BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

Predator biomass determines the magnitude of non-consumptive effects (NCEs) in both laboratory and field environments

Jennifer M. Hill · Marc J. Weissburg

Abstract Predator body size often indicates predation risk, but its significance in non-consumptive effects (NCEs) and predator risk assessment has been largely understudied. Although studies often recognize that predator body size can cause differing cascading effects, few directly examine prey foraging behavior in response to individual predator sizes or investigate how predator size is discerned. These mechanisms are important since perception of the risk imposed by predators dictates behavioral responses to predators and subsequent NCEs. Here, we evaluate the role of predator body size and biomass on risk assessment and the magnitude of NCEs by investigating mud crab foraging behavior and oyster survival in response to differing biomasses of blue crab predators using both laboratory and field methods. Cues from high predator biomass treatments including large blue crab predators and multiple small blue crab predators decreased mud crab foraging and increased oyster survival, whereas mud crab foraging in response to a single small blue crab did not differ from controls. Mud crabs also increased refuge use in the presence of large and multiple small, but not single small, blue crab predators. Thus, both predator biomass and aggregation patterns may affect the expression of NCEs.

Communicated by Pete Peterson.

J. M. Hill (✉) · M. J. Weissburg
Georgia Institute of Technology, 310 Ferst Drive,
Atlanta, GA 30332, USA
e-mail: jhill@disl.org

M. J. Weissburg
e-mail: marc.weissburg@biology.gatech.edu

J. M. Hill
Dauphin Island Sea Lab, 101 Bienville Boulevard,
Dauphin Island, AL 36528, USA

Understanding the impact of predator biomass may therefore be necessary to successfully predict the role of NCEs in shaping community dynamics. Further, the results of our laboratory experiments were consistent with observed NCEs in the field, suggesting that data from mesocosm environments can provide insight into field situations where flow and turbulence levels are moderate.

Keywords Antipredator behavior · Body size · Chemical cues · Trophic cascades · Blue crabs

Introduction

Predator–prey interactions, such as those responsible for trophic cascades, were originally thought to be purely consumptive interactions whereby predators reduced prey densities through lethal interactions and caused cascading indirect effects. However, increased attention has been focused on the non-lethal effects of predator intimidation and fear, labeled non-consumptive effects (NCEs), in which prey actively change traits such as behavior, morphology, and habitat use in response to the presence of a predator (Lima 1998; Werner and Peacor 2003). In many cases, these changes are mediated by chemical cues emanating from predators or injured conspecifics that warn prey of imminent risk (Kats and Dill 1998). Generally, NCEs can account for 85 % of the effects seen in trophic interactions based on meta-analysis of studies comparing NCEs with their traditional consumptive counterparts (Preisser et al. 2005). Further, NCEs can be even greater in individual systems (Grabowski 2004; Griffen and Byers 2006a). The importance of NCEs has prompted a number of studies into behavioral interactions and even revisitation of classic ecological predator–prey paradigms in order to

investigate the role of NCEs in trophic dynamics (Peckarsky et al. 2008).

Much like consumptive effects in traditional trophic cascades, investigations into NCEs find that the magnitude and direction of their effects are largely context-dependent based on a number of factors including habitat type and complexity (Trussel et al. 2006; Ferner et al. 2009), resource levels (Bolnick and Preisser 2005), and predator identity (Turner et al. 1999; Schmitz and Suttle 2001). This context dependence is driven largely by the evolutionary, sensory, and behavioral ecology of the prey that determine the set of conditions to which prey respond and their antipredator strategies (Kats and Dill 1998; Schmitz et al. 2004). Antipredator strategies frequently are dictated by the risk that prey assess using a variety of information about predators, such as type and activity (Stankowich and Blumstein 2005; Ferrari et al. 2010). Much of this information is perceived through chemical cues that mediate predator-specific behavioral responses in many prey species (Katz and Dill 1998; Turner et al. 1999; Schmitz and Suttle 2001). Here, risk assessment based on the intensity and composition of chemical cues causes different magnitudes of antipredator behavior. For instance, tadpoles respond to increasing cue concentration and to phylogenetic relatedness of predator diet causing varying levels of both behavioral and morphological responses (Van Buskirk and Arioli 2002; Schoeppner and Relyea 2005). These differential antipredator strategies based on risk assessment can then lead to context-dependent NCEs on resources and ecosystem dynamics (e.g., Schmitz 2008). Consequently, it is necessary to account for predator traits that lead to differences in predator risk assessment in order to predict the magnitude of NCEs across ecosystems.

One aspect of predators that often dictates risk to prey is predator body size (Werner and Gilliam 1984; Cohen et al. 1993), either as a result of size-dependent predation mechanics (i.e. gape-limited or crush-limited predation) or because predator body size often determines habitat choice, prey choice, and even consumption rates of organisms (Werner and Gilliam 1984). For instance, in freshwater ponds, larval salamanders prey selectively on larger zooplankton thereby releasing smaller zooplankton from competition and shifting community composition (Dodson 1970). Thus, predator body size affects the character and strength of many predator–prey interactions, both direct and indirect (Dodson 1970; Werner and Gilliam 1984; Rudolf 2006).

Just as predator body size mediates consumptive effects, it also alters the expression of both trophic and non-trophic NCEs (Werner and Peacor 2003; Crumrine 2005; Griffen and Byers 2006a, b; Rudolf 2006). For instance, Griffen and Byers (2006b) demonstrated changes in amphipod survival with differing body size combinations of invasive crab species through both predator interference (non-

trophic NCE) and behavioral responses to the larger crab predator (trophic NCE). Further, Rudolf (2006) showed larval salamander activity levels differed when exposed to differing sized heterospecific salamander predators demonstrating that prey perceive the difference in predator body sizes.

Although data indicate that predator sizes can change NCEs and the outcome of predator–prey interactions, the sensory mechanisms that mediate these changes are often unknown. This paucity is significant since the perceptual mechanisms may set limits on the ability of prey to detect or respond to predator body size, or different methods of encoding predator size may have different consequences for the expression of NCEs. Currently, our most detailed knowledge about the role of predator body size in risk assessment is from prey that respond visually. For example, fish, birds, and lizards flee at greater distances when approached by large predators compared to smaller ones, suggesting that large animals are perceived as riskier (Stankowich and Blumstein 2005).

In turbid aquatic systems such as estuaries, rivers, and ponds, many organisms rely on chemical cues rather than vision. In these systems, it may be difficult for chemosensory detection systems to encode predator size directly, but there is little information on size assessment (but see Chivers et al. 2001). Large versus small predators could be distinguished based on size-specific qualitative variation in chemical cues (i.e. differing chemical constituents, or blends; Kusch et al. 2004). Alternately, differing cue concentration dictated by predator biomass may also provide information on predator size, especially given observations that prey risk assessment can be based on chemical concentration (Chivers et al. 2001; Van Buskirk and Arioli 2002). The latter suggests that size per se may be less important than the combination of predator size, density, and degree of predator aggregation (i.e. biomass) for determining the magnitude of NCEs.

Previous studies have examined the role of predator biomass in modulating prey traits by constructing dosage-response curves using differing predator abundances (Anholt et al. 2000; Van Buskirk and Arioli 2002; Schoeppner and Relyea 2008). However, studies have rarely determined the role of predator biomass versus individual size in either influencing predator risk assessment (but see Chivers et al. 2001) or the propagation of size-based NCEs to trophic levels other than that of the focal prey. Further, aquatic studies that have examined the role of predator abundance in modulating prey behavior often use laboratory mesocosms where the concentration of chemical cues from multiple predators may become elevated. In many aquatic environments with moderate, or even slow, flow speeds, chemical cues move as odor plumes where cue concentration is often patchy and unpredictable (Weissburg 2000), suggesting that assessing predator size via chemical concentration in these environments may be problematic.

