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Growth response of an early successional assemblage of coralline algae and benthic diatoms to ocean acidification

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Abstract The sustained absorption of anthropogenically released atmospheric CO_2 by the oceans is modifying seawater carbonate chemistry, a process termed ocean acidification (OA). By the year 2100, the worst case scenario is a decline in the average oceanic surface seawater pH by 0.3 units to 7.75. The changing seawater carbonate chemistry is predicted to negatively affect many marine species, particularly calcifying organisms such as coralline algae, while species such as diatoms and fleshy seaweed are predicted to be little affected or may even benefit from OA. It has been hypothesized in previous work that the direct negative effects imposed on coralline algae, and the direct positive effects on fleshy seaweeds and diatoms under a future high CO_2 ocean could result in a reduced ability of corallines to compete with diatoms and fleshy seaweed for space in the future. In a 6-week laboratory experiment, we examined the effect of pH 7.60 (pH predicted to occur due to ocean acidification just beyond the year 2100) compared to pH 8.05 (present day) on the lateral growth rates of an early successional, cold-temperate species assemblage dominated by crustose coralline algae and benthic diatoms. Crustose coralline algae and benthic diatoms maintained positive growth rates in both pH treatments. The growth rates of coralline algae were three times lower at pH 7.60, and a non-significant decline in diatom growth meant that proportions of the two functional groups remained similar over the course of the experiment. Our results do not support our hypothesis that benthic diatoms will outcompete crustose coralline algae under future pH conditions. However, while crustose coralline algae were able to maintain their presence in this benthic rocky reef species assemblage, the reduced growth rates suggest that they will be less capable of recolonizing after disturbance events, which could result in reduced coralline cover under OA conditions.

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Introduction

The sustained absorption of anthropogenically released atmospheric CO_2 by the oceans is causing the seawater carbonate system to be perturbed at a rate that is unprecedented in the geological past (Pelejero et al. 2010), with increasing concentrations of H^+ (i.e., decreasing pH), CO_2 and HCO_3^- and decreasing concentrations of CO_3^{2-} (Raven 2005; Gattuso et al. 2010). These changes in seawater carbonate chemistry are termed 'ocean acidification' (OA) and by the year 2100, the mean surface oceanic seawater pH is predicted to drop by an average of 0.2–0.5 units from current values of 8.00–8.10 (McNeil and Matear 2008; Pörtner 2008; Doney et al. 2009; Ciais et al. 2013).

Increasing scientific effort has focused on assessing the responses of oceanic and coastal organisms to these predicted changes in seawater chemistry (Boyd 2011; Dupont and Pörtner 2013). Calcifying organisms are considered particularly susceptible to OA, as net calcification and growth are often impaired as pH declines (Ries et al. 2009; Rodolfo-Metalpa et al. 2011; Kroeker et al. 2013b). In contrast, some organisms, especially non-calcifying primary producers such as diatoms and 'fleshy' seaweeds, may respond positively to the additional dissolved inorganic carbon available for photosynthesis (Kübler et al. 1999; Hepburn et al. 2011; Raven et al. 2011; Cornwall et al. 2012). In coastal communities, the response of benthic organisms to OA varies with taxonomic group and can be species or strain specific, and this could lead to shifts in the relative dominance of different functional groups and the structure of near-shore communities (Hall-Spencer et al. 2008; Diaz-Pulido et al. 2011b; Doropoulos et al. 2012; Kroeker et al. 2013c).

Coralline algae are calcifying members of the red algae (Rhodophyta) and are a dominant component of near-shore communities from the tropics to the poles (Nelson 2009). They are foundation species that provide important ecosystem services and, along with providing a complex surface for settlement, they are known to release chemical cues that encourage settlement of invertebrate larvae and other algae (Rowley 1989; Roberts 2001; Scheibling and Robinson 2008). They are considered to be particularly susceptible to OA because they deposit high magnesium calcite, which is the most soluble form of calcium carbonate (Ries 2011; Smith et al. 2012). The majority of studies that have examined the direct response of corallines to increased CO_2 (decreased pH) report reduced rates of net calcification and growth (see reviews by Harley et al. 2012; Roleda and Hurd 2012; Koch et al. 2013). OA could also indirectly influence crustose coralline algae through increased competition with species that may benefit from the increased CO_2 available for photosynthesis, namely benthic diatoms and fleshy non-calcareous macroalgae (Hepburn et al. 2011; Connell et al. 2013; Kroeker et al. 2013a, c). In the few cases where community composition or species interactions have been studied, this hypothesis has been supported, with a transition from calcifying to non-calcifying species under conditions simulating OA (Hall-Spencer et al. 2008; Martin et al. 2008; Fabricius et al. 2011; Kroeker et al. 2013c).

