

LETTER

Interacting environmental mosaics drive geographic variation in mussel performance and predation vulnerability

Kristy J. Kroeker,^{1a*} Eric Sanford,^{2,3a} Jeremy M. Rose,⁴ Carol A. Blanchette,⁵ Francis Chan,⁴ Francisco P. Chavez,⁶ Brian Gaylord,^{2,3} Brian Helmuth,⁷ Tessa M. Hill,^{2,8} Gretchen E. Hofmann,⁹ Margaret A. McManus,¹⁰ Bruce A. Menge,⁴ Karina J. Nielsen,¹¹ Peter T. Raimondi,¹ Ann D. Russell⁸ and Libe Washburn^{5,12}

Abstract

Although theory suggests geographic variation in species' performance is determined by multiple niche parameters, little consideration has been given to the spatial structure of interacting stressors that may shape local and regional vulnerability to global change. Here, we use spatially explicit mosaics of carbonate chemistry, food availability and temperature spanning 1280 km of coastline to test whether persistent, overlapping environmental mosaics mediate the growth and predation vulnerability of a critical foundation species, the mussel *Mytilus californianus*. We find growth was highest and predation vulnerability was lowest in dynamic environments with frequent exposure to low pH seawater and consistent food. In contrast, growth was lowest and predation vulnerability highest when exposure to low pH seawater was decoupled from high food availability, or in exceptionally warm locations. These results illustrate how interactions among multiple drivers can cause unexpected, yet persistent geographic mosaics of species performance, interactions and vulnerability to environmental change.

Keywords

Biogeography, macroecology, multidimensional niche, multiple stressors, emergent effects, ocean acidification.

Ecology Letters (2016)

INTRODUCTION

In an era of unprecedented global environmental change, there is growing interest in understanding the mechanisms underlying geographic variation in species' performance (Doak & Morris 2010). Hutchinson's multidimensional niche hypothesis predicts that a combination of multiple abiotic and biotic parameters determines a species' performance (Hutchinson 1957), and recent advances in macroecology suggest that this concept also applies to understanding variation in performance across broad spatial scales (Brown 1995; Brown *et al.* 1995; Martínez-Meyer *et al.* 2013). Key to these macroecological extensions of Hutchinson's hypothesis is the observation that geographic variation in niche parameters appears to be a relatively permanent feature of the landscape (Brown 1995). Thus, persistent combinations of abiotic and biotic factors can establish geographic 'hot spots' and 'cool spots,' where the performance and fitness of a given species is high or low, respectively (Brown 1995). This perspective has helped spark

interest in predicting species' responses to global environmental change using niche-based modelling (Guisan & Thuiller 2005; Thuiller *et al.* 2005; Kearney *et al.* 2010).

Although models traditionally assumed niche parameters were independent from one another (Brown *et al.* 1995), a growing body of work suggests that multiple environmental drivers commonly interact in ways that are non-additive (Crain *et al.* 2008). Our understanding of non-additive effects is largely derived from laboratory studies (Crain *et al.* 2008), and the combined effects of multiple environmental parameters have rarely been explored in nature. This leaves open the question: do persistent, spatially explicit, environmental mosaics overlap to create regions of unanticipated susceptibility or resilience in the face of global environmental change?

Regional and local-scale processes can cause complex geographic mosaics in both abiotic and biotic conditions (Helmuth *et al.* 2002; Menge *et al.* 2003; Sanford *et al.* 2003; Feely *et al.* 2008; Seabra *et al.* 2011; Suggitt *et al.* 2011; Woodson *et al.* 2012; Rapacciolo *et al.* 2014; Ackerly *et al.*

¹Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA, USA

²Bodega Marine Laboratory, University of California Davis, Bodega Bay, CA, USA

³Department of Evolution and Ecology, University of California Davis, Davis, CA, USA

⁴Department of Integrative Biology, Oregon State University, Corvallis, OR, USA

⁵Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA, USA

⁶Monterey Bay Aquarium Research Institute, Moss Landing, CA, USA

⁷Department of Marine and Environmental Sciences, Northeastern University, Nahant, MA, USA

⁸Department of Earth & Planetary Sciences, University of California Davis, Davis, CA, USA

⁹Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA, USA

¹⁰Department of Oceanography, University of Hawaii at Manoa, Honolulu, HI, USA

¹¹Romberg Tiburon Center, San Francisco State University, San Francisco, CA, USA

¹²Department of Geography, University of California Santa Barbara, Santa Barbara, CA, USA

*Correspondence: E-mail: kkroeker@ucsc.edu

^aThese authors contributed equally to this work

2015). Here, we define an environmental mosaic as the spatial distribution of an abiotic or biotic parameter that varies in a non-monotonic way, rather than as a uniform gradient. If abiotic and biotic drivers are patchy over relevant spatial scales, and if they are not perfectly correlated over space, they can create a multivariate mosaic of interacting conditions that can cause differences in species performance over relatively small spatial scales (Fig. 1). For example, in coastal ecosystems, upwelling and other oceanographic features often generate strong alongshore variation in temperature, nutrients, pH and oxygen over spatial scales of tens to hundreds of kilometres (Bustamante *et al.* 1995; Menge *et al.* 1997; Menge 2000; Navarrete *et al.* 2005; Feely *et al.* 2008; Hofmann *et al.* 2014). These same oceanographic processes can generate spatial variation in the delivery of phytoplankton and larvae to coastal sites, with strong ecological influences on population dynamics and benthic communities (Menge & Menge 2013). Importantly, the spatial patterns in environmental and ecological factors are often persistent, as they are linked to geographic features of the seascape (Menge *et al.* 1997; Navarrete *et al.* 2005; Barth *et al.* 2007; Broitman *et al.* 2008; Woodson *et al.* 2012; Hofmann *et al.* 2014). Differences in the spatial variability of the dominant drivers can result in locations with different combinations of environmental conditions. If the effect of an environmental driver is context dependent (e.g. its effect on species performance is dependent on the occurrence or magnitude of another driver), the interactions among overlapping environmental mosaics could lead to complex geographic variability in species' vulnerability to future environmental change.

The California Current System (CCS) provides an opportunity to examine how interacting environmental mosaics influence species' performance and interactions, as well as to provide insight into the vulnerability of key species to anthropogenic changes in ocean chemistry. CO₂-driven ocean acidification is considered a major threat to marine species worldwide, and the process is especially accelerated in the CCS (Gruber *et al.* 2012). As in other eastern boundary upwelling systems, the prevailing winds during spring and summer bring cold, deep, nutrient-rich, high-CO₂ seawater into the nearshore environment in the CCS. Existing geographic variability in strength and persistence of upwelling and the chemistry of the source water create a spatial mosaic in carbonate chemistry, with exposure to low pH conditions occurring regularly in areas of strong upwelling along the Oregon and northern California coast and more stable conditions with less intense upwelling in southern California (Feely *et al.* 2008; Hofmann *et al.* 2014). This spatial variability in the upwelling system allows an examination of how carbonate chemistry affects species performance in the context of other abiotic and biotic drivers (Fig. 1), with implications for how these factors may mediate the effects of ocean acidification in the future.

