GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Climate shapes population variation in dogwhelk predation on foundational mussels

Gina M. Contolini[1] · Kerry Reid[1] · Eric P. Palkovacs[1]

Abstract

Trait variation among populations is important for shaping ecological dynamics. In marine intertidal systems, seawater temperature, low tide emersion temperature, and pH can drive variation in traits and affect species interactions. In western North America, *Nucella* dogwhelks are intertidal drilling predators of the habitat-forming mussel *Mytilus californianus*. *Nucella* exhibit local adaptation, but it is not known to what extent environmental factors and genetic structure contribute to variation in prey selectivity among populations. We surveyed drilled mussels at sites across Oregon and California, USA, and used multiple regression and Mantel tests to test the effects of abiotic factors and *Nucella* neutral genetic relatedness on the size of mussels drilled across sites. Our results show that *Nucella* at sites characterized by higher and less variable temperature and pH drilled larger mussels. Warmer temperatures appear to induce faster handling time, and more stable pH conditions may prolong opportunities for active foraging by reducing exposure to repeated stressful conditions. In contrast, there was no significant effect of genetic relatedness on prey size selectivity. Our results emphasize the role of climate in shaping marine predator selectivity on a foundation species. As coastal climates change, predator traits will respond to localized environmental conditions, changing ecological interactions.

Keywords Intraspecific variation · Climate change · Rocky intertidal · *Nucella* · *Mytilus*

Introduction

Intraspecific trait variation is an important component of biodiversity that can shape communities by changing ecological interactions (Palkovacs and Post 2009; Harmon et al. 2009; Palkovacs et al. 2009; Bolnick et al. 2011; Ingram et al. 2012; Royauté and Pruitt 2015; Fryxell and Palkovacs 2017; Des Roches et al. 2018). Variation in predator traits can alter entire food webs, yet evidence for this phenomenon comes almost entirely from freshwater and terrestrial ecosystems (Post et al. 2008; Palkovacs and Post 2009; Royauté

and Pruitt 2015). Only recently have ecologists begun to appreciate intraspecific trait variation among marine populations, long considered too open to exhibit local adaptation, which can fine-tune the traits of populations to suit their local environments (Kawecki and Ebert 2004; Sanford and Kelly 2011). To advance our understanding of ecologically important trait variation in the marine environment, it is important to examine this variation at the population level and identify the underlying drivers.

Climate variables like temperature and pH can alter foraging traits in marine predators. For example, temperature alters feeding rate in intertidal *Nucella* dogwhelks (Yamane and Gilman 2009; Miller 2013; King and Sebens 2018), and elevated seawater $p\text{CO}_2$ shifts prey size selectivity in *Nucella lapillus* (Sadler et al. 2018). Consistent differences in these abiotic factors can lead to population differences in foraging traits due to local adaptation and phenotypic plasticity. However, patterns of genetic relatedness among populations can also underlie trait similarities despite environmental differences (Endler 1973; Felsenstein 1985; Thorpe 1996; Hendry et al. 2001; Lenormand 2002). We evaluate the effects of local environment and genetic relatedness as drivers of

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trait variation among populations of a low-dispersing marine intertidal predator.

In intertidal zones in the California Current System of western North America, dogwhelks of the genus *Nucella* are important predators, consuming sedentary, foundational prey (West 1986). *Nucella* have direct-developing larvae and very low dispersal ability (Strathmann 1987), which gives them an increased ability to adapt to environmental conditions such as temperature and pH that affect foraging strategies (Yamane and Gilman 2009; Queirós et al. 2015; Cerny-Chipman 2016; King and Sebens 2018; Sadler et al. 2018). For example, populations of *N. canaliculata* exhibit local adaptation in mussel prey selectivity (Sanford et al. 2003; Sanford and Worth 2010). Here we examine differences in prey selectivity among populations of the *Nucella ostrina-emarginata* species complex (hereafter *Nucella*). This species complex is made up of individuals identified as *N. ostrina* or *N. emarginata,* which have conflicting morphological and molecular evidence for their distinctness (Marko 1998, 2005; Dawson et al. 2014); thus, we consider them together for ecological analyses. Differences in prey selectivity among populations could be due to patterns of genetic relatedness, adaptation, plasticity to local abiotic conditions, or some combination of these factors.

