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ECOLOGY OF POPULATION-LEVEL TRAIT VARIATION IN PREDATORS OF FOUNDATIONAL INTERTIDAL MUSSELS

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by

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Abstract

ECOLOGY OF POPULATION-LEVEL TRAIT VARIATION IN PREDATORS OF FOUNDATIONAL INTERTIDAL MUSSELS

by

Gina Marie Contolini

Recent research highlights the prevalence of intraspecific trait variation, even in relatively open ocean habitats. The ecological importance of intraspecific trait variation, however, while shown in freshwater and terrestrial ecosystems, remains unexplored in marine systems. While climates change rapidly and differentially across marine environments at scales within species ranges, population-level trait variation in response to abiotic drivers is inevitable. It is therefore timely and important to explore the climate drivers of intraspecific trait changes and their ecological consequences in marine systems. In this dissertation, I explore these dynamics in a model predator-prey system. The predators, *Nucella ostrina-emarginata* dogwhelks, exhibit low population connectivity and gene flow due to their life history. The prey, *Mytilus californianus*, the California mussel, is a foundational mussel that supports high intertidal diversity. These species exist throughout a mosaic of climate conditions in the California Current System, setting the stage for local scale climate effects on *Nucella* predation that have community consequences. In **Chapter 1**, I examine climate drivers of population-level variation in size selectivity of *Nucella* on *Mytilus*. I find that abiotic variables such as

temperature and pH are the strongest drivers of *Nucella* prey size selectivity rather than neutral genetic relationships among populations, which have no effect. In **Chapter 2**, I test for population-level differences in the responses to acute exposure to acidified seawater on *Nucella* size selectivity and consumption time. I find that populations are affected differently by acidification, showing that climate change can affect *Nucella* predation on local scales. In **Chapter 3,** I test for community effects of population-level differences in *Nucella* predation on mussel beds in the field. I find that *Nucella* predation affects mussel bed size structure and in turn, size structure affects community composition, showing differential predation on a foundation species can alter communities. My dissertation links climate change, trait variation, and community ecology, demonstrating how climate can indirectly alter communities by shaping predator traits on local scales, and expanding the study of population-level trait variation into marine ecosystems.

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Introduction

One of the central goals of the field of Ecology is quantifying and explaining the wonderful and seemingly endless diversity of life in the natural world. This is an enormous and daunting task, best approached at different scales. The scales of ecological diversity include ecosystem, community, species, and subspecies scales. Diversity at the subspecies scale, including population-level trait variation, has recently been more heavily studied due the discovery that it can be important for broader ecological processes (Bolnick et al. 2011; Des Roches et al. 2018). For example, alewife (*Alosa pseudoharengus*) from anadromous versus landlocked populations have differential effects on the community structure of zooplankton in lakes (Post and Palkovacs 2009). *Pisaurina mira* spiders from different thermal habitats exhibit differences in foraging that ultimately affect the composition of grass and forb species in old-field meadows (Barton 2011). The ecological effects of population-level trait variation can be as strong or stronger than species-level effects (Des Roches et al. 2018). Traits, i.e. phenotypes, are especially important in linking ecology to evolution because they are the scale at which selection acts, and thus provide a mechanism by which evolution interacts with ecology (Palkovacs and Hendry 2010).

The abiotic environment is an important driver of trait diversity. For example, adaptation to temperature leads to population-level trait variation in terrestrial and

freshwater systems (Barton 2011; Royauté and Pruitt 2015; Fryxell and Palkovacs 2017). Temperature is an especially relevant abiotic driver in our era of global warming. As climate changes, populations with different prior exposures to climate stressors may respond differently, and this can affect their ecological interactions. Predators have particularly important roles in structuring communities in systems under top-down control. Therefore, population-level trait variation in predators is an important part of how climate change alters natural systems. Despite the importance of predator traits in linking climate change to ecosystems, few studies have addressed climate effects on predator traits. To fill this gap, in this dissertation I characterize patterns of predation in a marine intertidal predator at the population scale, explore whether trait differences are driven by neutral genetic relationships or adaptation or acclimatization to climatic factors, and examine the community effects of differential foraging traits.

I characterize trait differences among populations of the intertidal gastropod predator species complex *Nucella ostrina-emarginata* (hereafter *Nucella*) in the California Current System of the United States. These drilling dogwhelks consume sessile prey including the foundational mussel *Mytilus californianus*. *Nucella* have very low dispersal and high genetic population structure, indicating low gene flow among populations and a high potential for local adaptation (Marko 1998; Sanford and Worth 2009; Dawson et al. 2014). They also exist along an environmentally heterogeneous coastline in the California Current System. Together, these attributes make it extremely likely that *Nucella* populations have developed trait differences

based on local abiotic conditions. In **Chapter 1,** I explore population-level differences in *Nucella* predation on *M. californianus* mussels in the field and relate this to environmental regimes and neutral genetic relationships among populations. In **Chapter 2,** I test for differential effects of seawater acidification on *Nucella* foraging traits. In **Chapter 3**, I test for community effects of population-level differences in *Nucella* foraging in the field.

In **Chapter 1,** "Climate shapes population variation in dogwhelk predation on foundational mussels," I used field surveys to quantify *Nucella* prey size selectivity on mussels at eight sites throughout the California Current System (Oregon and California, USA). I hypothesized there would be differences in size selectivity of *Nucella* on mussel prey that relate to environmental conditions because *Nucella* populations are isolated from each other and experience different abiotic regimes. By pairing data on mussel size selectivity with temperature (immersion and emersion) and pH data, I found that *Nucella* at sites with lower and more variable temperature and pH regimes drill smaller mussels. Drilling smaller mussels in cooler, more acidic, and more variable abiotic environments could reduce the risk of exposure to repeated stressful environmental conditions while drilling, which often takes several days and can be even slower in cooler temperatures. Neutral genetic relatedness at the mitochondrial gene cytochrome c oxidase subunit I (COI) among populations did not correspond to mussel size selectivity, indicating that abiotic factors are more important than phylogeny in determining *Nucella* foraging traits.

In **Chapter 2**, "Population-specific differences in the effects of seawater acidification on predator foraging traits," I examined *Nucella* population-level foraging responses to ocean acidification conditions. Ocean acidification threatens calcified marine life throughout the world, and the California Current System experiences even more intense acidification during the natural process of upwelling. To understand if *Nucella* populations with varying prior exposures to low pH seawater respond differently to acidification, I tested *Nucella* from three populations in ambient and acidified conditions in the lab. Each population came from a site with a unique pH regime that can broadly be categorized as high, intermediate, and low pH based on mean pH and frequency of exposure to pH below 7.8. I measured *Nucella* search and handling times while allowing them to choose among three sizes of *M. californianus* prey in ambient (pH 8.0) and acidified (7.6) treatments. I found that acidification affected search and handling times differently depending on the origin of the *Nucella*, and the population with the most prior natural exposure to low pH was least negatively affected by experimental acidification. This shows that prior exposure to climate stressors may increase acidification tolerance and highlights how population-specific responses to climate change can lead to differences in emergent ecological effects that may restructure prey communities at local scales.

In **Chapter 3**, "Population variation in an intertidal predator shapes habitat structure and community composition," I tested for differences in mussel bed matrix communities among mussel beds preyed on by *Nucella* from different populations with different foraging traits. After nine months of predation by *Nucella* from one of

three populations or no *Nucella* (control), I found that *Nucella* from different populations altered mussel beds differently. I also found that the sizes of altered (drilled or dislodged) mussels was related to the sizes of remaining mussels which in turn was related to community composition within the mussel bed matrix. Together, these findings show how differential predator foraging can lead to community changes.

The results of this dissertation highlight the importance of studying population-specific trait differences in a changing climate. Since intraspecific trait variation can have broad ecological effects, especially in predators consuming foundation species, it is critical to consider trait diversity alongside species diversity as we strive to understand ecological function and predict community changes with ongoing climate change. Furthermore, this dissertation presents some of the first studies of the ecological importance of intraspecific trait variation in marine systems and shows how trait variation can be a mechanism through which climate change indirectly affects ecological communities.

Chapter 1: Climate shapes population variation in dogwhelk predation on foundational mussels

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 adaptation or acclimatization to environmental factors and neutral 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* 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.

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 pCO_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 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 of *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 & 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 2000b). 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 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; Palmer et al. 1990; Suchanek 1992; 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 can therefore shape intertidal diversity (Kanter 1977; Suchanek 1992; Suchanek 1978).

Characterization of environmental variables

We studied *Nucella* drilling selectivity at eight intertidal sites in Oregon and California, USA with different climate regimes (Figure 1.1, Table A1.1). To describe the different regimes, we used three datasets: 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 ten-minute 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 of variation, various percentiles, and frequency of exposure below pH values known to induce pH stress (Figure A1.1, Table A1.2; 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 ten minutes. 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 (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 A1.2).

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 dataset reflects the characteristic immersed thermal environments which dogwhelk populations had experienced over a five-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 (Figure 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 five-year dynamics, providing support that the 2013 upwelling pH and emersion temperature dynamics were also similar to long term dynamics (Figure S3).

Finally, we used Principal Component Analysis (PCA) to characterize the combined environmental regimes of the sites, including pH, emersion and water temperature dynamics (*prcomp* function in *stats* package in *R*; R Core Team 2017). We performed PCA on all previously listed environmental metrics (Figure S1). 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 had not yet been removed, 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 eight months, so boreholes provide a long-term estimate of *Nucella* predation (Suchanek 1978; 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 by using average growth rates of *M. californianus* from mussel growth surveys in central California (Menge et al. 2004) and Oregon (Behrens Yamada & Dunham 1989), calculating

mean growth over eight 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. 1.51s; 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 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 performed all analyses in *R* v. 3.3.1 (R Core Team 2017) and plots were made with package *ggplot2* (Wickham 2016). 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 A1.3). 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. 2018a). 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.

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 (Figure A1.1; Table A1.2). 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). 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 high frequency of pH dropping below 7.6, and

negative values represented 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 ± SD; Kolmogorov-Smirnov tests, D = 0.24–0.64, $P < 0.001$; Figure A1.4), 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 (Figure 1.2). Larger *Nucella* occurred at the southern three sites (ANOVA, $F_{7,315} = 55.04$, $P < 0.0001$; Figure 1.2a). Mean available mussel length varied from about 1.5 to 5 cm (ANOVA, $F_{7,19} = 5.78$, $P = 0.001$; Figure 1.2b), and drilled mussel length from 1 cm to almost 6 cm, with smallest mussels at the northern two sites (ANOVA, $F_{7,19} = 20.12$, $P < 0.001$; Figure 1.2c).

Mitochondrial haplotype diversity and IBD

We generated a haplotype network using 135 COI sequences of 599 bp (n = 7 to 25 per site; Figure A1.5; GenBank accession numbers MK258758–MK258868 and MK265353–MK265375). There were fixed differences in COI among most *Nucella*

populations, and only the 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 A1.4) 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; Figure A1.6).

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 1.1; Table A1.3). 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; Figure 1.3a). 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; Figure 1.3b). Mean available mussel length and mean *Nucella* length were not significantly related to

mean drilled mussel length. (Table 1.1). 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 eight months, these results were qualitatively unchanged (Tables A1.5 and A1.6).

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 1.2).

Discussion

Intraspecific trait variation, including any phenotypic variation among populations, can have important effects on species interactions that shape communities and ecosystems (Palkovacs & Post 2009, Harmon et al. 2009, Palkovacs et al. 2009, Bolnick et al. 2011, Ingram et al. 2012, Royauté & Pruitt 2015, Fryxell & 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. While Palmer (1990) reported two species in this range, we found very low COI differentiation among populations, which does not clearly indicate separate species. Marko (1998) and Dawson (2014) found similarly low COI differentiation among these populations. 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 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 while feeding, so more stable conditions may allow them the option of consuming larger prey with longer handling times.

Temperature and pH are biologically important abiotic factors 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 decreased size selectivity 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 increases in the sizes of mussels drilled via reductions in 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.

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Tables and Figures

Table 1.1. Estimates for linear mixed effects model for mean drilled mussel length. Units are mm for lengths and standard deviations for PCs. An asterisk indicates significance at the $\alpha = 0.05$ level

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				

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

Table 1.2. Mantel and partial Mantel tests for correlations between genetic distance, environmental variables, and mussel length drilled. 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

Distance matrix 1	Distance matrix 2	Control matrix	Mantel correlation coefficient (*r*)	P
Mean drilled mussel length	K2P	NA	–0.170	0.99
Mean drilled mussel length	K2P	PC1	–0.300	0.99
Mean drilled mussel length	K2P	PC3	–0.209	0.99
Mean drilled mussel length	PC1	K2P	0.262	0.003*
Mean drilled mussel length	PC3	K2P	0.246	0.007*

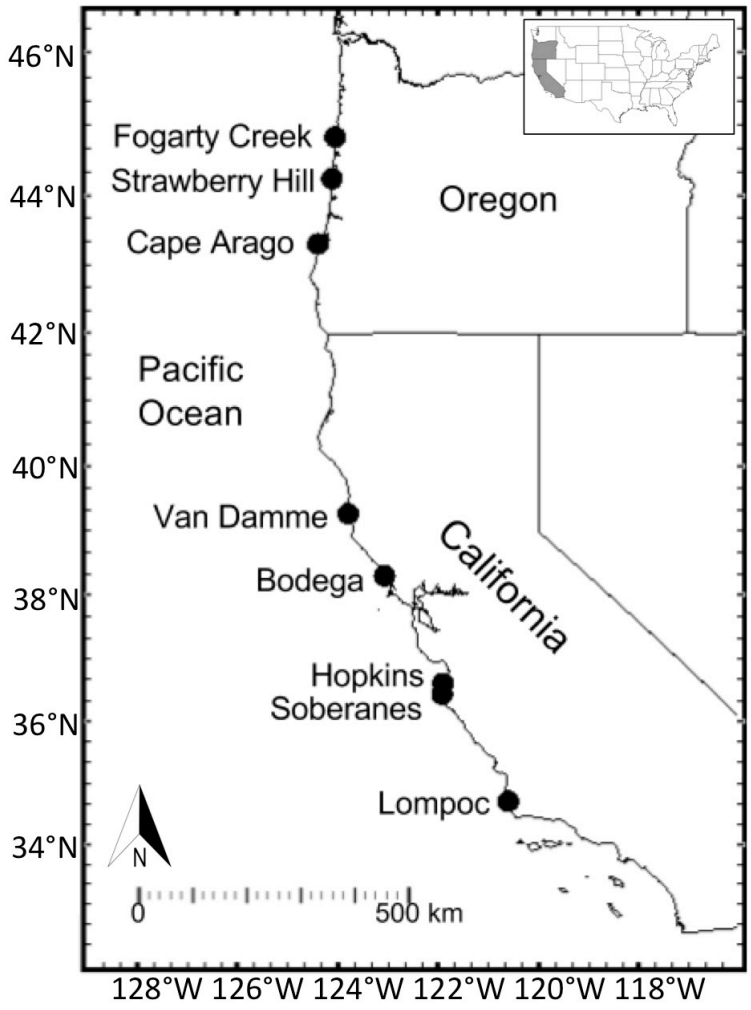

Figure 1.1. Map of study sites in Oregon and California (USA)

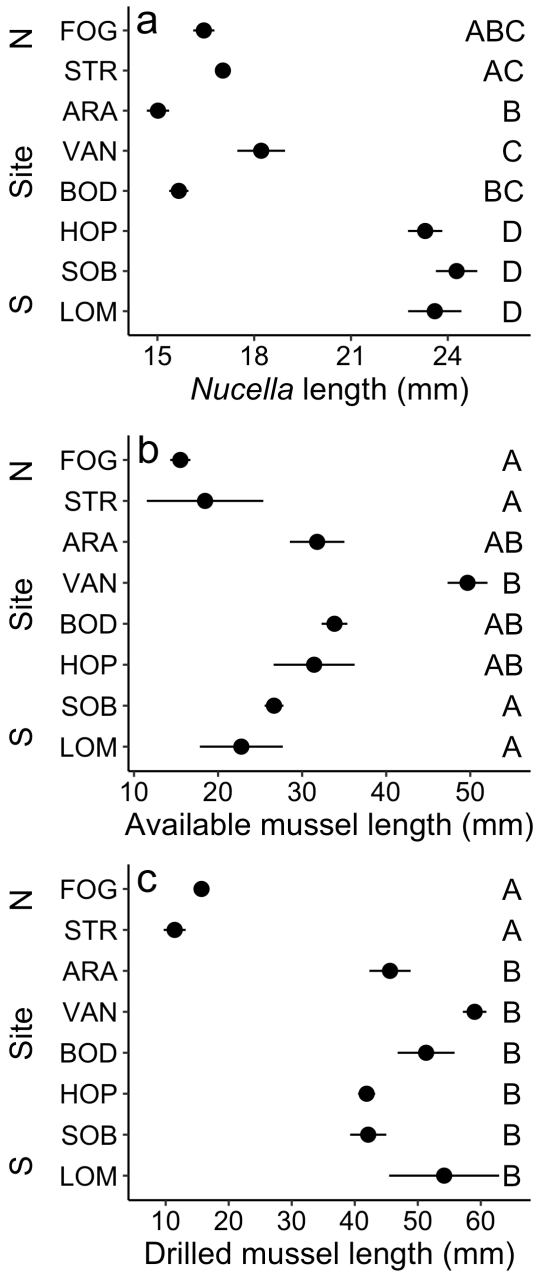

Figure 1.2. Site comparisons of mean ± S.E.M. of (a) *Nucella* length (n = 25–68 per site, total n = 341), (b) available mussel length (n = 271–1238 per site, total n = 5665), and (c) drilled mussel length (n = 39–154 per site, total n = 581). Sites are ordered north to south. Mussel length is the average 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

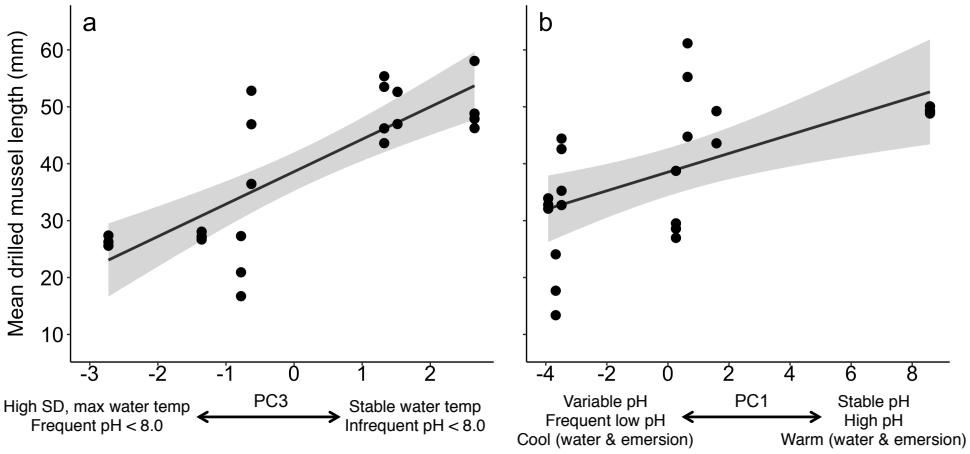

Figure 1.3. Relationships between the significant terms in the final model and the response variable, drilled mussel length (n = 24). Axes are mean drilled mussel length residuals (added back to the mean for easy interpretation) versus each predictor term. Lines and 95% confidence bands are from linear smoothing functions

Chapter 2: Population history of low pH exposure shapes the effects of acute seawater acidification on predator foraging traits

Abstract

Recent and ongoing evolution can cause predator populations to vary in traits and their effects on prey, but few studies have tested whether divergent predator traits respond similarly to acute environmental stressors. We examined how intertidal predators from populations with varying natural exposures to low pH seawater altered their foraging traits when experimentally exposed to acidified seawater. We tested how *Nucella ostrina-emarginata* dogwhelks from three populations with distinct pH regimes in the California Current System altered consumption of mussel prey (*Mytilus californianus*) in ambient (pH 8.0) and acidified (7.6) seawater. In both pH treatments, predators from the populations with least natural exposure to low pH showed increased consumption times. Exposure to acidification altered the individual components of consumption time—search and handling times—depending on both population and pH treatment. The population with least exposure to low pH increased search time under acidification, whereas the other populations decreased. The reverse pattern occurred for handling time. These results indicate that *Nucella* predation responses to acute acidification are population-specific and this may relate to prior exposure. Our study highlights how population-specific responses to climate change, i.e. ocean acidification, can lead to differences in emergent ecological effects that may restructure prey communities at local scales.

