

Native predator chemical cues induce anti-predation behaviors in an invasive marine bivalve

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Abstract The ability of non-native prey to detect native predators and respond with effective anti-predation behaviors may be an important factor mediating invasion success and biotic resistance. However, our current understanding of how native predator cues influence invasive prey is greatly limited. In estuaries and coastal seas—among the most heavily invaded ecosystems—olfaction of chemical cues is a primary mechanism by which sessile and sedentary organisms evaluate predation risk. We tested the hypothesis that chemical cues from a suite of predators native to southern California, USA, estuaries induce anti-predation behaviors in an invasive bivalve, the Asian nest mussel *Arcuatula senhousia*. In a laboratory experiment, we manipulated chemical cues from injured conspecifics and a functionally and taxonomically diverse group of native predators that may represent important agents of biotic resistance. We then measured several potential anti-predation behaviors that may be key to *Arcuatula*

survival due to its modest structural defenses. As predicted, *Arcuatula* changed behaviors in response to cues from predators and injured conspecifics. Interestingly, however, *Arcuatula* was able to discriminate among cues from different native predators: mussels fed less when exposed to cues from snails and stingrays, burrowed deeper in the presence of cues from injured conspecifics and lobsters, and increased aggregation in response to snail cues. Our findings demonstrate that native predators can induce potentially-defensive behavioral changes in an invasive marine bivalve. The ability for *Arcuatula* to detect and selectively respond to novel predators may play a role in their invasion success in southern California and other regions globally.

Keywords Anti-predation behavior · Chemical cues · Estuary · Inducible defenses · Native predators · Olfaction

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Introduction

The success of biological invasions relies in part on the capacity of native communities to resist invaders (Elton 1958; Stachowicz et al. 1999; Cheng and Hovel 2010; Kimbro et al. 2013). A major component of biotic resistance is the ability of native predators to consume non-native prey (Maron and Vilà 2001; Grosholz 2010). Therefore, biotic resistance is likely

influenced by individual predator–prey interactions (Lima 2002; Sih et al. 2010), including the ability of prey to detect and respond to predator cues, which can strongly mediate predation risk (Sih 1985; Weissburg et al. 2002). Just as the naïveté of native prey to invasive predators can exacerbate native mortality (the ‘naïve prey’ hypothesis; Sih et al. 2010), the response of invasive prey to native predators may influence invader predation risk (Weissburg et al. 2002; Carthey and Banks 2014; Berthon 2015). If invasive prey are capable of responding with effective anti-predation behaviors to cues from novel (i.e., native) predators, they may have higher invasion success or cause greater ecological change in invaded ranges. While there has been a growing body of literature describing how native prey react to invasive predator cues (Carthey and Banks 2014; Berthon 2015), relatively little is known about how *invasive* prey respond to *native* predator cues and whether this process may mediate biotic resistance (Werner and Peacor 2003; Czarnofęski et al. 2010; Grason and Miner 2012; Naddafi and Rudstam 2013; Berthon 2015).

Across a diverse range of ecosystems, olfaction is a key process by which prey assess and avoid predation risk (Hay and Steinberg 1992; Apfelbach et al. 2005). Chemical cues are especially important to predator–prey interactions in marine and aquatic environments due to the fluid mechanics of water, ubiquity of dissolved chemicals, and frequency of low visibility (Wisenden 2000; Webster and Weissburg 2009; Hay 2009; Ferrari et al. 2010). For sessile and sedentary organisms, such as those commonly found in benthic marine, estuarine, and aquatic habitats, the ability to detect and respond to predator cues may be particularly important because of inherent limitations in avoidance strategies. Coastal seas and estuaries are also among the most heavily invaded ecosystems and invasion rates are accelerating in these biomes (Ruiz et al. 1999; Williams 2007).

Non-native suspension-feeding bivalves are excellent organisms for testing the effects of native predator cues on invasive prey because they are ubiquitous invaders of benthic habitats in marine, estuarine, and freshwater ecosystems (Sousa et al. 2009) and are often consumed by a diverse array of native predators (Robinson and Wellborn 1988; Reusch 1998; Ruesink et al. 2005). Furthermore, bivalves exhibit a host of anti-predation responses to predator cues that can improve the probability of survival. Many bivalves

rely on inducible defenses in the form of morphological changes, such as producing thicker shells (Leonard et al. 1999; Nakaoka 2000; Cheung et al. 2004), stronger adductor muscles (Reimer and Tedenren 1996), or additional, sturdier byssal threads that improve the strength of attachment to the substrate (Côté 1995; Leonard et al. 1999; Cheung et al. 2006; Garner and Litvaitis 2013; Naddafi and Rudstam 2013). Bivalves also utilize behavioral strategies to avoid predation, including burrowing deeper into the sediment (Lin 1991; Griffiths and Richardson 2006; Flynn and Smee 2010), aggregating with conspecifics (Côté and Jelnikar 1999; Nicastro et al. 2007; Naddafi and Rudstam 2013), or reducing feeding, which can decrease the exposure of soft tissues and reduce chemical signaling to predators (Smee and Weissburg 2006a, b; Naddafi and Rudstam 2013). Bivalves and other prey species are commonly sensitive to chemical cues from particular predators, in which case they often adjust their defenses based on predator feeding mode (e.g., drilling vs. crushing), predator diet (Cheung et al. 2006), and perceived threat level (Palmer et al. 1982; Smith and Jennings 2000; Cheung et al. 2004). Many bivalves are also able to evaluate predation risk using ‘alarm cues’ associated with chemical effluent from injured conspecifics (Smee and Weissburg 2006b; Nicastro et al. 2007; Garner and Litvaitis 2013).

