



Physiological and ecological performance differs in four coral taxa at a volcanic carbon dioxide seep



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ARTICLE INFO

Article history:

Received 16 October 2014

Received in revised form 30 January 2015

Accepted 19 February 2015

Available online 26 February 2015

Keywords:

Ocean acidification

Volcanic carbon dioxide seep

Scleractinia

Calcification

Photosynthesis

Respiration

ABSTRACT

Around volcanic carbon dioxide (CO₂) seeps in Papua New Guinea, partial pressures of CO₂ (pCO₂) approximate those as predicted for the end of this century, and coral communities have low diversity and low structural complexity. To assess the mechanisms for such community shifts in response to ocean acidification, we examined the physiological performance of two hard corals that occur with increased or unaltered abundance at a seep site (mean pH_{Total} = 7.8, pCO₂ = 862 μatm) compared to a control site (mean pH_{Total} = 8.1, pCO₂ = 323 μatm), namely massive *Porites* spp. and *Pocillopora damicornis*, and two species with reduced abundance, *Acropora millepora* and *Seriatopora hystrix*. Oxygen fluxes, calcification, and skeletal densities were analyzed in corals originating from the seep and control site. Net photosynthesis rates increased considerably in *Porites* spp. and *A. millepora* and slightly in *P. damicornis* at increased pCO₂, but remained unaltered in *S. hystrix*. Dark respiration rates remained constant in all corals investigated from both sites. Rates of light calcification declined in *S. hystrix* at high pCO₂, but were unaffected by pCO₂ in the other three coral taxa. Dark and net calcification rates remained unchanged in massive *Porites* and *P. damicornis*, but were drastically reduced at high pCO₂ in *A. millepora* and *S. hystrix*. However, skeletal densities were similar at both seep and control sites in all coral taxa investigated. Our data suggest that the pCO₂-tolerant corals were characterized by an increased ability to acclimatize to ocean acidification, e.g. by maintaining net calcification. Thus, robust corals, such as *Porites* spp. and *P. damicornis*, are more likely to persist for longer in a future high pCO₂ world than those unable to acclimatize.

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1. Introduction

The world's oceans are a major sink for anthropogenic atmospheric carbon dioxide (Sabine et al., 2004; IPCC, 2014). Rising partial pressure of carbon dioxide (pCO₂) in seawater modifies the carbonate chemistry, lowering pH and increasing the concentration of bicarbonate ions [HCO₃⁻], at the expenses of carbonate ions [CO₃²⁻], in a process called ocean acidification (OA). This lowers the saturation state of carbonate minerals, such as calcite (Ω_{calc}) and aragonite (Ω_{arag}), which are used by marine calcifying organisms to build their calcium carbonate (CaCO₃) skeletons.

The responses of scleractinian corals and other marine calcifying organisms to OA have been investigated in numerous studies, mainly based on aquarium experiments. They report variable, sometimes severe responses to changing seawater carbonate chemistry including declining calcification rates, altered photophysiology, metabolic rates and recruitment success, and reduced survival rates (Hendriks et al., 2010; Hofmann et al., 2010; Kroeker et al., 2010; Erez et al., 2011;

Pandolfi et al., 2011). However, reported responses are species-specific and often contrast across studies even for the same species. Previous studies document both stimulation and inhibition of coral calcification, with rates ranging from +23% to -78% at twofold ambient atmospheric pCO₂ (Kleypas et al., 2006; Erez et al., 2011; Tambutté et al., 2011; Comeau et al., 2013b). Thereby, the responses of corals to OA are affected by the variability of experimental exposure times applied. For example, calcification of the cold water coral *Lophelia pertusa* declined by 26–29% during a short-term (1 week) high pCO₂ exposure while they showed slightly enhanced rates of calcification in long-term (6 months) incubations at similarly high levels of pCO₂ (Form and Riebesell, 2012).

