Effect of increased atmospheric CO_2 on shallow water marine benthos

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[1] The decision to sequester CO_2 in the deep ocean should ultimately be based not only upon what would happen to deep sea marine biota but also upon what would happen to surface organisms if nothing were done to limit atmospheric CO_2. Thus such a decision should be based on a proper understanding of long-term chronic effects, from the global-scale perturbation in near-surface ocean CO_2, in addition to acute effects, from large local increases in CO_2 caused by purposeful sequestration. Here we focus on the long-term chronic effects of CO_2 on shallow water benthic organisms that have calcium carbonate shells. With two duplicate 6 month manipulative experiments, we demonstrate that a 200 ppm increase in CO_2 adversely affects the growth of both gastropods and sea urchins. Thus even moderate increases in atmospheric CO_2 that could well be reached by the middle of this century will adversely affect shallow water marine benthic organisms. This provides another reason, beyond concerns for climate, to enhance efforts to limit increases in atmospheric CO_2 to the lowest possible levels.

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1. Introduction

[2] As one option of mitigating rapid increasing atmospheric CO_2, it has been proposed to sequester CO_2 in the deep sea [*Handa and Ohsumi*, 1995; *Haugan and Drange*, 1992; *Herzog and Edmond*, 1994; *Hoffert et al.*, 1979; *Kita and Ohsumi*, 2004; *Marchetti*, 1977; *Ohsumi*, 2004]. Higher concentrations of CO_2 in seawater that would come with purposeful ocean sequestration suggests that marine organisms could be affected [*Barry et al.*, 2004; *Carman et al.*, 2004; *Ormerod and Angel*, 1996; *Omori et al.*, 1998; *Takeuchi et al.*, 1997; *Shirayama*, 1997]. However, related physiological studies of the impacts of high CO_2 on deep sea organisms are inadequate to estimate related ecological impacts.

[3] During the 21st century, atmospheric CO_2 is likely to increase by more than 200 ppm; without serious reduction of fossil fuel emissions, the increase could be as high as 2000 ppm [*Intergovernmental Panel on Climate Change* (*IPCC*), 2001]. Increasing atmospheric CO_2 leads to lower surface ocean pH. We may thus speak of an acidification of the surface seawater (i.e., an increase in the number of hydrogen ions [H^+]) although surface ocean seawater will almost certainly never become acidic (pH < 7). Such acidification could affect shallow water organisms [*Ishimatsu et al.*, 2004; *Kurihara et al.*, 2004; *Pörtner et al.*, 2004]. Some may consider an increase of atmospheric CO_2 by 200 ppm to be moderate, but even that may produce chronic health problems in shallow water marine organisms. *Riebesell et al.* [2000] found notable effects of increased CO_2 concentrations on coccolithophores [*Riebesell*, 2004]. Here we focus on the effects on marine organisms exposed for 6 months to surface seawater in contact with atmospheric CO_2 of 560 ppm. This represents a 200 ppm increase above today's level, which is what the *IPCC* [2001] proposed would need to be maintained to avoid catastrophic climatic change. We focus our study on the potential impacts of elevated CO_2 at this level on shallow water benthos.

[4] Regardless of whether global warming occurs, increases in atmospheric CO_2 concentration will result in a decrease in seawater pH. As a result, it is likely that organisms with calcium carbonate shells will be affected more than others [*Shirayama*, 1997], because making calcium carbonate shells is one of the biological processes that are the most sensitive to the acidification of the seawater. In the present paper, we studied some marine organisms that have $CaCO_3$ skeletons, namely gastropods and sea urchins. Unfortunately few studies have focused on the effects of increasing CO_2 on these organisms [e.g., *Knutzen*, 1981; *Bamber*, 1990; *Adams et al.*, 1997]. Here we have used long-term exposure experiments, to evaluate if increased atmospheric CO_2 and the associated change in surface water pH will affect the growth rate and mortality of these shallow water species.

