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Respiration of Mediterranean cold-water corals is not affected by ocean acidification as projected for the end of the century

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Abstract

The rise of CO_2 has been identified as a major threat to life in the ocean. About one-third of the anthropogenic CO_2 produced in the last 200 yr has been taken up by the ocean, leading to ocean acidification. Surface seawater pH is projected to decrease by about 0.4 unit between the pre-industrial revolution and 2100. The branching cold-water corals *Madrepora oculata* and *Lophelia pertusa* are important, habitat-forming species in the deep Mediterranean Sea. Although previous research has investigated the abundance and distribution of these species, little is known regarding their eco-physiology and potential responses to global environmental change. A previous study indicated that the rate of calcification of these two species remained constant up to 1000 µatm CO_2, a value that is at the upper end of changes projected to occur by 2100. We examined whether the ability to maintain calcification rates in the face of rising pCO_2 affected the energetic requirements of these corals. Over the course of three months, rates of respiration were measured at a pCO_2 ranging between 350 and 1100 µatm to distinguish between short-term response and longer-term acclimation. Respiration rates ranged from 0.074 to 0.266 µmol O_2 (g skeletal dry weight)$^{-1}$ h^{-1} and 0.095 to 0.725 µmol O_2 (g skeletal dry weight)$^{-1}$ h^{-1} for *L. pertusa* and *M. oculata*, respectively, and were independent of pCO_2. Respiration increased with time likely due to regular feeding which may have provided an increased energy supply to sustain coral metabolism. Future studies are needed to confirm whether the insensitivity of respiration to increasing pCO_2 is a general feature of deep-sea corals in other regions.

1 Introduction

Cold-water corals form unique, deep-sea habitats containing a high biodiversity of organisms (Roberts et al., 2006). The habitat-forming cold-water corals *Lophelia pertusa* and *Madrepora oculata* are found in relatively deep waters at temperatures and salinities between 4 to 12 °C (Roberts et al., 2006) and 31.7 to 38.8 (Davies et al., 2008), respectively. Recent work on the distribution and abundance of these cold-water corals in the Mediterranean Sea (Taviani et al., 2005b; Freiwald et al., 2009; Orejas et al., 2009) indicates that they are found at depths below 200 m, at relatively warm (and stable) temperatures (12.5 to 13.5 °C) and high salinity (38 to 39) (Freiwald et al., 2009; Tursi et al., 2004). Biogeographic considerations indicate that the cold-water corals in the Mediterranean Sea occur at the warm edge of their range in thermal tolerance (Davies et al., 2008). *Madrepora oculata* is more abundant than *L. pertusa* in the region which suggests that the former may be better adapted than the latter to warmer temperature and more saline waters (Taviani et al., 2005a). A general decline in the presence of Mediterranean cold-water corals has been reported during the post-glacial time (Delibrias and Taviani, 1985) and appears to be more pronounced for *L. pertusa* than for *M. oculata*.

The oceans play a critical role in mitigating the effect of increased production of greenhouse gasses on global climate by removing ~ one fourth to one third of anthropogenic CO_2 from the atmosphere (Khatiwala et al., 2009; Sabine et al., 2004). The downside of this process is that, once dissolved in seawater, CO_2 is a weak acid which reduces seawater pH causing ocean acidification (Caldeira and Wickett, 2003; Gattuso et al., 1999). This process also increases the concentrations of bicarbonate ions (HCO^{3-}) and dissolved inorganic carbon (C_T) and decreases the concentration of carbonate ions (CO_3^{2-}). The saturation state of calcium carbonate, Ω, is a measure of the solubility of carbonate minerals (e.g. calcite (Ω_c) or aragonite (Ω_a)) in seawater (Kleypas et al., 1999; Feely et al., 2004; Cao et al., 2007) and provides a good indicator of whether calcifying organisms can build and maintain their exoskeletons (e.g., corals) and shells (e.g., pteropods). Calcium carbonate dissolution is favoured when Ω is below 1, while calcium carbonate precipitation is favoured when it is above 1. The saturation state decreases with increasing pressure (water depth) and decreasing temperature hence, Ω is lower at higher latitude (colder) and deeper waters than in lower latitude (warmer) and shallower waters (Orr et al., 2005). Calcifying organisms at high latitudes and/or deeper depths will be the first to be subjected to seawater favouring

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carbonate dissolution ($\Omega < 1$). At the end of the century, Ω_a is projected to be < 1 within > 70 % of the present habitat of cold-water corals (Guinotte et al., 2006 #2578).

Previous experiments examining the effect of ocean acidification on *L. pertusa* and *M. oculata* suggest that their rates of calcification remain positive even in waters where Ω_a is < 1 (Maier et al., 2009; Thresher et al., 2011; Form and Riebesell, 2012). Moreover, recent studies (Form and Riebesell, 2012; Maier et al., 2012, 2013) reported that calcification rates of these species remained positive at a partial pressure of CO_2 (pCO_2) of 1000 µatm, a value that is at the high end of projected changes by 2100 (IPPC, 2007). Calcification is an energy demanding process (Goreau, 1959; Allemand et al., 2004) and it is likely that the mechanism(s) responsible for these species maintaining positive rates of calcification at high pCO_2 (lower seawater pH) would be reflected in higher energetic costs. For example, it has been suggested that *M. oculata* and *L. pertusa* are able to regulate their internal pH over a large gradient of pCO_2 (McCulloch et al., 2012) which likely increases their metabolic requirements. Unfortunately, very little is known regarding the metabolic rate of these species. No metabolic research has been performed on *M. oculata* and respiration rates have only been reported in one study on specimens of *L. pertusa* collected from the North Atlantic and maintained under variable temperature (Dodds et al., 2007). In that study, a dramatic (50 %) increase in respiration rate occurred between 9 and 11 °C (Dodds et al., 2007), temperatures that are several degrees colder than those experienced by cold-water corals in the Mediterranean Sea.