Introduction

A primary focus in ecology is to understand how predators structure prey communities. The effects predators have on prey depend on predator feeding traits, which are shaped by prior and ongoing evolution (Hairston et al. 2005; Post and Palkovacs 2009; Schoener 2011). The effects of predator evolution on predator-prey interactions have been shown in aquatic systems, where fish predators diverge in feeding traits, which then differentially structure prey communities. For example, alewives with anadromous versus landlocked life histories evolved different gill raker morphologies, causing them to feed on zooplankton of different sizes (Palkovacs and Post 2008). Similarly, stickleback populations specializing in benthic or limnetic habitats within lakes differ in gill raker number and have different effects on zooplankton diversity than generalist stickleback that utilize both habitats (McPhail 2008; Des Roches et al. 2013). Evolution in response to other species, such as a predator or competitor, can also affect feeding traits. Stickleback that coevolve in lakes with sculpin consume more zooplankton than stickleback that evolve without sculpin, strengthening their effect on zooplankton biomass (Ingram et al. 2012). While there is now ample evidence that predator populations can evolve diverging traits with differential effects on prey, few studies have tested how these trait differences respond to environmental variation.

Environmental factors such as temperature and pH can alter predator foraging traits (Sanford 1999; Cripps et al. 2011; Barton 2011; Pistevos et al. 2015), but whether all populations respond similarly to changes in such conditions is poorly

known. In particular, decreasing seawater pH, or ocean acidification, alters marine predator feeding traits by disrupting brain function (Nilsson et al. 2012). For example, acute exposure to low pH seawater impairs neurotransmitter function in many fish predators, leading to reduced attraction to prey odors, increased search time, and reduced attack behaviors (Munday et al. 2009; Cripps et al. 2011; Pistevos et al. 2015; Dixson et al. 2015; Porteus et al. 2018). Acute acidification exposure also causes negative responses in invertebrate predators, such as increased handling time, decreased prey size selectivity, and reduced ability to capture and consume prey (de la Haye et al. 2012; Cerny-Chipman 2016; Watson et al. 2017; Spady et al. 2018; Contolini et al. in press). While it has been established that the pH environment can shape predator foraging traits, no studies have tested whether different predator populations have different responses to low pH conditions.

Nucella spp. dogwhelks are a model system to study the effects of pH on population-specific changes in predator foraging traits. *Nucella* are important intertidal predators that exhibit local adaptation for prey preference, likely due to their limited dispersal ability (Sanford and Worth 2009). They are calcified, drilling predators with calcified prey, making ocean acidification especially relevant to their feeding ability. In the California Current System (CCS), *Nucella* populations have high population genetic structure and exist across variable pH environments due to the heterogeneous oceanography and coastal geology of the region (Hofmann et al. 2014; Dawson et al. 2014; Chan et al. 2017). Therefore, *Nucella* populations that

naturally experience different pH regimes may show different foraging responses to changes in pH conditions.

We tested how *Nucella ostrina-emarginata* dogwhelks from populations with varying natural exposures to low pH seawater altered their foraging traits when acutely exposed to low pH seawater. We studied three populations of dogwhelks from sites with different pH regimes. Specifically, the populations varied in terms of mean pH and their frequency of exposure to pH below 7.8. We expected that acute exposure to low pH seawater would decrease *Nucella* foraging performance by increasing consumption time, including search and handling times, and by reducing prey size selectivity. However, we hypothesized these changes to be less pronounced for populations that are naturally more exposed to low pH events.

Materials & Methods

Study system

Nucella ostrina-emarginata (hereafter *Nucella*) is a species complex of muricid gastropod commonly found in rocky intertidal zones in the CCS. These dogwhelks have very low dispersal ability and high population-level genetic differentiation that does not correlate with morphological species identity (Marko 1998). Thus, we focus on population-level variation in this study. *Nucella* are predators of sedentary shelled invertebrates, leaving a characteristic ≈ 1 mm diameter hole in their prey, making it easy to track predation across space and time (Clelland and Saleuddin 2000a). *Nucella* consume *Mytilus californianus* mussels, which create

expansive beds of biogenic habitat that support diverse communities (Kanter 1977; Suchanek 1978b, 1992).

To test for population-level variation in predator foraging traits that could respond to acute exposure to low pH, we tested *Nucella* from three populations in central California that have naturally different pH regimes: Hopkins in the Monterey Bay (36.62°, –121.91°); Soberanes, located on the open coast south of Monterey Bay (36.45°, –121.93°); and Lompoc, furthest south and just north of the major oceanographic boundary Point Conception (34.72°, –120.61°; Figure 2.1). *In situ* pH loggers mounted in the mussel bed or offshore from these sites recorded pH and temperature intermittently between 2011 and 2013; detailed descriptions of these instruments can be found elsewhere (Menge et al. 2015; Kroeker et al. 2016; Rivest et al. 2016; Chan et al. 2017). We qualitatively compared natural pH regimes using these studies and quantitatively compared data recorded from July through September from the Ocean Margin Ecosystems Group for Acidification Studies (Hopkins and Soberanes) (Menge et al. 2015) and the Santa Barbara Coastal Long Term Ecological Research datasets (Lompoc) (Rivest et al. 2016). We calculated metrics of pH such as mean, median, minimum, maximum, standard deviation, and the frequency of pH 0.2 to 0.4 units lower than the mean. Such low pH events are associated with biological effects and are useful metrics not only of pH stress but also the progression of ocean acidification in an area (Kroeker et al. 2016). Hopkins is characterized by highest pH (mean: 8.10, frequency < 7.8: 0.026; hereafter the "high pH population"), Soberanes by intermediate pH (8.02, 0.051; hereafter the "intermediate pH population"), and

Lompoc by lowest pH (7.97, 0.082; hereafter the "low pH population;" Table 2.1, Figure 2.1; Hofmann et al. 2014; Kroeker et al. 2016).

Carbonate chemistry manipulation

To test population-level foraging responses to increased seawater acidity, we performed a predation experiment using an outdoor, flow-through seawater system at the University of California Santa Cruz Long Marine Lab in Jan–Mar 2016. The system consisted of twelve 22.7 L (46 x 38 x 13 cm) bins that were paired and randomly assigned either ambient (ambient Santa Cruz seawater of pH ≈ 8.0) or acidified seawater (experimentally acidified to pH ≈ 7.6; Figure A2.2). To manipulate carbonate chemistry, six 200 L header barrels received filtered, ambient seawater mixed with pre-equilibrated highly acidified seawater (pH ≈ 6.5) controlled by a custom-built system of controllers, sensors, and relays. The highly acidified seawater was created by bubbling 99.9% CO_2 gas into a separate recirculating tank of filtered ambient seawater, which was then mixed with the ambient water to reach pH 7.6. Controllers (Honeywell Inc. UDA) connected to Tris buffer-calibrated sensors (Honeywell Inc. Durafets) monitored pH in the acidified pH barrels, and when the pH value exceeded 7.6, a solenoid valve automatically opened to allow pH 6.5 water to enter the barrel until the pH reached the pH 7.6 set point. We chose the pH for the acidified treatment based on predictions that surface pH during upwelling will regularly reach 7.6 in a few decades (Gruber et al. 2012). The pH manipulation was

replicated six times in header barrels that each gravity-fed two bins containing animals (N = 12 bins). Temperature, salinity and light were held constant for all bins.

The pH and temperature in header barrels were recorded from the Durafet sensors every 15 seconds. Temperature in each bin was recorded every 15 minutes using HOBO temperature loggers (Onset Computer Corporation, Bourne, MA). Salinity was measured every other day in all barrels and bins using handheld sensors (YSI Inc., Yellow Springs, OH; Oakton Instruments, Vernon Hills, IL). Discrete water samples were collected once every twelfth day (N = 5) from all header barrels and bins to check against the sensor measurements and were analyzed following best practices for ocean CO_2 measurements (Dickson et al. 2007). We measured pH_T at 25 °C using a spectrophotometer (Shimadzu, UV-1800) and total alkalinity using a Metrohm 815 Robotic USB Sample Processor XL and Titrando 905. Finally, we used CO2Calc to calculate the pH at the temperatures experienced during the experiment using K1 and K2 constants from Hansson 1973 refit by Dickson and Millero 1987 (Robbins et al. 2010).

The pH treatments were successfully maintained near the targeted values: spectrophotometric and chemical analyses of bottle samples revealed the ambient pH treatment as mean pH_T 7.99 ± 0.01 and the acidified treatment 7.66 ± 0.01 (mean pH_T ± SE; Table 2.2). Neither temperature nor salinity of bins differed between pH treatments (temperature: ambient pH 13.96 ± 0.04, acidified pH 13.93 ± 0.04 °C, mean ± SE; ANOVA $F_{1,10} = 1.02$, $P = 0.34$; salinity: ambient pH 33.57 ± 0.01, acidified pH 33.58 ± 0.01 ppt; ANOVA $F_{1,10} = 0.04$, $P = 0.85$). Durafet automated pH

and temperature measurements matched well with measurements from discrete bottle samples and HOBO data loggers from the experimental bins (Table A2.1).

Predation experiment

Adult *Nucella* 23.08 ± 2.25 mm in length (mean ± SD) were collected in mid intertidal mussel beds from the three populations seven to nine weeks before the start of the experiment. *Nucella* were held in an indoor lab in flowing, filtered, ambient seawater, fed local California mussels *ad libitum*, then starved two weeks prior to the experiment to standardize hunger levels. Immediately prior to the start of the experiment, *Nucella* shell length was measured with electronic calipers and total wet mass (after patting dry for several minutes) and mass suspended in seawater (buoyant mass) were measured using an analytical balance. Buoyant mass reflects the mass of the shell since the body is neutrally buoyant (Palmer 1982). We calculated soft tissue mass by subtracting buoyant mass from total wet mass. We tested for differences in *Nucella* shell length, total wet mass, soft tissue mass, and shell mass using ANOVA. For all these variables, data met model assumptions of normality and homogeneity of variance. Mean *Nucella* length, total wet mass, and body mass did not differ significantly among populations, pH treatments, or bins (ANOVA $F < 2$, $P > 0.1$), though mean shell mass was slightly higher in the high pH than the intermediate pH population (1.06 ± 0.23 vs. 0.91 ± 0.28 g, ANOVA $F_{2,169} = 4.0$, $P = 0.02$; Tables A2.2, A2.3, A2.4).

We collected small (length 25 mm), medium (40 mm), and large (55 mm) *Mytilus californianus* mussels from a single site in Santa Cruz, CA (36.951, –121.043) to be used as prey and cleaned them of all epibionts. We placed one mussel of each size in a 11.43 x 9.53 x 6.60 cm plastic mesh basket (a modified pint-sized berry basket; hole size ≈ 1 cm) which was submerged in a bin, with N = 15 baskets per bin. Bins were paired and randomly assigned header barrels from which to receive treatment water (ambient or acidified). We acclimated mussels to experimental conditions for one week.

We initiated the experiment by adding one *Nucella* predator to each basket. *Nucella* added in the acidified treatment in this way would not have experienced an unusually extreme or stressful pH shift because intertidal organisms are subjected to extreme changes in abiotic conditions on a daily basis (Menge et al. 2015). *Nucella* were from one of the three populations (high, intermediate, and low pH). *Nucella* population was replicated four to five times per bin (depending on *Nucella* availability) and the arrangement of *Nucella* within bins was randomized (N = 14–15 baskets per bin; Figure A2.2). We crossed *Nucella* population and pH treatment in a full factorial design. Each bin was covered with a sheet of clear acrylic and shade cloth to prevent excessive algal growth and weighted with a cinder block to provide a tight-fitting lid to contain the *Nucella* and limit off-gassing of CO_2. Immediately after adding *Nucella*, we recorded their behavior every 12 h as either resting (not touching a mussel), mounted on a mussel (touching enough of the mussel that it could be consuming it), finished consuming a mussel (mussel shell empty with a drill hole in

it), or dead. Search time was recorded as days from the start of the experiment to when the *Nucella* mounted the mussel it would consume. Handling time was recorded as days from the end of search time to when the mussel shell was empty with a visible drill hole. Total consumption time was calculated as the sum of search and handling times. We excluded search and handling data where we could not clearly tell when feeding started or ended (e.g. if the *Nucella* moved on and off the mussel numerous times during feeding). Each *Nucella* was allowed to drill one mussel, and the experiment lasted 60 days.

Statistical analyses

We used censored survival regression models to test for treatment and population effects on *Nucella* response times when possible because this type of model can account for uncertainty in event-time data (*"survival"* package in *R*) (Therneau 2015). In our case, the start and end of a predation event was sometimes uncertain because the drilling site is obscured by the dogwhelk. To model search time, we used a parametric censored survival model with interval censored data, which are data where the exact value is known only to be between a specified interval, and thus excluded *Nucella* that died or never started handling a mussel (N = 138; 14 died and 9 did not handle). We used pH treatment, population, and their interaction as fixed effects and experimental bin as a random effect using gamma distributed frailty, which is the term used for random effects in censored models (Fox et al. 2015). For handling and total consumption times, we also included mussel size

and its interactions with population and pH treatment since prey size is likely to affect handling but not searching. Because including the extra factor of mussel size in the model reduced the degrees of freedom, we averaged mean handling and consumption times for each treatment, population, and mussel size across bins and used linear models (N = 72). For interval-censored data, e.g. if handling started between days 2 and 4, we used the average of the interval. To meet model assumptions of normality, we log-transformed the response variables. We reduced these models to a final model by sequentially removing nonsignificant interaction terms. We performed post-hoc analyses (Student's *t*-tests) on significant terms, log transforming as necessary to meet model assumptions. To model prey size selectivity, we used an ordered regression mixed model with the Laplace approximation (Christensen 2019). We used pH treatment, *Nucella* population, and their interaction as fixed effects, and bin as a random effect.

Finally, since *Nucella* from the lower pH populations may have been more resilient to the sudden shift in pH they experienced at the start of the experiment, leading to altered behaviors, we compared the number of *Nucella* from each population that drilled within the first two weeks, a common acclimation period. To test if mussel shells thinned within 60 d exposure to low pH, potentially reducing handling time for *Nucella* that drilled later (Sadler et al. 2018), we used linear regression on search time versus mussel thickness within each size class and overall after standardizing for length. All statistical analyses were done in *R* (R Core Team 2017).

Results

The final model for consumption time included the main effects of pH treatment, population, and mussel size, and showed consumption time differed significantly among *Nucella* populations (Table 2.3, Figure 2.2a). Specifically, *Nucella* from the low pH population took significantly less time to consume a mussel than the high pH population (Student's *t*-test on log-transformed values, $t = 2.64$, $df = 33.91$, $P = 0.012$). Neither pH treatment nor mussel size were significantly related with consumption time ($F < 1.3$, $P > 0.30$).

When consumption time was broken down into search and handling times, the interaction between population and pH treatment was significant, as *Nucella* from each population responded differently to pH. The model for search time included the main effects of pH treatment and population and their interaction. *Nucella* from the high pH site increased search time in the acidified treatment, while those from the intermediate and low pH populations decreased search time (Table 2.4, Figure 2.2b). The model for handling time included main effects pH treatment, population, and mussel size, as well as the interaction between pH treatment and population. There was a significant interaction between pH treatment and population where *Nucella* from each population showed different responses in the acidified treatment (Table 2.5, Figure 2.2c). Mussel size was also significant in this model, with large mussels on average requiring longer handling time (9.4 ± 4.2 d), than medium (5.8 ± 2.8 d), and small mussels (3.0 ± 1.2 d, mean ± SD; all pairwise *t*-tests $P < 0.02$).

We did not detect differences in prey size selectivity among populations, pH treatment, or their interaction (Table A2.5, Figure A2.3). To test if *Nucella* in the acidified treatment had altered behaviors before they acclimated to the treatment water, we considered the number of *Nucella* that drilled within the first two weeks (a common acclimation period; Sanford et al. 2014; Sadler et al. 2018) and whether they were evenly split among treatments. We found no evidence of differential acclimation. Of the *Nucella* that started drilling within the first two weeks, 30 were from the acidic treatment and 29 were from the ambient treatment. Finally, there was no evidence that mussels that spent longer in the acidified water became thinner and easier to handle, which would affect *Nucella* handling time (linear regression within size classes, $r^2 < 0.01$, $P > 0.3$; linear regression among size classes, $r^2 = 0$, $P > 0.6$).

Discussion

Predators play important roles in shaping ecosystems by the way they consume prey (Brooks and Dodson 1965; Palkovacs and Post 2008; Barton 2011; Des Roches et al. 2013). Though both environmental factors and evolutionary history play a role in determining predator foraging traits, variation in the foraging responses of different predator populations to ocean acidification has not been explored. We tested how *Nucella* from populations with varying natural exposures to low pH seawater altered their foraging traits when acutely exposed to acidified seawater. We expected acute exposure to low pH seawater to reduce predation rate by increasing consumption time and that *Nucella* from populations with greater natural low pH

exposure would be less affected. Our results confirm this general expectation. The low pH population showed significantly reduced consumption time compared to other populations and was least negatively affected by acidification. These results suggest that populations can develop localized responses to global change that will influence the outcomes of key interactions governing community structure.

Nucella total consumption time (the total amount of time it took to find and consume a mussel) was significantly different among populations. *Nucella* from the low pH population had the fastest consumption time, then the intermediate pH population, then the high pH population. This result provides evidence that *Nucella* from sites with more acidification exposure may have faster predation rates—perhaps if metabolism is increased to compensate for the higher energy costs of homeostasis (Beniash et al. 2010)—and consume more foundational mussels, which could restructure the mussel bed community. Though the pH treatment by population interaction was not statistically significant, there was a trend for *Nucella* from the high pH population to increase consumption time in the acidified treatment, while the other two populations showed decreases (Figure 2.2a). This suggests that *Nucella* from populations in high pH environments may be more likely to decrease predation rates under future ocean conditions, highlighting the context-dependent nature of the effects of acidification on predator-prey interactions.

To understand the mechanisms behind differences in total consumption time, we analyzed its two components: search and handling time. Search time contributed most to changes in consumption time—it was at least three times as long as handling

time for any given pH treatment-population combination. Acidification can affect search time by altering chemosensory abilities (Ashur et al. 2017; Draper and Weissburg 2019), but if prior exposure to acidification helps animals adjust their physiology or behavior to reduce the negative effects of acidification, we expected search time to be less impaired in acidified water for such *Nucella*. This hypothesis was confirmed. *Nucella* from the site with the highest natural pH had increased search time in the acidic treatment, while search times for those from the intermediate and low pH populations decreased (Figure 2.2b). While these results support our general hypothesis, a reduction in search time in acidified water was unexpected and reflects the complex nature of behavioral responses to acidification.

Similar to search time, the handling time response to acidification differed among populations. We expected acidified conditions to increase handling time, and that this increase would be greater for the high pH population. Results showed that the low and intermediate pH populations increased handling time, but the high pH population's search time actually decreased. This result may be explained in light of differences in temperature regimes between the experiment and each population's home site—the low and intermediate populations may also have been responding to relative warming. The temperature in the experiment (13.93 ± 0.81 °C) was warmer relative to the natural conditions of the low and intermediate pH populations only (respectively 13.14 ± 0.99 and 12.38 ± 0.85 °C, mean ± SD). This could have caused an increase in ingestion rate that sped up handling (Miller 2013), but this effect was then reduced in the acidified treatment because high CO_2 can dampen the effects of

warming on metabolism (Melatunan et al. 2011). *Nucella* from the high pH population did not experience experimental conditions warmer than their home site (15.1 ± 0.99 °C) and thus was not responding to interactive effects of warming and acidification but may have been primarily responding to changes in carbonate chemistry, which alone has complex effects on shellfish metabolism (Michaelidis et al. 2005; Beniash et al. 2010; Ivanina et al. 2013; Waldbusser et al. 2015). However, as handling time was on average between 12 and 23% of total consumption time for any given population in any given treatment, it contributed little to the differences in total consumption.

