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Predator populations differ in their foraging responses to acute seawater acidification

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ABSTRACT: Local adaptation can cause predator populations to vary in traits and their effects on prey, but few studies have tested whether divergent predator populations respond differently to acute environmental stressors. We tested how *Nucella* dogwhelks from 3 populations with natural exposure to distinct environmental regimes in the California Current System altered consumption of mussel prey (*Mytilus californianus*) in ambient (pH 8.0, 429 µatm partial pressure of CO_2 [pCO_2]) and acidified (pH 7.6, 1032 µatm pCO_2) seawater. Overall, experimental acidification increased the variation in consumption time observed among populations. We found reduced consumption time for the population that experienced more frequent exposure to low pH conditions in nature but not for populations with less prior exposure. Exposure to acidification also altered the individual components of consumption time — search time and handling time — depending on source population. These results indicate that impaired predator performance is not a universal response to acidification, that predation responses to acute acidification can be population specific, and that individual population responses may relate to prior exposure. Our study highlights how population-specific responses to climate change can lead to differences in ecological effects that may restructure prey communities at local scales.

KEY WORDS: Intraspecific trait variation · Predator–prey interaction · Ocean acidification · Climate change · Contemporary evolution · Rocky intertidal

1. INTRODUCTION

A primary focus in ecology is to understand how predators can influence the structure of 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 & Palkovacs 2009, Schoener 2011). Effects of predator evolution on predator–prey interactions have been shown in aquatic systems, where fish predators diverge in feeding traits that 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 & 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 (McPhail 1993, 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 ample evidence that predator populations differ in foraging traits, few studies have tested whether populations respond differently to acute environmental stressors.

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

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in such conditions is poorly known (Kroeker et al. 2013, but see Calosi et al. 2017). In particular, decreasing seawater pH, or ocean acidification, can alter marine predator feeding traits by disrupting olfactory function (Nilsson et al. 2012). For example, acute exposure to low pH seawater can alter olfactory transduction-related gene expression and impair 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, Dixson et al. 2015, Pistevos et al. 2015, Jiahuan et al. 2018, Porteus et al. 2018). Acute acidification exposure also causes negative responses in invertebrate predators, such as increased handling time 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). However, not all organisms respond negatively to acidification (Clark et al. 2020). While it is established that the pH environment can shape the foraging traits of some predators, no studies have tested whether predator populations from different environmental regimes have different responses to low pH conditions.

Nucella ostrina-emarginata dogwhelks (hereafter *Nucella*) are a model system to study the effects of pH on population-specific changes in predator foraging traits. *Nucella* is a species complex of muricid gastropods commonly found in rocky intertidal zones in the California Current System (CCS). These animals are dioecious with internal fertilization. Females lay egg capsules, each containing dozens of eggs, and glue them to the substrate. After about 3 mo, metamorphosed larvae crawl away and begin exogenous feeding. Due to this life history, *Nucella* dogwhelks have very low dispersal and high neutral population genetic differentiation (Marko 1998, Contolini et al. 2020). Patterns of neutral population structure do not correspond with patterns of prey selectivity, suggesting that local adaptation rather than population history is the primary force shaping ecological divergence among *Nucella* populations (Sanford & Worth 2009, Contolini et al. 2020).

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 & Saleuddin 2000). In central California, *Nucella* consume *Mytilus californianus* mussels, which create expansive beds of biogenic habitat that support diverse communities, setting the stage for local differences in predation to have widespread community effects (Kanter 1977, Suchanek 1978, 1992). *Nucella* are calcified, drilling predators with calcified prey, making ocean acidification especially relevant to their feeding ability. In the CCS, *Nucella* populations exist across variable pH environments due to the heterogeneous oceanography and coastal geology of the region (Marko 1998, Dawson et al. 2014, Hofmann et al. 2014, Chan et al. 2017, Contolini et al. 2020). As intertidal animals, *Nucella* are adapted to extreme changes in abiotic conditions (Menge et al. 2015); therefore, *Nucella* populations that naturally experience different pH regimes may be locally adapted to pH conditions and exhibit different foraging responses to changes in pH.