In the present study, respiration rates were measured for two habitat-forming cold-water coral species, *M. oculata* and *L. pertusa* from the Mediterranean Sea. Respiration rates were measured for corals maintained for both short and long periods of time at pCO_2 levels ranging from ambient (350 µatm) to elevated (1100 µatm) levels. This study utilized the same experimental set-up as a previous study demonstrating that elevated pCO_2 had no effect on the rate of calcification in these two species (Maier et al., 2013). Thus, we test the hypothesis that the ability to maintain positive rates of calcification at high pCO_2 is accompanied by higher energy requirements which could be expressed by increased rates of respiration.

2 Material and methods

2.1 Sampling of cold-water corals and experimental set up

Colonies of the cold-water corals *M. oculata* and *L. pertusa* were collected during the MedSeaCan cruise in June 2009 in the Lacaze-Duthiers canyon at water depths of 260 m (42°35.07′ N, 03°24.14′ E), 267 m (42°34.98′ N, 03°24.15′ E) and 500 m (42°32.98′ N, 03°25.21′ E), using a remotely operated vehicle. Corals were transported to the laboratory and maintained in a temperature-controlled room until the start of the experiments. Branches were carefully sub-divided into smaller fragments and placed into individual maintenance vials of 4.5 cm inner diameter and a volume of ca. 300 mL (Table 1). Surface water with a salinity of 38 was pumped into two, 110-L storage tanks and maintained at 11 °C in the temperature-controlled room. Water was delivered to maintenance vials at a flow rate of 32 ± 14 mL h^{-1}. The vials were maintained in four water baths and temperature was adjusted to 13 ± 0.1 °C using electronic temperature controllers (Corema) coupled with aquarium heaters (Tetratec HT75). Homogeneity of temperature was achieved by water circulation pumps (JBL Pro Flow 500, 500 L h^{-1}).

Circulation in the coral maintenance vials was obtained by air-lift with thin silicon tubes connected to a PVC tube (8 cm long and 1.0 cm in diameter), which was submerged inside each of the vials. The air flow was 50 mL min^{-1} in every vial. Corals were fed 1 and 3 times a week with frozen krill and freshly hatched *Artemia* nauplii, respectively. After an acclimation period of 1 month, pCO_2 was adjusted using pre-mixed air generated by high-precision mass flow controllers (MFCs; ANALYT MC-GFC17, 0–10 L for air and 0–10 mL for pure CO_2) and an air compressor (Jun-Air OF302-25B). Four pCO_2 treatments were established: A = 280 ppm (low), B = 400 ppm (ambient), C = 700 ppm (elevated) and D = 1000 ppm (above projected) as described in Maier et al. (2013).

The seawater of the water baths containing the maintenance vials was also adjusted to the intended pCO_2 by bubbling with an air stone (HOBBY ceramic air diffuser, 150 mm in length). Prior to feeding, the seawater of the waterbath was filtered (Tetratec EX 1200, 1200 L h^{-1}). Any leftover food was removed via siphon to prevent bacterial respiration and the build-up of nutrients and organic matter. Corals were maintained under these conditions throughout the 3 month duration of the experiment except during incubations aimed at determining rates of respiration (next section) or calcification (Maier et al., 2013).

2.2 Determination of respiration rates

Two days (T_1) after adjusting to different pCO_2 levels and at about monthly intervals for 3 months (T_2–T_4), rates of respiration were measured using the same coral fragments (repeated measures approach). Respiration was determined using optodes (Presens OXY-4 mini) equipped with polymer optical fibers (Presens, POF) and small sensor (5 mm diameter) placed inside the respiration vials. The respiration vials (8 cm × 5.5 cm height × diameter) with a screw cap were placed on 4 submersible magnetic stirrers in a temperature-controlled water bath (13 ± 0.1 °C). A magnet was placed below a grid on which the corals were placed during the incubations. Three vials containing coral fragments were incubated for 2.5 h while a separate vial, with no coral, served as blank and contained a temperature sensor (StarOddi, DST centi-T) logging every 30 s with an accuracy of ±0.1 °C to make sure temperature was constant during the 2.5 h duration of incubation. Any oxygen consumption rate within the blank, due to either minor changes in temperature or prokaryotic respiration, were subtracted from that measured in cold-water corals.

Prior to respiration measurements, pCO_2 levels were adjusted in bulk seawater in 10 L containers by aeration with the four air–CO_2 mixtures for 24 h. Respiration rates were determined from the depletion in O_2 during incubation period. Oxygen sensors

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were calibrated with oxygen-free (0 %) and oxygen-saturated (100 %) seawater. Oxygen consumption curves (% O_2) were established at 30 s intervals over an incubation period of 2.5 h and respiration rates are given as µmol O_2 (g skeletal dry weight)$^{-1}$ h^{-1} (Table 1, Fig. 1).