Contradictory results have also been reported for CO₂ effects on oxygen (O₂) production rates in corals. Several studies did not detect any CO₂ induced changes in the photophysiology of coral reef biota (Leclercq et al., 2002; Langdon et al., 2003; Schneider and Erez, 2006; Marubini et al., 2008). In contrast a pCO₂ of 600–790 μatm leads to increasing photosynthetic capacities in the zooxanthellae of *Acropora formosa* (Crawley et al., 2010), to higher photosynthetic yields and photosynthetic efficiency in *Acropora millepora* and *Seriatopora hystrix*, and to increased O₂ production rates and pigment concentrations in

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S. hystrix (unpublished data S.H.C. Noonan and K. Fabricius). The conflicting responses of corals to OA in laboratory experiments cannot only be attributed to species-specific potentials for acclimatization but also to the diversity of treatments employed to mimic OA (e.g. addition of acid vs. CO₂ bubbling), the different ancillary conditions (e.g. temperature, light intensity, flow etc.) and experimental exposure times (days to month) (reviewed in Erez et al., 2011; Edmunds et al., 2012).

Studies conducted in situ at volcanic CO₂ seeps in Papua New Guinea (PNG), Japan and the Mediterranean (Italy) provide data on the long-term effects of OA on marine ecosystems (Hall-Spencer et al., 2008; Fabricius et al., 2011; Kroeker et al., 2011, 2012; Inoue et al., 2013). These seeps are unique places where organisms are exposed for years/decades to increased *p*CO₂ and to altered carbonate chemistry parameters. These studies demonstrate substantial changes in community structure of benthic species in response to increasing *p*CO₂ and decreasing seawater pH. At a seep site in Italy, the taxonomic richness of benthic invertebrates covering 82 families was reduced by 22% in the low pH zones (mean pH_{Total} = 7.8, *p*CO₂ = 1000–1500 μatm) and by 60% in the extreme low pH zones (pH_{Total} = 6.6–7.2, *p*CO₂ ≥ 6000 μatm) (Kroeker et al., 2011). Similarly, the taxonomic richness of hard corals was reduced by 39% at the seep sites (pH_{Total} = 7.73–8.00, *p*CO₂ = 444–953 μatm) compared to the control sites in PNG (pH_{Total} = 7.97–8.14, *p*CO₂ = 296–494 μatm) (Fabricius et al., 2011). However, the total number of individuals in the Mediterranean and the hard coral cover in PNG remained similar between pH zones (Fabricius et al., 2011; Kroeker et al., 2011). Thus reduced diversity in acidified waters seems to be compensated through population blooms of generalists, robust enough to withstand extreme CO₂ conditions of up to 900 μatm and pH_{Total} of 7.8, values which are consistent with projections for the end of this century (Ciais et al., 2013; IPCC, 2014).

At the CO₂ seeps in PNG, long-lived and structurally simple eurytopic massive *Porites* spp. characterized by slow linear extension have established a dominance over fast-growing and structurally complex corals such as *A. millepora* and *S. hystrix* (Fabricius et al., 2011). At the high *p*CO₂ sites, the cover of *Porites* spp. doubles, whereas that of branching corals is reduced threefold, which reduces habitat availability and quality for many invertebrates (Fabricius et al., 2014). While ecological shifts in hard coral communities in areas of naturally decreased pH are well described, physiological data underlying these long-term shifts are sparse. The decline in recruitment success of hard coral cannot exclusively account for the observed community shifts in PNG as juvenile densities of all coral genera investigated, including *Porites* spp., are drastically reduced at high *p*CO₂ (Fabricius et al., 2011). Species-specific physiological performances of negatively affected and robust corals exposed to OA *in situ* and differing capacities to acclimatize to certain higher levels of *p*CO₂ might lead to the reported ecological changes in high-*p*CO₂ environments. Volcanic acidified waters in Japan are dominated by soft corals *Sacrophyton elegans*, which benefit from high *p*CO₂ by enhancing photosynthesis rates (Inoue et al., 2013). This increase in productivity is suggested to provide sufficient energy to allow these soft corals the ability to maintain stable rates of light calcification under acidified conditions, while dark decalcification (negative dark calcification rates) increased with enhanced *p*CO₂ (Inoue et al., 2013). It is hypothesized that the shift in coral community composition within the PNG seep sites is driven by species-specific differences in physiological processes that have been shown to respond to OA, namely photosynthesis, respiration and calcification dynamics in the light and in the dark. A better understanding of these processes might re-evaluate predictions of community shifts in tropical coral reefs for the next decades under projected *p*CO₂.