We examined the effect of reduced pH on an early successional community of crustose coralline algae from a cold-temperate (4–17 °C) region in southern New Zealand in a controlled laboratory experiment. Here, coralline algae are the most abundant functional group of nearshore communities, making up to 80 % of the benthic cover (Schiel 1988; Shears and Babcock 2007; Hepburn et al. 2011). The seaweed communities were obtained by placing small settlement plates in the field for 11 months, and these were then grown in a semi-autonomous culture system (modified from McGraw et al. 2010) at pH 8.05 (today) and 7.60 (worst case scenario projected pH by year 2100) for 6 weeks. We hypothesized that the growth rate of crustose coralline algae (measured as change in area) would be lower in the pH 7.60 treatment and that coralline algae would be replaced by fleshy algae or diatoms, which would overgrow crustose coralline algae in the low-pH treatment due to a combination of reduced growth rates of coralline algae and increased growth rates of diatoms.

Materials and methods

Settlement plates

Twenty 35-mm diameter Perspex® settlement plates (total surface area = 962 mm^2) were placed subtidally, underneath a *Carpophyllum flexuosum* canopy on the Northern coast of Huriawa Peninsula, Karitane, Otago, New Zealand (45°38′20″S, 170°40′15″E) in November 2009 (Spring). The surface of the plates was lightly sanded to roughen the glossy surface of the Perspex® to encourage the attachment of organisms (Foster 1975). The settlement plates were spaced 10 cm apart along a leaded rope, and the rope was positioned parallel to the shore at a depth of 2–3 meters. In mid-October 2010, the settlement plates, now containing an early successional stage of a natural algal assemblages, were collected and transported to the laboratory (taking approximately 1 h) submerged in seawater, in the dark in an insulated bin. At the laboratory, the settlement plates were placed in UV-filtered seawater and kept in the dark at 12 °C for 24 h of pre-experimental treatment. Digital images were taken of the plates with a Canon EOS 50D digital camera, and the plates were immediately placed into their randomly allocated experimental treatment.

Culture and treatment of algal communities

Seawater used in the experiment was obtained from the Portobello Aquarium, Otago Harbour (45°52.51′S, 170°30.9′E) and stored in a 1,000 L polypropylene tank. Twice a day, a 150-L storage tank was filled with this seawater filtered using Filter Pure® polypropylene spun melt (0.5 µm pore size) and ultraviolet sterilized with an Aquastep® 25 W Ultraviolet Sterilizer.

A modified version of the automated culture system of McGraw et al. (2010) was used to control and maintain pH in each of 24 culture chambers. The settlement plates were randomly allocated to individual 150-mL culture chambers and were randomly assigned either a present day seawater (pH 8.05) treatment or an OA seawater treatment (pH 7.60)

based on the worst case scenario for the year 2100, as per the best practices in ocean acidification guide (Barry et al. 2010). Recent models indicate that pH may reach ~7.75 by 2100 in Otago, New Zealand, by 2100 (Ciais et al. 2013); therefore, this scenario is beyond the worst case scenario for 2100. There were a total of 10 replicate tanks in each treatment. In addition, four clean Perspex® plates, identical to the settlement plates, were assigned to random culture chambers in present day seawater, to act as controls to detect any alien organisms entering the system from the filtered seawater. This system was housed in a walk-in temperature controlled chamber (Plant Growth 680, Contherm Scientific, Wellington, New Zealand) at 11.6 °C, with a mean photon flux density of 20 μmol m^{-2} s^{-1} and a 12:12 light: dark cycle. The daily dose of photons in culture was similar to that found in situ at 2 m underneath the *Carpophyllum flexuosum* canopy where the settlements plates were located prior to experiments (Hepburn et al. 2011).

