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Effects of ocean acidification on calcification of symbiont-bearing reef foraminifers

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Abstract

Ocean acidification (decreases in carbonate ion concentration and pH) in response to rising atmospheric pCO_2 is generally expected to reduce rates of calcification by reef calcifying organisms, with potentially severe implications for coral reef ecosystems. Large, algal symbiont-bearing benthic foraminifers, which are important primary and carbonate producers in coral reefs, produce high-Mg calcite shells, whose solubility can exceed that of aragonite produced by corals, making them the "first responder" in coral reefs to the decreasing carbonate saturation state of seawater. Here we report results of culture experiments performed to assess the effects of ongoing ocean acidification on the calcification of symbiont-bearing reef foraminifers using a high-precision pCO_2 control system. Living clone individuals of three foraminiferal species (*Baculogypsina sphaerulata*, *Calcarina gaudichaudii*, and *Amphisorus hemprichii*) were subjected to seawater at five pCO_2 levels from 260 to 970 µatm. Cultured individuals were maintained for about 12 weeks in an indoor flow-through system under constant water temperature, light intensity, and photoperiod. After the experiments, the shell diameter and weight of each cultured specimen were measured. Net calcification of *Baculogypsina* and *Calcarina*, which secrete a hyaline shell and host diatom symbionts, increased under intermediate levels of pCO_2 (580 and/or 770 µatm) and decreased at a higher pCO_2 level (970 µatm). Net calcification of *Amphisorus*, which secretes a porcelaneous shell and hosts dinoflagellate symbionts, tended to decrease at elevated pCO_2. These different responses among the three species are possibly due to differences in calcification mechanisms (in particular, the specific carbonate species used for calcification) between hyaline and porcelaneous taxa, and to links between calcification by the foraminiferal hosts and photosynthesis by the algal endosymbionts. Our findings suggest that ongoing ocean acidification might favor symbiont-bearing reef foraminifers with hyaline shells at intermediate pCO_2 levels (580 to 770 µatm) but be unfavorable to those with either hyaline or porcelaneous shells at higher pCO_2 levels (near 1000 µatm).

1 Introduction

The oceans have taken up about one-third of the anthropogenic carbon dioxide released into the atmosphere over the past 200 yr (Sabine et al., 2004). According to the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (SRES), atmospheric CO_2 will rise further, up to a partial pressure of 500–1000 µatm by the end of the century (Meehl et al., 2007). This absorption of CO_2 into the surface ocean changes seawater chemistry, resulting in decreases in pH and carbonate ion concentration, and increases in the concentrations of bicarbonate and hydrogen ions. It will also lead to a decrease in the saturation state of seawater with respect to calcite and aragonite, two common forms of calcium carbonate secreted by marine calcifying organisms (Orr et al., 2005). Calcification of marine calcareous organisms is strongly dependent on the carbonate saturation state of seawater, suggesting that ocean acidification will adversely affect marine calcifying taxa, with potentially severe implications for marine ecosystems such as coral reefs (Kleypas et al., 1999).

Culture experiments with reef calcifying organisms such as corals, coralline algae, molluscs, and foraminifers suggest that ocean acidification will adversely impact their calcification (e.g. Gattuso et al., 1998; Kuffner et al., 2008; Kuroyanagi et al., 2009; Ries et al., 2009), leading to a reduction in coral-reef biodiversity and the net accumulation of reef carbonates in the future (Hoegh-Guldberg et al., 2007). Large, reef-dwelling benthic foraminifers (defined as mature individuals >1 mm in diameter) are shelled protists that are host to algal endosymbionts (Lee, 1998; Hallock, 1999). They are one of the primary producers and carbonate producers in coral reefs (Hallock, 1981; Langer et al., 1997; Hohenegger, 2006; Fujita and Fujimura, 2008), secreting high-magnesium calcite (HMC; Raja et al., 2005), the solubility of which can exceed that of aragonite at a similar seawater pCO_2 level (Morse et al., 2006). Therefore, reef foraminifers with high-magnesium calcite shells may be the “first responders” among reef calcifying organisms to the decreasing saturation state of seawater caused by ocean acidification.