California mussels, *Mytilus californianus*, are a foundation species that support considerable biodiversity in rocky intertidal ecosystems (Suchanek 1992). The ability of mussels to create habitat-forming beds depends on their ability to overgrow competitors (Dayton 1971), and interest in the effects of carbonate chemistry on mussel growth has increased greatly

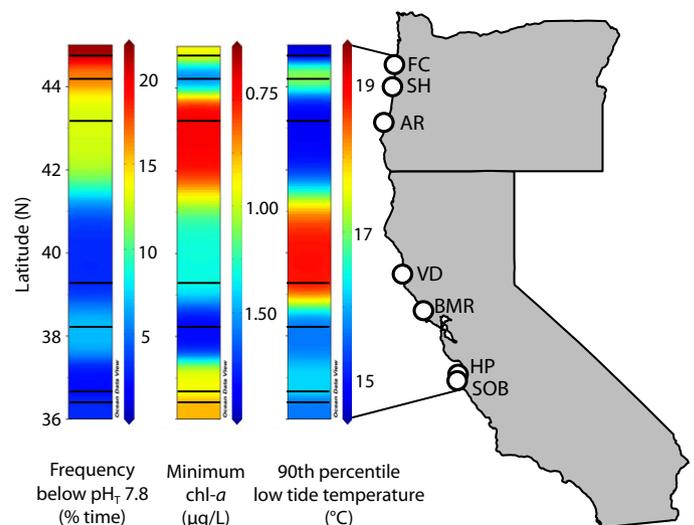


Figure 1 Conceptual figure illustrating how multiple environmental drivers can create complex geographic mosaics across the study region. Environmental mosaics were based on data for seawater pH, chlorophyll-*a* and mussel body temperature collected from April to October 2013 at the seven study sites, which are denoted by the horizontal black lines on the heat maps. **Values beyond the study sites were extrapolated linearly to illustrate the overlapping mosaic concept and do not represent actual environmental conditions.** FC = Fogarty Creek, OR; SH = Strawberry Hill, OR; AR = Cape Arago, OR; VD = Van Damme State Park, CA; BMR = Bodega Marine Reserve, CA; HP = Hopkins Marine Reserve, CA; SOB = Soberanes Point, CA.

with the growing awareness of ocean acidification (Wootton *et al.* 2008). Exposure to reduced pH, low saturation-state seawater has been shown to cause a thinning and weakening of larval shells of *M. californianus* (Gaylord *et al.* 2011) and reduced growth and performance in its congeners (Gazeau *et al.* 2007; Waldbusser *et al.* 2015). *M. californianus* growth and fitness are also linked to other environmental drivers, including food availability as measured by chlorophyll-*a* (chl-*a*) concentrations (Menge *et al.* 1997), immersion time (Seed & Suchanek 1992), water temperatures (Blanchette *et al.* 2007; Menge *et al.* 2008) and weather conditions during low tide (Blanchette *et al.* 2007). For example, warm body temperatures occurring during low tides can trigger physiological stress responses leading to higher energetic demands, reduced growth rates and reduced survival (Somero 2002; Schneider 2008). Food availability has been shown to mediate the effects of reduced pH/high *p*CO₂ seawater on growth and shell morphology in the congener *Mytilus edulis* (Melzner *et al.* 2011; Thomsen *et al.* 2013), suggesting an energetic basis for the effects of low pH/high *p*CO₂ on mussels. All of these environmental drivers vary in persistent mosaics across the CCS [carbonate chemistry [Feely *et al.* 2008; F. Chan (in prep), unpublished data]; temperature (Helmuth *et al.* 2002) and chl-*a* concentrations (Woodson *et al.* 2012)], and we hypothesized that interactions among these drivers could drive spatial patterns in mussel performance (Fig. 1).

Moreover, there is considerable potential for environmentally mediated variation in performance to influence mussel populations indirectly via altered species interactions (Wootton *et al.* 2008). In particular, in this study, we consider

vulnerability to drilling by predatory snails, an interaction that is closely linked to mussel size and shell thickness (Sanford & Worth 2009, 2010). Although the lower vertical boundary of *M. californianus* distribution on the shore is determined primarily by the predatory sea star *Pisaster ochraceus* (Paine 1974; Menge *et al.* 2004), within the mussel beds themselves, or in areas where sea star densities are low, predatory drilling snails (especially the Channeled Dogwhelk, *Nucella canaliculata*) can have strong effects on mussel populations (Navarrete & Menge 1996; Sanford *et al.* 2003; Sanford & Worth 2009).

Here, we examine the relationships between interacting environmental mosaics and juvenile mussel performance and vulnerability to drilling predation at seven sites spanning 1280 km within the CCS (Table 1). In particular, we examine the effects of low pH seawater associated with upwelling, food availability and body temperatures on the growth and morphology of juvenile California mussels in dynamic environments and determine how these environmentally mediated differences affect rates of predation by the dogwhelk *N. canaliculata*. To model the potential interactions among pH, chl-*a* and temperature on mussels, we coupled growth measurements of juvenile mussels in the field with high-resolution environmental monitoring. We used these data in separate principal components analyses (PCA) for key environmental variables (i.e. a separate PCA was performed for all pH-related variables, and this process was repeated for chl-*a*-related variables, as well as temperature-related variables) (Fig 2). In the absence of any *a priori* knowledge of what aspects of the pH, chl-*a* and temperature were related to mussel growth and morphology, the PCA analysis allowed us to explore whether mussel performance was more closely related to estimates of the mean conditions vs. the variability in these factors. This is important in the dynamic conditions of the CCS with extremely high variability in pH, chl-*a* and temperature. Moreover, the PCAs allowed us to create a set of independent variables derived from each set of environmental variables, which often are colinear. This approach allowed us to characterise pH, chl-*a* and temperature 'regimes.' We then used the explanatory factors (e.g. PC1, PC2) from the PCAs as predictor variables to model mussel growth, morphology and predation vulnerability with linear and non-linear approaches as indicated by the underlying distributions. Although pH, chl-*a* and temperature regimes are often related in nature, using the principal components allowed

identification of non-additive interactions among these environmental drivers that explain geographic variability in juvenile mussel performance and species interactions.

