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Exploring local adaptation and the ocean acidification seascape – studies in the California Current Large Marine Ecosystem

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Abstract. The California Current Large Marine Ecosystem (CCLME), a temperate marine region dominated by episodic upwelling, is predicted to experience rapid environmental change in the future due to ocean acidification. The aragonite saturation state within the California Current System is predicted to decrease in the future with near-permanent undersaturation conditions expected by the year 2050. Thus, the CCLME is a critical region to study due to the rapid rate of environmental change that resident organisms will experience and because of the economic and societal value of this coastal region. Recent efforts by a research consortium – the Ocean Margin Ecosystems Group for Acidification Studies (OMEGAS) – has begun to characterize a portion of the CCLME; both describing the spatial mosaic of pH in coastal waters and examining the responses of key calcification-dependent benthic marine organisms to natural variation in pH and to changes in carbonate chemistry that are expected in the coming decades. In this review, we present the OMEGAS strategy of co-locating sensors and oceanographic observations with biological studies on ben-thic marine invertebrates, specifically measurements of functional traits such as calcification-related processes and genetic variation in populations that are locally adapted to conditions in a particular region of the coast. Highlighted in this contribution are (1) the OMEGAS sensor network that spans the west coast of the US from central Oregon to southern California, (2) initial findings of the carbonate chemistry amongst the OMEGAS study sites, and (3) an overview of the biological data that describes the acclimatization and the adaptation capacity of key benthic marine invertebrates within the CCLME.

1 Introduction

A leading imperative in global change biology is forecasting the impact of environmental change on key species and ecosystems (Buckley and Kingsolver, 2012; Hoffmann and Sgrò, 2011; Williams et al., 2008; Dawson et al., 2011), and on critical natural resources (Gillson et al., 2013; Ibáñez et

al., 2013; Pettorelli, 2012). As exemplified by the study of ocean acidification (OA) (Boyd, 2011; Hofmann et al., 2011; Kroeker et al., 2013), the issues in this scientific endeavor are complex. In addition to the natural complexity in ecosystems emanating from biotic interactions and variability in biological responses to the environment, physical environmental parameters can also vary dramatically, as is evident when comparing disparate ecosystems such as tropical reefs and polar seas. From a biological perspective, one way to better predict the consequences of ocean change is to examine ways in which populations could potentially respond to environmental change. One mechanism is inherent physiological plasticity that confers tolerance to a changing environment (Chown, 2012; Chown and Gaston, 2008; Helmuth, 2009; Huey et al., 2012); a second is outright evolutionary adaptation to rapidly changing conditions (Hoffmann and Sgrò, 2011; Kelly and Hofmann, 2012; Visser, 2008; Sunday et al., 2013). Of the two responses, evolutionary adaptation may be the most difficult to study. The absence of extensive long-term data sets and the existence of complexity of biological processes combined with vast spatial expanses to cover have made studying evolution in the ocean a significant challenge.

In the oceans, major changes in temperature and carbonate chemistry are predicted in the coming decades (Feely et al., 2009; Gruber et al., 2012; Hauri et al., 2013; Orr et al., 2005) and in some ecosystems the rate of change will be rapid. For example, Australia is experiencing warming and extreme heat events (Wernberg et al., 2013) and the western Antarctic Peninsula has warmed significantly in the last two decades with significant decreases in sea ice that have already altered this polar marine ecosystem (Steinberg et al., 2012). In the California Current system, the focus of this article, aragonite saturation state in the upwelling zone is expected to decrease rapidly in the future (Gruber et al., 2012; Hauri et al., 2013). Here, within the next 30 yr, summer-long undersaturation conditions are expected in nearshore regions in the top 60 m. Thus, the California Current Large Marine Ecosystem (CCLME) is a critical region to study, both in terms of the pace at which associated biota might experience rapid environmental change and because of the economic and societal value of this coastal region (Costanza et al., 1997). From a biological perspective, we have limited information on how critical species might respond to this predicted shift in ocean chemistry. Major questions remain regarding whether marine species currently possess functional traits that would allow the tolerance of a changing environment, or whether they will be able to adapt to rapidly changing ocean conditions into the future.

Recently, a collaborative group of investigators, who have been studying biological, ecological and oceanographic conditions along the US west coast for decades, has begun to tackle these questions in the CCLME using a strategy that involves co-locating oceanographic sensors with biological observations. This group, called OMEGAS (Ocean Margin Ecosystems Group for Acidification Studies), has worked as a collaborative body since 2010 studying an area spanning from central Oregon (OR) to southern California (CA; Fig. 1). Research activities include gathering oceanographic observations (e.g., pH, pCO_2, alkalinity, temperature, salinity, currents) that are matched with biological data (physiological measurements, organismal-level responses to low pH conditions such as growth rates and calcification, and genetic data) for key species of calcifying benthic marine invertebrates. The central goal of the OMEGAS project is to consider physiological and ecological performance of organisms, and genetic variation within and between populations, within the broad spatial mosaic of pH and saturation states found across the CCLME. Ocean acidification is driven by absorption of anthropogenic CO_2 into surface waters and the commensurate change in ocean chemistry, both the reduction in pH and the decline in the concentration of carbonate ions, are physiologically challenging to calcifying marine organisms (Doney et al., 2009). Further, because pH and saturation state regimes vary widely across the CCLME, our research allows a "substitution of space for time" (Pickett, 1989) approach in an exploration of local adaptation of benthic marine invertebrates to carbonate chemistry (Sanford and Kelly, 2011). The combination of simultaneous oceanographic and biological research across a large latitudinal range will help identify areas on the coast that express a range of acidification conditions. This information may indicate areas that might be refuges from acidification in the future, and could reveal regions that are adaptation "hot spots"; i.e., places where selection for undersaturation-tolerant genotypes has been underway for long periods of time (Jacobs et al., 2004). Finally, discovery of tolerant populations within the environmental mosaic of the CCLME can provide an opportunity to identify mechanisms that underlie tolerance (Evans et al., 2013a; Evans and Hofmann, 2012). We also hope to address whether some species possess sufficient physiological and genetic variation to adapt to future change. Species that lack physiological plasticity may quickly become excluded from an environment when change occurs. Alternatively, organisms with the capacity to adapt should do so, and exploring the degree of standing genetic variation for pH tolerance may help us to forecast responses to environmental change (De Wit and Palumbi, 2012; Kelly et al., 2013; Pespeni et al., 2013a).