We tested the hypothesis that native predator chemical cues induce anti-predation behaviors in an invasive marine bivalve, the Asian nest mussel *Arcuatula* (previously *Musculista*) *senhousia* (hereafter referred to as *Arcuatula*; Benson in Cantor 1842). *Arcuatula* is a shallow-burrowing mytilid native to sandy and muddy benthic environments in shallow bays and estuaries of eastern Asia. Although diminutive (≤ 28 mm shell length), *Arcuatula* is fast growing, prolific, and gregarious (Crooks 1996), and is commonly found in densities of thousands of adults m^{-2} and sometimes exceeding 10,000 adults m^{-2} (Dexter and Crooks 2000; Williams et al. 2005). We suspected that *Arcuatula* might exhibit inducible anti-predation behaviors because of its modest structural defenses (i.e., small size and thin shell) and high predator-induced mortality rates (Reusch 1998; Kushner and Hovel 2006; Cheng and Hovel 2010; Castorani and Hovel 2015). In a laboratory experiment, we manipulated chemical cues from injured *Arcuatula* conspecifics and a functionally and taxonomically diverse

group of native predators that may represent important agents of biotic resistance, and measured the response through time of several key behaviors that may be important to reducing predation risk.

Methods

Study species

Arcuatula is a highly successful invasive species with introduced ranges in Australia, New Zealand, the Mediterranean Sea, and the Pacific Coast of North America (Crooks 1996 and references therein). In southern California, where we conducted our study, *Arcuatula* was first observed in the 1960s (MacDonald 1969) and is presently the most abundant bivalve in intertidal and shallow-subtidal soft-sediment habitats at several estuaries (Crooks 1998b, 2001; Dexter and Crooks 2000; M.C.N.C. personal observation). Introduction of *Arcuatula* has been a concern for scientists, managers, and conservation practitioners because it has been implicated in changes to assemblages of native bivalves and other infauna (Crooks 1998a, b, 2001; Reusch and Williams 1998; Crooks and Khim 1999; Dexter and Crooks 2000; Castorani and Hovel 2015), and because it may negatively affect habitat-forming seagrass (Reusch and Williams 1998).

Despite its strong invasion success, *Arcuatula* is highly vulnerable to predation by a suite of predators native to southern California, including gastropods, crustaceans, demersal fishes, and wading shorebirds (Reusch 1998; Crooks 2002; Kushner and Hovel 2006; Cheng and Hovel 2010; Castorani and Hovel 2015). We chose to examine the effects of chemical cues from three of the most abundant known predators of *Arcuatula* native to this region: the festive murex *Pteropurpura festiva* (a drilling snail), the spiny lobster *Panulirus interruptus*, and the round stingray *Urolophus halleri* (Reusch 1998; Crooks 2002; Cheng and Hovel 2010; M.C.N.C. unpublished data).

Field collections

We conducted our study with sediments and organisms collected from two estuaries in San Diego, California, USA: Mission Bay (32°46'N, 117°14'W) and San Diego Bay (32°43'N, 117°11'W). Both estuaries have typical Mediterranean seasonality in temperature

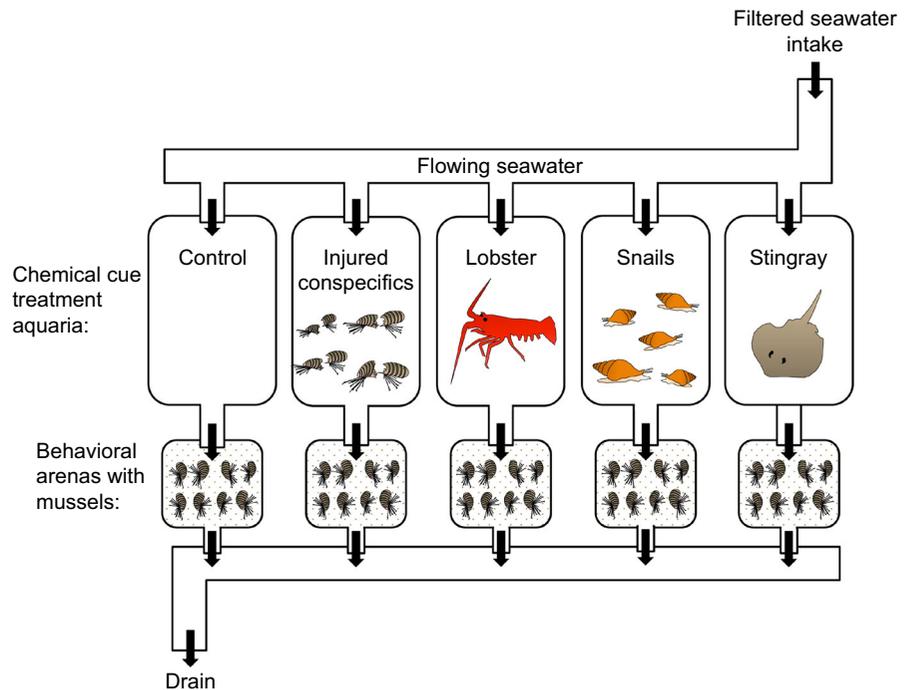
(~14–25 °C) and salinity (~32–36 PSU), with winter freshwater inflow and hypersalinity during long, dry summers (Largier et al. 1997). In April 2012, we excavated beach sand from intertidal areas in Mission Bay where *Arcuatula* is found, sieved sediments to remove fauna larger than 5 mm, and homogenized sediments by hand. Prior to being used in trials, sediment was stored under flow-through seawater in the dark at the San Diego State University Coastal and Marine Institute Laboratory (CMIL) in San Diego.