Our results add to an understanding of the effects of low pH on *Nucella* handling time. Previous research concerning *N. ostrina* and *N. canaliculata* feeding on *Mytilus trossulus* reported increased handling times when the snails were exposed to seawater at pH 7.5 and 12–13 °C over 14 days (Cerny-Chipman 2016). When we compare these results (using *Nucella* from a site with mean pH of 8.00, frequency of pH below 7.8 of 0.16, and mean temperature of 11.2 °C in 2011) with our populations with similar pH regimes that experienced experimental warming (our intermediate and low pH populations), our results also demonstrate an overall increase in handling time under acidified conditions. However, since our high pH population showed the opposite result, our findings stress the importance of studying climate effects on multiple populations from sites with varying environmental exposures.

Population-level variation can be an important source of variation in organisms' responses to climate change (Barton 2011; Fryxell and Palkovacs 2017).

We found population-specific differences in how seawater acidification affected *Nucella* consumption time that related to the populations' prior exposures to low pH. Populations with a history of exposure to low pH conditions appear to exhibit traits that increase tolerance to acidification and may therefore be more buffered from negative consequences. Our study highlights the importance of intraspecific trait variation for predator-prey interactions and the pitfalls of assuming that the traits of all populations will respond the same to environmental changes. By understanding the contributions of population-level variation in response to ocean acidification, we can gain insights into how organisms will respond to climate change and make more accurate predictions about the future of ecological communities.

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Tables and figures

Table 2.1. Summary of pH conditions for each population July through September

Population	Relative pH	Mean	Median	Min	Max	SD	Freq < 7.8
Hopkins	High	8.10	8.10	7.60	8.51	0.15	0.026
Soberanes	Intermediate	8.02	8.03	7.50	8.29	0.13	0.051
Lompoc	Low	7.97	7.97	7.67	8.24	0.12	0.082

Hopkins and Soberanes data are from intertidal sensors in 2013 (Menge et al. 2015) and Lompoc data are from an offshore sensor (Purissima) in 2011 (Rivest et al. 2016). Descriptions of pH regimes at these sties can also be found in (Hofmann et al. 2014; Kroeker et al. 2016; Chan et al. 2017).

Table 2.2. Seawater physiochemical properties from experimental bins during the 60-d experiment

Treatment	pH_T	Temperature (°C)	Salinity (ppt)	Alkalinity (μmol kg^{-1})	DIC (μmol kg^{-1})	pCO_2 (μatm)
Ambient	7.99 ± 0.01	13.96 ± 0.04	33.57 ± 0.01	2043.03 ± 24.20	1877.80 ± 26.40	429 ± 4.87
Acidified	7.66 ± 0.01	13.90 ± 0.04	33.58 ± 0.01	2094.54 ± 21.81	2041.99 ± 26.07	1032 ± 12.39

Temperature was recorded by loggers every 15 minutes. Salinity was measured directly from treatments with a handheld sensor. All other carbonate chemistry parameters were measured from bottle samples taken every 12th day and analyzed following best practices for ocean CO_2 measurements (Dickson 2007). Bottle pH values matched well with continuous pH measurements from Durafet sensors. Values are mean ± standard error

Table 2.3. Analysis of variance (type III) on linear model for total consumption time. An asterisk indicates significance at the $\alpha = 0.05$ level

	Sum Sq	Df	F	P
(Intercept)	104.01	1	484.44	<0.001*
pH treatment	0.14	1	0.64	0.43
Population	1.43	2	3.33	0.04*
Mussel size	0.52	2	1.26	0.29
Residuals	14.17	66	NA	NA

Table 2.4. Analysis of deviance (type III) on censored regression model for search time. An asterisk indicates significance at the $\alpha = 0.05$ level

	LR Chisq	Df	P
pH treatment	18.77	1	<0.001*
Population	17.95	2	<0.001*
pH treatment * Population	20.74	2	<0.001*

Table 2.5. Analysis of variance (type III) on linear model for handling time. An asterisk indicates significance at the $\alpha = 0.05$ level

	Sum Sq	Df	F	P
(Intercept)	40.58	1	132.91	<0.001*
pH treatment	1.51	1	4.93	0.03*
Population	1.02	2	1.67	0.20
Mussel size	13.52	2	22.14	<0.001*
pH treatment * Population	2.88	2	4.71	0.01*
Residuals	19.54	64	NA	NA

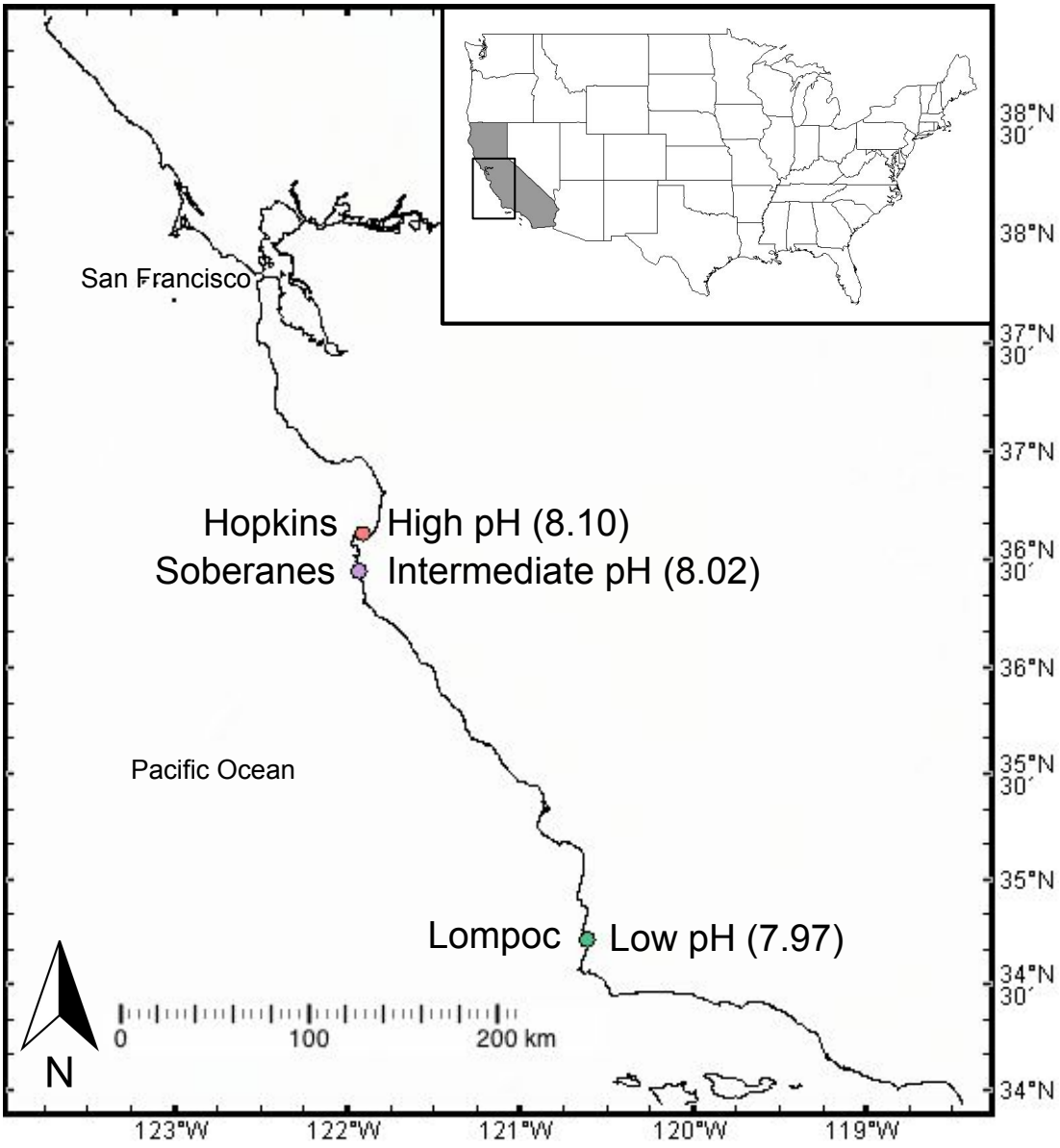

Figure 2.1. Map of study populations with mean pH during upwelling season

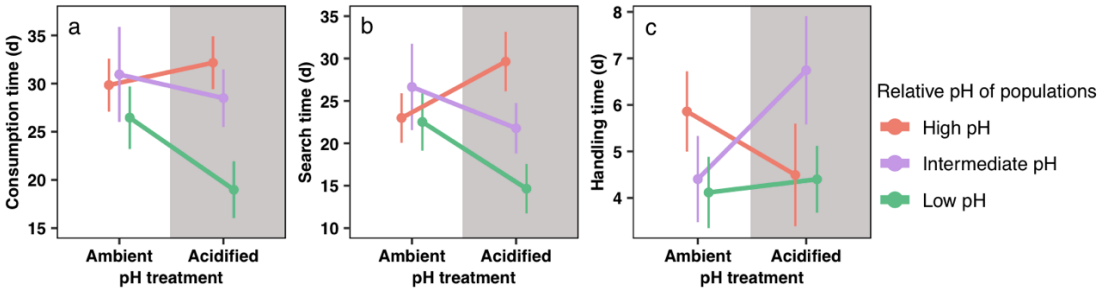

Figure 2.2. Predation responses for each population in each pH treatment. (a) Mean total consumption time, (b) mean search time, and (c) mean handling time. Points and error bars are mean and standard error of raw values

Chapter 3: Population variation in a marine intertidal predator shapes habitat structure and community composition

Abstract

Population-level trait variation is an important form of biodiversity that can alter community and ecosystem properties. While recent work shows the ecological importance of population-level trait variation, few studies describe this for predator-prey interactions, and none for predators consuming foundational prey. In marine systems, where populations are traditionally viewed as open and highly connected, much debate exists about the importance of intraspecific trait variation. Here we test the prediction that intraspecific foraging differences among populations of a marine intertidal predator (*Nucella ostrina-emarginata*) differentially alter California mussel bed communities by altering mussel bed structure. In a nine-month field experiment, we measured mussel bed structure and community composition within the bed matrix after treatment with *Nucella* from one of three populations or no *Nucella*. We found that *Nucella* treatment altered the size structure of mussel beds, and that *Nucella* predators from different populations differentially altered mussel bed structure by consuming different sizes of mussels. The size structure of drilled and dislodged mussels was related to the size structure of remaining mussels, which was related to multivariate community composition, revealing a mechanism by which *Nucella* alter communities. *Nucella* populations also had differential effects on crab biomass. Our results show that *Nucella* can have top-down effects on mussel bed communities by

changing mussel bed habitat. These results support the hypothesis that population-level variation in predators can have community consequences in marine ecosystems.

Introduction

Intraspecific trait differences among individuals within species can drive community and ecosystem characteristics by causing differential effects on ecological interactions like competition and predation (Hairston et al. 2005; Hughes et al. 2008; Harmon et al. 2009; Bolnick et al. 2011; Palkovacs et al. 2012, 2018; Des Roches et al. 2018). Intraspecific variation in predators can have an especially important role in determining community structure in ecosystems under top-down control, and studies show the ecological effects of predator trait variation in consumer controlled systems (Post et al. 2008; Urban 2013; Royauté and Pruitt 2015; Fryxell and Palkovacs 2017).

The importance of intraspecific trait variation in ocean predators remains virtually unexplored due to a widespread belief that marine populations are highly connected through planktonic dispersal. Thus, scientists have historically been skeptical of the prevalence of marine intraspecific trait variation. More recently, this paradigm is shifting, and there is now evidence of intraspecific variation in marine mammals and invertebrates (Baird et al. 1992, Estes et al. 2003, Sanford et al. 2003, Pruitt et al. 2012, Calosi et al. 2013, Kelly et al. 2013, Padilla-Gamiño et al. 2016, Foo et al. 2018, Contolini et al. in press, Contolini et al. in review). These variable predator traits can have differential community effects through top-down control. For example, otters that specialize on sea urchins, potent consumers of giant kelp, can

cause a trophic cascade that increases kelp habitat and restructures kelp forest communities (Estes et al. 1998). Similarly, variation in foraging among predators of foundational California mussels (e.g. sea stars or dogwhelks) can alter mussel bed structural complexity which is associated with species diversity (Paine 1966; Suchanek 1978b). However, the ecological consequences of intraspecific trait variation have yet to be explored in marine systems as well as in predators of foundation species.

Intertidal habitats are an excellent system in which to study the ecological effects of marine predator trait variation because they are diverse habitats with foundation species under consumer control (Paine 1966). In the California Current System (CCS), *Mytilus californianus* is the dominant mussel species on exposed shores and creates expansive intertidal biogenic habitat capable of supporting hundreds of species (Lafferty and Suchanek 2016; Paine 1966; Suchanek 1992; Suchanek 1978). *M. californianus* bed structural complexity, especially in terms of density and depth, is positively correlated with species richness, diversity and evenness, and altering these factors can affect community diversity (Kanter 1977; Suchanek 1992; Suchanek 1978). Anything affecting mussel bed structure, such as predation, can therefore affect the composition of the community within the mussel matrix.

Nucella ostrina-emarginata (hereafter "*Nucella*") is a species complex of dogwhelk commonly found on the west coast of North America. *Nucella* live in *M. californianus* beds and feed primarily on mussels and barnacles by drilling through

the prey's shell using a combination of chemical dissolution and mechanical scraping, leaving a characteristic ≈1 mm diameter hole (West 1986; Clelland and Saleuddin 2000b). *Nucella* are dioecious and reproduction occurs via copulation. Larvae develop and metamorphose to the juvenile stage inside egg capsules which are attached to the substrate, and upon emergence from the capsule, they crawl away and begin life in the same intertidal area as their parents. This life history limits gene flow and populations exhibit local adaptation in foraging traits (Marko 1998; Sanford and Worth 2010; Dawson et al. 2014). We focus on *Nucella* predation on mussels because it is a mechanism for top-down control on the mussel bed community; *Nucella* exhibit population-level differences in size selectivity and consumption rate on mussels, which could alter the size structure and complexity of mussel beds (Sanford et al. 2003, Sanford & Worth 2009, Contolini et. al. in press, Contolini et al. in review).

Here we test the prediction that *Nucella* foraging alters mussel bed matrix community composition via altering the structure of the mussel bed. We further test that variation in *Nucella* foraging among populations differentially alters mussel bed matrix community composition via differentially altering mussel bed structure. We predict that *Nucella* foraging will decrease the number and mean size of remaining mussels, changing bed complexity and mussel bed community composition. We further predict that *Nucella* from populations that drill more and larger mussels will have a greater effect on mussel bed complexity and consequently cause greater changes to community composition. Our study tests whether an emerging paradigm in

ecology—that intraspecific variation in predators shapes communities and ecosystems— applies to marine systems.

Materials & Methods

Nucella *collection*

We collected adult *Nucella* from three mid intertidal sites in September 2017: Hopkins (19 Sep; 36.62°, –121.91°), Soberanes Point (19 Sep; 36.45°, –121.93°), and Lompoc Landing (21 Sep; 34.72°, –120.61°; Figure 3.1). These sites naturally experience different pH and temperature regimes; Hopkins experiences warmest, highest pH, and most stable conditions; Lompoc is intermediate in mean temperature and lowest in mean pH; and Soberanes is coolest with intermediate mean pH (Table 3.1; Helmuth et al. 2006, Hofmann et al. 2014, Kroeker et al. 2016, Chan et al. 2017, Contolini et al. in press). *Nucella* from Lompoc on average drill larger mussels and consume them faster than those from both Hopkins and Soberanes, and Lompoc *Nucella* are less negatively affected by seawater acidification (Contolini et al. in press, Contolini et al. in review). *Nucella* were held in filtered, flowing seawater in the Long Marine Lab in Santa Cruz, CA until the start of the experiment on 17 October 2017.

Mussel bed predation experiment

To test the effects of population-level variation in *Nucella* foraging on mussel bed communities, we outplanted *Nucella* from all three populations to an

experimental array of plots at Terrace Point in Santa Cruz, CA, USA (39.49, –122.06; Figure 3.1) and allowed them to feed freely for 9 months. The array was on an existing bench of continuous, level mussel bed (Figure A3.1). We created the array by clearing all biological material 10 cm around thirty-two 20 x 20 cm plots so each was surrounded by a border of bare rock. We installed cages made from 0.4 cm Vexar mesh and bolted them to the rock using stainless steel lag screws and washers. Cages were 20 x 20 x 8 cm (L x W x H) with removable lids of the same material secured with cable ties. We arranged the cages in rows parallel to the shore and assigned them to one of four treatments: five adult *Nucella* from one of the three populations or no *Nucella* (control), each replicated eight times and in a blocked design (Figure A3.2). We measured all *Nucella* for length and wet mass prior to the start of the experiment, then marked them with bright nail polish and uniquely numbered them with bee tags (Bee Works, Canada). Mean *Nucella* length was 24.22 ± 1.43 mm (mean ± SD) which did not differ significantly among populations or cages (ANOVA for populations $F_{2,117} = 0.007$, $P = 0.99$; cages $F_{23,96} = 1.02$, $P = 0.45$; Tables A3.1 and A3.2). We opened all cages biweekly to record and collect dislodged mussels, remove invading non-experimental *Nucella*, and replace dead or lost *Nucella* with one of a similar size from the same population. We monitored temperature at the site every 15 minutes using HOBO temperature loggers (Onset Computer Corporation; Table A3.3) and compared this to previously published temperature and pH regimes at each of the *Nucella* population sites (Menge et al. 2015, Rivest et al. 2016; Table 3.1). Nine

months later on July 29–August 1, 2018 we measured the sizes of remaining *Nucella* (Table A3.4) and removed and froze all mussels and their associated communities.

Mussel bed structure and matrix community composition

We characterized the mussel beds at the end of the experiment in terms of number and size of dislodged, drilled, and remaining mussels. We counted all dislodged and drilled mussels and measured their length using digital calipers. We counted all live mussels remaining and measured a random sample of 100 from each cage. To characterize mussel bed matrix communities, we identified all organisms within the matrix to the lowest possible taxon. We cleaned organisms, dried them in a 56 °C oven (Chicago Surgical & Electrical Co. Imperial II, Thelco Precision Model 2, or Quincy Lab Model 40GC) for one week, and measured their dry mass using an analytical scale (Mettler Toledo AG104; Table A3.5).

Statistical analyses

We tested the following mechanism through which *Nucella* could affect community structure: *Nucella* predation alters the size structure of drilled and dislodged mussels, altering the size structure of remaining mussels, altering community structure. We then explored what aspects of the mussel matrix (i.e. which size classes) were associated with changes in specific taxa.

To test for differential predation among *Nucella* treatments (both presence vs. absence and *Nucella* populations vs. each other), we counted how many drilled and

dislodged mussels were in each of five size classes with upper limits defined by the 20^{th}, 40^{th}, 60^{th}, 80^{th}, and 100^{th} quantiles of drilled and dislodged mussel lengths. To test for differences in the size structure of mussels as a function of *Nucella* treatment, we used permutational analysis of variance (PERMANOVA) with Bray-Curtis dissimilarities and 999 permutations (function *adonis2* in package *vegan*; Oksanen et al. 2018). We used the PERMDISP2 procedure, the multivariate analog of Levene's test, to test for model assumptions of multivariate homogeneity of group dispersions and the data met this assumption (function *betadisper* in *vegan*). To determine which size classes contributed most to treatment dissimilarities, we calculated similarity percentages (SIMPER) using function *simper* in *vegan*. We used ANOVA to test for differences in mean drilled mussel length among *Nucella* populations, and pairwise *t*-tests to find which populations were significantly different. Data met assumptions of normality and homogeneity of variances.

