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HARD CLAMS (*Mercenaria mercenaria*) EVALUATE PREDATION RISK USING CHEMICAL SIGNALS FROM PREDATORS AND INJURED CONSPECIFICS

DELBERT L. SMEE* and MARC J. WEISSBURG

School of Biology, Georgia Institute of Technology, 310 Ferst Dr. Atlanta, GA 30332, USA

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Abstract—Hard clams, *Mercenaria mercenaria*, are sessile, filter-feeding organisms that are heavily preyed upon by blue crabs, which find their clam prey using chemical cues. Clams may evade blue crabs by reducing their pumping (feeding) behavior when a threat is perceived. The purpose of this study was to determine the type of signals that clams use to detect consumers. Clams decreased their pumping time in response to blue crabs and blue crab effluent, but not to crab shells, indicating that chemical signals and not mechanical cues mediated the response of clams to distant predators. Because predator diet can influence prey evaluation of predatory threats, we compared clam responses to blue crabs fed a steady diet of fish, clams, or that were starved prior to the experiment. In addition, we used injured clams as a stimulus because many organisms detect predators by sensing the odor of injured con- or heterospecifics. Clams reduced feeding in response to injured conspecifics and to blue crabs that had recently fed. Clams reacted similarly to fed crabs, regardless of their diet, but did not respond to starved blue crabs. Because blue crabs are generalist predators and the threat posed by these consumers is unrelated to the crab's diet, we should expect clam reactions to blue crabs to be independent of the crab's diet. The failure of clams to react to starved blue crabs likely increases their vulnerability to these consumers, but clam responses to injured conspecifics may constitute a strategy that allows animals to detect an imminent threat when signals emanating from blue crabs are not detectable.

Key Words—Blue crab, chemical cue, clam, diet, flume, foraging, predator avoidance, predator–prey interaction, risk evaluation.

* To whom correspondence should be addressed. E-mail: l_smee@hotmail.com

INTRODUCTION

Predators often have profound impacts on prey populations and on the organization and function of communities in general (Paine, 1966; Carpenter et al., 1985; Schmitz et al., 1997; Schmitz, 1998; Menge, 2000). The overall effect of predators on communities is determined by interactions between individual predators and prey (Lima, 1998, 2002). Therefore, the ability of predators to forage and the ability of prey to avoid consumers influence the magnitude of top-down forces in a given system (Menge, 2000; Werner and Peacor, 2003). Because decisions made by prey under the risk of predation have important consequences for both prey populations as well as entire communities, it is important to understand how prey evaluate and respond to predation risk (Lima and Dill, 1990; Werner and Peacor, 2003).

Although avoiding consumers is of great importance to prey, predator avoidance is often costly and results in decreased growth or fecundity (e.g., Lima and Dill, 1990; Peckarsky, 1996; Katz and Dill, 1998; Leonard et al., 1999; Nakaoka, 2000). Prey may minimize predator avoidance costs by using flexible avoidance strategies that balance the frequency or magnitude of predator avoidance responses with a perceived level of risk (Sih et al., 1985; Schmitz et al., 1997; Schmitz, 1998; Chivers and Smith, 1998; Katz and Dill, 1998; McIntosh and Peckarsky, 1999). Thus, prey require stimuli that accurately reveal the level of risk to determine when and how predator avoidance strategies should be employed.

Prey commonly use chemical signals to evaluate risk (Chivers and Smith, 1998; Katz and Dill, 1998) because chemical cues typically provide prey with accurate information concerning the location and intentions of predators (Chivers and Smith, 1998; Katz and Dill, 1998; Brown et al. 2000). This is particularly true in aquatic environments where visual or mechanical cues are often unavailable (Zimmer and Butman, 2000; Weissburg et al., 2002). Additionally, predators can more easily manipulate their posture or behavior to appear less threatening to prey than change their chemical signature (Katz and Dill, 1998; Brown et al., 2000).