2.3 Carbonate chemistry

Samples for total alkalinity (A_T) and dissolved inorganic carbon (C_T) were taken from bulk seawater (125 mL, $N = 3$ for each $p\mathrm{CO_2}$ treatment) prior to incubation and analysed as described in Maier et al. (2012). Other parameters of the carbonate chemistry, i.e. the partial pressure of CO_2 ($p\mathrm{CO_2}$), pH on total scale ($\mathrm{pH_T}$), and aragonite saturation state (Ω_a) were calculated using A_T, C_T, a salinity of 38, temperature of 13 °C and hydrostatic pressure of 0 atm using the software package seacarb running under R (Lavigne and Gattuso, 2011). The $p\mathrm{CO_2}$ cannot be adjusted during incubation. The carbonate chemistry therefore changed as function of respiration, calcification and ammonium excretion (Maier et al., 2009). These changes were estimated using a stepwise approach where A_T and C_T were calculated in hourly steps for the entire duration of the 2.5 h incubation for each coral fragment and repeated measurements of respiration rates (T_1–T_4) using the following equations:

$$\mathrm{A_T}(t+1) = \mathrm{A_T}(t) - 2 \times G + 0.875 \times \mathrm{NH_4} \quad (1)$$

$$\mathrm{C_T}(t+1) = \mathrm{C_T}(t) + R - G \quad (2)$$

with calcification rate (G), respiration rate (R) and ammonium excretion rate ($\mathrm{NH_4}$) in µmol kg^{-1} h^{-1}. Calcification decreases A_T by $2 \times G$ and C_T by $1 \times G$, respiration increases C_T by $1 \times R$ (assuming a respiratory quotient of 1), and ammonium increases A_T by $(14/16) \times \mathrm{NH_4}$ (Gattuso et al., 1999).

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2.4 Statistical analysis

Statistical analyses were conducted using the software Statistica 7.0. Data are given as mean ± standard deviation (SD). For the comparison of carbonate chemistry among the four pCO_2 treatments (A–D) of bulk seawater prepared at T_1–T_4, a one-way ANOVA was conducted followed by a Tukey HSD post-hoc comparison. A repeated measures ANOVA was used to compare respiration rates at the 4 pCO_2 levels from T_1 to T_4 for each coral fragment.

3 Results and discussion

3.1 Carbonate chemistry

The pCO_2 of bulk seawater prior to the incubations differed from the pCO_2 levels that were adjusted by aeration using pre-mixed air–CO_2 for treatment A (280 ppm), B (400 ppm), C (700 ppm) and D (1000 ppm). The seawater pCO_2 achieved by aeration was on average 350 ± 20, 497 ± 28, 826 ± 69 and 1108 ± 58 µatm for treatments A–D, respectively (Table 2). Therefore, all values tended to be higher than those of air–CO_2 mixtures. These levels covered a large range from slightly below ambient to above the level projected for the end of the century (IPPC, 2007). Unsurprisingly, A_T was not affected by changes in pCO_2 (1-way ANOVA, $p > 0.69$). The other parameters of the carbonate chemistry (C_T, pCO_2, pH_T and Ω_a) were significantly different between each of the four pCO_2 treatment levels (1-way ANOVA, $p \ll 0.001$ and Tukey HSD post-hoc comparison, $p < 0.05$ for pair-wise comparisons between any pair of the four pCO_2 treatments).

Also, the changes for parameters of the carbonate chemistry that took place during the 2.5 h closed-system incubation were estimated as a function of respiration, calcification and ammonium excretion (for details see Sect. 2.3.). During the 2.5 h incubations, there was an average increase of pCO_2 of 6 ± 2 % (range 3 to 13 %) and an average decrease of Ω_a of 5 ± 1 %. Changes in the other parameters were below 1 % of the initial values (Table 3).

3.2 Respiration rates at different pCO_2 levels and over time

The respiration rates ranged from 0.074 to 0.266 µmol O_2 (g skeletal dry weight)$^{-1}$ h^{-1} and 0.095 to 0.725 µmol O_2 (g skeletal dry weight)$^{-1}$ h^{-1} at different times of incubation and pCO_2 treatments for *L. pertusa* and *M. oculata*, respectively (Fig. 1). Despite the large range of pCO_2 levels across the four treatments, there was no effect between pCO_2 treatment levels on respiration rates (2-way repeated measures ANOVA, $p = 0.767$ and $p = 0.357$ for *M. oculata* and *L. pertusa*, respectively). For *L. pertusa*, there was an increase in respiration from T_1 to T_3 and a decrease again at T_4 independent of pCO_2 levels studied and a significant effect of time of incubation (2-way repeated measures ANOVA, $p \ll 0.001$). A similar pattern of increasing respiration from T_1 to T_3 could be observed for *M. oculata*, but it was not as consistent among the pCO_2 treatments as that for *L. pertusa*. In addition, there was no significant effect between repeated measurements T_1–T_4 (2-way repeated measures ANOVA, $p = 0.104$). To our best knowledge, this is the first report of the effect of pCO_2 on respiration on the two cold-water coral species *L. pertusa* and *M. oculata*. In contrast to our results, a significant decrease in respiration at elevated pCO_2 (D. Piepenburg and M. Bartz, unpublished results) was mentioned by Form and Riebesell (2012), but no data were provided. A decrease in respiration at elevated pCO_2 would be surprising as it would not be in agreement with the hypothesis that more energy must be allocated to upregulate internal pH and maintain constant calcification.