Thus, from a broad perspective, the OMEGAS strategy of co-locating sensors with biology allows one to explore the balance of physiological plasticity vs. capacity for adaptation in the light of present-day environmental conditions (Kelly and Hofmann, 2012). Such an assessment is critically important in allowing prediction of outcomes that rely on both species- and community-level responses (Kroeker et al., 2013; Wootton et al., 2008; Hall-Spencer et al., 2008). The goal of this article is to overview recent efforts of the OMEGAS consortium (http://omegas.science. oregonstate.edu) in the study of physiological plasticity and the capacity for adaptation in populations of benthic marine
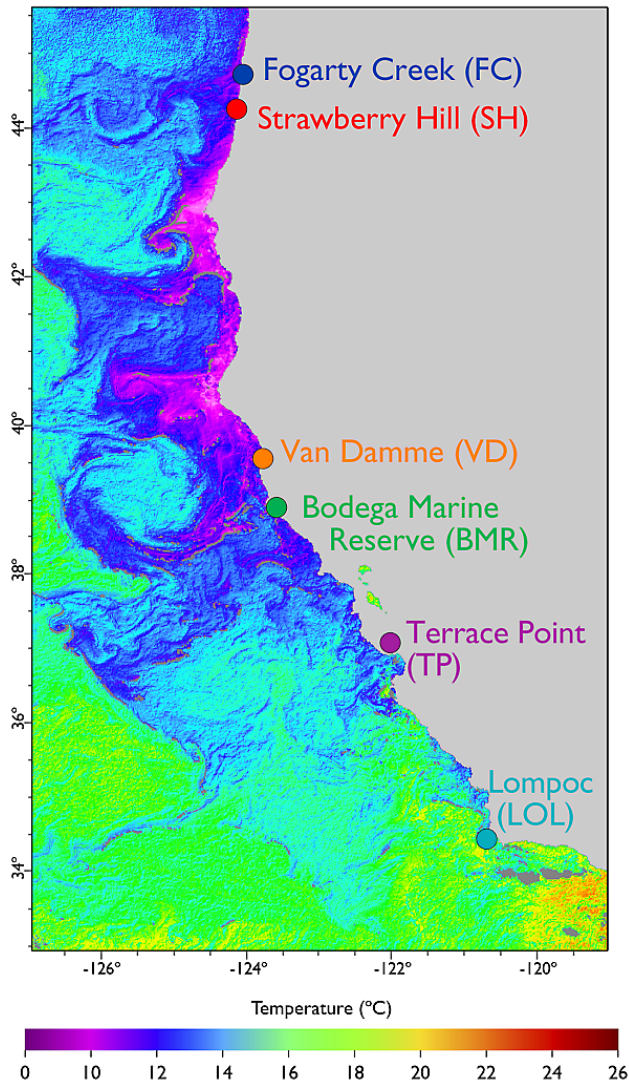
Fig. 1. Map of the OMEGAS study sites in the California Current Large Marine Ecosystem. The OMEGAS primary study sites are from north to south: Fogarty Creek (FC), Strawberry Hill (SH); Van Damme (VD); Bodega Marine Reserve (BMR); Terrace Point (TP) and Lompoc Landing (LOL). Note: colors in the image represent sea surface temperature (°C) from the NOAA CoastWatch database.

invertebrates across the CCLME. Here, we outline three lines of investigation that are integrated across the group and that frame our studies: (1) an overview of a spatially distributed sensor network for quantifying pH dynamics, (2) data on functional traits that may vary in populations and support physiological plasticity, and (3) data on genetic structure of the study populations that link to local adaptation in natural populations and the capacity to adapt to future environmental change in the CCLME.

