Ocean Acidification Accelerates Reef Bioerosion

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Abstract

In the recent discussion how biotic systems may react to ocean acidification caused by the rapid rise in carbon dioxide partial pressure (pCO₂) in the marine realm, substantial research is devoted to calcifiers such as stony corals. The antagonistic process – biologically induced carbonate dissolution via bioerosion – has largely been neglected. Unlike skeletal growth, we expect bioerosion by chemical means to be facilitated in a high-CO₂ world. This study focuses on one of the most detrimental bioeroders, the sponge Cliona orientalis, which attacks and kills live corals on Australia’s Great Barrier Reef. Experimental exposure to lowered and elevated levels of pCO₂ confirms a significant enforcement of the sponges’ bioerosion capacity with increasing pCO₂ under more acidic conditions. Considering the substantial contribution of sponges to carbonate bioerosion, this finding implies that tropical reef ecosystems are facing the combined effects of weakened coral calcification and accelerated bioerosion, resulting in critical pressure on the dynamic balance between biogenic carbonate build-up and degradation.

Introduction

Since the turn of the millennium, ocean acidification (OA) has been recognized as a key factor in marine ecology, attracting a growing pool of research which identified OA to have a multitude of mainly negative effects on reproduction, growth, survival, and diversity of marine biota [1–5]. Among the best studied victims in this respect are organisms that produce carbonate skeletons, and particularly scleractinian corals that show significantly reduced skeletal growth rates with declining pH and lowered seawater carbonate saturation state [4–8]. In contrast, bioeroding organisms have largely been ignored, although they play a key role in carbonate cycling by abrading or dissolving materials such as coral skeletons, and thus need to be included in any equation concerning reef health or growth. This omission needs to be addressed, because chemically achieved bioerosion is expected to be facilitated with progressing OA [9,10], potentially placing many biotoxins into the circle of “winners” of global climate change [11].

Marine bioerosion acts at different scales and is performed by a multitude of organisms employing different chemical and mechanical means in the process of attachment, grazing, or carbonate penetration [12]. On coral reefs, the largest proportion of internal bioerosion is often contributed by demosponges, which attacks and kills live corals on Australia’s Great Barrier Reef. Our model organism Cliona orientalis Thiele, 1900 belongs to one of the most competitive and abundant species complex and is one of the most competitive and abundant representatives of these bioeroders. It is widely distributed on Australia’s Great Barrier Reef (GBR), Indonesia and Japan [18,22] (Fig. 1).

Sponges erode at cellular level by means of biochemical dissolution that leads to the formation of minute cup-shaped grooves and the mechanical extraction of so-called sponge chips of a diameter between 10 and 100 μm [22]. In order to dissolve carbonate, the sponge lowers the pH at the tissue-substrate interface where the specialised etching cells act [22] (exact etching agent unknown to date). Sponge bioerosion is conducted extracellularly potentially making the process sensitive to environmental conditions and change. The lower the environmental pH is to begin with, the less pronounced is the gradient between ambient seawater and the site of dissolution, and the lower will be the metabolic cost required for bioerosion. Hence we hypothesise that the pH lowering inherent to OA will increase the efficiency of the bioerosion process, leading to a significant increase of sponge bioerosion rates with increasing pCO₂.