To test if the sizes of drilled and dislodged mussels affected remaining mussel bed structure, we counted and binned the sample of 100 premeasured remaining live mussels using 20^{th}, 40^{th}, 60^{th}, 80^{th}, and 100^{th} quantiles of remaining mussel lengths and calculated Bray-Curtis dissimilarities between all plots. We used a Spearman rank correlation test to test if the drilled/dislodged mussel size dissimilarity matrix was related with remaining mussel size dissimilarity matrix (function *cor.test* in package *stats*), and a linear mixed-effects model with block as random to test for a relationship between mean drilled and remaining mussel sizes (function *lme* in package *nlme*). Data met assumptions of normality and homogeneity of variances.

This relationship would link *Nucella* predation to the structure of the remaining mussel matrix, which can affect the community.

To test how remaining mussel bed structure was related to mussel bed community composition, we compared the dissimilarity matrix for remaining mussel size structure to a Bray-Curtis dissimilarity matrix of community biomass composition using a Spearman rank correlation test. We then found the mussel size classes that contributed most to these differences by computing Bray-Curtis dissimilarity matrices of each individual taxon and calculating which combination of mussel size classes created a Euclidean distance matrix with the maximum rank correlation with individual taxon dissimilarities (function *bioenv* in *vegan*). We identified the direction of the effect by examining relationships between the number of mussels in each size class and the biomass of each taxon in each plot.

Finally, to test if *Nucella* predation had direct effects on the community, we used PERMANOVA with Bray-Curtis dissimilarities and 999 permutations to test for differences in multivariate community composition as a function of *Nucella* treatment using mean size of remaining mussels as a covariate. We also used a linear mixed effects model with block as a random effect to test for differences in biomasses (and sizes and numbers when necessary) of individual taxa as a function of *Nucella* treatment, after confirming model assumptions of normality and homogeneity of variances. All statistical analyses were done in *R* (R Core Team 2017).

Results

Effects of Nucella *on mussel bed structure*

For the *Nucella* presence-absence contrast, PERMANOVA showed there were differences in the size structures of drilled/dislodged mussels (Table A3.6). SIMPER showed these differences were most attributable to the largest four size classes, each contributing 20–23% to the differences, while the smallest size class (up to the 20th percentile, 16.78 mm) contributed only 12%. For the *Nucella* population contrast, Lompoc *Nucella* drilled significantly larger mussels (mean ± SD, 35.6 ± 7.5 mm) than Hopkins (27.4 ± 2.9 mm), and Soberanes *Nucella* drilled intermediately sized mussels (31.06 ± 6.4 mm; ANOVA $F_{2,21} = 3.90$, $P = 0.04$; Table 3.2, Figure 3.2). There were no significant differences in the size structure of drilled/dislodged mussels among populations (PERMANOVA $F_{2,21} = 1.36$, $P = 0.2$).

The size structure of drilled/dislodged mussels was significantly related to the size structure of remaining mussels, linking the direct effects of dogwhelk predation to the remaining mussel bed structure (Spearman's *rho* = 0.28, $P < 0.01$). Mussel beds with larger drilled mussels had larger remaining mussels (ANOVA $\chi^2_1 = 13.71$, $P < 0.001$; Figure 3.3), which could suggest negative density dependent growth.

Effects of mussel bed structure on community composition

The Spearman rank correlation test comparing dissimilarity matrices of remaining mussel lengths and multivariate communities showed a significant correlation, linking mussel size structure to community composition (*rho* = 0.10, P = 0.03). The mussel sizes that were most correlated with multivariate community

dissimilarities were those over the 60th percentile (> 18.41 mm length). This was largely a result of *Nereis* spp. polychaetes, *Pachygrapsus crassipes* shore crabs, anemones, and *Acanthinucella spirata* being positively affected by large mussels and *Lacuna* and *Littorina* spp. (small gastropods) and *Cirolana* sp. (isopod) being negatively affected by large mussels (Table A3.7).

Direct effects of Nucella *on community composition*

PERMANOVA analysis on multivariate community composition showed a significant effect of remaining mussel length, but not of *Nucella* presence or population (Tables A3.8 and A3.9). Linear mixed effects models showed *Nucella* population had a significant effect on *Pachygrapsus crassipes* biomass where communities with Lompoc *Nucella* and no *Nucella* (control) had significantly higher biomass than communities with Soberanes and/or Hopkins *Nucella* (Table 3.3; Figure 3.4a). Treatments with Lompoc *Nucella* had increased *P. crassipes* width (Figure 3.4b), while control treatments had increased *P. crassipes* number (Figure 3.4c).

Discussion

Intraspecific trait variation in predators can have important consequences for communities and ecosystems, yet such consequences have not been studied in marine ecosystems. In this study, we tested the hypothesis that variable predation on foundational California mussels has community consequences in a marine intertidal system. The objective of our study was to test how, by preying on the mussels,

Nucella dogwhelks from different populations have differential effects on the physical and community structures of California mussel beds. We found that *Nucella* altered mussel bed structure, in part depending on *Nucella* population origin. We found that mussel size structure was related to community composition and this was largely due to differences in the biomass of gastropods, isopods, anemones, shore crabs and annelids. We also found that *Nucella* populations had different direct effects on shore crab biomass. Our results show that *Nucella* dogwhelks can have top-down effects on mussel bed communities directly and via changing mussel bed habitat, and these effects can differ among *Nucella* populations because of population-level variations in predation. These results provide evidence that predator intraspecific variation on foundational prey can have community consequences in marine ecosystems.

Nucella significantly deteriorated mussel beds by consuming mussels and causing more and larger mussels to be dislodged. As *Nucella* consume mussels, the mussels are no longer held to the substrate or to each other by byssal threads and the mussel matrix is weakened. These mussels eventually fall out and decrease the density and depth of the bed. Bed deterioration differed significantly among *Nucella* populations, where *Nucella* from Soberanes and especially Lompoc drilled larger mussels than those from Hopkins, matching prior work in this system (Contolini et al. in press). Such differences in foraging among populations could be the result of selection due to local abiotic or biotic drivers (Sanford et al. 2003, Contolini et al. in press). The process of attacking and consuming prey is likely under selection because

it is a time-intensive process that can take days, during which time the dogwhelk is unable to seek shelter from abiotic or biotic stressors. Abiotic conditions at these three sites are different: Soberanes and Lompoc experience cooler and less stable temperature conditions than Hopkins, where Soberanes is on average coolest, and Lompoc on average experiences lowest pH seawater (Table 3.1; Hofmann et al. 2014, Kroeker et al. 2016, Chan et al. 2017). In our experiment, the relatively warmer and less acidic seawater at the experiment location in Santa Cruz, CA, may have caused a relatively larger increase in metabolism for Soberanes and Lompoc *Nucella,* leading them to attack larger and more caloric prey (Miller 2013; Cerny-Chipman 2016).

The size structure of drilled and dislodged mussels was significantly related to remaining mussel size structure. This provides a direct mechanistic link to how *Nucella* predation alters the foundational mussel bed habitat. *Nucella* predation decreased the number of remaining mussels and increased their size, likely through negative density-dependent mussel growth. Thus, the overall effect of *Nucella* predation was to create mussel beds with fewer, larger mussels, leading to a less dense matrix with larger open spaces. This effect was greatest in beds with Lompoc *Nucella* since they drilled the largest mussels. Further, remaining mussel size structure was important for multivariate community composition, which aligns with previous work (Suchanek 1978). Specifically, we found that larger mussels, those greater than 18.41 mm in length, were associated with the differences in multivariate community composition, most likely because larger mussels are the largest contributors to mussel bed size and depth.

Beds with fewer larger mussels would be more susceptible to erosion and less protected from wave impact. These beds showed reduced biomass of *Chlorostoma funebralis, Littorina* spp., *Lacuna* spp. (small herbivorous gastropods) and *Cirolana* sp. (predatory isopods). Since *Nucella* treatments alone showed no significant direct effect on biomass of these taxa, we attribute these changes to the mussel bed matrix only. These gastropod species feed by scraping algae and diatoms off hard surfaces such as mussel shells and rocks. In beds with larger, fewer mussels, there would be fewer surfaces growing their preferred diet items, both in terms of mussel shells and rocks since the substrate was a shallow layer of sand. These conditions could have led the gastropods to seek areas with better habitat, leading to decreased biomass. *Cirolana* are predators of minute annelids and crustaceans and burry in sand at low tide. Beds with larger, fewer mussels would experience more erosion and would do poorly at retaining their minute prey items as well as providing deeper sand in which to burrow.

Larger mussels were also associated with greater biomass of *Nereis* polychaetes, *Pachygrapsus crassipes* shore crabs, anemones, and the predatory gastropod *Acanthinucella spirata*. These species are relatively large-bodied and can take advantage of larger spaces. Furthermore, *P. crassipes* and *Nereis* are scavengers, and the increased wave action in more deteriorated beds may increase the amount of large detrital material that can become lodged in the beds. For example, while maintaining the experiment, we observed large quantities of *Macrocystis pyrifera* and seagrass detritus in several plots.

Smaller mussels (< 11.14 mm length) were associated with a larger biomass of *Assiminea californa* (herbivorous gastropod)*, Epitonium tinctum* (anemone predator)*, Lottia* spp. and isopods in the genera *Cirolana* and *Idotea.* These taxa are all relatively small-bodied and either eat minute algae and/or burrow in sand. Beds with smaller mussels would support these needs by providing greater surface area (i.e. mussel shells) for microalgal growth as well as retaining sand for burrowing. Conversely, algae, *Eulithidium pulloides* (small gastropod), *A. spirata,* and anemone biomasses were negatively associated with smaller mussels. For algae, this is likely a result of herbivory, as herbivore biomass was positively associated with smaller mussels. Anemones and *A. spirata* are large-bodied and may utilize larger spaces, and the effects on *E. pulloides,* typically found in seagrass beds eating diatom films, is unexpected and may reflect processes occurring in the nearby low zone seagrass beds. Mussel beds with smaller mussels are also less able to retain large amounts of seagrass detritus that could transport the small epizoans.

By drilling different sizes of mussels, *Nucella* from different populations can create mussel beds with varying size structures and complexities. In our experiment, *Nucella* from Lompoc drilled significantly larger mussels than those from Hopkins. Prior work in this system showed that Lompoc *Nucella* also consume mussels faster than *Nucella* from Hopkins and Soberanes, and populations are differentially affected by acute exposure to acidification (Contolini in review). Given these differences in predation traits, *Nucella* from different populations should be able to change the foundational mussel bed habitat in ways relevant to the community, and these

changes will depend on abiotic factors influenced by climate change such as seawater pH and temperature. While in our experiment we did not detect significant effects of *Nucella* population directly on multivariate community composition, we found significant evidence for a causal pathway through changing biogenic habitat (mussel bed structure), which has not been shown before. By comparing biomasses of individual taxa to *Nucella* treatments, we found there were significant differences in *P. crassipes* biomass among *Nucella* populations: mussel beds treated with Lompoc *Nucella* or no *Nucella* (control) had greater biomass of *P. crassipes.* Biomass was higher for different reasons; Lompoc treatments had few very large individuals while control treatments had many small individuals. This suggests that *Nucella* have a direct effect on the crabs that differs by population; for example, Lompoc *Nucella,* by drilling larger mussels, may have directly provided habitat (large open mussels shells) for large *P. crassipes* individuals (Figure A3.3). Soberanes and Hopkins *Nucella* drilled smaller mussels and thus did not provide this unique habitat for large crabs. The presence of *Nucella* may deter smaller *P. crassipes* individuals, leading to lower biomass of small individuals in *Nucella* presence treatments and higher in the control treatment. Therefore, differential predation by *Nucella* may have direct community effects on taxa that can take advantage of the unique consequences of specific *Nucella* predation traits. This supports our hypothesis that *Nucella* that drill larger mussels may have greater effects on community composition via altering habitat complexity.

Intraspecific trait variation has important ecological effects in several well-studied systems (Hairston et al. 2005; Hughes et al. 2008; Harmon et al. 2009; Palkovacs et al. 2012, 2018; Des Roches et al. 2018), but it lacks assessment in marine habitats. Our study showed for the first time evidence of a mechanism through which predator trait variation can have differential community effects in a marine system. It also showed for the first time how differential predation on foundation species can alter communities. As we expand our understanding of the importance of intraspecific trait variation to more systems, we will be better able to understand the role of trait variation in producing the diversity we see in nature. As traits are the objects of selection, by studying the effects of trait change on ecological processes we begin to uncover the complex interactions between ecology and evolution.

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Tables and figures

Table 3.1. Summaries of temperature regimes during the experiment (in Santa Cruz) and temperature and pH regimes at *Nucella* population origin sites and Santa Cruz for available years during comparable seasons

	Temperature (°C)				pH (total)			
	Mean	Min	Max	SD	Mean	Min	Max	SD
Santa Cruz 2017–18	13.31	10.51	16.39	1.22				
Hopkins 2013	15.12	13.00	20.27	0.99	8.10	7.60	8.51	0.15
Soberanes 2013	12.38	10.28	15.04	0.85	8.02	7.50	8.29	0.13
Lompoc 2011	13.14	11.40	15.99	0.97	7.97	7.67	8.24	0.12
Santa Cruz 2012	14.70	12.48	17.63	0.77	8.15	7.78	8.36	0.09

Santa Cruz 2017–18 temperature is from a low zone intertidal logger 17 Oct 2017 to 1 Aug 2018 (the duration of the experiment). Hopkins 2013, Soberanes 2013, and Santa Cruz 2012 data are from intertidal pH sensors from 15 July to 22 September (Menge et al. 2015) and Lompoc data are from an offshore sensor (Purissima) from the same date range in 2011 (Rivest et al. 2016). Descriptions of pH regimes at these sites can also be found in (Hofmann et al. 2014; Kroeker et al. 2016; Chan et al. 2017)

Table 3.2. Summary of linear mixed effects model for mean drilled mussel length as a function of *Nucella* population. Soberanes and Lompoc populations are compared to the Hopkins population (intercept). An asterisk indicates significance at the $\alpha = 0.05$ level

	Estimate	**Std. Error**	**Df**	**t**	**Pr(>|t|)**
(Intercept)	27.39	2.09	14	13.09	< 0.001*
Soberanes	3.67	2.94	14	1.25	0.23
Lompoc	8.21	2.94	14	2.80	0.01*
Random effect		**% variance explained**			
block		10.5			

Table 3.3. Summary of linear mixed effects model for *P. crassipes* biomass as a function of *Nucella* treatment. Treatments are compared to the control (no *Nucella*; intercept). An asterisk indicates significance at the $\alpha = 0.05$ level

	Estimate	**Std. Error**	**Df**	**t**	**Pr(>|t|)**
(Intercept)	3.95	0.55	19.09	7.19	< 0.001*
Hopkins	–1.69	0.60	21.00	–2.80	0.01*
Soberanes	–2.03	0.60	21.00	–3.37	0.003*
Lompoc	–0.58	0.60	21.00	–0.95	0.35
Random effect		**% variance explained**			
block		39.4			

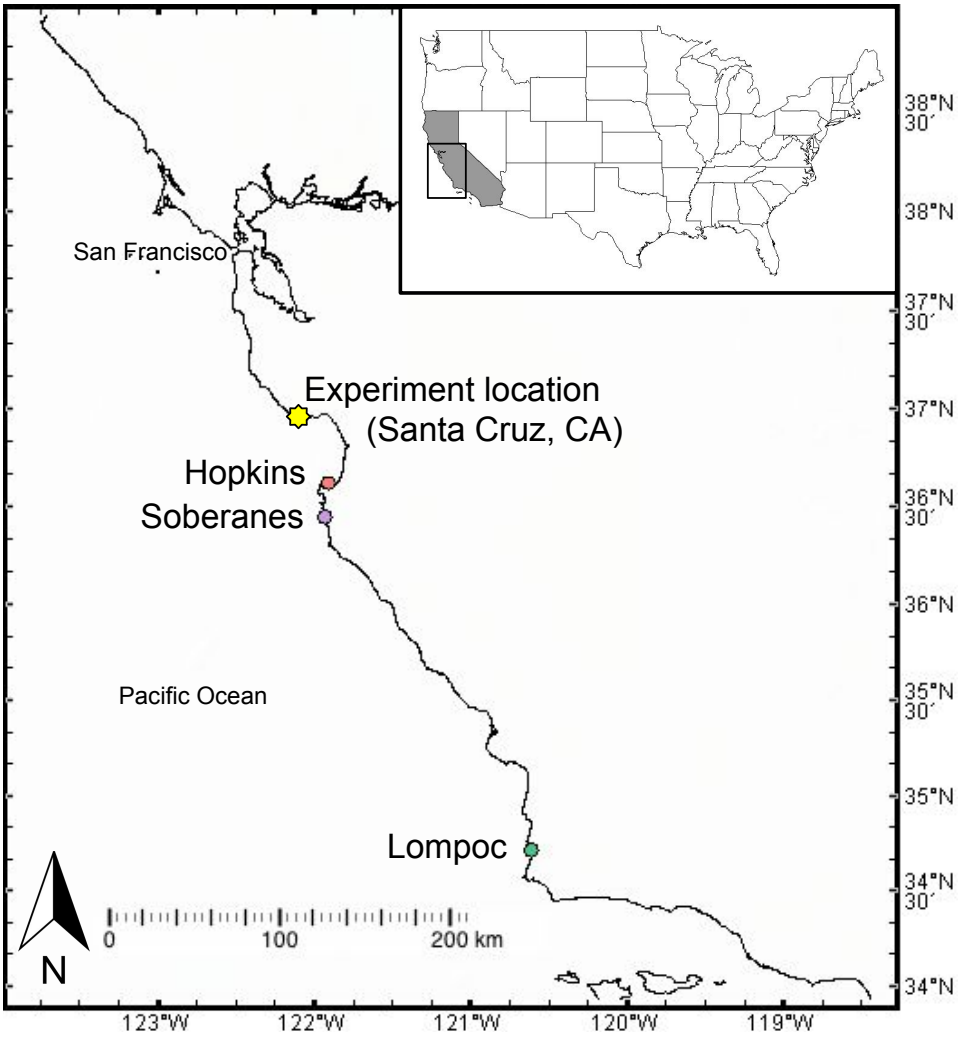

Figure 3.1. Map of study sites and experiment location

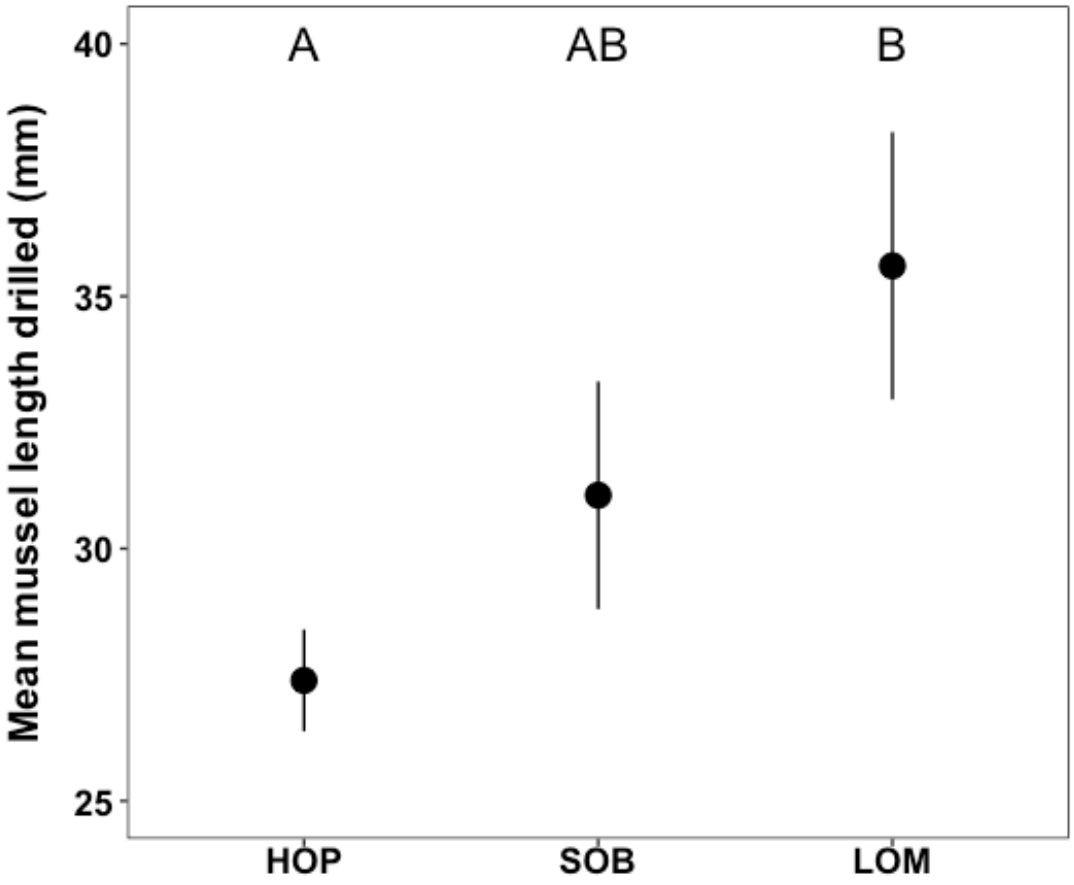

Figure 3.2. Mean drilled mussel length for each *Nucella* population. HOP, Hopkins; SOB, Soberanes; LOM, Lompoc. Means with different letters are significantly different at the $\alpha = 0.05$ level based on pairwise *t*-tests. Error bars are SEM