During calcification, foraminifers are able to elevate the pH at the site of calcification (vesicles or seawater vacuoles) by one unit above seawater pH (Erez, 2003; Bentov et al., 2009; de Nooijer et al., 2009). In acidified seawater, foraminifers would require more energy to elevate the intracellular pH, leading to a decrease in calcification. Previous culturing results have indicated that shell weights of both planktonic and benthic foraminifers reduce with decreasing [CO_3^{2-}] or pH (Bijma et al., 1999; Bijma et al., 2002; Dissard et al., 2010; Lombard et al., 2010). Calcification (measured as increments of shell weight and diameter) of *Marginopora*, a large, dinoflagellate symbiont-bearing benthic foraminifer, is reduced as pH becomes lower (Kuroyanagi et al., 2009). Culture experiments using ^{14}C tracer techniques of reef foraminifers have also shown that the carbon uptake ratio is dependent on pH and concentrations of inorganic carbon and calcium, and decreases when the pH or the concentrations of these elements are lower than those of the present seawater (ter Kuile et al., 1989).

However, the effects of ocean acidification on calcification of diverse large, algal symbiont-bearing and reef-dwelling benthic foraminifers has been assessed in only one species (*Marginopora kudakajimensis*; Kuroyanagi et al., 2009). Recent studies have shown that the response of marine calcifying organisms to ocean acidification varies both within and among species (e.g. Fabry, 2008; Ries et al., 2009; Ridgwell et al., 2009). Moreover, in our previous study (Kuroyanagi et al., 2009), we controlled the pH by adding an acid or base, rather than by bubbling CO_2-enriched air through the seawater, though the latter would better reproduce the present anthropogenic changes and the ocean's response. Therefore, in this study, we conducted a culture experiment using a high-precision pCO_2 control system to assess the effect of ocean acidification on calcification of symbiont-bearing reef foraminifers.

2 Materials and methods

2.1 Target species

Three species of large, algal symbiont-bearing benthic foraminifers were selected for this study: *Baculogypsina sphaerulata* (Parker and Jones, 1860), *Calcarina gaudichaudii* d'Orbigny in Ehrenberg, 1840, and *Amphisorus hemprichii* Ehrenberg, 1839 (hereafter referred to as *Baculogypsina*, *Calcarina*, and *Amphisorus*, respectively). These species are commonly found on macrophytes on coral-reef flats in the northwest Pacific (e.g. Hohenegger, 1994) and are important primary producers and carbonate producers in their environments (e.g. Sakai and Nishihira, 1981; Hohenegger, 2006; Fujita and Fujimura, 2008). Shells of all three species are composed of high-magnesium calcite (HMC; approx. 10 Mg mol%; Saraswati et al., 2004). Shell walls of *Baculogypsina* and *Calcarina* are perforate and have a hyaline (i.e. clear, glassy) appearance, whereas those of *Amphisorus* are imperforate and appear porcelaneous (i.e. shiny, white, and smooth like porcelain). *Baculogypsina* and *Calcarina* are host to diatom endosymbionts, whereas *Amphisorus* is host to dinoflagellate endosymbionts (Lee, 1998). In addition, these three species have been observed to reproduce asexually during spring and summer (Sakai and Nishihira, 1981; Hohenegger, 2006). Thus, asexually reproduced clone individuals can be used for culture experiments to exclude the effect of genetic variability on the experimental results. For more detailed information on the taxonomy, biology, and ecology of these species, see Röttger and Krüger (1990) and Hohenegger (1994).

