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Impacts of natural and manipulated variations in temperature, pH and light on photosynthetic parameters of coralline–kelp assemblages

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ABSTRACT

Increasing absorption of CO_2 by the world's oceans is lowering seawater pH and may have severe consequences for marine calcifying organisms. Understanding the ecological consequences of anthropogenic CO_2 emissions will require examination of how calcifying organisms and their associated communities respond to natural variation in CO_2 concentration. Many macroalgae may respond positively or neutrally to ocean acidification, but calcifying species such as coralline algae are predicted to be some of the most susceptible organisms to changing CO_2. Here I test the impacts of temperature and pH variation on important photosynthetic metrics of macroalgal assemblages composed of coralline turf, *Corallina vancouveriensis* and the associated canopy-forming kelp, *Saccharina sessilis* using in situ photorespirometry and laboratory mesocosms. In situ photorespirometry was done at two locations on the Oregon (USA) coast, an area with variable upwelling of high CO_2, low pH water. To complement in situ measurements, a series of laboratory mesocosms were used to disentangle the effects of pH and temperature on photosynthetic parameters across a light gradient. The acute effects of low pH were also tested across a temperature gradient, revealing an exacerbated effect of short duration, low pH events on respiration rates at increasing temperature. NPP (net primary productivity) was reduced by 10–20% within in situ coralline assemblages across a natural gradient of pH (8.1–7.9), but there was a mostly neutral effect of low pH on NPP of coralline–kelp assemblages. These results indicate varied responses of coralline and coralline–kelp assemblages to temperature and pH gradients, but under limiting light conditions primary production and growth of corallines are likely to decrease under modest scenarios of CO_2 increase. Assemblage composition could play an important role in modulating the impacts of ocean acidification on calcifying organisms, and results from this study suggest that canopy and sub-canopy interactions could determine the response of susceptible species to changing climatic parameters.
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1. Introduction

Increasing greenhouse gas emissions are already causing rapid changes in the Earth's climate (IPCC et al., 2013) and by the end of this century, seawater pH is expected to fall below 7.9 (scenario RCP 6.0) and global average sea-surface temperatures are projected to increase by an average of 1–3 °C. Anthropogenic emissions of CO_2 are shifting the pH of surface ocean waters and lowering carbonate saturation states (Fabry, 2008; Feely et al., 2004) with potentially dramatic consequences to calcifying organisms (Hall-Spencer et al., 2008; Martin and Gattuso, 2009). Temperature changes may severely impact the productivity and survival of marine organisms (Harley et al., 2006) and the combination of these two stressors has been shown to amplify the negative impacts of one stressor alone (Diaz-Pulido et al., 2012; Martin and Gattuso, 2009). Understanding the consequences of both pH and temperature changes on a key ecosystem function, primary productivity will help provide insight into the consequences of climate change on temperate reef ecosystems and may provide a useful metric to quantify the impacts of ocean acidification at a community scale.

Crustose and articulated coralline algae are a dominant component of the marine benthos from tropical to polar oceans and they play a crucial role in the ecology of coastal ecosystems (Adey, 1998; Chisholm, 2003; Kuffner et al., 2008; Nelson, 2009), including facilitating recruitment of invertebrates (Cameron and Schroeter, 1980; Morse and Morse, 1984), seagrass (e.g., *Phyllospadix scouleri*, Turner, 1983), and macroalgae (e.g., *Saccharina sessilis*, Milligan and DeWreede, 2000). Coralline algae are some of the most susceptible organisms to elevated partial pressure of carbon dioxide (Andersson et al., 2008; Büdenbender et al., 2011; Hurd et al., 2009; Kuffner et al., 2008; Martin and Gattuso, 2009; Martin et al., 2008; Price et al., 2011; Robbins et al., 2009; Russell et al., 2009; Sinutok et al., 2011), but the tolerance of these species to pH change within real ecosystems and the role of species interactions in modulating the ecological response to ocean acidification are poorly understood (Barry et al., 2011; Diaz-Pulido et al., 2012; Johnson et al., 2012). Many non-calcareous macroalgal species are able to tolerate a wide range of pH, with some benefiting from higher CO_2 (Connell and Russell, 2010; Fabricius et al., 2011; Roleda et al., 2012) and photosynthetic uptake of CO_2 has the potential to alleviate pH stress over localized scales (Cornwall et al., 2013; Hurd et al., 2011; Saderne and Wahl, 2012). Examining kelp–coralline interactions and the impacts of temperature and pH stress is

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vital to uncovering some of the potentially subtle impacts of climate change stressors on natural assemblages.

Although the impacts of decreasing pH at a species level are increasingly well documented (Anthony et al., 2008; Hofmann et al., 2012; Kuffner et al., 2008; Noisette et al., 2013), results across natural gradients of CO_2 concentration suggest that some calcifiers are able to tolerate decalcification and maintain high photosynthetic rates (Johnson et al., 2012). There is an increasing need to understand how ocean acidification and temperature change will manifest within complex systems, where modification of physical parameters (i.e., uptake of CO_2 by autotrophs; Middelboe and Hansen, 2007; Manzello et al., 2012) and shifts in biological interactions (Connell and Russell, 2010) could change the outcome of pH variations on community composition or ecosystem functioning. Assemblages have been shown to respond differently to irradiance and temperature compared to species studied in isolation (Binzer et al., 2006; Tait and Schiel, 2011, 2013) and testing the effects of pH and temperature variation across a full irradiance gradient in layered assemblages may provide insight into the energetic consequences of predicted CO_2 accumulation in seawater.