Given the importance of sensory perception to the study of NCEs, it is valuable to be able to link environmental properties affecting perception to the expression of NCEs. Many studies examining chemically-mediated NCEs are performed in laboratory mesocosm environments (Kats and Dill 1998), especially those examining factors such as chemical cue concentration (Anholt et al. 2000; Chivers et al. 2001; Van Buskirk and Arioli 2002; Schoeppner and Relyea 2008). Although these studies are applicable to environments such as ponds or intertidal pools, the relationship of these studies to patterns of NCEs in environments driven by currents, tides, and waves is unclear since they do not reproduce the characteristic patterns of water flow (i.e. moderate velocities and turbulence) that may alter the perception of predator chemical cues necessary for producing anti-predator behaviors (Weissburg 2000; Powers and Kittinger 2002; Smee et al. 2008; Ferner et al. 2009). Many other studies, including those examining chemically-mediated interactions, have documented NCEs in aquatic field environments with water flow (Forrester et al. 1994; Rochette et al. 1997; Trussel et al. 2002; McIntosh et al. 2004; O'Connor et al. 2008). Although these investigations clearly show that NCEs happen in the presence of flow and mixing, the actual flow dynamics are often unquantified (Zimmer and Zimmer 2008; but see Powers and Kittinger 2002; McIntosh et al. 2004; Smee et al. 2008; Ferner et al. 2009). Thus, it is currently difficult to establish more precise relationships between flow/mixing and NCE strength, or the effect of spatial and temporal variation in modulating the expression of NCEs. Intertidal oyster reefs are exemplar habitats where physical conditions affecting predator and prey perception can enhance or restrict the potential for CEs and NCEs, so that characterizing the flow environment likely provides insight into the importance and context-sensitivity of NCEs.

We examined the ability of prey to judge size and biomass-based predator risk using chemical cues and how prey responses to differing combinations of predator size and biomass propagate to lower trophic levels. The predation system consisted of adult and juvenile blue crabs, mud crabs, and their shared oyster prey. This intraguild (IG) crab predation system is ideal for examining size-based interactions because predation by crabs is crush-limited and size classes co-occur. The IG predators in this system, blue crabs (Callinectes sapidus), are important consumers and scavengers of estuarine environments (Micheli 1997) and prey on a variety of bivalve and crustacean species (Fitz and Weigert 1991; Micheli 1997). The IG prey, mud crabs (Panopeus herbstii), are small cryptic xanthid crab predators that occupy oyster beds at high densities (Lee and Kneib 1994; Hollebone and Hay 2007) and prey on a number of bivalve species (Seed 1980; Gibbons and

Castagna 1985; Bisker and Castagna 1987). Blue crabs and mud crabs both utilize shared oyster prey (Crassostrea virginica) and therefore may contribute to top-down control of oyster reefs that provide a wide variety of ecological services (Newell 2004). Blue crabs readily eat mud crabs in the laboratory (Grabowski et al. 2008; Hill 2011) and xanthid crabs and other non-portunid crabs make up approximately 43 % of the blue crab diet (Fitz and Weigert 1991). Predation risk from blue crabs is size based; large adult blue crabs (>100 mm carapace width; CW) are voracious predators on mud crabs, whereas small juvenile blue crabs (40–60 mm CW) rarely present a threat to mud crabs greater than 15 mm CW (Hill and Weissburg, in review). This suggests mud crab prey may benefit from information on predation risk by assessing blue crab body size (or biomass). Previous studies have documented NCEs between blue crabs and mud crabs in oyster reef systems that indirectly affect the survival of basal oyster prey (O'Connor et al. 2008; Grabowski et al. 2008). Chemosensation likely is important in driving these NCEs, but this has not been confirmed. Further, the role of predator size versus biomass in transmitting information about the degree of predation risk has not been evaluated.

In order to examine the connections between predator size and biomass in risk assessment and the expression of NCEs, we compared the predation rates of mud crabs on oyster prey in conditions where information on potential predation risk was transmitted via chemical cues. We employed predator treatments designed to differentiate the effects of size versus biomass. Similar to previous studies in aquatic NCEs, these experiments were first performed in laboratory mesocosms. However, NCEs were then examined in the field where tidally driven-flows could affect the perception of chemical cues and thus the outcome of the NCE. The goals of our study were to: (1) investigate whether blue crabs affect the foraging behavior of mud crabs on oyster prey through chemically-mediated NCEs; (2) examine the effects of predator traits (size, biomass) on the expression of NCEs propagated by chemical cues; (3) document whether NCEs occur in the field in moderate velocities (5–15 cm s^{-1}) often characteristic of tidal estuarine environments (Ferner et al. 2009); and (4) characterize the flow environment under which NCEs occur and examine potential variation in NCEs due to differences in temporal flow parameters.

Materials and methods

Animal collection and maintenance

All experiments were performed at the Skidaway Institute of Oceanography (SkIO), Skidaway Island, Georgia, USA.

Both blue crabs and mud crabs were collected from Wassaw Sound and associated tributaries. Hatchery-reared oysters (10–16 mm in length) were obtained from Bay Shellfish (Tampa, FL, USA). All animals were maintained in covered outdoor flow-through seawater tanks at SkIO for a minimum of 48 h before experiments began. Blue crabs were maintained on a diet of shrimp and/or clams and were fed an ad libitum diet of shrimp and oysters once a day for 48 h prior to experiments. Mud crabs were maintained on a clam diet and were starved 48 h prior to experiments.

Laboratory mesocosm experiment

In order to examine how potential NCEs on mud crabs and their oyster prey are modulated by either blue crab biomass or size, we monitored mud crab foraging on oysters in response to differing treatments of caged blue crab predators in laboratory mesocosms supplied with flow-through filtered seawater. Mesocosms (0.7 m × 0.4 m × 0.3 m) consisted of artificial oyster reefs constructed over approximately 2.5 cm of sand and shell hash substrate. Artificial reefs were constructed by gluing 10 sun-bleached oyster shells (obtained from natural shell banks) to create similar small clusters (approximately 6 cm in diameter), and then bundling clusters with rubber bands to build a reef (21 clusters per tank). One juvenile oyster (10–15 mm in length) was secured on the face of each cluster using cyanoacrylate glue (21 oysters per tank). Artificial reef structure allowed us to control the placement of juvenile oysters within reefs; natural heterogeneous clusters prevented us from minimizing variation between tanks and also changed the ability of mud crabs to access oyster prey. One liter of shell hash was scattered around reef edges to mimic the natural structure of the habitat since small oyster clusters surrounded by either mud or shell hash are characteristic of many oyster habitats in Wassaw Sound, GA. Twenty mud crabs (similar to natural size classes and densities: 13 of 15–20 mm; 4 of 20–25 mm; 3 of 25–30 mm CW; Lee and Kneib 1994; Hollebone and Hay 2007) were then added to the tank. One of four caged predator treatments was submerged in the tank once mud crabs were added; one large blue crab (>100 mm CW; approximately 130–180 g), one small blue crab (40–60 mm CW; 8–20 g), multiple small blue crabs (40–60 mm CW; totaling 130–180 g, ~9–14 crabs), and a no-predator control. Predator cages consisted of plastic containers (0.34 m × 0.20 m × 0.12 m) with multiple holes drilled through the side and a vexar mesh cover in order to allow diffusion of chemical cues into mesocosms, but prevent blue crabs from having any direct contact with mud crabs. Blue crabs were fed an ad libitum diet of shucked oysters every day. This diet was chosen because oysters are common prey for both adult and juvenile blue crabs (Eggleston

1990). Mud crabs were allowed to forage on oysters in mesocosms for 2.5 days. Oyster survival in the tank was recorded every 24 h. The total number of oysters eaten was recorded at the conclusion of the experiment, as well as the number of surviving mud crabs. Due to limited mesocosm space, 3 replicates of each treatment were run at one time in a randomized block design, with 6 runs in all, totaling 18 replicates for each treatment. Since there was no significant block effect, the percent of oysters eaten was arcsine-transformed to meet assumptions of normality and analyzed by a two-factor ANOVA for the effects of run and predator size (Zar 1999). The number of mud crabs surviving was also analyzed via a two-factor ANOVA with predator size blocked by run.

Field experiment

In order to examine the size- or biomass-dependent effects of blue crabs on mud crabs in the field, we caged mud crabs onto artificially constructed oyster reefs in the intertidal zone at Priest's Landing, Skidaway Island, GA, USA. This site is located along the Wilmington River entrance to Wassaw Sound and is characterized by a combination of *Spartina* grasses, loose cluster and fixed oyster reefs, and slow to moderate water velocities (3–10 cm s^{-1}; Smee et al. 2010). Blue crabs and mud crabs are common predators of oysters at this site.