Chemical cues indicative of danger may emanate from predators, from injured conspecifics, and sometimes from sympatric species (Petranka et al., 1987; Mathis and Smith, 1993; Chivers and Smith, 1998; Katz and Dill, 1998). Prey may use one or combinations of these signals to evaluate risk (Chivers and Smith, 1998; Katz and Dill, 1998; Bryer et al., 2001; Smith and Belk, 2001) and respond differently to chemical signals depending on other factors such as time of day (e.g., Peckarsky, 1996). Signals released from predators provide the most accurate indication of a predatory threat, and prey may minimize their predator avoidance costs by exclusively responding to these signals (reviewed by Katz and Dill, 1998). Although cost effective, an avoidance strategy in which prey

respond only to predator odors may increase their vulnerability when these chemicals are difficult to detect or when predators reach prey prior to the arrival of their chemical signals (e.g., when olfactory predators find prey by searching upstream). In contrast, chemical cues released by injured conspecifics may provide a stronger but less reliable indication of danger (reviewed by Katz and Dill, 1998). Yet, prey may overutilize predator avoidance tactics and incur high costs if they depend on less reliable signals (Lima and Dill, 1990; Katz and Dill, 1998).

Some prey limit their responses to predators that have eaten conspecifics or closely related species (e.g., Chivers and Smith, 1998; Katz and Dill, 1998; Chivers and Mirza, 2001; Mirza and Chivers, 2001; Smith and Belk, 2001; Brown and Dreier, 2002; Madison et al., 2002), and this predator detection strategy has been hypothesized to minimize predator avoidance costs. However, prey that depend on predator diet cues before initiating antipredator measures may be vulnerable to generalist predators that switch diets frequently (Bryer et al., 2001; Chivers and Mirza, 2001). Bryer et al. (2001) and Chivers and Mirza (2001) hypothesized that prey responses that are dependent on predator diets should only occur in systems where the threat posed by a predator is directly related to that predator's most recent foraging activity.

In this study, we examined the effects of a generalist predator's diet on the response of a common prey organism using blue crabs *Callinectes sapidus* and hard clams *Mercenaria mercenaria* as model organisms. Blue crabs *C. sapidus* are important predators and scavengers in southeastern estuaries (Eggleston et al., 1992; Micheli, 1997) and are the primary consumer of juvenile hard clams *M. mercenaria* in these areas (Micheli, 1995, 1997). Blue crabs are also a threat to adult clams, as they can nip their siphons and decrease their feeding efficiency, growth, and fecundity (Peterson, 1986; Coen and Heck, 1991; Irlandi, 1994). Clams release attractive chemicals into the water as they feed, and blue crabs follow these waterborne chemical odor plumes to locate their clam prey (Weissburg and Zimmer-Faust, 1993; Weissburg et al., 2002). Irlandi and Peterson (1991) found that clams responded to the presence of predators by reducing their feeding time and hypothesized that feeding reductions would make clams less apparent to consumers. Indeed, caging predators near clam beds decreases clam mortality (Smee and Weissburg, in press), but clam growth and reproductive output are diminished by long-term exposure to predators (Nakaoka, 2000). Thus, clam responses to predators are adaptive and costly.

We hypothesized that clams detect approaching blue crab predators by using chemical signals or hydrodynamic signals or both. We exposed clams to both chemical and hydrodynamic signals from blue crabs to verify the type of cue that clams used to detect blue crabs. The results indicate that clams were responding to chemical cues emanating from blue crabs, and we conducted a second experiment to determine the nature of these signals. In the second

experiment, we compared changes in clam behavior when exposed to blue crabs that had been fed different diets and to injured conspecifics. Our results suggest that prey respond to a generalist predator regardless of diet, presumably because the dietary history of such a predator does not predict the risk to its potential prey. Furthermore, there are limits to prey perceptual abilities that may result in increased predation risk. For example, prey may be unable to detect starved predators, although a highly motivated consumer increases the chance that potential prey may be attacked.

METHODS AND MATERIALS

Animal Capture and Maintenance. Animals were collected from Wassaw Sound, GA, USA, and associated tributaries. Hard clams *M. mercenaria* were hand dug with clam rakes and fingers in the intertidal zone, and blue crabs *C. sapidus* were captured with commercially purchased crab pots. After capture, animals were returned to the Skidaway Institute of Oceanography (SkIO) near Savannah, GA, and housed in flow-through sea tables supplied by water pumped from the Skidaway River. Sea table water was filtered through both gravel and sand filters, and the water temperature and salinity in the sea tables ranged from 25 to 30°C and from 25 to 30 ppt, respectively. Clams acclimated in the sea tables for at least 6 hr prior to behavioral assays (see below) and were used in behavioral assays within 48 hr after removal from the field. Blue crabs were kept in the sea tables for at least 1 wk prior to use in the behavioral assays. Crabs were fed with a daily diet of either fish (*Menhaden* sp.) or clams (*M. mercenaria*) or were starved during the 1-wk acclimation period. We returned each clam or crab to the field after a single use (except for a few clams that were injured as part of the experiment or used for food; see below).