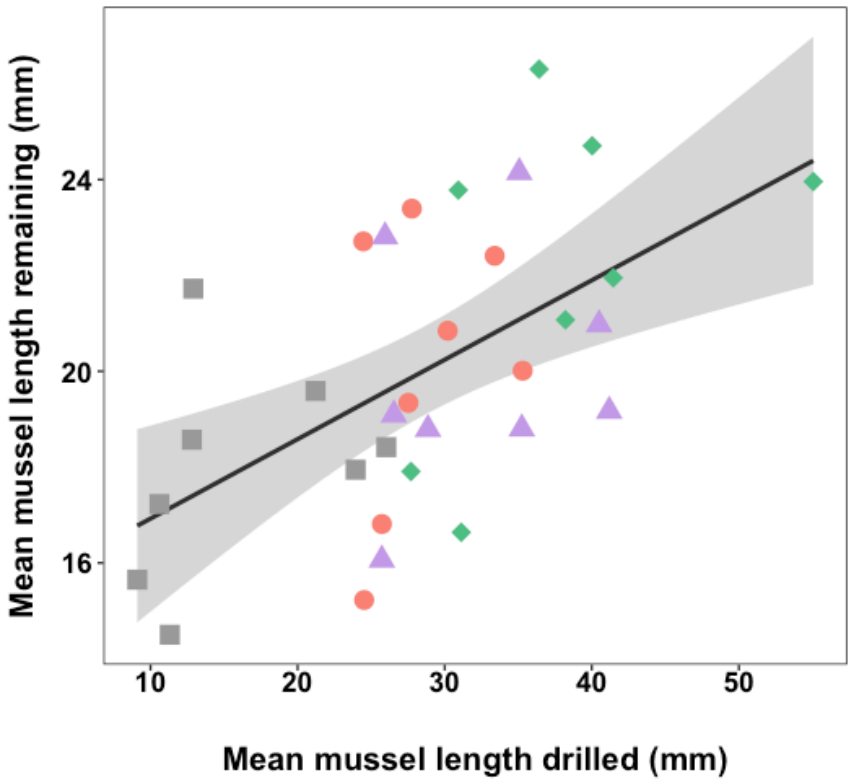

Figure 3.3. Relationship between mean drilled mussel length and mean remaining mussel length at the end of the 9-month experiment. Grey squares, control (no *Nucella*); red circles, Hopkins; purple triangles, Soberanes; green diamonds, Lompoc. Line is a linear regression with 95% CI shading. $P < 0.001$, $r^2 = 0.29$

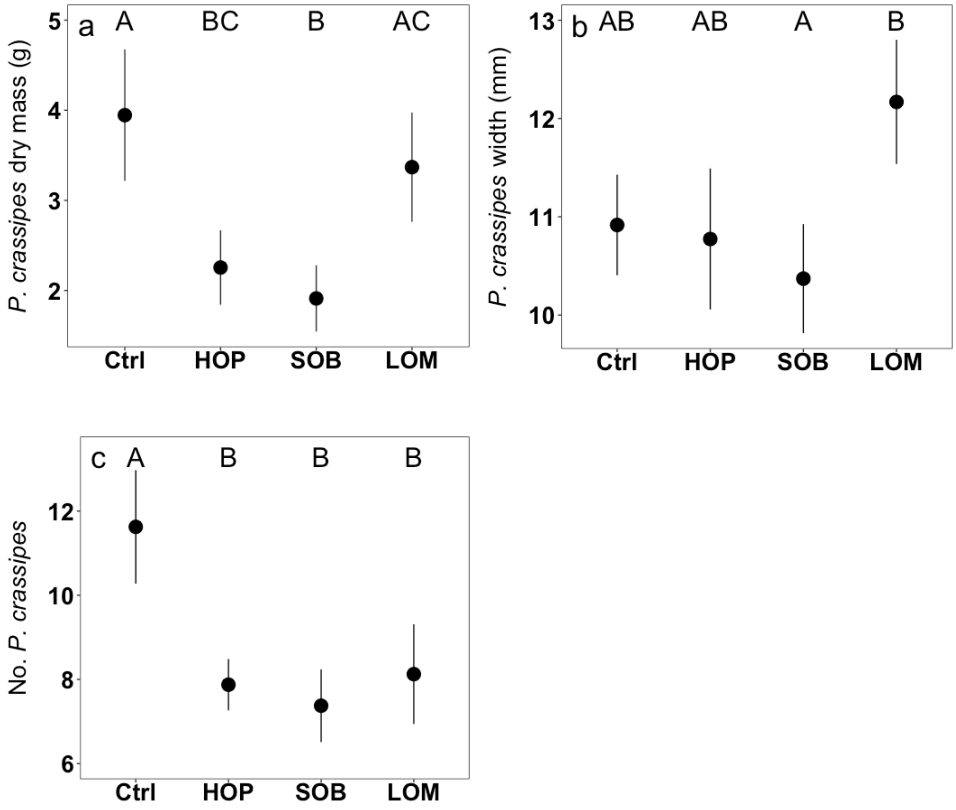

Figure 3.4. Effects of *Nucella* treatment on *P. crassipes*. (a) Mean dry mass, (b) width, and (c) number of *P. crassipes* as a function of *Nucella* treatment (Ctrl = *Nucella* absence). Points with different letters are significantly different based on linear mixed effects models. Sample size is 32 and error bars are SEM

Synthesis

My dissertation advances the study of the ecological importance of intraspecific trait variation by exploring population-level variation among intertidal predators consuming foundational mussels. I found significant variation in size selectivity and consumption rates among *Nucella* predator populations that were related to climate rather than neutral genetic relationships, and that some of these traits are affected by seawater pH. I also related differential prey size selectivity to mussel bed structure and the community composition of the mussel bed matrix, thus expanding the study of ecologically relevant trait variation to marine systems. Intertidal systems are classical ecological systems that have grounded our understanding of community regulation by disturbance, competition, predation, temperature, and desiccation (Menge and Sutherland 1987). Now, in addition to these processes, my work paves the way to use intertidal systems to develop our understanding of the ecological importance of trait variation.

In Chapter 1, I assessed how size selectivity on California mussel prey varied among populations of *Nucella ostrina-emarginata* across their range in the California Current System. I found that size selectivity was correlated with the different pH and temperature regimes experienced by each population and not neutral genetic relationships. This is consistent with the idea that local adaptation or acclimatization to climate rather than phylogenetic relationships shapes foraging traits. This study

showed the important role of climate in shaping *Nucella* population-level trait variation.

In Chapter 2, I assessed how seawater pH affected population-level variation in *Nucella* foraging. By testing the effects of acute exposure to acidified seawater on *Nucella* from three populations with varying pH regimes, I could assess if *Nucella* with a history of increased low pH exposure performed in acidification better than *Nucella* without prior exposure. I found this was true for some foraging traits, namely search time and total consumption time. While populations showed different handling time responses to acidification, the result did not support the idea of increased tolerance for populations with prior low pH exposure. Thus, other aspects of the abiotic environment may be important for handling, such as pH variability and temperature.

In Chapter 3, I explored community effects of *Nucella* population-level trait variation. Using populations with known foraging differences such as size selectivity and consumption rate, I measured changes in the mussel bed matrix community after predation by *Nucella* from one of three populations for nine months. First, I found that, on average, *Nucella* populations drilled different sizes of mussels. These differences could be a result of *Nucella* prior adaptations to biotic or abiotic conditions at their home sites. I found that the sizes of mussels drilled was directly related to the sizes remaining, and that remaining mussel size structure was important for community diversity, especially for small gastropods, annelids, isopods, anemones, and crabs. This illuminates a mechanism by which *Nucella* can alter

intertidal mussel bed communities. Together with Chapters 1 and 2, these results suggest that *Nucella* foraging traits play a role in regulating intertidal mussel bed communities and are mediated by climate. Thus, my work demonstrates a pathway through which climate can have indirect effects on communities.

Since *Nucella* traits differ on local scales and alter foundational habitat, *Nucella* may be able to shape their own selective environment in an eco-evolutionary feedback loop. Local adaptation (as well as transgenerational plasticity) to abiotic conditions can drive *Nucella* foraging traits, differentially altering mussel beds, which has the potential to feed back to alter the selective environment for *Nucella*. This eco-evolutionary process could be another driver of diversity, contributing to our understanding of the forces governing intertidal systems and natural systems more generally.

Population-level trait diversity is an important form of diversity that can have broad ecological consequences. My dissertation explored climate drivers of population-level trait diversity and their community consequences in an intertidal system. As climate continues to change rapidly, it is critical to characterize how ecologically important traits respond to abiotic changes on local scales. By examining community effects of local scale trait differences in predation in a marine system, my research develops and expands the study of ecologically important trait variation.

Appendices

A1: Supplemental Material for Chapter 1

Table A1.1. Site codes and coordinates.

Site name	Code	Latitude	Longitude
Fogarty Creek	FOG	44.83686°	–124.05871°
Strawberry Hill	STR	44.24944°	–124.11432°
Cape Arago	ARA	43.08730°	–124.40113°
Van Damme	VAN	39.28147°	–123.80226°
Bodega	BOD	38.31819°	–123.07365°
Hopkins	HOP	36.62108°	–121.90653°
Soberanes	SOB	36.44769°	–121.92880°
Lompoc	LOM	34.71862°	–120.60878°

Table A1.2. Principal component loadings of environmental variables.

Variable	PC1	PC2	PC3
min pH	0.315400361	0.76758287	-0.480719913
max pH	-0.252530523	-0.917458992	-0.111897291
mean pH	0.864654363	-0.479845411	-0.088503568
median pH	0.718030834	-0.6175664	-0.132811293
pH 5%	0.965543562	0.098001909	0.063920415
pH 10%	0.980418046	-0.035306032	0.139776469
pH 15%	0.972716579	-0.121214656	0.189339433
pH 20%	0.948590057	-0.212104163	0.220161089
pH 25%	0.91165385	-0.286239744	0.252432876
SD pH	-0.738743145	-0.509189344	-0.410455261
CV pH	-0.783321323	-0.445562752	-0.410884367
pH<7.6	-0.514169061	-0.616905826	0.376698496
pH<7.7	-0.660098176	-0.58050594	0.08422889
pH<7.8	-0.821193988	-0.135080596	-0.539856164
pH<7.9	-0.882395583	0.197669876	-0.416341149
pH<8.0	0.076313823	0.65679754	-0.671140833
median emersion	0.907478902	-0.285773562	-0.093743047
max emersion	0.747087204	0.144882133	-0.594966386
min emersion	0.212861927	-0.944968983	0.047571498
SD emersion	0.068401745	0.784890738	-0.150987123
emersion>24	0.76221024	0.522995843	0.022579632
emersion>26	0.807104642	0.460057058	-0.079411364
emersoin>28	0.846703297	0.425999967	-0.13133302
emersion>30	0.82570689	0.239358971	-0.338818974
mean water	0.951522634	-0.209277051	-0.082178432
min water	0.924248339	-0.325874176	-0.125380725
max water	0.359729	-0.736035064	-0.552535137
median water	0.954798661	-0.155879794	0.03395242
sd water	-0.567654458	-0.257048771	-0.728698587
water>10	0.961968131	0.119352006	0.046934242
water>12	0.936974108	-0.243243773	-0.187435635
water>14	0.817662778	-0.392556442	-0.406183744

Table A1.3. AIC statistics from linear models (regression) of drilled mussel length

Terms	AICc	ΔAICc	Weight	Cum. weight	Log likelihood	Sig terms (P<0.05)
NL, PC1, PC3	173.47	0.00	0.60	0.60	–78.26	NL, PC1, PC3
MLA, NL, PC1, PC3	174.81	1.34	0.31	0.91	–78.93	NL, PC1, PC3
MLA, NL, PC1, PC2, PC3	177.2	3.73	0.09	1.00	–78.10	NL, PC1, PC3

NL = *Nucella* length; MLA = mussel length available; PC1, PC2, and PC3 are principal component axes of environmental variables (seawater temperature, emersion temperature, and seawater pH (see Table S2)).

Table A1.4. Pairwise Kimura-2-paramter genetic distances calculated from a 599 bp section of COI. Sample sizes: FOG (15), STR (7), ARA (25), VAN (17), BOD (8), HOP (22), SOB (18), LOM (23)

	FOG	STR	ARA	VAN	BOD	HOP	SOB	LOM
FOG	0.000							
STR	0.048	0.764						
ARA	0.150	0.199	0.581					
VAN	1.269	1.014	1.421	0.530				
BOD	2.548	2.167	2.703	1.010	0.429			
HOP	6.980	7.038	7.062	8.283	9.59	0.091		
SOB	4.713	4.767	4.798	6.006	7.307	5.939	0.321	
LOM	4.027	4.081	4.102	5.316	6.613	5.036	0.897	0.000

Table A1.5. AIC statistics from linear models (regression) of drilled mussel length using growth-corrected available mussel length

Terms	AICc	ΔAICc	Weight	Cum. weight	Log likelihood	Sig terms (P<0.05)
NL, PC1, PC3, gcMLA	173.69	0.00	0.95	0.95	–78.37	NL, PC1, PC3
PC3, gcMLA	180.25	6.56	0.04	0.98	–85.07	gcMLA
gcMLA	181.52	7.84	0.02	1.00	–87.16	gcMLA

Table A1.6. Summary for linear mixed effects model for mean drilled mussel length using growth-corrected available mussel length

Fixed effects	**Estimate**	**Std. Error**	**df**	**t**	**P**
Intercept	92.71	26.83	16	3.44	0.003*
PC3	6.85	2.10	3	3.27	0.047*
PC1	3.47	1.16	3	3.00	0.058
Mean *Nucella* length	–3.18	1.35	3	–2.36	0.10
Mean growth-corrected available mussel length	0.18	0.17	16	1.05	0.31
Random effect	**% variance explained**				
Site	69.9				

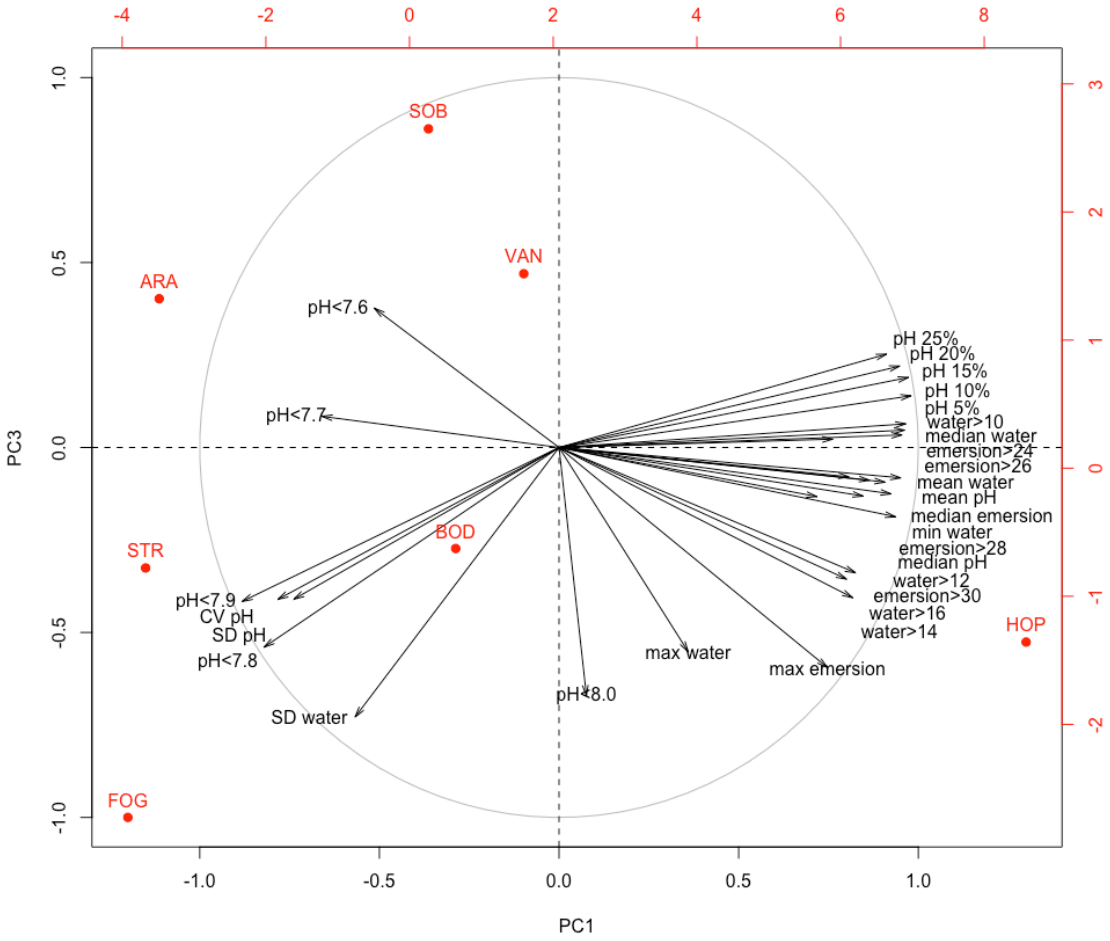

Figure A1.1. Principal component biplot of environmental variables used in the final model (PC1 and PC3). The lengths and directions of the arrows are determined by the eigenvectors that relate each variable to the two principal components. For clarity, only eigenvectors with an absolute value greater than 0.5 for either PC1 or PC3 are plotted. For values of PC1 greater than 0.5, labels are placed around the edge of the circle for clarity and correspond to the vertical order of the arrows. pH < x = percent of time spent below pH x; % = percentile; water or emersion > y indicates the percent of time spent above temperature y; SD = standard deviation; CV = coefficient of variation. Site codes are plotted in red using the red axes based on their PC scores

