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Interactions between filamentous turf algae and coralline algae are modified under ocean acidification

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ABSTRACT

Ocean acidification is a decrease in seawater pH and carbonate ion concentration due to increased uptake of atmospheric carbon dioxide by the world's oceans. This has major implications for many marine organisms, particularly the calcifiers. Crustose coralline algae (CCA) are among the most sensitive calcifying organisms to ocean acidification. In contrast, filamentous turf algae, which compete with CCA for space on the substratum, could potentially benefit from high pCO_2 conditions, suggesting that the effects of filamentous turf on coralline algae may be amplified in a high pCO_2 environment. The effect of ocean acidification on the growth of coralline algae, however, has rarely been investigated in combination with ecological interactions such as competition with filamentous turfing algae. Here we tested the combined effects of ocean acidification and overgrowth by filamentous turf algae on CCA calcification, photosynthetic capacity and quantum yield of photosynthesis. We observed a positive effect of algal turfs on CCA calcification but a negative effect on photosynthesis in the high pCO_2 treatments, however, these effects were variable over time. Our results have demonstrated the importance of investigating how inter-species interactions such as competition will complicate the impacts of ocean acidification.

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1. Introduction

Crustose coralline algae (CCA) are a ubiquitous component of euphotic benthic communities from the tropics to the poles and from the intertidal to the deepest recorded depths for a photosynthetic organism. They also form biotic reefs over sediments (maerl) that occupy large areas of the continental shelf e.g. (Ryan et al., 2007). CCA require seawater conditions favouring the precipitation of calcium carbonate during the process of biogenic calcification for normal growth and production, and as the partial pressure of carbon dioxide (pCO_2) in seawater increases, the saturation state of carbonate minerals decreases, adversely affecting the rate of calcification (Hoegh-Guldberg et al., 2007). Higher levels of pCO_2 negatively affect coralline algal recruitment, growth, mortality, productivity and calcification (Anthony et al., 2008; Diaz-Pulido et al., 2012; Kuffner et al., 2008; Martin et al., 2013). Indeed, ocean acidification threatens the growth of these important organisms more so than other calcifying organisms such as aragonite-forming corals (Anthony et al., 2008; Jokiel et al., 2008; Ries et al., 2009), potentially due to the high solubility of their magnesium calcite skeletons (Feely et al., 2004; Morse et al., 2006) and possibly their biological response to changing seawater pH (McCulloch et al., 2012).

CCA provide substrata for the settlement and growth of many marine invertebrates and seaweeds (Adey, 1998; Borowitzka et al., 1978; Morse, 1996). Space on primary substratum in benthic marine environments is often limiting (Sebens, 1986) and competition for this space, or its associated resources, leads to the exclusion of all but a small number of competitively dominant species (Connell, 1961). Overgrowth is a frequent mechanism of interference between space-limited organisms (Olson and Lubchenco, 1990; Sebens, 1986) and this is presumed to be a disadvantage for underlying species since epibionts may reduce light, O_2 and nutrients available to the underlying host, resulting in reduced growth, fecundity or death (D'Antonio, 1985; Dittman and Robles, 1991; Harris, 1996; Seed and O'Connor, 1981; Stevens, 1987). Indeed, recruitment and growth of CCA can be heavily impacted by overgrowth of filamentous turfs (Kendrick, 1991; Sebens, 1986; Underwood, 1980), and CCA are often considered subordinate in their capacity to compete for space (Dethier, 1994; Littler and Littler, 1980; Steneck and Dethier, 1994). In contrast, when irradiance levels are high or when there is a risk of desiccation (in intertidal environments), overgrowth by turf algae or shading by macroalgal canopy species can be beneficial for underlying corallines, providing protection from harmful environmental conditions (Figueiredo et al., 2000; Melville and Connell, 2001). Thus, the nature of the interaction between turf and coralline algae is variable, depending primarily on environmental conditions.

Despite the implications, few studies have investigated the potential effects of ocean acidification on ecological interactions (Johnson and

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Carpenter, 2012; Kroeker et al., 2010), which may define the fate of many species in the coming decades. In contrast to the CCA, the growth and metabolism of filamentous turf algae may increase under high pCO_2 conditions (Diaz-Pulido et al., 2012; Kuffner et al., 2008; Levitan et al., 2007; Tribollet et al., 2009). As such, the effects of filamentous turf on coralline algae may be synergistic with those associated with a high pCO_2 environment. Here we examined the effects of ocean acidification in combination with overgrowth by filamentous turf algae on calcification, photosynthesis and mortality of a temperate *Hydrolithoideae* crustose coralline alga. We hypothesized that in the absence of competitive interactions, CCA calcification and productivity would decrease and mortality rates would increase under elevated pCO_2. In a light-limited environment representative of a temperate fringing reef during autumn and early winter, we expected a negative effect of overgrowth by filamentous turf on coralline algae, thus, in the presence of filamentous turf we anticipated that the negative effects of elevated pCO_2 would be amplified.