2.2 Maintenance until asexual reproduction

Adult individuals just before asexual reproduction (agamont or shizont) were collected during low tide on nearshore reef flats: *Baculogypsina* and *Calcarina* northeast of Ikei Island, Okinawa, Japan (26°23′ N, 128°00′ E) on 26 April and 22 May 2009, and *Amphisorus* on a reef moat along the Oudo coast, south of Okinawa Island (26°05′ N, 127°42′ E) on 28 May 2009. Collected individuals were maintained separately in small Petri dishes filled with natural seawater at room temperature (approximately 25 °C) under a natural light:dark cycle near a window (light intensity, ~100 μmol m^{-2} s^{-1}). Because *Calcarina* and *Baculogypsina* are commonly found in high-energy reef-flat environments (Hohenegger, 1994), these species were maintained under continuous water motion produced by using a continuous-action shaker (approximately 30 rpm; in vitro Shaker, Wave-PR, TAITEC Inc., Saitama, Japan). In contrast, *Amphisorus* individuals were maintained under stagnant conditions on a flat shelf, because they are commonly found in relatively calm reef-moat environments (Hohenegger, 1994). These individuals were not fed during maintenance, and the culture medium was changed weekly.

After a few weeks, these adult individuals reproduced asexually. Juveniles of the clone populations were kept under the same conditions as the adults for 4 to 6 weeks until the experiments were started. To determine differences in characteristics within species under experimental conditions, two clone populations of each species were used, tagged as populations α (alpha) and β (beta).

2.3 High-precision pCO$_2$ control system

Clone individuals of the three foraminiferal species were placed into culture cages and subjected to seawater with different $p\text{CO}_2$ levels. $p\text{CO}_2$ in each culture cage was adjusted by bubbling CO_2 gas through the seawater, and a constant $p\text{CO}_2$ level was maintained by a high-precision $p\text{CO}_2$ control system developed with the cooperation of Kimoto Electric Co., Ltd. (Osaka, Japan). This system is composed of CO_2 dissolution and measurement towers (height, 1.78 m), into which gaseous CO_2 is dissolved in seawater by bubbling it from the bottom of the towers. The seawater $p\text{CO}_2$ is continually monitored in the equilibrated air flowing out from the measurement tower surface and adjusted as needed by controlling the CO_2 concentration in the air by mixing CO_2 and dilution-air (dried air with a low CO_2 concentration) into the filtered (pore size, 1μm) seawater.

The $p\mathrm{CO}_2$ of the culture medium was adjusted to one of five $p\mathrm{CO}_2$ levels (approximately 260, 360, 580, 770, and 970 µatm, Table 1) corresponding to the estimated preindustrial value, the present value, and future values predicted by IPCC SRES (Meehl et al., 2007), respectively. Seawater chemistry (temperature, salinity, pH, and total alkalinity) was measured twice a week, and the averaged values were used for calculating the saturation state of seawater with respect to calcite (Table 1).

2.4 Culture protocol

Each foraminifer culture cage consisted of a clear vinyl hose (5 cm long; inside diameter, 2.5 cm) with a cell strainer (100 µm mesh, BD Falcon, Inc) at each end. For each clone population, 40 individuals of each species (i.e. a total of 120 individuals per cage) were put into a cage. A set of five cages for the five $p\mathrm{CO}_2$ levels were prepared for each of the two clone populations α and β. Before the start of experiment, another 40 clone individuals of each species were preserved in ethanol. Each cage was placed in a water bath and attached to the tank wall with a suction cup. Thus, there were a total of 10 water baths (five treatments × two clone populations). Seawater within the culture cages was circulated by fixing them in a path of a water jet within the water bath. Culture cages containing clone individuals were maintained for approximately 12 weeks (from 6 July to 30 September 2009) at a constant water temperature ($28.5 \pm 0.7\,^{\circ}\mathrm{C}$), light intensity ($60\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$), and photoperiod (12 h). During the culture experiments, filamentous algae attaching to the surfaces of the culture cages were removed biweekly with brushes. Small air bubbles inside the cages, probably produced by the photosynthesis of the algal symbionts, were removed with a pipette.

At the end of the experiment, the cages were removed from the water baths and kept cool until later analysis. Cultured individuals were picked from each cage, cleaned with a brush and distilled water, and air-dried. Of the 40 cultured individuals, 20 were selected randomly for measurements, excluding dead individuals (i.e. those that did not grow or had no protoplasm). Mortality during the experiments was very low, less than 2.5% for each population. Twenty individuals from those preserved in ethanol at the start of the experiment (hereafter, "initial individuals") were also randomly selected for comparison with the cultured individuals.