Experiments were performed on mud substrates in the lower section of the intertidal zone, approximately one tidal foot below the level of local oyster reefs. The foraging success of mud crabs on juvenile oysters within experimental cages was monitored in response to predator biomass treatments from laboratory experiments; one large blue crab (>100 mm CW; approximately 130–180 g), one small blue crab (40–60 mm CW; 8–20 g), multiple small blue crabs (40–60 mm CW; totaling 130–180 g), and a no-predator control. Because cage recovery was limited to a short period at low tide, three replicates were run at a time in a randomized block design. Each treatment cage within a block was approximately 5 m apart and each experimental block was 30 m apart (i.e. block site). Three runs were completed, totaling 9 replicates.

Experimental enclosure cages (0.7 m × 0.7 m × 0.3 m) were constructed of polyvinyl chloride (PVC) frames and covered with vexar mesh (mesh size: 1 cm^2). An oyster reef was constructed on one side of the caged area from a combination of both natural reef and artificial oyster clusters (Fig. 1). The majority of the reef structure was comprised of four natural sun bleached oyster clusters (~0.20 m diameter), which maintained the structure of oyster reefs while removing live organisms that could serve as an alternate food source. Further, these small oyster clusters are common to the local area where they are often
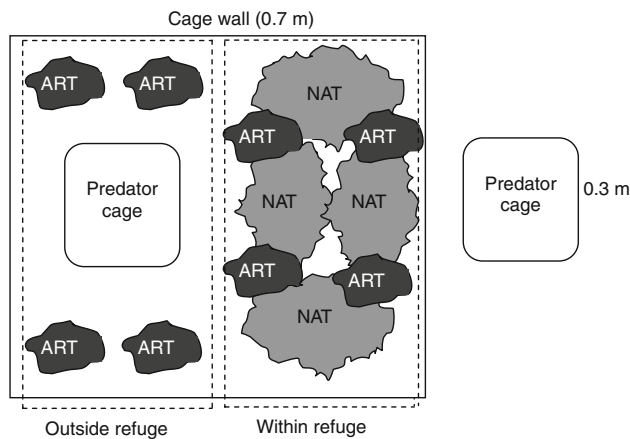
Fig. 1 Diagram of caged reef design in field experiment showing natural dried oyster reef clusters (*NAT*) and artificial oyster clusters with 4 attached live juvenile oysters (*ART*). Oysters eaten on artificial reef among natural reef structure were designated as 'Within refuge predation'. Oysters consumed on artificial clusters separated from natural reef were designated 'Outside refuge predation'. Predator cages were placed on either side of the oyster reef refuge so that predator cues reached the refuge in both tidal directions

interspersed with either intertidal shell hash or mud flats. Artificial oyster clusters were used to control for the placement oysters within the cage and each cluster had four oysters (10–16 mm length) secured to its face with cyanoacrylate glue. Within each enclosure (Fig. 1), four artificial clusters each were placed inside the reef (within the refuge) and outside the reef (outside the refuge) for a total of 16 juvenile oysters both inside and outside the habitat refuges. We estimated the level of refuge use by mud crabs by measuring the number of oysters eaten both inside and outside the refuge. This information provided insight on the risk assessment behaviors of mud crabs; higher numbers of oysters eaten outside refuge would suggest that mud crabs perceived the environment as less risky. Fifteen mud crabs (8 of 15–20 mm CW; 4 of 20–25 mm CW; 3 of 25–30 mm CW—similar to local population size structure and densities; Lee and Kneib 1994; Hollebone and Hay 2007) were placed within the oyster reef refuge. Each mud crab was marked with paint to differentiate it from potential mud crab immigrants into the cages. The influence of predator chemical cues was examined by placing caged predators on either side of the oyster reef refuge so that predator cues reached the refuge in both tidal directions. One predator cage was placed inside the main enclosure among the artificial clusters outside the main reef refuge. The second predator cage was placed on the other side of the refuge outside the enclosure walls (Fig. 1). We thought this design was a reasonable compromise between two potentially counter-acting influences of the enclosure cage mesh, which can restrict cue exchange across the mesh, but result in greater mixing of cues passing through the mesh. As we

describe below, flow measurements suggest the cages did not strongly alter the hydrodynamic environment inside the cage.

Predator cages consisted of half-cylinder vexar cages (0.30 m diameter × 0.30 m long, mesh size: 1 cm²) placed on their side. Cage bottoms were covered with mesh screening to prevent blue crabs from accessing any mud crabs that sometimes sheltered under the cage as well as to prevent mud crabs from accessing predator food. All cages were secured to the substrate with stakes of reinforcement bar. Predators were fed a diet of crushed oysters every day to ensure they were always producing cues. In addition, crab pots baited with three chicken necks were used to assess local abundance of blue crabs during each experimental run, as cues from mobile blue crabs could affect experimental outcomes. The number of oysters remaining on each artificial cluster was counted every 24 h for 48 h. Any mud crabs found within cages and all oyster clusters were collected at the end of the 48-h period, and were then transported back to the laboratory. Clusters were rinsed, and sorted for mud crabs to assure our counts of mud crabs were as accurate as possible. We determined the number of experimentally marked mud crabs as well as the number and carapace width of any immigrant mud crabs.

Preliminary analysis showed that experimental run (i.e. time), but not site (block) had a significant effect on the percent of oysters eaten; thus, all data from sites were pooled and subsequent analysis was blocked by experimental run (time). The percent of oysters eaten after 48 h was analyzed by a two-factor ANOVA for the effects of run and predator size. The number of oysters eaten inside and outside the refuge was compared using a two-factor repeated measures (or split-plot) ANOVA with oysters eaten inside the refuge and outside the refuge treated as a within-block/repeated measures factor. The number of mud crabs (>15 mm CW) found in the cage at the conclusion of the experiment (both experimental and immigrant crabs) was also analyzed by a two-factor ANOVA. All mud crab immigrants above 15 mm CW were included in this count as they may also have contributed to predation on oysters within cages (Hill, unpublished data).

Flow measurements in the field

Flow conditions vary over space and time in tidal-driven estuaries (Smee et al. 2010; Wilson 2011), and differing flow conditions could have significantly impacted the perception of chemical cues and thus the outcome of NCEs in each of our experimental runs. Consequently, we measured flow conditions over the course of our experiments in an attempt to determine if any changes in NCEs observed throughout our field experiment could be attributed to changing flow characteristics. Flow conditions were

monitored over the course of each experimental run using one acoustic Doppler velocimeter (ADV; Nortek). The flow was monitored in the same location and tidal height, over mud substrates and several meters away from experimental cages. The ADV was mounted so that flow measurements occurred at approximately 15 cm over the substrate, and aligned so that the u-velocity component was in the primary tidal-flow direction. Flow velocities were measured at a frequency of 16 Hz for 5 min every 15 min over the course of the experiment.

As our experiments were performed within cages, we performed additional measurements examining the effect of our cages on local flow parameters. Caging can often affect the magnitude of multiple flow parameters (Nowell and Jumars 1984; Miller and Gaylord 2007) and potentially inhibit (i.e. increase turbulence) or facilitate (i.e. decrease velocity) the ability of animals to perceive cues. Flow measurements taken inside the cage were compared to those taken outside the cage at two locations for each experimental block position. One cage was modified by cutting a 10-cm swath from the top to allow for an ADV to be mounted in the center and measure flow velocities inside the cage. The cage was then secured with reinforcement bar stakes. Two other ADVs were mounted outside the cage; one 30 cm directly upshore from the cage and the other 5 m away at the same tidal height. These comparisons were repeated at the position of each block position of the predation trials in order to examine whether cage effects differ between blocks. All ADVs were mounted so that flow measurements occurred at 17 cm above the substrate, slightly greater than mid-height within the cage. Flow velocities were measured at a frequency of 16 Hz for 5 min every 15 min for approximately 12 h. Both the total velocity and turbulent kinetic energy were calculated from these measurements.