Experimental Arena. Experiments were conducted in a paddle-driven racetrack flume at SkIO (4.8-m-long working section × 1 m wide × 0.33-m water depth). The upstream bend of the flume is divided into five 23-cm channels to reduce secondary circulation. Flow is further conditioned by honeycomb baffling (5 cm thick with 7-mm openings) at the downstream end of this bend and by a polyvinyl chloride (PVC) flow straightener (10 × 4.5-cm openings) placed at the end of the working section to prevent backflow. The working section contains a false bottom (0.30-m diam. × 0.15 m deep) located 2.3 m downstream from the entrance point of the working section and is in the center of the flume to minimize wall effects. Both the working section and false bottom of the flume were filled to a uniform depth of 1 cm with commercially purchased sand (grain size 0.04 ± 0.04 cm). The flume was supplied by the same water source as the sea tables and had similar temperature and salinity. Flume water passed through both gravel and sand filters as

well as a 10-μm filter bag. Flow speed was maintained at 3 cm sec^{-1} in all experiments. This flume produces stable and reproducible boundary layers at current speeds ranging from 1 to 15 cm sec^{-1}. See Ferner and Weissburg (2005) for a detailed flume description and characterization of the flow environment boundary.

Behavioral Assays. Experiments utilized changes in clam pumping (feeding) behavior as assays for the ability of clams to detect predation risk. Although previous investigators have assumed that clams are actively pumping only when their siphons are extended (e.g., Irlandi and Peterson, 1991), we performed preliminary experiments to verify this supposition. We visualized the excurrent from clams by carefully pipetting a 0.1% solution of fluorescein dye above the excurrent siphon of a clam. Thirty-six clams that had their siphons extended were tested in this manner, and all were releasing an excurrent. We tested 15 clams with open shells but withdrawn siphons, and only three were pumping. Thus, we concluded that siphon extension was indicative of pumping.

Behavioral trials consisted of challenging clams to detect and respond to blue crab predators, injured clams, predator-conditioned water, and predator shells. We judged clam responses to predation risk by determining if clam feeding (no. of siphon extension observations) was significantly less in response to these treatments when compared to a control that lacked predators or injured conspecifics. In each assay, we placed five clams in the false bottom of the flume and allowed them to acclimate for 30 min. Clam density in these experiments was five clams per 0.07 m^2 and mimics densities observed in natural habitats (Walker, 1987; Smee and Weissburg, unpublished data). We introduced predators, crushed conspecifics, or predator-conditioned water at the conclusion of the 30-min acclimation period by placing a tethered crab, injured clam, or the nozzle (see below) from our delivery system 0.5 m upstream from the clam bed. We recorded the siphon position of each clam (extended or not) prior to introduction of the predator treatments and at 5-min intervals after introduction for 30 min. Thus, each clam could have been observed feeding (pumping) a maximum of seven times, and we used the total number of observations in which clams were pumping as our measure of clam pumping time. That is, the response of each clam in a trial was measured by a single number between 0 and 7, which indicated how many times we observed an individual clam pumping.

The order of treatments and controls in these experiments was randomly assigned each day, and each treatment and the control were replicated at least five times (5 trials $\times$ 5 clams per trial = 25 clams for each treatment and control). Each clam and predator was used only once. Clams that neither pumped nor burrowed were excluded from the analysis, and we excluded approximately 25% of the clams from the experiment by using this criterion.

Including inactive clams in our analysis would have enhanced our results, but we excluded them because we could not clearly determine the causes of clam inactivity.

