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Food availability and pCO_2 impacts on planulation, juvenile survival, and calcification of the azooxanthellate scleractinian coral, *Balanophyllia elegans*

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Abstract

Ocean acidification, the assimilation of atmospheric CO_2 by the oceans that decreases the pH and $CaCO_3$ saturation state (Ω) of seawater, is projected to have severe consequences for calcifying organisms. Strong evidence suggests that tropical reef-building corals containing algal symbionts (zooxanthellae) will experience dramatic declines in calcification over the next century. The responses of azooxanthellate corals to ocean acidification are less well understood, and because they cannot obtain extra photosynthetic energy from symbionts, they provide a system for studying the direct effects of acidification on the energy available for calcification. The orange cup coral *Balanophyllia elegans* is a solitary, azooxanthellate scleractinian species common on the California coast where it thrives in the low pH waters of an upwelling regime. During an 8 month study, we addressed the effects of three pCO_2 treatments (410, 770, and 1230 µatm) and two feeding frequencies (High Food and Low Food) on adult *Balanophyllia elegans* planulation (larval release) rates, and on the survival, growth, and calcification of their juvenile offspring. Planulation rates were affected by food level but not pCO_2, while juvenile survival was highest under 410 µatm and High Food conditions. Our results suggest that feeding rate has a greater impact on calcification of *B. elegans* than pCO_2. Net calcification was positive even at 1230 µatm (∼ 3 times current atmospheric pCO_2), although the increase from 410 to 1230 µatm reduced overall calcification by ∼ 25–45 %, and reduced skeletal density by ∼ 35–45 %. Higher pCO_2 also altered aragonite crystal morphology significantly. We discuss how feeding frequency affects azooxanthellate coral calcification, and how *B. elegans* may respond to ocean acidification in coastal upwelling waters.

1 Introduction

As aqueous CO_2 concentrations continue to rise over the next century, pH of the surface oceans will decline in a process known as ocean acidification (Caldeira and Wicket, 2003, 2005; Sabine et al., 2004). Growing evidence suggests that calcifying organisms, including reef-building scleractinian corals, will be heavily impacted by a decrease in pH from 8.1 to 7.8 (Orr et al., 2005; Hoegh-Guldberg et al., 2007; Fabry et al., 2008; Doney et al., 2009). Both laboratory and field investigations suggest that calcification rates of many tropical coral species decrease as the pH and aragonite saturation state (Ω_{arag}, a measure of ease of $CaCO_3$ formation) decrease (Fine and Tchernov, 2007; Anthony et al., 2008; Jokiel et al., 2008; Krief et al., 2010). A majority of tropical corals have algal symbionts (zooxanthellae) whose photosynthesis contributes to the host's nutrition and increases calcification rates. Most cold-water corals lack zooxanthellae and their responses to ocean acidification are poorly known, but as the saturation state of seawater decreases, they may face similar declines in calcification rates and changes in geographical distributions (Turley et al., 2007; Andersson et al., 2008; Fabry et al., 2009; Maier et al., 2009). Some widespread cold-water species have a range of sensitivities in CO_2 manipulation experiments (Form and Riebesell, 2012; Maier et al., 2011), and some deep-water species can maintain positive net calcification at or below the carbonate saturation horizon, the depth below which $\Omega < 1$, and $CaCO_3$ dissolves readily (Form and Riebesell, 2012; McCulloch et al., 2012). Because azooxanthellate corals lack symbionts and rely solely on heterotrophy for energy, they can be used to shed light on the role of nutrition and energetic resources in controlling calcification.

Balanophyllia elegans is a solitary, azooxanthellate scleractinian coral common in shallow coastal waters around Monterey Bay, California, where it often thrives in cool, upwelling waters. Ocean acidification is predicted to have especially severe impacts in upwelling regions where low saturation waters occur naturally (Feely et al., 2008; Fabry et al., 2009; Hauri et al., 2009). The western North American coastline experiences

strong seasonal upwelling which brings CO_2 rich, low pH water from intermediate depths to the surface, and coastal organisms may be exposed to low and even undersaturated waters for several months of the year (Feely et al., 2008; Hauri et al., 2009). With anticipated increases in surface ocean pCO_2 and shoaling of the carbonate saturation horizon, calcifying organisms living in these coastal waters are likely to experience seasonal increases in the magnitude, duration, and extent of low pH waters (Feely et al., 2008; Hauri et al., 2009). Understanding the impacts of ocean acidification on calcification and on the interplay between calcification and nutritional status is critically important in upwelling regions where many organisms may already be living at their lower thresholds for pH tolerance (Barton et al., 2012) and therefore may be particularly vulnerable to ocean acidification. Several recent studies have described likely negative consequences of future ocean acidification events for several key species in the CA coastal upwelling zone (Gaylord et al., 2011; Barton et al., 2012; Hettinger et al., 2012; Timmins-Schiffman et al., 2012).