MATERIALS AND METHODS

Site characterisations

We used seven rocky intertidal sites across the CCS (Fig 1). At each site, we continuously monitored seawater pH and temperature using autonomous sensors from April to October 2013. Seawater pH and temperature were measured with a modified DuraFET pH sensor (Honeywell) adapted for the intertidal zone. The pH sensors were calibrated with a Certified Reference Material (seawater or TRIS buffer) from the Dickson Lab at Scripps Institute of Oceanography, bolted to the substrate at +0 m Mean Lower Low Water (MLLW) and collected every 4–8 weeks for maintenance. We collected discrete water samples once or twice a month for dissolved inorganic carbon and total alkalinity. Water samples were processed following best practices (Dickson *et al.* 2007), and the carbon system was calculated using CO2SYS with K_1 and K_2 dissociation constants from Roy *et al.* (1993) and KHSO_4 from Dickson *et al.* (2007). The discrete water samples collected every 2–4 weeks for chl-*a* concentrations ($n = 4\text{--}17/\text{site}$) were measured by pumping 50 mL of seawater through a 25 mm GF/F filter immediately after collection in the field and analysed using the non-acidification technique (Welschmeyer 1994) or the standard fluorometric procedure (Holm-Hansen *et al.* 1965). To test the ability of our limited number of discrete water samples collected in 2013 to explain longer term variation in chl-*a* among sites, we compared our results with a climatology in chl-*a* based on sampling data collected during 1993–2012. Specifically, we compared the mean and minimum chl-*a* concentration from the bottle samples collected during this study against the mean and minimum from all bottle samples collected during April to October, regardless of year ($n = 37\text{--}360$ samples per site). The mean and minimum chl-*a* concentrations from discrete water samples from 2013 are closely correlated with the mean and minimum chl-*a* concentration calculated over this longer period (Table S1, Fig. S1–2). In addition, previous analyses suggest discrete water samples can reliably predict site differences measured by continuous fluorometry (see Menge *et al.* 2015 for a comparison of a subset of the sites used in this study).

Table 1 Summary statistics of environmental conditions at each study site. Site codes are as in Fig. 1

Site	Mean pH _T	Frequency pH _T < 7.8 (% time)	Mean low-tide body temp (°C)	75% percentile low-tide body temp (°C)	Mean high- tide temp (°C)	Mean chl- <i>a</i> (µg L ⁻¹)	Min chl- <i>a</i> (µg L ⁻¹)
FC	7.99	21.7	11.2	12.6	10.6	11.9	0.9
SH	8.00	16.5	12.9	14.8	10.5	11.7	1.6
AR	8.03	12.7	11.8	13.2	10.3	6.0	0.4
VD	8.01	2.5	13.0	14.1	10.7	3.2	1.3
BMR	8.02	7.1	12.7	14.0	11.7	9.7	1.9
HP	8.14	1.2	15.4	15.4	14.3	5.3	1.0
SOB	8.03	3.7	12.7	13.3	11.5	6.9	0.6

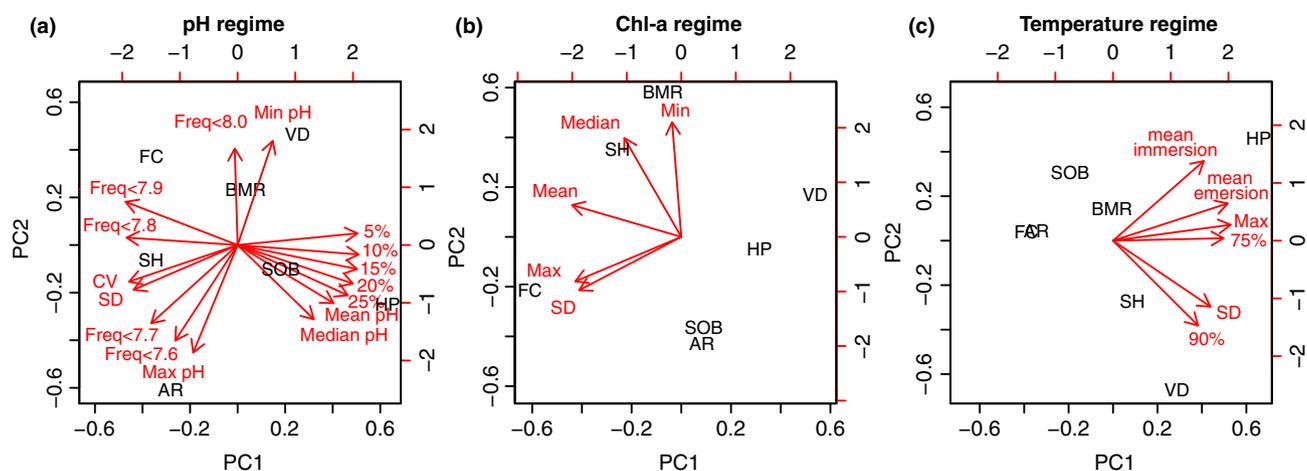


Figure 2 PCA biplots of the (a) pH, (b) chlorophyll-*a* and (c) temperature regimes for the study sites. Site codes are as in Fig. 1. The direction of the arrows is determined by the eigenvectors that relate each variable to the two primary principal components, and the site placements are based on component scores. The direction of the arrows indicates that the values of that variable increase in that direction, and the placement of the sites indicate how each site is related to the principal components. PC1 and PC2 from each regime were then used to model mussel growth. Freq = % time below a specific value; % = percentiles; CV = coefficients of variation; SD = standard deviations. The 75% and 90% temperature percentiles and Max, refer to mussel body temperatures from low tide (emersion), whereas SD refers to the combined immersion and emersion body temperatures.

We estimated mussel body temperature using two small bio-mimic temperature data-loggers (Fitzhenry *et al.* 2004) that were attached with marine epoxy to the substrate near the mussel outplants (recording temperature at 10-min intervals). We calculated the mean immersion temperature during a 6-h period centred on each high-tide, and mean emersion temperature by identifying the greatest low-tide tidal height when the temperatures were at least 5 °C warmer (i.e. likely out of water) than the preceding mean high-tide temperature and calculating the mean temperature for all 2-h periods below that tidal height. We calculated maximum seawater temperature as the greatest immersion temperature recorded. We determined relative emersion time by calculating the number of low tides where the temperature data-logger was 5 °C greater than the preceding high-tide temperature, divided by the total number of low tides during the deployment (Harley & Helmuth 2003). All statistics were based on the mean of the two data-loggers at each site.

