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*p*CO2 effects on species composition and growth of an estuarine phytoplankton community

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ABSTRACT

The effects of ongoing changes in ocean carbonate chemistry on plankton ecology have important implications for food webs and biogeochemical cycling. However, conflicting results have emerged regarding species-specific responses to *p*CO2 enrichment and thus community responses have been difficult to predict. To assess community level effects (e.g., production) of altered carbonate chemistry, studies are needed that capitalize on the benefits of controlled experiments but also retain features of intact ecosystems that may exacerbate or ameliorate the effects observed in single-species or single cohort experiments. We performed incubations of natural plankton communities from Narragansett Bay, RI, USA in winter at ambient bay temperatures (5–13 °C), light and nutrient concentrations. Three levels of controlled and constant CO_2 concentrations were imposed, simulating past, present and future conditions at mean pCO_2 levels of 224, 361, and 724 μatm respectively. Samples for carbonate analysis, chlorophyll *a*, plankton size-abundance, and plankton species composition were collected daily and phytoplankton growth rates in three different size fractions (<5, 5–20, and >20 μm) were measured at the end of the 7-day incubation period. Community composition changed during the incubation period with major increases in relative diatom abundance, which were similar across pCO_2 treatments. At the end of the experiment, 24-hr growth responses to pCO_2 levels varied as a function of cell size. The smallest size fraction (<5 μm) grew faster at the elevated pCO_2 level. In contrast, the 5–20 μm size fraction grew fastest in the Present treatment and there were no significant differences in growth rate among treatments in the >20 μm size fraction. Cell size distribution shifted toward smaller cells in both the Past and Future treatments but remained unchanged in the Present treatment. Similarity in Past and Future treatments for cell size distribution and growth rate (5–20 μm size fraction) illustrate non-monotonic effects of altered pCO_2 on ecological indicators and may be related to opposing physiological effects of high CO_2 and low pH both within and among species. Interaction of these effects with other factors (e.g., nutrients, light, temperature, grazing, initial species composition) may explain variability among published studies. The absence of clear treatment-specific effects at the community level suggests that extrapolation of species-specific responses or experiments with only present day and future pCO_2 treatments levels could produce misleading predictions of ocean acidification impacts on plankton production.

1. Introduction

Ocean chemistry is changing due to absorption of anthropogenic carbon dioxide (CO_2) from the atmosphere (Caldeira and Wickett, 2003; Sabine et al., 2004). This change in chemistry is anticipated to have significant effects on ocean biology (Riebesell, 2008). According to recent meta-analyses, the effects of lowered pH on traits

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such as calcification, growth, and early life stage survival in diverse marine organisms are highly variable, but on balance, are generally negative (Kroeker et al., 2013). Although *in situ* effects have been reported from a few field experiments and in natural gradients (Hall-Spencer et al., 2008), the extent to which laboratory results are predictive of ecological effects in marine environments is one of the major unknowns in ocean acidification science (Fabry et al., 2008). Despite the predictable effects of ocean acidification on biological processes (Kroeker et al., 2013), it is not yet clear how often these biological responses would persist in populations, communities, or ecosystems in ways that scientists, environmental advocates, or society would consider important. To address this gap, experiments are needed that capitalize on the error control of manipulative experiments and yet retain features of intact ecosystems that may exacerbate or ameliorate the effects observed in single-species or single cohort experiments.

Most studies of ocean acidification effects have focused on physiological responses of individual phytoplankton species. Elevated pCO_2 (CO_2 partial pressure) levels are theoretically expected to have a “fertilizer” effect on phytoplankton, given the low CO_2 affinity of the primary carboxylating enzyme RuBisCO (Badger et al., 1998) and the existence of other carbon concentrating mechanisms (Reinfelder, 2011). Indeed, several studies have observed such fertilizing effects for some species, while other species were intolerant of lowered pH levels and primary production rates decreased (e.g., Hutchins et al., 2007; Iglesias-Rodriguez et al., 2008; Rost et al., 2003; Sun et al., 2011; Wolf-Gladrow et al., 1999). Calcifying phytoplankton species have diverse and, at times, contradictory biological responses to altered carbonate chemistry (Iglesias-Rodriguez et al., 2008; Kroeker et al., 2010; Riebesell et al., 2000).

Attempts to scale up from the effects of increased pCO_2 on individual species to inferences about entire taxonomic groups, populations, or communities abound in the literature (e.g., Hendriks et al., 2009). However, strong biological sensitivity at the organismal level is neither a prerequisite for nor a predictor of strong sensitivity at higher levels of biological organization. In addition, the nature and magnitude of ecological changes that would be considered negative is often poorly defined, creating fertile ground for intractable speculation (Duarte et al., 2015).