We tested how *Nucella* dogwhelks from 3 populations altered their foraging traits when acutely exposed to low pH seawater. The 3 source populations varied in pH and temperature regimes including mean, SD, and their frequency of exposure to stressful pH and temperature events. We expected that acute exposure to low pH seawater would decrease *Nucella* foraging performance by increasing consumption time, including search and handling times, and cause them to choose smaller prey. However, we expected the effects of acute acidification to be less severe for populations naturally more exposed to low pH events.

2. MATERIALS AND METHODS

2.1. Study system

To test for population-level variation in predator foraging traits that could respond to acute exposure to low pH, we collected *Nucella* from 3 populations in central California that have naturally different environmental regimes: Hopkins in the Monterey Bay (36.62° N, 121.91° W); Soberanes on the open coast south of Monterey Bay (36.45° N, 121.93° W); and Lompoc, furthest south and just north of the major oceanographic boundary Point Conception (34.72° N, 120.61° W; Fig. 1). *In situ* pH loggers mounted in the mussel bed or offshore from these sites recorded pH and temperature during the upwelling season between 2011 and 2013. These loggers were Durafet®-based (Honeywell) sensors modified to be bolted to the bedrock. They recorded seawater pH and temperature in approximately 10 min intervals and were serviced and calibrated every 4 to 8 wk using certified reference material from Dr. Andrew Dickson's laboratory (Scripps Institute of Oceanography; Menge et al. 2015, Kroeker et al. 2016, Rivest et al. 2016, Chan et al. 2017). We compared the pH and temperature regimes among these sites using sensor

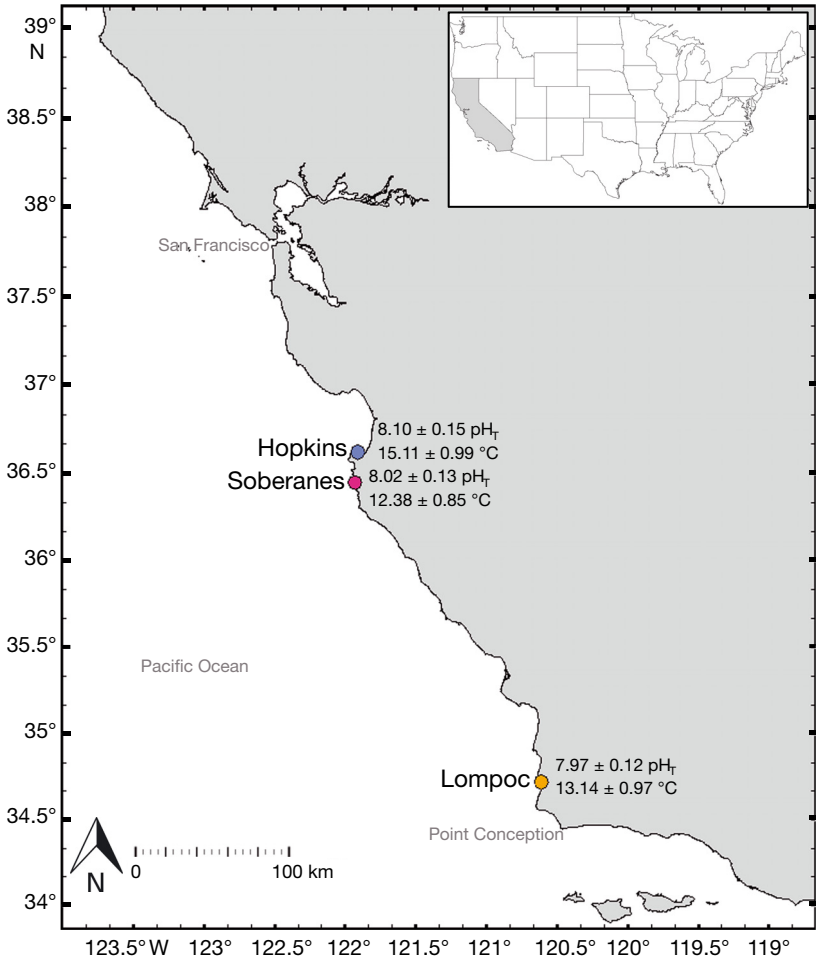

Fig. 1. Study populations in central California, USA, with total pH (pH$_T$) and temperature (°C) (mean ± SD) during upwelling season