2. Materials and Methods

[5] The gastropod *Strombus luhuanus* and two sea urchins, *Hemicentrotus pulcherrimus* and *Echinometra mathaei*, were chosen as representative near-shore calcareous species. We used juveniles (<1 year old) to be able to evaluate possible changes in growth rate. We made two experiments under nearly identical conditions. However, in the second experiment, seawater temperatures were higher and initial animal body size was larger. At the beginning of

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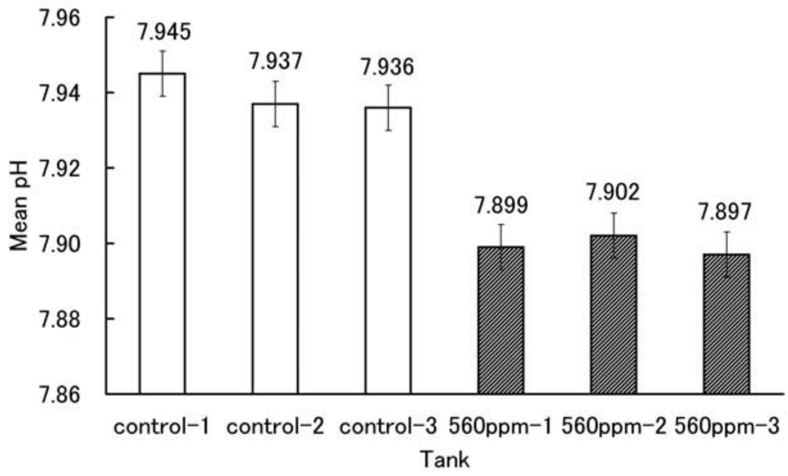

Figure 1. Mean pH of seawater in the control and high-CO_2 tanks.

these two experiments, the mean body size of *Strombus luhuanus* was 22 mm (experiment 1) and 24 mm (experiment 2) in terms of shell height; corresponding wet shell weights were 1.9 and 2.6 g. Mean body weights of *Hemicentrotus pulcherrimus* and *Echinometra mathaei* at the beginning of experiment 1 were 0.84 and 2.7 g, whereas in the experiment 2, they were 4.1 and 8.5 g.

[6] Thirty individuals (ten individuals for each species) were kept in one 30 L tank. Six tanks were prepared and hooked up to individual aeration systems. Three tanks were supplied with air to which an additional 200 ppm of CO_2 was added. The other three tanks were used as controls, i.e., they were supplied with ambient air flowing at the same rate, but with no additional CO_2. Food (sea weed and chopped krill) was supplied twice a day so that it would not be limiting. Approximately two thirds of the seawater was changed once a week using natural seawater pumped up through the subtidal intake situated near our coastal laboratory. Light exposure was not controlled. Seawater temperature was not controlled except during mid summer when it was not allowed to go beyond 30°C.

[7] Tank water pH and temperature were measured once a day. We recorded the deaths of individuals and subsequently removed them from the tanks. All individuals were marked and their growth was monitored. Once every two weeks, we measured the shell height of each snail with a slide gauge. We also measured the wet weight of the snails and the sea urchins with a digital balance. After these measurements, animals were returned to their tanks.

3. Results

3.1. Physical Data of Sea Water

[8] Throughout the first experiment, the mean water pH in the high-CO_2 tanks was significantly lower than in the control tanks (t-test, $p < 0.05$), although the difference was only 0.03 (Figure 1). Similar differences in pH were observed in the second experiment. The temperature of the seawater fluctuated with the natural conditions. In experiment 1, it ranged from 20.0° to 23.9°C, and in experiment 2, it ranged from 24.1° to 25.5°C. In both experiments, there was no significant difference in the mean water temperature among high-CO_2 and control tanks (t-test, $p > 0.05$). We used natural sea water pumped up from the subtidal zone (2 m water depth) off the shore close to our laboratory. The DIC in the control tank of the first experiment was measured as 1990 μmol/L.