2. Materials and methods

2.1. Field site and sample collection

In April 2013, CCA 'chips' were collected using a hammer and chisel at ~5 m depth at Whitford Rock (S31°48′, E115°42′) in Marmion Lagoon, a relic fringing reef-lagoon system located on the southwestern coast of Western Australia. CCA chips collected were members of the *Corallinaceae* sub-family *Hydrolithoideae*, which is the dominant CCA sub-family in Marmion Lagoon. This was identified via amplification of the psbA gene by Dr. Judith Sutherland at the University of Auckland. Ambient pCO_2 at Whitford Rock ranges from ~210 to 400 ppm seasonally (Short et al., Unpublished results) and sea surface temperatures range seasonally from ~16 to 24 °C (Smale and Wernberg, 2009).

CCA chips collected from the reef were transported in bins of seawater to an onshore laboratory, where they were cut into pieces ~3 to 15 cm^2 and cleaned of all visible epiphytes. CCA chips were then allowed to acclimate in aquaria under ambient conditions for 3 weeks prior to the application of experimental treatments. At the end of the acclimation period epiphytes were removed from all CCA chips.

2.2. Experimental design

To explore the potentially interactive effects of ocean acidification and filamentous turfing algae on CCA, a flow-through aquarium system was set up at the Department of Fisheries Research Laboratories in Hillarys, WA. The system comprised of twelve 25-L aquaria, each containing 20 CCA chips, receiving seawater from two 200-L header tanks (Fig. 1). Seawater entering the system was pumped directly from Marmion Lagoon and filtered to 30 μm. Turnover time of water within each treatment aquarium was ~90 min. Independent variables were (1) dissolved pCO_2 (ambient: ~300 ppm & high: ~900 ppm, chosen to represent the SRES worst-case scenario (RCP8.5) by 2100) and (2) the presence or absence of filamentous turf algae. The result was a fully factorial set up with four distinct treatments of three replicate aquaria each: (i) Ambient pCO_2 without filamentous turf (300), (ii) Ambient pCO_2 with filamentous turf (300 + F), (iii) High pCO_2 without filamentous turf (900) and (iv) High pCO_2 with filamentous turf (900 + F).

A CO_2 control system (Aqua Medic) was used to increase pCO_2 in the 'high pCO_2' treatments by direct injection of pure (food grade) CO_2 gas. To control the level of filamentous turf algae, all visible epiphytes were removed from CCA chips twice weekly with a soft brush in 6 of the 12 treatment tanks, while filamentous turf was allowed to colonise CCA chips in the remaining 6 tanks over the course of the experiment. Epiphytic filamentous turf in the current study was composed of a mixture of thin upright filaments, ~1–10 cm tall, resembling Fig. 2E. in Connell et al. (2014). We conducted the experiment for 10 weeks during late autumn–winter 2013 (May through July).

2.3. Seawater measurements

Downwelling PAR irradiances of ~100 μmol photons m^{-2} s^{-1} were maintained using Maxspect S-series LED lights on a diurnal cycle with 10 h of light and 14 h of darkness to reflect the low-end of light conditions and natural day length during winter in Marmion Lagoon. Ambient temperature was maintained in all of the treatment tanks over time. In order to represent natural seasonal variation, temperature was allowed to fluctuate over time, mimicking that in Marmion Lagoon. pH on the total scale (pH_T) was measured three times weekly in each of the treatment aquaria and header tanks just prior to midday using a Schott Handylab pH 12 equipped with a Blueline Elektrode. The electrode and pH metre were calibrated before each sampling day against seawater ('Tris') and NBS buffers. Salinity (±1) was measured once per week in both header tanks using a portable refractometer. Samples for the analysis of total alkalinity (TA ± 5 μeq kg^{-1}) were taken once per week in each treatment aquarium. These were filtered using glass fibre filters with 0.7 μm nominal pore size (Whatman GF/F), collected in Nalgene HDPE containers and stored on ice. These samples were

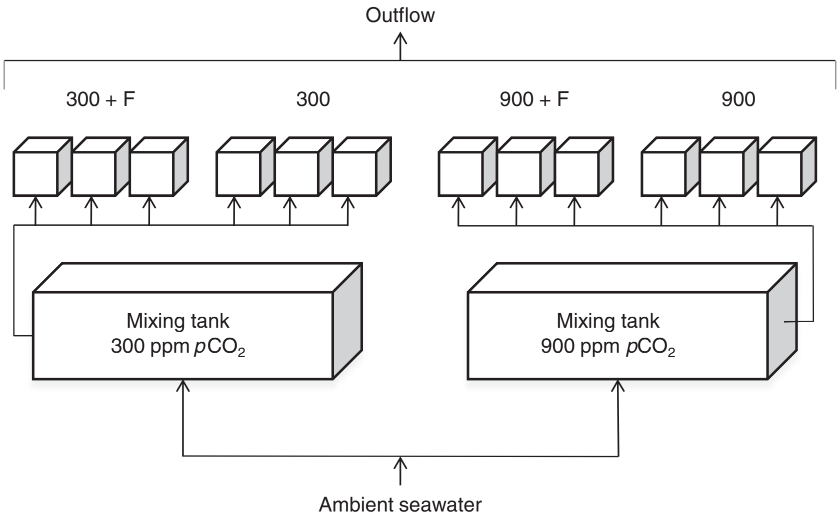

Fig. 1. Experimental setup with 2 pCO_2 conditions (300 and 900 ppm) and 2 levels of filamentous turf (present and absent). Arrows indicate direction of water flow from mixing tanks into treatment aquaria and exiting the system. Each aquarium contained 20 CCA chips.

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