The 150-mL culture chambers were each connected to an independent 1-L header tank. The pH in each header tank was controlled by automatically refilling the tank with seawater from a 1-L mixing tank. Target pH_T levels were achieved in the mixing tank by adding exactly equal amounts of 0.2 M HCl and $NaHCO_3$ (a process chemically identical to adding CO_2) (Hurd et al. 2009; Gattuso et al. 2010) to 1 L of seawater that was pumped from the 150-L storage tank. Before the newly mixed seawater was transferred to the appropriate header tank, pH_T was measured at 12 °C using the automated spectrophotometric system. If the measured pH was within 0.03 units of the target pH_T, the seawater was transferred to the appropriate 1-L header tank. If the pH varied more than 0.03 pH units from the target value, the seawater in the mixing tank was sent to waste and the process repeated until the correct pH was achieved. Using this method, the automated system delivered new seawater at the target pH to each of the 20 header tanks approximately every 37.5 min. The temperature of the sample solution was measured using a PT1000 temperature sensor (Pico Technology, PT-104) attached to the outflow of the optical cell. A second sensor, submerged in an unused 150-mL culture tank, was used to estimate the temperature in the experimental culture tanks. The order in which the seawater was refreshed in each of the 24 treatment chambers was randomly allocated at the beginning to avoid potential artifacts. The inflow rate from each header tank to the corresponding culture tank was 4 mL min^{-1}. The culture tanks were placed on orbital shaker tables and shaken continuously to minimize the formation of diffusion boundary layers. While pH was only measured in the mixing tank, other experiments using the same culture system determined that pH change due to metabolic activity of the coralline algae would be <0.02 units over 37.5 min in this system (Cornwall et al. 2013a). However, this was with a greater biomass of coralline algae and with no diatoms, and the change in this experiment will most likely be less that <0.02.

Seawater carbonate system

Every 5 days during the 6-week experimental period, 1-L seawater samples (filtered and UV-sterilized) were taken from the 150-L storage tank and poisoned with Mercuric chloride. Total alkalinity (A_T) was determined via closed-cell potentiometric titration using methods described by Dickson et al. (2007). The accuracy of the method was estimated to be ± 3.7 μmol kg^{-1} based on reference material provided by Andrew Dickson (Scripps Institution of Oceanography). A_T, pH on the total scale (pH_T), salinity measurements, and temperature were used to calculate DIC. Using these values, [CO_2], [CO_3^{2-}], and [HCO_3^-] were calculated using the constants of Mehrbach et al. (1973) refitted by Dickson and Millero (1987). Carbonate chemistry was calculated using the software $SWCO_2$ (Hunter 2007).

Assemblage growth and structure

To measure the growth and structure of the communities on the plates, digital images were taken using a Canon EOS 50D digital camera of each settlement plate immediately after they were removed from culture chambers at the end of the 6-week experiment. These images were compared with the images of the settlement plates at the start of the experiment. Functional groupings were used to classify the individuals for ease of identification and comparison among the plates. These functional groups were defined as: corallines, diatoms, fleshy seaweed, ploychaetes, and bare space. Using the computer program ImageJ (Rasband 1997), the surface area of each functional group was measured on each of the plates and the change in area (mm^2) from before and after the experiment was calculated to determine growth each functional group.

To assess whether pH treatment influenced the structure of the communities on the plates, each individual organism present on each plate at the start of the experiment was identified. At the end of the experiment, these individuals were re-examined and categorized as: 1. no change (i.e., the same functional group was present); 2. overgrown by a different functional group (e.g., corallines overgrown by diatoms or fleshy seaweed).

Statistical analysis

Paired 2-tailed tests were conducted to determine whether the growth of each functional group over 6 weeks was significant in each treatment. Separate one-way ANOVAs were used to test for the effect of pH on the growth of

diatoms and coralline algae and the change in bare space (mm^2) at the end of the experiment. A MANOVA was conducted to test the treatment effect of pH 7.60 and pH 8.05 on the beginning and end abundances (% of the three main functional groups on the plates corallines, diatoms and bare space). Fleshy seaweed and polychaetes were not included in the test as the sample size of these functional groups was too small to conduct any valid statistical tests. Generalized linear models (GLMs) using the binomial function were used to determine whether there was a significant effect of pH treatment on the overgrowth each of three functional groups (coralline algae, diatoms growing on Perspex substratum, and diatoms growing on coralline algae) by another group. The data were examined for homoscedasity and normality, and all data passed these assumptions except GLM data, which was binomially distributed. A P value <0.05 was considered statistically significant for all models. All statistics were performed in Minitab version 16.0 and R version 3.0.2.