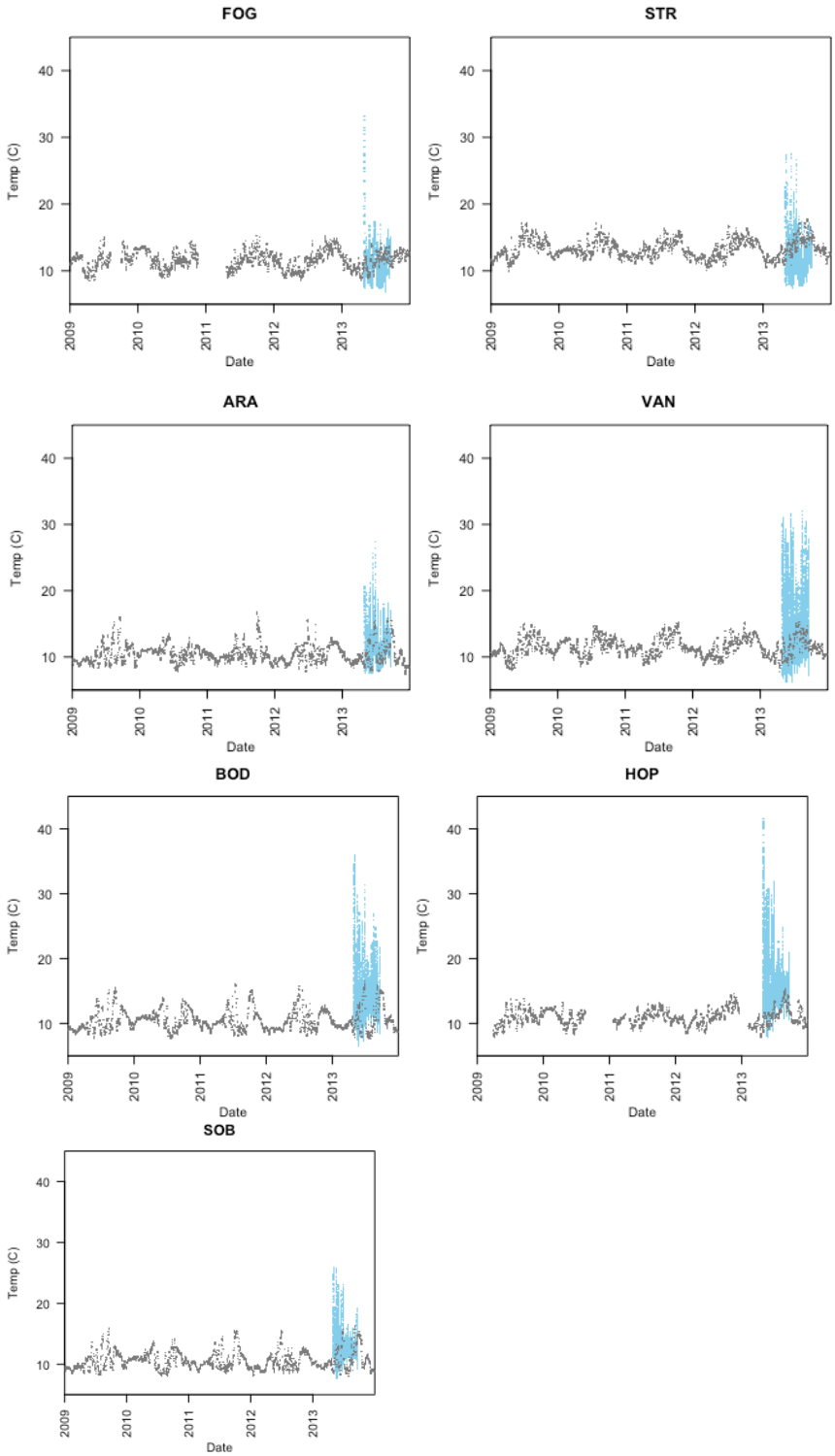

Figure A1.2. Mean daily water temperatures from 2009–2013 (grey) and 2013 emersion temperatures in 10-minute intervals (blue) at each site

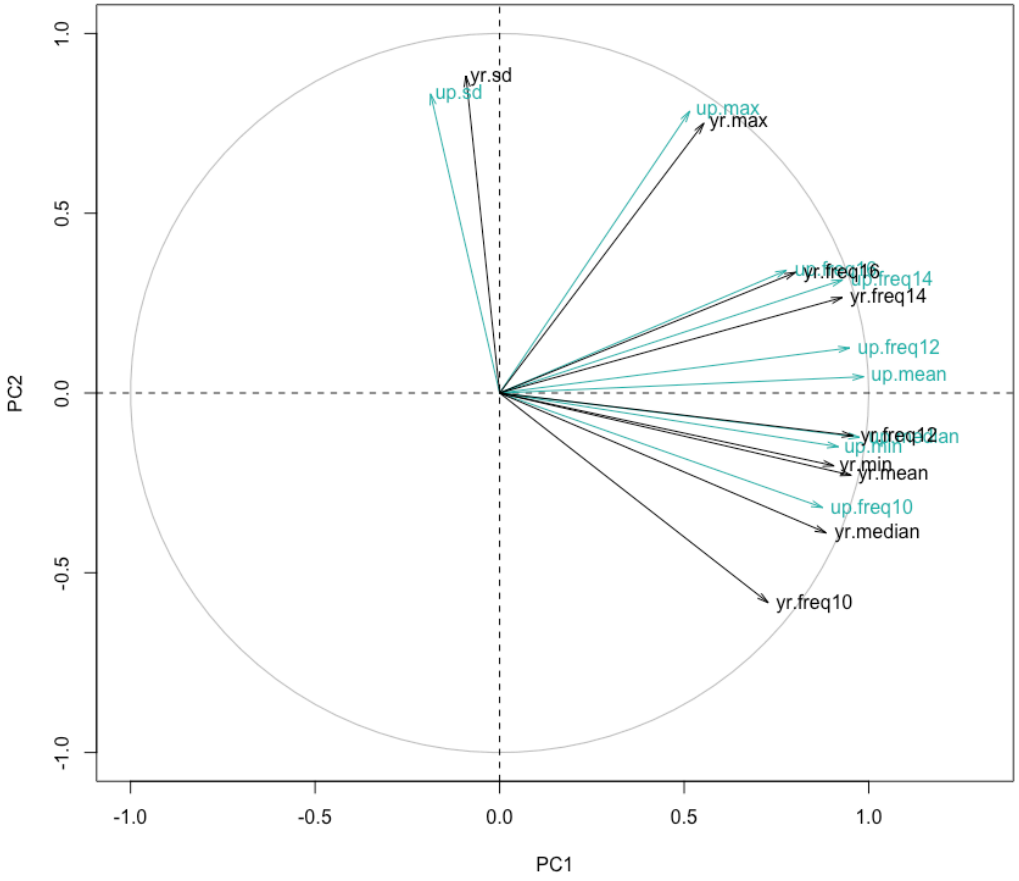

Figure A1.3. PCA on seawater temperature regimes for all sites comparing upwelling (April to September; blue) to full year regimes from 2009 through 2013

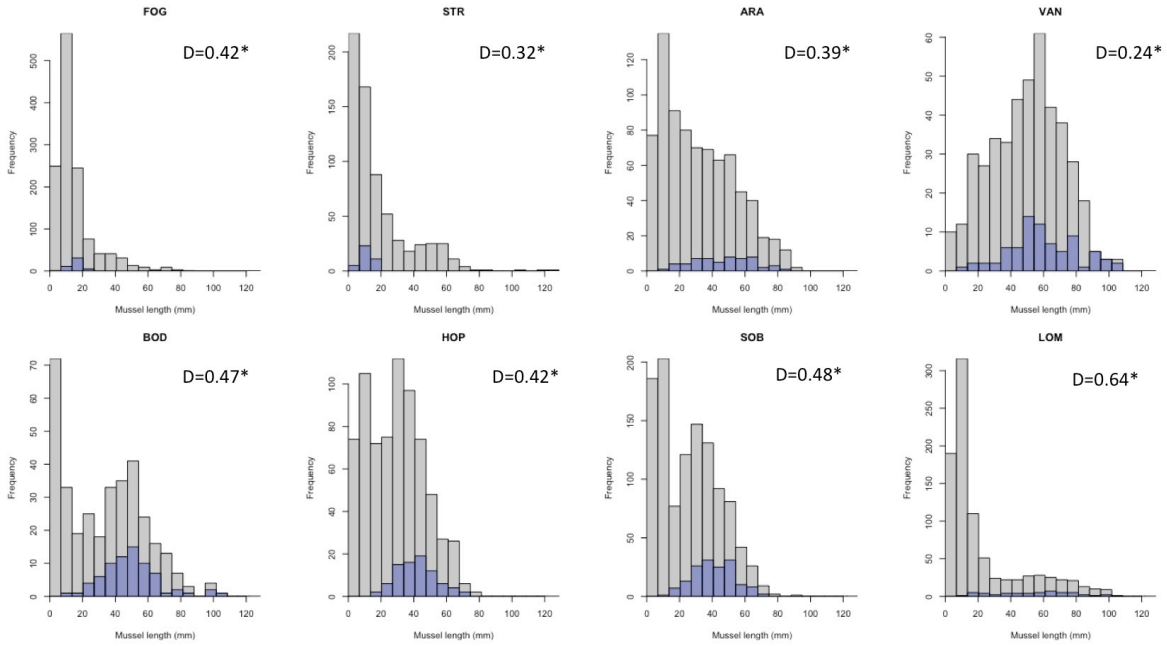

Figure A1.4. Histograms of drilled and available mussels from all plots pooled at each site. Available mussels include drilled and undrilled mussels. D is the Kolmogorov-Smirnov statistic for the difference between distributions. An asterisk indicates significance at the 0.001 level

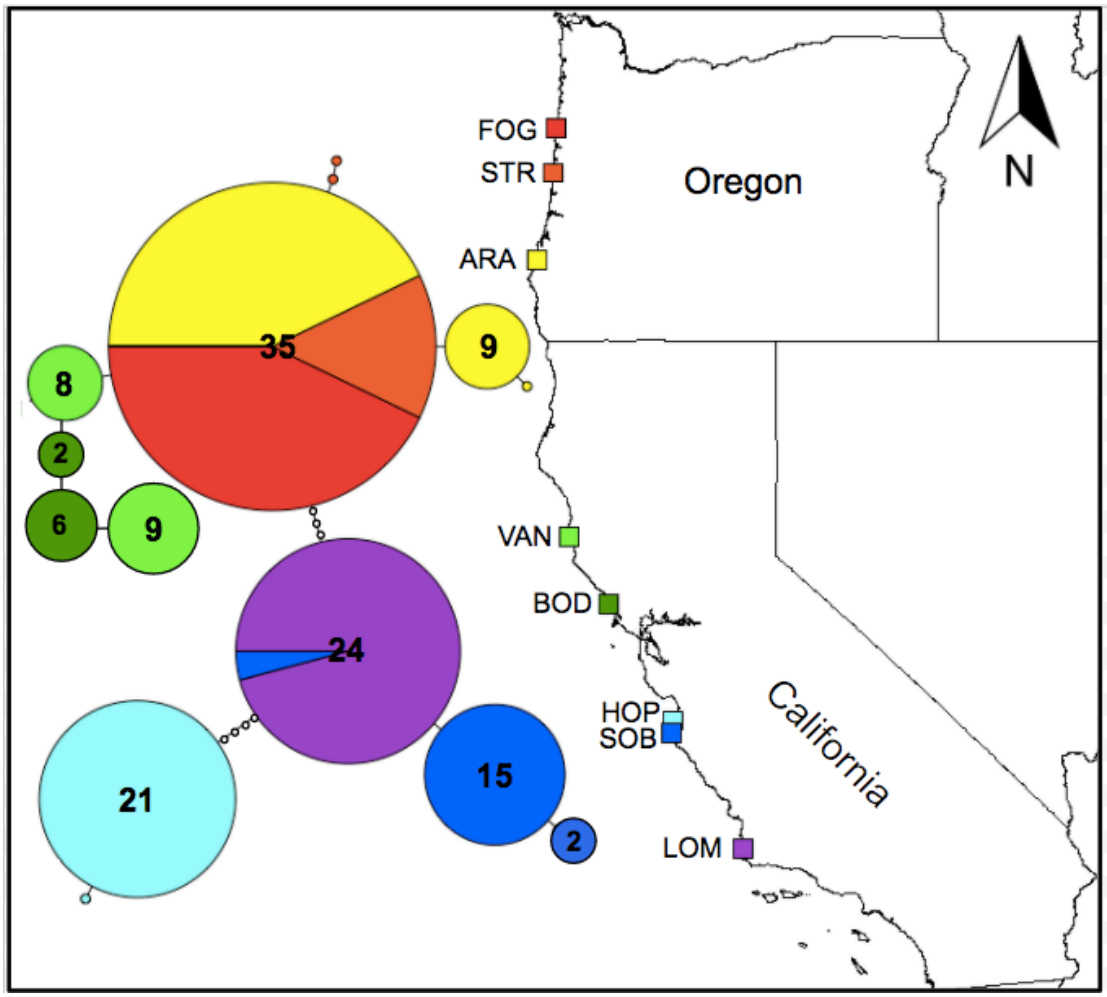

Figure A1.5. Map of study sites and cytochrome c oxidase subunit I (COI) haplotype network for *Nucella* specimens used in this study. Sequence length is 599 bp and total N = 135. Colored circles represent unique sampled haplotypes and small white dots between them represent missing haplotypes. Colors represent sites and correspond to the map. Wedges represent the portion of the haplotype found at the site. Site codes: Fogarty Creek (FOG), Strawberry Hill (STR), Cape Arago (ARA), Van Damme (VAN), Bodega (BOD), Hopkins (HOP), Soberanes (SOB), Lompoc (LOM)

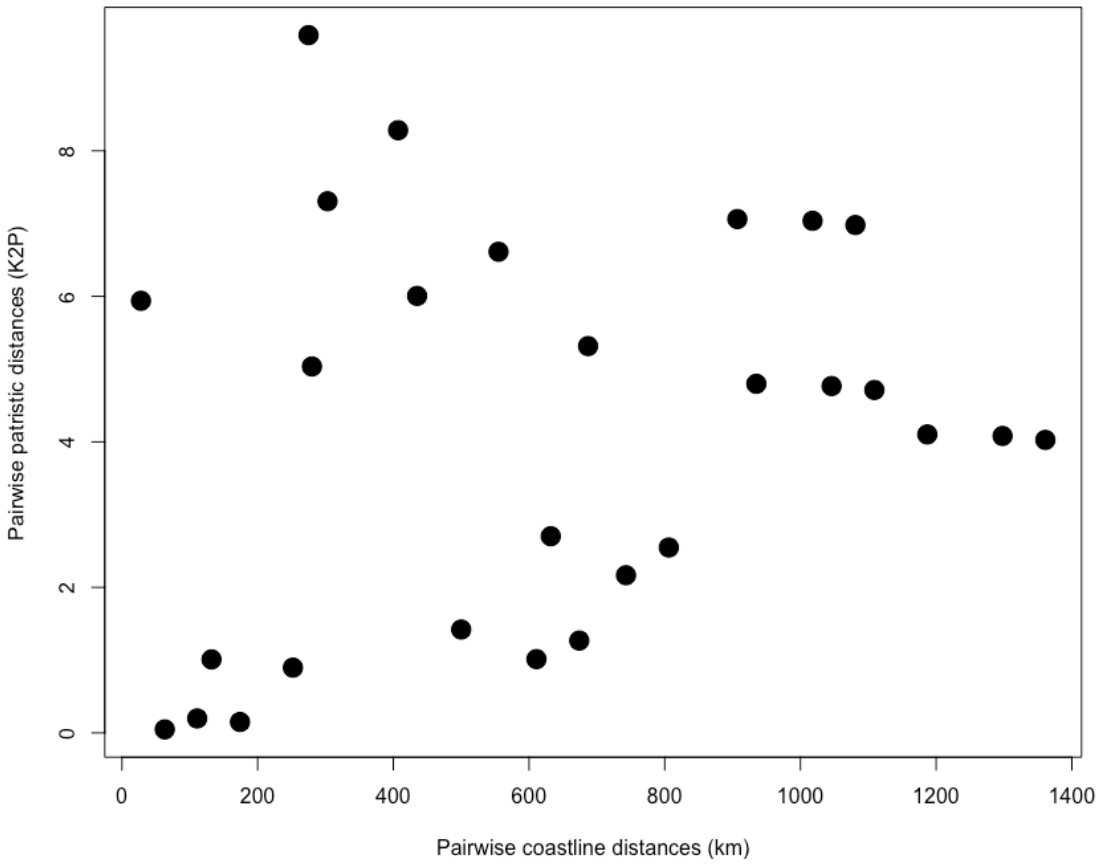

Figure A1.6. Isolation by distance plot of pairwise patristic distances (K2P) vs. pairwise coastline distance (km). Linear regression was nonsignificant ($P > 0.2$), indicating no pattern of isolation by distance

A2: Supplemental Material for Chapter 2

Table A2.1. Header barrel and bin comparisons. pH and temperature in header barrels were measured continuously in 15 s intervals with Durafet pH sensors. Bin pH was measured using bottle samples taken every twelfth day following the guide to best practices for ocean CO_2 measurements (Dickson 2007). Bin temperature was measured continuously in 15 min intervals with temperature loggers. Values are mean ± standard error

	Header barrel		Experimental bin	
Treatment	pH	Temperature (C)	pH	Temperature (C)
Ambient	8.03 ± 0.00	13.81 ± 0.00	7.99 ± 0.01	13.96 ± 0.04
Acidified	7.60 ± 0.00	13.80 ± 0.00	7.66 ± 0.01	13.90 ± 0.04

Table A2.2. Mean dogwhelk length (mm) and masses (g) of each population at the start of the experiment. Shell mass was measured by weighing the dogwhelk immersed in seawater

Population	N	Length	SD	Total wet	SD	Shell	SD	Body	SD
High	60	23.381	1.511	2.536	0.473	1.056	0.226	1.480	0.261
Intermediate	60	22.966	2.395	2.355	0.740	0.913	0.283	1.443	0.465
Low	53	22.876	2.736	2.546	0.813	1.000	0.327	1.547	0.542

Table A2.3. Mean dogwhelk length (mm) and masses (g) in each pH treatment at the start of the experiment

pH treatment	N	Length	SD	Total wet	SD	Shell	SD	Body	SD
Ambient	86	22.900	2.090	2.39	0.659	0.956	0.263	1.435	0.408
Acidic	87	23.262	2.389	2.56	0.706	1.021	0.301	1.538	0.453

Table A2.4. Mean dogwhelk length (mm) and masses (g) in each bin at the start of the experiment

Bin	N	Length	SD	Total wet	SD	Shell	SD	Body	SD
2a	15	23.275	2.711	2.556	0.834	1.035	0.335	1.521	0.512
2b	14	23.862	2.446	2.700	0.783	1.079	0.303	1.621	0.488
3a	14	23.164	1.432	2.355	0.432	0.924	0.194	1.431	0.253
3b	14	22.463	2.166	2.273	0.640	0.922	0.239	1.351	0.406
4a	15	22.257	1.900	2.165	0.571	0.853	0.247	1.312	0.333
4b	15	23.723	2.720	2.691	0.871	1.067	0.335	1.623	0.553
5a	14	23.416	1.813	2.559	0.618	1.034	0.259	1.525	0.366
5b	15	23.142	2.343	2.487	0.559	0.993	0.207	1.494	0.367
6a	14	22.342	2.393	2.438	0.721	1.008	0.347	1.430	0.385
6b	15	23.525	2.639	2.621	0.777	0.985	0.371	1.637	0.590
7a	14	23.628	1.645	2.648	0.629	1.073	0.255	1.575	0.387
7b	14	22.208	2.134	2.225	0.636	0.901	0.242	1.324	0.401

Table A2.5. Analysis of deviance (type III) on ordered regression mixed model for size of mussel drilled

	LR Chisq	Df	Pr(>Chisq)
pH treatment	0.000	1	1.000
Population	0.000	2	1.000
pH treatment * Population	1.928	2	0.381

Random effect of bin had variance 0.13.