Materials and Methods

Experimental Setup

In order to test the physiological response in the bioerosion capacity of Cliona orientalis to simulated OA, we core-sampled sponge tissue with dead coral substrate from infested, but live,
massive *Porites* sp. colonies in Little Pioneer Bay at Orpheus Island, central GBR (Fig. 1A). Sampling was achieved with an air-drill and hole-saw (inner diameter 30 mm), cores were trimmed to 25 mm in length with an air-cutter, and kept 4 days outdoors in a seawater flow-through raceway for recovery allowing the tissue to fully heal (Fig. 1D). Cores included sponge-penetrated material at the surface and clean dead coral skeleton below. Entirely clean cut-off parts of cores from the same colonies were prepared as controls and treated in exactly the same way. The condition of the physiologically important photosymbiosis with intracellular dino-flagellates was monitored with pulse amplitude modulated fluorescence (PAM) [20] by measuring their photosynthetic efficiency Fv/Fm and the proxy for chlorophyll *a* concentration F0 at the surface of dark-adapted sponge cores before and after the experiment (Maxi-iPAM, Walz, Germany). This analysis excluded significant differences between treatments and only in case of F0 it showed a moderate decrease over the course of the experiment, probably due to a partial retraction of the photosymbionts as a reaction to the experimental conditions (Table 1). Cores were transferred to a flow-through open system (Fig. 2) that was set up in a constant-temperature room (25°C), allowing 24 h of acclimatisation. Incoming ambient seawater taken from few hundred metres south of the sampling site in Pioneer Bay, was filtered to 25 μm, thereby retaining pico- and nanoplankton (<20 μm) as the sponges’ natural food. The water was temperature-adjusted in a reservoir tank coupled to two chiller/heater units (TC 15, Teco, Italy). Four outlets delivered controlled, constant flow (~30 l/h) to the four treatment lines. The range of target *p*CO₂ levels and the respective carbonate system parameters dissolved inorganic carbon (DIC), pH, and the resulting saturation state for aragonite and calcite in seawater (*Ω*ₐₐ and *Ω*₉₉), were established via perturbation with specifically mixed gases in sealed 30 l tanks (Table 1, Figs. 2–3). This approach is accepted as an effective and the most appropriate method for simulating future carbonate system scenarios in closed, and particularly in open experimental systems [23]. The present-day level (pCO₂ = 395 μatm; pH(total scale) = 8.05) was provided in form of compressed air. Gases for the three manipulated pCO₂ treatments were mixed with Digamix 5KA 36A/9 pumps (H. Wosthoff, Germany). The below present level (pCO₂ = 339 μatm; pH(total scale) = 8.10) was mixed from ‘scrubbed’ air, generated via CO₂-assimilation by soda lime pellets (DiveSorb Pro, Dräger, Germany), and CO₂. The elevated (pCO₂ = 571 μatm; pH(total scale) = 7.91) and the strongly elevated treatment levels (pCO₂ = 1410 μatm; pH(total scale) = 7.57) were mixed using food-grade CO₂ and compressed air with ambient pCO₂. The gas-adjusted seawater was led into 80 l treatment tanks. These were covered with lids of transparent acrylic glass to minimise evaporation and to stabilise the pCO₂ in the headspace that was also filled with the respective gas mixture. Each flow-through treatment tank carried 8 replicate sets of 4 sponge-bearing cores taken from different coral colonies (Fig. 1D; 32 cores in total per treatment tank), and 3 sets of control cores (12 cores per treatment). In each tank, current was generated by a pump placed centrally, spout pointing upwards. The experiment ran for 10 days.

**Simulating a Diurnal Rhythm**

The sponge-bearing cores were kept in a 12/12 h light/dark rhythm. This was achieved with two Sylvania Oracle lamps per treatment tank with 150W HIS-TD Coral-Arc bulbs suspended 85 cm above each treatment tank (Sylvania, Sydney). The light intensities per lamp and at different positions in the tanks were measured with an Exttech EA33 dome-sensor light meter (Triosmartcal, Australia), and lamps as well as sponge sets per
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Monitoring Carbonate System Parameters

Temperature in the treatments was recorded in 10 min intervals with Starmon Mini high-resolution loggers (Star Oddi, Iceland; accuracy ±0.02°C). Salinity (PSS scale) and pH (NBS scale; for monitoring purposes only) were measured daily with a SevenGo DUO meter (Mettler-Toledo, Switzerland) equipped with an InLab 738-ISM conductivity probe and an InLab Expert Pro-ISM pH probe (both calibrated daily with NIST certified buffer solutions). Water samples were taken at the start, the 3rd, 6th and 10th day of the experiment. Sampled water was sterile-filtered with 0.2 μm PES filters. Samples for DIC and Total Alkalinity (TA) were treated with 0.02 vol % saturated HgCl₂ solution to arrest biological activity while samples for nutrients were left untreated. The relative order and timing of all sampling procedures between 9:30 and 10:30 h was kept constant in order to minimise influence of daily fluctuations in temperature, pH, and sponge-dinoflagellate biorhythms. During this time window, pH and T were closest to their mean values (see below). Nitrate, nitrite, phosphate, and silicate were measured photometrically (U-2000, Hitachi, Japan) with precision levels of ±0.5, ±0.02, ±0.05, and 1 μmol/l; ammonium was quantified fluorometrically (SFM 25, Kontron Instruments, Germany) with a precision of ±0.08 μmol/l. TA was measured photochemically using an automated segmented flow analyser (QuAtrO, Bran+Luebbe, USA) equipped with an autosampler (±5 μmol/kg precision). Both, TA and DIC were measured photochemically using an automated segmented flow analyser (QuAtrO, Bran+Luebbe, USA) equipped with an autosampler (±5 μmol/kg precision). Both, TA and DIC were measured using a segmented flow analyser (QuAtrO, Bran+Luebbe, USA) equipped with an autosampler (±5 μmol/kg precision). Both, TA and DIC were measured using a segmented flow analyser (QuAtrO, Bran+Luebbe, USA) equipped with an autosampler (±5 μmol/kg precision). Both, TA and DIC were measured using a segmented flow analyser (QuAtrO, Bran+Luebbe, USA) equipped with an autosampler (±5 μmol/kg precision). Both, TA and DIC were measured using a segmented flow analyser (QuAtrO, Bran+Luebbe, USA) equipped with an autosampler (±5 μmol/kg precision).
measured temperature, salinity, TA and DIC concentrations using the CO2SYS program (EXCEL macro v. 1.02 in default settings). All nutrient levels were very low with values near or below precision and detection levels, rendering consideration for correcting the carbonate system calculations unnecessary. As a cross-check, calculated (via DIC and TA) and directly measured pH values were compared and showed a highly significant correlation and no outliers (pH\text{total scale} = 0.9176 pH\text{NBS}) + 0.5453; r² = 0.99; p < 0.0001). This regression was used to convert measured pH values to total scale. Numerical data of the experimental settings and selected calculated carbonate system parameters are given in Table 1 and are illustrated figure 3.

