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EFFECTS OF ELEVATED SEAWATER CO_2 CONCENTRATION ON THE MEIOFAUNA

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Key words: CO_2, decreased pH, nematoda, harpacticoid copepoda.

ABSTRACT

An increase in atmospheric CO_2 concentration leads to a rise in CO_2 concentrations and a decrease in pH of the ocean surface water due to continuous gas exchange between air and seawater, which may have serious impacts on neritic marine organisms. In this study, we assessed the impacts of elevated CO_2 concentrations on meiobenthic organisms by exposing them to seawater equilibrated with air (control: CO_2 concentration 380 ppm) or CO_2-enriched air (2,000 ppm higher than control, CO_2 concentration predicted by the year 2300) for 56 days in microcosms. We observed no significant differences in the abundance of total meiofauna, nematodes, harpacticoid copepods (including adults and copepodites) and nauplii by the end of the experiment. These results suggest that the projected atmospheric CO_2 concentration in the year 2300 does not have acute effects on the meiofauna. However, further studies are needed to evaluate longer-term effects of elevated CO_2 on meiobenthic organisms.

INTRODUCTION

The atmospheric concentration of carbon dioxide (CO_2) has increased from the pre-industrial level of 280 parts per million (ppm) to 380 ppm as a result of anthropogenic CO_2 emission associated with industrialization [11]. The resulting global warming has already impacted terrestrial and marine ecosystems [18, 24], and a further rise in temperature is predicted to intensify sea surface stratification and drastically alter marine ecosystem [1, 19]. In addition to the indirect effects of CO_2 due to global warming, recent studies have revealed direct effects of CO_2 on terrestrial ecosystems, and have predicted serious impacts on interactions between plants and insects [4, 7].

Due to continuous gas exchange between air and seawater [22], an increase in atmospheric CO_2 concentrations will raise CO_2 concentrations at the ocean surface, and decrease seawater pH through the dissociation of carbonic acid formed by the increased CO_2 [5]. The atmospheric CO_2 concentration is predicted to increase to above 2,100 ppm, and thereby reducing the pH of the ocean surface water by about 0.77 units by the year 2300 [5]. These chemical changes in seawater likely have significant impacts on neritic marine organisms.

Most published studies on the effects of CO_2 on marine organisms have focused on calcification responses to elevated seawater CO_2 concentration (for review, see Supporting Online Material of Feely *et al.* [8]). Riebesell *et al.* [17] also demonstrated that the growth rate of marine diatoms *Thalassiosira punctigera* and *Rhizosolena* cf. *alata* increased with CO_2 concentration. These previous studies mostly employed short-term exposure protocols and only very few evaluated long-term effects of increased CO_2 on marine organisms. Recently Michaelidis *et al.* [15] reported that the growth and metabolic rates of the marine mussels *Mytilus galloprovincialis* decreased when exposed to CO_2-acidified seawater (pH 7.3) for 3 months. Shirayama and Thornton [21] demonstrated that growth of sea urchins *Hemicentrotus pulcherrimus* and *Echinometra mathaei* was suppressed by 6-month exposure to seawater equilibrated with CO_2-enriched air (580 ppm). It is therefore conceivable that long-term exposure of marine organisms to elevated CO_2 concentration seawater for several generation could potentially result in decreases of population size.

In the present study, we incubated meiobenthic communities under elevated CO_2 conditions (2,000 ppm above ambient) for 56 days to investigate changes in abundance and biomass of nematodes and harpacticoid copepods. Meiofauna is suitable for studying long-term effects because of its short generation time, rapid growth, and high abundance in a small area. In addition, despite their small size, meiobenthic faunas are important in the energy flow of marine benthic ecosystems [9]. Here, we focused on nematodes and harpacticoid copepods because they usually account for more than 90% of the total meiofauna in mud environments [10], and owing to their confinement in the oxidized layers of sediment (usually in the top 1 cm, [6]), they may be more suscep-

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tible to the direct and indirect effects of seawater CO_2. We also investigated the effects on nauplius larvae, because the early developmental stages are thought to be particularly sensitive to environmental changes [14].

MATERIAL AND METHODS

Sediments were sampled with a Smith McIntyre grab from the seafloor (approximately 10 m in depth) of the Tanabe Bay, in the Kii Peninsula, Japan (33° 42.2'N, 135° 22.9'E) on 30 January 2001. The top 5 cm layer was used for the experiment.