Responses of calcifying corals to ocean acidification depend on species-specific energy allocations for calcification. Corals expend energy to remove protons from their calcifying compartments, the extracellular medium between the coral's basal layer and the skeleton below (Al Horani et al., 2003; Allemand et al., 2004; Cohen and McConnaughey, 2003). Removing protons facilitates calcification by increasing pH and saturation state in the calcifying fluid. In zooxanthellate tropical corals, this proton pumping raises the saturation state in the calcifying fluid by up to 5–10 times ambient (Al Horani et al., 2003; Cohen and Holcomb, 2009), and recent evidence suggests that deep-water azooxanthellate corals can create even steeper gradients (McCulloch et al., 2012). Lower saturation states in the external seawater require corals to expend more energy to remove excess protons (Ries, 2011; McCulloch et al., 2012), potentially at the cost of other critical life processes (Wood et al., 2008). A flexible energy budget would enable corals to vary the energy expended to raise the pH and saturation states of the calcifying fluids, and perhaps enable them to maintain calcification despite acidification. Some research indicates that zooxanthellate coral calcification

is energetically costly and that a coral's energy budget is fixed under normal circumstances (Cohen and Holcomb, 2009). It has also been shown that, when provided with excess nutrients, some species can maintain 100 % of their calcification rates despite near under-saturation conditions (Langdon and Atkinson, 2005; Holcomb et al., 2010, Ries et al., 2009; Cohen et al., 2009). This may be due to the nutrient surplus stimulating increased photosynthesis by zooxanthellae, which gives the coral more energy available for calcification. Because azooxanthellate corals cannot obtain extra photosynthetic energy from symbionts, they provide a system for studying the direct effects of acidification and energy availability on calcification.

We assessed the effects of pCO_2 and food availability on planulation rates of adult *B. elegans*. We also explored the effects of the same treatments on survival, growth, and calcification of juvenile *B. elegans* during an 8 month incubation experiment. The duration was based on recommendations of Doney et al. (2009) and Widdicombe et al. (2010) for long-term manipulation experiments. Recent evidence suggests that long-term exposure more accurately predicts responses to acidification than short-term experiments (Form and Riebesell, 2012). We address how azooxanthellate corals respond to lower ocean pH, and the role of nutrition level on their calcification and survival in low saturation upwelling regimes.

2 Materials and methods

2.1 Organisms

The orange cup coral *Balanophyllia elegans* Verrill, 1964 is a solitary (single polyp) species living on rocky substrates from the low intertidal to ~300 m depth along the west coast of North America, from southern Alaska to Baja California. It is a gonochoric (has separate sexes) species with a sex ratio of approximately 1 : 1. Fertilization is internal and zygotes are brooded for an average of 15 months in the mother's coelenteron until they develop into mature planula larvae (Fadlallah and Pearse, 1982). On release

(planulation) the larvae crawl down the mother's column and settle and metamorphose into juvenile corals, usually within a few centimeters of the mother (Gerrodette, 1981). *B. elegans* is an azooxanthellate species (lacking photosynthetic symbiotic algae) that depends on heterotrophic feeding on zooplankton or dissolved organic molecules for all of its energy and nutrients. It grows slowly and can survive for months without feeding.

2.2 Experimental design

The experiment used a full factorial design with two factors: pCO_2 (3 levels) and feeding frequency (2 levels). The seawater pCO_2 levels were based on present day atmospheric concentrations (380 ppm, $pH_T = 8.0$) and two IPCC emissions scenarios projected for the year 2100, the A1B "business as usual" (750 ppm, $pH_T = 7.8$), and a high emissions scenario (A1F1) approximately 3 times current atmospheric pCO_2 (1200 ppm, $pH_T = 7.6$) (Solomon et al., 2007). Actual pCO_2 in the seawater differed slightly from these atmospheric targets, and were 410 µatm ($pH_T = 8.0$), 770 µatm ($pH_T = 7.8$), and 1230 µatm ($pH_T = 7.6$). High Food corals were fed newly hatched brineshrimp (*Artemia*) nauplii larvae every 3 d to represent a plentiful food supply, while Low Food corals were fed once every 3 weeks, corresponding to a minimal food supply.

Each experimental unit was a 4 L glass jar with an airtight screw cap containing an inlet for CO_2-enriched air, an outlet for excess air and a sampling port (a stoppered rubber valve) for taking pH readings and water samples. The sampling port provided quick access to the water in the jars without having to break the airtight seal of the lid. An oscillating paddle inserted through a double-layered rubber membrane provided continuous water movement by mechanical stirring. There were 2 replicate jars per treatment, with 16–17 juvenile corals assigned randomly to each jar, for a total of 33 juveniles per treatment.

Temperature was maintained close to ocean ambient by placing the jars in a water table with running seawater. A daily light regime that alternated 12 h of light (overhead fluorescent bulbs) with 12 h of darkness was maintained throughout the experiment.

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Corals were fed through the sampling port in the jar lid using a 50 mL syringe with concentrated *Artemia nauplii* in filtered seawater. The brineshrimp remained in the jars for several hours to ensure the corals had eaten their fill. Every jar, lid, and paddle were cleaned once every 3 d (after feeding was finished). Corals were removed for approximately 30 min and placed in small glass dishes with filtered seawater equilibrated to their experimental pCO_2. The jars and lids were then scrubbed and rinsed, and new filtered, equilibrated seawater was siphoned into the jars to prevent air exchange.

Our first experiment aimed to determine whether pCO_2 and feeding treatment affected planulation rates. Ten adult corals of equal size (sex unknown) were assigned to each treatment (i.e. 5 adults per jar) for the first 3 months of the experiment (October 2011 to January 2012). The 60 adults had previously been held in the same tank at the UCSC marine laboratory for two years and, because they brood larvae for ~ 15 months (Fadlallah and Pearse, 1982), all females should have been equally likely to produce larvae. Every 3 d we counted numbers of larvae produced and removed them from the experimental jars.