Total velocity (U) was calculated by the formula, $U = \sqrt{u^2 + v^2 + w^2}$, where u, v, and w represent the velocity components x (along-stream), y (cross-stream), and z (vertical) directions. Turbulent kinetic energy (TKE) represents the magnitude of the velocity fluctuations (i.e. turbulence) that mix chemical cues and potentially decrease perception. TKE was calculated by the formula $TKE = 1/2\left(\overline{u'^2} + \overline{v'^2} + \overline{w'^2}\right)$, where u', v', and w' represents the magnitude of deviations of each velocity sample from the mean burst velocity in the x, y and z directions, averaged per burst. Data for total velocity and TKE taken over the three experimental runs were unable to be transformed for normality. However, as ANOVAs are typically robust for non-normal distributions (Zar 1999), we completed the analysis for this dataset by a two-factor ANOVA for run (1, 2, 3) and tide status (Incoming, Outgoing). We confirmed significance values for run and tide status using

a one-way non-parametric Kruskal–Wallis (K–W). We also examined the effects of total velocity on the percent of oysters eaten using a univariate ANCOVA in which the average total velocity of each run was used as a covariate for each replicate block and treatment within that experimental run. The ANCOVA was first completed with an interaction term of treatment × average total velocity to confirm slopes were homogenous and then run as a univariate ANCOVA without interactions (Engqvist 2005). Additionally, to examine the effect of the cages on the flow environment, measurements of the total velocity and TKE in and adjacent to cages were square root-transformed to meet assumptions of normality and analyzed by a three-factor ANOVA for ADV position (inside the cage, outside the cage, 5 m away from cage), Site (Block position 1, 2, 3), and Tide Status (Incoming, Outgoing).

Results

Laboratory experiment

Chemical cues from blue crab predators had a significant biomass-dependent effect on the percentage of oysters eaten by mud crabs (Fig. 2a; $F_{3,48} = 7.75$, $P < 0.001$). Cues from high biomass treatments (large and multiple small caged blue crabs) suppressed the percent of oysters consumed by mud crabs by approximately 20–25 %. In contrast, single small blue crabs did not suppress mud crab foraging and consumption was not significantly different from no predator controls (Fig. 2a). The experimental run also affected the number of oysters eaten ($F_{5,48} = 5.41$, $P = 0.001$), but there was no run × predator treatment interaction ($F_{15,48} = 1.62$, $P = 0.l0$). The number of mud crabs surviving the duration of the experiment varied significantly with run ($n = 18$, $F_{5,48} = 3.02$, $P = 0.019$), but not by predator treatment ($F_{3,48} = 0.73$, $P = 0.53$). We obtained the same results for ANOVA and post hoc tests when the number of oysters eaten in each tank was corrected for mud crab survivorship by dividing predation by the number of surviving mud crabs (data not shown).

Field experiment

Cues from blue crab predator treatments significantly affected the percentage of oysters eaten by mud crabs (Fig. 2b; $n = 9$, $F_{3,23} = 16.01$, $P < 0.001$), as did the experimental run ($F_{2,23} = 5.06$, $P = 0.015$). Consistent with laboratory results, high biomass treatments (large and multiple small blue crabs) suppressed mud crab predation on oysters by approximately 50 % relative to controls
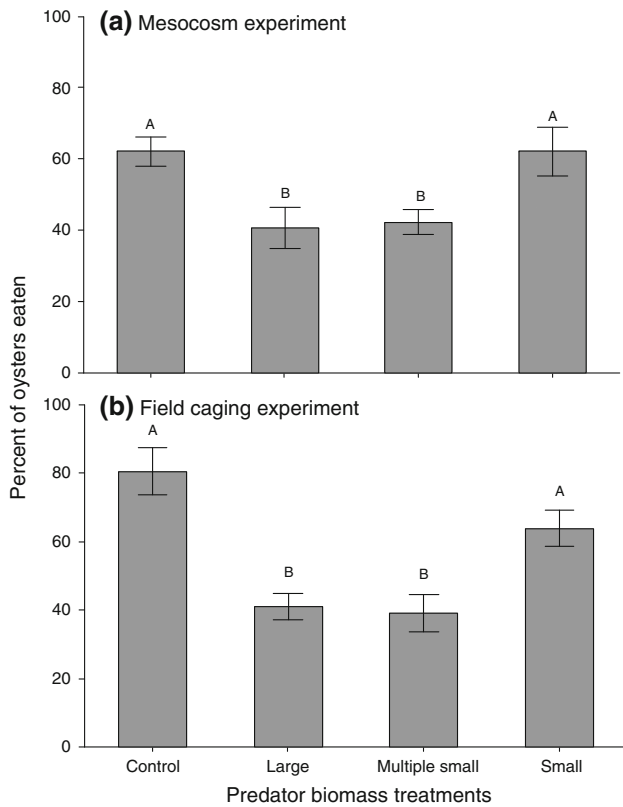
Fig. 2 The percent of oysters eaten by mud crabs (mean ± SE) in **a** laboratory mesocosms and **b** field caging experiments in response to four predator biomass treatments ($n = 18$ in **a**; $n = 9$ in **b**). *Different letters* denote means that are significantly different based on Tukey post hoc tests ($P < 0.05$)

Fig. 3 The number of oysters eaten outside and within the refuge (mean ± SE; $n = 9$)

(Fig. 2b). Oyster survival in response to cues from small blue crabs was not significantly distinguishable from the control. Analysis revealed no run × treatment interaction ($F_{6,23} = 0.75$, $P = 0.61$). The number of mud crabs recovered varied significantly with run ($F_{2,21} = 9.83$, $P = 0.001$) but not by treatment ($F_{3,21} = 0.97$, $P = 0.42$). Approximately 65, 50, and 75 % of mud crabs were recovered on Runs 1, 2, and 3, respectively. Despite differences in mud crab abundance, the ANOVA and post hoc analysis were not different when correcting for the number of recovered mud crabs by dividing the oyster predation by average number of mud crabs recovered by run (data not shown). The number of blue crabs in the environment surrounding the cages was low, with less than 1 crab per trap per day caught on average. Thus, ambient crabs in the environment likely did not influence mud crabs within experimental cages.

As the amount of foraging outside the refuge may indicate the perception of risk by mud crabs (i.e. increased predation outside the refuge indicates a low risk environment), a repeated measures (or split-plot) ANOVA was used to analyze differences in the number of oysters eaten inside and outside the refuge (within-subject factor).
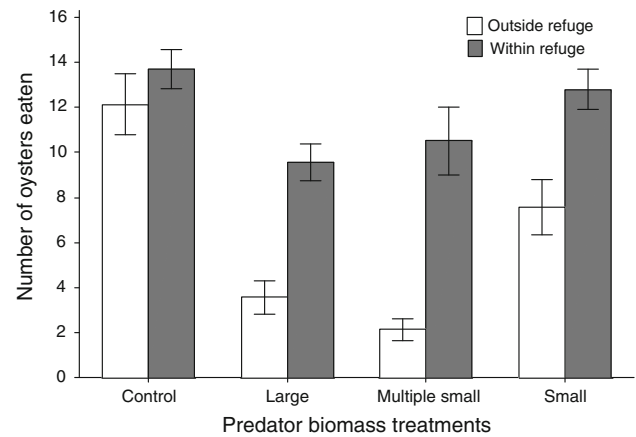
Both blue crab predator treatment (Fig. 3; $F_{3,23} = 16.23$, $P < 0.001$) and run ($F_{2,23} = 4.93$, $P = 0.017$) significantly affected the number of oysters eaten inside and outside the refuge, but there was no predator treatment × run interaction ($F_{6,23} = 0.812$, $P = 0.57$). Predation on oysters was significantly different as a function of position (inside or outside refuge; $F_{1,23} = 120.39$, $P < 0.001$), but the magnitude of this effect was dependent upon the predator treatment (Position × Treatment; $F_{3,23} = 8.24$, $P = 0.001$) and run (Position × Run; $F_{2,23} = 5.39$, $P = 0.012$). The greatest amount of predation in either position occurred in no predator controls where there was no apparent preference for oysters inside or outside the refuges (Fig. 3). Mud crabs showed a small preference for oysters within the refuge in response to single small blue crabs, but predation rates were high in both positions, averaging 8 and 12 oysters eaten outside and inside the refuge (of 16 total in each position). Mud crabs strongly preferred to forage within the refuge in the presence of high biomass treatments (large and multiple small blue crabs); on average, only 3 oysters were consumed outside reef refuges whereas approximately 10 were consumed inside the refuge (Fig. 3). The full interaction term was not significant (Position × Treatment × Run; $F_{6,23} = 1.62$, $P = 0.18$).