2.5 Measurements

The shell diameter and shell weight of each initial and cultured individual was measured. The shell diameter (the average of the maximum diameter from the final chamber and that crossing the first at the center of the test and perpendicular to it) was measured to the nearest 0.001 mm on microscope photographs using image analysis software (Photomeasure, Kenis Inc., Osaka, Japan). Shell weight was measured to the nearest 0.1µg using a microbalance (Thermo Cahn C-35 microbalance, Thermo Electron Corporation).

2.6 Statistical analysis

The shell diameter and weight data sets were analyzed by one-way analysis of variance (ANOVA) for differences among the five $p\text{CO}_2$ levels. When significant differences were observed within a data set, the difference between each pair of means was analyzed with a Tukey's Honestly Significant Difference (HSD) test. These statistical analyses were performed with JMP 7.0.2 (SAS Institute Inc.)

3 Results

All individuals cultured at different $p\text{CO}_2$ levels grew more than twice as large as the initial individuals during the experimental period (Figs. 1–3). Shell weight was positively correlated with shell diameter, but the statistical analysis indicated that shell weight was more dependent on $p\text{CO}_2$ than shell diameter, as reported by Kuroyanagi et al. (2009) as well. This difference is partly because shell diameter does not exactly reflect three-dimensional shell growth, in particular in *Baculogypsina* and *Calcarina*, which have subglobular to bilenticular shells with spines. Thus, the following description of culturing results is focused on foraminiferal shell weight.

3.1 *Baculogypsina*

Mean shell weight of *Baculogypsina* individuals varied from 15 to 25 µg (Fig. 1). Shell weight was relatively heavier at intermediate $p\mathrm{CO}_2$ levels in both clone populations. One-way ANOVA indicated significant differences in shell weight among the different $p\mathrm{CO}_2$ levels in both populations ($F = 4$; $P < 0.001$ for population α, $P < 0.0001$ for population β). Tukey's HSD post hoc test of each population showed that individuals grown at a $p\mathrm{CO}_2$ of 770 µatm had significantly heavier shell weights than those grown at 360 or 970 µatm ($P < 0.05$). Mean shell weights of individuals grown at a $p\mathrm{CO}_2$ of 580 µatm were significantly heavier than those of individuals grown at 970 µatm ($P < 0.05$). In population β, individuals grown at 580 µatm were also significantly heavier than those grown at 260 or 360 µatm ($P < 0.05$). Moreover, in both populations, individuals grown at 260 µatm were found to be heavier than those grown at 360 µatm, although mean shell weight was not statistically significant between these two treatments.

3.2 *Calcarina*

Mean shell weight of *Calcarina* individuals was generally lower at elevated $p\mathrm{CO}_2$, but higher at intermediate $p\mathrm{CO}_2$ levels (Fig. 2). It varied from 30 to 50 µg in population α, and from 35 to 55 µg in population β. One-way ANOVA indicated significant differences in shell weight among different $p\mathrm{CO}_2$ levels in both populations ($F = 4$, $P < 0.0001$). Tukey's HSD post hoc test of each population showed that individuals grown at a $p\mathrm{CO}_2$ of 260 µatm had significantly heavier shell weights than those grown at 970 µatm ($P < 0.05$). In population α, individuals grown at 260 and 770 µatm were significantly heavier than those grown at 580 or 970 µatm ($P < 0.05$). In population β, individuals grown at 260 and 580 µatm were significantly heavier than those grown at 360, 770, or 970 µatm ($P < 0.05$).

3.3 *Amphisorus*

Mean shell weight of *Amphisorus* individuals tended to decrease at elevated $p\mathrm{CO_2}$ (Fig. 3). One-way ANOVA indicated significant differences in shell weight among different $p\mathrm{CO_2}$ levels in both populations ($F = 4$; $P < 0.01$ for population α, and $P < 0.0001$ for population β). Tukey's HSD post hoc test showed that in population α, individuals grown at a $p\mathrm{CO_2}$ of 580 µatm had significantly heavier shell weights than those grown at 770 or 970 µatm ($P < 0.05$). In population β, individuals grown at a $p\mathrm{CO_2}$ of 260 µatm had significantly heavier shell weights than those grown at $p\mathrm{CO_2}$ levels of 580 µatm or more ($P < 0.05$). Mean shell weights of individuals grown at 770 µatm were significantly lighter than those grown at other $p\mathrm{CO_2}$ levels in population β ($P < 0.05$).