Juveniles used in the second experiment came from a stock of adult *B. elegans* maintained for several generations in the laboratory. Approximately 85 adults were placed in a tank with flowing ambient (pH ~ 7.9–8.0) seawater during the peak planulation season (October to December 2011). Emerging larvae were collected weekly, placed in glass dishes in a separate tank with flowing seawater, and allowed to settle on polypropylene plastic sheets pre-conditioned with a living biofilm and crustose coralline algae (Fig. 1). After settlement, small pieces of plastic, each holding one larva, were cut and glued to 5 × 5 cm ceramic tiles (approximately 5 per tile), and immediately exposed to their randomly assigned experimental treatments. Since skeletal formation does not begin for at least 2 weeks after settlement, there was no calcification before exposure to experimental conditions. All juvenile corals started with approximately equal weights and volumes, and initial skeletal weights of 0 g (i.e. no calcium carbonate). This experiment began in late November 2011 and ran for approximately 8 months until July 2012. Survival was monitored by recording deaths as they occurred.

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2.3 Seawater carbonate chemistry

Certified cylinders of CO_2-air mixtures were obtained from PraxAir (CO_2 at 380, 750, and 1200 ppmV). Seawater was filtered to 0.2 µm and collected in 20 L carboys, and bubbled with the appropriate gas mixture in each carboy for at least 4 d to equilibrate pCO_2 and stabilize pH before siphoning into the experimental jars. Jars were sealed with the appropriate pCO_2 gas mixture flowing continuously into the headspace.

pH was measured daily in each jar with an Oakton WD-35613 hand-held meter, and 40 mL water samples were taken from each jar every 3 d for dissolved inorganic carbon (DIC) and total alkalinity (TA) analysis. DIC and TA were measured using a CM5011 Carbon Coulometer (UIC, Inc.) and an automated, open-cell potentiometric titration procedure, respectively. Certified Reference Materials (batch 118) from the Andrew Dickson lab at UC San Diego were used to calibrate each instrument. DIC and TA were used to calculate aragonite saturation state and pH (Ω_{arag}) via CO_2 sys (Pierrot et al., 2006). pH is reported in total scale (pH_T).

2.4 Skeletal growth

At the end of the experiment, each living coral was imaged under a microscope at 40 ×, and then dried in a 50 °C oven for 48 h. All tissue was removed from skeletons in a 1 : 1 solution of 30 % H_2O_2 buffered with 0.1 M NaOH. As the juvenile corals are roughly elliptic cylinders in shape, linear measurements of height and diameter (both the major and minor axes) were taken with vernier calipers (+0.1 mm) and the volume of each coral calculated. Weight (+0.01 mg) was determined on an analytical balance and overall density of the entire skeleton calculated by dividing weight by volume. Five randomly selected skeletons from each of four treatments (High Food and Low Food with pCO_2 of 410 and 1230 µatm, excluding 770 µatm) were imaged with 10k × magnification on a Hitachi TM1000 Tabletop SEM scanning electron microscope at the UCSC MACS facility at NASA/Ames. The same region of each skeleton (the septa) was used for measurements. The length and width of individual crystals were measured using

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Imaging Processing and Analysis in Java (Image J, US National Institute of Health) from the SEM images.

2.5 Statistics

The software R was used for all statistical analyses (R Core Team 2013). Planulation, volume, weight, density and crystal structure were analyzed using 2-factor ANOVAs with pCO_2 and feeding frequency as fixed factors. For planulation, an additive model was applied because interaction terms could not be assessed with a single count per treatment. All other ANOVAs used a full model to investigate both the main effects and the interaction between pCO_2 and feeding frequency. Coral volumes and weights were log-transformed to satisfy normality assumptions. For crystal structure analyses, the individual corals from which crystals were sampled were treated as random factors nested within the two main effects. Where statistical significance is indicated, Tukey's HSD tests were used to compare treatments. Juvenile survival was assessed by a logistic regression against the two categorical predictor variables, pCO_2 and feeding frequency. The interaction term was not significant (Tukey's test for additivity; $p = 0.37$) and was therefore excluded from the logistic regression model. All results are expressed as mean ± standard error of the mean (s.e.m.).

3 Results

3.1 Water chemistry

The average pH (total scale, pH_T) of each treatment was 8.02 ± 0.01 (410 ± 20 µatm), 7.78 ± 0.006 (770 ± 12 µatm), and 7.59 ± 0.005 (1230 ± 10 µatm). The saturation state (Ω_{arag}) of each group, calculated from measurements of DIC and TA from discrete water samples, was 2.1 ± 0.05 (pH_T 8.0), 1.3 ± 0.1 (pH_T 7.8), and 0.9 ± 0.04 (pH_T 7.6). Temperature in the jars varied with the temperature of the external seawater, but averaged

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13.6 °C (±1.5) over the duration of the experiment. For a full data report, including a summary of water chemistry, see Supplement.

3.2 Planulation and juvenile survival

B. elegans planulae were collected as they emerged from adults and the total number per treatment were counted and compared. Adult corals released approximately 120 % more planulae in the High Food treatments than in the Low Food treatments ($p = 0.06$), but pCO_2 had no effect on numbers of larvae released ($p = 0.62$, Fig. 2a).

Approximately 5–15 % more juvenile corals survived in the High Food than in the Low Food treatment ($p = 0.04$, Fig. 1b). In both the Low Food and High Food groups, 10–15 % more juveniles died in the pH 7.6 treatment than in the control treatment ($p = 0.01$, Fig. 2b); mortality in the pH 7.8 treatment was intermediate, but did not differ significantly from the control ($p = 0.34$).

3.3 Impacts on growth calcification, density, and crystal structure

Juvenile coral skeletons from the High Food treatments had significantly greater volumes (6–7 times; $p < 0.001$) and heavier weights (4–5 times; $p < 0.001$) than the Low Food treatments (Fig. 3a, b). pH had no significant effects on volume ($p = 0.29$), but, for the Low Food regime, the pH_T 8.0 corals weighed significantly more (by ~ 45 %) than the pH_T 7.8 ($p < 0.001$) and pH_T 7.6 corals ($p = 0.001$). In the High Food regime, pH_T 8.0 corals also weighed more than the lower pH treatments, but the difference was smaller (~ 25 %) and not statistically significant ($p = 0.35$, $p = 0.06$).