Mussel outplants

To measure growth of juvenile mussels at the seven sites, juvenile California mussels (*Mytilus californianus*) were collected from the lower half of the mussel bed in wave-exposed areas during the low-tide series two weeks prior to deployment at each site. Care was taken to minimize confounding factors by selecting similar sized mussels (mean starting length = 21.0 mm \pm 2.7 SD) from similar tidal heights and wave-exposure regimes. Mussels were transported to flow-through seawater tanks at local marine laboratories, where we measured the total length of each mussel and added a 1.0–1.5 mm triangular notch in the growing (posterior) end of the shell with a file. We outplanted 76 juvenile mussels to each of five stainless steel mesh cages that were bolted and epoxied onto a relatively horizontal, rocky substrate at approximately + 0.30 m above MLLW at each site. The mussels were

deployed to each cage inside plastic mesh bags (with 7-mm-square openings) to limit movement and facilitate byssal thread attachment. We did not include cage controls in the experiment because juvenile mussels exposed to sea star and whelk predation at this low intertidal height would have been rapidly eliminated, yielding few or no data regarding growth of uncaged mussels. Although cages likely reduced wave forces to some extent, cages were cleaned every 2–4 weeks with wire brushes and thus were not overgrown by algae, barnacles or other organisms. After ~ 5 months, we retrieved the mussels and measured shell length, width, girth and new growth with calipers. New growth was measured as the length between the top of the notch (i.e. previous shell edge) and the posterior end (new edge) of the shell. Lastly, for a subset of the mussels ($n = 13$ –21/cage), we dissected the mussels for measurements of shell and soft tissue mass. The soft tissue and shells were dried separately in a drying oven at 50 °C for 48 h before weighing.

Predation experiments

To test the vulnerability of juvenile mussels from each site to drilling predation, we collected 100 dogwhelks (*Nucella canaliculata*) from Van Damme State Park, CA in August 2013. The Van Damme population was selected because previous research indicated that snails from this population consistently drill *M. californianus* (Sanford & Worth 2009). Snails of a similar size (shell length = 25.5–30.5 mm) were acclimated at Bodega Marine Laboratory for 6 weeks prior to the start of the experiment. During acclimation, snails were fed an *ad libitum* diet of *M. californianus* from a common source (Bodega Marine Reserve; BMR) for 4 weeks, and then starved for 2 weeks in separate flow-through containers prior to the start of the experiment. For the experiment, 16 mussels were haphazardly chosen from each field cage and separated into two 1-L containers with eight mussels each ($n = 68$

containers). We randomly assigned one snail to each container and opened the containers every ~ 14 days to inspect each mussel for a borehole. A mussel was recorded as 'drilled' if a borehole passed all the way through the shell. We returned all live and drilled mussels to the container following inspection for the 46-day experiment.

Models of mussel growth

To create statistical models of juvenile mussel growth, we calculated descriptive statistics (i.e. mean, median, standard deviation, upper and lower quartiles and frequency of exposure below specific pH values; Fig. 2). We then standardized all of the descriptive statistics to account for differences in measurement units. For standardization, we subtracted the minimum from the value of interest, and then divided by the difference of the maximum and the minimum value. Next, we performed a separate correlation-based PCA for all (1) pH-related variables, (2) chl-*a*-related and (3) temperature-related variables (Tables S2–4). Lastly, we used the scores of the first two principal components for pH, chl-*a* and temperature-related variables, along with the relative emersion time, as explanatory variables in multiple regression analyses of mussel growth and morphology (e.g. growth, shell thickness and tissue mass). Given the number of dependent variables ($n = 7$ sites), models could only contain a maximum of five predictor variables (including interactions). We first fit several models that incorporated five factors, using all possible combinations of interactions and predictor variables. We compared the alternate models that incorporated five factors using delta Akaike Information Criterion (AIC) scores, with a delta AIC threshold of 10 for model selection. The model with the lowest AIC value always had a delta AIC value > 10 compared to model with the next lowest AIC score. This model was then used for subsequent model simplification with backwards elimination using the same delta AIC model selection.

We used linear regression to determine whether the principal components from each PCA were related to others. The only significant correlation ($P < 0.05$) was between PC1 of the pH regime and PC1 of the chl-*a* regime, which were not included in the final model based on our model selection procedure. In addition, we used variance inflation factor (VIF) scores to test for issues with collinearity in the final model. All VIF scores in the final model were less than 2.1, suggesting that multicollinearity was low. There was strong leverage produced by three data points, which is not unexpected in models with limited data points. In addition, growth, tissue mass and shell thickness measurements were standardized and tested for correlations using linear models. The normal Q–Q plots and residual vs. fitted plots met expectations for parametric statistics. Lastly, we tested for spatial autocorrelation in mussel growth using Moran's I, which calculates the correlation among sites as a function of distance. This statistic varies between -1 and 1 depending on whether the variable is negatively or positively spatially correlated. Spatial autocorrelation is typified by high I-index at shorter distances eventually decreasing to zero at longer distances. This pattern would indicate that the patterns are more similar at locations that

are closer together and unrelated at sites that are farther apart (i.e. clustering). All analyses were performed in R (V 2.15.3).

Predation analyses

We tested for differences in susceptibility to drilling predation by using linear regression with mussel size and morphology as predictor variables and the number of mussels drilled over time as the dependent variable. The number of shells drilled was log-transformed after visual inspection of scatter plots, and the length, soft tissue mass (measured as the dry weight minus the ash-free dry weight) and shell thickness (calculated as the mass of the mussel shell, divided by the surface area of the shell) were standardised to account for right skew. Shell surface area was calculated as $SA = \text{length} \times (\text{width}^2 + \text{girth}^2)^{0.5} \times \pi/2$ (Reimer & Tedengren 1996). Soft tissue mass and shell thickness were calculated as mean values for a given site, based on a subset of mussels that were not included in the predation trials ($n = \sim 20/\text{cage}$ for 5 cages/site). The length estimates included all mussels collected from the site ($n = \sim 37/\text{cage}$ for 5 cages/site). Because size, thickness and tissue mass were correlated and had VIF scores above 10, we did not include more than one predictor variable in the model.

RESULTS

PCA highlighted complex differences in pH, chl-*a* and temperature regimes among the seven sites in the CCS (Fig. 2). Mussel growth and morphology varied among sites (Fig. S3), and PCA regression revealed an interaction between the principal components of the pH regime (PC2) and chl-*a* regime (PC2), as well as the principal components of the temperature regime (PC1) on mussel growth (Table 2). There were no other statistically significant models for mussel growth, and this model was substantially better than models incorporating other principal components or relative emersion time based on delta AIC scoring. For all model comparisons, the delta AIC values between the one with the lowest AIC score and other competing models were at least 10, indicating that the competing models were very unlikely to be superior (Burnham & Anderson 2002).