3.2. Survival

[9] In the first experiment, all animals remained alive for 6 months in the control tanks. This suggests that the culture conditions were suitable for carrying out these long-term experiments (Figure 2a). In the high-CO_2 tanks, however, several individuals died after just the 10th week. For *Hemicentrotus pulcherrimus*, which proved the most sensitive to the elevated CO_2, eight individuals (27%), died before the end of experiment. For *Echinometra mathaei*, one individual died during week 14, and three individuals (10%) died before the end of experiment. For the snail *Strombus luhuanus* no individuals died during the first 20 weeks; yet three individuals (10%) died by the end of the experiment (Figure 2b).

[10] In the second experiment, survival rates for both gastropods and sea urchins in the high-CO_2 tanks were not significantly less than those in the control tanks. For the control tanks, one *Hemicentrotus pulcherrimus* individual (3.3% of the population) died during week 10, and one gastropod (3.3%) died during week 14 (Figure 3a). In the high-CO_2 tanks, one *Echinometra mathaei* individual (3.3%) died during week 8, and another two individuals (10%) died by the end of experiment. Only one individual (3.3%) of *Hemicentrotus pulcherrimus* died during week 26. For the gastropod, one individual (3.3%) died during week 8 and another one died during week 20 (Figure 3b).

3.3. Growth

[11] The growth of each individual was calculated as a percentage of relative growth 100 × ((value at time T) − (initial value))/(initial value). For example, if an animal were to double its weight, the relative growth rate would be 100%.

[12] The impact of elevated CO_2 on marine organisms was more evident in terms of growth rate than in terms of

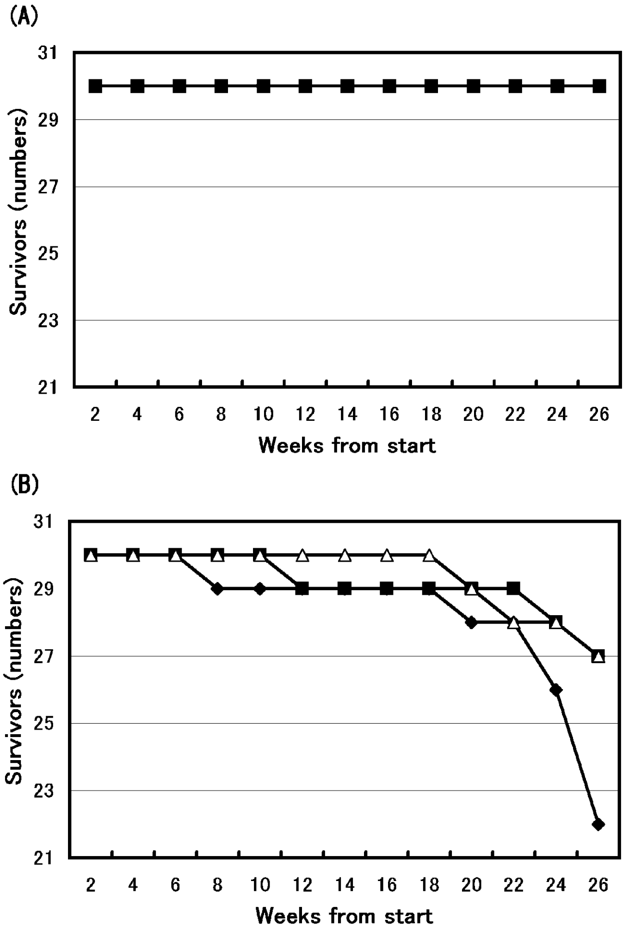

Figure 2. Survival of animals in (a) the control tanks and (b) the high-CO_2 tanks in experiment 1 (filled diamond, sea urchin *Hemicentrotus pulcherrimus*; filled square, sea urchin *Echinometra mathaei*; open triangle, snail *Strombus luhuanus*). The survival rates of animals in the high-CO_2 tanks were significantly lower than in the control tanks (two-way ANOVA, $F = 10.3$, $p = 0.0075$).

