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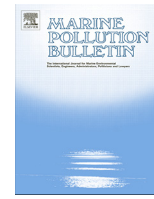

Long-term effects of elevated CO_2 and temperature on the Arctic calanoid copepods *Calanus glacialis* and *C. hyperboreus*

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ABSTRACT

The sensitivity of copepods to ocean acidification (OA) and warming may increase with time, however, studies >10 days and on synergistic effects are rare. We therefore incubated late copepodites and females of two dominant Arctic species, *Calanus glacialis* and *Calanus hyperboreus*, at 0 °C at 390 and 3000 μatm pCO_2 for several months in fall/winter 2010. Respiration rates, body mass and mortality in both species and life stages did not change with pCO_2. To detect synergistic effects, in 2011 *C. hyperboreus* females were kept at different pCO_2 and temperatures (0, 5, 10 °C). Incubation at 10 °C induced sublethal stress, which might have overruled effects of pCO_2. At 5 °C and 3000 μatm, body carbon was significantly lowest indicating a synergistic effect. The copepods, thus, can tolerate pCO_2 predicted for a future ocean, but in combination with increasing temperatures they could be sensitive to OA.

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1. Introduction

Ocean acidification (OA), i.e. the uptake of atmospheric CO_2 by the oceans and the subsequent decline in pH, and ocean warming may severely affect the performance of marine organisms and their trophic interactions (e.g. reviews by Fabry et al., 2008; Richardson, 2008). OA can thus be an important driver influencing marine ecosystem processes to date and in future (e.g. Raven et al., 2005; Solomon et al., 2007). With elevated seawater pCO_2, the carbonate concentration decreases (e.g. Raven et al., 2005), and thus, most studies at the beginning of OA research have focused on marine calcifiers (e.g. Riebesell et al., 2000; Orr et al., 2005). Recent studies have, however, shown that not only calcification processes but also reproduction, growth and behavior can be affected by elevated seawater pCO_2 (e.g. Munday et al., 2010; Kawaguchi et al., 2011; Fitzer et al., 2012, see review in Wittmann and Pörtner, 2013, their Fig. 1). As a consequence, increasing attention has recently been paid to the response of soft-bodied organisms to OA.

Among the non-calcifying zooplankton organisms, calanoid copepods play a key role in pelagic marine ecosystems as they account for up to 80% of the zooplankton biomass (Longhurst, 1985), link primary production to higher trophic levels (e.g. Runge, 1988; Węsławski et al., 1999) and contribute to the carbon transport from the surface to the deep sea (e.g. Schnack-Schiel and Isla, 2005). Short-term laboratory studies (⩽10 days) which investigated the ecological effects of OA on calanoid copepods indicated that mortality, development, egg production rates and hatching success may be impaired by CO_2 partial pressures (pCO_2) ⩾2000 μatm, whereas pCO_2 levels predicted for the end of the century seem to have no impact on most of the copepod species yet studied (Kurihara et al., 2004; Watanabe et al., 2006; Mayor et al., 2007; Kurihara and Ishimatsu, 2008; Zhang et al., 2011; Mayor et al., 2012; Vehmaa et al., 2012; Weydmann et al., 2012; McConville et al., 2013). Only in *Centropages tenuiremis*, a pCO_2 of 1000 μatm affected respiration and grazing rates during a 90 h incubation experiment (Li and Gao, 2012).

The sensitivity of marine animals to high pCO_2 and low pH can increase with exposure time (Yamada and Ikeda, 1999; Kurihara et al., 2008). Long-term studies are thus crucial to evaluate the impact of OA on copepods, however, to date such studies are rare. In a 30-day mesocosm experiment in an Arctic fjord, the impact of OA on a plankton community was studied under near-natural conditions (Riebesell et al., 2013). During this study abundance and developmental stage composition of *Calanus* spp., *Acartia longiremis*, *Oithona similis* and *Microsetella norvegica* were not affected by increasing pCO_2 (185–1420 μatm) (Niehoff et al., 2013). However, the grazing rates of *Calanus* spp. decreased with increasing pCO_2 (de Kluijver et al., 2013), but it cannot be distinguished whether this was due to indirect (via trophic interactions) or direct effects of OA. In laboratory experiments, CO_2 incubations for 20 days and longer have only been conducted with three copepod species. In *Acartia tsuensis*, the effects of OA were studied over two generations (20 days), revealing that a pCO_2 of 2380 μatm (pH = 7.32) had no influence on egg production and hatching rate (Kurihara and Ishimatsu, 2008). In contrast, growth and