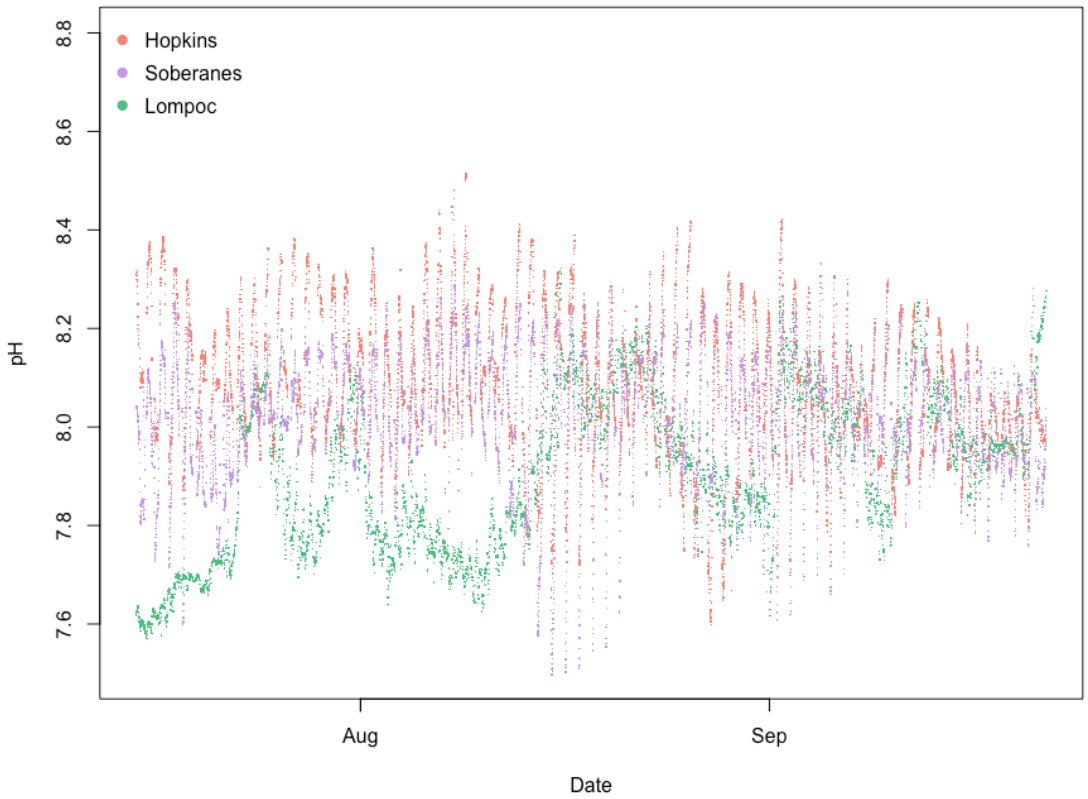

Figure A2.1. Time series of pH at study locations in 2011 (Lompoc) and 2013. Lompoc intertidal pH is approximated with pH data from an offshore mooring at Purisima (34.73, -120.63)

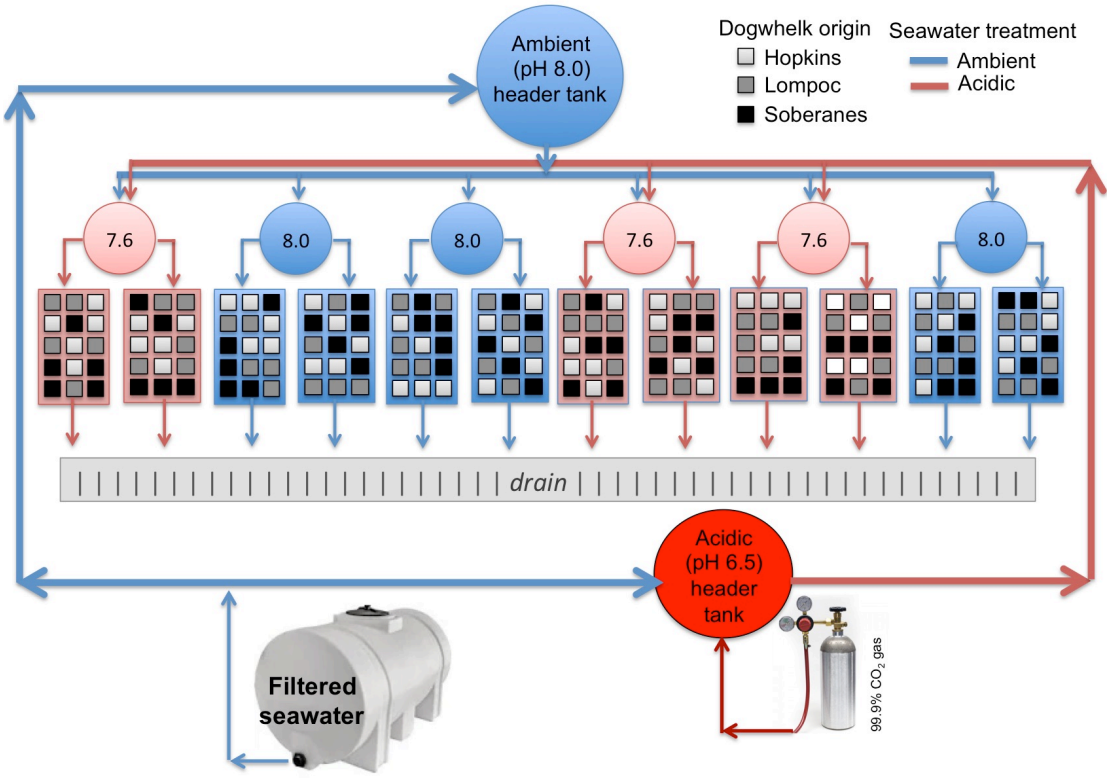

Figure A2.2. Diagram of experimental setup with carbonate chemistry manipulation. Red indicates acidified seawater and blue indicates ambient seawater. Red and blue circles labeled with pH are header barrels where pH was manipulated and Durafets continuously recorded pH. Water from header barrels flowed to rectangular bins each with 15 dogwhelks from the three populations

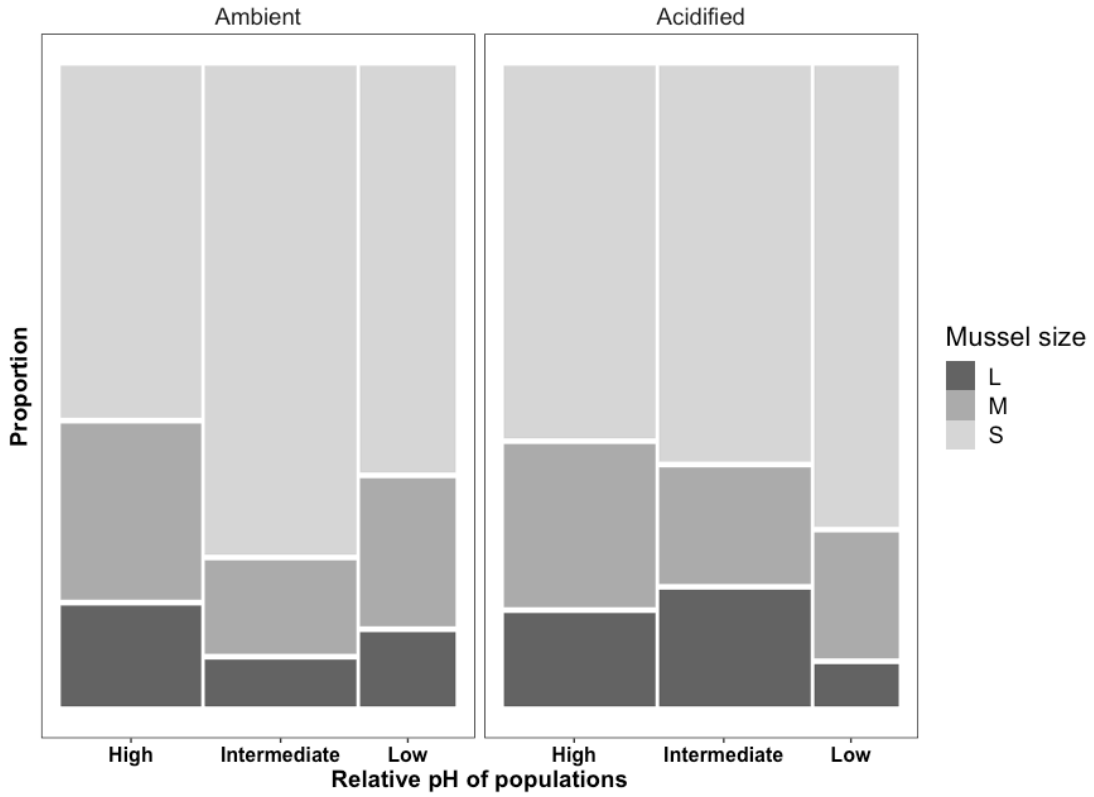

Figure A2.3. Proportion of each size of mussel drilled by dogwhelk population and pH treatment. Bar widths indicate sample sizes

A3: Supplemental Material for Chapter 3

Table A3.1. Initial sizes of *Nucella* by population origin

Population	N	Mean.length	SD.length	Min.length	Max.length	Mean.mass	SD.mass	Min.mass	Max.mass
HOP	40	24.20	1.01	22.68	26.33	2.41	0.32	1.90	3.04
LOM	40	24.23	1.21	22.03	26.00	2.47	0.44	1.71	3.48
SOB	40	24.23	1.93	20.55	26.76	2.19	0.53	1.38	3.36

Table A3.2. Initial sizes of *Nucella* by cage

Cage ID	N	Mean.length	SD.length	Min.length	Max.length	Mean.mass	SD.mass	Min.mass	Max.mass
A04	5	23.84	1.50	22.30	25.87	2.25	0.52	1.83	3.09
A05	5	23.24	1.92	20.74	25.84	1.81	0.39	1.38	2.34
A06	5	23.72	0.74	22.69	24.47	2.28	0.23	1.90	2.47
A07	5	24.77	1.06	23.76	25.99	2.67	0.64	2.05	3.48
A09	5	24.52	1.19	22.94	26.00	2.73	0.56	1.88	3.25
A10	5	24.61	1.19	22.69	25.81	2.52	0.25	2.20	2.85
A12	5	24.57	2.35	20.76	26.75	2.40	0.68	1.41	3.07
A13	5	24.36	1.70	22.38	25.94	2.44	0.41	1.96	2.93
A15	5	25.25	2.01	21.76	26.75	2.41	0.61	1.65	3.36
A16	5	24.51	0.80	23.24	25.29	2.53	0.34	2.14	3.04
B03	5	24.09	1.21	22.68	25.80	2.40	0.45	1.94	3.01
B04	5	23.12	1.91	21.01	25.48	2.02	0.63	1.43	2.82
B05	5	24.35	1.08	23.24	25.67	2.49	0.29	2.17	2.90
B07	5	23.75	1.29	22.04	24.94	1.94	0.29	1.61	2.28
B08	5	24.44	1.16	23.47	26.33	2.46	0.40	2.04	2.94
B10	5	23.08	2.24	20.55	25.48	1.85	0.46	1.40	2.51
B11	5	23.98	1.45	22.03	25.56	2.54	0.43	2.11	3.06
B12	5	24.42	1.35	22.87	26.18	2.46	0.27	2.13	2.82
B13	5	23.99	1.08	22.73	25.09	2.35	0.42	1.98	2.81
B14	5	25.20	1.11	23.91	26.60	2.42	0.31	2.20	2.94
B15	5	23.74	1.14	22.10	25.28	2.20	0.36	1.71	2.59
C14	5	23.81	0.76	22.71	24.65	2.28	0.26	1.99	2.60
C15	5	24.24	0.96	23.09	25.57	2.48	0.24	2.24	2.75
C16	5	25.63	1.29	23.53	26.76	2.66	0.21	2.43	2.95

Table A3.3. Daily temperature profile during the experiment based on two temperature loggers recording temperature inside easternmost and westernmost cages (east and west, 25 Jan 2018 to 1 Aug 2018) and one low zone site logger (PISCO, 17 Oct 2017 to 1 Aug 2018). Loggers recorded temperature every 15 minutes

logger	N	Mean	Median	Min	Max	SD
east	169	13.91	14.02	8.63	22.98	1.80
west	189	13.98	14.10	8.37	23.31	1.84
PISCO	289	13.31	13.31	10.51	16.39	1.22

Table A3.4. Final sizes of *Nucella* by population origin

site	N	Mean.length	SD.length	Min.length	Max.length	Mean.mass	SD.mass	Min.mass	Max.mass
HOP	40	24.13	1.36	21.83	26.86	2.42	0.45	1.53	3.32
LOM	39	25.69	1.36	22.81	28.67	3.05	0.43	1.93	4.07
SOB	43	25.74	2.34	19.83	31.63	2.70	0.58	1.34	3.87

Table A3.5. Dry biomass in g of all taxa found in each cage

	Acanthinucella spirata	Adula diegensis	algae	Amage auricula	amphipod	annelid	Anthopleura	Assiminea californica
A03	0.0452	0.0000	17.9804	0.0000	0.0525	0.0550	1.4097	0.0020
A04	0.2146	0.0000	0.4450	0.0000	0.0082	0.4215	3.3583	0.0000
A05	0.0000	0.0000	0.9309	0.0000	0.0120	0.0033	0.7372	0.0000
A06	0.0000	0.0000	1.1793	0.0000	0.0090	0.0000	4.6285	0.0000
A07	0.0000	0.0000	0.7704	0.0000	0.0095	0.0060	2.0790	0.0000
A08	0.2233	0.0000	0.5412	0.0000	0.0207	0.1082	2.7748	0.0000
A09	0.0000	0.0000	0.2896	0.0000	0.0163	0.0000	1.2942	0.0000
A10	0.0483	0.0000	0.0147	0.0000	0.0142	0.0694	2.0689	0.0000
A11	0.0000	0.0000	0.1033	0.0000	0.0081	0.0000	1.7461	0.0000
A12	0.2867	0.0057	0.5945	0.0000	0.0125	0.0748	1.0317	0.0000
A13	0.0000	0.0000	1.1617	0.0000	0.0110	0.0184	0.8032	0.0000
A14	0.0000	0.0000	1.3235	0.0000	0.0158	0.0000	0.5684	0.0017
A15	0.0000	0.0000	0.3896	0.0000	0.0438	0.0000	0.4661	0.0000
A16	0.0000	0.0000	0.0000	0.0000	0.0231	0.0000	0.7215	0.0000
B03	0.0000	0.0000	5.0242	0.0000	0.1049	0.0848	3.0433	0.0000
B04	0.0235	0.0000	0.7660	0.0097	0.0910	0.0397	2.0499	0.0000
B05	0.4173	0.0000	1.7318	0.0000	0.0038	0.0477	0.0000	0.0000
B06	0.0000	0.0000	3.7627	0.0000	0.0102	0.0055	1.5244	0.0004
B07	0.0000	0.0000	0.7933	0.0000	0.0224	0.0545	0.4162	0.0022
B08	0.2698	0.0000	1.4681	0.0000	0.0364	0.0586	0.3932	0.0064
B09	0.0000	0.0000	0.0000	0.0000	0.0060	0.0000	2.8836	0.0000
B10	0.0623	0.0000	0.0000	0.0000	0.0141	0.0042	0.8123	0.0000
B11	0.0000	0.0000	2.3607	0.0000	0.0133	0.0110	1.2554	0.0059
B12	0.7969	0.0000	0.0000	0.0000	0.0766	0.0827	2.3921	0.0000
B13	0.0000	0.0000	0.1234	0.0000	0.0177	0.0186	0.7000	0.0011
B14	0.0586	0.0000	0.8336	0.0000	0.0040	0.0000	2.3080	0.0065
B15	0.0000	0.0000	0.4970	0.0000	0.0003	0.0047	6.0208	0.0000
B16	0.0000	0.0000	4.8147	0.0000	0.0013	0.1161	0.4181	0.0003
C13	0.0000	0.0000	0.0000	0.0000	0.0193	0.0000	0.2292	0.0011
C14	0.0000	0.0000	0.0000	0.0000	0.0017	0.0404	0.2331	0.0150
C15	0.0000	0.0000	0.0000	0.0000	0.0096	0.0825	1.1607	0.0000
C16	0.0000	0.0000	2.8261	0.0000	0.0000	0.0324	0.3358	0.0000

Table A3.5 continued (1)

	Chaetopterus	Chlorostoma funebralis	Cirolana	clam	Cyanoplax dentiens	Cyanoplax hartwegii	Epitonium tinctum
A03	0.0000	13.2914	0.0000	0.0313	0.0000	0.0036	0.0000
A04	0.0000	34.7129	0.0000	0.0400	0.0000	0.0000	0.0000
A05	0.0000	11.8781	0.0000	0.0000	0.0000	0.0000	0.0122
A06	0.0000	17.7309	0.0000	0.0000	0.0000	0.0000	0.0000
A07	0.0000	19.3589	0.0000	0.0000	0.0000	0.0000	0.0000
A08	0.0000	36.9786	0.0076	0.0000	0.0000	0.0000	0.0000
A09	0.0293	30.5099	0.0287	0.0000	0.0000	0.0000	0.0000
A10	0.0000	21.5066	0.0000	0.0000	0.0000	0.0000	0.0000
A11	0.0000	19.4381	0.0000	0.0036	0.0000	0.0000	0.0000
A12	0.0391	8.7738	0.0000	0.0000	0.0000	0.0000	0.0275
A13	0.0000	16.3999	0.1460	0.0000	0.0000	0.4440	0.0000
A14	0.0000	13.3258	0.0232	0.0000	0.0000	0.0000	0.0000
A15	0.0000	15.7189	0.0675	0.0000	0.0000	0.0000	0.0000
A16	0.0000	25.4166	0.0000	0.0000	0.0000	0.0000	0.0000
B03	0.0000	10.6893	0.0205	0.0000	0.0000	0.0000	0.0082
B04	0.0000	17.7629	0.0060	0.0000	0.0000	0.0000	0.0000
B05	0.0000	5.9860	0.0000	0.0000	0.0000	0.0000	0.0000
B06	0.0000	11.2779	0.0328	0.0040	0.0000	0.0000	0.0164
B07	0.0000	11.6023	0.0000	0.0031	0.0000	0.0000	0.0000
B08	0.0000	21.8810	0.0524	0.9711	0.0000	0.0000	0.0000
B09	0.1559	26.3332	0.0000	0.0019	0.0011	0.0000	0.0321
B10	0.0000	11.9957	0.0000	0.0000	0.0000	0.0000	0.0000
B11	0.0000	12.7097	0.0000	0.0000	0.0000	0.0000	0.0000
B12	0.0000	9.0580	0.0170	0.0000	0.0000	0.0000	0.0000
B13	0.0000	16.5510	0.0000	0.0000	0.0000	0.0000	0.0000
B14	0.0000	29.1492	0.0000	0.0011	0.0000	0.0000	0.0000
B15	0.0000	14.8194	0.0000	0.0000	0.0000	0.3061	0.0000
B16	0.0000	8.8460	0.0776	0.0132	0.0000	0.0000	0.0000
C13	0.0000	8.7581	0.0093	0.0000	0.0000	0.0000	0.0000
C14	0.0000	11.1514	0.0286	0.0565	0.0000	0.0000	0.0000
C15	0.0000	13.9193	0.0589	0.0000	0.0000	0.0000	0.0000
C16	0.0000	10.0375	0.1040	0.0107	0.0000	0.0000	0.0000

Table A3.5 continued (2)