We gathered *Arcuatula* [27.1 ± 2.7 (SD) mm shell length; 0.15 ± 0.05 g dry of soft tissue per mussel] and predatory snails (*P. festiva*) by hand from intertidal areas in Mission Bay. We collected adult lobsters (*P. interruptus*) and adult stingrays (*U. halleri*) from San Diego Bay using commercial lobster traps. We kept all mussels and predators under flow-through seawater at CMIL for 2 weeks prior to the beginning of each sequential behavioral trial. While in captivity we fed lobsters and stingrays a diet of commercially-available frozen California squid (*Doryteuthis opalescens*) and fed snails a diet of California mussels (*Mytilus californianus*). A pilot study demonstrated that *Arcuatula* exposed to lobster cues behaved similarly regardless of lobster diet (starved or fed squid, California mussels, or *Arcuatula*; M.C.N.C. unpublished data). Still, to avoid possible conflation between predator identity and diet, we starved all predators for 72 h before the start of each trial.

Experimental design and laboratory set-up

To test the hypothesis that chemical cues from native predators and injured conspecifics alter *Arcuatula* behaviors, we conducted a laboratory experiment at CMIL using a randomized complete block design. Our approach was to perform a series of sequential behavioral trials ($n = 7$ blocks) in which we observed *Arcuatula* for changes through time in three potential anti-predation behaviors in response to exposure with seawater that was unmanipulated (i.e., 'control') or impregnated with chemical cues from injured conspecifics or one of three native predators (see Fig. 1 for conceptual diagram). In each replicate trial, we randomly assigned one of each of the five chemical cue treatments to separate aquaria, measured the response of a dozen *Arcuatula* within each aquarium, and then calculated the collective (i.e., aquarium-scale) behavioral response through time.

Fig. 1 Conceptual diagram of the experimental set-up. Flowing seawater entered each chemical cue treatment aquaria then flowed into the behavioral arenas, which contained sediment and mussels (12 per arena). The number and size of organisms are for illustrative purposes only and not drawn to scale



Our experimental set-up consisted of five 75 l opaque polyethylene ‘chemical cue aquaria’ (61 cm × 40 cm × 31 cm height) that were supplied with flowing filtered seawater (60 ml s⁻¹; ~18 °C) pumped from San Diego Bay. Seawater then flowed (14 ml s⁻¹) through a small nozzle at the bottom of each chemical cue aquarium into separate 9 l clear glass ‘behavioral arena aquaria’ (28 cm × 16 cm × 20 cm height), each of which contained a 5 cm layer of sediment and 12 *Arcuatula* for observation. Seawater gently overflowed behavioral arenas and drained onto a seawater table. The entire experimental set-up was housed in a sound-insulated, constant air-temperature (20 °C), light-controlled room with light–dark cycles set to local conditions.

Behavioral trials

Before initiating each trial ($n = 7$ sequential trials), we ensured that seawater flow rates were equal among all five chemical cue aquaria. We added a 5 cm layer of sediment at the bottom of each empty behavioral arena aquarium and allowed the sediment to stabilize overnight. Next, we transferred 12 *Arcuatula* to the bottom of each behavioral arena in a Cartesian grid with equal spacing among all individuals. We allowed

24 h for mussels to establish because a pilot study indicated that this amount of time was sufficient for transplanted mussels to burrow, attach byssal threads, and resume feeding (M.C.N.C. unpublished data).

We commenced all behavioral trials the following evening (16:00), when our nocturnal predators (lobsters and stingrays) tend to increase foraging (Tegner and Levin 1983; Vaudo and Lowe 2006). We randomly assigned each chemical cue aquarium one of five treatments: (1) control (empty), (2) injured conspecifics, (3) lobster (1 individual, ~8 cm carapace length), (4) snails (20 individuals), or (5) stingray (1 individual, ~15–20 cm diameter). We chose a higher abundance of snails to compensate for their small size (mean shell length = 5 cm) and because this predator aggregates in patches of *Arcuatula* in situ (Kushner and Hovel 2006; Castorani and Hovel 2015). For the injured conspecifics treatment, we simulated predation to *Arcuatula* by a crushing predator (such as lobsters and stingrays) by introducing 30 mussels (~4.4 g dry of soft tissue) to the chemical cue aquarium and immediately crushing them using a pestle. We selected this abundance of crushed mussels because predation on *Arcuatula* in invaded ranges by native snails, crustaceans, and fishes is relatively intense, even at high *Arcuatula* densities (Reusch

1998; Kushner and Hovel 2006; Cheng and Hovel 2010; Castorani and Hovel 2015).