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 (Lompoc; Rivest et al. 2016) datasets. We calculated metrics of pH such as the mean, median, minimum, maximum, SD, and frequency of pH 0.2 to 0.4 unit lower than the mean. Such low pH events are associated with biological effects and are useful metrics of not only pH stress but also the progression of ocean acidification in an area (Kroeker et al. 2016). Hopkins was characterized by the highest and most variable seawater pH; Soberanes by an intermediate mean, SD, and frequency of pH below 7.8 and the lowest minimum pH over the measured timeframe; and Lompoc by the lowest mean and SD pH and the highest frequency of pH below 7.8. We calculated seawater temperature metrics such as the mean, median, minimum, maximum, and 90th percentile. Hopkins had the highest mean, SD, and 90th percentile temperature; Lompoc was intermediate; and Soberanes had the lowest mean, SD, and 90th percentile temperature (Table 1, Table S1 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m646p069_supp.pdf; Hofmann et al. 2014, Kroeker et al. 2016, Contolini et al. 2020).

2.2. 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 Laboratory in January to March 2016. The system consisted of twelve 22.7 l (46 × 38 × 13 cm) bins that were paired and randomly assigned either ambient (ambient Santa Cruz seawater of pH ~8.0) or acidified (experimentally acidified to pH ~7.6; Fig. S2) seawater. 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 continuously bubbling 99.9% CO_2 gas into a separate recirculating tank of filtered ambient seawater, keeping it far below pH 7.6.

Table 1. Summary of pH conditions for each population, July through September. Hopkins and Soberanes data are from intertidal sensors in 2013 (Menge et al. 2015), and Lompoc data are from an offshore sensor (Purisima) 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), and Chan et al. (2017). SW: seawater

Population	pH		Freq pH	SW temp (°C)		
	Mean	SD	<7.8	Mean	SD	90th percentile
Hopkins	8.10	0.15	0.026	15.11	0.99	16.57
Soberanes	8.02	0.13	0.051	12.38	0.85	13.52
Lompoc	7.97	0.12	0.082	13.14	0.97	14.59

This water was then mixed with the ambient water to achieve the acidified treatment water of pH 7.6. Controllers (Universal Dual Analyzer, Honeywell) connected to Tris buffer-calibrated sensors (Durafet, Honeywell) 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 pH reached the 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 6 times in header barrels that each gravity-fed 2 bins containing animals (n = 12 bins). All bins experienced similar natural fluctuations in temperature, salinity, and light.

Temperature and pH in the header barrels were recorded from the Durafet sensors every 15 s. Temperature in each bin was recorded every 15 min using HOBO temperature loggers (Onset Computer Corporation). Salinity was measured every other day in all barrels and bins using handheld sensors (YSI, Oakton Instruments). Discrete water samples were collected once every 12th day (n = 5) from all header barrels and bins to check against the sensor measurements and analyzed following best practices for ocean CO_2 measurements (Dickson et al. 2007). We measured total pH (pH_T) at 25°C using a spectrophotometer (UV-1800, Shizmadzu) and total alkalinity using a Metrohm 815 Robotic USB Sample Processor XL and Titrando 905. Finally, we used CO2Calc to calculate pH at the temperatures experienced during the experiment using *K*1 and *K*2 constants from Hansson (1973) refit by Dickson & 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 7.99 ± 0.01 pH_T (429 ± 4.87 µatm partial pressure of CO_2 [pCO_2], mean ± SE) and the acidified treatment as 7.66 ± 0.01 pH_T (1032 ± 12.39 µatm pCO_2; Table 2). Neither temperature nor salinity of the bins differed between pH treatments (temperature: ambient 13.96 ± 0.04, acidified 13.93 ± 0.04°C, ANOVA, $F_{1,10} = 1.02$, p = 0.34; salinity: ambient 33.57 ± 0.01, acidified 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 S2).