The Low Food corals were approximately 35–40 % more dense than the High Food corals for both the pH_T 7.8 ($p = 0.008$) and pH_T 7.6 treatments ($p = 0.04$, Fig. 3c), but there was no significant difference in density between the feeding treatments at pH_T 8.0 ($p = 0.11$). At pH_T below 8.0, skeletal density declined by approximately 35–45 % in both the High Food ($p = 0.03$, $p = 0.001$) and Low Food ($p = 0.01$, $p = 0.04$) treatments.

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Aragonite crystals were significantly longer (by ~ 18 %) at pH_T 8.0 than at pH_T 7.6 ($p < 0.001$), and at pH_T 7.6, crystals were ~ 15 % longer in the High Food than the Low Food ($p < 0.001$, Fig. 4a). Crystal width did not significantly differ with pH ($p = 0.93$) or feeding group ($p = 0.41$, Fig. 4b).

4 Discussion

Responses of calcifying organisms to ocean acidification are likely to vary at different stages of their life cycles, and several studies provide evidence that early (larval and juvenile) stages of many marine taxa in upwelling regions are particularly sensitive to acidification (Kroeker et al., 2010, 2013; Hettinger et al., 2012). Hettinger et al. (2012) also showed that adverse effects of stressors experienced during larval stages can "carry-over" to the next life stage and be compounded by the time adulthood is reached. In the present study, high food levels increased the numbers of brooded planula larvae released by 50–200 %. This suggests that females may delay release of larvae until feeding conditions are optimal, either for completing maturation of the larvae conceived many months earlier, or for sustaining the larvae after release. High pCO_2 had no effect on either the timing or numbers of larvae released, but the 15 months of brooding before release means that this experiment provides no information about whether prolonged exposure to high pCO_2 negatively impacts such processes as gametogenesis, fertilization, cleavage or early larval development that have been seen in other organisms (Kurihara, 2008; Kroeker et al., 2010, 2013; Nakamura et al., 2011). It is possible that prolonged exposure to low pH may divert energetic resources away from reproduction, but this experiment provides no information about possible impacts of prolonged low pH or low food on adult nutrition or reproduction.

While pCO_2 did not affect numbers of planulae released, subsequent survival of the juvenile corals was substantially reduced at the highest pCO_2 level (1230 µatm, $pH_T = 7.6$) where average survival was about 10 % lower (across both food levels) than in the other two pCO_2 treatments (410 and 770 µatm). Within the 1230 µatm CO_2

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treatments, survival was up to 15 % higher in the High Food than the Low Food treatment. This pattern suggests that, if atmospheric pCO_2 increases beyond the projected 750 ppm over the next century, the numbers of corals surviving to the adult stage might decline, even if food is plentiful.

In the juvenile incubation experiment, food availability was the major factor controlling the growth (and final size) of *B. elegans*; pCO_2 had no significant effects on final length or volume. At the end of the experiment, the High Food corals had up to 7 times greater volumes than the Low Food corals at every pCO_2 level. Although corals within a food level had similar sizes (length and volume) across all pCO_2 treatments, their skeletal weights, and hence bulk densities, declined significantly from 410 µatm to 1230 µatm pCO_2. This suggests that with increasing pCO_2, either the shapes of skeletal elements changed, or there was less secondary thickening of the initial skeleton. One possible mechanism is that energy available for calcification is allocated first to ensuring full skeletal extension, at the cost of a less heavily calcified skeleton.

Calcification rates in reef-building corals are commonly measured as the annual linear extension multiplied by the density, and expressed in $g\,cm^{-2}\,yr^{-1}$. Because *B. elegans* is a solitary species, its radial expansion must be considered in the calculation of calcification rates. Therefore, we expressed calcification as the change in the total skeletal weight measured over known intervals and normalized to $g\,yr^{-1}$. In this study, higher food led to both greater extension and greater calcification within every pCO_2, a trend that is consistent with more energy being available for allocation to skeletal formation. Although the linear dimensions of corals were unaffected by increased pCO_2, and well-fed corals had heavier skeletons within each pCO_2 level, the trend to less dense skeletons with increasing pCO_2 suggests that the structural integrity of the skeleton may decline and leave the coral more vulnerable to predation, bioerosion, and dislodgement (Hoegh-Guldberg et al., 2007).

However, the differences in bulk density due to high pCO_2 are small compared to those between the feeding levels, with the Low Food corals actually being denser than the High Food corals. While the Low Food corals did not grow as quickly or weigh

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as much as the High Food corals, their bulk density was higher. This response may be analogous to that of certain reef-building corals in which rapid linear extension dominates when conditions are favorable, while slower growing, denser skeletons are formed during less favorable conditions (Highsmith, 1979).