Throughout the course of each trial, we monitored all *Arcuatula* for three activities that are known to be chemically-inducible anti-predation behaviors in other marine bivalves: cessation of feeding (to reduce detection by predators; Smee and Weissburg 2006a, b), burrowing (to avoid predators; Lin 1991; Griffiths and Richardson 2006; Flynn and Smee 2010), and aggregating (to create a safety-in-numbers effect; Côté and Jelnikar 1999; Nicastro et al. 2007). We measured feeding behavior as the proportion of mussels suspension feeding (i.e., valves gaped and siphons extended). We assessed burrowing activity in the form of burial depth, visually estimated (to the nearest 5 %) as the mean percentage of the shell exposed above the sediment–water interface. Lastly, we characterized aggregation behavior as the mean estimated nearest neighbor distance between mussels (this was a relative measure of aggregation because we estimated nearest neighbor distance noninvasively using calipers at a constant height level with the top of the arena and just above the water surface). We measured *Arcuatula* behaviors just after applying treatments (‘0 h’) and 0.5, 1, 2, 24, and 48 h subsequently. Following each behavioral trial and before beginning the next trial, we disposed of sediments and thoroughly cleaned, rinsed (under flowing seawater for 72 h), and randomized the arrangement of all aquaria. Mussels and predators were not reused among separate trials.

Statistical analyses

We chose an information-theoretic approach to simultaneously determine the strength of evidence supporting multiple statistical models that we specified a priori (Burnham and Anderson 2002). We examined changes in each response variable separately using random-intercept linear mixed-effects models (LMMs), with chemical cue treatment and time of observation (fixed factors) nested within behavioral trial (a blocked random factor). For each response variable, we generated a set of eight LMMs (see Table 1) by factorially varying (1) the presence or absence of each fixed effect, (2) the presence or absence of a fixed-effects interaction term (in the case of two fixed factors), and (3) including or excluding autoregressive temporal correlation in the covariance structure (using a first-order autoregressive [AR(1)]

process, in which the autocorrelation lag = 1 time step), which accounts for non-independent repeated measures taken from the same behavioral arena through time.

We analyzed models using the package ‘nlme’ (Pinheiro et al. 2014) in R 3.1.2 (R Core Team 2014) and selected the most parsimonious models based on comparisons of Akaike information criterion values corrected for sample size bias (AIC_C) to optimize goodness-of-fit but avoid model overfitting (Hurvich and Tsai 1989; Aho et al. 2014). Because the only factors to vary among models were fixed, we calculated AIC_C values by the maximum-likelihood method (Pinheiro and Bates 2000; Zuur et al. 2009) using the R package ‘AICcmodavg’ (Mazerolle 2014). We ranked models based on delta- AIC_C values (a measure of the strength of evidence of each model relative to the best model, which has the lowest AIC_C value; $\Delta_i = AIC_{C,i} - AIC_{C,\min}$)—and considered $\Delta_i < 2$ to indicate substantial model support, $4 < \Delta_i < 7$ to indicate considerably less support, and $\Delta_i > 10$ to indicate very low support for model i (Burnham and Anderson 2002). We report model comparisons as Δ_i , Akaike weights (the probability that model i is best among all candidate models; $w_i = (e^{-\Delta_i/2}) / \sum_{i=1}^R [e^{-\Delta_i/2}]$), and evidence ratios for the best model relative to each other model i (w_{\max}/w_i), given the set of candidate models and data (Burnham and Anderson 2002).

To further evaluate the goodness-of-fit of competing models, for each response variable we used likelihood ratio tests to compare the most parsimonious model (based on Δ_i) with all possible nested models (e.g., models containing one fixed effect only or an intercept-only null model; Zuur et al. 2009). After selecting the best model for each response variable by comparisons of Δ_i and likelihood ratio tests, we performed an omnibus test of model terms using analysis of variance (ANOVA; Underwood 1997) with denominator degrees of freedom calculated by the Satterthwaite method (Pinheiro and Bates 2000; Pinheiro et al. 2014). Where ANOVAs revealed significant treatment effects, we tested whether each experimental treatment differed from the control treatment using Dunnett’s test (Dunnett 1955) and report model coefficients \pm 95 % confidence intervals.

We also describe overall temporal trends. To visualize the results, at each time point within each trial we calculated the difference between the value measured in the control treatment and values measured in each experimental treatment. Because there

Table 1 Delta-AIC_C values (Δ_i), Akaike weights (w_i), and evidence ratios (w_{max}/w_i) from comparisons of general linear mixed-effects models (random effect of trial not shown) as a function of the response variable analyzed

Model number and factors	Response variable								
	Feeding			Burrowing			Aggregating		
	Δ_i	w_i	(w_{max}/w_i)	Δ_i	w_i	(w_{max}/w_i)	Δ_i	w_i	(w_{max}/w_i)
No temporal autocorrelation in covariance structure									
Treatment	47.92	<0.01	>88	193.62	<0.01	>93	106.48	<0.01	>85
Time	21.36	<0.01	>88	185.72	<0.01	>93	125.00	<0.01	>85
Treatment, time	5.16	0.07	12.6	158.10	<0.01	>93	105.18	<0.01	>85
Treatment, time, (treatment \times time)	12.16	<0.01	>88	159.22	<0.01	>93	111.55	<0.01	>85
Temporal autocorrelation [AR(1)] in covariance structure									
Treatment	37.35	<0.01	>88	86.46	<0.01	>93	5.62	0.05	17.0
Time	7.30	0.02	44	18.68	<0.01	>93	7.35	0.02	42.5
Treatment, time	0	0.88	1	0	0.93	1	0	0.85	1
Treatment, time, (treatment \times time)	7.15	0.02	44	5.04	0.07	13	4.78	0.08	10.6

For each response variable, the best model is shown in boldface type

was very weak support for a treatment \times time interaction (see “Results” section; Table 1), for each experimental treatment we then calculated the average relative response (difference from the control) over time for each trial, and generated mean and 95 % confidence intervals among replicate trials.