mortality rate. Under both control and high-CO_2 conditions, *Hemicentrotus pulcherrimus* grew at the same rate for 12 weeks during the first part of experiment 1. From week 14 onward, the wet weights of these animals were lower in the high-CO_2 tanks than in the control tanks (Figure 4a). In the second experiment, growth in the control and high-CO_2 tank were similar until week 14. Growth rate diverged in week 16 with animals in the high-CO_2 tank weighing significantly less than those in the control tank. After week 22, growth continued in the control tanks, but there was no significant growth in the high-CO_2 tanks (Figure 4b).

[13] The effect of elevated CO_2 on growth rate was most pronounced in *Echinometra mathaei*. During the first 12 weeks of the first experiment, there was no difference in the growth rate between the control and high-CO_2 tanks; the same was found for *Hemicentrotus pulcherrimus* (see above). Afterward, *E. mathaei* continued to grow in the control tanks, but not in the high-CO_2 tanks (Figure 5a). In the second experiment, differences in growth rates were not significant during the first 14 weeks. After week 16, animals in the control tank continued to grow, whereas the size of those in the high-CO_2 tank actually diminished. At the end of the experiment, the mean wet weight in the high-CO_2 tank was 8% less than at the beginning of the experiment (Figure 5b). A final visual inspection revealed that these sea urchin shells had become so brittle that they were easily broken during handling. Thinning of the calcium carbonate tests of the sea urchins in the high-CO_2 tank might explain part of their loss in body weight.

[14] For *Strombus luhuanus*, we measured both shell height and wet weight of the whole individual. In the two experiments, like both species of sea urchins, the growth rates in the control and high-CO_2 tanks were not substantially different in the beginning of experiments but were statistically significant at the end of experiments. In the first experiment, both shell height (Figure 6a) and wet weight (Figure 6c) were not statistically different during the first 12 weeks. However, at week 14, average values of both shell height (t-test, $p < 0.05$) and wet weight (t-test, $p < 0.01$) were significantly larger in the control tank than in the