5 The aspect ratio (length divided by width) of aragonite crystals in coral skeletons has been used as an indirect proxy for saturation state of the seawater in a coral's calcifying compartment (Cohen and Holcomb, 2009; Holcomb et al., 2009). Longer, thinner crystals are associated with high saturation states while shorter, broader crystals are indicative of low saturation states (Cohen and McConnaughey, 2003). Cohen and Holcomb (2009) used abiogenic aragonites precipitated in seawater with known saturation
10 states to derive a formula in which crystal aspect ratio linearly approximates the saturation state of the calcifying fluid (Ω_{cf}) in a coral's calcifying compartment (Cohen and Holcomb, 2009):

$$\Omega_{cf} = 0.93\ (\pm 0.06) \times \text{crystal aspect ratio}\ + 0.20\ (\pm 0.89) \quad (1)$$

15 In our experiment, high $p > CO_2$ significantly reduced crystal length, with crystals being approximately 18 % longer in the 410 µatm than the 1230 µatm corals. While the crystal width did not vary between any of the treatments (feeding frequency or pCO_2), the crystal aspect ratio was higher for the ambient corals. Using Eq. (1) we calculate that Ω_{cf} was ~21 and 20 for High and Low Food 410 µatm corals, respectively, and ~17
20 and 16 for High and Low Food 1230 µatm corals (Fig. 4c). Even in well-fed corals at 1230 µatm, Ω_{cf} was lower than in corals grown at ambient pCO_2. At 1230 µatm, High Food significantly increased crystal length by about 15 % over those in Low Food corals resulting in a slight increase in both crystal aspect ratio and Ω_{cf}. This is consistent with the calcification results and may indicate that excess food enables corals to partially
25 counteract some of the negative impacts of low saturation state. The changes in crystal length and calculated Ω_{cf} indicate that these corals may not be able to expel enough protons under high pCO_2 conditions to calcify at rates similar to those of corals at ambient pCO_2, even when provided with plentiful high energy food.

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Combined, these lines of evidence suggest that *Balanophyllia elegans* are able to maintain moderate rates of calcification even during extreme acidification events, provided they have an adequate nutritional supply. *B. elegans* and other efficient grazers that do not depend on zooxanthellae may be able to increase their feeding rates to increase their energy reserves (provided prey is available). As seen in our experiment, even feeding once every three weeks was still sufficient to maintain positive growth at high pCO_2, albeit very slowly. We suggest that removing protons to increase the pH and saturation state of the calcifying compartment may be energetically costly and that as energetic demands for maintaining the saturation state of the calcifying fluid rise with increasing pCO_2, the total amount of $CaCO_3$ deposited will decline even as extension rates are maintained. This decrease in calcification at moderate to high pCO_2 was observed regardless of feeding amount, suggesting that even well-fed corals can not entirely overcome the stress of acidification.

Our observation that heterotrophic feeding rate has a greater impact on calcification than pH may explain the success of *B. elegans* and other calcifying organisms endemic to upwelling coastal waters, despite low saturation. During upwelling, when the pH is at its lowest, nutrient and plankton concentrations are also at their highest. Indeed, nutrient concentrations during the upwelling months can be up to 20 times the nutrient concentration during non-upwelling periods in Monterey Bay (Pennington and Chavez, 2000). This nutrient surplus drives phytoplankton (and subsequent zooplankton) production, and is therefore likely to increase the amount of food available to the corals. In fact, zooplankton concentrations during upwelling months can be up to 10 times the concentration during non-upwelling months, and often peak in the fall when planulation occurs (Marinovic et al., 2002). Thus, along the California coast when pH is at its lowest, food availability is at its highest and the corals may naturally be able to feed at higher rates. This may suggest that if acidification is decoupled from upwelling, *B. elegans* may be negatively impacted due to lower food concentrations. However, if food availability remains high, *B. elegans* may be able to compensate for the extra

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energy required for calcification at low saturation, even if calcification occurs at slightly lower rates than at modern pCO_2.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/10/7761/2013/ bgd-10-7761-2013-supplement.pdf.

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References

Al-Horani, F. A., Al-Moghrabi, S. M., and de Beer, D.: The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral, *Galaxea fascicularis*, Mar. Biol., 142, 419–426, 2003.

Allemand, D., Ferrier-Pagès, C., Paola Furla, P., Houlbrèque, F., Puverel, S., Reynaud, S., Tambutté, E., Tambutté, S., and Zoccola, D.: Biomineralisation in reef-building corals: from molecular mechanisms to environmental control, General Palaeontology, 3, 453–467, 2004.

Andersson, A. J., Mackenzie, F. T., and Bates, N. R.: Life on the margin: implications of ocean acidification on Mg-calcite, high latitude and cold-water marine calcifiers, Mar. Ecol.-Prog. Ser., 373, 265–273, 2008.

Anthony, K. R. N., Kline, D. I., Diaz-Pulido, D., Dove, S., and Hoegh-Guldberg, O.: Ocean acidification causes bleaching and productivity loss in coral reef builders, P. Natl. Acad. Sci. USA, 105, 17442–17446, 2008.

Atkinson, M. J., Carlson, B., Crow, G. L.: Coral growth in high- nutrient, low-pH seawater: a case study of corals cultured at the Waikiki Aquarium, Honolulu, Hawaii, Coral Reefs, 14, 215–223, 1995.