Results

Seawater carbonate system

The total alkalinity (A_T) of both treatments was 2,288 ± 2.5 μmol kg^{-1} (mean ± SE, $n = 8$), and temperature was 11.6 ± 0.3 °C (mean ± SD, $n = 6{,}125$). The average pH of the present day treatment was 8.05 ± 0.03 (mean ± SD, $n = 3{,}413$), and calculated concentrations of DIC, HCO_3^-, and CO_3^{2-} were 2,091 ± 5, 1,932 ± 8, and 143 ± 3 μmol kg^{-1}, respectively. The average pH in the OA treatment was 7.60 ± 0.01 ($n = 2{,}425$), and calculated concentrations of DIC, HCO_3^-, and CO_3^{2-} were 2,256 ± 2, 2,148 ± 18, and 56 ± 1 μmol kg^{-1}, respectively.

Assemblage growth and structure

The % cover of all functional groups on the settlement plates increased after 6 weeks in both the pH 8.05 and 7.60 treatments (Fig. 1). Coralline algae were the most abundant group present, covering 32 % of the surface area on the plates in each treatment before the experiment began. After 6 weeks, there was a 25 % increase in the abundance of coralline algae in the present day treatment compared with a 9 % increase in the pH 7.60 treatment (Fig. 2). The coralline algae grew significantly in both treatments (present day: $t_{19} = 4.15$, $P < 0.01$; pH 7.60: $t_{19} = 4.16$, $P < 0.01$), and overall, the pH level that plates were grown in had a significant effect on the change in abundance that occurred over the course of the 6-week experiment (ANOVA: $F_{3.16} = 7.11$, $P = 0.03$). The increase in surface area (mm^2) of coralline algae at pH 8.05 was three times higher than at pH 7.60 and was statistically significant (ANOVA: $F_{1.19} = 6.42$, $P = 0.02$). Coralline algae remained the most abundant functional group at the end of the experiment, covering 57 and 41 % of the pH 8.05 and pH 7.60 treatments, respectively. At the end of the experiment, the crustose coralline algae had produced a total of nine and eight upright fronds at pH 8.05 and 7.60, respectively.

The surface area of the plates that was covered by benthic diatoms also increased in both pH treatments (pH 8.05: $t_{19} = 2.59$, $P = 0.03$; pH 7.60: $t_{19} = 4.18$, $P < 0.01$), but there was no significant difference in diatom growth rates between treatments ($F_{1.19} = 1.9$, $P = 0.18$). At the start of the experiment, benthic diatoms covered 14 % of the surface area on the plates assigned to the pH 8.05 treatment, and 16 % of the area on the pH 7.60 plates. After 6 weeks, there was a 21 % increase in the cover of benthic diatoms at pH 8.05 and a 9 % increase at pH 7.60. The percent of bare space on the plates decreased significantly in the pH 8.05 treatment, but not the in the pH 7.60 treatment (pH 8.05: $t_{19} = 6.82$, $P = 0.02$; pH 7.60: $t_{19} = 0.55$, $P = 0.47$). The amount of bare space in the pH 8.05 treatment decreased by 25 % and by 10 % in the pH 7.6 treatment; this difference between pH treatments was significant. ($F_{1.19} = 5.42$, $P = 0.03$). Non-calcifying, fleshy red algae appeared on two of the settlement plates in the pH 7.60 treatment (e.g., Figs. 1c and 2). Polychaete worms from the Spirorbinae subfamily were present on 2 of the pH 8.05 and 2 of the pH 7.60 treatment plates before the experiment began, and they remained on the plates for the duration of the experiment (Fig. 3). No organisms were observed on any of the four control plates.