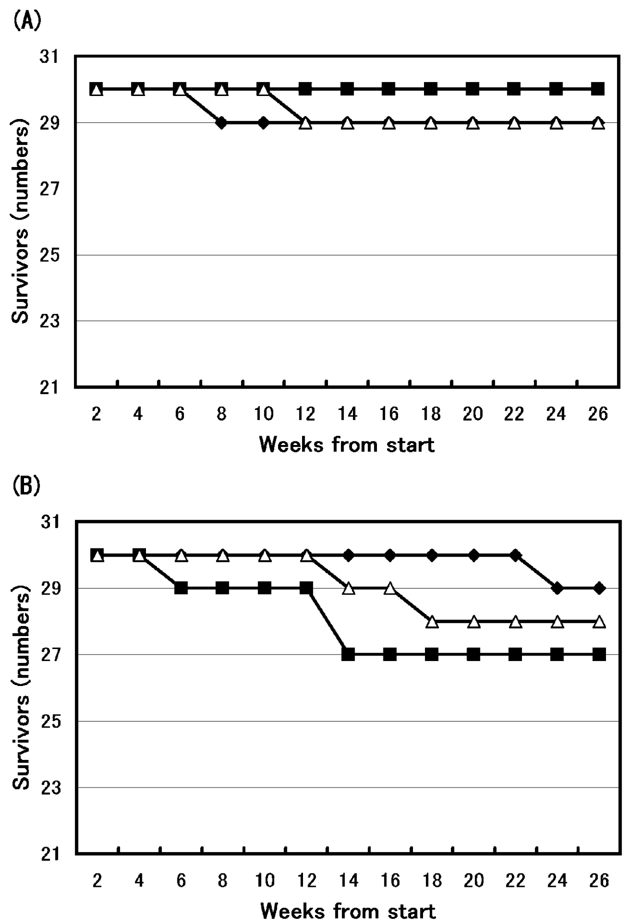

Figure 3. Survival of sea urchins in (a) the control tanks and (b) the high-CO_2 tanks in experiment 2 (filled diamond, *Hemicentrotus pulcherrimus*; filled square, *Echinometra mathaei*; open triangle, snail *Strombus luhuanus*). Survival rates of animals in the high-CO_2 tanks were not significantly lower than in the control tanks (two-way ANOVA, $F = 2.29$, $p = 0.16$).

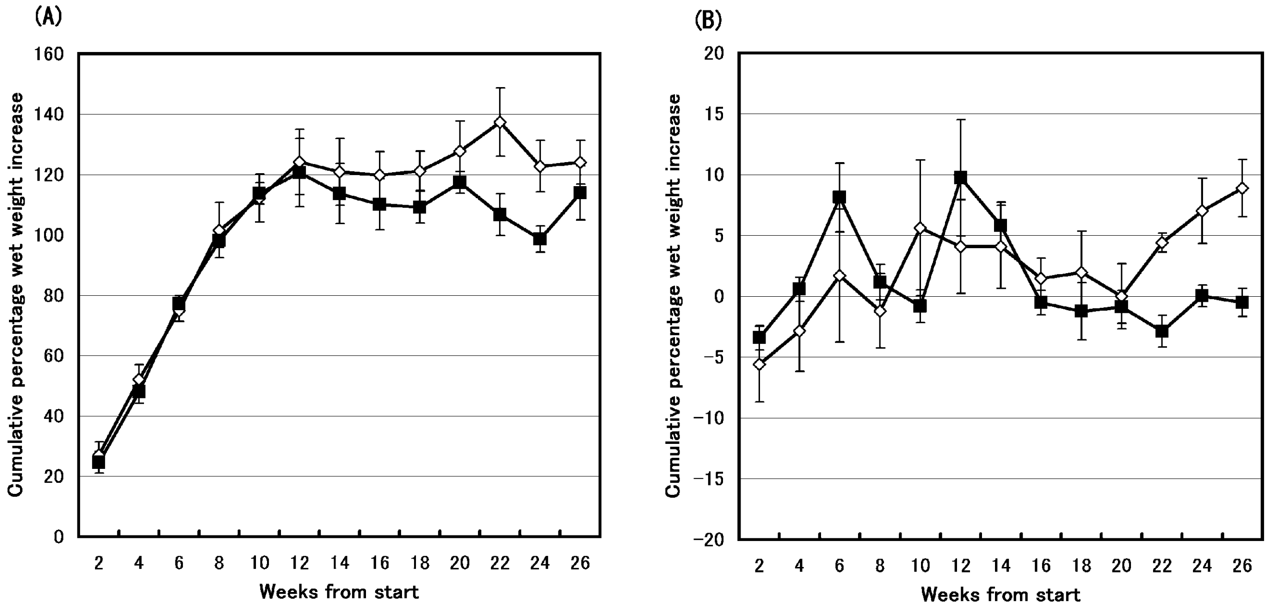

Figure 4. Relative growth rate from the wet weight of the sea urchin *Hemicentrotus pulcherrimus* (open symbol, control; filled symbol, higher CO_2 concentration) in experiments (a) 1 and (b) 2. A three-way ANOVA as a function of time (week 2–26), experiment (experiment 1 and 2), and treatment (control versus high CO_2) confirmed that increased CO_2 significantly decreased the growth rate of this sea urchin species ($F = 11.2$, $p < 0.001$). In addition, a significant difference was found between experiments 1 and 2 ($F = 3767$, $p < 0.0001$).