2 The OMEGAS sensor network: identifying a pH mosaic in the CCLME

A central goal of researchers within the OMEGAS consortium is to link biological performance with environmental variability in ocean carbonate chemistry along what we hypothesized would be a mosaic or gradient of conditions that might foster local adaptation. Long-term observations have been invaluable in defining the rate of OA progression in low-latitude, open ocean biomes and records from sub-tropical gyre time-series stations (e.g., Bermuda Atlantic Time Series "BATS", http://www.bios.edu/research/bats.html; Hawaiian Ocean Times Series "HOT", http://hahana.soest.hawaii.edu/hot/hot_jgofs.html; European Station for Time Series in the Ocean "ESTOC" http://www.eurosites.info/estoc.php) show a decline of ocean pH from −0.02 to −0.04 pH units over a 20 yr period against low-frequency seasonal oscillations of similar magnitude (Bates et al., 2012; Dore et al., 2009; Santana-Casiano et al. 2007). For coastal regions, the scientific community is just now assessing the longer-term variability in pH. Recent analyses of long-term data sets indicate that pH is changing rapidly in coastal Washington (Wootton and Pfister, 2012), in coastal upwelling zones along the US Pacific coast (Harris et al., 2013; Chan et al., 2014), at a coastal region in the Netherlands (Provoost et al., 2010), and in the Monterey Bay area where low pH water is associated with low oxygen water masses that reach the shallow, nearshore regions (Booth et al., 2012). Cruise data have provided snapshots of carbonate chemistry along the coast of the CCLME (Feely et al., 2008), and suggested that at some locations in northern California, undersaturated waters shoaled in the inner shelf. Prior to OMEGAS, however, no coordinated inner-shelf time series were available that would allow evaluation of the frequency, intensity and spatial expanse with which coastal ecosystems experience rapid acidification.

The recent development of autonomously recording pH sensors (Martz et al., 2010) has helped to bridge this data gap. Easily deployed on either moorings or benthic (e.g., rocky intertidal) locations, these sensors facilitate the collection of environmental pH data in a variety of habitats and support the collection of long-term data sets that more comprehensively characterize the OA seascape (Hofmann et al., 2013). Recent deployments of these sensors has highlighted that different ocean ecosystems display a great deal of natural variability in pH (Frieder et al., 2012; Hofmann et al., 2011; Kroeker et al., 2011; Price et al., 2012). Importantly, these sensors have created an affordable option for marine scientists to describe spatial patterns in ocean chemistry across dynamic coastal systems. In these environments, characterization of local-scale differences can be ecologically and economically critical, but require discrete sampling efforts that are often logistically and cost-prohibitive. Additionally, this strategy facilitates identification of refuges from future ocean acidification, information that would provide information to managers of coastal ecosystems and resources. It also allows the

exploration of patterns of local adaptation to carbonate chemistry across large marine ecosystems such as the CCLME, where previous studies have demonstrated possible genetic differences among populations (De Wit and Palumbi, 2012; Kelly et al., 2013; Pespeni et al., 2012, 2013a, b, c).

In summer 2011, OMEGAS scientists deployed a network of environmental sensors on the US west coast at locations that span ~ 1300 km of the CCLME. The sensor network included intertidally deployed instruments paired with instruments mounted on inner-shelf moorings (depth = 15–25 m), initially at eight sites ranging from central Oregon to Santa Barbara, CA (Fig. 1). Descriptions of intertidal sensors and sites and mooring configurations can be found elsewhere (Washburn et al., 2011; Evans et al., 2013; Pespeni et al., 2013c; Adams et al., 2013), but briefly, pH records shown in Fig. 2 are from custom-designed Durafet®-based sensors deployed in open coast, intertidal rocky habitats to record at 10 min intervals. Sensors were calibrated directly against certified reference materials (CRM) or indirectly against CRM-calibrated spectrophometric pH samples. Periodic (2–4 weeks) discrete samples were collected for checks on sensor performance in situ and for characterization of carbonate system chemistry via paired total alkalinity and total CO_2 or total alkalinity and spectrophotometric pH samples. Information on the range of alkalinity in conjunction with the tight covariation between pH and pCO$_2$ served to constrain the range of possible pCO$_2$ values for the system and to inform treatment selection for laboratory studies. This region is well known for patterns of episodic upwelling that vary from relatively intermittent to the north and relatively persistent to the south (Checkley Jr and Barth, 2009; Menge and Menge, 2013). Recent efforts to characterize the nearshore carbonate chemistry of the California Current system (Fassbender et al., 2011; Feely et al., 2008; Hauri et al., 2009) suggest that biota of this region experience natural variation in pH due to latitudinally and temporally variable upwelling. Results from the OMEGAS sensor network indicate that acidification of coastal waters extends into the nearshore environments of the CCLME with low pH, undersaturated water reaching the rocky intertidal zone (Evans et al., 2013; Pespeni et al., 2013c; Chan et al., 2014). Importantly, these data indicate that biota in the plankton and benthic marine organisms on shore face an exposure regime to low pH and undersaturated waters that is tremendously dynamic in time and space (Evans et al., 2013; Chan et al., 2014). Across the OMEGAS network, the frequency of low pH events encountered in intertidal sensors ranged widely (Fig. 2). In central Oregon, as much as 20 % of pH values fell below 7.8. In contrast, sites in central and southern California experienced exposure to pH values below 7.8 less than 2 % of the time. This pattern of spatial separation is even more pronounced when we consider pH exposure at even lower-thresholds. For example, the frequency of exposure to low pH conditions of 7.7 or less at Bodega Marine Reserve (BMR) – a site in the geographic center of the network – is most similar to a station 700 km
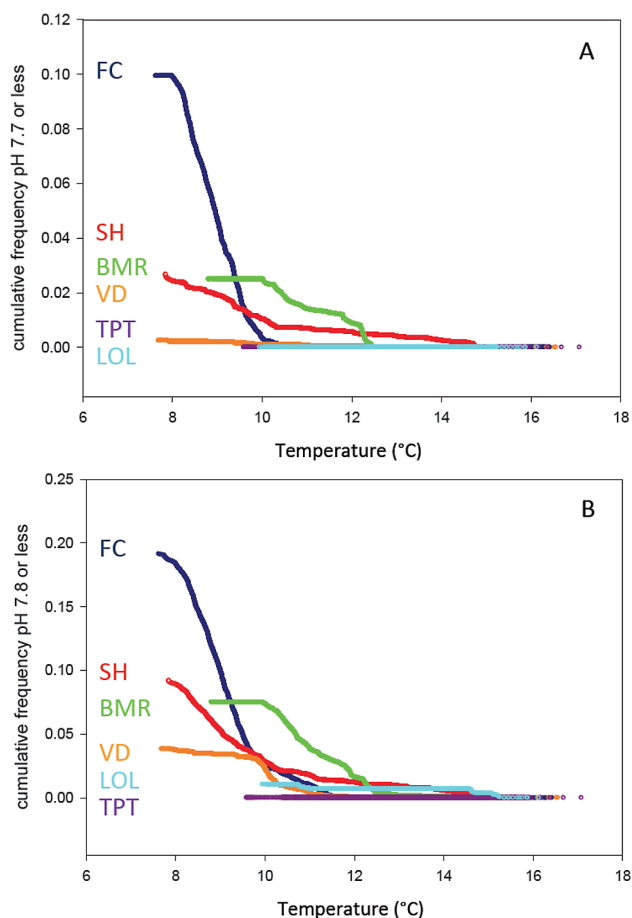