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10, 7761–7783, 2013

Barton, A., Hales, B., Waldbusser, G. G., Langdon, C., and Feely, R. A.: The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: implications for near-term ocean acidification effects, Limnol. Oceanogr., 57, 698–710, doi:10.4319/lo.2012.57.3.0698, 2012.
5 Caldeira, K. and Wickett, M. E.: Anthropogenic carbon and ocean pH, Nature, 425, p. 365, 2003.
Caldeira, K. and Wickett, M. E.: Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean, J. Geophys. Res., 110, C09S04, doi:10.1029/2004JC002671, 2005.
10 Cohen, A. L. and Holcomb, M.: Why corals care about ocean acidification: uncovering the mechanism, Oceanography, 22, 118–127, 2009.
Cohen, A. L. and McConnaughey, T. A.: Geochemical perspectives on coral mineralization, Rev. Mineral. Geochem., 54, 151–187, 2003.
Cohen, A. L., McCorkle, D. C., de Putron, S., Gaetani, G. A., and Rose, K. A.: Morphological
15 and compositional changes in the skeletons of new coral recruits reared in acidified seawater: insights into the biomineralization response to ocean acidification, Geochem. Geophys. Geosyst., 10, Q07005, doi:10.1029/2009GC002411, 2009.
Doney, S. C., Balch, W. M., Fabry, V. J., and Feely, R. A.: Ocean acidification: a critical emerging problem for the ocean sciences, Oceanography, 22, 16–25, 2009.
20 Fabry, V. J., Seibel, B. A., Feely, R. A., and Orr, J. C.: Impacts of ocean acidification on marine fauna and ecosystem processes, ICES J. Mar. Sci., 65, 414–432, 2008.
Fabry, V. J., McClintock, J. B., Mathis, J. T., and Grebmeier, J. M.: Ocean acidification at high latitudes: the bellwether, Oceanography, 22, 160–171, 2009.
Fadlallah, Y. H. and Pearse, J. S.: Sexual reproduction in solitary corals: overlapping oogenic
25 and brooding cycles, and benthic planulas in *Balanophyllia elegans*, Mar. Biol., 71, 223–231, 1982.
Feely, R. A., Sabine, C. L., Hernandez-Ayon, J. M., Ianson, D., Hales, B.: Evidence for upwelling of corrosive “acidified” water onto the continental shelf, Science, 320, 1490–1492, 2008.
Fine, M. and Tchernov, D.: Scleractinian coral species survive and recover from decalcification,
30 Science, 315, p. 1811, 2007.
Form, A. U. and Riebesell, U.: Acclimation to ocean acidification during long-term CO_2 exposure in the cold-water coral *Lophelia pertusa*, Glob. Change Biol., 18, 843–853, 2012.

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Gaylord, B., Hill, T. M., Sanford, E., Lenz, E. A., Jacobs, L. A., Sato, K. N., Russell, A. D., and Hettinger, A.: Functional impacts of ocean acidification in an ecologically critical foundation species, J. Exp. Biol., 214, 2586–2594, 2011.

Gerrodette, T.: Dispersal of the solitary coral *Balanophyllia elegans* by demersal planular larvae, Ecology, 62, 611–619, 1981.

Hauri, C., Gruber, N., Plattner, G. K., Alin, S., Feely, R. A., Hales, B., and Wheeler, P. A.: Ocean acidification in the California current system, Oceanography, 22, 60–71, 2009.

Hettinger, A., Sanford, E., Hill, T. M., Russell, A. D., Sato, K. N. S., Hoey, J., Forsch, M., Page, H. N., and Gaylord, B.: Persistent carry-over effects of planktonic exposure to ocean acidification in the Olympia oyster, Ecology, 93, 2758–2768, 2012.

Highsmith, R. C.: Coral growth rates and environmental control of density banding, J. Exp. Mar. Biol. Ecol., 37, 105–125, 1979.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A., and Hatziolos, M. E.: Coral reefs under rapid climate change and ocean acidification, Science, 318, 1737–1742, doi:10.1126/science.1152509, 2007.

Holcomb, M., Cohen, A. L., Gabitov, R. I., and Hutter, J. L.: Compositional and morphological features of aragonite precipitated experimentally from seawater and biogenically by corals, Geochim. Cosmochim. Ac., 73, 4166–4179, 2009.

Holcomb, M., McCorkle, D. C., and Cohen, A. L.: Long-term effects of nutrient and CO_2 enrichment on the temperate coral *Astrangia poculata* (Ellis and Solander, 1786), J. Exp. Mar. Biol. Ecol., 386, 27–33, 2010.

Jokiel, P. L., Rodgers, K. S., Kuffner, I. B., Andersson, A. J., Cox, E. F., and Mackenzie, F. T.: Ocean acidification and calcifying reef organisms: a mesocosm investigation, Coral Reefs, 27, 473–483, 2008.

Krief, S., Hendy, E. J., Fine, M., Yam, R., Meibom, A., Foster, G. L., and Shemesh, A.: Physiological and isotopic responses of scleractinian corals to ocean acidification, Geochim. Cosmochim. Ac., 74, 4988–5001, 2010.

Kroeker, K. J., Kordas, R. L., Crim, R. N., and Singh, G. S.: Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms, Ecol. Lett., 13, 1419–1434, doi:10.1111/j.1461-0248.2010.01518.x, 2010.

Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M., and Gattuso, J.-P.: Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming, Glob. Change Biol., 13 pp. doi:10.1111/gcb.12179, 2013.
Kurihara, H.: Effects of CO_2-driven ocean acidification on the early development stages of invertebrates, Mar. Ecol.-Prog. Ser., 373, 275–284, doi:10.3354/meps07802, 2008.
Langdon, C. and Atkinson, M. J.: Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment, J. Geophys. Res., 110, C09S07, doi:10.1029/2004JC002576, 2005
McCulloch, M., Trotter, J., Montagna, P., Falter, J., Dunbarf, R., Freiwaldg, A., Försterrah, G., Correai, M. L., Maier, C., Rüggeberg, A., and Taviani, M.: Resilience of cold-water scleractinian corals to ocean acidification: boron isotopic systematics of pH and saturation state up-regulation, Geochim. Cosmochim. Ac., 87, 21–34, 2012.
Maier, C., Hegeman, J., Weinbauer, M. G., and Gattuso, J.-P.: Calcification of the cold-water coral *Lophelia pertusa*, under ambient and reduced pH, Biogeosciences, 6, 1671–1680, doi:10.5194/bg-6-1671-2009, 2009.
Maier, C., Watremez, P., Taviani, M., Weinbauer, M. G., and Gattuso, J. P.: Calcification rates and the effect of ocean acidification on Mediterranean cold-water corals, P. Roy. Soc. B.-Biol. Sci., 279, 1716–1723, 2011.
Marinovic, B. B., Croll, D. A., Gong, N., Benson, S. R., and Chavez, F. P.: Effects of the 1997–1999 El Nino and La Nina events on zooplankton abundance and euphausiid community composition within the Monterey Bay coastal upwelling system, Prog. Oceanogr., 54, 265–277, 2002.
Nakamura, M., Ohki, S., Suzuki, A., and Sakai, K.: Coral larvae under ocean acidification: survival, metabolism, and metamorphosis, PLoS ONE, 6, e14521, doi:10.1371/journal.pone.0014521, 2011.
Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R. M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R. G., Plattner, G. K., Rodgers, K. B., Sabine, C. L., Sarmiento, J. L., Schlitzer, R., Slater, R. D., Totterdell, I. J., Weirig, M. F., Yamanaka, Y., and Yool, A.: Anthropogenic ocean acidification over the 21st century and its impact on calcifying organisms, Nature, 437, 681–686, 2005.

Pennington, J. T. and Chavez, F. P.: Seasonal fluctuations of temperature, salinity, nitrate, chlorophyll and primary production at station H3/M1 over 1989–1996 in Monterey Bay, California, Deep-Sea Res. Pt. II, 47, 947–973, 2000.
Pierrot, D., Lewis, E., and Wallace, D. W. R.: MS excel program developed for CO_2 system calculations, ORNL/CDIAC-105a Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, 2006.
R Core Team: R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, 2013.
Ries, J. B., Cohen, A. L., and McCorkle, D. C.: Marine calcifiers exhibit mixed responses to CO_2 induced ocean acidification, Geology, 37, 1131–1134, 2009.
Ries, J. B.: A physicochemical framework for interpreting the biological calcification response to CO_2 induced ocean acidification, Geochim. Cosmochim. Ac., 75, 4053–4064, 2011.
Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., Wanninkhof, R., Wong, C. S., Wallace, D. W. R., Tilbrook, B., Millero, F. J., Peng, T- H., Kozyr, A., Ono, T., and Rios, A. F.: The oceanic sink for anthropogenic CO_2, Science, 305, 367–371, 2004.
Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L. (Eds.): Climate Change 2007: The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK, New York, USA, 2007.
Timmons-Schiffman, E., O'Donnell, M. J., Friedman, C. S., and Roberts, S. B.: Elevated pCO_2 causes developmental delay in early larval Pacific oysters, *Crassostrea gigas*, Mar. Biol., 1–10, doi:10.1007/s00227-012-2055-x, 2012.
Turley, C. M., Roberts, J. M., and Guinotte, J. M.: Corals in deep water: will the unseen hand of ocean acidification destroy cold-water ecosystems?, Coral Reefs, 26, 445–448, 2007.
Widdicombe, S., Dupont, S., and Thorndyke, M.: Laboratory experiments and benthic mesocosm studies, in: Guide to Best Practices for Ocean Acidification Research and Data Reporting, Luxembourg Publications Office of the European Union, Luxembourg, 113–122, 2010.
Wood, H. L., Spicer, J. I., and Widdicombe, S.: Ocean acidification may increase calcification rates, but at a cost, P. Roy. Soc. B.-Biol. Sci., 275, 1767–1773, 2008.

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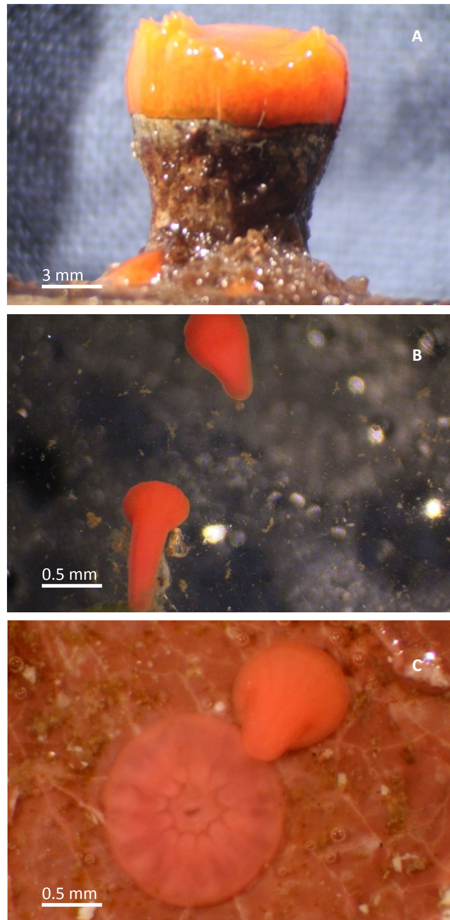

Fig. 1. Adult **(a)**, larvae **(b)**, and newly settled juvenile **(c)** *Balanophyllia elegans*.