Flow measurements

Ranges of both the velocity and TKE generally overlapped over the course of the experimental runs, indicating that organisms experienced similar conditions (Fig. 4). Total velocity, but not TKE, was significantly different over the course of experimental runs (Fig. 4; ANOVA $F_{2,386} = 11.49$, $P < 0.001$, K–W $P = 0.005$; ANOVA, $F_{2,386} = 2.96$, $P = 0.053$; K–W $P = 0.40$ for velocity and TKE, respectively). Both total velocity ($F_{1,386} = 153.09$, $P < 0.001$; K–W $P = 0.005$) and TKE ($F_{1,386} = 20.73$, $P < 0.001$; K–W $P < 0.001$) were significantly higher on
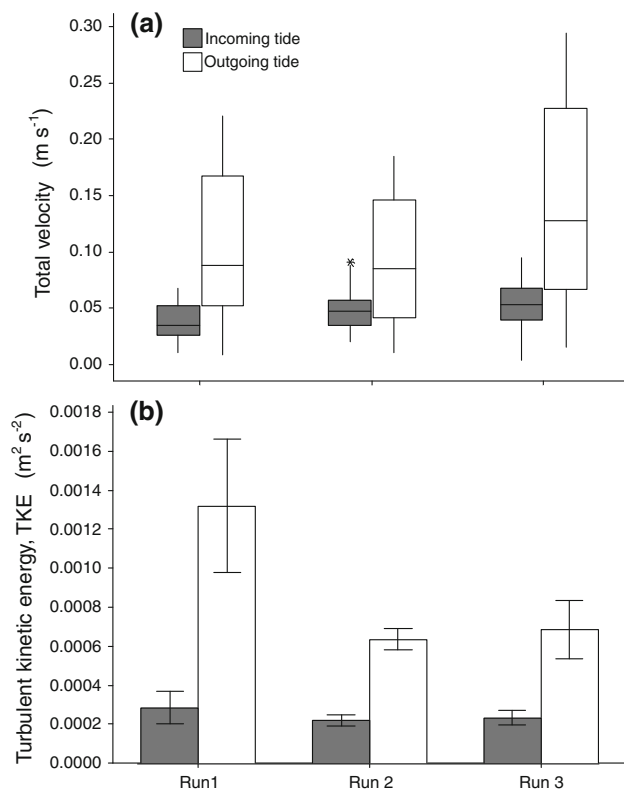
Fig. 4 Environmental flow characteristics of seawater measured during incoming and outgoing tides on three experimental runs in the field. **a** Box plot of total velocity. Each *box* represents the median, upper, and lower quartiles of data distribution. *Whiskers* represent 95 % confidence intervals and the *asterisk* denotes an outlier that was not excluded in analysis. **b** Turbulent kinetic energy (*TKE*; mean ± SE)

outgoing tide versus the incoming tide (Fig. 4). The difference in total velocity was more pronounced in run three where outgoing tide velocities were higher than the previous two runs (Fig. 4a; Run × Tide Status, $F_{2,386} = 6.66$, $P = 0.001$). As the significant changes in total velocity across the experimental runs could have contributed to differences in NCEs over time, we examined the effect of velocity and predator treatment on the percent of oysters eaten in a univariate ANCOVA, with and without interactions terms with the covariate. The interaction term in the initial ANCOVA of predator treatment × total velocity was not significant ($F_{3,27} = 0.79$, $P = 0.50$), demonstrating that the slopes of the treatment groups were homogenous (Engqvist 2005). In the univariate ANCOVA, the percent of oysters eaten was significantly dependent on both the predator treatment ($F_{3,30} = 16.66$, $P < 0.001$) and the average total velocity ($F_{1,30} = 9.01$, $P = 0.005$), indicating that flow had some effect on the behavioral suppression of mud crabs by blue crab predators. The effect size (partial η^2) indicated that total velocity was responsible for 23 % of the variance in the amount of oysters eaten. However, since we used an average velocity for each

experimental run, we cannot clearly distinguish a velocity effect from a time (run) effect as reported in the previous ANOVA. Consequently, this variance may be attributable to varying velocities in addition to other time-sensitive factors (i.e. hunger levels, seasonality, etc.).

ADVs placed in and around cages characterized the flow environment at the site of each experimental block. Unfortunately, beam correlation values were less than 60 % (i.e. an object was blocking the sensor) for one of the ADVs at Site 1, so data from Site 1 were excluded. Flows were slightly, but significantly, modified by cage walls. Analysis of flow data by ANOVA revealed that cages significantly dampened the total velocity (Fig. 5a; $F_{2,189} = 11.32$, $P < 0.001$), but the magnitude of the dampening tended to be affected by flow velocities related to tide status (ADV Position × Tide Status, $F_{2,189} = 2.28$, $P = 0.10$). Flow velocity was generally greater by ∼4 to 6 cm s^{-1} on the outgoing versus incoming tide (Tide Status, $F_{1,189} = 88.90$, $P < 0.001$). During the higher velocities of outgoing tides, cage mesh dampened velocities to a greater extent than on the incoming tide. Velocities were dampened ∼1 cm s^{-1} on the incoming tide but ∼3 to 4 cm s^{-1} on the outgoing tide. Total velocities were also significantly impacted by block site ($F_{1,189} = 9.63$, $P = 0.002$). However, this difference reflects taking measurements on different days during which tide was transitioning from spring to normal tide levels. Despite these differences, the ranges of velocities in each ADV position overlap, indicating that similar velocity fluctuations were occurring inside cages.

Similar to total velocity, TKE was higher on outgoing tide than incoming tide (Fig. 5b; Tide Status, $F_{1,189} = 10.15$, $P = 0.002$). Cages did modify turbulence levels ($F_{2,189} = 5.73$, $P = 0.004$) but, like velocity, this effect was dependent on the tide status (Tide Status × ADV Position, $F_{2,189} = 6.39$, $P = 0.002$). Cage effects on TKE tended to act opposite to the effects of cages on velocity. Cages increased TKE a very small amount during incoming tides when turbulence levels were generally low. Cages did not affect turbulence levels during outgoing tides when turbulence was generally higher. TKE was not significantly different based on site ($F_{1,189} = 0.62$, $P = 0.43$).

Discussion

Body size has long been recognized as an important factor in structuring ecological communities (Werner and Gilliam 1984; Rudolf 2006; Shackell et al. 2010). Our results extend the importance of this concept by indicating that predator body size and density can significantly impact the magnitude of NCEs through differential behavioral
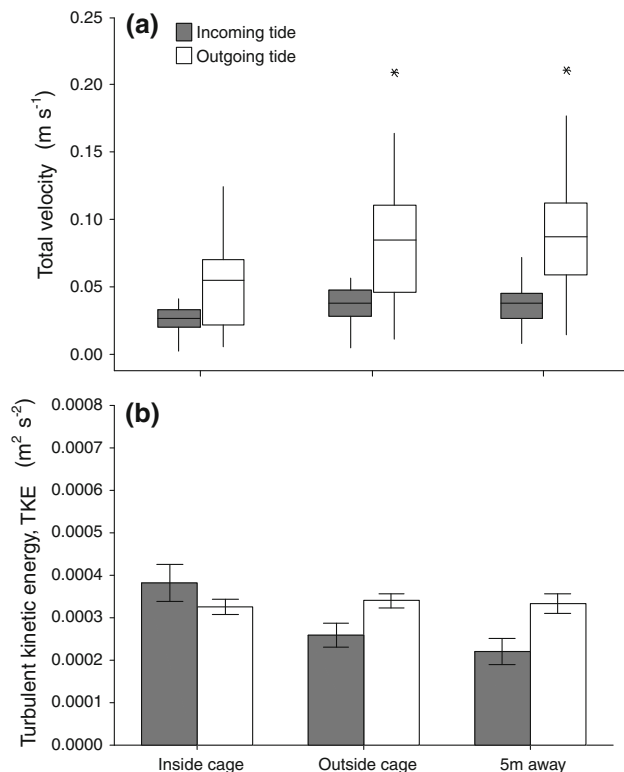
Fig. 5 Flow characteristics measured on incoming and outgoing tide by acoustic Doppler velocimeters (ADVs) placed inside, directly outside, and 5 m away from cages. **a** Box plot of total velocity; each *box* represents the median, upper, and lower quartiles of data distribution. *Whiskers* represent 95 % confidence intervals and *asterisks* denote outliers that were not excluded in analysis. **b** Turbulent kinetic energy (*TKE*; mean ± SE)

responses to predator biomass. These responses include changes in both the overall intensity of predation and refuge use.