The experiment was conducted for two months (from 1 February to 29 March, 2001) in an indoor microcosm system. The sediments were homogenized by stirring and were placed in six microcosms (capacity 30L) to a depth of 7 cm and covered with seawater. Microcosms were placed in a flow-through container into which coastal seawater was pumped continuously. Air was supplied at a rate of 500 ml min^{-1} to the water in three microcosms, (CO_2 concentration 360 ppm, control groups) whereas the water in the other three microcosms were aerated with CO_2-enriched air (CO_2 concentration 2,000 ppm higher than the air, CO_2 groups). The flow rates of air (500 ml min^{-1}) and CO_2 (1 ml min^{-1}) were controlled using flow meters (Kofloc). The pH and temperature of water in each microcosm was measured daily using a pH meter (Horiba, D-25). No food was supplied. The entire volume of seawater in each microcosm was renewed once a week throughout the experiment. The photoperiod was set to 14L:10D.

To monitor changes in the meibenthic community, sediment was sampled on days 0 (untreated cores), 7, 14, 21, 28, and 56. At each sampling, one sediment core (1-cm deep) was taken from each microcosm using a plastic syringe, the tip of which was cut off to make a cylinder (2.0 cm internal diameter). Sediment samples were preserved in 5% borax-buffered formalin seawater. Rose Bengal was added to stain the meiofaunae. The samples were sieved through stainless steel sieves with mesh size of 500, 250, 125, 63, and 32 μm, and the number of meiofauna was counted under a dissecting microscope. The biomass of the meiofauna was calculated by using the standard ash-free dry weight per individual as reported by Shirayama [20]. Treatment effects were evaluated statistically using Student t-test and two-way ANOVA. Values are given as means ± S.D..

RESULTS

1. Temperature and pH

During the experiment, seawater temperature of each microcosm varied between 13.0°C to 17.8°C (Figure 1). The difference in water temperature was less than 0.1°C between any two microcosms throughout the experiment. The average seawater pH values of the control and CO_2 groups were 8.20 ± 0.05 and 7.40 ± 0.07, respectively (Figure 1).

2. Effects on the abundance and biomass of meiofauna

The abundance of total meiofauna was significantly lower in the CO_2 groups than in the control of the same day only on day 7 (t-test, $p < 0.05$, Figure 2). The total biomass fluctuated in both control and CO_2 groups during the experiment (2-way ANOVA, $p < 0.05$, Figure 2), but there was no difference between the two groups at any given day of observation throughout the experiment (*t*-test, Figure 2).

The composition of meiobenthic community in this study consisted of nematodes (67.8 ± 7.5%), harpacticoid copepods (24.4 ± 4.4%), nauplii larvae (4.3 ± 2.7%), ostracods (1.6 ± 1.6%), turbellarians (1.9 ± 1.4%) and polychaeta (0.1 ± 0.3%). The foraminiferans were excluded from our analysis because of their fragile nature.

The abundance and the biomass of the two dominant taxa, nematodes and copepods (including adults and copepodites), were further investigated to examine possible changes in meiofauna composition. The abundance of nematodes varied significantly with time in both control and CO_2 groups (2-way ANOVA, $p < 0.05$, Figure 3), whereas there was no difference between the

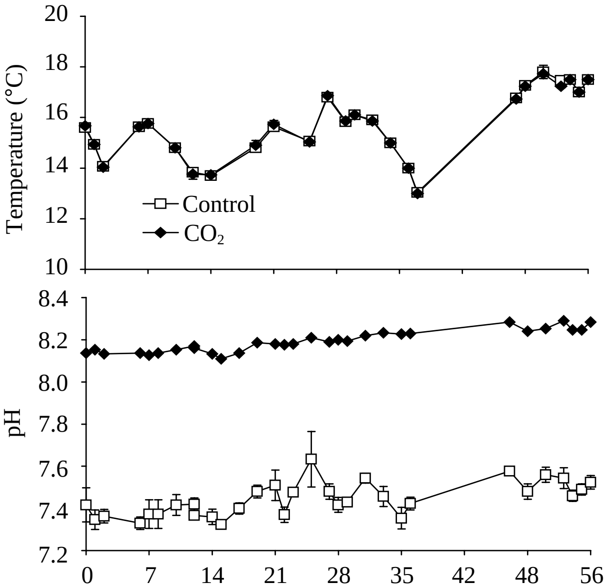

Fig. 1. **Mean seawater temperature and pH of the control and CO_2 microcosms during the experimental period.**