4 Discussion

Experimental results indicate that responses of foraminiferal calcification (measured by the increment of shell weight and diameter) to different $p\mathrm{CO_2}$ levels varied both among individuals within a clone population, and between two clone populations within a species. These are probably due to the heterogeneity of micro-environments around individuals in culture cages or in water baths (e.g. irradiance levels, nutrient regime). Alternatively, the intra-species variability suggests the presence of diverse genotypes or ecotypes within a foraminiferal species, which have different physiological adaptations to $p\mathrm{CO_2}$, as suggested for *Emiliania huxleyi* (Ridgwell et al., 2009). Here we will discuss mainly statistically significant results that were common to the two clone populations within a species.

4.1 Increased calcification at intermediate $p\mathrm{CO_2}$ levels

Calcification was enhanced at intermediate $p\mathrm{CO_2}$ levels in the two species with a hyaline shell (*Baculogypsina* at 580 and 770 µatm and *Calcarina* at 580 or 770 µatm), compared with that at the present $p\mathrm{CO_2}$ level. This result is similar to the findings of previous culture experiments by Iglesias-Rodrigues et al. (2008) and Ries et al. (2009). Iglesias-Rodrigues et al. (2008) reported increased calcification and net primary production in the coccolithophore *Emiliania huxleyi* at high $p\mathrm{CO}_2$ (750 µatm). Ries et al. (2009) obtained parabolic calcification response patterns (i.e. positive at intermediate $p\mathrm{CO}_2$ [600 to 900 µatm] and negative at the highest $p\mathrm{CO}_2$ [2856 µatm]) in four of the 18 benthic marine taxa that they examined.

Enhanced calcification at intermediate $p\mathrm{CO}_2$ levels might be due to an increased bicarbonate ion concentration and/or to increased photosynthesis by the algal endosymbionts. According to ter Kuile (1991), in hyaline (perforate) species, inorganic carbon is initially taken up in the form of bicarbonate in a diffusion-limited step. Uptake for photosynthesis and for incorporation into the skeleton are not obligatorily linked in perforate species; instead, the two processes may compete for the same inorganic carbon source. In the cytoplasm, algal symbionts take up inorganic carbon in the form of CO_2 for photosynthesis. Inorganic carbon for calcification is not taken up directly from the cytoplasm, but is first concentrated as carbonate in an inorganic carbon pool (i.e. vesicles or seawater vacuoles) (Erez, 2003; Bentov et al., 2009; de Nooijer et al., 2009). Thus, an increased bicarbonate ion concentration associated with increased $p\mathrm{CO}_2$ in the culture medium may enhance diffusion of bicarbonate, thereby promoting calcification.

Photosynthesis by algal symbionts might be enhanced under intermediate $p\mathrm{CO}_2$ levels. Foraminifers with algal symbionts have several advantages over non-symbiotic foraminifers in clear, nutrient-deficient environments (Hallock, 1999). The photosynthesis by algal symbionts provides host foraminifers with substantial photosynthate, which becomes a source of energy for calcification. The removal of host metabolites such as NH_4^+ and PO_4^{3-} by symbionts might also aid calcification of the host foraminifers because such metabolites can interfere with crystal formation (ter Kuile et al., 1989). Enhancement of calcification by photosynthesis has been also demonstrated by Iglesias-Rodrigues et al. (2008) in *E. huxleyi*, and suggested by Ries et al. (2009) in coralline red and calcareous green algae. Although experimental results have suggested that photosynthesis by isolated in situ diatom symbionts is saturated at the inorganic carbon concentration of the present seawater (ter Kuile et al., 1989), further studies are needed to measure photosynthetic rates of algal symbionts at various $p\mathrm{CO}_2$ levels.

