while the consequences for food web interactions remain largely unknown. This study carried out experimental manipulations of natural pelagic communities at different high latitude sites in both the northern (Nordic Seas) and southern hemispheres (Scotia and Weddell Seas). The aim of this study was to identify more generic responses and achieve greater experimental reproducibility through implementing a series of short term (4 d), multilevel (3 treatment) carbonate chemistry manipulation experiments on unfiltered natural surface-ocean communities, including grazing copepods. The experiments were successfully executed at six different sites, covering a diverse range of environmental conditions and differing plankton community compositions. The study identified the interaction between copepods and dinoflagellate cell abundance to be significantly altered by elevated levels of dissolved CO_2 (pCO_2), with dinoflagellates decreasing relative to ambient conditions across all six experiments. A similar pattern was not observed in any other major phytoplankton group. The patterns indicate that copepods show a stronger preference for dinoflagellates when in elevated pCO_2 conditions, demonstrating that changes in food quality and altered grazing selectivity may be a major consequence of ocean acidification. The study also found that transparent exopolymeric particles (TEP) generally increased when pCO_2 levels were elevated, but the response was dependent on the exact set of environmental conditions. Bacteria and nannoplankton showed a neutral response to elevated pCO_2 and there was no significant relationship between changes in bacterial or nannoplankton abundance and that of TEP concentrations. Overall, the study illustrated that, although some similar responses exist, these contrasting high latitude surface ocean communities are likely to show different responses to the onset of elevated pCO_2.

1. Introduction

The on-going shift in seawater carbonate chemistry and related reduction of ocean pH (termed ocean acidification, OA) caused by increasing atmospheric carbon dioxide (CO_2) levels has the potential to affect a wide range of marine organisms (Fabry et al., 2009; Cooley et al., 2009). Taxa that inhabit oceanic surface layers are particularly at risk since that is where the greatest changes are being observed. Some taxa respond sensitively to elevated CO_2 levels, whereas the response in others is mixed and often highly species-specific (Engel et al., 2008; de Nooijer et al., 2009; Doney et al., 2012; Beaufort et al., 2011; Whiteley, 2011). Our present understanding of OA impacts is largely limited to single species responses while the consequences for food web interactions remain relatively unknown (Rossoll et al., 2012). For instance, the response at the community level may dampen the overall impact to elevated CO_2 levels through altered physiological performance, prey switching and species replacement (Rossoll et al., 2013).

* Corresponding author.
E-mail address: gant@bas.ac.uk (G.A. Tarling).

http://dx.doi.org/10.1016/j.dsr2.2016.02.008
0967-0645/

The solubility of CO_2 increases with decreasing temperatures, such that polar oceans have naturally higher CO_2 and correspondingly lower carbonate ion concentrations (Sabine et al., 2004). With a low buffer capacity and a relatively low starting baseline, polar oceans are particularly susceptible to ocean acidification and are expected to be the first to experience carbonate mineral undersaturation and large decreases in pH (McNeil and Matear, 2008; Steinacher et al., 2009). As a result, the polar regions, and particularly the Arctic, have been a focus for studies into the effects of projected OA on the marine environment (Riebesell et al., 2013).

Most studies of the effect of OA on pelagic organisms have involved laboratory and mesocosm experiments. Laboratory monoculture experiments allow experimental conditions to be tightly controlled and are valuable at identifying possible mechanisms and impacts. However, the outcomes of these experiments cannot be fully realistic because species are studied in isolation from the natural ecosystem in which there may be shifts from more pH-sensitive to more pH-tolerant species. Furthermore, the experimental conditions themselves (e.g. nutrient levels) may not be representative of typical oceanic conditions. Some of these shortcomings are overcome in carrying out mesocosm experiments, where large volumes (50–75 m^3) of natural planktonic communities are incubated in situ and manipulated by artificially altering pH, carbonate chemistry and nutrient levels (Riebesell et al., 2010). The logistical demands of such operations have, nevertheless, restricted their deployment to inshore regions which may not adequately cover the range of conditions and communities found in the open ocean.