Before constructing LMMs, we determined normality of the residuals using normal probability plots and homoscedasticity of the residuals by visually examining the relationship between residuals and fitted values, and by using Cochran’s test for homogeneity of variances (Cochran 1941; Underwood 1997). We used a logit transformation ($\log[x/(1-x)]$) for the proportion of mussels feeding and a log transformation ($\log[x+1]$) for estimated nearest neighbor distances to meet the assumptions of our parametric analyses (Underwood 1997; Warton and Hui 2011).

Results

Model selection

Chemical cues from native predators and injured conspecifics induced *Arcuatula* behaviors that are generally associated with reduced bivalve predation risk (Tables 1, 2; Figs. 2, 3, 4). For each potential anti-

predation behavior we measured, comparisons of delta-AIC_C values (Δ_i) clearly indicated the parsimony of a single model that included chemical cue treatment and time of observation without an interaction of these fixed effects ($w_i \geq 0.85$; for less parsimonious competing models, $\Delta_i \geq 4.78$ and $w_i \leq 0.08$; Table 1). Including AR(1) autocorrelation in the covariance structure greatly improved model parsimony for all behaviors (for less parsimonious competing models, $\Delta_i \geq 5.16$, $w_i \leq 0.07$; Table 1), indicating a very high likelihood that anti-predation behaviors were temporally autocorrelated. In other words, the proportion of mussels feeding, depth of burrowing, and degree of aggregating at a given point in time were not independent of the previous point in time. Likelihood ratio tests comparing full and nested models confirmed the superiority of a single full model for all response variables (likelihood ratio > 7.82 ; $P < 0.0052$). Because behaviors changed through time similarly for all chemical cue treatments, we focus here on temporally-averaged relative responses (differences from the control; see “Methods” section) and overall temporal trends.

Feeding behavior

When exposed to chemical cues from stingrays and snails, *Arcuatula* reduced feeding activity relative to

mussels in the control treatment, with the trend being slightly weaker for snails than for stingrays (Fig. 2; Table 2; ANOVA, $F = 4.37, P = 0.0021$). Exposure to cues from injured conspecifics or lobsters, on the other hand, elicited no change in feeding activity (Fig. 2; Table 2). Among all treatments, the proportion of mussels feeding declined during the course of each 48 h trial by $\sim 20\text{--}30\%$ (see Table 2 for effect size estimates).

Burrowing behavior

Chemical cues from injured conspecifics and lobsters increased *Arcuatula* burrowing activity (i.e., reduced shell exposure above the sediment) relative to mussels in the control treatment (Fig. 3; Table 2; ANOVA, $F = 8.42, P < 0.0001$). By contrast, cues from snails and stingrays had no effect on mussel burial (Fig. 3; Table 2). Among all treatments, shell exposure decreased during the course of each 48 h trial by $\sim 10\%$, indicating that, overall, mussels were slowly burrowing deeper into the sediment (Table 2).

Aggregating behavior

Exposure to chemical cues from snails enhanced *Arcuatula* aggregation (i.e., reduced mean estimated nearest neighbor distance) relative to mussels in the control treatment (Fig. 4; Table 2; ANOVA, $F = 4.23, P = 0.0027$). Cues from injured conspecifics, lobsters, and stingrays had little impact on aggregation (Fig. 4; Table 2). Among all treatments, nearest neighbor distances increased slightly during the course of each 48 h trial by $\sim 1\text{--}3\text{ mm}$, suggesting that mussels were generally dispersing away from each other (Table 2).

Discussion

We have demonstrated that chemical cues from a suite of native predators induce potential defensive behaviors in an invasive marine bivalve. Olfaction is a key way for bivalves and other prey to evaluate predation risk (Hay and Steinberg 1992; Apfelbach et al. 2005; Ferrari et al. 2010) and, as predicted, *Arcuatula* changed its feeding, burrowing, and aggregating behaviors in response to chemical cues from injured conspecifics and three prominent predators native to

Table 2 Estimated model coefficients ($\pm 95\%$ confidence intervals; CIs) for time and experimental treatments (relative to the control treatment) from the best models indicated in Table 1

Factors	Response variable								
	Feeding (logit transformed)			Burrowing			Aggregating (log transformed)		
	Coefficient	95 % CI	P	Coefficient	95 % CI	P	Coefficient	95 % CI	P
Time (units h^{-1})	-0.028	-0.037 to -0.020		-0.21	-0.25 to -0.17		1.2×10^{-3}	3.7×10^{-4} to 2.1×10^{-3}	
Crushed mussels	-0.58	-1.2 to -6.9×10^{-3}	0.14	-9.6	-14 to -4.9	<0.001	-0.10	-0.020 to -5.3×10^{-3}	0.11
Spiny lobster	0.24	-0.33 to 0.81	0.81	-9.1	-14 to -4.6	<0.001	0.028	-0.066 to 0.12	0.93
Festive murex	-0.64	-1.2 to -0.077	0.078	-2.3	-6.7 to 2.0	0.64	-0.12	-0.22 to -0.031	0.027
Round stingray	-0.71	-1.3 to -0.14	0.044	-1.8	-6.5 to 2.8	0.84	-0.029	-0.13 to 0.069	0.93