Fig. 2. Cumulative frequencies of exposure to pH (total scale) less than 7.7 (**A**) and 7.8 (**B**) as recorded at 10 min intervals by in situ Durafet®-based pH sensors deployed in intertidal environment between April and September (maximum record length). Exposure frequencies at a given pH threshold are normalized to expanding windows of maximum to minimum in situ water temperature to illustrate the response of pH to the progressive strengthening of seasonal upwelling at each site.

to the north in central Oregon at Strawberry Hill (SH), than adjacent stations within 150 km to the north at Van Damme (VD) and the southern site Terrace Point (TP). At 14 °C, this pH corresponds to a pCO$_2$ value of 1200 µatm in our system. Such values were used to inform experiments described below (Fig. 3). Our emerging understanding from this first year of operational deployment of the OMEGAS network thus suggests a mosaic-like coastal pH seascape where organism's exposure to OA is both geographically defined and variable over spatial scales of dispersal of marine larvae (Gouhier et al., 2010; Navarrete et al., 2008).

Further, analysis of the time series data show that there is a mosaic of OA where sites in the northern portion of the study region (in central Oregon) have a greater intensity of exposure to low pH than sites in the southern portion of the study region (Fig. 2). Specifically, when parsing the data as
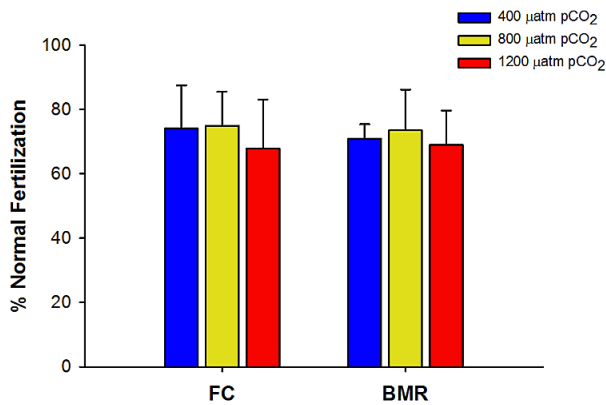
Fig. 3. Fertilization success of *Strongylocentrotus purpuratus* gametes across populations and pCO_2 treatments. Adult urchins were collected from two locations that spanned the CCLME and the OMEGAS study sites: Fogarty Creek (FC), OR, and Bodega Marine Reserve (BMR), CA. Adult pairs from the same site were spawned in the laboratory (FC $N = 12$ pairs; BMR $N = 8$ pairs). Eggs were fertilized at 14 °C under control (400 µatm) and elevated (800 µatm, 1200 µatm) pCO_2 conditions at an ecologically relevant sperm concentration of 7×10^3 sperm mL^{-1}. Gametes were allowed a 30 min contact time and at least 200 eggs were scored per pair after the second cleavage. There was no significant effect of pCO_2 by population (two-way ANOVA; $pCO_2 \times$ site effect $p = 0.8577$; pCO_2 effect $p = 0.3168$; site effect $p = 0.7147$). A similar pattern was observed at higher and lower sperm concentrations (data not shown).

a function of measurements below pH 7.7, Fogarty Creek (FC) in Oregon has a much greater number of measurements below pH 7.7 whereas sites in California, Lompoc Landing (LOL), have the lowest frequency (Fig. 2a). If that filter is changed to pH 7.8, Fogarty Creek continues to maintain its position as the site with the greatest frequency of low pH exposure, other sites in central California begin to show elevated frequency of low pH but LOL in the south persists in being a low OA site (Fig. 2b).

3 The biology: assessing physiological plasticity and functional traits

Having demonstrated the mosaic of pH experienced by organisms at study sites across the CCLME, OMEGAS investigators began to explore whether there are functional traits and physiological performance profiles in key calcification-dependent organisms that are acclimatized to this pattern of carbonate chemistry conditions. Although it is difficult to pin any one phenotypic element on a single selection factor in the environment (e.g., temperature or pH alone), the importance of the phenotype and tolerance traits has been increasingly recognized as a key mechanism by which a species might respond to environmental change in a number of systems (Buckley and Kingsolver, 2012; Chown, 2012; Chown and Gaston, 2008; Helmuth, 2009). Recently within the

OMEGAS research community, functional traits and physiological tolerances have been measured in an environmentally relevant context (Evans et al., 2013; Kelly et al., 2013; Padilla-Gamiño et al., 2013; Pespeni et al., 2013a; Yu et al., 2011). The OMEGAS group hypothesized that such phenotypic traits would show variation across space if benthic invertebrates are acclimatized to the local conditions (Chown, 2012) such that they might also contribute to how species respond to environmental change.