Characterization of Predator Cues. Preliminary observations suggested that clams pumped significantly less when tethered blue crabs were placed upstream. We hypothesized that potential predators created hydrodynamic signals, chemical signals, or both that mediated the response of clam prey. Therefore, we conducted two experiments to determine the cue that clams use to detect predators. We tested responses of clams to hydrodynamic cues by placing an empty predator shell 0.1 m upstream from the clams and comparing clam pumping between this treatment and the control. Qualitative flow visualization with dye indicated that the turbulence created by the predator shells dissipated within the first 0.25 m downstream, although we could not exclude the possibility that a more exacting analysis of flow would reveal that perturbations induced by the shell extended farther downstream. Thus, we placed the predator shell 0.1 m upstream from the clam bed to ensure that the clams were in its turbulent wake.

To determine if clams were detecting chemical signals from predators, we designed a chemical delivery system to transport blue crab effluent to the experimental clams. The delivery system pumped water out of the flume and into a container ($0.31 \times 0.24 \times 0.36$ m) that was left empty (control) or that housed a blue crab that had recently eaten clams. The water from the container was released into the flume 0.5 m upstream from the clam bed via a 0.076-m diam PVC pipe oriented parallel to the flow. Water moved through the delivery system at a velocity of 3 cm sec^{-1}, which matched the free stream flow velocity in the flume. The large diameter pipe was selected because it was of similar size to a blue crab, which allowed us to simulate water passing over the crab at a rate similar to that occurring in experiments with clams exposed to a live predator.

We realize that the flow diversion method may only crudely approximate the flux of chemicals experienced by a prey organism directly upstream of a crab predator. Although our approach replicates the rate of water movement over the animal, mixing in the delivery system and introduction through a pipe will probably change the chemical signal dynamics relative to that produced by water flowing over an individual crab. However, the flow diversion method we employed is a more realistic alternative than prey soaks or body washes because the volumetric rate at which water passes over the crabs in the diversion system is roughly equal to that passing over a crab in the flume. In contrast, soaks or body washes concentrate predator metabolites using arbitrarily determined volumes and time periods, and so produce unknown metabolite concentrations that will not be experienced by naturally foraging animals.

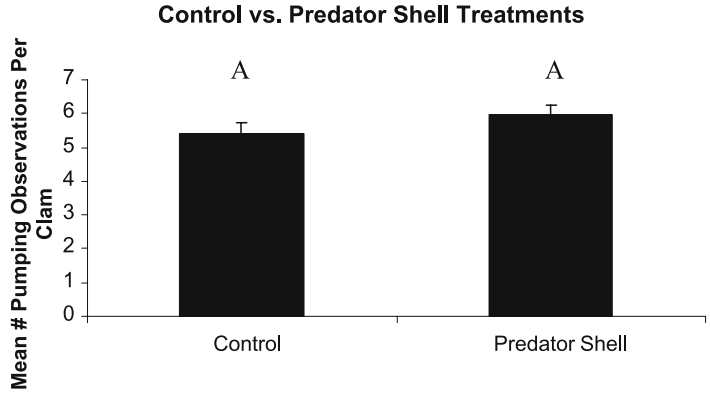
Effects of Predator Diet and Response of Clams to Injured Conspecifics. In this experiment, we measured the responses of clams when presented with odors from injured conspecifics as well as crabs that were fed with different diets prior to behavioral assays. The injured clam treatment was prepared by striking a clam with the blunt edge of a kitchen knife, removing the top valve, and making multiple lacerations on the visceral mass. This treatment mimicked crab feeding and insured that clam metabolites were released into the water. To measure the impact of crab diet on clam responses, collected blue crabs were fed with a daily diet of fish or clams for 1 wk or were starved for 1 wk prior to the experiment. We allowed clams to acclimate in the flume using the same methodology previously described, then placed a tethered blue crab or injured clam 0.5 m upstream from the clam bed, and monitored clam feeding.

Data Analysis. We initially examined the percentage of times that adjacent clams were feeding simultaneously to determine if interactions occurred between clams. Clams in control trials pumped during 87% of our observations. Thus, the proportion of time that two adjacent clams should be pumping simultaneously is 0.87^2 (0.76), assuming that adjacent animals do not influence each other. Adjacent clams (N = 25 pairs) in control trials pumped simultaneously in 70% of our assays, a value not significantly different from the random expectation (Sokal and Rohlf, 1995).