Units for each response variable are shown in parentheses. P values indicate results of Dunnett's tests comparing experimental treatments to the control treatment. P values <0.05 are shown in boldface type

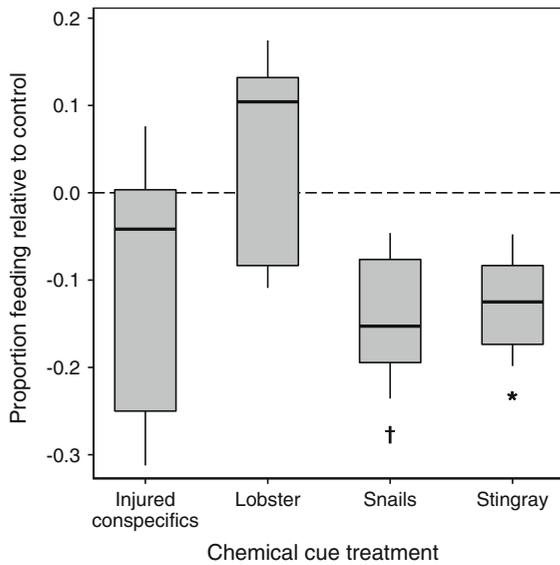


Fig. 2 Box plot of the proportion of mussels feeding in experimental chemical cue treatments relative to those in the control treatment. Data have been averaged across multiple observations through time and, therefore, depict variation among replicate trials. For each trial, differences between each experimental treatment and the control treatment were calculated at each time point of observation and averaged because there was very weak support for a treatment \times time interaction (see “Results” section; Table 1). Grey boxes and horizontal lines show interquartile ranges and median values, respectively. Vertical lines extending above and below boxes depict 95 % confidence intervals. Asterisks and daggers indicate $P < 0.05$ and $P < 0.1$, respectively, by Dunnett’s test comparing experimental treatments to the control treatment using the best model (see “Results” section; Table 1). Because statistical analyses were conducted on the full model, the 95 % confidence intervals depicted do not necessarily correspond to significance by Dunnett’s test

southern California. Therefore, introduced *Arcuatula* are not naïve to the threat of predation from native lobsters, drilling snails, or stingrays, which are among the most important agents of biotic resistance in San Diego estuaries (Reusch 1998; Crooks 2002; Cheng and Hovel 2010; M.C.N.C. unpublished data).

Our study adds to a small but growing body of work illustrating adaptive behavioral plasticity of invasive prey in response to chemical cues from native predators. Similar to our findings, invasive oyster drills (*Ocenebrina inornata* and *Urosalpinx cinerea*) spend more time hiding and less time feeding in the presence of cues from native crabs (*Cancer productus*; Grason and Miner 2012). Likewise, non-native zebra and quagga mussels (*Dreissena* spp.) aggregate when

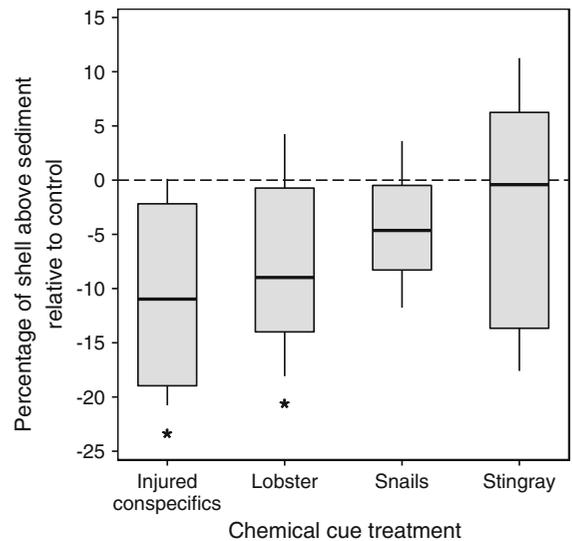


Fig. 3 Box plot of the mean percentage of mussel shells exposed above the sediment surface in experimental chemical cue treatments relative to those in the control treatment. See Fig. 2 for explanation

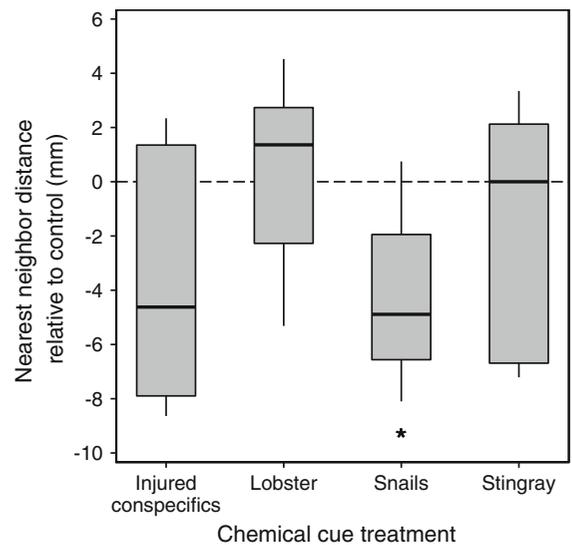


Fig. 4 Box plot of the mean estimated nearest neighbor distance among mussels in experimental chemical cue treatments relative to those in the control treatment. See Fig. 2 for explanation

exposed to native predator chemical cues (Naddafi and Rudstam 2013). On the other hand, European mussels (*Mytilus galloprovincialis*) introduced to South Africa are naïve to cues from native lobsters (Nicastro et al. 2007). The ability of invasive prey to

detect native predators and respond with effective anti-predation behaviors may be an important factor mediating native predation, biotic resistance (Sih 1985; Maron and Vilà 2001; Weissburg et al. 2002; Lima 2002; Grosholz 2010), and subsequent invasion success (Stachowicz et al. 1999; Kimbro et al. 2013). However, more research is needed to determine the mechanisms underpinning how invasive prey detect and respond to cues from novel native predators, and whether variation in this process mediates invasion success and biotic resistance (Werner and Peacor 2003; Czarnoński et al. 2010; Naddafi and Rudstam 2013).