In our experiment, high biomass predator treatments composed of large and multiple small blue crabs resulted in increased oyster survivorship in both laboratory mesocosms and in the field (Fig. 2). This increase in oyster survival is likely driven by mud crabs decreasing their movement, foraging activity, and patterns of distribution (Grabowski and Kimbro 2005; Hill 2011). In contrast to the effects of high predator biomass, low predator biomass (i.e. a single small blue crab) did not significantly alter the number of oysters eaten relative to control cages in the laboratory or in the field (Fig. 2), and patterns of predation outside the refuge habitats indicated that perception of risk in response to low predator biomass was low (Fig. 3). The biomass specific behavioral response allows mud crabs to respond with risk appropriate behaviors to individuals of the two predator size classes. Large blue crabs are high risk predators able to consume large numbers of mud crabs especially in low habitat complexity environments (Hill and Weissburg, in review). In contrast, small blue crabs

were a low risk predator, rarely preying on mud crabs that were greater than 15 mm CW. Mud crab foraging was suppressed by caged single large, but not single small, blue crabs. However, the response of mud crabs to aggregations of small blue crabs versus a single large blue crab was statistically indistinguishable; in other words, mud crabs could not disambiguate individual size from aggregate biomass. Consequently, mud crabs responded equally to multiple small versus single large blue crabs despite the fact that only large blue crabs represented a significant predation risk (Hill and Weissburg, in review).

This apparent inability of mud crabs to distinguish individual size from aggregate predator biomass suggests that risk perception is related to quantitative as opposed to qualitative chemical signal properties. This is the most parsimonious explanation, and is consistent with at least one other report showing that sculpin do not discriminate between water conditioned by single large versus multiple smaller predators using activity level as the assessment metric (Chivers et al. 2001). Whether these densities of small blue crabs produce NCEs in natural conditions is dependent on their distribution; we know of no data examining blue crab aggregations in the field. However, differing size classes of blue crab predators often overlap (Fitz and Weigert 1991; Orth and Montfrans 1987) and densities are highly variable (i.e. 0–6.9 > 25 mm CW m^{-2}; 0–89.2 < 25 mm CW m^{-2}). Thus, aggregate biomass of differing size classes of smaller blue crabs may be sufficient to trigger a response in mud crab prey.

This biomass-specific risk perception introduces another important type of context-sensitivity in NCEs where body size, density, and aggregation will affect the expression of NCEs, at least when risk perception is based on chemical cues. There are two important consequences to this observation. First, since concentration or flux of chemical cues is dependent on both the size of the individual predator and predator density, we may be misestimating both the magnitude and importance of NCEs in natural systems by not including individual predator body mass as an experimental variable, and by ignoring the degree of aggregation. For instance, highly aggregated small predators may have as great an effect as a single larger consumer, and be more likely to induce risk responses, than small predators at lower densities. Similarly, the effects of high small predator densities may have been different in our experiment if these predators were not aggregated away from mud crabs. Consequently, the body mass as well as the distribution and density of predators can influence NCEs, and may have important consequences for direct and cascading effects when those species interactions are often chemically mediated. Future field or modeling studies of chemically-mediated NCEs should be cognizant of the potential role of predator density and size

distributions and explore the role of biomass in modulating risk perception and the expression of NCEs.

Second, the detection of size-based risk via chemical cues appears to operate differently when compared to other sensory modalities, such as vision, and suggests that the role of biomass in the expression of size-based NCEs may be specific to the sensory modality by which predators are detected. By example, several previous studies have demonstrated that individual predator body size affects risk perception when predators are perceived visually (Chivers et al. 2001; Stankowich and Blumstein 2005; Rudolf 2006). Further, visual detection of predators likely also allows prey to differentiate predator size from biomass. For instance, larval spring salamanders (*Eurycea cirrigera*) decrease their activity levels in response to cohorts of large salamander predators (*Gyrinophilus porphyriticus*), but not to small individuals who are less likely to prey upon them (Rudolf 2006). The response to small predators does not differ if the predator density is increased (i.e. increased biomass), although it is unclear if the increase in predator density was enough to produce the cues of a large predator. Consequently, the sensory modality by which risk is determined may have large impacts on how predator size versus biomass affects the expression of NCEs in natural communities. One potential caveat is that prey can combine information from different modalities for better assessment of risk (Chivers et al. 2001), and our experimental design limited other sensory information, particularly visual cues, which may have affected how mud crab prey perceive predator size and biomass. Given the extremely poor visibility in our system, and the presence of complex oyster substrates that further limit visual cues, we consider this a potentially minor effect. Nonetheless, it will be important to recognize, and if possible account for, multimodal risk assessment in many experimental systems, potentially including ours.

Our study also shows that NCEs are expressed in relatively unaltered field conditions in estuarine systems that experience significant changes in water velocity and turbulence over relatively short time periods. A limited number of prior studies in natural conditions (Powers and Kittinger 2002; Smee et al. 2008) indicate that the fluid environment can change the scale and likelihood of prey perception of predator cues, and, thus, the potential for NCEs to be expressed. In our study, we found that the field environment did not impede the NCEs between blue crabs and mud crabs, as results were similar in both the laboratory and the field. Although this is only one observation, our results suggest that estimating NCEs in laboratory settings may provide an accurate understanding of effects in moderate flow environments such as ours.

Estuaries display considerable variation in hydrodynamic properties that change over both time and space

(e.g., Smee et al. 2010; Wilson 2011). Not all conditions are permissive of prey perception (Smee et al. 2010), making it important to establish those situations in which NCEs do occur. We found that flow ranges were similar over the course of experimental runs, but the overall average magnitude of total velocity was significantly different, as run 3 exhibits a slightly higher total velocity (Fig. 4a). This is not unexpected as tidal flow is generally extremely variable over time due to differences in waves, tides, and wind. Despite these differences in flow characteristics, NCEs are still expressed over the course of the experiment, and overall patterns of predation in response to blue crabs over the course of the experiment remained unchanged (data not shown). The magnitude of the NCE varies over the course of the runs, as does the average total velocity, a significant covariate. Consequently, differing velocities over time could have contributed to mud crab foraging behavior and aversion to blue crab chemical cues. However, these differences may have also been attributable to other unmeasured time-sensitive variables. Since the velocity covariate was potentially confounded with other variables, and NCEs still occurred over the course of the experiment, we consider the flow effects within our experiment to be minimal.