In contrast to *Baculogypsina* and *Calcarina*, calcification in *Amphisorus* did not increase significantly at intermediate $p\mathrm{CO}_2$ levels. This different result may be due to the different calcification mechanism between *Baculogypsina*/*Calcarina* (hyaline species) and *Amphisorus* (porcelaneous species) (ter Kuile et al., 1989). *Amphisorus* takes up inorganic carbon for photosynthesis and for calcification in two separate flows that do not interfere with each other (ter Kuile, 1991). However, the photosynthetic activity of algal endosymbionts under saturating irradiance contributes to an increase in pH above the shell surface of up to 0.2 pH units, which increases the total alkalinity of the surrounding seawater (Köhler-Rink and Kühl, 2000). This alkalinity increase is favorable for imperforate species, which take up carbonate ions for calcification directly from seawater. However, in seawater with high $p\mathrm{CO}_2$ (i.e. low pH), an increase in pH above the shell surface due to symbiont photosynthesis does little to increase the alkalinity or carbonate ion concentration there. Thus, calcification in *Amphisorus* is reduced in seawater at high $p\mathrm{CO}_2$ levels.

4.2 Reduced calcification in seawater at $p\mathrm{CO}_2$ near 1000 µatm

In spite of the differences in calcification mechanisms between hyaline and porcelaneous species, calcification in all three species studied tended to be reduced at the highest $p\mathrm{CO}_2$ treatment level (970 µatm). In porcelaneous species (*Amphisorus*), this reduced calcification can be explained by the decreased carbonate ion concentration in the high $p\mathrm{CO}_2$ seawater. However, calcification in the two hyaline species at 970 µatm was also reduced compared with that at lower $p\mathrm{CO}_2$ levels, indicating that an increased bicarbonate ion concentration and increased photosynthesis of algal endosymbionts may not be effective in enhancing calcification at $p\mathrm{CO}_2$ levels of around 1000 µatm. This result is consistent with the findings of Ries et al. (2009), who demonstrated that in some calcareous algae enhanced calcification peaked at $p\mathrm{CO}_2$ levels between 580 and 900 µatm. Results of culturing experiments using ^{14}C tracer techniques have indicated that the rate of photosynthetic incorporation of carbon by *Amphistegina lobifera* (a hyaline, perforate species with diatom symbionts) changes gradually over a pH range (NBS scale) between 6.0 and 9.6, with the optimum rate being around pH 8.2 (present seawater pH) (ter Kuile et al., 1989). These results suggest that $p\text{CO}_2$ levels of around 1000 µatm and higher (pH of 7.7 on the seawater scale) may be a limiting factor for photosynthesis by symbiotic algae, which may in turn affect calcification by the host foraminifer. Another cause of reduced calcification may be metabolism effects. Le Cadre et al. (2003) showed that in low pH seawater, pseudopodial emission of a hyaline species (*Ammonia*) was reduced or stopped, implying a disturbance of the metabolic activity of the foraminifer. Further studies are needed to investigate metabolic activity in relation to calcification of foraminifers with algal symbionts in seawater at high $p\text{CO}_2$.

4.3 Reduced calcification between 260 and 360 µatm $p\text{CO}_2$

Calcification tended to decrease from $p\text{CO}_2$ of 260 to 360 µatm in the three species examined, although not all observations were statistically significant. This result suggests that ocean acidification since preindustrial times has already caused reef foraminifers to reduce their calcification, as suggested by Kuroyanagi et al. (2009). Culture experiments using ^{14}C tracer techniques (ter Kuile et al., 1989) have demonstrated that in perforate species the optimum pH for calcification is between pH 8.2 and 8.9 (NBS scale), but in an imperforate species (*A. hemprichii*), they found no optimum pH for calcification, which increased very steeply above pH 8.4 (NBS scale). These results indicate that reef foraminifers with both hyaline and porcelaneous shells can calcify more effectively in seawater at a pH higher than the present level.