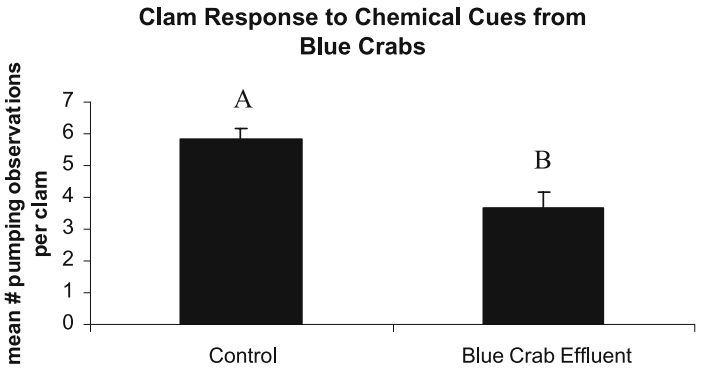
Since clams were not influencing each other, observations of pumping behavior of individual clams (number of siphon extensions observed for each clam) were arcsine transformed to meet analysis of variance (ANOVA) assumptions and were then compared using a nested ANOVA that examined the effects of predator treatment and trial nested within treatment (Sokal and Rohlf, 1995). The use of a nested ANOVA allowed us to determine if variations in clam responses were affected by variability in cue quality or quantity across replicate treatments, which is a source of uncontrolled variation in the experiments. The P value for the nest effect was greater than 0.20 in all experiments, indicating that clams in different groups were reacting similarly to the same treatments. The lack of a significant nest effect permitted us to lump trials within treatments and test the significance of the main effect by using the pooled error variance (Sokal and Rohlf, 1995). The absence of a nest effect suggests that cues from predators and injured conspecifics were roughly similar between replicate trials.

Experiments using tethered predators, predator effluents, and predator shells were conducted at different times over a period of several months. Therefore, each experiment was analyzed separately because it would be inappropriate to compare treatments to one another under these conditions. Separate control experiments were performed for each experiment to account for any variation in animal or general experimental conditions. Trials that used different predator diets or injured conspecifics were intermingled and, on a daily

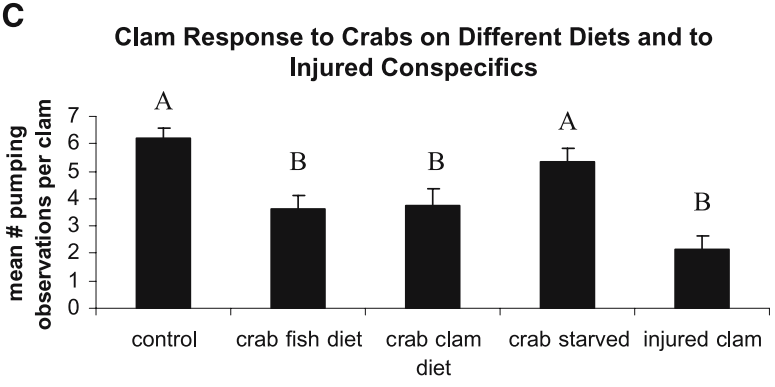
A


Control vs. Predator Shell Treatments
Mean # Pumping Observations Per Clam
0
1
2
3
4
5
6
7
A
A
Control
Predator Shell

B


Clam Response to Chemical Cues from Blue Crabs
mean # pumping observations per clam
0
1
2
3
4
5
6
7
A
B
Control
Blue Crab Effluent

C


Clam Response to Crabs on Different Diets and to Injured Conspecifics
mean # pumping observations per clam
0
1
2
3
4
5
6
7
A
B
B
A
B
control
crab fish diet
crab clam diet
crab starved
injured clam

basis, were presented in random order to test clams. After completing the nested ANOVA, a Tukey–Kramer *post hoc* analysis was employed to test for pairwise differences between treatments (Sokal and Rohlf, 1995).

RESULTS

Characterization of Predator Cues. Data from experiments using the predator shells indicated that there were no significant differences in clam pumping between the predator shell treatments and the controls ($F_{1,83} = 2.56$, $P > 0.11$, Figure 1A). Although not significant, we observed a higher clam-pumping rate in trials with predator shells. Thus, turbulence generated by the predator shell did not alter clam pumping, which suggested that clams were not using a hydrodynamic cue to detect predators.