In this study I explore the impacts of temperature and pH on coralline–kelp assemblages to understand how changes in ocean pH may influence rates of net primary productivity (NPP) and the importance of the light environment for sub-canopy coralline algae. Upwelling water along the Pacific North-West can be high in pCO_2, with pH values falling below 7.6 (Feely et al., 2008) making it an ideal location to examine how natural communities are responding to large pH fluctuations. This included testing the acute impacts of a natural pH gradient (caused by upwelling) on rates of in situ NPP of coralline assemblages (predominantly *Corallina vancouveriensis*) and coralline–kelp assemblages (*C. vancouveriensis* sub-canopy with an overlying canopy of *S. sessilis*). Furthermore, I manipulated pH under laboratory conditions through control of pCO_2 using mass flow controllers (MFC) to obtain three pH treatments; 8.1, 7.9 and 7.6 and temperature was manipulated to four levels (9, 11, 13, 15 °C). The effects of temperature and pH on NPP and respiration across a light gradient were tested using photorespirometry to generate photosynthesis–irradiance curves (*P–E*). I tested the hypotheses that; 1) NPP of in situ coralline assemblages will respond negatively to decreasing ambient pH, while NPP of coralline–kelp assemblages will respond positively, 2) variation in temperature will affect both coralline and coralline kelp assemblages, while pH variation will have a negative impact only on coralline assemblages and 3) combined temperature and pH changes will amplify the negative effects on coralline dominated assemblages.

2. Materials and methods

To understand the consequences of temperature and pH variation on important photosynthetic parameters of assemblages dominated by the calcareous alga *C. vancouveriensis* and the kelp *S. sessilis* (hereafter referred to as "coralline" assemblages and "coralline–kelp" assemblages), photorespirometry was used to evaluate NPP using both in situ pH gradients caused by temporal variation in upwelling intensity and manipulated variations of pH and temperature in laboratory mesocosms. Since upwelling was associated with decreasing temperature and increased nutrients, the separate effects of temperature and pH across an irradiance gradient were tested in laboratory mesocosms. Using laboratory manipulations I varied temperature and pH independently and in a separate experiment, exposed coralline and coralline–kelp assemblages acclimated to four different temperatures to acute changes in pH and measured respiration rates and net primary productivity (NPP).

2.1. Impacts of natural pH variation on NPP of in situ assemblages

NPP of in situ coralline assemblages (dominated by *C. vancouveriensis*) and coralline–kelp assemblages (*C. vancouveriensis* and *S. sessilis*) was tested at Fogarty Creek (44°50′N, 124°03′W; hereafter FC) and Strawberry Hill (44815.39 N, 124806.79 W; hereafter SH). This was done using custom built photorespirometry chambers sealed around attached assemblages of macroalgae (Fig. 1). These chambers were attached with screws threaded into rawl plugs secured in the substratum and formed a seal with the reef surface using a thick foam gasket. Chambers were fitted with a submerged bilge pump to circulate water within the chambers and oxygen was sampled with a probe fitted into the chamber. Further details on in situ chamber attachment protocol can be found in Tait and Schiel (2010).

To understand the potential impacts of varying pH on in situ coralline and coralline–kelp assemblages ($n = 3$ for each assemblage type), NPP measurements were done on three separate occasions of different upwelling intensities at two field sites, FC and SH. Assemblages were composed of 72% (SE, ±5) *C. vancouveriensis* and 81% (SE, ±7) *S. sessilis*. Due to natural variation in light intensities, NPP data was pooled into two irradiance ranges, 800–1000 μmol m^{-2} s^{-1} ("moderate" irradiance) and 1500–1700 μmol m^{-2} s^{-1} ("high" irradiance). Several environmental parameters were measured during in situ incubations including pH, O_2 (Hach® LDO probe and pH probe), and temperature and irradiance, both measured with HOBO Pendant loggers (Onset©). Average outside-canopy and sub-canopy irradiances were measured during incubations using HOBO light and temperature loggers fixed within the chambers. Proportional light transmittance through the canopy ranged from 0.03 to 0.10 (3–10% of ambient light) which equated to irradiance of 20–50 μmol m^{-2} s^{-1} in the sub-canopy. Although nutrient analysis was not done for this study, even during periods of non-upwelling, nitrogen concentrations are typically between 20 and 30 μmol L^{-1}, but with diurnal reductions due to biological uptake (Sigleo et al., 2005). Furthermore, nutrient concentrations are unlikely to have a large impact on instantaneous measurements of NPP (Bracken and Stachowicz, 2006), and are unlikely to limit growth of macroalgae in this system (Pfister and Van Alstyne, 2003).

Algal richness and percent cover surveys were done at FC and SH. Percent cover of each algal taxon was visually estimated in each plot ($n = 12$ at each site). Cross shore transects were set up across the low shore zone with 0.50 m^2 gridded quadrats randomly assigned along

Fig. 1. In situ photo-respirometry chamber fixed around an assemblage dominated by *Corallina vancouveriensis*.

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