We explore the effects of temperature, pH, and neutral population genetic relatedness in shaping variation in *Nucella* size selectivity for the foundational mussel *Mytilus californianus* throughout Oregon and California, USA. Our main questions are: (1) How do temperature and pH regimes shape variation among populations in *Nucella* size selectivity for *M. californianus*? and (2) Do populations with higher genetic relatedness exhibit more similar size selectivity? We predict that temperature will have important effects on size selectivity because it is known to influence *Nucella* foraging and ingestion rates (Largen 1967; Bayne and Scullard 1978; Sanford 2002; Yamane and Gilman 2009; Miller 2013; King and Sebens 2018). We further expect that pH will shape prey size selectivity because it affects prey detection and predation rate across a wide range of taxa (de la Haye et al. 2012; Pistevos et al. 2015; Watson et al. 2017), including other *Nucella* species (Queirós et al. 2015; Cerny-Chipman 2016; Sadler et al. 2018). We hypothesize that neutral genetic relatedness will not have a strong effect on size selectivity because *Nucella* populations have limited dispersal, providing ample opportunity for local adaptation and plasticity to modify feeding traits (Strathmann 1987; Marko 1998; Sanford et al. 2003; Dawson et al. 2014). Temperate mussel beds provide habitat for hundreds of species and are strongly influenced by top-down interactions (Paine 1966); therefore, understanding the drivers of variation in predator selectivity, such as *Nucella* prey size selectivity, will help link larger ecological and climate processes to mussel bed structure and diversity.

Materials and methods

Study species

Nucella are dogwhelk predators that feed on sedentary shelled animals including *Mytilus* spp. mussels. Members of the *Nucella ostrina-emarginata* species complex are the primary mussel drilling predators in the mid-intertidal, as other *Nucella* species like *N. canaliculata* inhabit lower shore levels (Morris et al. 1980). *Nucella* feed by drilling, leaving a characteristic ≈ 1 mm diameter hole in their prey, making it easy to track predation across space and time (Clelland and Saleuddin 2000). Though it may take days for a dogwhelk to consume one mussel, *Nucella* in high densities can have significant negative effects on mussel density (Hughes and de Dunkin 1984; Suchanek 1986; Menge et al. 1994; Navarrete and Menge 1996; Sanford et al. 2003). We focus on predation of *Mytilus californianus* rather than congeners like *M. trossulus* because *M. californianus* is competitively dominant, more abundant, and important for intertidal community diversity (Kanter 1977; Suchanek 1978b, 1992; Palmer et al. 1990; Navarrete 1994, 1996; Lafferty and Suchanek 2016). *M. californianus* mussel bed structural complexity, which is largely determined by mussel size, is positively correlated with species diversity. Anything that affects mussel size structure can therefore shape intertidal diversity (Kanter 1977; Suchanek 1992; Suchanek 1978a, b).

Characterization of environmental variables

We studied *Nucella* drilling selectivity at eight intertidal sites in Oregon and California, USA with different climate regimes (Fig. 1, Table S1). To describe the different regimes, we used three data sets: seawater pH from the Ocean Margins Ecosystem Group for Acidification Studies (OMEGAS, Menge et al. 2015), low tide emersion temperatures from intertidal biomimetic temperature sensors (Helmuth et al. 2016), and seawater temperatures from the Partnership for the Interdisciplinary Studies of Coastal Oceans (PISCO; http://www.piscoweb.org/access-data). For the pH data, we used 10-min interval measurements of pH made using Durafet® pH sensors modified by OMEGAS and secured to the intertidal zone from Apr-2013 to Oct-2013 (Chan et al. 2017). The OMEGAS group monitored seawater chemistry during this time, the core upwelling season, to capture pH profiles during the most dynamic and biologically stressful period, and because winter deployments are often unfeasible due to increased wave stress. We calculated summary statistics on seawater pH including mean, median, standard deviation, coefficient