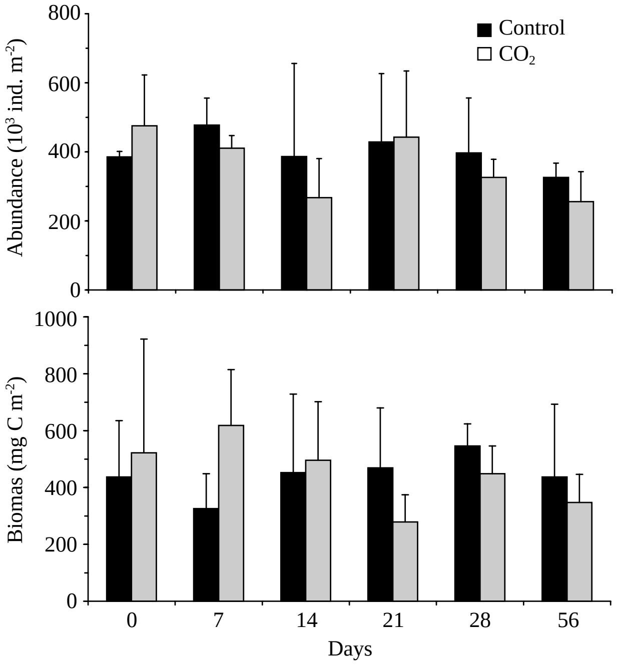

Fig. 2. **Change in abundance and biomass of total meiofauna in control and CO_2 groups from day 0 to day 56. Initial abundance of total meiofauna was 385 × 10^3 ± (16 × 10^3) ind. m^{-2} (control) and 475 × 10^3 ± (147 × 10^3) ind. m^{-2} (CO_2 groups). Initial biomass of total meiofauna was 437 × 197 mgC m^{-2} (control) and 521 ± 400 mgC m^{-2} (CO_2 microcosms). Mean ± SD of three replicate microcosms. * Significant difference between control and CO_2 groups ($p < 0.05$, *t*-test).**

two except on day 7 (*t*-test, $p < 0.05$, Figure 3). There was a decreasing tendency in nematode biomass in both groups (2-way ANOVA, $p < 0.05$, Figure 4), although no significant difference was detected between the two groups at any given day of observation (*t*-test, Figure 4).

No difference in the abundance of harpacticoid copepods was either detected throughout the experiment between the two groups (*t*-test, Figure 3). On day 7, the biomass of harpacticoid copepods in CO_2 groups was significantly higher than control groups, whereas the reverse was true on day 21 (*t*-test, $p < 0.05$, Figure 4).

No difference in the abundance of harpacticoid nauplii was detected throughout the experiment between the two groups (*t*-test, Figure 3). The abundance of other components of meiofauna, such as polychaetes, ostracods, and turbellarians, were also unaffected by CO_2.

3. Effects on the different sizes of meiofauna

We analyzed the size structure of nematodes and harpacticoid copepods to evaluate the size dependency