Assessment of Bioerosion Rates

Bioerosion rates were determined gravimetrically by applying the buoyant weight method [24] at the beginning and the end of the experiment after 10 days of exposure. This method allows an accurate determination of substrate weight loss, while the sponge tissue (<2% of the dry weight) is removed with accuracy. The mean penetration depth was determined gravimetrically by applying the buoyant weight method and the calculated values differed from the directly measured dry weight by only 0.06 ± 0.05%. The sponge tissue was then removed with ~ 5% hydrogen peroxide and the weighing procedure was repeated for determining the weight difference corresponding to the sponge biomass. The mean penetration depth of C. orientalis was quantified with a digital calliper from the two deepest and two shallower penetration depths of each core.

Statistical Analyses

Linear regression models were computed with SigmaPlot (v. 12). Normality tests, One-way ANOVA, and the Kruskal-Wallis analysis were carried out with PAST (v. 2.03). Two-way ANOVA of PAM data was undertaken with the software R (v. 2.13).

Results and Discussion

Before testing a possible pH dependency of sponge bioerosion, we assessed biologically-driven daily pH fluctuations in the treatment tanks as evidenced during a 24 h series of measurements logged both with and without sponge replicates in place (Fig. 4). Despite the flow rate of ~30 l/h, a pH oscillation of 0.07 points was determined at present-day pCO₂ when sponges were in the tank. The rise in pH coincided with the beginning of the 12 h irradiance period (simulated daylight), and values declined again after lights were turned off. This signal reflects the uptake of CO₂ (and linked rise of pH) during active photosynthesis of the symbionts in the sponge tissue. This flux was higher than the simultaneous generation of CO₂ from the sponge respiration, resulting in net photosynthesis during daytime. In contrast, during the following dark phase only respiration was taking place, both by the sponge and its photosymbionts, and led to a decrease in pH. In
comparison, the photosynthetic activity of phytoplankton and some early algal turfs in the treatment tanks amounted to a change of only 0.01 pH points. The temperature in all treatment tanks also followed a synchronous light-dependent rhythm due to the warming by the lamps, thereby simulating daily temperature fluctuation. The carbonate saturation states for aragonite and calcite never became undersaturated ($\Omega < 1$), neither in the highest experimental $p$CO$_2$ nor when considering the diurnal pH and temperature fluctuations. Nevertheless, a relevant abiotic dissolution or microbial bioerosion of the coral substrate was ruled out by including clean dead coral cores of similar size and from the same source as controls – none of these lost weight, despite the larger exposed surface in the sponge-free cores (Table 1). Estimates of proportional biomass [25] additionally indicate that microbial bioerosion by phototrophic or chemotrophic euendoliths in the sponge cores is negligible. We furthermore checked mean penetration depth and sponge tissue weight per sponge-bearing core after the experiment (Table 1), which did not vary significantly between treatments and confirmed that our data were not biased by sponge biomass or tissue shrinkage, so that the change in buoyant weight recorded in our experiment can be addressed with confidence to the chemical and mechanical bioerosion activity of *Cliona orientalis*.