Fig. 1 Map of study sites in Oregon and California (USA)
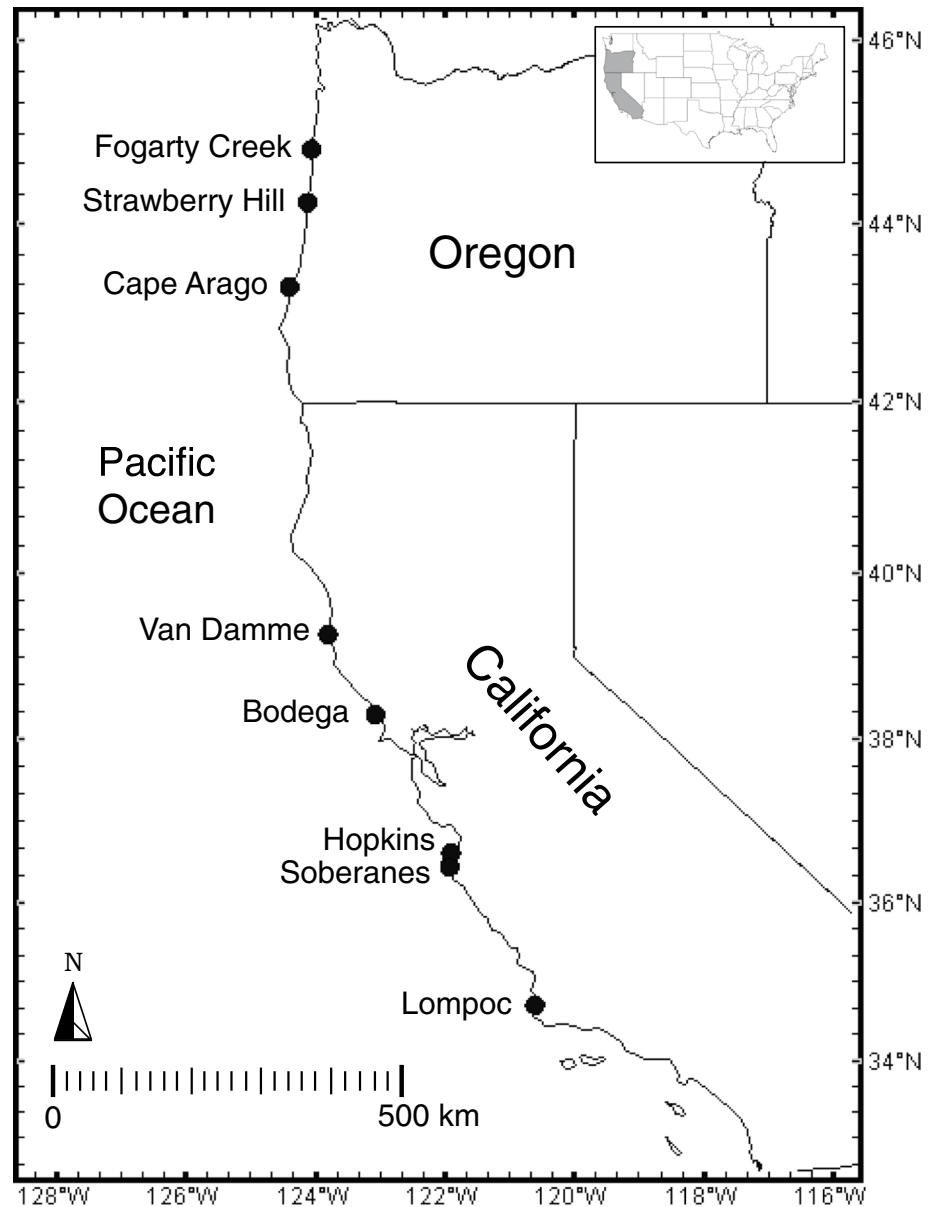
of variation, various percentiles, and frequency of exposure below pH values known to induce pH stress (Fig. S1, Table S2; Hofmann et al. 2014; Kroeker et al. 2016). We excluded all environmental data from our southernmost site, Lompoc, where the pH sensor was damaged.

To characterize the emersion thermal dynamics of intertidal mussel beds, we used data from the intertidal biomimetic temperature sensors (Helmuth et al. 2016). We include emersion temperature in addition to water temperature because in intertidal zones, the two temperature regimes can be different in unexpected ways (e.g., not following a latitudinal gradient) and elicit different biological responses (Helmuth et al. 2006; Yamane and Gilman 2009; King and Sebens 2018). Biomimetic loggers are preferred to traditional temperature loggers for emersion temperature

because traditional loggers often record highly unrealistic values due to their unnatural color and shape (Fitzhenry et al. 2004). Rather than act as approximations of dogwhelk body temperatures, these temperature data were used to represent the site-specific emersion temperature of the mussel bed to which dogwhelks would adjust foraging behaviors; for example, dogwhelks can face a tradeoff between foraging and seeking thermal refugia at low tide (Burrows and Hughes 1989; Hayford et al. 2015). The biomimetic sensors were fashioned out of marine epoxy to the size, shape, and color of *M. californianus* mussels and secured in the mussel bed, recording temperature every 10 min. We used data as available for all sites in low and lower-mid intertidal zones from 02-May-2013 to 21-Sep-2013. Since high emersion temperatures are thought to limit intertidal organisms, the

cooler low-zone thermal dynamics provided conservative estimates of heat stress for our study (Connell 1961). To parse emersion and water temperatures, we aligned these temperature data to tidal height using the "WWW Tide/Current Predictor" (http://tbone.biol.sc.edu/tide) and identified at what tidal height low tide temperatures differed noticeably from high tide temperatures (i.e., the sensor was emersed vs. immersed). We determined the appropriate emersion tidal height for each site and used it as a threshold for when to classify temperature as emersed versus immersed, excluding temperature values ± 0.15 m around the threshold height when it is difficult to tell whether the sensor is immersed. After parsing emersion and immersion temperatures, we calculated summary statistics for emersion including median, minimum, maximum, standard deviation, and, since upper thermal tolerance determines the distribution of many intertidal organisms, the frequency of temperatures over 24, 26, 28, and 30 °C (Connell 1961; Table S2).

While OMEGAS pH and biomimetic temperature logger data were only available for spring and summer 2013, intertidal water temperature was available for all seasons from a larger time range. We used PISCO temperature loggers (HOBO, Onset Corporation) to characterize seawater temperature dynamics over the upwelling season and throughout the entire year for 2009 through 2013. This data set reflects the characteristic immersed thermal environments which dogwhelk populations had experienced over a 5-year period prior to our field sampling. This approach allowed us to characterize the long-term patterns of seawater temperatures at the sites and to compare water to emersion thermal dynamics and the upwelling season to the full year (Fig. S2). We calculated summary statistics (mean, median, min, max, frequency of water temperature above 10, 12, 14, and 16 °C) on the daily average temperature at each site for each year, then averaged across years. Upwelling thermal dynamics matched well with full year dynamics, so we used temperature data for full years in our analyses. The 2013 upwelling water temperature dynamics were similar to the 5-year dynamics, supporting that the 2013 upwelling pH and emersion temperature dynamics were also similar to long-term dynamics (Fig. S3).