Studies initiated by the OMEGAS research teams first focused on populations of ecologically important calcification-dependent benthic marine invertebrates, the purple sea urchin, *Strongylocentrotus purpuratus*, and the mussel, *Mytilus californianus*, across the OMEGAS study sites. Experiments conducted by the group included field experiments at different OMEGAS sites and laboratory mesocosms that tested the response of organisms from various populations to variation in pH. The overall results of the laboratory component demonstrated that the two study organisms displayed different degrees of sensitivity to shifts in ocean chemistry with sea urchins appearing to be more resilient to variation in partial pressure of carbon dioxide (pCO_2) than mussels. Specifically, larval culturing of purple sea urchins in CO_2 mesocosms showed sea urchin larvae were tolerant of pCO_2 levels that are representative of present-day pCO_2 levels documented by OMEGAS field sensors. That is, growth, morphology, early development to echinopluteus and development to metamorphosis were rarely affected (Kelly et al., 2013; Padilla-Gamiño et al., 2013; Pespeni et al., 2013a), although minor decreases in the size of the larval skeleton were seen at elevated pCO_2s of around 1000 µatm (Padilla-Gamiño et al., 2013). The mechanistic underpinning of this tolerance and physiological plasticity is currently being examined in greater detail. However, in the analyses of urchin larvae from the CO_2 mesocosm experiments, the transcriptome displayed variable gene expression during development that likely compensates for carbonate under-saturation and challenges to calcification and pH_i homeostasis (Evans et al., 2013a). In contrast, laboratory studies on mussel larvae (*M. californianus*) showed that low pH conditions reduced growth and shell strength (Gaylord et al., 2011). In light of the pH mosaic data from the sensors, these results suggest that mussel recruits will vary across the CCLME in terms of their susceptibility to drilling and crushing predators, and that susceptibility will increase through time.

When functional traits were compared from animals in populations across the OMEGAS study sites, we found a more complicated story. However, for the most part, results thus far highlight a resilience of function in the study's marine invertebrate organisms. First, in line with the robustness of the early-life embryonic stages of sea urchins in mesocosm studies, analysis of fertilization kinetics using adult, purple sea urchins collected from OMEGAS sites showed that fertilization success was not affected by elevated pCO_2 (Fig. 3), with populations from both FC and further south

at BMR showing the same insensitivity to elevated $p\text{CO}_2$. Similarly, larval culturing of sea urchins demonstrated that larvae from northern and southern populations have similar and more resilient metabolic responses to $p\text{CO}_2$ (Kelly et al., 2013). Specifically, oxygen consumption rates in early pluteus did not change between larvae reared under different $p\text{CO}_2$ conditions (Fig. 4a), and this response was consistent between populations exposed to different upwelling regimes (Kelly et al., 2013). Examining a feature of juvenile and adult sea urchins – the mineralogy of the calcium carbonate skeleton– LaVigne et al. (2013) found that for the most part the composition of the skeleton was not different in urchins collected across the latitudinal gradient of the OMEGAS study sites. Adult spine composition (Mg / Ca and Sr / Ca ratios) was not different between populations from Fogarty Creek, Oregon, in the north to others near Lompoc Landing in southern California (LaVigne et al., 2013) (Fig. 4b).

Finally, field experiments examined mussel growth at all the OMEGAS sites and, surprisingly, evidence to date suggests that adult mussel growth was *not* reduced at low pH sites across the OMEGAS regions (Fig. 4c). The results are more strongly correlated to other characteristics of the sites and growth may be driven by other factors such as food availability (Thomsen et al., 2013) and temperature (Blanchette et al., 2007; Menge et al., 2008). These results that highlight different responses in life history stages of mussels (adult vs. larval forms) are intriguing, and our emphasis in future research will be to investigate the changes in physiology and ecology that underlie this apparent ontogenetic shift in sensitivity in *M. californianus*.

Taken together, studies initiated by the OMEGAS research teams have made two critical observations: species display a range of sensitivities to OA in the laboratory, and patterns of functional traits in natural populations show unexpected divergences from expectations (e.g., faster growth at sites with more extreme exposure to pH). Additional insights and resolution of these patterns await further study in the coming field seasons for OMEGAS research. Finally, it should be noted that only a very few species from the rich biota of the CCLME have been studied in an OA context (Table 1) and determining the OA tolerance across a larger number of species occupying similar pH environments in the CCLME is a critical research need.

4 Local adaptation and benthic marine invertebrates of the CCLME

In addition to studying functional traits of study organisms, several lines of investigation within the OMEGAS group have been designed to address local adaptation. Local adaptation occurs when there is genetic variation among populations that matches some aspect of the environment, so that on average "local" genotypes outperform "foreign" genotypes

when they compete against one another in the home environment (Kawecki and Ebert, 2004). An understanding of local adaptation is relevant to forecasting a species' capacity to adapt to global change for two reasons. First, adaptation depends on genetic variation. Local adaptation to a particular gradient (temperature, pH) implies the existence of variation that will allow for adaptation to changes in that gradient in the future. In addition, the capacity to adapt to an environmental variable in *space*, suggests the capacity to adapt to changes in that variable through *time*. And conversely, limits to adaptation in space (for example failure to adapt to maximum temperatures above 20 °C at a southern range limit) suggest possible limits to adaptation in the face of future changes.