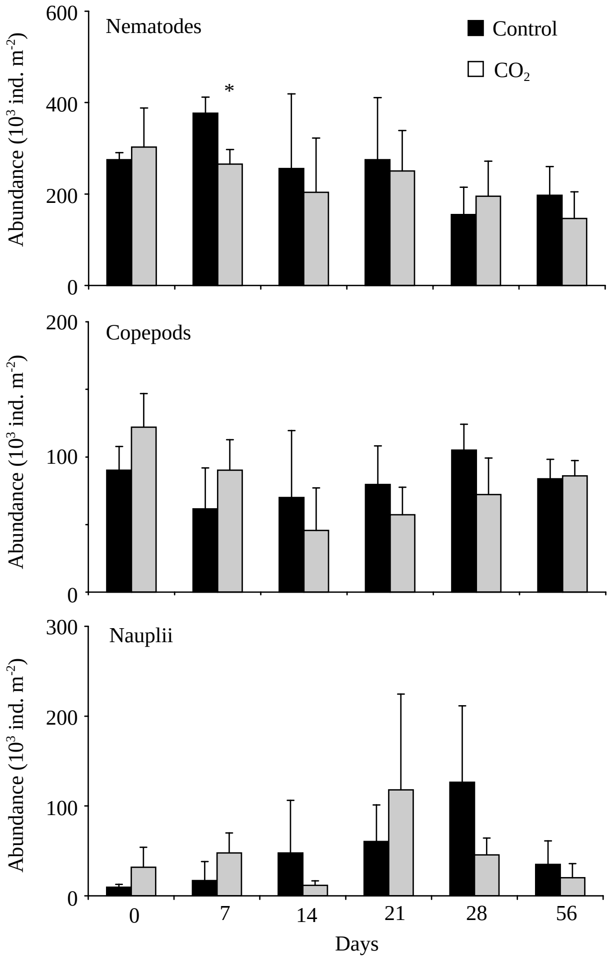

Fig. 3. **Changes in the abundance of nematodes, harpacticoid copepods and nauplii in sediment in control and CO_2 groups from day 0 to day 56. Initial abundance of nematodes was 274 × 10^3 ± (16 × 10^3) ind. m^{-2}, copepods was 90 × 10^3 ± (18 × 10^3) ind. m^{-2}, and nauplii was 10 × 10^3 ± (3 × 10^3) ind. m^{-2} (control). Initial abundance of nematodes was 302 × 10^3 ± (86 × 10^3) ind. m^{-2}, copepods was 122 × 10^3 ± (25 × 10^3) ind. m^{-2}, and nauplii was 31 × 10^3 ± (22 × 10^3) ind. m^{-2} (CO_2 groups). Mean ± SD of three replicate microcosms. * Significant difference between control and CO_2 groups ($p < 0.05$, *t*-test).**

of CO_2 tolerance. The most abundant sizes of nematodes and harpacticoid copepods were between 250 and 125 μm (Figures 5, 6). For nematodes, there was a significant difference between treatments in the abundance of 250- to 125 μm size classes on day 7 (*t*-test, $p < 0.05$, Figure 5c), but not in the other size classes (Figure 5). For harpacticoid copepods, no significant differences were observed between treatments in any size class throughout the experiment (Figure 6).

DISCUSSION

Our results suggest that atmospheric CO_2 concen-

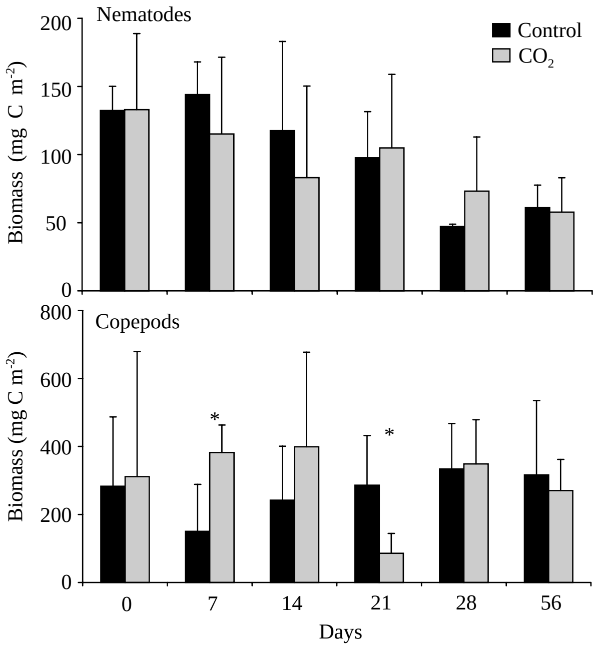

Fig. 4. **Change in the biomass of nematodes and harpacticoid copepods in control and CO_2 groups from day 0 to day 56. Initial abundance of nematodes was 132 ± 17 mgC m^{-2} and copepods was 282 ± 203 mgC m^{-2} (control). Initial abundance of nematode was 310 ± 367 mgC m^{-2} and copepods was 133 ± 55 mgC m^{-2} (CO_2 groups). Mean ± SD of three replicate microcosms. * Significant difference between control and CO_2 groups (p < 0.05, *t*-test).**

tration projected by the year 2300 (2,000 ppm higher than the control) does not induce lethal effects on most meiofaunae, at least within 56 days. In contrast, Shirayama and Thornton [21] showed that increased mortality of sea urchins and a gastropod after 6 months, when they were exposed to only 200 ppm above ambient or 580 ppm CO_2. Similarly, we observed increased mortality of shrimps *Palaemon pacificus* exposed to 1,000 ppm CO_2 for 30 weeks and to 2,000 ppm CO_2 concentrations for 15 weeks (submitted). Thus, CO_2 tolerance differs markedly among marine organisms. The apparent higher tolerance of the benthic meiofauna may be attributable to several factors. First, the sea urchins, gastropod and shrimps are epibenthos, exposing themselves to ambient seawater, whereas the organisms examined in the present study largely confine themselves in sedimentary mud. Because of larger fluctuations of CO_2 concentration in pore water, species dwelling in sediments may be more tolerant to CO_2 than pelagic organisms [16]. Second, calcified marine organisms such as snails, echinoderms and crustaceans are thought to be more sensitive to CO_2 than other organisms due to the high sensitivity of CO_2 effects on calcification mechanisms [8]. Specific difference in the response to elevated CO_2 may change community