The flow regime measured within our experiment matches many other sites within the Wassaw Sound system. Ferner et al. (2009), Smee et al. (2010), Berry (2009), and Wilson (2011), all have measured flow within multiple sites in Wassaw sound and various associated tributaries for periods of several hours to several days, and have found that, typically, flow velocity ranges between 3–17 cm s^{-1} (u) and turbulence levels of 1.5–8 cm s^{-1} root mean square of velocity. Velocities within these sites can exceed 20 cm s^{-1} (turbulence levels measured as TKE > 1 m^2 s^{-2}), but these high measurements are typically associated with the 2- to 3-h peak flow period during outgoing tides (Berry 2009; Wilson 2011). Areas within Herb and Moon River (small tributaries furthest from the mouth of Wassaw Sound) experience average flow velocities of approximately 17–20 cm s^{-1} and 23–27 cm s^{-1}, respectively (Smee et al. 2010). These high velocity sites show decreased predation intensity that may result from drag-imposed limits on foraging and decreased predator perception of prey odors, whereas predation at most other sites seems to reflect the balance between the ability of predators and prey to perceive one another (Ferner et al. 2009; Smee et al. 2010). Although measurements of velocity in oyster reef systems are limited, Breitburg et al. (1995) reports similar velocities (4–19 cm s^{-1}) around oyster reefs in Flag Pond, Maryland. Further, Leonard and Luther (1995) document estuarine flow speeds along salt marsh edges as 1–5 cm s^{-1} in southeastern Louisiana and 0.75–12 cm s^{-1} in west-central Florida. Powers and Kittenger (2002)

measured and manipulated bulk flow velocity in intertidal flats in Back Sound, North Carolina, and found that flow velocities exceeded 15 cm s^{-1} only 30 % of the time (again centered around times of peak incoming and outgoing flows), even when flows were enhanced using specially designed flow channels. The commonality of flow regimes within and across multiple estuarine systems suggests that the chemically-mediated NCEs we document likely occur in many of the oyster reef communities along the US Atlantic and Gulf coasts. However, given that flow rates exhibit substantial spatial and temporal (within and across tidal cycles) variability, further field experiments are needed to establish if and how the intensity of the NCEs we document vary with physical regime.

In order to fully examine the interactions of flow and NCEs, it may be more appropriate to sample NCEs on smaller time scales such as incoming versus outgoing tide, where flow characteristics are significantly different (Fig. 4). In our experiment, it is possible that any effects of water flow on NCEs average out over several days. Measuring flow at each of the cages per run could also have helped distinguish the role of flow on NCEs and differentiate time from velocity effects. However, given the difficulty of these measurements, investigating interactions of flow and NCEs is likely better accomplished by performing experiments at sites with differing flow regimes or by manipulating flow in laboratory or field flumes. For instance, Smee et al. (2010) demonstrates differences in clam survival over multiple sites with differing flow characteristic suggesting that perceptive abilities can change across sites with different velocity and mixing levels. Further, flow measurements within and between sites in Wassaw Sound suggest that the flow parameters within sites separated by <10 m are highly correlated (Wilson 2011), suggesting that perceptive abilities of organisms may be more likely to vary between widely separated areas and not within sites.

Performing field experiments on NCEs requires cages that may alter the flow environment (Nowell and Jumars 1984; Miller and Gaylord 2007), but our results suggest we can perform the required manipulations in the field with only small effects. Cages increased TKE by a small, albeit statistically significant, amount during incoming tides when turbulence levels were the lowest (Fig. 5b). This increased turbulence within cages would disperse chemical cues inhibiting perception of predators and NCEs (Smee et al. 2008). In contrast, the impact of cages on water velocities may have increased perception of predators, as cages generally dampened the total water velocity, possibly allowing cues to remain in cages for longer periods (Fig. 5a). Thus, the different cage-related effects have opposite effects on perception, suggesting the overall impact was minor. In addition, it is important to note that,

although cages did affect water flow characteristics, both velocity and TKE still fell within ranges of those seen outside the cage.

Finally, although our field experiment is a necessary attempt to characterize NCEs under environmental parameters consistent with many estuarine environments, it does not address all potential difficulties commonly encountered when examining NCEs in both the laboratory and the field. As in most studies to date, the necessity of confining predators to experimental plots resulted in a 'press' experiment where blue crab predators were present throughout the course of the experiments that spanned a short period of time. Although we did not measure cue output or persistence, this design conceivably allowed for blue crab chemical cues to reach mud crabs at all times. Since blue crabs are typically mobile predators, both the confinement of predators and the short time scale of our experiment may have increased the strength of the NCEs (Lima and Bednekoff 1999; Werner and Peacor 2003). As in many systems, examinations of the strength of NCEs over longer time scales are still needed to accurately estimate the role of NCEs.

In conclusion, our results demonstrate cues from blue crabs can suppress mud crab foraging on oyster prey and affect the degree of refuge use. The magnitude of this NCE is significantly modulated by predator biomass where large risky predators and multiple small predators cause large suppressions of mud crab foraging and increased refuge use, in contrast to effects seen in the presence of individual small non-risky blue crabs. Furthermore, these interactions occur in the field in tidally-driven flow environments suggesting that NCEs can be an important structuring force in intertidal communities where water flow is produced by waves and tides. This study also contributes to a growing number of investigations suggesting that fisheries managers may need to account for body size distributions of fished species in order to understand cascading interactions (Benoit and Swain 2008; Darimont et al. 2009; Shackell et al. 2010), since local biomass will be the product of density and body size. Blue crabs are among many species currently experiencing shifts to smaller body size distributions as a result of over exploitation (Lipcius and Stockhausen 2002). This alteration of size structure and its resulting impacts to NCEs may have significant negative consequences for oyster reefs if the loss of larger sized individuals is not replaced by high densities of juveniles that can trigger similar risk responses in oyster mesopredators. Future efforts should further examine the role of consumers and their body size on NCEs in order to determine the full impact to fished species and estuarine communities. In the future, it may be necessary to protect species from overfishing to preserve the stability of food webs, and also to preserve their biomass and/or population size structure to

maintain predator traits and cascading NCEs (Shackell et al. 2010).

References

Anholt BR, Werner E, Skelly DK (2000) Effect of food and predators on the activity of four larval ranid frogs. Ecology 81:3509–3521. doi:10.1890/0012-9658(2000)081[3509:EOFAPO]2.0.CO;2

Benoit HP, Swain DP (2008) Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. Can J Fish Aquat Sci 65:2088–2104

Berry WA (2009) A hydrodynamic characterization of tidal ecosystems with respect to predation. MS thesis, Georgia Institute of Technology, Atlanta

Bisker R, Castagna M (1987) Predation on single spat oysters *Crassostrea virginica* by blue crabs *Callinectes sapidus* and mud crabs *Panopeus herbstii*. J Shellfish Res 6:37–40

Bolnick DI, Preisser EL (2005) Resource competition modified the strength of triat-mediated predator-prey interactions: a meta-analysis. Ecology 86:2771–2779. doi:10.1890/04-1249

Breitburg DL, Palmer MA, Loher T (1995) Larval distributions and the spatial patterns of settlement of an oyster reef fish: responses to flow and structure. Mar Ecol Prog Ser 125:45–60. doi:10.3354/meps125045

Chivers DP, Mirza RS, Bryer PJ, Kiesecker JM (2001) Threat-sensitive predator avoidance by slimy sculpins: understanding the importance of visual versus chemical information. Can J Zool 79:867–873

Cohen JE, Pimm SL, Yodzis P, Saldana J (1993) Body sizes of animal predators and animal prey in food webs. J Anim Ecol 62:67–78

Crumrine PW (2005) Size structure and substitutability in an odonate intraguild predation system. Oecologia 145:132–139. doi:10.1007/s00442-005-0084-6

Darimont CT, Carlson CM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC (2009) Human predators outpace other agents of trait change in the wild. PNAS 106:952–954. doi:10.1073/pnas.0809235106

Dodson SI (1970) Complementary feeding niches sustained by size-selective predation. Limnol Oceanogr 15:131–137

Eggleston DB (1990) Functional responses of blue crabs *Callinectes sapidus* feeding on juvenile oysters *Crassostrea virginica* (Gmelin)—effects of predator sex and size, and prey size. J Exp Mar Biol Ecol 143:73–90. doi:10.1016/0022-0981(90)90112-P

Engqvist L (2005) The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. Anim Behav 70:967–971. doi:10.1016/j.anbehav.2005.01.016

Ferner MC, Smee DL, Weissburg MJ (2009) Habitat complexity alters lethal and non-lethal olfactory interactions between predators and prey. Mar Ecol Prog Ser 374:13–22. doi:10.3354/meps07764

Ferrari MCO, Wisenden BD, Chivers DP (2010) Chemical ecology of predator-prey interactions in aquatic ecosystems: a review and prospectus. Can J Zool 88:698–724. doi:10.1139/Z10-029

Fitz HC, Weigert RG (1991) Utilization of the intertidal zone of a salt marsh by the blue crab *Callinectes sapidus*: density, return frequency, and feeding habits. Mar Ecol Prog Ser 76:249–260

Forrester GE (1994) Influences of predatory fish on the drift dispersal and local density of stream insects. Ecology 75:1208–1218