There was no significant effect of pH treatment on the composition of the functional groups on the plates (MANOVA: $F_{3.34} = 0.38$, $P = 0.77$), nor was there an interaction between time and pH treatment ($F_{3.34} = 0.82$, $P = 0.49$), but there was a significant change over time ($F_{3.34} = 4.40$, $P = 0.01$). Fifty percent of the coralline algae in the pH 8.05 treatment and 56 % at pH 7.60 remained free of any organisms on their surface (Fig. 3). Forty percent of coralline algae at pH 8.05 and 32 % at pH 7.60 became overgrown with diatoms. At the end of the experiment, diatoms had become attached to 10 % of the polychaete individuals in the present day treatment and 17.5 % of the polychaeta individuals in the pH 7.60 treatment (Fig. 3). Ninety-three percent of diatoms at pH 8.05 and 100 % in the pH 7.60 treatment were not overgrown by other functional groups. There was no significant effect of pH treatment on the measured overgrowth of one group of species by another (Fig. 3; GLMs: coralline algae $F_{1.17} = 0.33$, $P = 0.74$, diatoms on Perspex $F_{1.7} = 0.43$, $P = 0.67$, diatoms on coralline algae $F_{1.6} = 0.70$, $P = 0.48$).

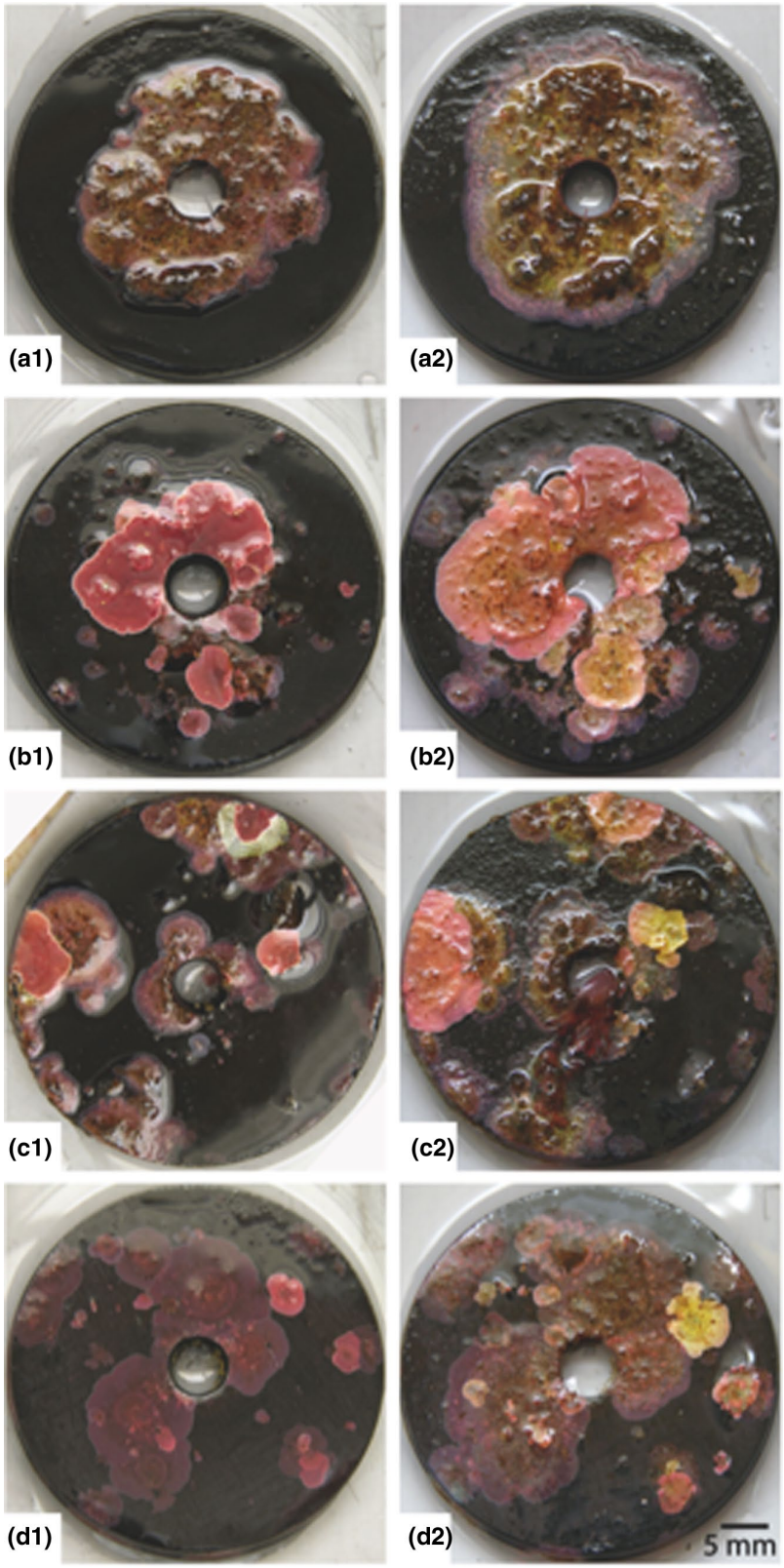