2.3. Predation experiment

Adult *Nucella* 23.08 ± 2.25 mm (mean ± SD) in length were collected in mid intertidal mussel beds where mussel cover was 70 to 100% and *Nucella* were seen grappling or actively consuming California mussels. Collections were done on 9 November 2015 (Soberanes), 10 November 2015 (Hopkins), and 23 November 2015 (Lompoc). *Nucella* were held in an indoor laboratory in flowing, filtered, ambient seawater — the same pH 8.0 seawater used in the experiment — and fed local California mussels ad libitum, then starved 2 wk 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 and mass suspended in seawater (buoyant mass) were measured using an analytical balance. Wet mass was measured after squeezing closed the operculum and absorbing all water possible with a paper towel for 1 to 2 min. Buoyant mass reflects the in-water weight of only the shell since the body is neutrally buoyant (Palmer 1982). We estimated body mass by subtracting buoyant mass from total wet mass. This overestimates body mass since the shell weighs less in water than in air, so it was used as a comparison rather than an accurate measurement of body mass. We tested for differences in *Nucella* shell length, total wet mass, estimated body mass, and in-water shell mass (buoyant mass) using ANOVA. For all these vari-

Table 2. Seawater physiochemical properties from experimental bins during the 60 d experiment. Temperature was recorded by loggers every 15 min. Salinity was measured directly from treatments with a handheld sensor. All other carbonate chemistry parameters were measured from bottle samples taken every 12th day (n = 5) and analyzed following best practices for ocean CO_2 measurements (Dickson et al. 2007). Bottle pH values matched well with continuous pH measurements from Durafet sensors. Values are mean ± SE. pH_T: total pH; DIC: dissolved inorganic carbon; pCO_2: partial pressure of carbon dioxide

Treatment	pH_T	Temperature (°C)	Salinity (ppt)	Alkalinity (µmol kg^{-1})	DIC (µmol kg^{-1})	pCO_2 (µmol)
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

ables, data met model assumptions of normality and homogeneity of variance. Mean *Nucella* length, total wet mass, and estimated body mass did not differ significantly among populations, pH treatments, or bins (ANOVA, $F < 2$, $p > 0.1$), though mean in-water shell mass was slightly higher for Hopkins than Soberanes *Nucella* (1.06 ± 0.23 vs. 0.91 ± 0.28 g, ANOVA, $F_{2,169} = 4.0$, $p = 0.02$; Tables S3–S5).

We collected small (length 25.30 ± 1.45 mm), medium (39.97 ± 1.63 mm), and large (54.80 ± 1.81 mm) *Mytilus californianus* mussels from a single site in Santa Cruz, California (36.951° N, 121.043° W) to be used as prey and cleaned them of all epibionts. We placed 1 mussel of each size in a 11.43 × 9.53 × 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 1 wk.

We initiated the experiment by adding 1 *Nucella* predator to each basket (n = 173 *Nucella*). *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 3 populations — Hopkins, Soberanes, or Lompoc — that naturally experience different environmental regimes including pH regimes. The *Nucella* population was replicated 4 to 5 times per bin (depending on *Nucella* availability), and the arrangement of *Nucella* within bins was randomized (n = 14–15 baskets per bin; Fig. S2). 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. Bins were weighted with a cinder block to provide a close-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 the 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; n = 12). The experiment was terminated for each individual *Nucella* after it consumed 1 mussel. After 60 d, the experiment was terminated for all remaining *Nucella.*

2.4. 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 start handling). 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). To model 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 models reduced the degrees of freedom, we could not use censored regression models. Instead, 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. For significant main effects, we used post hoc Tukey's HSD tests to test which level pairs were significantly different. 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, to test if *Nucella* in the low pH treatment altered behaviors during acclimation, we compared the number of *Nucella* that drilled in the first 2 wk,

a common acclimation period, among pH treatments (Sanford et al. 2014, Sadler et al. 2018). 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 v. 3.6.1 using RStudio v. 1.1.463 (R Core Team 2017).

3. RESULTS

The final reduced model for consumption time included the main effects of pH treatment, population, and mussel size. Consumption time differed significantly among *Nucella* populations, where *Nucella* from Lompoc took significantly less time to consume a mussel than those from Hopkins (Tukey's HSD, p = 0.03; Table 3, Fig. 2a). Neither pH treatment nor mussel size was significantly related with consumption time ($F < 1.3$, $p > 0.30$).

Table 3. ANOVA (type III) on linear model for total consumption time. NA: not applicable. *Significant at α = 0.05 level

	SS	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

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 final reduced model for search time included the main effects of pH treatment, population, and their interaction. *Nucella* from Hopkins, the high temperature and pH site, increased search time in the acidified treatment, while those from Soberanes and Lompoc decreased (Table 4, Fig. 2b). The final reduced model for handling time included the 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 5, Fig. 2c). Namely, *Nucella* from Hopkins decreased handling time in the acidified treatment, those from Soberanes increased, and those from Lompoc remained relatively unchanged. Mussel size was also significant in this model, with large mussels on average requiring the longest handling time (9.1 ± 5.2 d, mean ± SD), then medium (5.9 ± 3.9 d), then small (3.2 ± 1.8 d; Tukey's HSD, $p < 0.01$ for all pairwise differences).