high-CO_2 tank, and the differences remained significant during the rest of the experiment. In the second experiment, the differences between control and elevated CO_2 conditions became statistically significant also at week 14 in the case of shell height (Figure 6b; *t*-test, $p < 0.001$). On the other hand, the differences of wet weight were significant as early as at week 8 (Figure 6d; *t*-test, $p < 0.01$). Throughout the rest of the experiment, both shell height and wet weight

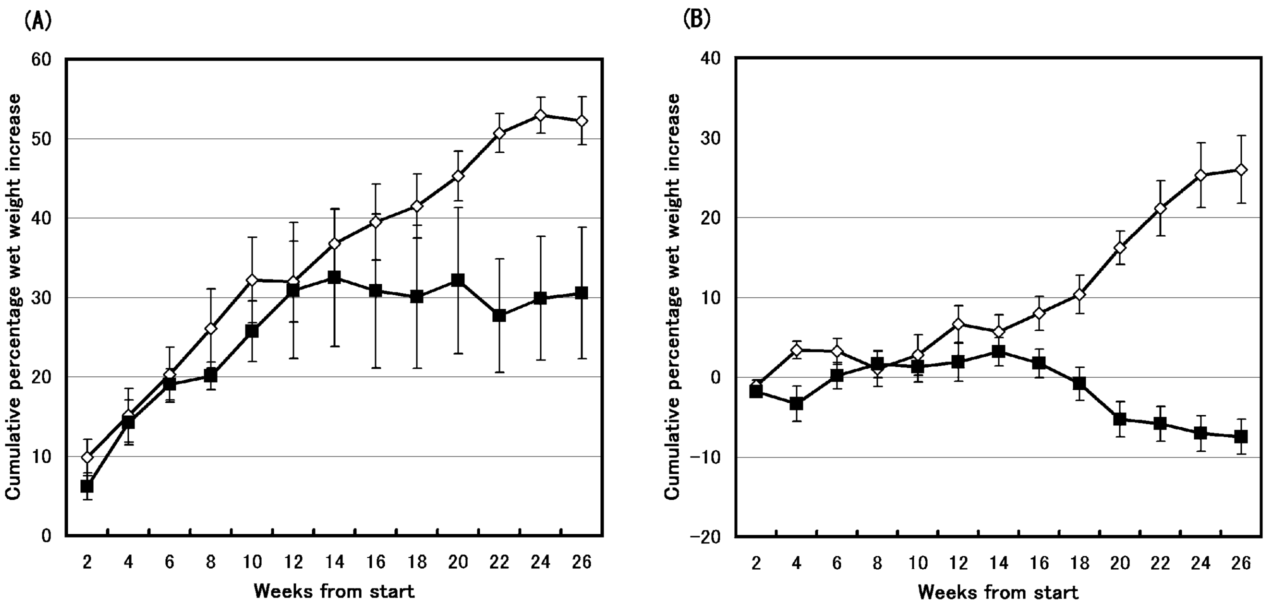

Figure 5. Relative growth rate based on the wet weight of the sea urchin *Echinometra mathaei* (open symbol, control; filled symbol, higher CO_2 concentration) in experiments (a) 1 and (b) 2. A three-way ANOVA as a function of time (week 2–26), experiment (experiment 1 and 2), and treatment (control versus high CO_2) confirmed increased CO_2 significantly decreased the growth rate ($F = 27.9$, $p < 0.0001$). There was also a significant difference between experiments 1 and 2 ($F = 283$, $p < 0.0001$).