Sponge bioerosion rates reached a mean of $2.23 \pm 0.15$ kg m$^{-2}$ yr$^{-1}$ in the present-day treatment (Table 1). Bioerosion rates significantly increased with rising $p$CO$_2$ (Fig. 5A, Table 2). At moderately elevated $p$CO$_2$ the mean bioerosion rate was $2.60 \pm 0.25$ kg m$^{-2}$ yr$^{-1}$, which corresponds to a 17% increase relative to the present-day rate. At strongly elevated $p$CO$_2$, bioerosion was further enhanced, attaining a mean rate of $3.59 \pm 0.40$ kg m$^{-2}$ yr$^{-1}$ and representing a 61% change compared to the present-day value. This increase in bioerosion rate reflects the enhanced efficiency of the sponges’ bioerosion process as a result of the lowered environmental pH, causing a shallower gradient between the environment and the etching site. The sponge apparently ‘takes advantage’ of the facilitated dissolution in the more acidic environment, as opposed to keeping bioerosion rates constant and only lowering the metabolic cost. In contrast to this distinct trend, a decrease in bioerosion rate of $2.22 \pm 0.45$ kg m$^{-2}$ yr$^{-1}$ in the slightly lowered $p$CO$_2$ level was less than 1% lower and thus not significantly different compared to the present-day treatment (Table 2). The physiological interpretation for our findings in the lowered $p$CO$_2$ is that the sponge is partly able to compensate for the less favourable conditions (hindered dissolution in more alkaline conditions), possibly at the cost of increasing the metabolic rate. The overall linear regression of bioerosion rate versus $p$CO$_2$ is highly significant ($r^2 = 0.76$; $p < 0.0001$) and clearly supports the initial hypothesis that sponge bioerosion can be expected to accelerate with progressing OA.

Based on the linear regression, the relationship between $p$CO$_2$ [μatm] and *C. orientalis* bioerosion rates [kg m$^{-2}$ yr$^{-1}$] can be formulated as in Eq. 1, and the respective relationship converted to changes in pH in Eq. 2.

$$\text{bioerosion rate} = 0.0013p\text{CO}_2 + 1.7875$$  \hspace{1cm} (1)

$$\text{bioerosion rate} = -2.6836p\text{H(total scale)} + 23.882$$  \hspace{1cm} (2)

Keeping the limitation in ecological relevance inherent to short-term lab experiments in mind, this relationship translates to a predicted 25.4% increase in sponge bioerosion by the end of this century, following the BERN-CG reference model based on the SRES A2 emission scenario that corresponds to a predicted $p$CO$_2$ level of 836 μatm by the year 2100 [26]. The most optimistic SRES B1 model with a predicted 2100 $p$CO$_2$ of only 540 μatm would result in an 8.6% increase and the intermediate SRES A1B
model with a $2100 \mu$atm $pCO_2$ of 703 atm equates to a potential 17.7% increase in sponge bioerosion (Fig. 5B). A similar range of predictions can be made when applying the new Representative Concentration Pathways (RCPs) [27] with an 8.6%, 15.8%, and 30.9% increase for the RCP 4.5, 6, and 8.5 scenarios, respectively.

Due to the important role of bioeroding sponges, and of ‘C. viridis complex’ species in particular, this finding suggests severe consequences for coral reef health. Coral reef calcification and bioerosion are antagonistic processes in a dynamic balance [28,29]. This balance will become seriously strained when bioerosion is accelerated by OA, while at the same time, coral net calcification rates are declining [4–8]. This situation will push the carbonate budget towards negative values, and on some reefs negative carbonate budgets have already been recognised as result of intensive sponge bioerosion [16,17].

Pioneer experimental evidence for an increase of bioerosion rates generated by specific bioeroders due to seawater acidification was provided for euendolithic microborers. Biosphere 2 experiments showed that particularly the dominant microboring chlorophyte Ostreobium quekettii grows faster under elevated $pCO_2$ (750 atm) [10]. However, in contrast to endolithic algae which occasionally even support stressed calcifiers [30], bioeroding sponges are always in antagonism to calcifiers, and the species we worked with is known to often overwhelm and kill live corals [18,21]. Several mesocosm experiments and field studies demonstrated an increase of total dissolution – including bioerosion, but rarely addressed as such – partly leading to a net loss of carbonate [31]. Coral reefs in the eastern tropical Pacific, where cool, CO2-rich upwelling water masses lead to naturally low pH and saturation states, are poorly cemented and prone to intense bioerosion [17], serving as a model for coral reef development in a high-$CO_2$ world [9]. Lowest mean pH(seawater scale) values of 7.88 and a corresponding $\Omega_{AR}$ of 2.49 were reported from Galápagos [9]. Hence at least part of pH conditions predicted by OA
Figure 5. Increasing sponge bioerosion as a function of increasing $p$CO$_2$. (A) Weight loss per replicate set translated to bioerosion rates for the four $p$CO$_2$ treatments. The linear regression of the 32 replicates (8 per treatment) is highly significant ($r^2 = 0.76; p < 0.0001$). (B) Projected percent increase in sponge bioerosion relative to the present-day level, calculated for the BERN-CC model based on the SRES A2 (red), A1B (blue), and B1 (green) emission scenarios.