3.3 Respiration and calcification

To date, calcification is the only parameter investigated with respect ot the effects of ocean acidification on cold-water corals. It generally appears to be constant over a large range in pCO_2 levels (Thresher et al., 2011; Form and Riebesell, 2012;

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Maier et al., 2012, 2013). It has been proposed that cold-water corals can upregulate their internal pH and maintain a constant rate of calcification even when seawater is under-saturated in aragonite (McCulloch et al., 2012). Since the upregulation of internal pH and maintenance of high calcification rates is an energy-requiring process mediated through Ca-ATPase (McConnaughey et al., 1997; Allemand et al., 2004; Zoccola et al., 2004), the question arises whether upregulation of internal pH at elevated $p\mathrm{CO_2}$ alters the energy balance. For example, more energy would be required to upregulate the internal pH if ambient pH decreases, and it was therefore expected that this would induce a higher rate of respiration. However, the results presented here reveal that respiration is independent of $p\mathrm{CO_2}$ level in the corals tested. The response of calcification of the same coral fragments is similar over $p\mathrm{CO_2}$ levels ranging from 380 to 930 µatm (Maier et al., 2013). Calcification correlates significantly with respiration (Fig. 2), indicating a strong coupling of calcification and general metabolic performance. The slope of the regression equation between skeletal growth (G) and respiration rates (R) was steeper for *L. pertusa* than for *M. oculata*, which suggests that more energy is allocated to calcification in *L. pertusa* than in *M. oculata* (Fig. 2).

For zooxanthellate corals, it had been proposed that the energy for calcification is derived to a large part from photosynthesis (Gattuso et al., 1999; Al-Horani et al., 2003), an energy source that is not available to cold-water corals. It is unclear, what caused the synchronous increase of calcification and respiration during the 2–3 months-long experiment at different $p\mathrm{CO_2}$ levels (this study and Maier et al., 2013). One likely explanation is that the regular feeding triggered an increase in coral metabolism (calcification and respiration) compared to in situ.

3.4 Energy requirements and temperature

A study of the cold-water coral *Desmophyllum dianthus*, revealed that both respiration and calcification rates were lower in starved than fed colonies (Naumann et al., 2011). Also, feeding increases both the skeletal and tissue growth in zooxanthellate corals (Ferrier-Pagès et al., 2003; Houlbrèque et al., 2003; Rodolfo-Metalpa et al., 2008).

Mean respiration rates pooled for pCO_2 treatment levels and repeated measurements (T_1–T_4) were 0.16 ± 0.08 µmol O_2 (g skeletal dry weight)$^{-1}$ h^{-1} and 0.45 ± 0.45 µmol O_2 (g skeletal dry weight)$^{-1}$ h^{-1} for *L. pertusa* and *M. oculata*, respectively (Table 1). So far, only one study (from Mingulay reef, Northeast Atlantic) has reported the respiration rates for *L. pertusa* (Dodds et al., 2007) and respiration rates of *M. oculata* have, to the best knowledge, never been measured. For *L. pertusa,* Dodds et al. (2007) reported respiration rates of specimens from the NE Atlantic at ambient temperature that were higher than those measured here in individuals collected from the Mediterranean Sea (0.23 vs 0.16 µmol O_2 (g skeletal dry weight)$^{-1}$ h^{-1}; Table 1). This is surprising since Mediterranean cold-water corals live in habitats that are, on average, 4 °C warmer than temperatures reported at the Mingulay collection site (13 vs 9 °C). Furthermore, Dodds et al. (2007) showed that respiration increased by 50 % (0.23 to 0.33 µmol (g skeletal dry weight)$^{-1}$ h^{-1}) with an increase of 2 °C (from 9 to 11 °C) suggesting that respiration rates for Mediterranean cold-water corals subjected to 13 °C would be expected to be well above those found for North Atlantic specimen. The temperature coefficient of respiration (Q_{10}) of Mediterranean *L. pertusa* is lower than that of North Atlantic *L. pertusa* (on average of 4.0 and 7.2, respectively; SI 1 and Dodds et al., 2007). A lower Q_{10} might be indicative of acclimation (Barnes, 2001), and the lower Q_{10} for a temperature of up to 16.7 °C could mean that cold-water corals, due to their adaptation to the higher Mediterranean temperature, might be less sensitive to temperature changes than their North Atlantic congeners.