In contrast to the results obtained with empty predator shells, clam pumping was significantly reduced (≈40%) when clams were exposed to water released from the delivery system that had passed over a blue crab as compared to water passing through the empty system without blue crabs present ($F_{1,35} = 8.69$, $P < 0.01$, Figure 1B). Additionally, clam feeding was affected similarly by predator-conditioned water and (nonstarved) predators placed directly in the flume (see below). The failure of clams to cease pumping in response to hydrodynamic signals, combined with the positive response to predator-conditioned water delivered under environmentally realistic conditions, suggested that clam responses to predators were chemically mediated.

Effects of Predator Diet and Response of Clams to Injured Conspecifics. The data revealed that clam feeding decreased by 40% when exposed to blue crabs that had recently been fed and by 65% in the presence of injured conspecifics as compared to controls that lacked predators or injured clams ($F_{4,84} = 10.28$, $P < 0.001$, Figure 1C). Starved blue crabs caused a slight (15%) but insignificant reduction in clam feeding. Additionally, *post hoc* analysis revealed that clams pumped significantly more in the presence of starved blue crabs than those that were recently fed, and clam responses to crab predators

FIG. 1. Mean number of pumping observations per clam (±SE). Letters denote means that are significantly different based on a Tukey–Kramer *post hoc* test. Each clam could have been observed pumping a maximum of seven times during the 30-min observation period. (A) Control vs. predator shell placed 0.1 m upstream, $N = 42$ and 43 clams, respectively. (B) Control vs. blue crab effluent released from our delivery system, $N = 16$ and 21 clams, respectively. (C) Clam pumping in the presence of crabs fed with different diets and injured conspecifics. Sample sizes for each treatment are 24, 16, 15, 19, and 15 for the control, crab fed with fish, crab fed with clams, starved crab, and injured clam treatments, respectively. Differences in sample size result from exclusion of inactive clams from analyses.

were similar regardless of their diet. Although not significantly different from responses to fed crabs, clams reduced their feeding time almost 40% more after detecting an injured conspecific than a crab that had recently eaten (Figure 1C). Thus, clam feeding was affected more by the presence of injured clams than by the odors of fed predators, although both caused significant reductions in clam feeding as compared to controls and starved crab treatments.

DISCUSSION

Our results indicate that clams use chemical signals to detect upstream blue crabs and respond to these predators by reducing their feeding (pumping) behavior. Other bivalves (e.g., mussels) also use chemical cues to detect predators and respond by changing their morphology (e.g., Leonard et al., 1999) or behavior (e.g., Cote' and Jelnikar, 1999). Previous studies have shown that blue crabs depend on chemical cues to locate clam prey (Weissburg and Zimmer-Faust, 1993; Finelli et al., 2000; Weissburg et al., 2002). The modulation of the blue crab–clam predatory interaction by chemicals is perhaps unsurprising given that the water in our study area is extremely turbid, and chemical cues are likely the only signals that can be detected from a distance in this habitat. Both blue crabs and their prey use the same sensory modality to detect each other, so the conditions that affect the transmission of chemical signals will affect the sensory abilities of both organisms. Thus, the outcome of interactions between these organisms may differ considerably between areas that enhance chemical signaling as compared to those that impede it.

In nature, clam feeding rates may be influenced by other factors (e.g., food availability, temperature) that were not considered in the present study. Reactions to predators may change in the field depending on a variety of factors besides the perceived level of risk. Still, long-term exposure to predators has been shown to significantly decrease clam growth in the field (Nakaoka, 2000). In a related field study, Smee and Weissburg (in press) found that clam survival was significantly higher in clam plots with predators caged nearby as compared to control plots with empty cages. These studies indicate that clam reactions to predators, while costly, reduce mortality and suggest that clams react to predators across a range of natural conditions. Therefore, the clam reactions to predators and injured conspecifics observed in the present study should be indicative of the cues used by clams to avoid predation in the field.

Clams only responded to cues released by blue crabs if the crabs had recently been fed and not if they had been starved for 1 wk. Clams responded similarly to fed crabs regardless of whether the crab's diet consisted of fish or clams prior to behavioral assays. In addition, clams altered their feeding behavior in the pres-

ence of injured conspecifics, suggesting that they also use these signals to detect predatory threats.