Behavioral responses to chemical cues from injured conspecifics

In response to cues from injured conspecifics, *Arcuatula* burrowed deeper into the sediment. This finding is consistent with other studies indicating that alarm cues from dead or injured conspecifics can invoke potential anti-predation behaviors in bivalves, such as suppressed feeding (Smee and Weissburg 2006b), reduced mobility (Czarnoński et al. 2010), and increased aggregating (Nicastro et al. 2007). Similar observations have been made for a diverse range of other taxa (Chivers and Smith 1998; Katz and Dill 1998; Ferrari et al. 2010) but rarely in the context of invasive prey species (but see Grason and Miner 2012).

However, feeding and aggregation of *Arcuatula* in the presence of cues from injured conspecifics were no different than those of mussels in control arenas. While this observation may be surprising, it agrees with previous investigations showing that some bivalve taxa react strongly to cues from predators but not from injured conspecifics (Griffiths and Richardson 2006). By contrast, other invasive marine species such as mussels (Nicastro et al. 2007) and whelks (Grason and Miner 2012) respond stronger to cues from injured conspecifics rather than to cues from novel native predators. It is also possible that the generally modest behavioral responses of *Arcuatula* to conspecific alarm cues may have been an artifact of our experimental design because the strength of anti-predation responses is often related to the concentration of conspecific cues or the biodegradation of cues through time (reviewed in Ferrari et al. 2010).

Predator-specific behavioral responses

The ability for prey to interpret chemical information from specific predators and selectively modulate their anti-predation behaviors is a widespread phenomenon (Wudkevich et al. 1997; Smee and Weissburg 2006a, b; Bourdeau et al. 2013). Indeed, it appears that *Arcuatula* is able to discriminate among cues from different native predators. Spiny lobster (*Panulirus interruptus*) cues had little effect on feeding or aggregating. This was surprising because spiny lobsters are the main predator of *Arcuatula* in parts of some southern California estuaries (Cheng and Hovel 2010). However, lobsters triggered an increase in burial depth comparable to that caused by cues from injured conspecifics. Lobsters and other predatory crustaceans can easily excavate *Arcuatula* and other small, surface-dwelling bivalves from soft sediments (M.C.N.C. personal observation). It is possible that small increases in burial reduce detection by or mortality from digging predators, as has been documented for ribbed mussels (*Geukensia demissa*) attacked by blue crabs (*Callinectes sapidus*; Lin 1991). Similarly, some clams and cockles (*Macoma balthica* and *Cerastoderma edule*, Griffiths and Richardson 2006; *Mya arenaria*, Flynn and Smee 2010) increase burial in response to effluent from green crabs (*Carcinus maenas*). Within seagrass meadows, where *Arcuatula* are often found, burrowing only a few millimeters deeper may place mussels below the depth of roots and rhizomes, conferring structural protection or crypsis. However, physiological constraints (e.g., siphon length) limit the depths to which *Arcuatula* and other shallow-dwelling bivalves can remain burrowed for extended periods of time when confronted by a predatory threat (Griffiths and Richardson 2006; Smee and Weissburg 2006a, b; Flynn and Smee 2010).

Cues from drilling snails (*P. festiva*) and stingrays (*U. halleri*) had weak influences on burrowing but suppressed the proportion of mussels feeding. Drilling snails can be superior trackers of prey scent relative to other predators (Smee and Weissburg 2006b) and elasmobranchs are well known for their olfactory sensitivities (Meredith and Kajiura 2010), whereas spiny lobsters have modest attraction to uninjured mussels (*Mytilus californianus*; Zimmer-Faust and Case 1982). Because of the fitness costs associated with cessation of feeding, it is possible that *Arcuatula*

reduced suspension feeding in the presence of cues from snails and stingrays, but not lobsters, to reduce their signals to only for the most chemically sensitive predators. The ability of *Arcuatula* to discern cues among native predators and regulate feeding accordingly echoes observations of hard clams (*Mercenaria mercenaria*) that cease feeding in the presence of predatory whelks (*Busycon carica*) but not blue crabs, because whelks are superior trackers of clam scent in high flow environments (Smee and Weissburg 2006a, b).

Chemical cues from snails also induced changes to *Arcuatula* aggregation relative to the control treatment. Analogously, blue mussels (*Mytilus edulis*) aggregate more quickly and form more clumps in response to chemical cues from European lobsters (*Homarus gammarus*), probably through chemotaxis (Côté and Jelnikar 1999). Tradeoffs in growth and reproduction may confer benefits to solitary behavior in the absence of predatory threats (Fréchette et al. 1992; Stiven and Gardner 1992). In the presence of predators, however, aggregation can increase the per capita likelihood of survival (Hamilton 1971) and this ‘safety-in-numbers’ phenomenon has been observed in intertidal mussels (Bertness and Grosholz 1985). The consumption rate of *Arcuatula* by *P. festiva* decreases with increasing *Arcuatula* density (i.e., a Type II functional response) within seagrass meadows (Kushner and Hovel 2006). Thus, *P. festiva* may satiate on *Arcuatula* in high densities and thereby incentivize aggregative behavior. While this may explain why *Arcuatula* aggregates in the presence of cues from *P. festiva*, further research is needed to determine why cues from other native predators did not elicit a similar aggregative response. Solitary behavior may be favored where aggregating increases detectability by predators (Ferrari et al. 2010), and this could be the case for *Arcuatula* exposed to cues from lobsters and stingrays.