This is the first study to measure the respiration rates of *M. oculata* and, consequently, no data for comparison are available. Due to the lack of data from other regions and temperature ranges, it remains unknown, whether *M. oculata* is better adapted to the relatively warm temperatures experienced in Mediterranean Sea deep water habitats. However, respiration not only depends on temperature, but also on other parameters, e.g. salinity (Ferrier-Pagès et al., 1999), food availability (Naumann et al., 2011) and intrinsic factors regulating metabolism (Hochachka and Somero, 2002). *M. oculata* is more commonly found in the Mediterranean than *L. pertusa* (Freiwald et al., 2009;

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Gori et al., 2013), which suggests that it is better adapted to environmental factors prevailing in that region. Respiration rate normalized by the skeletal dry weight was 2.7 times higher in *M. oculata* than in *L. pertusa,* and with higher respiration, more energy would be required to sustain coral metabolism. However, respiration is a surface dependent process (Barnes, 2001) and skeletal weight might thus not be a good biomass estimator to normalize metabolic processes. Surface area, tissue biomass or number of polyp are likely more suitable units to relate metabolic processes or prey capture. The ratio of skeletal area versus polyp number is approximately 3 times higher in *L. pertusa* than in *M. oculata* (373 vs 126 mm^2 $polyp^{-1}$) (Maier et al., 2011). Using this ratio and the ratio of polyp number to skeletal weight (Table 1) reveals that respiration normalized to surface is similar in *L. pertusa* and *M. oculata* (0.022 and 0.024 µmol O_2 cm^{-2} h^{-1}, respectively).

Since the food uptake plays a significant role for both respiration and calcification (Naumann et al., 2011), the similar respiration rate for the two species does not allow to draw any conclusion as to whether both species would be similarly well acclimatized to high Mediterranean temperatures. *L. pertusa* has bigger, but less numerous, polyps than *M. oculata*, which might indicate that the efficiency of prey capture differs in the two species, depending on the amount and size of food available. Food capture rates were not measured in the present study, but Tsounis et al. (2010) reported total carbon uptake rates of 3731 and 1072 µg C $polyp^{-1}$ h^{-1}, respectively in *L. pertusa* and *M. oculata* from the Mediterranean Sea (Tsounis et al., 2010). This translates to a carbon uptake of 83.4 µmol C cm^{-2} h^{-1} and 70.9 µmol C cm^{-2} h^{-1} (Maier et al., 2011 and Table 1). Therefore, both species have a similar prey capture efficiency despite the difference of polyp size, which is possibly compensated by the higher number of polyps per unit surface area or skeletal weight in *M. oculata*. It can therefore be inferred that the two species ingested a similar amount of C in our experiment. It should be pointed out that calcification rates normalized to surface area were also similar in the two species (0.010 and 0.008 µmol $CaCO_3$ cm^{-2} h^{-1}) for *L. pertusa* and *M. oculata*, respectively; Maier et al., 2013). There is a relative uniformity of the two species with the overall

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lack of response to pCO_2, as well as the similar rates of carbon uptake, respiration, calcification and the reported increase over time of respiration rates independent of pCO_2. This could indicate that *M. oculata* and *L. pertusa* will exhibit a similar response to future global environmental change. However, more studies are needed to confirm this hypothesis.

3.5 Perspective on the response of cold-water corals to global environmental change

In the range of pCO_2 studied so far, up to 1215 µatm, no significant change in respiration was found as a function of increasing pCO_2. However, to better predict future responses of organisms to global change it is critical to identify potential interactive effects between ocean acidification and other parameters such as temperature and food availability. Considering all published information, a potential tipping point for calcification of the two cold-water species would be above a pCO_2 of 1000 µatm and at an Ω_a below 1 (Maier et al., 2009, 2012, 2013; Thresher et al., 2011; Form and Riebesell, 2012; McCulloch et al., 2012 #3512) and the same might be true for the respiration response as indicated in the present study. For calcification rates of *L. pertusa*, there is an indirect evidence from short-term closed system incubations (Maier et al., 2009) that this tipping point would be well above 1000 ppm and at an Ω_a below 0.9 (Table 3; Maier et al., 2009).

This study provides the first evidence, that respiration rates of cold-water corals are not affected by elevated pCO_2 and that the ability of our two target species to maintain rates of calcification at high pCO_2 was not via compensatory responses in metabolic losses. This means that for the maintenance of high calcification rates over a large range of pCO_2 of up to 1000 ppm, there is no evidence for a direct energy allocation from food uptake to calcification to compensate for higher energy required to maintain calcification constant despite a decrease in pH. However, it is possible that as yet unidentified changes in metabolic pathways enable a more efficient supply of necessary energy for pH upregulation to maintain constant calcification rates at increasing

pCO_2. It is also possible that cold-water corals use lipid reserves, which would be reflected in a lower respiratory quotient. However, this would mean, that respiration would not be sustainable over a longer time scale as lipid reserves would get exhausted and would not be replenished due to the higher energy allocated to calcification. Therefore, future studies are needed to investigate in more detail the mechanisms that allow cold-water corals to cope with high pCO_2 levels. For zooxanthellate corals, molecular techniques looking at gene expression revealed that ocean acidification strongly suppresses metabolism and enhanced extracellular organic matrix synthesis and had complex effects on genes involved in calcification (Moya et al., 2012; Kaniewska et al., 2012). The response of other parameters important for coral functioning, e.g. reproduction and resilience to other environmental stressors (food reduction, temperature rise, predation etc.) also needs attention to better predict whether and how cold-water corals will be able to cope with global environmental changes.