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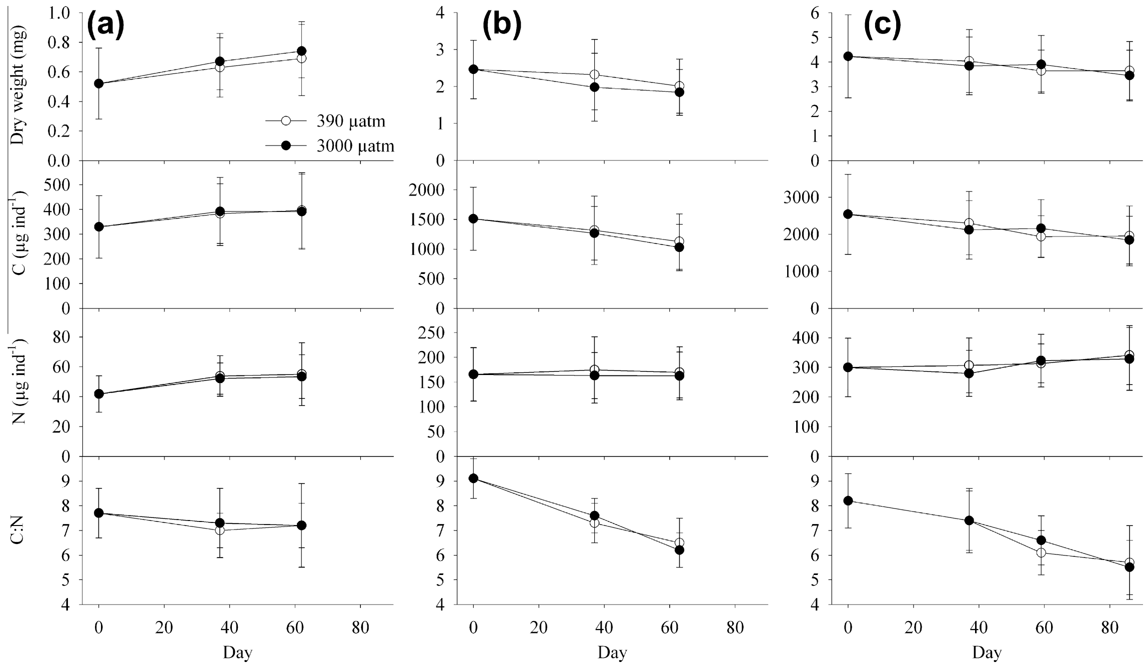

Fig. 1. Dry weight, carbon (C) and nitrogen (N) content and C:N ratio of *Calanus glacialis* CV (a), *C. hyperboreus* CV (b) and *C. hyperboreus* females (c) incubated at 0 °C and 390 (white circles) and 3000 µatm pCO_2 (black circles). Please note different scaling of the y axes.

reproductive rates of the harpacticoid copepod *Tisbe battagliai*, incubated for four generations (approx. 56 days), decreased at a $pCO_2 \geqslant 394$ µatm and a corresponding pH $\leqslant 7.82$ (Fitzer et al., 2012). Just recently, Pedersen et al. (2013) published a study on boreal *Calanus finmarchicus*, raised from eggs to adults at very high pCO_2, showing that the generation time increased at $\geqslant$7300 µatm.