There are several approaches to describing local adaptation. The gold standard for demonstrating local adaptation is a set of reciprocal transplants among sites, followed by a comparison of some aspect of performance for "local" vs. "foreign" genotypes in each environment. However, when local genotypes can be shown to have the highest performance in a particular environment it will not always be clear to which aspect of the environment they are responding to, as aspects of the environment (e.g., temperature, pH, biotic interactions) often co-vary. To test for adaptation to a specific environmental variable of interest, it will often be necessary to bring organisms from different populations into the laboratory, and examine variation in performance along a particular axis of environmental variation.

This type of laboratory experiment was done by OMEGAS investigators with sea urchins. Kelly et al. (2013) performed quantitative genetic crosses among purple sea urchins (*Strongylocentrotus purpuratus*) from two different sites with different upwelling regimes, and then reared the offspring of these crosses under high and low $p\text{CO}_2$. They found abundant genetic variation for the response to high $p\text{CO}_2$, but only minor differences between the offspring of males from the two sites. However these small differences were consistent with local adaptation to pH, with offspring from the site with more exposure to extreme pH levels showing a lesser sensitivity to low pH (Fig. 5). The lack of large differences among populations is also consistent with the biology of purple urchins, which have long-lived planktonic larvae, and therefore relatively homogenized populations (Edmands et al., 1996).

Another way to demonstrate genetic differences among populations is to identify differences in actual gene sequences. Pespeni et al. (2012) performed a genome-wide scan of polymorphisms for two distant populations of the purple urchin *S. purpuratus*. They found many polymorphisms whose frequencies differed strongly among populations, indicating that they were targets of selective forces that differed among these populations. Similarly, De Wit and Palumbi (2013) used transcriptome sequencing of three populations of the red abalone (*Haliotis rufescens*) to identify single nucleotide polymorphisms (SNPS) in genes that

Table 1. Ocean acidification studies on functional traits of organisms in the California Current Large Marine Ecosystem.