Table 4. Analysis of deviance (type III) on censored regression model for search time. LR χ^2: likelihood ratio chi-squared test. *Significant at α = 0.05 level

	LR χ^2	df	p
pH treatment	18.77	1	<0.001*
Population	17.95	2	<0.001*
pH treatment × Population	20.74	2	<0.001*

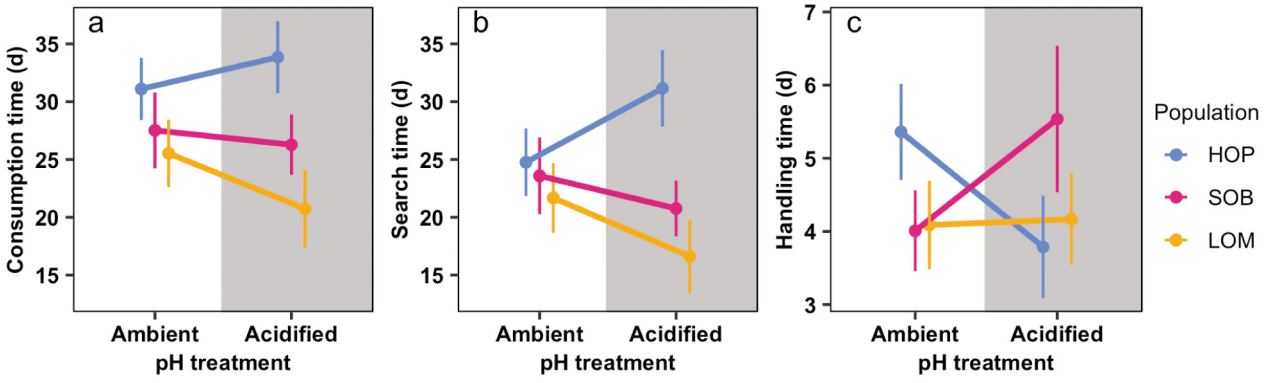

Fig. 2. Predation responses for each population (HOP: Hopkins; SOB: Soberanes; LOM: Lompoc) in each pH treatment. (a) Mean total consumption time (n = 137), (b) mean search time (n = 138), and (c) mean handling time (n = 137). Note the different scale for handling time. Points and error bars are mean ± SE of raw values. All data exclude *Nucella* that died (n = 14) and never started handling (n = 9). Consumption and handling times do not include *Nucella* that finished searching but not handling (n = 1)

Table 5. ANOVA (type III) on linear model for handling time. NA: not applicable. *Significant at α = 0.05 level

	SS	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

We did not detect differences in prey size selectivity among populations, pH treatment, or their interaction (Table S6, Fig. S3). We found no evidence of differential acclimation of *Nucella* among pH treatments, suggesting our results were not skewed by altered behaviors during acclimation to low pH. Of the *Nucella* that started drilling within the first 2 wk, 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 treatment became thinner and easier to handle, which would affect *Nucella* handling time (linear regression on time spent in acidified treatment before being attacked [search time] vs. thickness: within size classes, $r^2 < 0.01$, $p > 0.3$; among size classes, $r^2 = 0$, $p > 0.6$).

4. DISCUSSION

Environmental factors and evolutionary history can both play a role in determining predator foraging traits; however, variation in the foraging responses of different predator populations to ocean acidification has not been explored. We tested how *Nucella* from populations along an environmental gradient altered their foraging traits when acutely exposed to acidified seawater. Our results did not confirm the expectation that acute exposure to low pH seawater increases consumption time across all populations. Rather, we found that populations varied significantly in their foraging responses to acute acidification, and this was only somewhat related to prior exposure to low pH. Overall, feeding responses were generally more variable across populations under acidified relative to ambient conditions (Fig. 2). These results demonstrate that populations can display localized responses to global change drivers that will influence the outcomes of key ecological 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 (Fig. 2a). *Nucella* from Lompoc had the fastest consumption time, especially under acute seawater acidification. Adaptation to low pH is the most likely explanation for this result: Lompoc had the lowest mean pH and highest frequency of low pH events, which could lead to local adaptation to low pH. In contrast, adaptations to seawater temperature or local mussels are less plausible explanations. Seawater temperature at Lompoc was intermediate compared with the other sites, and mussels from Lompoc are on average thinner than those from the other sites, including those used in the experiment (G. M. Contolini unpubl. data). If Lompoc *Nucella* had feeding traits (e.g. radula morphology or acid composition) adapted for their local thin-shelled prey, we would expect Lompoc *Nucella* to take longer to consume the thick-experiment mussels.