Finally, we used principal component analysis (PCA) to characterize the combined environmental regimes of the sites, including all previously listed pH, emersion and water temperature metrics (Fig. S1; *prcomp()* function in *stats* package in *R*; R Core Team 2017). These climate regime axes were later used as predictors in a multiple regression of drilling selectivity.

Drilling selectivity

To measure *Nucella* drilling selectivity, we surveyed mid intertidal *M. californianus* mussel beds for drilled mussels between Mar-2015 and Jun-2015 (except Lompoc in Nov-2015). At sites where pH sensors were still present, we performed our surveys as close as possible to the sensor, often a few meters away. At each site, we collected all dead mussels with a borehole within 2 m diameter plots ($n = 3$–4 per site, total $n = 27$) where *Nucella* were present. Dead mussel shells can remain in the mussel bed for as long as 8 months, so boreholes provide a long-term estimate of *Nucella* predation (Suchanek 1978a, b; Sanford and Worth 2009). To determine if *Nucella* are size-selective for prey, we subsampled undrilled mussels in the 2 m diameter plots by haphazardly placing four 15 cm diameter quadrats within the plots and collecting all mussels in them. Since the ranges of congeners *M. trossulus* and *M. galloprovincialis* overlap with *M. californianus*, we identified mussels to species level morphologically and confirmed they were absent or very uncommon in our plots (< 20 at any site and < 40 overall). We accounted for mussel growth between the time of dogwhelk drilling and our collection using average growth rates of *M. californianus* from mussel growth surveys in central California (Menge et al. 2004) and Oregon (Behrens Yamada and Dunham 1989), calculating mean growth over 8 months, subtracting this potential growth from our sample means, then redoing all analyses.

We measured shell length of all drilled ($n = 39$–154 per site, total $n = 581$) and undrilled ($n = 271$–1238 per site, total $n = 5665$) mussels in each plot. We measured length as the tip of the beak to the posterior edge using either electronic calipers or, for mussels ≤ 20 mm, from photos using ImageJ software (v. 1.51 s; Abràmoff et al. 2004). Quadrats were nested within plots, so we averaged mussel lengths across quadrats within plots, then averaged plots to get site means and variance. We also measured shell thickness across the whole shell and found that length and thickness were highly colinear (linear regression $R^2 = 0.871$, $P < 0.001$); therefore, we considered only length in our final analyses. To understand if *Nucella* are selective predators, we tested if the sizes of drilled mussels were different from the sizes of available mussels (which includes drilled and undrilled) by performing Kolmogorov–Smirnov tests of the respective distributions at each site.

To compare dogwhelk sizes among sites, we collected 25–68 *Nucella* at each site from in and around our plots. We measured length with calipers as the distance from the shell apex to the tip of the siphonal canal and calculated mean and variance for the whole site. We used analysis of variance (ANOVA) and pairwise *t* tests to examine variation in *Nucella* length and drilled and available mussel lengths across the eight study locations, transforming data when necessary to meet model assumptions of normality.

Mitochondrial haplotype diversity and IBD

From our previously collected *Nucella,* we took a foot tissue sample from each specimen and preserved it in 95% EtOH. We collected additional specimens in 2017 from Fogarty Creek, Strawberry Hill and Bodega to increase sample size (final $n = 20$–39). To compare genetic differences among populations, we sequenced a region of the mitochondrial gene cytochrome *c* oxidase subunit I (COI) which is widely used in mollusk studies to distinguish both between closely related species and among populations within species (Marko 1998, 2004; Hebert et al. 2003; Marko et al. 2014; Dawson et al. 2014). We extracted DNA using a Thermo Scientific GeneJET Genomic DNA purification kit (ThermoFisher Scientific), following instructions for mammalian tissue genomic DNA purification. To amplify the COI gene, we used primers LCO1490 and HCO2198 (Folmer et al. 1994) or the modified versions jgLCO1490 and jgHCO2198 (Geller et al. 2013). We prepared polymerase chain reactions (PCR) with 1.5–3 μL genomic DNA, 11.08 μL GoTaq Green master mix (Promega), 1.46 μL of each primer stock solution (20–100 μM; Sigma-Aldrich), and 2 μL BSA. PCR conditions were 94 °C for 2 min followed by 30 cycles of 94 °C for 1 min, 48 °C for 1 min and 72 °C for 1 min. We visualized PCR products on 2% agarose gels before purification and sequencing at the UC Berkeley DNA Sequencing Facility (Berkeley, USA). We edited chromatograms of sequences in CLC Bio Workbench v. 7.9.1 (CLC Bio A/S, Aarhus, Denmark) and cropped and aligned them using MEGA v. 7.0.26 (Kumar et al. 2016). We calculated haplotype frequencies in the *R* package *pegas* (v. 0.10; Paradis 2010). To quantify genetic relatedness between populations, we calculated Kimura-2-parameter distance (K2P) within and between all sites using Arlequin v. 3.5.2.2 (Excoffier and Lischer 2010). We tested for isolation by distance (IBD) by plotting pairwise K2P distance against coastline distance estimated from Google Earth Pro v. 7.3.1.4507 and used linear regression to test for a significant correlation.