| Taxonomic Group	Species Name	Life Stage	Variable Measured	Response	Source
Invertebrate	*Strongylocentrotus franciscanus*	Larvae	Transcription of *hsp70*	Larvae that were raised under enhanced CO_2 displayed compromised expression of the thermally induced molecular chaperone *hsp70*.	O'Donnell et al. (2009)
Invertebrate	*Lytechinus pictus*	Larvae	Morphometrics transcriptomics	Larvae cultured under high CO_2 were smaller and had a more triangular body. Downregulation of genes related to metabolism and biomineralization. Upregulation of a few genes related to ion regulation and acid-base pathways.	O'Donnell et al. (2010)
Invertebrate	*Mytilus californianus*	Larvae	Shell strength and size	Larvae raised under high CO_2 developed thinner, weaker and smaller shells as compared to controls.	Gaylord et al. (2011)
Invertebrate	*Mytilus trossulus* and *Strongylocentrotus franciscanus*	Larvae	Developmental rate	Decrease in larval body size in both the sea urchin and the mussel.	Sunday et al. (2011)
Invertebrate	*Haliotis kamtschatkana*	Larvae	Development, size and survivorship	Exposure to high CO_2 during development resulted in lower survival, abnormal development and smaller size in the northern abalone.	Crim et al. (2011)
Invertebrate	*Strongylocentrotus purpuratus*	Larvae	Development size	No differences in development between low and high CO_2 treatments. Smaller larvae in the high CO_2 treatment.	Yu et al. (2011)
Microbes	Nitrifiers	n/a	Ammonia oxidation rates	Microbial nitrification rates decreased when pH was experimentally reduced.	Beman et al. (2011)
Invertebrate	*Ostreola conchaphila*	Larvae Juvenile	Shell growth rate, shell area	Carryover effects of water chemistry experienced at early stage (larvae) to the later post-larval juvenile stage. Juveniles exposed to acidified conditions in their larval stages failed to attain the same size as juveniles derived from larvae exposed to less acidic conditions.	Hettinger et al. (2012)
Algae	*Pseudo-nitzschia fraudulenta*	n/a	Domoic acid production, cellular $Si : C$ ratios	Strong synergism between high CO_2 levels and silicate-limited growth, which greatly increases cellular toxicity relative to growth under lower CO_2 conditions.	Tatters et al. (2012)
Invertebrate	*Strongylocentrotus purpuratus*	Juvenile Adults	Mg / Ca, Sr / Ca	Composition of skeleton precipitated during early and adult life history stages appears relatively robust to spatial gradients and predicted changes in seawater chemistry.	LaVigne et al. (2012)
Invertebrate	*Strongylocentrotus purpuratus*	Larvae	Morphometrics and biochemical responses	Lipid utilization rates and protein content did not vary with pCO_2, larval growth was reduced at elevated pCO_2 despite similar rates of energy utilization, and relationships between egg phospholipid content and larval length were found under control but not high pCO_2 conditions.	Matson et al. (2012)
Invertebrate	*Strongylocentrotus purpuratus*	Larvae	Transcriptomics	Upregulation of several calcium transporters and binding proteins in a population of urchins from an intertidal site characterized by low and fluctuating pH.	Evans et al. (2013a)
Invertebrate	*Strongylocentrotus purpuratus*	Larvae	Development, size, respiration, transcriptomics	Additive effects of high temperature and high CO_2 conditions induce metabolic depression and a major downregulation of histone encoding genes. No differences in development between CO_2 treatments were found.	Padilla-Gamiño et al. (2013)
Invertebrate	*Strongylocentrotus purpuratus*	Larvae	Heritability, genetic variation, size	Genetic variation in the response to ocean acidification, indicating potential for adaptation. Smaller larvae under high CO_2 conditions.	Kelly et al. (2013)
Invertebrate	*Mytilus trossulus*	Adults	Strength of byssal threads	Threads grown under high pCO_2 conditions exhibited compromised mechanical characteristics.	O'Donnell et al. (2013)
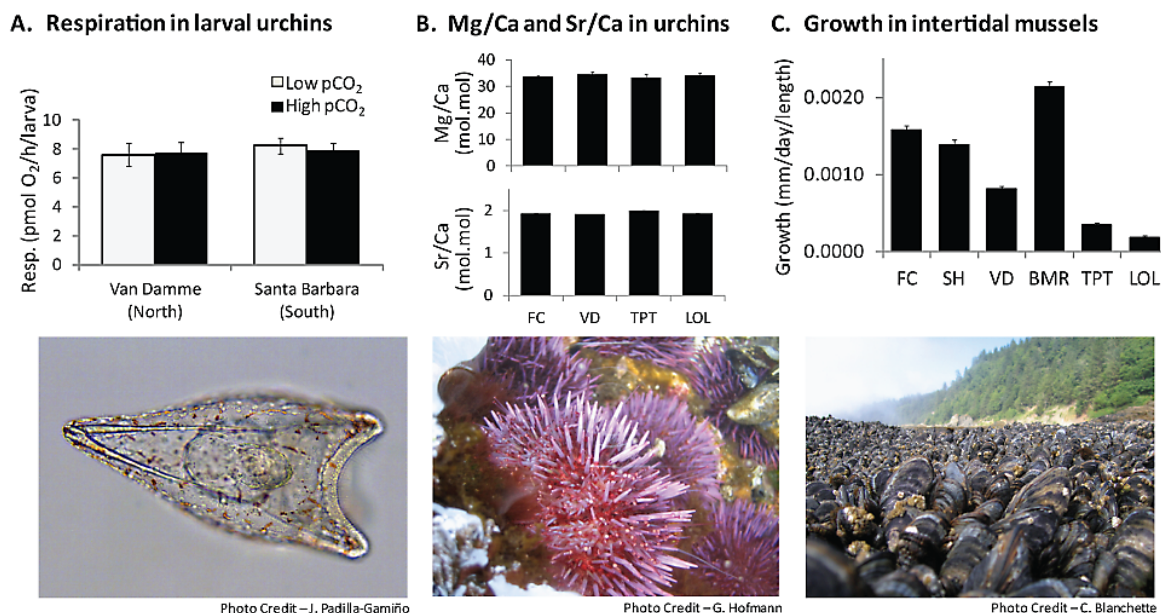
Fig. 4. Responses of marine calcifiers at the OMEGAS sites. **(A)** Respiration rates in larval sea urchins of *Strongylocentrotus purpuratus*; Sea urchin larvae from the Santa Barbara area and Van Damme were raised at 13 °C under high (1100 µatm) and low (400 µatm) pCO_2 using a flow-through CO_2 mixing system. Rates of oxygen consumption were obtained 92 h after fertilization in early pluteus larvae. Larval respiratory rates did not differ among sites or pCO_2 treatments. **(B)** Biomineral composition of the spines of adult *S. purpuratus*; data shown are mean Mg / Ca (upper panel) and Sr / Ca (lower panel) ratios for spines collected from adult urchins at OMEGAS study sites: Purisma Point (PP), CA, near Lompoc Landing, Terrace Point (TPT), CA, Van Damme State Park (VD) and Fogarty Creek (FC), OR; **(C)** Growth of intertidal mussels, *Mytilus californianus*, during the 2011 summer upwelling season. Mussels ∼ 40 mm in length were collected in April 2011 from the OMEGAS sites, notched at the posterior lip of the shell, and outplanted back to each site. Mussels were retrieved in October 2011, and growth was measured as the increase in shell length. Growth rate is expressed as millimeters per day, standardized by initial length; results shown here are scaled by the number of days for the study duration at each site and the individual mussel length at study initiation. Site abbreviations as in Fig. 1 and the text.

appeared to be under spatially varying selection. A limitation of the approach used in both of these studies is that variation in gene sequences often cannot be directly tied to variation in organismal performance. Furthermore, because of co-variation in environmental variables it is often difficult to know which aspect of the environment is selecting for differences in allele frequencies among populations. However studies like these provide a rich foundation for ongoing work attempting to identify the genetic basis of local adaptation. Notably, in a mesocosm experiment where urchin larvae from OMEGAS study sites were cultured under ecologically relevant pCO_2 conditions for the CCLME, Pespeni et al. (2013a) found significant allelic change in 40 classes of functional proteins in gene classes for ion homeostasis and biomineralization, suggesting that standing genetic variation does exist within these study populations at the OMEGAS sites.