The interaction between the second principal components of the pH and chl-*a* regimes in the model indicates that the effects of pH and chl-*a* on mussel growth were interdependent (Fig. 3). At lower values of PC2 of pH (e.g. more frequent events below pH 7.6, lower minimum pH values and higher maximum pH values; Fig. 2a), the higher values of PC2 of

Table 2 Linear model (regression) statistics for mussel growth

	Estimate	SE	<i>t</i> -value	<i>p</i> -value
(Intercept)	0.786	0.025	31.90	< 0.001
PC2 pH	-0.192	0.015	-12.96	< 0.01
PC2 chl- <i>a</i>	0.082	0.02	4.16	0.05
PC1 temp	-0.061	0.012	-5.03	0.04
PC2 pH \times PC2 chl- <i>a</i>	-0.150	0.011	-13.56	< 0.01
Residual		0.053		

chl-*a* had a greater positive effect on mussel growth (modelled by the blue line representing more consistent chl-*a* concentrations, defined by higher minimum and median chl-*a* concentrations in Fig. 3). This suggests consistent chl-*a* concentrations were more important for supporting growth in dynamic pH environments than in relatively less variable, higher pH environments. In contrast, PC2 of the pH regime had very little effect on mussel growth at low values of PC2 of chl-*a* (modelled by the red line, representing less consistent

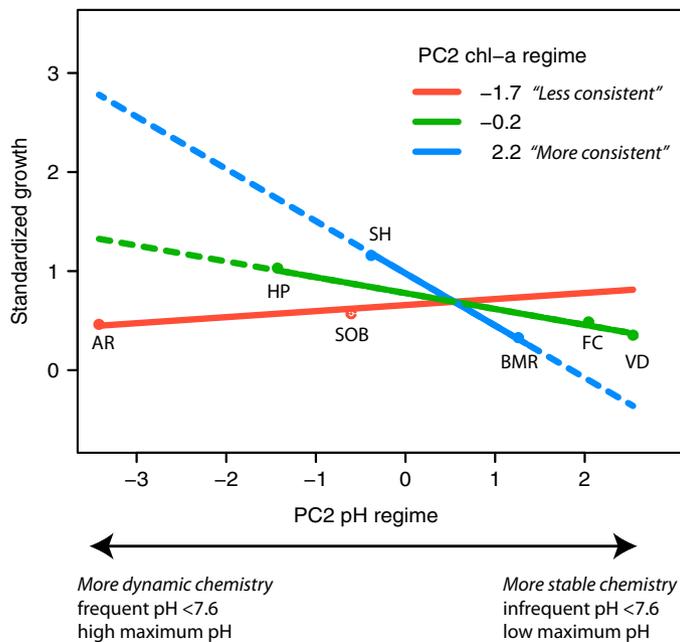


Figure 3 The interaction between pH and chl-*a* regimes based on linear model results. Mussel growth is modelled as a function of PC2 of the pH regime for the 10th (red line), 50th (green line) and 90th (blue line) percentiles of PC2 of the chl-*a* regime. Data points are represented by small dots, and an interpretation of PC axes is added for clarification (e.g. the 10th percentile of PC2 of the chl-*a* regime represent low-minimum and median chl-*a* concentrations). The solid lines indicate where the available data informed the model, and the dotted lines indicate the model predictions beyond the available data.

chl-*a* concentrations, defined by low minimum and median chl-*a* concentrations in Fig. 3). Mussel growth was also related to PC1 of the temperature regime (Table 2; $P = 0.04$). This principal component captured some of the variation in the extremes in mussel body temperatures during low tide (e.g. the maximum and the 75th percentile of body temperatures during emersion; Fig. 2c), indicating that new growth decreased as the extremes of body temperature increased.

We did not detect a correlation between growth and shell thickness ($P = 0.09$ Fig. S4A). Growth and soft tissue mass, as well as shell thickness and soft tissue mass were significantly correlated (Fig S4B–C). Patterns in the linear model of growth vs. pH, chl-*a* and temperature regimes (Table 2) were mirrored in the tissue mass, although the explanatory power was slightly less for this variable.

We did not detect spatial autocorrelation in mussel growth in our dataset (Global $I = 0.15$, $P = 0.2$). Similarly, the I-index did not show a clear pattern of higher values for sites that were closer vs. further apart (Table S5).

Total length (correlated to growth; Adj. $R^2 = 0.77$, $P = 0.005$), shell thickness and soft tissue mass all successfully predicted the vulnerability of mussels to predation by dogwhelks using log-linear models (Fig. 4; Table S6). As each of these mussel traits decreased, the number of mussels that were drilled by dogwhelks increased exponentially.

DISCUSSION

Our results demonstrate that spatially explicit knowledge of interacting environmental mosaics is essential to predicting geographic variation in species' performance. The interaction between the pH regime and the chl-*a* regime on juvenile mussel growth suggests that the effects of carbonate chemistry and food availability are interdependent and vary geographically. Juvenile mussel growth was highest in locations with frequent low pH events and consistent food availability (e.g. high-minimum and median chl-*a* concentrations). Such sites experience frequent shifts between upwelling and downwelling conditions (i.e. 'intermittent' upwelling), with both low-minimum and high-maximum pH (characterised by low values of PC2 in the pH PCA). We hypothesise that filter feeding

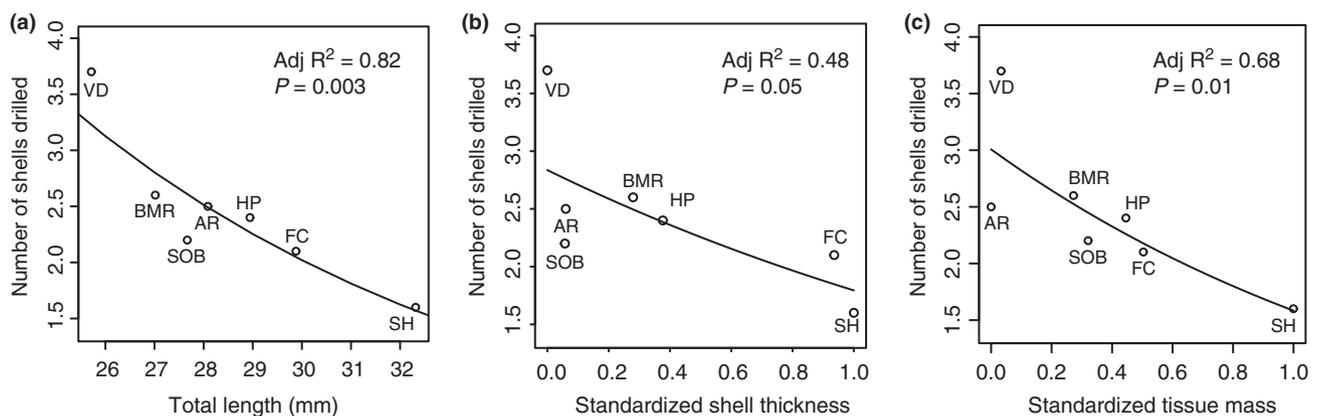


Figure 4 Log-linear models of drilling predation and (a) mussel growth, (b) shell thickness and (c) tissue mass. Predation vulnerability quantified as number of mussels drilled during a 46-day experiment when mussels from each site were held in the laboratory with dogwhelks (*Nucella canaliculata*).