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Table 1. Mean physical and chemical conditions in each $p\mathrm{CO}_2$ treatment. Standard deviations are shown for pH_T and $p\mathrm{CO}_2$. The mean salinity and total alkalinity, which were measured repeatedly during the experiments, were 34.4 and 2188 $\mathrm{mol\,kg}^{-1}$, respectively. The value of Ω_cal and Ω_arg (saturation state of seawater with respect to calcite and aragonite) was calculated from the total alkalinity and $p\mathrm{CO}_2$.

Treatment	Temperature (°C)	pH_T at 25 °C	$p\mathrm{CO}_2$ (µatm)	Ω_cal	Ω_arg
Preindustrial	27.5	8.170 ± 0.028	261 ± 29	6.39	4.24
Present	27.4	8.072 ± 0.033	360 ± 19	5.32	3.53
Future 1	27.5	7.926 ± 0.039	580 ± 30	3.91	2.60
Future 2	27.5	7.826 ± 0.035	774 ± 56	3.18	2.11
Future 3	27.6	7.756 ± 0.038	972 ± 43	2.69	1.78

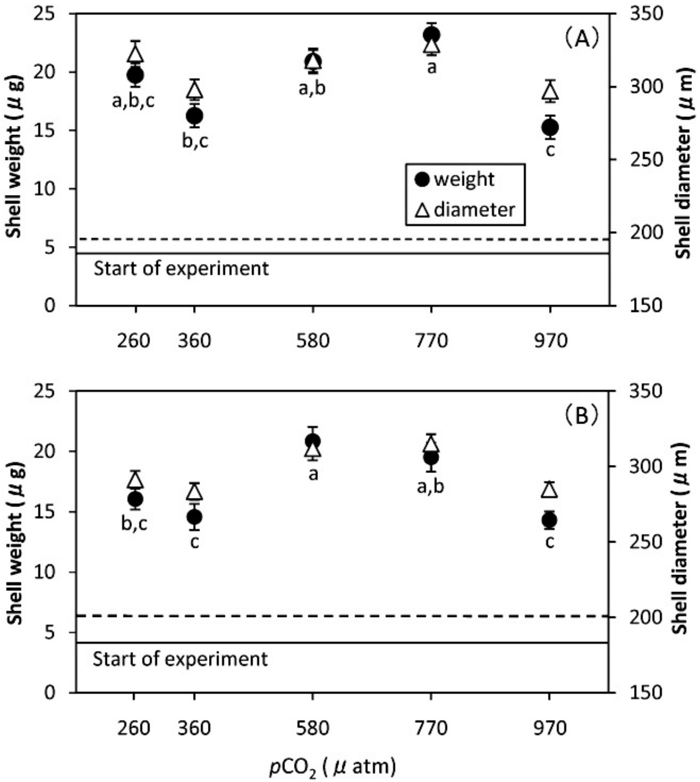

Fig. 1. Mean shell diameter and weight of *Baculogypsina sphaerulata* after culture for about 12 weeks at five $p\mathrm{CO}_2$ levels. Values are means ± SE of the 20 clone individuals sampled in each treatment. Different letters above plotted treatment values indicate a significant difference ($\alpha = 0.05$) in shell weight according to Tukey's HSD post hoc test. Dashed and solid lines show mean shell diameter and mean weight of clone individuals, respectively, at the start of the experiment. **(A)** Population α, **(B)** population β.