We are currently testing for local adaptation to carbonate chemistry in another species from the CCLME with a very different life history and dispersal mode from purple urchins. Coralline algae are an ecologically important group of marine calcifiers that live in almost every habitat in the world's

oceans, from the tropics to the polar regions (Johansen, 1981). Coralline algae are very abundant along the CCLME (Abbott and Hollenberg, 1976) providing substrata and settlement cues to invertebrate larvae and serving as habitat for many marine species (Johansen, 1981). Coralline algae are highly vulnerable to ocean acidification (Koch et al., 2013) and, to date, it is unclear how more acidified waters will affect algal physiological mechanisms dependent on HCO$_3$- and CO_3^{2-} availability such as photosynthesis and calcification. Coralline algae reproduce by releasing spores (Johansen, 1981) that can fully attach to the bottom within hours of release (Miklasz, 2012) and recruit near the parental alga. This feature of coralline algae life history could limit dispersal distance and increase the potential for local adaptation in this group. We are currently examining how ocean acidification can affect the growth of spores from the articulated coralline algae *Corallina vancouveriensis*, which is an abundant species in the intertidal zone within the CCLME (Abbott and Hollenberg, 1976). Using populations exposed to different oceanographic conditions we are examining whether there is genetic variation among individuals and how this genetic variation is distributed among populations. Differences
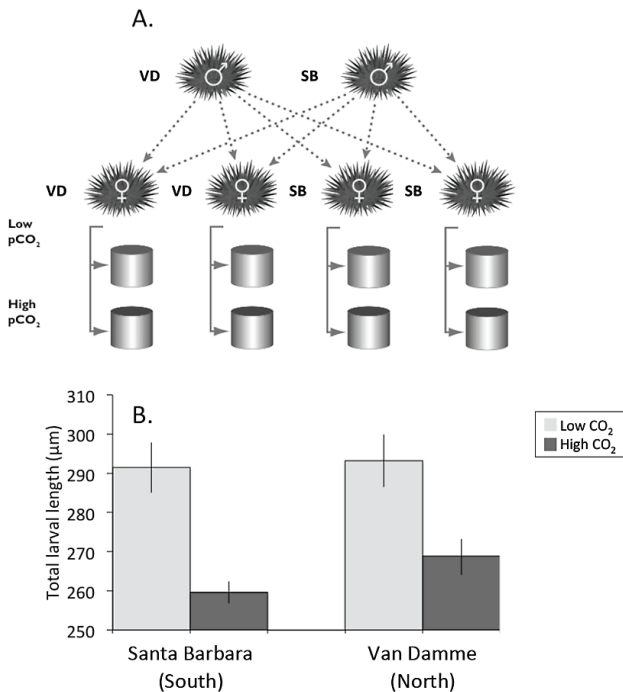
Fig. 5. Breeding experiment conducted using purple urchin adults collected from two OMEGAS study sites. **(A)** Cross design: we crossed adult urchins from two sites in California, US (inset), known to differ in their carbonate chemistry regimes (OMEGAS sites: northern CA, Van Damme; southern CA, Santa Barbara). In the lab, we crossed each male with two females from his own site, and two females from the opposite site, and split embryos from each cross into low and high pCO_2 rearing conditions. **(B)** Total larval length ($\pm$SD) of *S. purpuratus* raised for five days under low pCO_2 and high pCO_2 conditions. Offspring of northern CA sires are larger than the offspring of southern CA sires under high pCO_2 (pMCMC = 0.012) but not under low pCO_2 (pM-CMC = 0.27). Modified from Kelly et al 2013.

in the potential for adaptation could have important implications for the distribution of *C. vancouveriensis* and the organisms in the CCLME that depend on them.

5 Summary and future directions

The OMEGAS consortium has used a strategy of co-locating sensors and biological observations to begin to describe patterns of acclimatization and local adaptation in the CCLME. Ultimately, the goal of this research consortium is to use this information to forecast the impacts of future acidification in coastal regions around the globe. Co-locating sensors with measures of physiological performance makes sense, but should be more deeply appreciated in a biological context. Since it is the physical environment that makes a large contribution to genetic variation in populations, we would predict that regions characterized by large variation in pH

and changes in saturation state may have organisms with different physiological tolerances and with different genetics in terms of OA tolerance (Kelly and Hofmann, 2012; Kelly et al., 2013; Pespeni et al., 2013a). Thus, from a global change biology perspective, this strategy also allows us to explore the extent to which physiological plasticity vs. the capacity for adaptation might play a role in species response to environmental change.

Our emerging understanding of a spatial mosaic of coastal pH has facilitated studies of biological responses to system-relevant, mean-state changes in carbonate chemistry. As we gain insights from this first-order coupling between field observations and laboratory studies, we anticipate that a deepening understanding of the temporal variability of OA stress, its scope for future changes and covariation with other global change stressors will similarly enable a new generation of physiological, ecological and evolutionary studies. For example, organisms in the CCLME will face changes in exposures to both the severity and frequency of low pH and saturation state conditions (Hauri et al., 2013), with impacts that can interact with exposures to declining oxygen concentrations (Rykaczewski and Dunne 2010, Cocco et al., 2012). While capacity for resolving mean state vs. variability impacts and interactions between multiple stressors remains a limiting factor in the field, development of new experimental systems (Bockmon et al., 2013) can enable experimental treatments that mimic exposure regimes that organisms are observed and forecasted to face in situ. Such advances will be crucial to making more robust forecasts regarding the ecological consequences of future ocean change (Boyd, 2011; Harvey et al., 2013). Finally, as the complexity of this issue unfolds it will require that scientists engage more actively with policy makers, conservation biologists, and managers of critical marine ecosystems (Dawson et al., 2011; Ibáñez et al., 2013; Kelly et al., 2011).

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