species in such areas may be more resilient to low pH seawater than generally expected because intermittent upwelling allows the development of phytoplankton blooms that provide food for these species (Menge & Menge 2013). In contrast, juvenile mussel growth was most limited in locations where mussels experienced (1) frequent exposure to low pH conditions and less consistent food availability (e.g. low minimum chl-*a* concentrations, such as Cape Arago, OR, or Soberanes Point, CA) or (2) extremes in low-tide body temperatures (e.g. Van Damme State Park, CA). The interaction between the pH and chl-*a* regimes supports previous evidence suggesting increased food availability may mediate the predicted negative effects of low pH seawater on mussel growth (Thomsen *et al.* 2013). Mussels are also able to use particulate organic carbon (POC) for food, which was not measured in this study, and attention to POC or food quality could refine our understanding of the relationship between carbonate chemistry and mussel performance.

Our results highlight the importance of considering context when inferring ecological vulnerability to environmental change, as well as the need to incorporate interactions among multiple environmental drivers in species niche models related to climate change. The mean pH values at each site were higher than those expected in near future scenarios for the surface waters of the CCS (i.e. pH_T 7.8 in 2050; Gruber *et al.* 2012) and other naturally acidified systems (Feely *et al.* 2010; Thomsen *et al.* 2010), although some sites were intermittently exposed to pH values relevant to future acidification (e.g. Fogarty Creek pH_T was below 7.8 for 22% of the time; Table 1). Although correlative in nature, our results suggest mussel performance was better predicted by frequency of exposure to low pH events than mean conditions (as well as other aspects of variability in the pH regime). Although continued acidification will likely create novel conditions not captured in our study, our results suggest mussels can maintain growth in response to short-term exposure to low pH conditions expected in the future, and the relationship between exposure to low pH seawater and mussel growth is strongly mediated by food availability.

Our results also illustrate how interactions between overlapping mosaics of environmental drivers can cause differences in post-settlement processes, including species performance and interactions over relatively small spatial scales. For example, Cape Arago and Strawberry Hill are only separated by ~130 km (Fig. 1), but show some of the most striking differences in mussel growth. Lower growth at Cape Arago can be explained by the decoupling of low pH and high chl-*a* concentrations, as previously noted. Differences in species' vulnerability and resiliency to environmental change over relatively fine geographic scales could have important implications for management and climate adaptation strategies. For example, our results suggest that individuals from closely spaced sites could differ sharply in their fitness and reproductive output (Lester *et al.* 2007). When coupled with dispersal models, this information could be used to inform the placement of protected areas or management actions that would protect robust populations (e.g. in this example mussel populations exposed to high chl-*a* concentrations) to serve as sources that could replenish populations in more vulnerable locations.

Our results also highlight how small changes in prey growth rates caused by environmental change could affect population dynamics or community structure via species interactions. For example, in the laboratory assay, mussels were most vulnerable to drilling predation when they came from sites with high exposure to low pH seawater and inconsistent chl-*a* concentrations, as well as sites characterized by high body temperatures during low tides. Given the positive correlations between size and soft tissue mass, as well as shell thickness and soft tissue mass, it remains unclear whether increased predation on these smaller mussels was a result of thinner shells, or lower handling time and energetic content, all of which could influence their vulnerability to this and other predators (e.g. sea stars or other drilling whelks) (Kroeker *et al.* 2014).

The strong relationship among the environmental drivers, mussel traits and vulnerability to drilling predation suggests pathways through which environmental change could alter population dynamics and community structure via species interactions (Coleman *et al.* 2006; Poloczanska *et al.* 2008; Thomsen *et al.* 2013). Along the West Coast of North America, the predatory sea star *Pisaster ochraceus* often plays a keystone role in rocky intertidal communities through its effects on the mussel *M. californianus* (Paine 1974; Menge *et al.* 2004). In areas where sea star densities are reduced (e.g. by disease), or within mid-intertidal mussel beds above the vertical foraging range of *Pisaster*, dogwhelk predation on mussels can partially fill the functional role of this sea star (Navarrete & Menge 1996; Sanford *et al.* 2003). Our results suggest that interacting environmental mosaics influence the vulnerability of mussels to drilling predation, although geographic variation in predation rates will also be affected by a variety of additional factors [e.g. spatial variation in predator abundance and behaviour, and thermal or CO₂ effects on predators (Menge *et al.* 2004; Sanford & Worth 2009)].

Persistent spatial variation in environmental factors may also define geographic mosaics of selection that shape predator-prey interactions (Sanford *et al.* 2003; Sanford & Worth 2010). Geographic mosaics of both environmental and ecological conditions can create a landscape of 'hot spots' and 'cold spots', where selection on a focal species interaction ranges from strong to weak (Benkman 1999; Thompson 1999). Indeed, prior work has documented striking geographic variation in the interaction between *N. canaliculata* and *M. californianus* (Sanford *et al.* 2003; Sanford & Worth 2009, 2010) that likely has a genetic basis (Sanford & Worth 2009). The spatial differences in mussel performance reported here may be an important selection force that shapes the evolution of drilling capacity in dogwhelks. Smaller and thinner mussels likely reduce handling time and increase the relative profitability of *M. californianus* as a prey item for dogwhelks at some sites (although lower tissue mass associated with smaller or thinner shells in the juvenile mussels studied here could decrease the profitability). Interestingly, Cape Arago stands out as a site where the *N. canaliculata* population has a greater frequency of mussel drillers in F2-generation family lines than other nearby populations, such as Strawberry Hill and Fogarty Creek (Sanford & Worth 2009). Thus, persistent environmental mosaics leading to thinner shells at Cape Arago than other nearby sites may have contributed to

selection for dogwhelks that can prey upon these more vulnerable *M. californianus*. These patterns suggest that differentiation in drilling capacity may have been shaped by spatial variation in mussel shell thickness, and highlight the potential for complex feedbacks among environmental, ecological and evolutionary processes.