Contributions of environment and genetic relatedness

To determine the contributions of the environment and genetic relatedness to drilling selectivity, we used two approaches: multiple regression and stepwise model selection (environmental data) and Mantel tests (genetic data). We used two approaches because the response variable and most predictor variables are measured values, but the genetic data were a distance matrix that cannot be used in multiple regression analyses. First, we used multiple regression to fit environmental models of the mean length of drilled mussels using the *lm()* function in package *stats* in *R* (R Core Team 2017). The total sample size was 24, as one site (Lompoc)

did not have environmental data available. For predictors, we used principal component axes one through three (PC1–PC3) from the environmental data as well as mean *Nucella* length, mean available mussel length, and the density of drilled mussels as a proxy for *Nucella* density. Predictor variables were noncolinear and independent, meeting model assumptions (VIF < 6, Zuur et al. 2007). Assumptions of normality and homogeneity of variance were checked visually using Q–Q and residuals versus fitted plots and no assumptions were violated. We performed forward and backward stepwise model selection using the *step()* function in package *stats* and compared models using the Akaike Information Criteria corrected for small sample sizes (AICc) to determine which model best explained drilled mussel length (*aictab()* function in package *AICcmodavg*; Mazerolle 2019; Table S3). We selected the model with the lowest AICc score that included mussel length available since this was an important a priori biological predictor. We then incorporated random effects and correlations among quadrats with a compound symmetry correlation structure using the *lme()* function in package *nlme* (Pinheiro et al. 2019). Our final model included PC1, PC3, mean mussel length available and mean *Nucella* length as fixed effects and site as a random effect. We calculated effect sizes using the coefficients of linear regressions on mean drilled mussel length residuals and each predictor variable.

To test for correlations between genetic distance and drilled mussel length while taking into account covariates, our second approach was to convert all non-matrix data into separate Euclidean distance matrices using the *dist()* function in package *vegan* (Oksanen et al. 2018). First, we used a Mantel test to test for an effect of genetic distance on drilled mussel length (function *mantel()* in package *vegan*). Next, we used partial Mantel tests to evaluate the correlation between genetic distance and drilled mussel length while controlling for significant model terms individually (function *mantel.partial()* in package *vegan*). Lastly, we used partial Mantel tests to evaluate the correlation between each significant model term and drilled mussel length while controlling for genetic relatedness. It is important to note the interpretation of these analyses differs from those of the multiple regression as all variables are distance matrices, not raw measured values. We performed all analyses in R v. 3.3.1 (R Core Team 2017) and plots were made with package ggplot2 (Wickham 2016).

Results

Characterization of environmental variables

Principal component axis one (PC1) explained 59.49% of the variability in the environmental variables and showed

differences in pH and temperature regimes among the sites, roughly reflected in latitude. Sites with low median emersion and water temperatures also had high values for standard deviation in pH, standard deviation in water temperature, and frequency of low pH events, conditions that especially characterized the northern three sites (Fig. S1; Table S2). On the other end of this environmental axis were sites with high median emersion and water temperatures, high frequencies of very warm emersion and water temperatures, and high mean pH, most notably Hopkins, which is in the Monterey Bay, CA.

Positive values on the second PC axis (PC2) represented high standard deviation of emersion temperatures and stable pH (i.e., high minimum, low maximum, low frequency below 7.6) and this axis explained 22.36% of the total environmental variation among sites. One of the central sites (Van Damme) had the highest value on this axis, showing it had the most variable emersion temperatures but a relatively stable pH regime. For the third PC axis (PC3), accounting for 10.78% of the total variation, positive values represented higher frequency of pH dropping below 7.6, and negative values represented high frequency of pH below 8.0, high standard deviation of water temperature and high maximum water and emersion temperatures.

Drilling selectivity

Distributions of drilled and available mussels differed significantly at all sites, indicating that *Nucella* were selective for mussel size. Nearly all sites had larger mean drilled mussels than the mean available (mean selectivity [mean drilled − mean available] across sites: 14.02 ± 9.51 mm, mean $\pm$ SD; Kolmogorov–Smirnov tests, $D = 0.24$–0.64, $P < 0.001$; Fig. S4), except Strawberry Hill where the drilled mussels were on average smaller (mean selectivity: -7.48 ± 14.28; Kolmogorov–Smirnov test, $D = 0.312$, $P < 0.001$). Mean *Nucella* shell length, mean available mussel length, and mean drilled mussel length all varied significantly among sites (Fig. 2). Larger *Nucella* occurred at the southern three sites (ANOVA, $F_{7,315} = 55.04$, $P < 0.001$; Fig. 2a). Mean available mussel length varied from about 1.5 to 5 cm (ANOVA, $F_{7,19} = 5.78$, $P = 0.001$; Fig. 2b), and drilled mussel length from 1 cm to almost 6 cm, with smallest drilled mussels at the northern two sites (ANOVA, $F_{7,19} = 20.12$, $P < 0.001$; Fig. 2c).