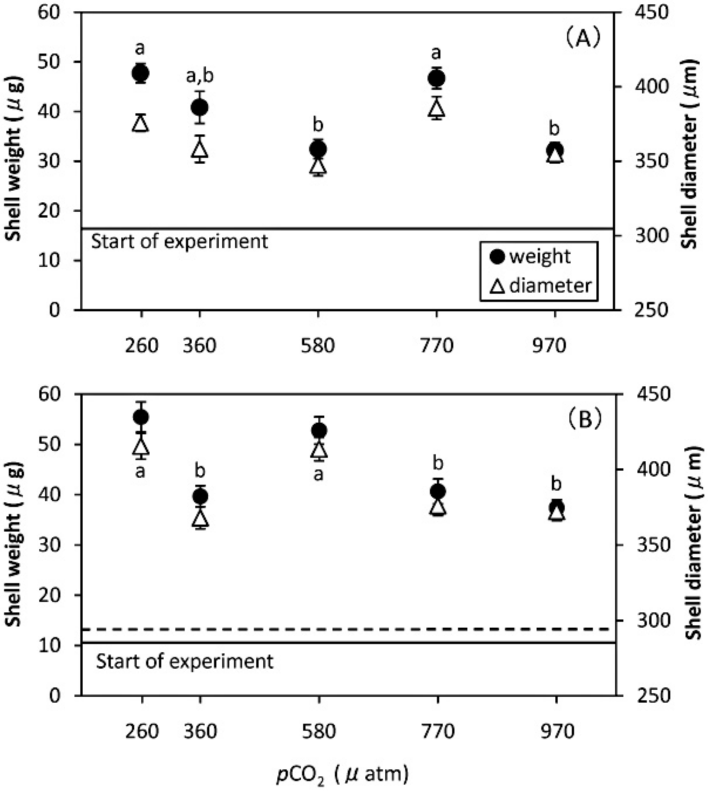

Fig. 2. Mean shell diameter and weight of *Calcarina gaudichaudii* after culture for about 12 weeks at five pCO$_2$ levels. Values are means ± SE of the 20 clone individuals sampled in each treatment. Different letters above plotted treatment values indicate a significant difference ($\alpha = 0.05$) in shell weight according to Tukey's HSD post hoc test. Dashed and solid lines show mean shell diameter and weight of clone individuals, respectively, at the start of the experiment. **(A)** Population α, **(B)** population β.

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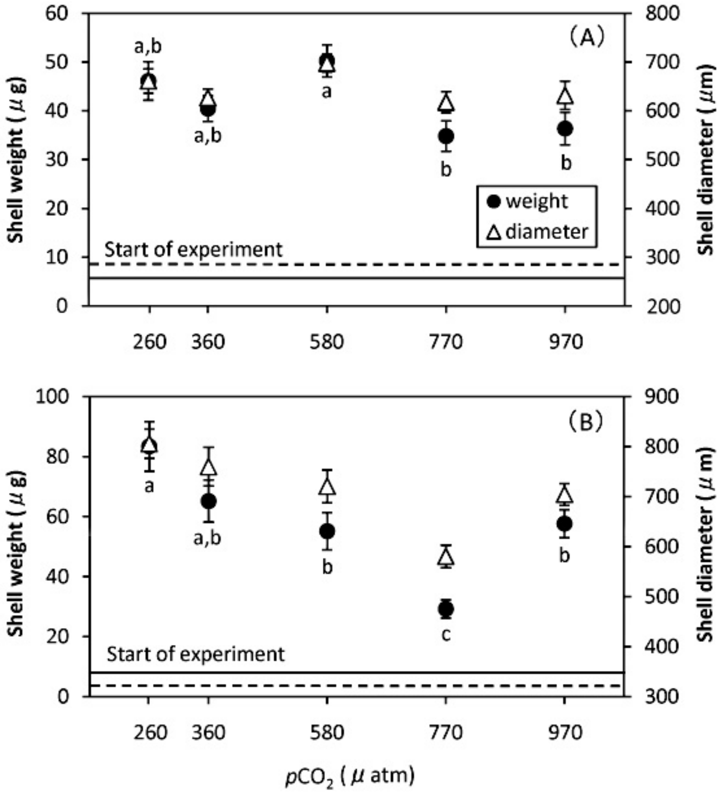

Fig. 3. Mean shell diameter and weight of *Amphisorus hemprichii* after culture for about 12 weeks at five $p\mathrm{CO}_2$ levels. Values are means ± SE of the 20 clone individuals sampled in each treatment. Different letters above plotted treatment values indicate a significant difference ($\alpha = 0.05$) in shell weight according to Tukey's HSD post hoc test. Dashed and solid lines show mean shell diameter and weight of clone individuals, respectively, at the start of experiment. **(A)** Population α, **(B)** population β.