Gibbons MC, Castagna M (1985) Biological control of predation by crabs in bottom cultures of hard clams using a combination of crushed stone aggregate, toadfish, and cages. Aquaculture 47:101–104. doi:10.1016/0044-8486(85)90056-0

Grabowski JH (2004) Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. Ecology 85:995–1004. doi:10.1890/03-0067

Grabowski JH, Kimbro DL (2005) Predator avoidance behavior extends trophic cascades to refuge habitats. Ecology 86:1312–1319. doi:10.1890/04-1216

Grabowski JH, Hughes AR, Kimbro DL (2008) Habitat complexity influences cascading effects of multiple predators. Ecology 89:3413–3422. doi:10.1890/07-1057.1

Griffen BD, Byers JE (2006a) Partitioning mechanisms of predator interference in different habitats. Oecologia 146:608–614. doi:10.1007/s00442-005-0211-4

Griffen BD, Byers JE (2006b) Intraguild predation reduces redundancy of predator species in multiple predator assemblage. J Anim Ecol 75:959–966. doi:10.1111/j.1365-2656.2006.01115.x

Hill JM (2011) Predator biomass and habitat characteristics affect the magnitude of consumptive and non-consumptive effects (NCEs): experiments between blue crabs, mud crabs, and oyster prey. PhD dissertation. Georgia Institute of Technology, Atlanta

Hollebone AL, Hay ME (2007) Propagule pressure of an invasive crab overwhelms native biotic resistance. Mar Ecol Prog Ser 342:191–196. doi:10.3354/meps342191

Kats LB, Dill LM (1998) The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5:361–394

Kusch RC, Mirza RS, Chivers DP (2004) Making sense of predator scents: investigating the sophistication of predator assessment abilities of fathead minnows. Behav Ecol Sociobiol 55:551–555. doi:10.1007/s00265-003-0743-8

Lee SY, Kneib RT (1994) Effects of biogenic structure on prey consumption by the xanthid crabs *Eurytium limosum* and *Panopeus herbstii* in a salt marsh. Mar Ecol Prog Ser 104:39–47

Leonard LA, Luther ME (1995) Flow hydrodynamics in tidal marsh canopies. Limnol Oceanogr 40:1474–1484

Lima SL (1998) Non-lethal effects in the ecology of predator prey interactions. Bioscience 48:25–34

Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredatorbehavior: the predation risk allocation hypothesis. Am Nat153:649–659

Lipcius RN, Stockhausen WT (2002) Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Mar Ecol Prog Ser 226:45–61. doi:10.3354/meps226045

McIntosh AR, Peckarsky BL, Taylor BW (2004) Predator-induced resource heterogeneity in a stream food web. Ecology 85:2279–2290. doi:10.1890/03-0196

Micheli F (1997) Effects of predator foraging behavior on patterns of prey mortality in marine soft bottoms. Ecol Monogr 67:203–224. doi:10.1890/0012-9615(1997)067[0203:EOPFBO]2.0.CO;2

Miller LP, Gaylord B (2007) Barriers to flow: the effects of experimental cage structures on water velocities in high energy subtidal and intertidal environments. J Exp Mar Biol Ecol 344:215–228. doi:10.1016/j.jembe.2007.01.005

Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension feeding bivalve molluscs: a review. J Shellfish Res 23:51–61

Nowell ARM, Jumars PA (1984) Flow environments of aquatic benthos. Annu Rev Ecol Syst 15:303–328

O'Connor NE, Grabowski JH, Ladwig LM, Bruno JM (2008) Simulated predator extinctions: predator identity affects survival and recruitment of oysters. Ecology 89:428–438. doi:10.1890/06-2029.1

Orth RJ, van Montfrans J (1987) Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus* I. Season and annual variations in abundance with emphasis on post settlement juveniles. Mar Ecol Prog Ser 41:283–294

Peckarsky BL, Abrams PA, Bolnick DI, Dill LM, Grabowski JH, Luttbeg B, Orrock JL, Peacor SD, Preisser EL, Schmitz OJ, Trussel GC (2008) Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology 89:2416–2425. doi:10.1890/07-1131.1

Powers SP, Kittinger JN (2002) Hydrodynamic mediation of predator-prey interactions: differential patterns of prey susceptibility and predator success explained by variation in water flow. J Exp Mar Biol Ecol 273:171–187. doi:10.1016/S0022-0981(02)00162-4

Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501–509. doi:10.1890/04-0719

Rochette R, Dill LM, Himmelman JM (1997) A field test of threat sensitivity in a marine gastropod. Anim Behav 54:1053–1062. doi:10.1006/anbe.1997.0488

Rudolf VHW (2006) The influence of size-specific indirect interactions in predator-prey systems. Ecology 87:362–371. doi:10.1890/05-0961

Schmitz OJ (2008) Effects of predator hunting mode on grassland ecosystem functioning. Science 319:952–954. doi:10.1126/science.1152355

Schmitz OJ, Suttle KB (2001) Effects of top predator species on direct and indirect interactions in a food web. Ecology 82:2072–2081. doi:10.1890/0012-9658(2001)082[2072:EOTPSO]2.0.CO;2

Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait mediated indirect interactions. Ecol Lett 7:153–163. doi:10.1111/j.1461-0248.2003.00560.x

Schoeppner NM, Relyea RA (2005) Damage, digestion, and defence: the roles of alarm cues and kairomones for inducing prey defences. Ecol Lett 8:505–512. doi:10.1111/j.1461-0248.2005.00744.x

Schoeppner NM, Relyea RA (2008) Detecting small environmental differences: risk-response curves for predator-induced behavior and morphology. Oecologia 154:743–754. doi:10.1007/s00442-007-0862-4

Seed R (1980) Predator-prey relationships between the mud crab *Panopeus herbstii*, the blue crab *Callinectes sapidus* and the atlantic ribbed mussel *Geukensia demissa*. Estuar Coast Mar Sci 11:445–458

Shackell NL, Frank KT, Fisher JAD, Petrie B, Leggett WC (2010) Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. Proc R Soc Lond B 277:1353–1360. doi:10.1098/rspb.2009.1020

Smee DL, Ferner MC, Weissburg MJ (2008) Alteration of sensory abilities regulates the spatial scale of nonlethal predator effects. Oecologia 156:399–409. doi:10.1007/s00442-008-0995-0

Smee DL, Ferner MC, Weissburg MJ (2010) Hydrodynamic sensory stressors produce nonlinear predation rates. Ecology 91:1391–1400. doi:10.1890/09-0017.1

Stankowich T, Blumstein DT (2005) Fear in animals: a meta-analysis and review of risk assessment. Proc R Soc Lond B 272:2627–2634. doi:10.1098/rspb.2005.3251

Trussel GC, Ewanchuck PJ, Bertness MD (2002) Field evidence of trait mediated indirect interactions in a rocky intertidal food web. Ecol Lett 5:241–245. doi:10.1046/j.1461-0248.2002.00304.x

Trussel GC, Ewanchuk PJ, Matassa CM (2006) Habitat effects on the relative importance of trait and density mediated indirect interactions. Ecol Lett 9:1245–1252. doi:10.1111/j.1461-0248.2006.00981.x

Turner AM, Fetterolf SA, Bernot RJ (1999) Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail. Oecologia 118:242–247. doi:10.1007/s004420050724

Van Buskirk J, Arioli M (2002) Dosage response of an induced defense: how sensitive are tadpoles to predation risk? Ecology 83:1580–1585. doi:10.1890/0012-9658(2002)083[1580:DROAID]2.0.CO;2

Weissburg MJ (2000) The fluid dynamical context of chemosensory behavior. Biol Bull 198:188–202

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425

Werner EE, Peacor SD (2003) A review of trait mediated indirect interactions in ecological communities. Ecology 84:1083–1100. doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Wilson ML (2011) Sensory landscape impacts on odor-mediated predator-prey interactions at multiple spatial scales in salt marsh communities. PhD dissertation, Georgia Institute of Technology, Atlanta

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, Upper Saddle River

Zimmer RK, Zimmer CA (2008) Dynamic scaling in chemical ecology. J Chem Ecol 34:822–836. doi:10.1007/s10886-008-9486-3