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Table 1. Number of samples (N), number of polyps per coral fragment (NP), skeletal dry weight (SDW), and rates of respiration (R) and calcification (G, Maier et al., 2013) of coral fragments of *L. pertusa* (LP) and *M. oculata* (MO). Values of R and G of periods T_1 to T_4 were pooled.

pCO$_2$ treatment	Coral species	N	N polyps mean	S.D.	SDW [g] mean	S.D.	R [µmol g^{-1} h^{-1}] mean	S.D.	G [µmol g^{-1} h^{-1}] mean	S.D.
A	LP	5	9.2	4.8	5.7	4.2	0.146	0.073	0.082	0.076
B	LP	4	11.0	5.0	4.6	2.8	0.216	0.092	0.066	0.068
C	LP	4	14.3	5.0	5.4	1.9	0.117	0.030	0.053	0.046
D	LP	4	12.5	5.6	7.6	5.8	0.162	0.096	0.081	0.050
mean	LP	17	11.6	5.0	5.8	3.8	0.160	0.078	0.071	0.057
A	MO	3	26.7	8.4	2.6	1.9	0.193	0.045	0.117	0.043
B	MO	6	29.3	7.5	2.0	1.6	0.483	0.453	0.166	0.098
C	MO	3	29.3	10.3	1.8	0.8	0.450	0.365	0.113	0.047
D	MO	4	29.5	11.3	1.5	1.0	0.577	0.711	0.169	0.080
mean	MO	16	28.9	8.3	2.0	1.3	0.446	0.453	0.148	0.076

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Table 2. Parameters of the carbonate chemistry at the beginning of the incubations. Total alkalinity (A_T) and dissolved inorganic carbon (C_T) were measured while pH on total scale (pH_T), partial pressure of CO_2 (pCO_2) and the aragonite saturation state (Ω_a) were calculated. T is the period at which the incubations were performed (at approximately monthly intervals). T_{1-4} displays the pooled data for T_1 to T_4.

T	pCO_2 treatment	N	**A_T [µmol kg^{-1}]**		**C_T [µmol kg^{-1}]**		pH_T		pCO_2 [µatm]		Ω_a	
			mean	**S.D.**	**mean**	**S.D.**	mean	S.D.	mean	S.D.	mean	S.D.
1	A	3	**2565**	**1.5**	**2297**	**6.6**	8.10	0.01	380	11.0	2.90	0.06
2	A		n/a		n/a							
3	A	3	**2548**	**1.6**	**2261**	**3.0**	8.14	0.01	342	6.1	3.08	0.04
4	A	3	**2552**	**7.7**	**2255**	**3.2**	8.15	0.02	327	14.4	3.18	0.11
T_1–T_4	A	3	**2555**	**6.5**	**2271**	**17.5**	8.13	0.02	350	20.3	3.05	0.10
1	B	3	**2540**	**0.4**	**2341**	**12.5**	7.97	0.03	530	34.6	2.24	0.11
2	B	3	**2544**	**1.3**	**2341**	**4.6**	7.98	0.01	520	13.5	2.28	0.04
3	B	3	**2549**	**3.3**	**2331**	**1.1**	8.01	0.00	481	4.8	2.42	0.02
4	B	3	**2555**	**7.1**	**2327**	**1.2**	8.03	0.01	459	16.6	2.52	0.08
T_1–T_4	B	4	**2547**	**4.8**	**2335**	**6.3**	8.00	0.02	497	27.5	2.37	0.10
1	C	3	**2549**	**1.5**	**2440**	**13.0**	7.76	0.03	910	75.4	1.48	0.11
2	C	3	**2552**	**4.1**	**2438**	**9.8**	7.78	0.01	879	33.8	1.52	0.04
3	C	3	**2536**	**1.3**	**2408**	**5.0**	7.81	0.01	798	21.6	1.63	0.03
4	C	3	**2564**	**2.8**	**2415**	**11.2**	7.86	0.02	716	38.2	1.81	0.07
T_1–T_4	C	4	**2550**	**7.9**	**2425**	**13.6**	7.80	0.03	826	68.9	1.61	0.11
1	D	3	**2553**	**1.5**	**2482**	**2.2**	7.67	0.01	1164	28.1	1.20	0.03
2	D	3	**2554**	**7.5**	**2482**	**7.9**	7.66	0.02	1169	58.9	1.20	0.05
3	D	3	**2538**	**5.6**	**2455**	**3.6**	7.70	0.01	1075	22.0	1.27	0.03
4	D	3	**2554**	**3.8**	**2463**	**6.3**	7.72	0.02	1025	50.2	1.34	0.06
T_1–T_4	D	4	**2549**	**6.0**	**2470**	**11.6**	7.69	0.02	1108	58.3	1.25	0.05

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Table 3. Estimated parameters of the carbonate chemistry at the end of the incubations of coral fragments of *L. pertusa* (LP) and *M. oculata* (MO). Mean values $A_{T,2.5h}$ and $C_{T,2.5h}$ were used to calculate the other parameters of carbonate chemistry ($pH_{T,2.5h}$, $pCO_{2,2.5h}$ and $\Omega_{a,2.5h}$). The difference between the end and the beginning of the incubations is also shown (Δ). *T* is the period at which the incubations were performed (at ca. monthly intervals). T_{1-4} displays the pooled data for T_1 to T_4.