As atmospheric CO₂ concentrations continue to increase, many locations will experience novel environmental regimes not captured in existing environmental mosaics. For example, upwelling is forecasted to intensify in some regions (Wang *et al.* 2015) and the source water is predicted to become more acidic in the near future (Gruber *et al.* 2012), potentially leading to pH and chl-*a* regimes beyond the ranges of those represented in our study. Our findings suggest that studies examining predicted geographic shifts in the patterns of co-occurrence and interactions among multiple environmental drivers are of critical importance in determining how the emergent effects of environmental changes, such as ocean acidification, will develop in the future.

ACKNOWLEDGEMENTS

We are grateful to the University of California Natural Reserve System and State Parks of California and Oregon for access to these study sites. We thank F. Choi, G. Dilly, R. Focht, S. Gerrity, J. Hosfelt, L. Hunter, A. Johnson, K. Laughlin, M. Poole, J. Robinson, R. Williams and M. Wood for field and lab assistance. This work is a contribution from OMEGAS, funded by NSF grants OCE 10-41240 and OCE 12-20338. Additional funding was provided by grants from the UC MRPI and David and Lucile Packard Foundation in support of PISCO (publication #465).

AUTHORSHIP

ES designed the study, KJK, ES, JMR, CAB, FC, BG, BH, TMH, GEH, MAM, BAM, KAJ, PTR, ADR and LW performed the research, KJK performed the statistical analyses and modelling and KJK and ES wrote the manuscript with comments from co-authors.

REFERENCES

- Ackerly, D.D., Cornwell, W.K., Weiss, S.B., Flint, L.E. & Flint, A.L. (2015). A geographic mosaic of climate change impacts on terrestrial vegetation: which areas are most at risk? *PLoS ONE*, 10, e0130629.
- Barth, J.A., Menge, B.A., Lubchenco, J., Chan, F., Bane, J.M., Kirincich, A.R. *et al.* (2007). Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California Current. *Proc. Natl Acad. Sci. USA*, 104, 3719–3724.
- Benkman, C.W. (1999). The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *Am. Nat.*, 154, S75–S91.
- Blanchette, C.A., Helmuth, B. & Gaines, S.D. (2007). Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at point conception, California, USA. *J. Exp. Mar. Biol. Ecol.*, 340, 126–148.
- Broitman, B.R., Blanchette, C.A., Menge, B.A., Lubchenco, J., Krenz, C., Foley, M. *et al.* (2008). Spatial and temporal patterns of invertebrate recruitment along the west coast of the United States. *Ecol. Monogr.*, 78, 403–421.
- Brown, J.H. (1995). *Macroecology*. University of Chicago Press, Chicago, Illinois.
- Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995). Spatial variation in abundance. *Ecology*, 76, 2028–2043.
- Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag New York.
- Bustamante, R.H., Branch, G.M., Eekhout, S., Robertson, B., Zoutendyk, P., Schleyer, M. *et al.* (1995). Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia*, 102, 189–201.
- Coleman, R.A., Underwood, A.J., Benedetti-Cecchi, L., Åberg, P., Arenas, F., Arrontes, J. *et al.* (2006). A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia*, 147, 556–564.
- Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.*, 11, 1304–1315.
- Dayton, P.K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.*, 41, 351–389.
- Dickson, A.G., Sabine, C.L. & Christian, J.R. (2007). Guide to best practices for ocean CO₂ measurements. PICES Special Publication, 3.
- Doak, D.F. & Morris, W.F. (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature*, 467, 959–962.
- Feeley, R.A., Sabine, C.L., Hernandez-Ayon, J.M., Ianson, D. & Hales, B. (2008). Evidence for upwelling of corrosive ‘acidified’ water onto the continental shelf. *Science*, 320, 1490–1492.
- Feeley, R.A., Alin, S.R., Newton, J., Sabine, C.L., Warner, M., Devol, A. *et al.* (2010). The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. *Estuar. Coast. Shelf Sci.*, 88, 442–449.
- Fitzhenry, T., Halpin, P.M. & Helmuth, B. (2004). Testing the effects of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design. *Mar. Biol.*, 145, 339–349.
- Gaylord, B., Hill, T.M., Sanford, E., Lenz, E.A., Jacobs, L.A., Sato, K.N. *et al.* (2011). Functional impacts of ocean acidification in an ecologically critical foundation species. *J. Exp. Biol.*, 214, 2586–2594.
- Gazeau, F., Quiblier, C., Jansen, J.M., Gattuso, J.P., Middelburg, J.J. & Heip, C.H.R. (2007). Impact of elevated CO₂ on shellfish calcification. *Geophys. Res. Lett.*, 34, 1–5.
- Gruber, N., Hauri, C., Lachkar, Z., Loher, D., Frolicher, T.L. & Plattner, G.-K. (2012). Rapid progression of ocean acidification in the California Current System. *Science*, 337, 220–223.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.*, 8, 993–1009.
- Harley, C.D.G. & Helmuth, B.S.T. (2003). Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnol. Oceanogr.*, 48, 1498–1508.
- Helmuth, B., Harley, C.D.G., Halpin, P.M., O’Donnell, M., Hofmann, G.E. & Blanchette, C.A. (2002). Climate change and latitudinal patterns of intertidal thermal stress. *Science*, 298, 1015–1017.
- Hofmann, G.E., Evans, T.G., Kelly, M.W., Padilla-Gamino, J.L., Blanchette, C.A., Washburn, L. *et al.* (2014). Exploring local adaptation and the ocean acidification seascape - studies in the California Current Large Marine Ecosystem. *Biogeosciences*, 11, 1053–1064.
- Holm-Hansen, O., Lorenzen, C.J., Holmes, R. & Strickland, J.D. (1965). Fluorometric determination of chlorophyll. *Conseil International pour l’Exploration de la Mer; Charlottenlund (Denmark)* 30, 3–15.
- Hutchinson, G.E. (1957). Concluding remarks. In: *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427.
- Kearney, M., Simpson, S.J., Raubenheimer, D. & Helmuth, B. (2010). Modelling the ecological niche from functional traits. *Philos. Trans. R. Soc. B*, 365, 3469–3483.