The ability of clams to react to injured conspecifics may compensate for their inability to detect hungry blue crabs. Prey organisms may benefit from living in close proximity to conspecifics or related species, as neighbors can provide for shared vigilance against consumers or early warnings of danger (Hamilton, 1971; Powell, 1974; Sullivan, 1984; Fitzgibbon, 1990; Aukema and Raffa, 2004). The benefit provided by neighbors is particularly strong in organisms that respond to the odors of injured conspecifics or heterospecifics, as consumption of neighbors reveals a predatory threat (e.g., Mathis and Smith, 1993). Hard clams are commonly found in dense beds and can reach densities in excess of 50 clams m^{-2} in our study area (Walker, 1987; Smee and Weissburg, unpublished data). Clams living in dense beds may be better able to avoid unapparent predators, as neighbors that are eaten may warn of imminent peril.

Responses of prey that are dependent on predator diets have been found in many predator–prey systems (Crowl and Covich, 1990; Chivers et al., 1996; Stabell and Lwin, 1997; Chivers and Mirza, 2001; Smith and Belk, 2001) but are notably absent from others (Petranka and Hays, 1998; Bryer et al., 2001). The existence of diet-dependent responses may be contingent on whether the recent dietary history of the predator is correlated with risk to prey. For instance, seasonally hunting predators may pose a risk for prey only at certain times, so that predator diet may predict the potential threat level to that prey species (Chivers and Mirza, 2001). Alternatively, Bryer et al. (2001) suggest that diet-dependent responses to predators may not be beneficial when prey are hunted by generalist predators, such that the risk level posed by the predator is unrelated to its foraging habits. Bryer et al. (2001) observed that slimy sculpin responses to brook trout predators were unaffected by the trout's diet. They reasoned that the threat posed by brook trout to sculpins is unrelated to the trout's foraging habits, and thus, it would not be advantageous for the sculpin to base risk evaluation on predator diet cues.

The response of clams to blue crabs in our experiment was not dependent on the crab's diet. Because blue crabs are generalist consumers and eat almost anything alive or dead (Virnstein, 1977; Eggleston et al., 1992; Micheli, 1995, 1997), the threat of predation by crabs is unrelated to the crab's recent foraging activity. As in the previous example with slimy sculpins, knowledge of a blue crab's diet provides no valuable information for their prey, suggesting that it is not advantageous for clams to rely on diet cues as their sole means of evaluating risk.

Cost-benefit analyses are often used to explain the variability in responses to predators across predator–prey systems. However, cost-benefit explanations currently are focused on response specificity as opposed to response sensitivity and may be inadequate when prey fail to detect actual predatory threats because predators have not recently fed (Howe and Harris, 1978). If predators stop

releasing chemical signals or release chemicals that are difficult to detect, then organisms may not adequately perceive the true risk level. Starved predators often show enhanced search responses relative to those that are well fed, as revealed by increases in the duration and frequency of search bouts in response to a given stimulus level or decreases in the threshold stimulus levels that are required to initiate or maintain search (Mackie and Shelton, 1972; Zimmer-Faust and Case, 1982). Therefore, the threat posed by a starved crab is equal to, or possibly greater than, that posed by a crab that has recently foraged. Thus, it would be prudent for clams to respond to starved crabs, and their failure to do so suggests that starvation renders blue crabs less detectable to clam prey. Prey may be more likely to depend on the odors of injured con- or heterospecifics to detect consumers when predators are commonly undetectable, although this hypothesis has not been empirically tested.

We have yet to develop risk-based models for the sensitivity of potential prey to cues derived from their consumers, and research that attempts to quantify the stimulus levels necessary to elicit prey reactions is lacking. Prey with low sensitivity thresholds may experience large costs (e.g., reductions in the opportunity to feed), particularly if prey use general metabolites to detect their predators, as these substances may come from a variety of sources. In contrast, prey with higher sensitivity thresholds may decrease predator avoidance costs but may also be more vulnerable to their enemies. Recent technological advances in our ability to characterize and identify chemical signals (e.g., Millar and Haynes, 1998), as well as our ability to examine chemical signal transport in aquatic systems (e.g., Webster and Weissburg, 2001; Weissburg et al., 2002), may allow us to investigate threshold sensitivity and its relationship to predation risk in a more thorough manner than has been previously attempted.

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