T	pCO_2 treatment	Coral	*N*	A_T2.5 h [µmol kg^{-1}] mean	S.D.	Δ	C_T2.5 h [µmol kg^{-1}] mean	S.D.	Δ	pH_T2.5 h	Δ	$pCO_2$2.5 h [µatm]	Δ	Ω_a2.5 h	Δ
1	A	LP	5	2560	1.37	−4.63	2303	8.07	5.76	8.08	−0.02	398	18	2.79	−0.10
2	A	LP	5	*n/a*			*n/a*								
3	A	LP	5	2541	5.46	−6.89	2269	9.15	8.61	8.11	−0.03	365	24	2.93	−0.15
4	A	LP	5	2546	2.15	−6.57	2259	7.76	4.77	8.14	−0.02	342	15	3.07	−0.11
T_{1-4}	A	LP	**3**	**2549**	**7.43**	**−6.03**	**2277**	**17.06**	**5.77**	**8.11**	**−0.02**	**368**	**19**	**2.93**	**−0.12**
1	B	LP	4	2535	2.73	−4.92	2348	3.99	6.82	7.95	−0.02	563	33	2.13	−0.11
2	B	LP	4	2539	3.01	−5.22	2348	4.07	6.26	7.96	−0.02	552	33	2.17	−0.11
3	B	LP	4	2543	2.75	−5.85	2344	11.63	13.40	7.97	−0.04	530	49	2.25	−0.18
4	B	LP	4	2551	3.31	−4.39	2337	7.08	9.90	8.00	−0.03	492	33	2.39	−0.13
T_{1-4}	B	LP	**4**	**2542**	**4.80**	**−5.09**	**2344**	**3.76**	**9.10**	**7.97**	**−0.03**	**534**	**37**	**2.23**	**−0.13**
1	C	LP	4	2543	2.96	−5.27	2442	3.45	2.50	7.74	−0.02	952	43	1.41	−0.07
2	C	LP	4	2545	6.86	−7.26	2443	6.33	5.14	7.75	−0.03	947	68	1.42	−0.10
3	C	LP	4	2525	10.07	−10.87	2412	7.62	4.74	7.78	−0.04	872	74	1.50	−0.13
4	C	LP	4	2562	1.76	−2.16	2424	3.47	8.61	7.84	−0.03	762	46	1.72	−0.09
T_{1-4}	C	LP	**4**	**2544**	**9.61**	**−6.39**	**2430**	**12.14**	**5.25**	**7.78**	**−0.03**	**883**	**58**	**1.51**	**−0.10**
1	D	LP	4	2551	1.81	−2.64	2489	2.89	6.97	7.64	−0.03	1245	81	1.13	−0.07
2	D	LP	4	2547	5.20	−6.72	2491	4.22	8.58	7.62	−0.04	1296	127	1.09	−0.11
3	D	LP	4	2527	6.37	−10.75	2463	13.35	8.19	7.64	−0.05	1214	140	1.14	−0.14
4	D	LP	4	2544	3.82	−9.56	2465	5.95	1.86	7.69	−0.03	1104	79	1.25	−0.09
T_{1-4}	D	LP	**4**	**2542**	**7.66**	**−7.42**	**2477**	**12.93**	**6.40**	**7.65**	**−0.04**	**1215**	**107**	**1.15**	**−0.10**
1	A	MO	3	2561	2.16	−3.43	2303	6.59	6.37	8.08	−0.02	397	17	2.80	−0.09
2	A	MO	3	*n/a*			*n/a*								
3	A	MO	3	2541	2.96	−7.74	2266	1.89	4.72	8.12	−0.02	360	19	2.95	−0.12
4	A	MO	3	2546	3.44	−6.46	2256	1.37	1.17	8.14	−0.01	337	10	3.10	−0.08
T_{1-4}	A	MO	**3**	**2549**	**8.13**	**−5.88**	**2275**	**19.00**	**4.08**	**8.11**	**−0.02**	**365**	**15**	**2.95**	**−0.10**
1	B	MO	6	2537	1.69	−3.16	2346	3.00	4.70	7.96	−0.02	551	21	2.17	−0.07
2	B	MO	6	2540	2.57	−4.40	2347	4.59	5.50	7.96	−0.02	547	27	2.19	−0.09
3	B	MO	6	2538	10.38	−10.82	2333	5.30	2.44	7.99	−0.02	511	30	2.30	−0.12
4	B	MO	6	2549	3.52	−5.77	2331	3.32	4.59	8.01	−0.02	481	22	2.42	−0.10
T_{1-4}	B	MO	**4**	**2541**	**4.14**	**−6.04**	**2339**	**7.11**	**4.31**	**7.98**	**−0.02**	**523**	**25**	**2.27**	**−0.10**
1	C	MO	3	2546	0.73	−2.66	2443	3.46	3.04	7.75	−0.01	942	32	1.43	−0.05
2	C	MO	3	2550	0.37	−2.21	2445	4.91	7.36	7.75	−0.02	931	52	1.45	−0.07
3	C	MO	3	2532	2.25	−4.21	2415	6.19	7.51	7.79	−0.03	853	56	1.53	−0.09
4	C	MO	3	2560	1.19	−4.50	2424	8.39	8.32	7.83	−0.03	770	55	1.70	−0.11
T_{1-4}	C	MO	**4**	**2547**	**7.97**	**−3.39**	**2432**	**12.21**	**6.56**	**7.78**	**−0.02**	**874**	**49**	**1.53**	**−0.08**
1	D	MO	4	2550	1.37	−2.72	2484	0.82	1.90	7.65	−0.02	1211	47	1.16	−0.04
2	D	MO	4	2552	2.05	−1.83	2487	4.53	4.82	7.65	−0.02	1220	51	1.15	−0.05
3	D	MO	4	2536	1.60	−1.23	2460	7.56	5.15	7.68	−0.02	1122	48	1.22	−0.05
4	D	MO	4	2548	1.99	−5.29	2465	7.00	2.73	7.70	−0.02	1077	51	1.28	−0.06
T_{1-4}	D	MO	**4**	**2547**	**5.23**	**−2.77**	**2474**	**11.27**	**3.65**	**7.67**	**−0.02**	**1158**	**49**	**1.20**	**−0.05**