To date, the main approach to considering planktonic community responses to OA in open-ocean environments has been through short-term (1–14 d) incubations of natural communities on scientific vessels using on-deck microcosms (1–50 L; Riebesell et al., 2000; Tortell et al., 2002; Hutchins et al., 2007; Richier et al., 2014). Although the incubation volumes are relatively small compared to mesocosms, this approach does allow identical experiments to be repeated across natural gradients in carbonate chemistry, temperature and nutrients. The approach has the advantage of examining a range of natural communities adapted to their particular environmental ranges. Comparisons can be made on how each community responds to the same stressor (i.e. changes in carbonate chemistry). The disadvantage of this approach is in the sudden induced change in pH and carbonate chemistry to which the community is given little time to adapt. Nevertheless, alternative longer-term, multigenerational approaches (Cripps et al., 2014) are best suited to studies of single species, and over timescales that are unfeasible for spatially extensive, vessel-based research. We used the short-term on-deck microcosm approach to consider the response of planktonic foodwebs, from a range of polar and sub-polar environments, to acute OA perturbations.

OA may affect food-webs in a number of ways, each with their own feedbacks to other parts of the system. Short-term acute-change experiments of this sort cannot characterise all such changes. However, in performing identical experiments across a range of environmental starting conditions, they can identify where there are common responses to acute change, or otherwise, how responses vary according to the initial environmental conditions and community composition. In particular, we investigate two separate, but not mutually exclusive, hypotheses:

i) that acute OA change will lead to the accumulation of transparent exopolymeric particles (TEP) which will stimulate the microbial food web;
ii) that acute OA change will alter the nutritional quality of individual phytoplankton species and lead to a change in zooplankton grazing preferences, so altering phytoplankton community composition and potentially zooplankton body condition.

i) *Stimulation of TEP production.* TEP are gel-like particles that form through coagulation of the polysaccharide fraction of dissolved organic matter (Passow, 2002). It has been proposed that increasing levels of pCO_2 in the surface ocean leads to more partitioning of the organic carbon fixed by marine primary production into the dissolved rather than the particulate fraction. This enhances the accumulation of dissolved organic carbon (DOC) in the surface ocean, and the concurrent accumulation of TEP. Such an accumulation was first noted by Engel (2002) in on-board experiments under increased pCO_2, although whether the accumulation was due to increased production or modification of TEP structure remains uncertain (Weinbauer et al., 2011). Enhanced TEP has also been associated with nutrient stress (Engel, 2002; Engel et al., 2004; Bellerby et al., 2008). Increased TEP aggregation can result in higher abundances and production of bacteria by attracting cells to a microbial hotspot (Simon et al., 2002). Nevertheless, contrasting relationships between TEP and bacteria have been found across diverse ocean areas (Corzo et al., 2005; Passow et al., 2001; Hung et al., 2003; Santschi et al., 2003; Passow and Alldredge, 1994; Bhaskar and Bhosle, 2006). We investigated if TEP production is affected by acute pH change and whether there is evidence of an enhancement of the microbial community as a result. Furthermore, we also considered whether any such patterns are altered by an additional trophic level (i.e. copepod grazers), given that copepods can directly feed on clusters of TEP (Passow and Alldredge, 1999; Ling and Alldredge, 2003).
ii) *Changes to grazing preferences.* There is growing evidence that enhanced pCO_2 levels alter the nutritional quality of individual phytoplankton species available to grazers via species specific changes in their biochemistry (Riebesell and Tortell, 2011). One major factor is taxonomic differences in the kinetic properties of carbon acquisition. Diatoms, for instance, have a much higher enzymatic specificity for carbon than dinoflagellates (Tortell, 2000), which affects the rate of carbon enrichment per unit pCO_2. pCO_2 increase may also alter carbohydrate and fatty acid content in certain phytoplankton (Wynn-Edwards et al., 2014). Zooplankton have specific stoichiometric dietary requirements (Nobili et al., 2013) and an ability to select the prey species that suit their overall needs (Kleppel, 1993). Therefore, this study will consider how zooplankton grazing preferences may alter between different acute OA treatments, and whether zooplankton body condition is affected.

We conducted short-term bioassay CO_2 perturbation experiments using natural seawater collected from the surface ocean and brought into a controlled laboratory on the deck of the research ship. This natural unfiltered seawater was manipulated to raise pCO_2 to future predicted levels, albeit at an acute rate. Locally-caught herbivorous copepods were subsequently introduced into certain incubation chambers to simulate natural food-web scenarios. The procedure was repeated in a number of Arctic and Southern Ocean oceanic settings, with contrasting environmental characteristics. In so doing, the study examines both short-term physiological responses, through acute exposure to raised pCO_2 levels, alongside adaptive community variability, given that the communities being incubated were extracted directly from their natural setting. This means that responses will be dependent on initial community structure alongside community changes resulting from competition between the multiple genotypes present within the incubation. Overall, this study examines the effects of acute changes to CO_2 levels on real-world planktonic food-webs found in both polar oceans.