doi:10.1371/journal.pone.0045124.g005

Table 2. Results ($p$ values) from the pairwise comparison of bioerosion rates in the four $p$CO$_2$ treatments (Mann-Whitney test; Bonferroni corrected $p$ values in lower left triangle of matrix) performed after Kruskal-Wallis analysis ($H = 21.25; H_c = 21.25; p < 0.0001; n = 8$ per treatment) and rejection of normal distribution for the present-day (393 μatm) and the elevated treatment (571 μatm) via Shapiro-Wilk test.

|                      | below present $p$CO$_2$ 339 μatm | present-day $p$CO$_2$ 393 μatm | elevated $p$CO$_2$ 571 μatm | strongly elevated $p$CO$_2$ 1410 μatm |
|----------------------|----------------------------------|--------------------------------|-----------------------------|--------------------------------------|
| below present $p$CO$_2$ 339 μatm | –                               | 0.7132                         | 0.0831                      | 0.0009*                              |
| present-day $p$CO$_2$ 393 μatm | 1.0000                          | –                              | 0.0063*                     | 0.0009*                              |
| elevated $p$CO$_2$ 571 μatm | 0.4987                          | 0.0379*                        | –                           | 0.0014*                              |
| strongly elevated $p$CO$_2$ 1410 μatm | 0.0056*                      | 0.0056*                        | 0.0082*                     | –                                    |

*significant difference.

doi:10.1371/journal.pone.0045124.t002
scenarios is already experienced by tropical reef corals and bioeroding sponges at present time. This may apply not only for the eastern Pacific but for many shallow coral reefs with relative long water residence times, as a result of carbon fluxes related to calcification and the remineralisation of organic matter [32]. At the PEBB-REEF for instance, spatial and temporal pH fluctuations are in the magnitude of 0.4 pH units [33]. Hence, the three lower \( \text{pCO}_2 \) treatments of the present experiment were within the range of natural fluctuations currently experienced on some coral reefs, whereas the strongly elevated treatment looks far into the future and may never be reached.

Intriguingly, another important factor in climate change – global warming – may partly counteract the development caused by OA. Rising temperatures reduce the physicochemical dissolution capacity of calcium carbonate in seawater [34] and could also slow down chemical bioerosion. However, within tolerance limits of physiological processes, i.e. chemical reactions can be accelerated by elevated temperature, and interaction of \( \text{pCO}_2 \) and temperature may have complex effects as has been demonstrated with respect to coral calcification rates [35,36]. This observation calls for multifactorial experiments that consider both, the isolated as well as concerted effects of \( \text{pCO}_2 \) and temperature on sponge bioerosion and other bioerosion processes. And, as an indispensable step, the impact of climate change on bioerosion needs to be addressed in long-term in-situ experiments. Ultimately, these data will convey critical insights into global trends of biologically caused dissolution and the possible threat of increasing bioerosion on the balance between skeletal growth and bioerosion on tropical coral reefs.

**Acknowledgments**

Supreme logistical support by AIMS staff members including M. Donaldson and D. Stockham, and the OIRS team S. Kelly, H. Burgess, R. Wiley, I. Fennel, and N. Salmon. Fieldwork greatly profited from the commitment of the scientific volunteers R. and D. Wisdom, N. Lee and C. Ansell. Statistical analyses supplemented by R. O’Leary.

**Author Contributions**

Conceived and designed the experiments: MW CHLS A. Freiwald. Performed the experiments: MW CHLS. Analyzed the data: MW CHLS A. Form. Contributed reagents/materials/analysis tools: MW CHLS A. Form. Wrote the paper: MW CHLS A. Freiwald. Initiated the study and obtained the funding: CHLS A. Freiwald.

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