Evolutionary history, the ‘naïve prey’ hypothesis, and invasion success

The ‘naïve prey’ hypothesis predicts that prey lacking an evolutionary history with their predators will suffer greater predation rates because of their inability to produce effective anti-predation responses (Nicastro et al. 2007; Sih et al. 2010; Carthey and Banks 2014; Berthon 2015). *Arcuatula* does not have a long

evolutionary history with any of the specific predators used in our study (it is believed that *Arcuatula* was introduced to southern California in the 1960s; MacDonald 1969). Strong and consistent selective pressure by invasive predators can drive rapid evolution of anti-predation behaviors in native prey (Thompson 1998; Yoshida et al. 2003; Nunes et al. 2014). Given their high vulnerability to predation (Kushner and Hovel 2006; Castorani and Hovel 2015), it is possible that introduced *Arcuatula* have evolved relatively rapidly (less than ~50 year, or ~25–50 generations; Crooks 1996) the ability to detect cues from novel native predators. On the other hand, in their native range *Arcuatula* co-occurs with many taxonomically-similar predators: the ornate spiny lobster *Panulirus ornatus* (a congener of *P. interruptus*), muricid snails (Muricidae) including *Pteropurpura* spp., and many species of rays and skates, including *Urolophus* spp. (Ponder and Vokes 1988; Michael 2005). If chemical cues are relatively consistent within these genera due to taxonomic similarity (Sih et al. 2010) or *Arcuatula* utilizes broad behavioral anti-predation strategies, *Arcuatula* may be ‘pre-adapted’ to detecting cues from a wide range of native predators in invaded ranges (Payne et al. 2004). The ability and plasticity of invasive species to recognize and respond to native consumers may have important implications for invasion success and the potential for biotic resistance (Weissburg et al. 2002; Payne et al. 2004; Sih et al. 2010), but this hypothesis is largely unexplored (Werner and Peacor 2003; Czarnołęski et al. 2010; Naddafi and Rudstam 2013; Berthon 2015). Future studies pairing multiple functionally or taxonomically similar predators from an invader’s native and invaded ranges (e.g., combining *Arcuatula* with drilling snails from eastern Asia and southern California) offer the promise of parsing out the relative influences of predator cues and evolutionary history (Nicastro et al. 2007; Bourdeau et al. 2013; Berthon 2015).

Conclusions and future directions

In summary, chemical cues from a diverse suite of native predators induce specific potential anti-predation behaviors in the invasive mussel *Arcuatula senhousia*. The three predators we chose for our experiment are important consumers of *Arcuatula* in invaded areas of southern California, suggesting that the ability of *Arcuatula* to effectively respond to native

predator cues may reduce the potential for biotic resistance. The behavioral changes we observed in *Arcuatula* are generally associated with greater survival for bivalves, but further experiments are needed to determine how native predator cues influence *Arcuatula* behavior in situ and how effectively anti-predation responses affect demographic rates (e.g., survival and fecundity; Carthey and Banks 2014). If behavioral responses to native predators improve the persistence and spread of *Arcuatula* populations, there will likely be cascading effects on the structure and function of southern California estuaries because *Arcuatula* can change abundances of native habitat-forming seagrass (Reusch and Williams 1998), infauna (Crooks 1998b; Crooks and Khim 1999), and bivalves (Castorani and Hovel 2015).

Together with previous studies, our work demonstrates that native predators can induce behavioral defenses in invasive prey. Although many studies have focused on the physiological and behavioral responses of native prey to invasive predators, understanding how *invasive* prey react to *native* predators may be equally valuable to determining the ecological impacts of non-native species and assessing the potential for biotic resistance to invasion (Carthey and Banks 2014; Berthon 2015). Trait-mediated indirect effects caused by predation cues (e.g., predators or injured conspecifics) can have substantial effects on community dynamics and, in many cases, exceed the direct effects of predation (Werner and Peacor 2003; Trussell et al. 2004; Ferrari et al. 2010; Berthon 2015). At present, understanding the degree to which invasive prey can detect and respond to native predator cues are largely restricted to a few case studies (Nicastro et al. 2007; Czarnoński et al. 2010; Grason and Miner 2012; Naddafi and Rudstam 2013). Future investigations should resolve the evolutionary drivers and biochemical mechanisms underlying the ability of invasive prey to detect native predator cues, the consequences for population dynamics of invasive prey, native predators, and native competitors (Castorani and Hovel 2015), and the implications for invasion success and biotic resistance (Grosholz 2010; Kimbro et al. 2013; Berthon 2015). Studies are especially urgent in estuaries and coastal seas, where invasions are accelerating and understudied (Ruiz et al. 1999; Williams 2007), and chemical cues play a central role in predator–prey dynamics (Webster and Weissburg 2009; Hay 2009; Ferrari et al. 2010).

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