Fig. 1 Examples of the benthic community growing on settlement plates before and after the 6-week laboratory experiment. Photographs of four (of the twenty) experimental settlement plates, taken immediately before (*left hand panel*) and after (*right hand panel*) the plates were cultured for 6 weeks at pH 8.05 (*top four photographs*) and pH 7.60 (*bottom four photographs*)

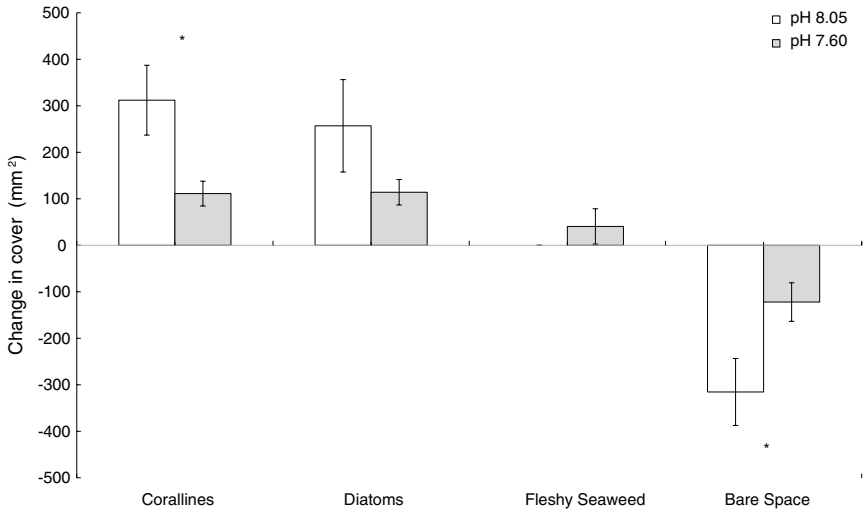

Fig. 2 The growth rate (mm^2) of the algal functional groups (coralline algae, diatoms and fleshy seaweed) during a 6-week laboratory culture experiment at seawater pH 8.05 (present day) and 7.60 (beyond the worst case scenario for 2100). *Bars* represent mean ±1 SE ($n = 10$)

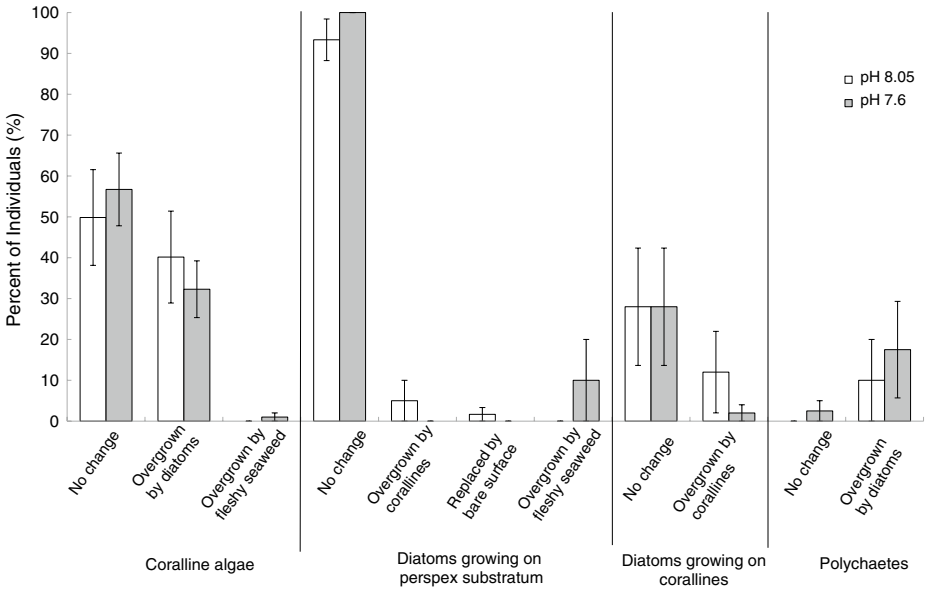

Fig. 3 The percent of individuals for each defined transition observed on the settlement plates. The *x*-axis denotes the initial functional group at the beginning of the laboratory culture, followed by a breakdown for each group, indicating whether they were overgrown by another group after 6-week culture at pH 8.05 (present day) and pH 7.60 (beyond the worst case scenario for 2100). *Bars* represent means ±1 SE ($n = 10$)