- Kroeker, K.J., Sanford, E., Jellison, B.M. & Gaylord, B. (2014). Predicting the effects of ocean acidification on predator-prey interactions: a conceptual framework based on coastal molluscs. *Biol. Bull.*, 226, 211–222.
- Lester, S.E., Gaines, S.D. & Kinlan, B.P. (2007). Reproduction on the edge: large-scale patterns in individual performance in a marine invertebrate. *Ecology*, 88, 2229–2239.
- Martínez-Meyer, E., Díaz-Porras, D., Peterson, A.T. & Yáñez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biol. Lett.*, 9, 20120637.
- Melzner, F., Stange, P., Trübenbach, K., Thomsen, J., Casties, I., Panknin, U. *et al.* (2011). Food supply and seawater pCO₂ impact calcification and internal shell dissolution in the blue mussel *Mytilus edulis*. *PLoS ONE*, 6, e24223.
- Menge, B.A. (2000). Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J. Exp. Mar. Biol. Ecol.*, 250, 257–289.
- Menge, B.A. & Menge, D.N.L. (2013). Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. *Ecol. Monogr.*, 83, 283–310.
- Menge, B.A., Daley, B.A., Wheeler, P.A., Dahloff, E., Sanford, E. & Strub, P.T. (1997). Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? *Proc. Natl Acad. Sci. USA*, 94, 14530–14535.
- Menge, B.A., Lubchenco, J., Bracken, M.E.S., Chan, F., Foley, M.M., Freidenburg, T.L. *et al.* (2003). Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proc. Natl Acad. Sci. USA*, 100, 12229–12234.
- Menge, B.A., Blanchette, C.A., Raimondi, P.T., Gaines, S.D., Lubchenco, J., Lohse, D. *et al.* (2004). Species interactions strength: testing model predictions along an upwelling gradient. *Ecol. Monogr.*, 74, 663–684.
- Menge, B.A., Chan, F. & Lubchenco, J. (2008). Response of a rocky intertidal ecosystem engineer and community dominant to climate change. *Ecol. Lett.*, 11, 151–162.
- Menge, B.A., Gouhier, T.C., Hacker, S.D., Chan, F. & Nielsen, K.J. (2015). Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats. *Ecol. Monogr.*, 85, 213–233.
- Navarrete, S.A. & Menge, B.A. (1996). Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecol. Monogr.*, 66, 409–429.
- Navarrete, S.A., Broitman, B.R., Wieters, E.A. & Castilla, J.C. (2005). Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top down control. *Proc. Natl Acad. Sci. USA*, 102, 18046–18051.
- Paine, R.T. (1974). Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, 15, 93–120.
- Poloczanska, E.S., Hawkins, S.J., Southward, A.J. & Burrows, M.T. (2008). Modeling the response of populations of competing species to climate change. *Ecology*, 89, 3138–3149.
- Rapacciuolo, G., Maher, S.P., Schneider, A.C., Hammond, T.T., Jabis, M.D., Walsh, R.E. *et al.* (2014). Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. *Glob. Change Biol.*, 20, 2841–2855.
- Reimer, O. & Tedengren, M. (1996). Phenotypical improvement of morphological defenses in the mussel *Mytilus edulis* induced by exposure to the predator *Asterias rubens*. *Oikos*, 75, 383–390.
- Roy, R.N., Roy, L.N., Vogel, K.M., Porter-Moore, C., Pearson, T., Good, C.E. *et al.* (1993). The dissociation constants of carbonic acid in seawater at salinities 5 to 45 and temperatures 0 to 45 °C. *Mar. Chem.*, 44, 249–267.
- Sanford, E. & Worth, D.J. (2009). Genetic differences among populations of a marine snail drive geographic variation in predation. *Ecology*, 90, 3108–3118.
- Sanford, E. & Worth, D.J. (2010). Local adaptation along a continuous coastline: prey recruitment drives differentiation in a predatory snail. *Ecology*, 91, 891–901.
- Sanford, E., Roth, M.S., Johns, G.C., Wares, J.P. & Somero, G.N. (2003). Local selection and latitudinal variation in a marine predator-prey interaction. *Science*, 300, 1135–1137.
- Schneider, K.R. (2008). Heat stress in the intertidal: comparing survival and growth of an invasive and native mussel under a variety of thermal conditions. *Biol. Bull.*, 215, 253–264.
- Seabra, R., Wetthey, D.S., Santos, A.M. & Lima, F.P. (2011). Side matter: microhabitat influence on intertidal heat stress over a large geographical scale. *J. Exp. Mar. Biol. Ecol.*, 400, 200–208.
- Seed, R. & Suchanek, T.H. (1992). Population and community ecology of *Mytilus*. In: *The Mussel Mytilus: Ecology, Physiology, Genetics and Culture*. (ed Gosling, E.). Elsevier, Amsterdam, the Netherlands, pp. 87–169.
- Somero, G.N. (2002). Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integr. Comp. Biol.*, 42, 780–789.
- Suchanek, T.H. (1992). Extreme biodiversity in the marine environment mussel bed communities of *Mytilus californianus*. *Northwest Environ. J.*, 8, 150–152.
- Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B. *et al.* (2011). Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, 120, 1–8.
- Thompson, J.N. (1999). The evolution of species interactions. *Science*, 284, 2116–2118.
- Thomsen, J., Gutowska, M.A., Saphorster, J., Heinemann, A., Trübenbach, K., Fietzke, J. *et al.* (2010). Calcifying invertebrates succeed in a naturally CO₂-rich coastal habitat but are threatened by high levels of future acidification. *Biogeosciences*, 7, 3879–3891.
- Thomsen, J., Casties, I., Pansch, C., Körtzinger, A. & Melzner, F. (2013). Food availability outweighs ocean acidification effects in juvenile *Mytilus edulis*: laboratory and field experiments. *Glob. Change Biol.*, 19, 1017–1027.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005). Climate change threats to plant diversity in Europe. *Proc. Natl Acad. Sci. USA*, 102, 8245–8250.
- Waldbusser, G.G., Hales, B., Langdon, C.J., Haley, B.A., Schrader, P., Brunner, E.L. *et al.* (2015). Saturation-state sensitivity of marine bivalve larvae to ocean acidification. *Nat. Clim. Chang.*, 5, 273–280.
- Wang, D., Gouhier, T.C., Menge, B.A. & Ganguly, A.R. (2015). Intensification and spatial homogenization of coastal upwelling under climate change. *Nature*, 518, 390–394.
- Welschmeyer, N.A. (1994). Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. *Limnol. Oceanogr.*, 39, 1985–1992.
- Woodson, C.B., McManus, M.A., Tyburczy, J., Barth, J.A., Washburn, L., Caselle, J.E. *et al.* (2012). Coastal fronts set recruitment and connectivity patterns across multiple taxa. *Limnol. Oceanogr.*, 57, 582–596.
- Wootton, J.T., Pfister, C.A. & Forester, J.D. (2008). Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *Proc. Natl Acad. Sci. USA*, 105, 18848–18853.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Editor, Sergio Navarrete

Manuscript received 3 December 2015

First decision made 12 January 2016

Second decision made 8 March 2016

Manuscript accepted 4 April 2016