In the present study four coral taxa were investigated for their physiological performance after lifelong exposure to OA: massive *Porites* spp. and *Pocillopora damicornis*, which occur with increased and unaltered abundance at a seep site, respectively, and *A. millepora* and *S. hystrix*, which were less abundant at high *p*CO₂. Rates of net photosynthesis,

dark respiration, light and dark calcification, and skeletal densities were compared between corals from a CO₂ seep and a control site.

2. Material and methods

2.1. Site description and coral cover

The study was conducted at Upa-Upasina Reef (Normanby Island, Milne Bay Province, Papua New Guinea) in June 2013. The 'seep' site with elevated *p*CO₂ (latitude 9.82410 S, longitude 150.81759 E) was within an area where numerous bubble streams of gas consisting of 99% CO₂ and 1% of O₂, N₂ and CH₄ emerge from the sea floor (Fabricius et al., 2011). A control site (9.82821 S, 150.82052 E) was located 500 m south of the seep site with ambient *p*CO₂ (Table 1). Samples of sea water were collected repeatedly at the seep and control site, to determine temperature and pH_{Total} potentiometrically, as described in detail in Vogel et al. (2014). The samples were then processed for determination of Total Alkalinity (A_T) following standard operational procedures (Dickson et al., 2007). The A_T of 0.05 L subsamples was determined by acid titration (0.05 M HCl) on a Methrom 855 robotic titrosampler (Methrom 855, Methrom, Switzerland), as described in Uthicke and Fabricius (2012). An in-house seawater standard and certified reference material (CRM Batch No. 106, A. Dickson, Scripps Oceanographic Institute) were used to assess the accuracy (replicate readings were ~0.2% standard deviations of the means) and bias of the A_T measurements and to correct for slight differences between acid batches used for acid titration. Carbonate system parameters (Table 1) were calculated from pH_{Total} and A_T using the software CO₂ calc (Robbins et al., 2010) and CO₂ standards as reference material (Lueker et al., 2000). Mean pH_{Total} over a period of 14 days was 7.83 at the seep site and 8.14 at the control site. Calculated mean values of *p*CO₂ and aragonite saturation state (Ω_{arag}) were 848 μatm and 2.41 for the seep site, and 323 μatm and 4.25 for the control site (Table 1). These values are close to long-term averages measured during several field trips (Fabricius et al., 2011; Uthicke and Fabricius, 2012; Fabricius et al., 2014) and thus, are representative for the conditions the corals live in.

To confirm and quantify observations on coral abundances (Fabricius et al., 2011) in higher resolution, fifteen belt transects (0.5 m wide, 10 m long), each at the control and the seep site, were used to determine the cover of specific coral taxa in March 2014.

2.2. Sampling of corals and incubation water

Four coral taxa with differential *p*CO₂ sensitivity were chosen for physiological investigations in June 2013: *A. millepora* and *S. hystrix*, were hypothesized to be vulnerable to elevated *p*CO₂, as structurally complex corals are less abundant at the seep site compared to the control site (Fabricius et al., 2011). In contrast, *Porites* spp. and *P. damicornis* were presumed as more robust species as they were found in high numbers at both sites (Fabricius et al., 2011). For incubation experiments, coral branches 5–6 cm in height and fragments of *Porites* spp. 3–5 cm² in diameter were collected by SCUBA diving in 4–5 m of depth at the seep and control site, and transported to the ship in partitioned, perforated plastic boxes, to conduct incubation experiments. Seawater for incubation experiments was collected at the control and the seep site (pH_{Total} 8.12 ± 0.03 and 7.80 ± 0.02, respectively, *n* = 4 per site) in large buckets.

2.3. Physiological measurements

To determine rates of photosynthesis, respiration and calcification, 8–10 replicate branches/fragments per species were incubated in the light and in the dark under controlled conditions on the ship deck. Coral branches/fragments were transferred into bins with O₂ saturated seawater from their collection site, and placed upright (kept in place with a plastic screw) into the lids of custom-made, inverted clear acrylic

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