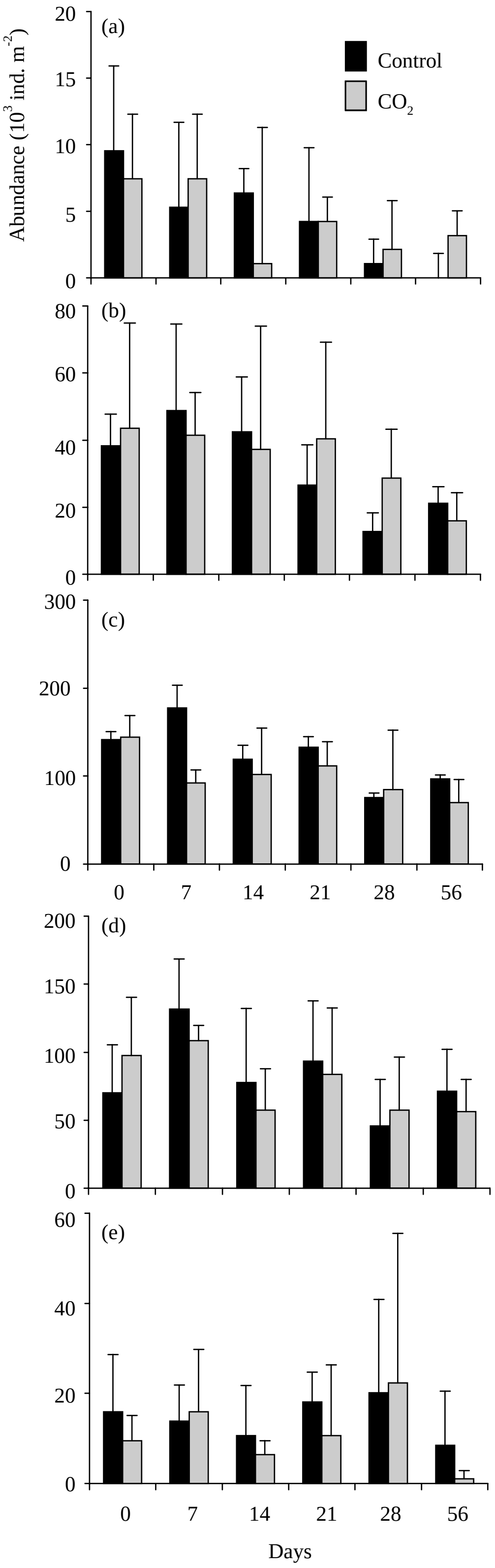

Fig. 5. **Changes in the abundance of nematodes of different size classes: (a) > 500 µm, (b) 500-250 µm, (c) 250-125 µm (d) 125-63 µm, and (e) 63-32 µm in control and CO_2 groups from day 0 to day 56. Mean ± SD of three replicate microcosms. * Significant difference between control and CO_2 groups (p < 0.05, *t*-test).**