Mitochondrial haplotype diversity and IBD

We generated a haplotype network using 135 COI sequences of 599 bp ($n = 7$–25 per site; Fig. S5; GenBank accession numbers MK258758–MK258868 and MK265353–MK265375). There were fixed differences in COI among most *Nucella* populations, and only the
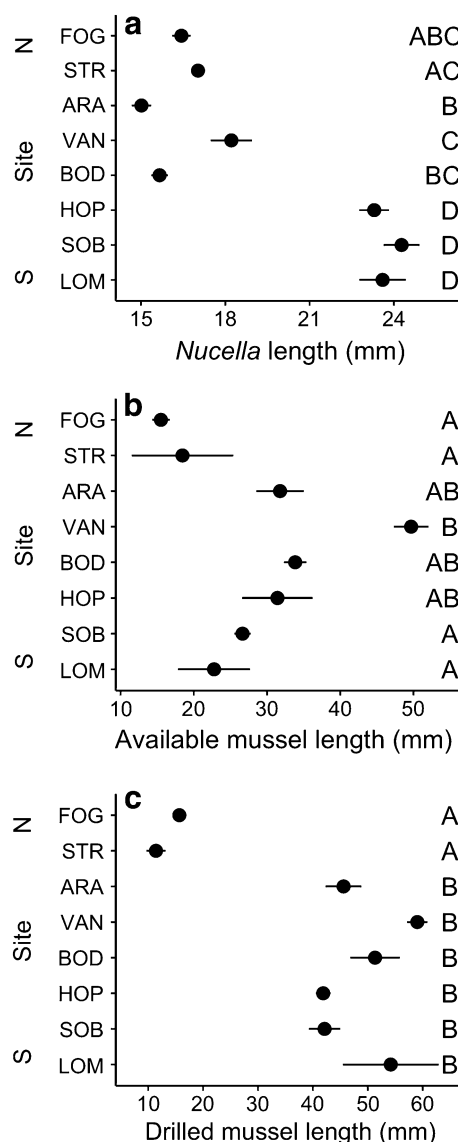

Fig. 2 Site comparisons of mean $\pm$ SEM of **a** *Nucella* length ($n = 25$–68 per site, total $n = 341$), **b** available mussel length ($n = 271$–1238 per site, total $n = 5665$), and **c** drilled mussel length ($n = 39$–154 per site, total $n = 581$). Sites are ordered north to south. Mussel length is the average of $n = 3$–4 plots per site. *Nucella* length is the average of all dogwhelks collected at a site since they were found in and out of plots. Points with different letters are significantly different at the $\alpha = 0.05$ level based on paired t tests

northern three populations shared a substantial number of haplotypes, suggesting that populations in the south are more isolated. In the south, Hopkins did not share haplotypes with the two other southern locations (Soberanes and Lompoc) and none of the northern sites shared any haplotypes with the southern sites. Estimates of K2P (Table S4) indicate these northern populations are less divergent from each other than populations in the south.

A pattern of isolation by distance was not supported, suggesting isolation on a very localized scale ($R^2 = 0.017$, $P = 0.24$; Fig. S6).

Contributions of environment and genetic relatedness

In the multiple regression of environmental variables on mean drilled mussel length, the two best models (lowest AICcs, less than 2 units apart) for mean drilled mussel length showed 91% of the cumulative weighting in the set of competing models and included the significant predictor terms *Nucella* length, PC1, and PC3 ($P < 0.02$), plus the nonsignificant term mean available mussel length (Table 1; Table S3). We used these four terms as fixed effects while accounting for correlations among replicate quadrats and site as random in our final linear mixed effects model. PC3, representing more stable water temperature and pH, was significantly positively related to mean drilled mussel length ($P = 0.045$; Fig. 3a). PC1, representing greater and more stable temperatures and pH, was also positively related to drilled mussel length, though it was marginally insignificant ($P = 0.052$; Fig. 3b). Mean available mussel length and mean *Nucella* length were not significantly related to mean drilled mussel length (Table 1). A one-unit increase in PC3 had about twice the effect on mean drilled mussel length as PC1 (7.0 vs. 3.6), with total effect sizes of 27.12 and 20.25 mm, respectively. The random effect of site explained 71.05% of the residual variance. After subtracting potential mussel growth over 8 months, these results were qualitatively unchanged (Tables S5 and S6).

Genetic distance was not significantly correlated with the matrix of mean drilled mussel length, even when controlling for significant model terms using a partial Mantel test. PC1 and PC3 were significantly correlated with drilled mussel length after controlling for genetic distance (Table 2).