Discussion

The pH level used in our OA treatment (7.60) is among the lowest used in a manipulative experiment to examine the effects of OA on coralline algae (see Table 3 in Koch et al. 2013), but contrary to our hypothesis; it did not result in increased overgrowth of coralline algae by diatoms or fleshy seaweed. This result is in sharp contrast to studies that have shown major changes from coralline algal-dominated systems to those dominated by non-calcareous "biofilm" species such as benthic diatoms under pH conditions that were generally higher than those used here, in the order of 7.80–7.90 (Kroeker et al. 2013a, c; Porizo et al. 2013). Growth rates of coralline algae were lower at pH 7.60, as we hypothesized, but there was no evidence of net dissolution or mortality that has been reported for coralline algae in some other experiments (Anthony et al. 2008; Kuffner et al. 2008; Martin and Gattuso 2009; Diaz-Pulido et al. 2011a). Also contrary to our predictions, the benthic diatoms did not benefit from the high CO_2 seawater of the

pH 7.60 treatment, in terms of space occupied. In fact, their growth rates declined, albeit non-significantly. The reduced growth rate of corallines in the pH 7.60 treatment suggests a decreased ability to occupy new space that could alter their competitive ability in a future high CO_2 ocean, but overall, this severe OA treatment had a relatively small effect on the ability of coralline algae to maintain space in this benthic rocky reef assemblage.

Our experiment was conducted under conditions where light and temperature were optimal for the growth of coralline algae (based on preliminary experiments), suggesting that once established, coralline algae could maintain space within a community in situations where there is no disturbance. In the field, however, coralline-dominated communities are continually modified by numerous physical (e.g., storm waves, sedimentation, temperature) and biological (e.g., whiplash and grazing) disturbances (Lawrence 1975; Steneck 1986; Sousa 2001; Airoldi 2003). Under disturbed conditions, the 14 % reduction in growth at pH 7.60 could reduce the ability of coralline algae to quickly colonize new space through growth; i.e., they will have a reduced ability to respond to disturbance via re-colonization (Doropoulos et al. 2012). The frequency and magnitude of disturbance events may therefore play a more dominant role in determining coralline algal abundance in future low-pH seawater.

The fact that diatoms did not replace coralline algae in our experiment could be explained by several possible reasons. First, the responses of coralline algae and diatoms to low pH observed here could be species specific, where differences in the physiology of the species in this ecosystem resulted in both our coralline algae being more robust to the negative effects of OA and the diatoms benefiting less from any potential positive effects of OA than previous studies (i.e., Kroeker et al. 2013a, b). Secondly, it is logical that in different ecosystems, different ecological processes and interactions will be occurring. Responses to OA will be ecosystem specific, and the differences in ecological interactions that could be occurring in the shallow subtidal in New Zealand compared to those in the Mediterranean could have contributed to differences in observed responses. Thirdly, differences in variability in pH between that used in this study and at vent sites could contribute to differences in responses to "low" and "ambient" pH treatments. Lastly, the shorter duration here could have prohibited us from observing a strong effect of pH on the early successional communities. The rest of the discussion will be devoted to discussing these points.

It is possible that there were underlying physiological or inorganic skeletal changes that reduced the fitness of the coralline assemblages, which we did not assess. For example, a reduction in hardness of their skeleton could make them less robust to herbivore grazing (Johnson and Carpenter 2012; Ragazzola et al. 2012) or make them poorer competitors for space with other encrusting species (McCoy 2013; McCoy and Pfister 2014). However, we have found similar results in our all work on cold-temperate coralline algae, with reduced growth rates at pH 7.60 compared to 8.05, but no change in other physiological diagnostics (Fv:Fm, photosynthesis; McGraw et al. 2010; Cornwall et al. 2013a; Roleda et al. in prep). Our consistent findings that reduced pH did not alter any other aspect of temperate coralline algal physiology are in line with the trends seen in some other recent work (Hofmann et al. 2012b; Egilsdottir et al. 2013; Noisette et al. 2013; Yildiz et al. 2013) and could indicate that these species are more tolerant to the negative effects of OA.