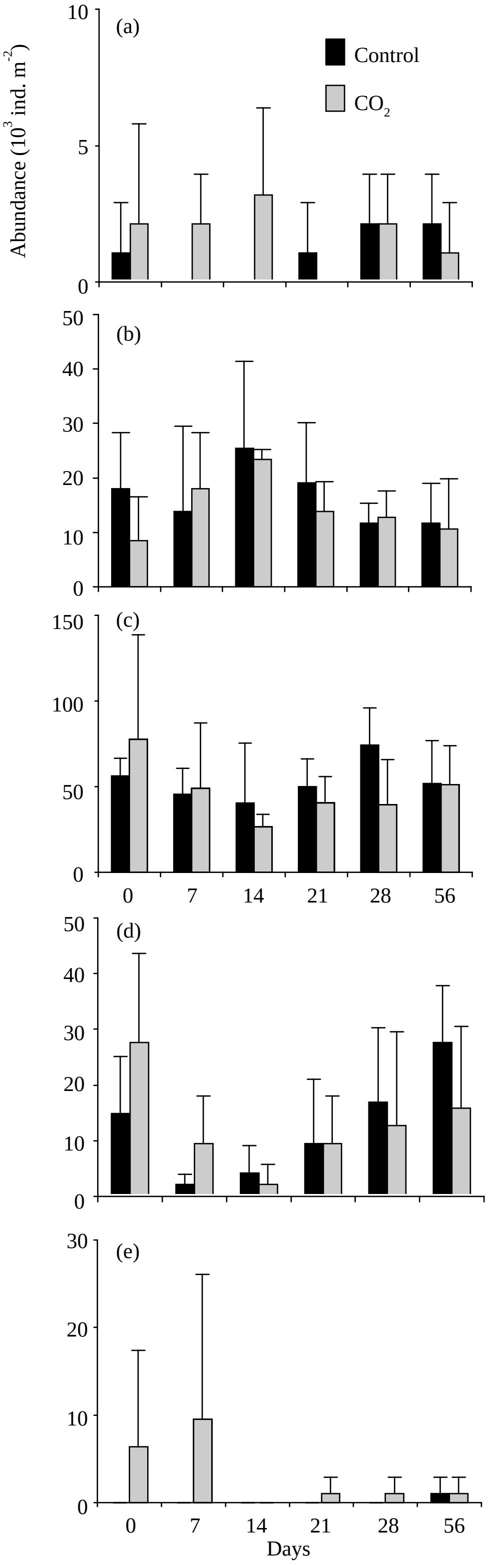

Fig. 6. Changes in the abundance of harpacticoid copepods of different size classes: (a) > 500 μm, (b) 500-250 μm, (c) 250-125 μm (d) 125-63 μm, and (e) 63-32 μm in control and CO_2 groups from day 0 to day 56. Mean ± SD of three replicate microcosms. * Significant difference between control and CO_2 groups ($p < 0.05$, *t*-test).

structure, and thereby have ecosystem-level consequences.

Even though meiobenthos are not lethally affected by elevated CO_2, it is highly possible that raised CO_2 have sub-lethal effects on reproduction, metabolism and growth rate. Michaelidis *et al.*, [15] reported that long-term exposure (3 months) of the marine mussels to CO_2-acidified seawater (pH 7.3) resulted in a depression of respiration rate. Similarly, reduced growth rate and feeding activity under low pH were observed in clams and oysters [2, 3]. When sea urchin eggs were reared under elevated CO_2 levels, the fertilization rate of the eggs tended to decrease with increasing CO_2 concentration [13]. In the present study, the abundance of small-sized nematodes (Figure 5e) and nauplius embryos (Figure 3) never disappeared throughout the experiment, although their abundance fluctuated in both control and CO_2 microcosms. This suggest that may have been successful recruitments under elevated CO_2 conditions, and therefore elevated CO_2 had not impacted the reproduction of nematodes and harpacticoid copepods. However, it is possible that, there could have been a change in the species composition of nematodes or harpaticoid copepods, in spite of no observed change in the abundance or biomass of meiofauna in the elevated microcosms. Indeed, Takeuchi *et al.* [23] demonstrated in CO_2 tolerance between marine nematode species. Analyses of nematodes and harpacticoids to a lower taxonomic level are needed to more closely evaluate impacts of raised CO_2 on these meiofaunal taxa.

Investigating biological impacts of elevated CO_2 is of importance in the context of understanding environmental impacts of not only ocean acidification due to increasing atmospheric CO_2, but also of potential seepage from sub-seabed geological CO_2 storage, for which no scientific information is currently available [12]. Biological impacts should differ depending on the extent (from geologically localized to spatially dispersed), duration (slow gradual to sudden intermittent), the magnitude of CO_2 flux leaked, and the phase of CO_2 (supercritical, liquid or gas), let alone the local fauna and flora of seepage sites. However, endobenthic organisms may well be subjected to much higher CO_2 concentrations than the projected maximum concentrations of atmospheric CO_2. Appropriate experimental protocols must be employed to evaluate the risk of potential seepage from sea-bed geological storage, because the expected hazards are distinctly different from the impact of CO_2 injection into mid-water depths [12].

In conclusion, the results demonstrated that the increased seawater CO_2 concentration used in the present study does not have acute impacts on the abundance and biomass of the meiofauna. Yet, it is possible that the meiofauna is sublethally affected when exposed to raised

CO_2 concentration for longer durations and that the meiobenthic community structure changes due to differences in CO_2 tolerance among species. Further studies are needed to understand the future impacts of increasing atmospheric CO_2 on the marine ecosystem.

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