



Responses of calcification of massive and encrusting corals to past, present, and near-future ocean carbon dioxide concentrations



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ARTICLE INFO

Article history:

Available online 17 October 2014

Keywords:

Ocean acidification
Coral
Calcification
The industrial revolution
Bayesian modeling

ABSTRACT

In this study, we report the acidification impact mimicking the pre-industrial, the present, and near-future oceans on calcification of two coral species (*Porites australiensis*, *Isopora palifera*) by using precise $p\text{CO}_2$ control system which can produce acidified seawater under stable $p\text{CO}_2$ values with low variations. In the analyses, we performed Bayesian modeling approaches incorporating the variations of $p\text{CO}_2$ and compared the results between our modeling approach and classical statistical one. The results showed highest calcification rates in pre-industrial $p\text{CO}_2$ level and gradual decreases of calcification in the near-future ocean acidification level, which suggests that ongoing and near-future ocean acidification would negatively impact coral calcification. In addition, it was expected that the variations of parameters of carbon chemistry may affect the inference of the best model on calcification responses to these parameters between Bayesian modeling approach and classical statistical one even under stable $p\text{CO}_2$ values with low variations.

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1. Introduction

Ocean acidification (OA) caused by increased atmospheric CO_2 partial pressure ($p\text{CO}_2$) through human activities has attracted many concerns mainly as the future threat for marine calcifying organisms due to the decrease of seawater carbonate ion concentrations inducing the difficulty of maintaining calcium carbonate skeletons (reviewed in Orr et al., 2005; Hoegh-Guldberg et al., 2007). Laboratory experiments have demonstrated that calcification of marine calcifying organisms (e.g. corals, mollusks, echinoderms) decrease according to the increase of $p\text{CO}_2$ in the seawater (reviewed in Kleypas et al., 2006; Raven et al., 2005). Since pre-industrial times, it is thought that surface ocean pH has already decreased by 0.1 units (Caldeira and Wickett, 2003), which would have also caused the decrease of calcification of marine calcifying organisms although there have been few evidence that calcification has really decreased from the past to the present

day (e.g., Talmage and Gobler, 2010; Ohki et al., 2013). In the Intergovernmental Panel on Climate Change the fourth assessment report (IPCC AR4), the stabilization scenarios have been discussed to suppress the increase of atmospheric CO_2 based on six categories (IPCC, 2007) and the near-future $p\text{CO}_2$ concentrations have been expected to arrive around 600–1100 ppm (200–700 ppm increase from the present ocean (around 400 ppm)) which equals to the decrease of pH around 0.2–0.4 units. To judge when the decrease of calcification will apparently occur in the near-future CO_2 emission scenarios, laboratory experiments using acidified seawater based on the stabilization scenarios on IPCC AR4 would be persuasive to promote social awareness on the impact of OA.

Scleractinian corals are the most important calcifying organisms which support coral reef ecosystems characterized by high biodiversity. Although corals have been threatened by various kinds of disturbances from local (e.g., inputs of sediment and nutrient; Bellwood et al., 2004) to global scales (e.g., global warming which is often considered as a key stressor for coral bleaching; Hoegh-Guldberg, 1999), OA has been recently recognized as a threat for corals because coral calcification is generally reduced by the decrease of carbonate ion concentrations (Kleypas et al.,

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2006; Hoegh-Guldberg et al., 2007) while some exceptions also have been reported (e.g., Ries et al., 2009; Takahashi and Kurihara, 2013; Ohki et al., 2013), and other factors of carbon chemistry such as bicarbonate ions are also known to affect coral calcification (Marubini et al., 2008; Jury et al., 2010; Comeau et al., 2013; Jokiel, 2013). The carbonate ion concentrations are higher in tropical areas where coral reefs exist than in arctic or antarctic areas, and it is suggested that the decrease of carbonate ion concentrations from pre-industrial to the present is larger in the tropics (29 $\mu\text{mol/kg}$) than in the Southern Ocean (18 $\mu\text{mol/kg}$; Orr et al., 2005). However, the extent to which the decrease of carbonate ion concentrations that has occurred after the industrial revolution has affected coral calcification remains almost unknown (Ohki et al., 2013).

When preparing $p\text{CO}_2$ adjusted seawater, addition of acid or base (e.g. HCl, NaOH) is an easy way to adjust seawater pH, but this is different from the condition produced by CO_2 bubbling (e.g. change of alkalinity and co-varying parameters such as pH, HCO_3^- , CO_3^{2-} ; Atkinson and Cuet, 2008). In usual CO_2 bubbling system, however, it is difficult to produce seawater with stable $p\text{CO}_2$ values due to the difficulty of the maintenance of homogenized $p\text{CO}_2$ water because simple CO_2 bubbling for culture tanks was not able to give $p\text{CO}_2$ in equilibrium especially in case of flow-through system which is better to keep sessile marine organisms like corals healthy (Leclercq et al., 2002; Suwa et al., 2010; Iguchi et al., 2012; Takahashi and Kurihara, 2013). This makes it difficult to perform laboratory experiments to evaluate the effects of near-future OA reflecting the future CO_2 emission scenarios proposed in IPCC AR4. To overcome these problems, we developed precise $p\text{CO}_2$ control system which can produce stable $p\text{CO}_2$ with comparatively low variations in the seawater. In addition, this system uses dried air which includes low concentration CO_2 and can produce lower $p\text{CO}_2$ seawater than the present seawater (around 300 μatm , namely, pre-industrial level).