	Eulithidium pulloides	Halosydna brevisetosa	Harfordia	Idotea	Lacuna	Limonia marmorata	Littorina	Lottia
A03	0.0000	0.0000	0.0000	0.0027	0.0826	0.0000	1.3833	1.5436
A04	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.1784	0.8119
A05	0.0000	0.0000	0.0000	0.0012	0.0165	0.0000	0.6895	1.4315
A06	0.0163	0.0000	0.0000	0.0000	0.0000	0.0000	0.4732	2.1554
A07	0.0115	0.0000	0.0000	0.0000	0.0000	0.0000	0.2127	2.4507
A08	0.0000	0.0000	0.0000	0.0000	0.0420	0.0000	1.3197	1.3910
A09	0.0000	0.0000	0.0000	0.0026	0.0000	0.0000	0.4217	1.8176
A10	0.0000	0.0000	0.0000	0.0000	0.0374	0.0000	1.1391	3.4667
A11	0.0060	0.0000	0.0000	0.0059	0.0178	0.0000	0.5068	1.0285
A12	0.0000	0.0000	0.0000	0.0000	0.0287	0.0000	1.0980	2.0186
A13	0.0000	0.0000	0.0000	0.1013	0.0100	0.0000	0.8716	0.9600
A14	0.0000	0.0000	0.0000	0.0213	0.0514	0.0000	3.0326	0.9476
A15	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.6241	0.9412
A16	0.0000	0.0000	0.0000	0.0077	0.0000	0.0000	0.4431	2.3129
B03	0.0000	0.0000	0.0000	0.0150	0.0297	0.0000	0.8626	2.5777
B04	0.0000	0.0000	0.0000	0.0000	0.0935	0.0000	1.5938	1.6096
B05	0.0000	0.0000	0.0000	0.0000	0.0694	0.0000	1.6099	1.7511
B06	0.0000	0.0000	0.0000	0.0000	0.1076	0.0000	0.5402	1.0800
B07	0.0000	0.0000	0.0000	0.0000	0.0399	0.0000	1.4005	2.1294
B08	0.0000	0.0000	0.0261	0.0000	0.1220	0.0000	1.9434	4.3676
B09	0.0047	0.0000	0.0000	0.0000	0.0294	0.0000	1.1476	1.0948
B10	0.0000	0.0000	0.0000	0.0331	0.0018	0.0000	1.8449	1.1716
B11	0.0063	0.0000	0.0000	0.0000	0.0240	0.0000	1.2547	1.7688
B12	0.0094	0.0000	0.0000	0.0000	0.0238	0.0000	1.8603	1.1677
B13	0.0073	0.0000	0.0000	0.0000	0.0090	0.0000	0.6947	0.8981
B14	0.0000	0.0759	0.0000	0.0000	0.0424	0.0000	1.0168	0.9988
B15	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.6658	1.3200
B16	0.0000	0.0000	0.0000	0.0000	0.0212	0.0056	0.8839	0.4510
C13	0.0000	0.0000	0.0000	0.0000	0.0069	0.0000	1.6579	0.9152
C14	0.0000	0.0000	0.0000	0.0000	0.2325	0.0000	1.2855	0.2968
C15	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9205	0.7681
C16	0.0000	0.0000	0.0000	0.0000	0.0152	0.0063	0.6902	0.5982

Table A3.5 continued (3)

	Modiolus	Mopalia muscosa	Neolepton	Nereis	Nuttalina californica	Pachygrapsus crassipes	Pagurus	Petrolisthes cinctipes
A03	0.0000	0.3030	0.000	1.2882	0.0000	4.9745	0.0000	0.0048
A04	0.0000	0.0000	0.000	0.0000	0.0000	2.5575	0.0000	0.0786
A05	0.0000	0.0000	0.000	1.6183	0.0000	3.6703	0.0026	0.0000
A06	0.0000	0.0000	0.000	1.5945	0.0000	2.3784	0.0000	0.0000
A07	0.0000	0.0000	0.000	0.7025	0.0000	4.8846	0.0000	0.0000
A08	0.0000	0.0000	0.000	0.1814	0.0000	4.3062	0.0403	0.0000
A09	0.7024	0.0000	0.000	1.3284	0.0000	6.7351	0.0000	0.0000
A10	0.0000	0.0000	0.000	0.8461	0.0000	4.7995	0.0000	0.0000
A11	0.0000	0.0000	0.000	0.0284	0.0000	6.1934	0.0000	0.0000
A12	0.0000	0.0000	0.002	1.2381	1.5245	2.3771	0.0000	0.0000
A13	0.0000	0.0000	0.000	0.6370	0.0000	2.6193	0.0000	0.0000
A14	0.0000	0.2172	0.000	0.0264	0.0000	1.2005	0.0000	0.0000
A15	0.0000	0.0000	0.000	0.0000	0.0000	1.6323	0.0000	0.0000
A16	0.0000	0.0000	0.000	0.3853	0.0000	1.4723	0.0000	0.0000
B03	0.0000	0.0000	0.000	0.2772	0.0000	2.4497	0.0000	0.0000
B04	0.0000	0.0000	0.000	1.7832	0.0000	1.2011	0.0000	0.3828
B05	0.0000	0.0000	0.000	0.8466	0.0000	1.2703	0.0000	0.0000
B06	0.0000	0.0000	0.000	0.8469	0.0000	1.8318	0.0000	0.0000
B07	0.0000	0.0000	0.000	0.4052	0.0000	2.5255	0.0000	0.0000
B08	0.0000	0.0000	0.000	2.1729	0.0000	2.2445	0.0000	0.0000
B09	0.0000	0.0000	0.000	0.0000	0.0000	7.0113	0.0000	0.0000
B10	0.0000	0.0000	0.000	1.0674	0.0000	2.4948	0.0000	0.0000
B11	0.0000	0.0000	0.000	0.3972	0.0000	3.1949	0.0000	0.0000
B12	0.0000	0.0000	0.000	1.7787	0.0000	1.2872	0.0000	0.0000
B13	0.0000	0.0000	0.000	0.0000	0.0000	2.3703	0.0000	0.0000
B14	0.0000	0.0000	0.000	0.0387	0.0000	0.8089	0.0000	0.0000
B15	0.0000	0.0000	0.000	1.5173	0.0000	2.2335	0.3252	0.0000
B16	0.1249	0.0000	0.000	0.0000	0.0000	3.5034	0.0000	0.0000
C13	0.0000	0.0000	0.000	0.0498	0.0000	2.5444	0.0000	0.0048
C14	0.0000	0.0000	0.000	1.5872	0.0000	1.0378	0.0000	0.0000
C15	0.1001	0.0000	0.000	0.3752	0.0000	3.4567	0.0000	0.3534
C16	0.0000	0.0000	0.000	0.3474	0.0000	0.5871	0.0000	0.0000

Table A3.5 continued (4)

	Phascolosoma agassizii	Pseudoalloioplana	Pugettia	Pycnogonida	Septifer bifurcatus	Serpula	unknown Cerithioidea	unknown Littorinidae	unknown snail 1
A03	0.0000	0.0000	0.0000	0.0000	3.6161	0.0000	0.0000	0.0000	0.000
A04	0.0000	0.0000	0.0392	0.0000	1.2959	0.0000	0.0000	0.0000	0.000
A05	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
A06	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
A07	0.0000	0.0000	0.0000	0.0000	0.0000	0.0097	0.0000	0.0000	0.000
A08	0.0000	0.0000	0.0000	0.0017	0.0000	0.0000	0.0000	0.0000	0.000
A09	0.0000	0.0000	0.0000	0.0000	0.0000	0.0063	0.0000	0.0000	0.000
A10	0.0000	0.0000	0.0000	0.0000	0.1026	0.0229	0.0344	0.0000	0.000
A11	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
A12	0.0000	0.0000	0.0000	0.0028	0.0000	0.0000	0.0000	0.0000	0.000
A13	0.0791	0.0000	0.0000	0.0000	0.0000	0.0789	0.0000	0.0000	0.000
A14	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
A15	0.0000	0.0000	0.0000	0.0000	0.0000	0.0045	0.0000	0.0000	0.000
A16	0.0000	0.0000	0.0000	0.0000	0.1506	0.0000	0.0000	0.0000	0.000
B03	0.0080	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
B04	0.0000	0.0000	0.0000	0.0000	0.3459	0.0000	0.0000	0.0000	0.000
B05	0.0000	0.0000	0.0100	0.0000	0.9065	0.0000	0.0000	0.0000	0.032
B06	0.0000	0.0000	0.0000	0.0000	0.0516	0.0014	0.0000	0.0000	0.000
B07	0.1508	0.0000	0.0000	0.0000	0.7797	0.0076	0.0000	0.0174	0.000
B08	0.0748	0.0000	0.0000	0.0000	0.7755	0.0000	0.0000	0.0055	0.000
B09	0.0000	0.0000	0.0000	0.0000	3.8102	0.0000	0.0000	0.0220	0.000
B10	0.0442	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
B11	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
B12	0.0000	0.0000	0.0000	0.0000	0.0000	0.0110	0.0000	0.0000	0.000
B13	0.0000	0.0000	0.0000	0.0000	0.0000	0.0134	0.0000	0.0000	0.000
B14	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
B15	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
B16	0.0000	0.0000	0.0000	0.0000	0.3538	0.0039	0.0000	0.0000	0.000
C13	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
C14	0.0000	0.0000	0.0000	0.0000	0.1631	0.0000	0.0000	0.0000	0.000
C15	0.0000	0.0095	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
C16	0.0000	0.0000	0.0000	0.0053	0.0000	0.0000	0.0000	0.0000	0.000

Table A3.6. PERMANOVA indicating effects of *Nucella* presence on drilled/dislodged mussel size structure. An asterisk indicates significance at the α = 0.05 level

	Df	**SumOfSqs**	**R2**	**F**	**Pr(>F)**
Nucella presence	1	2.28	0.45	24.34	0.001*
Residual	30	2.81	0.55		
Total	31	5.09	1.00		

Table A3.7. Effects of size classes of remaining mussels that were most influential for the biomass of each taxon. Minus indicates a negative effect, plus indicates positive, and an asterisk indicates 3 or fewer observations. The upper limits of bins were defined by 20th (6.16 mm), 40th (11.14), 60th (18.41), 80th (29.38), and 100th (90.14) percentiles

	Percentile				
Taxon	20	40	60	80	100
Assiminea californica	+		+		
Epitonium tinctum	+				
algae	–				
Eulithidium pulloides	–				
clam	–	+	+		–
Pagurus	+*			+*	+*
Cyanoplax dentiens	+*				
unknown *Cerithoidea*	+*				
Mopalia muscosa	–*			+*	
Phascolosoma agassizii		+	+		
Cirolana		+		+	–
Idotea		+			
Lottia		+			
Acanthinucella siprata		–	+	+	
Anthopleura		–	–		+
unknown Littorinidae		–	–*		
Amphipoda		–			–
Pycnogonida		+*		+*	–*
Harfordia		+*			
Limonia marmoarata		+*			
Adula diegensis		–*			
Amage auricla		–*			
Chaetopterus		–*			
Neolepton		–*			
Nuttalina californica		–*			
Petrolisthes cinctipes		–*			+*
Annelida			–	+	
Septifer bifurcates			–		
Serpula			–		
unknown gastropod 1			+*		
Cyanoplax hartwegii			–*		–*
Pugettia			–*		
Nereis				+	
Pachygrapsus crassipes				+	
Chlorostoma funebralis				–	–*
Halosydna brevisetosa				+*	
Modiolus				+*	
Pseudoalloioplana				+*	+*
Lacuna					–
Littorina					–

Table A3.8. PERMANOVA indicating effects of *Nucella* presence and mean remaining mussel length on multivariate community composition. An asterisk indicates significance at the $\alpha = 0.05$ level

	Df	**SumOfSqs**	**R2**	**F**	**Pr(>F)**
Nucella presence	1	0.09	0.05	1.50	0.19
Mean mussel length remaining	1	0.15	0.08	2.70	0.04*
Residual	29	1.66	0.88		
Total	31	1.89	1.00		

Table A3.9. PERMANOVA indicating effects of *Nucella* population and mean remaining mussel length on multivariate community composition. An asterisk indicates significance at the $\alpha = 0.05$ level

	Df	**SumOfSqs**	**R2**	**F**	**Pr(>F)**
Nucella population	2	0.05	0.04	0.48	0.86
Mean mussel length remaining	1	0.15	0.12	2.99	0.04*
Residual	20	1.00	0.82		
Total	23	1.23	1.00		

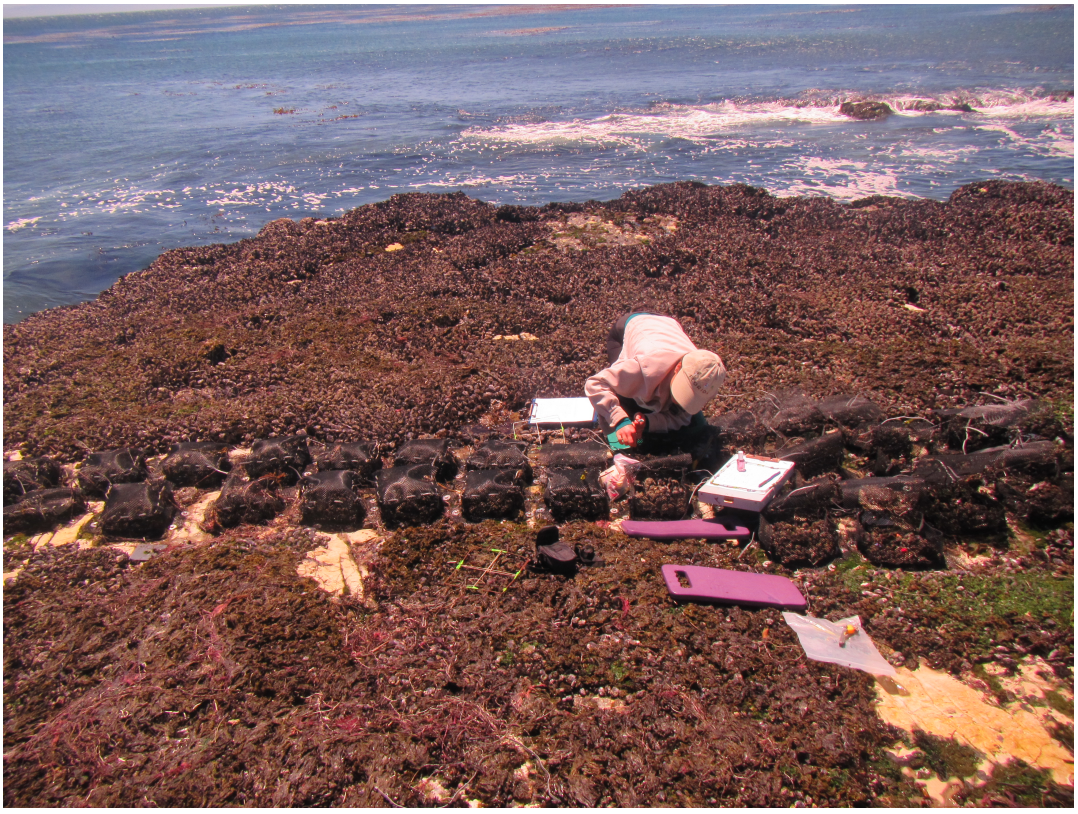

Figure A3.1. Cage array in the field

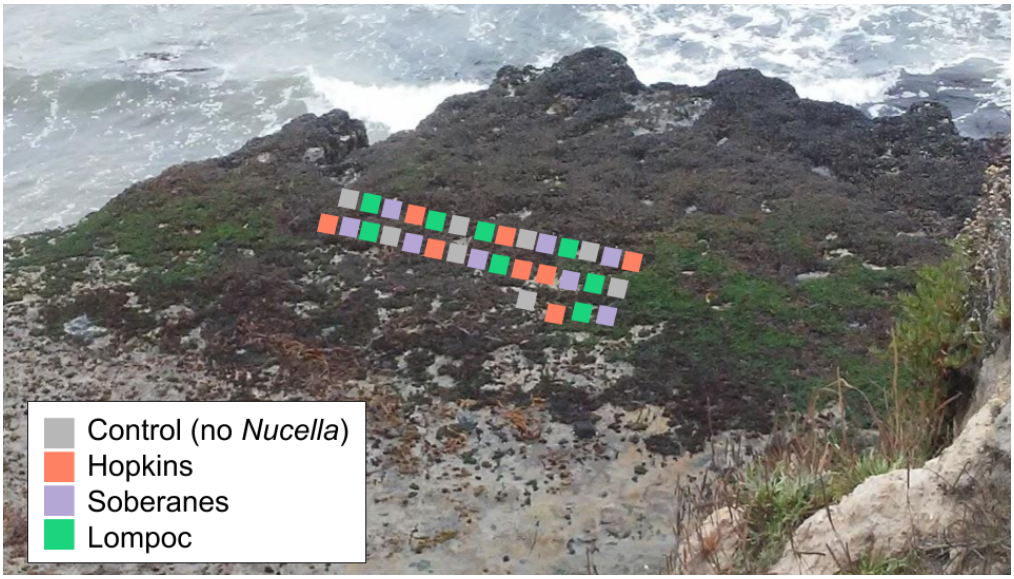

Figure A3.2. Diagram of cage array treatments

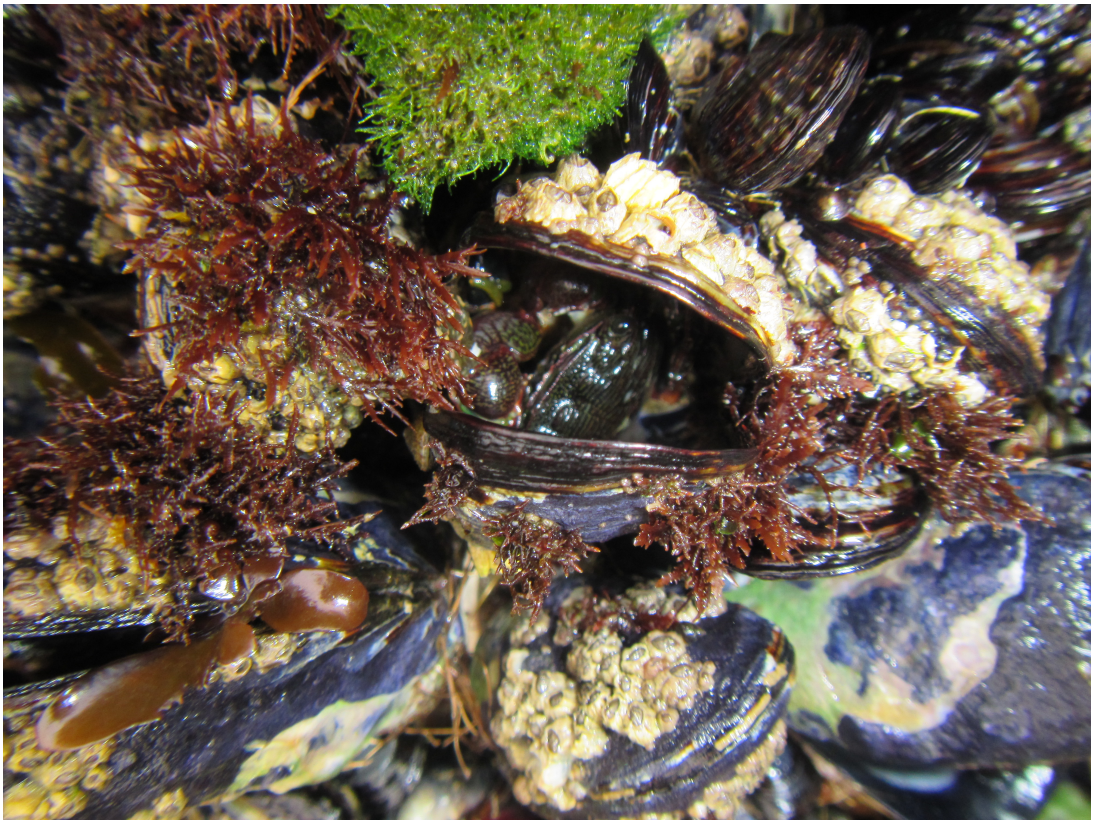

Figure A3.3. Large *P. crassipes* occupying an empty mussel shell as a result of *Nucella* predation

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