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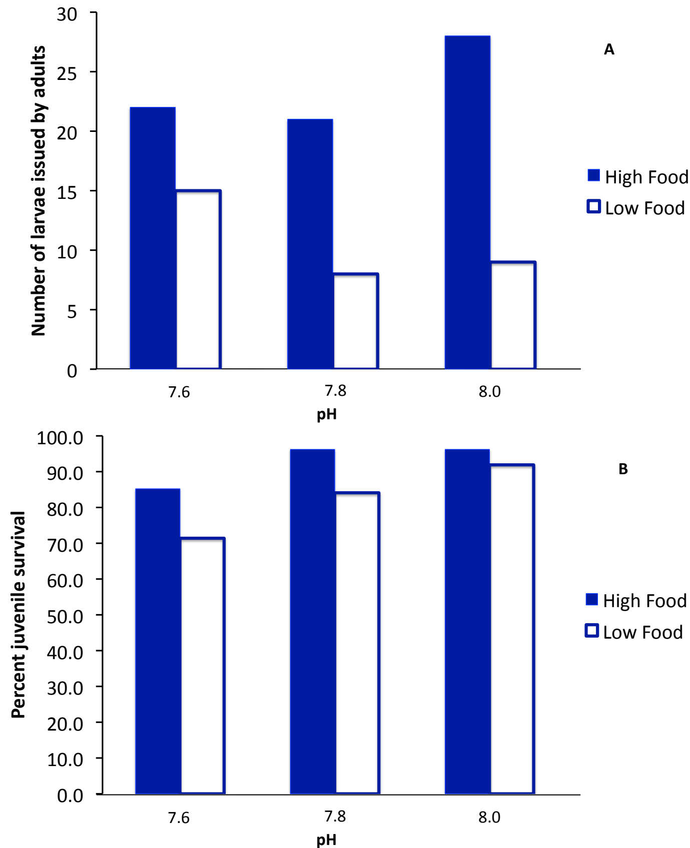

Fig. 2. Planulation rates of adults **(a)** and percent juvenile survival **(b)** by pH_T and feeding frequency. Planulation rates were determined by placing 10 adults/treatment (60 total adults) in experimental conditions for three months, and larvae were counted as they emerged. Percent juvenile survival was determined by counting deaths as they occurred (198 initial juvenile corals).

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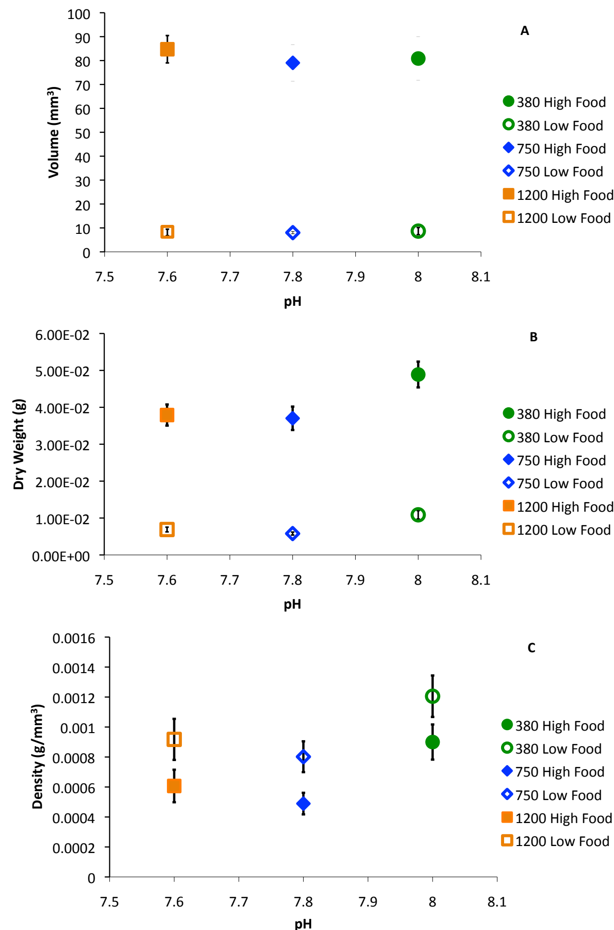

Fig. 3. Volume **(a)**, dry weight **(b)**, and bulk density **(c)** of juvenile *B. elegans* after 8 months exposure to experimental conditions (33 juveniles/treatment). High Food corals were fed once every 3 days while Low Food corals were fed once every three weeks. Mean ± s.e.m displayed.

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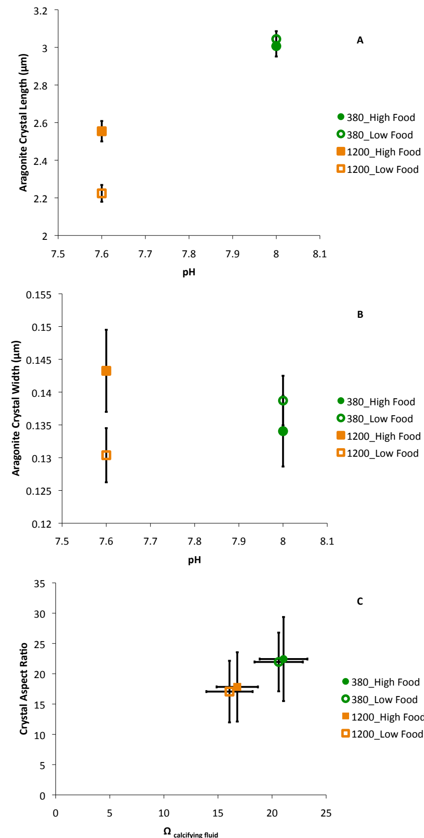

Fig. 4. Aragonite crystal length **(a)**, and aragonite crystal width **(b)**, obtained from scanning electron microscope (SEM) images taken from a subset of 20 juvenile coral samples (mean ± s.e.m.). In **(c)**, the crystal aspect ratio (aragonite crystal length divided by the width) was used to calculate the saturation state in the calcifying fluid (Ω_{cf}) using Eq. (1) (mean ± s.d.).

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