In this study, by setting five $p\text{CO}_2$ treatments (pre-industrial under 300 μatm , the present, and three future treatments under 1000 μatm), we evaluated the effects of $p\text{CO}_2$ adjusted seawater on coral calcification by using two massive and encrusting coral species (*Porites australiensis*, *Isopora palifera*). In addition, we estimated calcification responses of these coral species to parameters of carbon chemistry for deeply understanding coral responses to acidified seawater condition. In the analyses, we adopted Bayesian modeling approaches incorporating the variations of $p\text{CO}_2$ to evaluate these effects on coral calcification and compared the results between our modeling approach and classical statistical one. Massive *Porites* corals are important reef builders and often used to predict past environmental conditions (e.g., Gagan et al., 2000). *I. palifera* fossil corals have a merit for viewpoint from geology and geosciences. This species is reported to be dominated in the Last Glacial Maximum section of the Great Barrier Reef, which was drilled during the Integrated Ocean Drilling Program IODP Expedition 325 (Yokoyama et al., 2011; Nishida et al., 2014; Felis et al., 2014). In addition, fossil *Isopora* corals dominate Quaternary coral reef terraces in Kikai Islands of the northern Ryukyu Islands, Japan (Webster et al., 1998). Because *Porites* spp. round-shape colonies are relatively rare at those sites, *Isopora* corals are important materials for age dating and proxy-based Paleoclimatic reconstruction.

2. Materials and methods

2.1. Preparing $p\text{CO}_2$ adjusted seawater

To produce $p\text{CO}_2$ adjusted seawater, we used precise $p\text{CO}_2$ control system (called as AICAL system) developed by cooperating with Kimoto Electric CO., Ltd., Japan (Ohki et al., 2013). This system

includes CO_2 dissolution and measurement towers (height: 1.78 m) which facilitate the effective dissolution of gaseous CO_2 into seawater by bubbling from the bottom of towers, and record the accurate seawater $p\text{CO}_2$ and adjust $p\text{CO}_2$ values to target ones constantly during experimental periods. This system uses mixed gases (CO_2 and dried air which includes low concentration CO_2) and can produce not only higher $p\text{CO}_2$ seawater but also lower $p\text{CO}_2$ seawater than the present seawater bubbled with air. Five $p\text{CO}_2$ treatments were prepared by this system (pre-industrial level around 300 μatm , the present, and three future level under 1,000 μatm). The $p\text{CO}_2$ values and the variations are summarized in Tables 1 and 2.

2.2. Preparation for coral nubbins

Three colonies of *P. australiensis* were collected from a fringing reef of Sesoko Island, Okinawa, Japan. Of these, one colony of *P. australiensis* was selected after checking the healthy condition by pulse amplitude modulation fluorometry (data not shown). One colony of *I. palifera* was collected from a fringing reef of Bise, Okinawa, Japan. All samples were collected with permission by Okinawa Prefecture. Collected colonies were kept in a running seawater tank under natural light conditions at Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, Okinawa, Japan before starting experiment. Similar sized cubes, hereafter referred to as nubbins (approximately 4 cm^2), were cut from parent colonies and combined with acrylic plates by using superglue. Nubbins were kept in a running seawater tank under natural light conditions until coral tissues started to spread on the surface of top of plastic plates.

2.3. Experimental setup

During the experiment, the seawater temperature was maintained at approximately 27 °C which is the ambient water temperature during the coral spawning season in Okinawa with a 12:12 light:dark photoperiod (*Porites* experiment: 80–100 $\mu\text{mol m}^{-2} \text{s}^{-1}$; *Isopora* experiment: 190–200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) under metal-halide lamps (Funnel2 150 W, Kamihata, Japan). The seawater temperature in each aquarium was maintained with a thermostat and a heater. The seawater in each aquarium was circulated (approx. 5 cm s^{-1}) with a water-jet pump. Temperature was recorded every 30 min by using data loggers (Water Temp Pro, Onset, MA), but unfortunately, the data of treatment d ($p\text{CO}_2$ around 800 μatm) in *Isopora* experiment was lost. Thus, we used the data of treatment c which was manually measured. Filtered Seawater (FSW) was made by inline filter system (1 μm). The seawater adjusted to each $p\text{CO}_2$ as above was supplied into aquarium (12 L) to establish a flow-through system (150 ml min^{-1}). A 100 mL of unfiltered seawater sample was collected and immediately treated with a saturated solution of HgCl_2 . Total alkalinity was determined on aliquots of 50 mL by the potentiometric acid titration method with a Radiometer automated burette (Model ABU91) at 25 °C (Kawahata et al., 2000). The precision of the method has been estimated to be 0.15% for total alkalinity. Primary standardization of the instrument was done using reference material solutions prepared in KANSO TECHNOS Co., Ltd. (Osaka, Japan) by a similar procedure of the Certified Reference Material (CRM) preparation (Dickson et al., 2003). The chemical and physical conditions of each treatment are summarized in Tables 1 and 2. The pH, HCO_3^- , CO_3^{2-} , CO_2 , Ω_{arg} were estimated from $p\text{CO}_2$, temperature, mean total alkalinity of $2,257 \pm 19 \mu\text{mol/kg}$ (mean \pm standard deviation) in *Porites* experiment ($n = 4$, which were measured during the same season in the same laboratory) and $2,226 \pm 28$ in *Isopora* one ($n = 5$, which were measured around the experimental period), and salinity of 34.5 which represents the average previously measured in the

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