Benthic diatoms did not show enhanced competitive abilities in the low-pH treatment. In fact their growth rates decreased, albeit this was not a statistically significant reduction. Rather than competing with coralline macroalgae at low pH, an alternate hypothesis that has not yet been explored is that it is possible that the benthic diatoms could facilitate the growth of coralline algae. Benthic diatoms are able to modify their local pH environment; when they photosynthesize, they will raise the pH at their surface (Roberts et al. 2007) like all marine primary producers (Hurd et al. 2011; Flynn et al. 2012; Glas et al. 2012). Regardless of water motion or exchange, some degree of metabolic alteration will take place at the surface of the corallines within the diffusion boundary layer (Hurd et al. 2011), with the diatoms increasing the thickness of the diffusion boundary layer, leading to greater changes in pH. Hence, at the surface of the underlying coralline algae, pH could be higher during the day in the presence of diatoms; possibly buffering the crustose coralline algae from the low-pH seawater of our 7.60 treatment (Hurd et al. 2011). Reductions in pH at the surface of marine primary producers due to respiration tend to be less than the increases in pH due to photosynthesis, meaning that these types of natural interactions may increase the ability of marine organisms to tolerate the effects of ocean acidification (Cornwall et al. 2013b). Thus, it is important to conduct ocean acidification experiments with more complex communities so that the response of the organisms encompasses both the competition and facilitation encountered in situ.

This laboratory experiment with highly controlled pH revealed no change in community composition under pH conditions mimicking worst case scenario for 2100, whereas field-based experiments in natural laboratories with greater variability in pH reveal major community shifts (Kroeker et al. 2013a, c). While laboratory experiments are usually limited in their environmental and ecological realism, and limited in duration, they provide a setting where pH can be highly controlled. Variability in pH can have a large influence on the physiology of a variety

of species which could either mask or enhance the effects of ocean acidification (Dufault et al. 2012; Cornwall et al. 2013a; Munguia and Alenius 2013; Comeau et al. 2014; Frieder et al. 2014; Johnson et al. 2014). If the laboratory experiment here continued for a longer period of time, then corallines algal crusts and diatoms could conceivable spread to cover more surface area of the plates and even onto the walls of the culture tanks. Under this scenario, competition for space could be more intense and larger differences in coralline algal/diatom abundances may have been observed. That aside, diatoms in this experiment were already observed growing on coralline crusts within both pH treatment levels, indicating that if competition was likely to ever occur between these two groups, it would already be occurring. Laboratory and field research provides different suites of information, and one or the other should not be discounted. It is paramount that future research utilizes both laboratory and field studies in a variety of different ecosystems in order to enhance our ability to predict the future effects of OA on temperate rocky reef ecosystems.

Within OA research, there is a need to quantify observed competitive interactions between groups of species and attribute them to specific causes. For example, an increase in the abundance of non-calcareous species at high CO_2 vents (Hall-Spencer et al. 2008; Kroeker et al. 2013c) could be due to either direct effects (such as increased growth rates, increased recruitment, etc. [e.g., (Russell et al. 2009, 2011; Connell et al. 2013)] or indirect effects (competitive release from coralline species). The next step in accurately predicting how competition between calcifying and non-calcifying species could change in a high CO_2 ocean will require research with a dual approach that measures specific physiological changes in each of the competitor groups directly due to carbonate chemistry and changes due to altered ecological interactions (i.e., competition and facilitation) between competitor groups or species. Current published observations predicting how whole temperate rocky reef ecosystems will respond to OA are currently limited by their geographical range to areas with CO_2 vents (e.g., Hall-Spencer et al. 2008; Kroeker et al. 2013a; Porizo et al. 2013) or to simplified species assemblages in the laboratory (e.g., Jokiel et al. 2008; Russell et al. 2009; Hofmann et al. 2012a; and here). Using the framework, we propose will us to more accurately predict how rocky reef ecosystems will response to future high CO_2, by understanding the specific mechanisms behind observed changes in species abundances and by determining whether general patterns will occur within different ecosystems.

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