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The ocean acidification seascape and its relationship to the performance of calcifying marine invertebrates: Laboratory experiments on the development of urchin larvae framed by environmentally-relevant pCO_2/pH

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ABSTRACT

Variation in ocean pH is a dynamic process occurring naturally in the upwelling zone of the California Current Large Marine Ecosystem. The nearshore carbonate chemistry is under-characterized and the physiology of local organisms may be under constant challenge from cyclical changes in pH and carbonate ion concentration of unexpectedly high magnitude. We looked to environmental pH conditions of coastal upwelling and used those values to examine effects of low pH on 4-arm larvae of purple sea urchin *Strongylocentrotus purpuratus*. We deployed a pH sensor at a nearshore shallow benthic site for 3 weeks during summer 2010 to assess the changes in pH in the Santa Barbara Channel, a region considered to have relatively less intense upwelling along the US Pacific Coast. Large fluctuations in pH of up to 0.67 pH units were observed over short time scales of several days. Daily pH fluctuations on a tidal pattern followed temperature fluctuations over short time scales, but not over scales greater than a day. The lowest pH values recorded (~7.70) are lower than some of those pH values predicted to occur in surface oceans at the end of the century. In the context of this dynamic pH exposure, larvae were raised at elevated pCO_2 levels of 1000 ppm and 1450 ppm CO_2 (pH 7.7 and 7.5 respectively) and measured for total larval length (from the spicule tip of the postoral arm to the spicule tip of the aboral point) along the spicules, to assess effects of low pH upwelling water on morphology. Larvae in all treatments maintained normal development and developmental schedule to day 6, and did not exhibit significant differences in larval asymmetry between treatments. At day 3 and day 6, larvae in the 1450 ppm CO_2 treatment were significantly smaller ($p < 0.001$) than the control larvae by only 7–13%. The observation of smaller larvae raised under high pCO_2 has an as yet undetermined physiological mechanism, but has implications for locomotion and feeding. These effects of small magnitude in these urchin larvae are indicative of a potential resilience to near-future levels of ocean acidification. Using environmental monitoring of pH to inform experimental parameters provides a means to improve our understanding of acclimatization of organisms in a dynamic ecosystem.

1. Introduction

Research on the effects of ocean acidification (OA) on organismal function has now been conducted on a variety of marine species (see Kurihara, 2008; Przeslawski et al., 2008; Doney et al., 2009; Dupont and Thorndyke, 2009; Ries et al., 2009; Hofmann et al., 2010; Crim et al., 2011-this issue). As the empirical evidence from these CO_2 manipulation experiments continues to grow, it is increasingly clear that many species are sensitive to OA conditions whereas other species are quite tolerant. Notably, the majority of these studies employ IPCC (2007) emission scenarios to determine the pCO_2 levels (or pH levels) used in the experimental design (e.g., from our laboratory: Todgham and Hofmann, 2009; O'Donnell et al., 2010). One of the ultimate goals of our physiologically-inclined research in the field of OA is to perform our laboratory experiments in the context of the actual environmental conditions experienced by the study organisms in nature; that is, to consider the ocean acidification seascape in an experimental context.

The benefits of such an approach are considerable — experimental results can be interpreted in a manner that better supports forming predictions about individual species' responses (e.g., Melzner et al., 2009) and, thus ecosystem vulnerability to OA (see Widdicombe and Spicer, 2008). Additionally, knowing environmental conditions opens the door to asking questions about physiological performance across a species' range (i.e., macrophysiology in a climate change context —

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see Chown and Gaston, 2008; Gaston et al., 2009 for a review). This contribution to the special edition on ‘Global environmental change in marine ecosystems’ highlights the emerging research activities in our laboratory. Here, we report data on the development and morphology of the larvae of the purple sea urchin (*Strongylocentrotus purpuratus*) from laboratory experiments that are framed within the estimated present-day environmental exposure for pelagic stages of this species (see Hauri et al., 2009). In addition, we present field observations of pH collected using a SeaFET pH sensor (Martz et al., 2010). This latter data set is preliminary but illustrates a technical approach that may be useful to marine ecologists and ecophysiologists interested in linking environmental exposures to physiological performance in the lab.