In Arctic waters, *Calanus glacialis* Jaschnov, 1955 and *Calanus hyperboreus* Krøyer, 1838 dominate the mesozooplankton biomass and are major components of the food web. *C. glacialis* is a polar species (Grainger, 1961) and inhabits the Arctic shelf regions, from where it is transported into the Fram Strait with the East Greenland Current (Jaschnov, 1970; Conover, 1988). The main distribution areas of *C. hyperboreus* are the Greenland Sea, the Canadian Archipelago and the Baffin Bay (Conover, 1988; Hirche, 1991). It also occurs in the Arctic Ocean (Dawson, 1978; Hirche and Mumm, 1992) and is advected southwards into the Norwegian Sea and the Gulf of Maine (Conover, 1965, 1988). Both, *C. glacialis* and *C. hyperboreus* have multi-year life cycles in Arctic waters (e.g. Tande et al., 1985; Conover, 1988; Hirche, 1997). From copepodite stage III (*C. hyperboreus*) and stage IV (*C. glacialis*) on (Hirche, 1998), the species spend the period of scarce food in winter in diapause in deep waters (*C. glacialis*: 200–300 m (Falk-Petersen et al., 2007); *C. hyperboreus*: 500–3000 m (Hirche, 1991)). During this time the copepods are torpid, their development is arrested, metabolic and digestive enzyme activities are low, and they rely on internal lipid reserves only (Conover and Corner, 1968; Hallberg and Hirche, 1980; Head and Conover, 1983; Head and Harris, 1985; Auel et al., 2003). If the copepods experienced elevated temperatures during this resting stage due to ocean warming, the lipid stores may faster be depleted and, thus, the maximum duration of the diapause may be shortened as models suggest for *C. finmarchicus* (Saumweber and Durbin, 2006; Pierson et al., 2013). Also, exposure to elevated CO_2 concentrations can affect the energy budget (Li and Gao, 2012). As diapausing copepods cannot compensate for energetic losses, they might be especially vulnerable to climate change.

In both *C. glacialis* and *C. hyperboreus*, reproduction and survival have been studied during short-term exposure to high pCO_2 (Weydmann et al., 2012; Lewis et al., 2013) while there is no information on effects during long-term exposure. Also, no data are available on the response of diapausing individuals and, in addition, there are no studies on synergistic effects of ocean warming and OA on these two species. The aims of this study were therefore (1) to compare the long-term responses of two Arctic *Calanus* spp. to elevated seawater pCO_2 as well as temperatures during fall/winter and (2) to detect possible synergistic effects of OA and ocean warming. To get a comprehensive view on different ecological and physiological parameters, we measured mortality, respiration rates, body mass in terms of carbon and nitrogen content and, in females, gonad development during incubation experiments with copepodite stage V (CV) of *C. glacialis* and *C. hyperboreus* and with female *C. hyperboreus* over two to four months at pCO_2 of 390 and 3000 µatm and 0 °C. To study synergistic effects of elevated pCO_2 and temperatures, in an additional experiment *C. hyperboreus* females were incubated at different temperatures (0, 5 and 10 °C).

2. Methods

2.1. Field work

The copepods were collected with vertical bongo and multi net hauls during two expeditions with RV *Polarstern* to the Fram Strait, ARK-XXV/2 in June/July 2010 and ARK-XXVI/2 in July/August 2011 (see Table 1 for details). Immediately after capture, the samples were diluted in surface seawater.

In 2010, *Calanus* spp. were picked by eye from the samples with glass pipettes and maintained in filtered seawater at 0 °C for up to four weeks. Every two to three days, the copepods were fed with natural phytoplankton that was sampled from the chlorophyll *a* maximum layer with a rosette. For transport in a cooling box by airplane, the copepods were transferred to 1 and 2 liter plastic bottles. At the Alfred Wegener Institute, *C. glacialis* and *C. hyperboreus* were sorted under a binocular and separated according to sex and developmental stage. The copepodite stage V (CV) was abundant in both species as were female *C. hyperboreus*. Therefore, these three

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