Table 1 Estimates for linear mixed effects model for mean drilled mussel length

Fixed effects	Estimate	Std. error	df	t	P
Intercept	92.68	27.85	16	3.33	0.004*
PC3	7.01	2.10	3	3.33	0.045*
PC1	3.59	1.15	3	3.13	0.052
Mean *Nucella* length	−3.22	1.38	3	−2.34	0.10
Mean available mussel length	0.17	0.17	16	0.97	0.34
Random effect	% variance explained				
Site	71.05				

Units are mm for lengths and standard deviations for PCs. An asterisk indicates significance at the $\alpha = 0.05$ level

The model was fitted using restricted maximum likelihood with the *nlme* package in *R*

Discussion

Intraspecific trait variation, including phenotypic variation among populations, can have important effects on species interactions that shape communities and ecosystems (Palkovacs and Post 2009; Harmon et al. 2009; Palkovacs et al. 2009; Bolnick et al. 2011; Ingram et al. 2012; Royauté
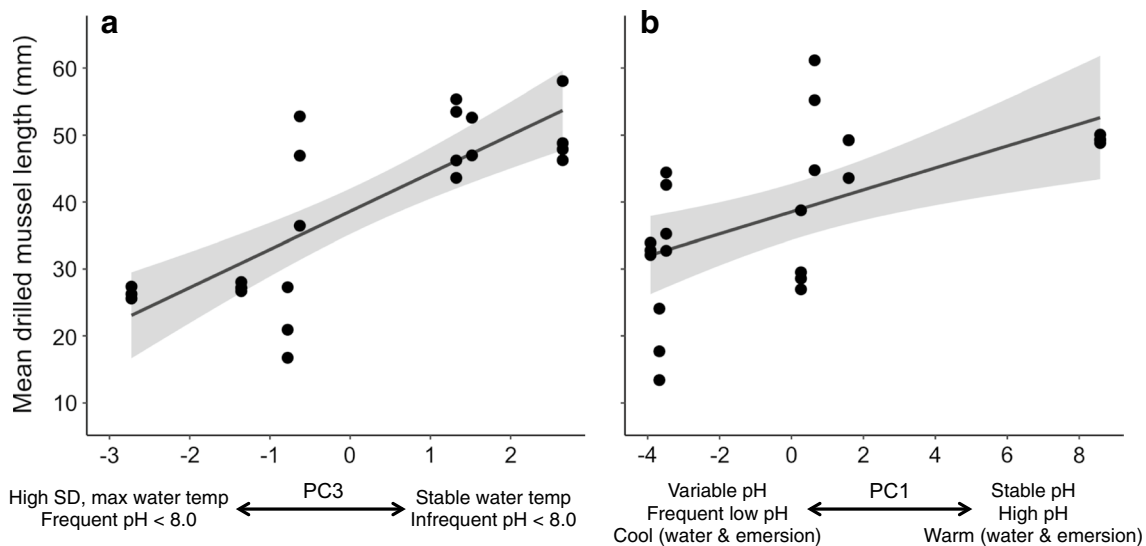

Fig. 3 Relationships between the significant terms in the final model and the response variable, mean drilled mussel length ($n = 24$). Axes are mean drilled mussel length residuals (added back to the mean for easy interpretation) versus each predictor term. Lines and 95% confidence bands are from linear smoothing functions

Table 2 Mantel and partial Mantel tests for correlations between genetic distance, environmental variables, and mussel length drilled

Distance matrix 1	Distance matrix 2	Control matrix	Mantel correlation coefficient (r)	P
Mean drilled mussel length	K2P	NA	-0.17	0.99
Mean drilled mussel length	K2P	PC1	-0.30	0.99
Mean drilled mussel length	K2P	PC3	-0.21	0.99
Mean drilled mussel length	PC1	K2P	0.26	0.003*
Mean drilled mussel length	PC3	K2P	0.25	0.007*

Correlation coefficients for distance matrices 1 and 2 are computed after controlling for the control matrix. An asterisk indicates significance at the $\alpha = 0.05$ level

and Pruitt 2015; Fryxell and Palkovacs 2017; Des Roches et al. 2018). Our study explored the drivers of trait variation among populations of a predator that preys on a foundation species. Our goal was to determine how environmental variation and neutral genetic relatedness contribute to variation among populations in *Nucella* selectivity of *Mytilus californianus* prey. We found significant trait variation among populations of *Nucella* is largely related to temperature and pH and not significantly related to neutral genetic relatedness. Specifically, we found that *Nucella* select larger mussels at sites characterized by greater and more stable temperatures and pH. These results provide evidence that *Nucella* predation can be altered by climate change, which is reducing seawater pH, increasing temperature, and lengthening the duration of upwelling in the California Current System (Gruber et al. 2012; Hauri et al. 2013; Wang et al. 2015; Turi et al. 2016; Xiu et al. 2018). As changes occur, environmental conditions interacting at different scales will influence the size selectivity of *Nucella* with the potential to change the structure of the mussel bed and associated community.