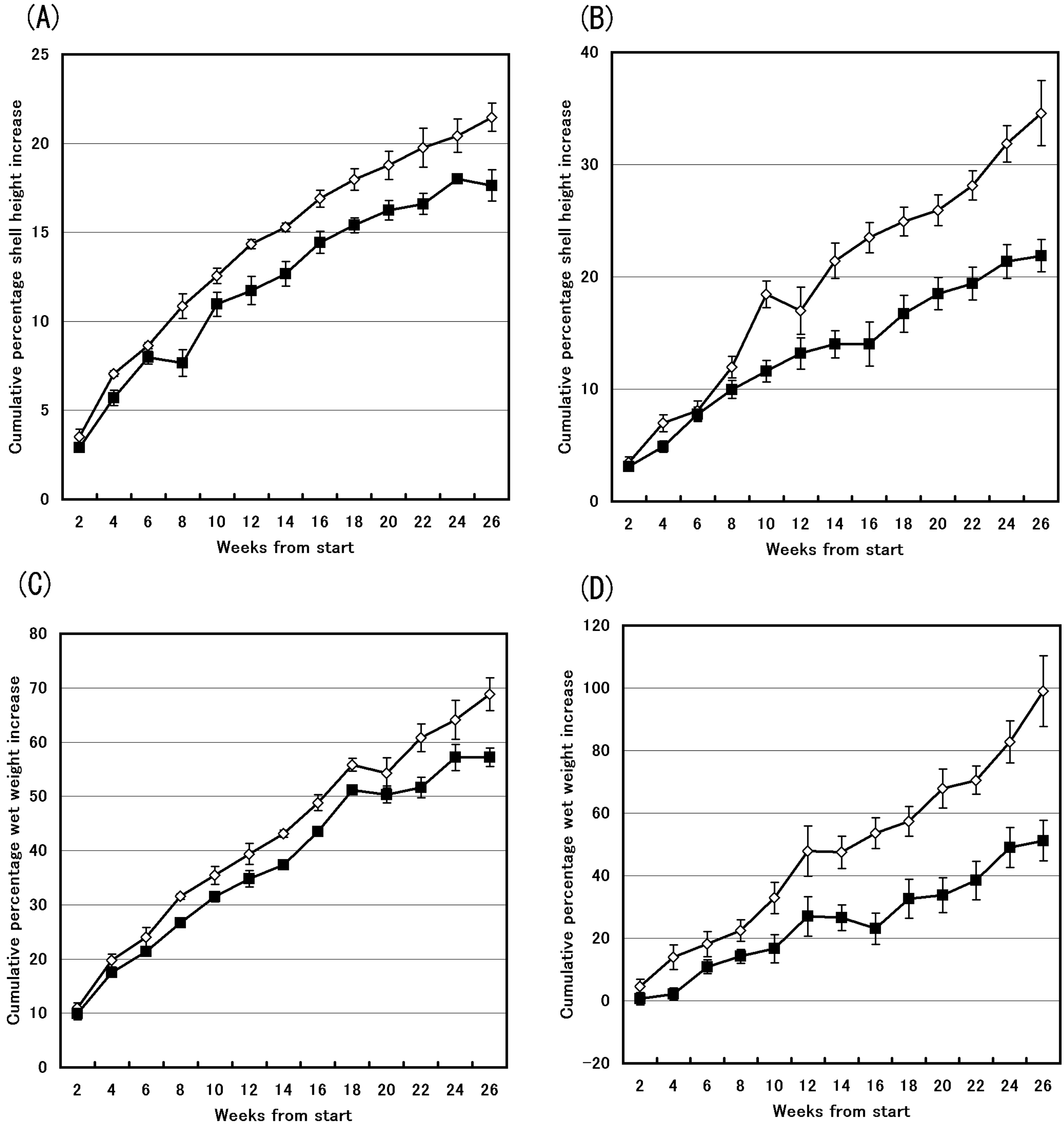

Figure 6. Relative growth rate based on shell height as well as wet weight for the snail *Strombus luhuanus* (open symbol, control; filled symbol, high CO_2) in experiments (a, c) 1 and (b, d) 2. A three-way ANOVA as a function of time (week 2–26), experiment (experiment 1 and 2), and treatment (control versus high CO_2) confirmed that increased CO_2 concentration significantly decreased the growth rate in terms of both shell height ($F = 57.0$, $p < 0.0001$) and wet weight ($F = 113$, $p < 0.0001$). There was also a significant difference between experiments 1 and 2 ($F = 30.9$, $p < 0.0001$ and $F = 37.9$, $p < 0.0001$, respectively).

were significantly larger in the control tank than in the high-CO_2 tank.