Local adaptation to low pH could result in higher predation rates — perhaps if metabolism is increased to compensate for the higher energy costs of homeostasis (Beniash et al. 2010) — and greater consumption of foundational mussels, which could restructure the mussel bed community. Though the pH treatment by population interaction was not statistically significant for consumption time, there was a trend for *Nucella* from Hopkins to increase consumption time in the acidified treatment, while the other 2 populations decreased (Fig. 2a). Hopkins had on average relatively higher pH and temperature, so in this experiment it is not possible to discuss how these 2 environmental variables individually relate to the increased consumption time. Temperature and pH are often coupled in this way in the CCS due to upwelling. This result suggests that *Nucella* from populations exposed to less upwelling may be more likely to decrease predation rates under expected increases in upwelling (Bakun et al. 2015, Turi et al. 2016, Xiu et al. 2018), highlighting the context-dependent nature of the effects of climate change on predator–prey interactions.

To understand the mechanisms behind differences in total consumption time, we analyzed its 2 components: search and handling times. Search time contributed most to changes in consumption time — it was at least 3 times as long as handling time for all treatment combinations. Acidification can affect search time by altering chemosensory abilities (Ashur et al. 2017, Jiahuan et al. 2018, Draper & Weissburg 2019). However, 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 for *Nucella* with prior exposure. This hypothesis was somewhat confirmed. As expected, *Nucella* from the population experiencing naturally high pH, Hopkins, showed an increase in search time under acidified conditions; however, *Nucella* from the other populations did not (Fig. 2b). This result shows that impaired predator performance is not a universal response to acidification, and acidification can increase the variability in performance among predator populations (Clark et al. 2020).

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 smaller for *Nucella* that naturally experience lower pH. Our results showed that *Nucella* from the populations with intermediate to low pH regimes (Soberanes and Lompoc, respectively) increased or did not change handling time, but those from the site with higher pH (Hopkins) decreased. This unexpected finding could be the result of relative differences in temperature regimes between the experiment and each population's home site and the complex way temperature interacts with pH to alter traits (Tables 1 & S1, Fig. S1; Wood et al. 2010, Melatunan et al. 2011, Ivanina et al. 2013). For example, the mean temperature of the experiment was much cooler than the mean temperature at Hopkins and much warmer than the mean temperature at Soberanes, leading them to have divergent responses. However, as mean handling time was between 11 and 27% of total consumption time for any given population in any given treatment, it contributed little to the differences in total consumption time.

Our results add to an understanding of the effects of low pH on *Nucella* handling time. Previous research concerning *Nucella* feeding on *Mytilus trossulus* reported increased handling times when the dogwhelks were exposed to seawater at pH 7.5 and 12 to 13°C over 14 d using *Nucella* from a site with mean pH during the upwelling season of 8.00, mean temperature of 10.6°C, and frequency of pH <7.8 of 0.16 (Cerny-Chipman 2016). These findings align most closely with results from our population with a similar environmental regime, Soberanes, demonstrating an overall increase in handling time under acidified conditions. However, since our other populations showed no change or decreased handling time, 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 the responses of organisms to climate change (Barton 2011, Fryxell & Palkovacs 2017), but population-level responses are rarely considered in ocean acidification studies (Munday et al. 2009, Barton et al. 2012, Kroeker et al. 2014, Queirós et al. 2015, Lord et al. 2019). We found population-specific differences in how acute seawater acidification affected *Nucella* consumption time. Population-specific responses related to the abiotic regimes of source populations, including exposure to low pH conditions. Populations with different histories of exposure to pH and temperature conditions appear to exhibit different responses to acidification that may buffer them from the negative consequences of acidification. 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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