Until recently there has been a paucity of nearshore environmental pH data that are available to the research community within experimental marine biology and ecology (e.g., Yates and Halley, 2006; Yates et al., 2007; Hall-Spencer et al., 2008; Wootton et al., 2008; Chierici and Fransson, 2009; Gagliano et al., 2010). In general, high quality pCO_2 data are limited to snapshots taken during large field campaigns (e.g. World Ocean Circulation Experiment “WOCE”, http://woce.nodc.noaa.gov/wdiu/; U.S. Joint Ocean Global Flux Study “JGOFS”, http://www1.whoi.edu/; Climate Variability and Predictability “CLIVAR”, http://www.clivar.org/), a few time-series locations (e.g. Bermuda Atlantic Time Series “BATS”, http://www.bios.edu/research/bats.html; Hawaiian Ocean Times Series “HOTS”, http://hahana.soest.hawaii.edu/hot/hot_jgofs.html), and occasional process studies that would best pair with a study system or study organisms in the open ocean. Furthermore, for an individual research group interested in linking environmental variables of OA to experimental biology, collecting these types of data can be a logistical and technical challenge, involving time-consuming and expensive carbonate chemistry sampling and analysis, and a relative lack of affordable and deployable sensors for pH equivalent to those available for measuring temperature (e.g. *i*buttons and StowAway® TidbiT™ loggers). The recent development of autonomous pH sensors (Seidel et al., 2008; Martz et al., 2010) has enabled the collection of pH data at study sites in a manner that can support studies on local to larger whole ecosystem scales. As of February 2011, 45 autonomous Durafet sensors have been deployed by 13 research groups at multiple sites along the North American West Coast, Pacific Islands, Gulf of Mexico, and Mediterranean Sea (Martz et al., unpublished data: http://martzlab.ucsd.edu/data.html). In this study, we deployed a sensor on the near-shore benthos at a site in the Santa Barbara Channel. This site is in the southern biogeographic range of the study organism, the purple urchin *S. purpuratus*, and larvae in the water column would encounter chemistry typical of this location. In addition to being a developmental model organism, *S. purpuratus* is also a model in the study of calcium biomineralization (Wilt, 2005; Mann et al., 2008a, 2008b), thus affording us a model study organism about which there is already a substantial body of research into the formation of calcified structures. The objective of this aspect of the study was to begin to characterize the heterogeneity of coastal waters of the California Current Large Marine Ecosystem (CCLME), an upwelling-dominated system on the west coast of the U.S., and relate these values to the physiological performance and tolerances of our study organism, the purple sea urchin.

In terms of what is known regarding the pCO_2 of waters of the CCLME, the observations suggest that there is heterogeneity in the physical nature of coastal waters. Further, these observations indicate that organisms in the CCLME experience low pH and high pCO_2 values that are not expected for the open ocean for another ~100 years or longer. Globally, the Northeastern Pacific region has both the shallowest aragonite and calcite saturation depth horizons ($\Omega = 1$); on average, the West coast of North America from Alaska down to the tip of Central America is undersaturated with respect to calcite below 500 m depth (Feely et al., 2004). Specifically, Feely et al. (2008) report that in summer 2007, the aragonite saturation horizon had shoaled (>20 m) during peak upwelling on the coast of the Oregon–California state line. These investigators estimate that the aragonite saturation horizon in the eastern North Pacific has shoaled by 50–100 m since the pre-industrial era. High resolution time series by Hales et al. (2005) demonstrate high short-term dynamic variability in pCO_2 (reported as X_{CO2}) with shifting wind stress, and the large differential between offshore and nearshore conditions, with sharp pCO_2 gradients occurring over <10 km. More recently, pCO_2 levels ranging from 200 to 1400 μatm have been recorded along the Oregon coast near Cape Perpetua and Newport, OR during the period of April–October 2009 (Francis Chan, unpublished observations).

Given the variability in pH exposure that larvae could experience during the pelagic stage in the waters of the CCLME, we explored the effects of elevated pCO_2 on the development of larvae of the purple urchin. We predicted that purple urchin larvae would mostly develop normally with possible minor perturbations, as they may be more adapted to conditions of variable and elevated pCO_2. Evidence from other studies indicate that larvae of sea urchins show a range of negative responses (from decreased fertilization success, to smaller sizes and altered gene expression) under elevated pCO_2 levels that generally vary according to the intensity of the treatments (reviewed by Dupont et al., 2010). Though we were certain the effects on larvae were sublethal, we nonetheless expected some effect on overall performance/growth given the metabolic costs of functioning at lower pH.

Larval size and in particular, larval length and arm length, is a highly plastic character in echinoid larvae. While it is only moderately reliable as a proxy for feeding physiological state (Fenaux et al., 1994; Reitzel et al., 2004), the shape and size of the arms is directly controlled by spicule length. Multiple studies on echinoplutei have shown a consistent pattern of decreased larval and arm length resulting from acidification treatments, with a wide range of responses observed among the different treatments used (Kurihara and Shirayama, 2004; Brennand et al., 2010; Dupont et al., 2010; O'Donnell et al., 2010). The mechanism responsible for reduced size has not been determined, but could result from a combination of factors including developmental delay (e.g., Dupont and Thorndyke, 2008), reduced growth from depressed metabolism, and decreased ability to deposit calcium carbonate due to greater energetic cost (Cohen and Holcomb, 2009).

In this study, we present morphometric analysis of larval endoskeletons cultured under variable pCO_2 treatments that bracket a range of environmental exposures that would be characteristic of waters in the North Pacific coastal upwelling system (see Feely et al., 2008). In addition, we provide a small data set of environmental pH collected from the Santa Barbara Channel using a SeaFET sensor (Martz et al., 2010). These are the first data in our possession that will assist us in performing manipulative laboratory CO_2 exposure culturing experiments that are framed using realistic environmental data.

2. Material and methods

2.1. Larval culturing

Gravid adult purple urchins (*S. purpuratus*) were collected by SCUBA divers off Goleta Pier, Goleta (34° 24.854 N 119° 49.711 W) at a depth of 5.5 m in November 2009, and maintained in flowing seawater aquaria (ambient temperature) until spawning at the University of California, Santa Barbara. Adult urchins were fed *ad libitum* with *Macrocystis pyrifera* until use in experiments. *S. purpuratus* has a biogeographic distribution that ranges from Alaska to the northern half of the Baja Peninsula, Mexico.

Gametes were obtained by coelomic injection of 0.5 M KCl. The eggs were resuspended in 0.35 μm filtered, UV-sterilized seawater (FSW) at ambient temperature and pCO_2 for fertilization. The sperm