We found fixed genetic differences in COI haplotypes among populations, but these differences were not correlated with variation in prey selectivity, even after accounting for important environmental variables, indicating that prey size selectivity is not related to neutral genetic distance. Marko (1998) and Dawson et al. (2014) found similarly low COI differentiation among many of these populations. While Palmer et al. (1990) reported two species in this range, the very low COI differentiation we found among populations does not clearly indicate separate species. Since environmental predictors remained important after controlling for genetic relationships, climate effects on *Nucella* feeding ecology appear relatively unconstrained by phylogeny. This result has important implications for how populations will respond to rapid changes in coastal climate.

Abiotic and biotic stressors may make predation risky for *Nucella* as the dogwhelk is immobilized and vulnerable for several days during handling (drilling) of their prey. The larger the mussel, the longer the handling time, and the longer the dogwhelk is exposed to these stressors (Hughes and de Dunkin 1984). Temperature and pH are two important stressors that alter *Nucella* foraging behavior and can influence size selectivity via risk of prolonged handling. Acidified seawater increases handling time (Queirós et al. 2015; Cerny-Chipman 2016) and causes shell dissolution in *Nucella* (Nienhuis et al. 2010), so dogwhelks exposed to low pH face a tradeoff between foraging and hiding from their own predators. This tradeoff could lead dogwhelks in lower pH to choose smaller mussels with shorter handling times. Temperature has more complex effects on *Nucella* foraging. Warm emersion temperatures have negative effects on *Nucella* predation rate, while warm water has strong positive effects and can mitigate the negative effects of warming during emersion (Yamane and Gilman 2009; King and Sebens 2018). *Nucella* may have been able to drill larger mussels at the sites with warm water despite the associated warm emersion temperatures due to the overwhelmingly positive effects of water temperature on predation rate and growth. Finally, wave exposure, which we did not measure, can affect foraging (Burrows and Hughes 1991), and is often correlated with temperature (higher wave exposure, lower temperature; Harley and Helmuth 2003; Blanchette et al. 2007). Therefore, cold temperature could be confounded with high wave stress as a driver of prey selectivity, leading dogwhelks to drill smaller mussels to reduce handling time and the associated risk of dislodgement by waves.

Environmental variability was the most important factor explaining mussel size selectivity. *Nucella* drilled larger mussels—with longer handling times—at sites with greater PC3 values, representing more stable water temperature and pH conditions. It is possible that the risk of repeated exposure to stressful abiotic events while handling a large mussel was lower at the more stable sites. Marine organisms initiating thermal stress repair (e.g., heat shock protein expression) may take days to return to baseline levels, and many repeated stressful events can add up and increase recovery time (Gunderson et al. 2016); therefore, sites characterized by high abiotic variability could put *Nucella* in a prolonged stress response. During handling, *Nucella* cannot seek refuge from these stressful events, so more stable conditions may allow them the option of consuming larger prey with longer handling times.

Temperature and pH are important components of climate that are changing worldwide due to recent climate change. Global climate models predict sea surface temperatures to rise, pH to decrease, and upwelling intensity and duration in the California Current System to increase in the coming decades (Bakun et al. 2015; Turi et al. 2016; Xiu et al. 2018). In our study, warmer temperatures and low pH were oppositely correlated with the size of mussels drilled, suggesting that the effects of climate change on the *Nucella–Mytilus* interaction will depend on which stressor has the stronger effect in a given local environment. For example, *Nucella* predation in areas with strong and persistent upwelling, such as sites between Cape Blanco and Point Conception, may be more affected by decreases in pH since upwelling primarily brings low pH, cold water to the coast. This trend would reduce the size of mussels *Nucella* select, weakening their effect on mussel bed structure. One possible mechanism for selecting smaller prey in low pH is increased handling time if the energetic reward for consuming large mussels ceases to exceed the energy required to drill them (Queirós et al. 2015; Cerny-Chipman 2016). In contrast, *Nucella* at sites outside the region of strong upwelling may be more affected by warming temperatures, leading to increased selection of larger mussels by reducing handling time (Miller 2013), strengthening *Nucella's* effect on mussel bed structure. However, pH and temperature also affect mussel traits like size and shell thickness (Kroeker et al. 2014a; Sadler et al. 2018), so net changes in the *Nucella–Mytilus* interaction ultimately depend on the responses of both predator and prey to changing climate (Kroeker et al. 2014b).

Our study suggests that variation among populations in predator foraging patterns in intertidal zones is more related to climate conditions than neutral genetic relatedness, showing the importance of environmental conditions in driving trait variation among populations of marine organisms. As ocean conditions continue to change, populations of marine organisms will face increasingly stressful abiotic conditions that vary based on the interactions between global, regional, and local climate dynamics. As each population faces unique conditions, organisms will respond by changing behavioral, morphological, or physiological traits, which can change species interactions and community dynamics. Increasingly, predictions of biodiversity will depend not only on effects of climate on species persistence but also on population-specific changes in ecologically important traits.

Compliance with ethical standards

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