The responses of whole communities to elevated pCO_2 have been examined in a number of experiments. Increased pCO_2 has been shown to drive shifts in abundance or composition of primary producers and their consumers (Aberle et al., 2006; Hare et al., 2007; Rost et al., 2003; Tortell et al., 2002) as well as community rates of photosynthesis and productivity (Egge et al., 2009; Feng et al., 2009; Fu et al., 2007). For instance, increased pCO_2 had little effect on primary production in a coastal sub-arctic system (e.g., Egge et al., 2009) whereas in Southern Ocean waters, increased pCO_2 acted to increase overall productivity of the community through the growth of chain-forming diatoms (Tortell et al., 2008). Similarly, increased pCO_2 led to dramatic increases in diatom abundance in the North Atlantic (Feng et al., 2009). The variability in responses to increased pCO_2 observed thus far does not allow responses to be extrapolated from one phytoplankton species, community or functional group to another. Moreover, responses are dependent on plankton community composition and environmental conditions at the time of pCO_2 manipulation. For example Gao et al. (2012) observed pH-dependent shifts in primary production that differed between haptophyte- and diatom-dominated communities. It seems likely that experiments with highly unstable carbonate chemistry, as would be expected when large blooms and crashes occur during incubations, would exacerbate these contributors to variability. Although many experiments have been conducted, they span a variety of environments (estuaries, fjords, coasts, open ocean) and very few have reported measurements of carbonate chemistry with sufficient temporal detail to assess stability (but see, e.g., Bach et al., 2016; Brussaard et al., 2013; Endo et al., 2013; Silyakova et al., 2013).

Ocean acidification (OA) alters the carbonate system and results in both increased CO_2 and decreased pH, the responses to which are expected to have opposing energetic costs. The net sum of these opposing costs is likely to vary with a number of traits, one of the most important of which is cell size (Gao and Campbell, 2014; Wolf-Gladrow et al., 1999; Wu et al., 2014). Since these net costs are affected by light and temperature gradients that may or may not coincide with gradients in carbonate chemistry, there is an enormously complex array of potential species-specific outcomes. There are also likely to be differing degrees of genetic variation, phenotypic plasticity and adaptive potential among species (Collins et al., 2014). This may lead to evolutionary shifts in important physiological characteristics like growth rate as species respond to the selective pressure of increased pCO_2 (Scheinin et al., 2015). Thus, it is not surprising that opposing predictions about OA effects on size-abundance spectra have emerged and remain unresolved (e.g., Finkel et al., 2010; Wu et al., 2014). Given these considerations, more experiments are needed that include detailed monitoring of carbonate chemistry and consider the effects of both increases and decreases in CO_2 relative to modern-day concentrations.

Phytoplankton cell size is an easily measured and physiologically important characteristic that is often discussed in the context of responses to environmental change (Barton et al., 2013; Finkel et al., 2010), including OA (Schlüter et al., 2014). Using cell size abundance in the fossil record, Hannisdal et al. (2012) described periods of declining coccolithophore cell size during the pCO_2 decline in the Oligocene (34-23 million years before present). Within a few well-studied species, responses of mean cell size to temperature, pCO_2, and/or light perturbations have been reported (Xu et al., 2014). Gao and Campbell (2014) reviewed 17 studies of species-level responses to elevated pCO_2; results were roughly evenly split between positive, neutral and negative effects. Effects on the full size spectrum of observed phytoplankton communities are rarely reported (Engel et al., 2008), but may have greater predictive value for ecosystem science because of the biomass, energetic and carbon cycling implications of cell size (Menden-Deuer and Lessard, 2000).

In this study, we tested whether CO_2 enrichment could cause changes in community-level plankton community composition, size-abundance and production on scales large enough to motivate concern about effects on trophic transfer. We used outdoor untempered chemostat experiments to control and stabilize the carbonate chemistry while maintaining natural light and temperature cycles and inoculated the chemostats with natural seawater to retain complex phytoplankton community structure. We measured effects on specific taxa as well as community level metrics to assess linkages from species to communities and ecosystem function, such as trophic transfer and primary production rates. The pCO_2 level in our “future” treatment resembled levels that were uncommon in surface waters but already present in bottom waters during a recent study of Narragansett Bay and other northeast U.S. estuaries (Wallace et al., 2014).

2. Methods

2.1. Source water preparation and collection

Surface water samples containing source plankton were collected on 17 February 2014 as part of the Long Term Plankton Time Series station in the West Passage of Narragansett Bay (41° 34.5′ N, 71° 24.3′W); see Fig. 1 in Lawrence and Menden-Deuer