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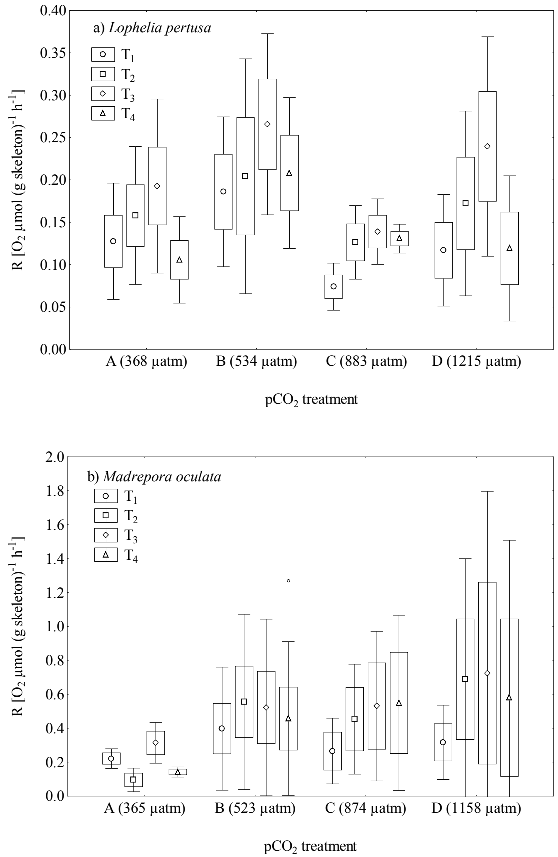

Fig. 1. Respiration rates of **(a)** *L. pertusa* (LP) and **(b)** *M. oculata* (MO) for repeated measurements (T_1–T_4) at 4 pCO_2 treatments (A–D; see Tables 2 and 3). Values for pCO_2 treatments A–D (parentheses) are mean at end of incubation (Table 3).

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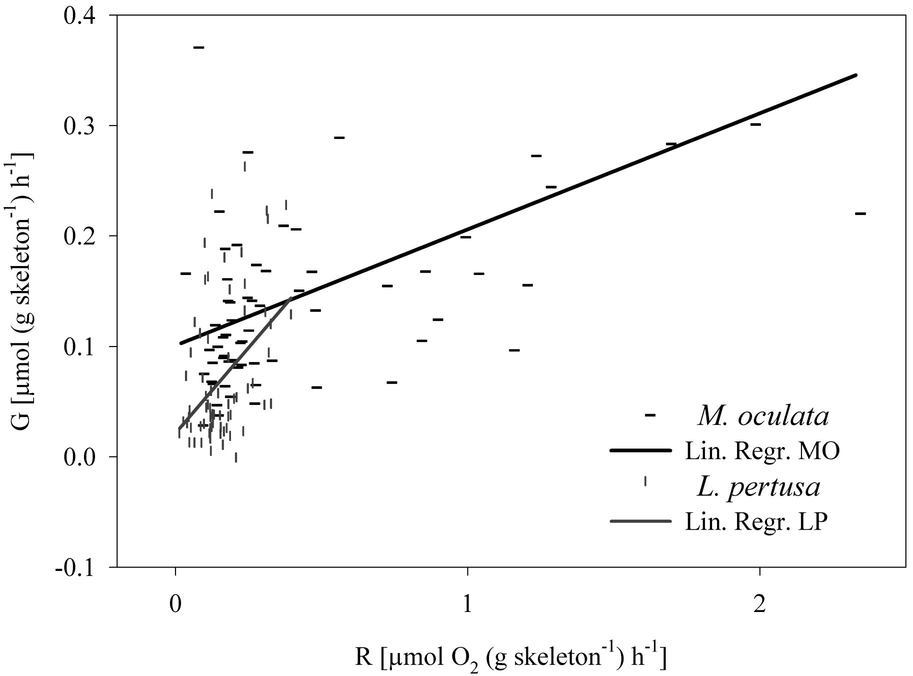

Fig. 2. Rate of calcification (G, from Maier et al., 2013) as a function of respiration rate (R) for *L. pertusa* (LP) and *M. oculata* (MO). The equations of the regression lines are: $G_{LP} = 0.0217 + 0.3091 \times R$; ($r = 0.4182$, $p = 0.0004$, $n = 68$), and $G_{MO} = 0.1009 + 0.1051 \times R$; ($r = 0.4877$, $p = 0.00004$; $n = 64$).

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