4. Discussion

[15] To our knowledge, only *Michaelidis et al.* [2005] have tried to elucidate the impact of small increases in atmospheric CO_2 concentration on marine organisms through a long-term study. They monitored the growth of a mussel species, *Mytilus galloprovincialis* for three months and found that the growth of the mussel was significantly reduced by moderate hypercapnia. Here we have shown that an atmospheric CO_2 increase of just 200 ppm would have negative consequences on the

growth rates of other groups of animals, gastropod and echinoids.

[16] Sea urchins were affected more by increased CO_2 than were snails. Sensitivity among these species differed significantly in both experiment 1 (three dimensional ANOVA: $F = 1045$, $p < 0.0001$) and experiment 2 (three dimensional ANOVA: $F = 302$, $p < 0.0001$). Differences may be partly explained by the larger surface area/body weight ratio of the sea urchins and their inability to regulate changes in their internal body condition, i.e., because of their direct connection with the ambient seawater through their madreporites. Moreover, sea urchin tests are made of high magnesian calcite, which is substantially more soluble than snail shells (calcite).

[17] If the influence of elevated CO_2 were limited to reduced calcification of the $CaCO_3$ test, the shells in the experimental tank should be thinner than in the control. However, the shell height should be the same because the physiological condition of the gastropods should not have been affected, and the animals should grow at the same rate. Yet we found that increased CO_2 affected both shell height and body mass, which suggests that increased CO_2 also affected the physiology of these organisms.

[18] Stronger effects were evident in experiment 2 relative to experiment 1. The only differences were that experiment 2 had larger animals and higher seawater temperatures. Animals with higher metabolic activity are more sensitive to elevated CO_2 [*Pörtner and Reipschläger*, 1996]. The metabolic activity of poikilothermal marine animals increases with an increase in seawater temperature. Both findings are consistent with our observation of the greater influence of higher CO_2 in experiment 2, which also had higher seawater temperature.

[19] The level of pCO_2 plays an important role not only because it affects the saturation state of $CaCO_3$, but probably even more so because of its effect on the cells of animals. In shallow water ecosystems, surface water pCO_2 is lower than that in the atmosphere as a result of daytime primary productivity of both phytoplankton and benthic macroalgae. At night this balance is reversed and pCO_2 becomes higher in the seawater than in the atmosphere due to the respiration of all organisms including plants. Thus in situ, animals under an atmospheric CO_2 of 560 ppm would experience even higher pCO_2 than in our controlled study, were they not also exposed to equivalent increases due to plant respiration. Such diurnal fluctuations will also need to be accounted for in future efforts to evaluate impacts of increasing CO_2 levels on the marine ecosystem.

[20] Our results rely on experiments using only a few species. We have ignored possible interactions between species that would occur under natural conditions. To understand the impact of elevated CO_2 on shallow water marine organisms at the ecosystem level, laboratory experiments are just a beginning. It would be desirable to carry out small-scale open-water CO_2 enrichment experiments.

[21] As with corals, elevated seawater temperatures must also affect benthic organisms [*Pörtner et al.*, 2004]. The combined effects due to elevated CO_2 and elevated temperature could have a larger impact than simply adding the two effects individually, particularly in regard to the species with calcium carbonate shells.

[22] Our results are inadequate by themselves to evaluate the impact of elevated CO_2 on shallow water marine benthic ecosystems. Nonetheless, they point out the high sensitivity of some marine organisms to what many may consider as moderate increases in atmospheric CO_2. This provides an added reason, beyond worries about climate, why there is an even more pressing need to thoroughly explore all opportunities to limit atmospheric levels of this greenhouse gas.

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