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Crabs interpret the threat of predator body size and biomass via cue concentration and diet

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Greater predator body size is often associated with greater predation risk. According to the threat-sensitive predator avoidance hypothesis, prey should display graded responses to increasing predator body size; in turn, these differences in behaviour should also cause differing indirect effects. Yet, in aquatic systems, where prey often use chemical cues to judge predator threats, the role of chemically mediated perception of predator body size and the propagation of indirect effects are still unclear. To differentiate intraspecific predator size via chemical cues, prey must judge predator threat quantitatively (i.e. via concentration) or qualitatively (i.e. via differing cues and/or diets). We investigated the role of individual and aggregate predator body size (i.e. biomass, cue concentration) and qualitative diet cues in antipredator behaviour and indirect interactions by examining the behavioural responses of the mud crab *Panopeus herbstii* and the survival of oyster prey (*Crassostrea virginica*) in response to various blue crab, *Callinectes sapidus*, biomass and diet treatments. Mud crabs increased their refuge use and decreased foraging in response to chemical cues from large, but not small, individual blue crabs. The perception of predator size appeared to be related to predator biomass as multiple small blue crabs and large crabs elicited similar foraging responses in mud crabs. However, multiple small blue crabs failed to affect mud crab refuge use, indicating that some measures of behaviour may not always be predictive of indirect effects. Predator diet also influenced mud crab behaviour and foraging: predators fed mud crabs elicited a greater antipredator response than crushed conspecifics or predators fed oyster diets, suggesting that qualitative cues also influence intraspecific threat perception and indirect interactions. These experiments demonstrate that we cannot successfully predict indirect interactions without considering predator population size structure and measuring indirect effects.

Predation is an important force in structuring ecological communities and imposes high selection pressure on prey to develop strategies to avoid being eaten (Dawkins & Krebs, 1979). One such strategy is predator threat assessment, in which prey use a variety of sensory cues to determine the likelihood of danger from an individual predator and the need to perform antipredator behaviours that increase survivorship (Lima, 1998). Yet, assessing predator threats can be complex as predation risk can vary both between predators and between individuals of a single predator species. For instance, snails differentiate between predator cues and crawl underneath leaf litter to escape sunfish, but crawl towards the water surface in response to crayfish cues (Turner, Fetterolf, & Bernot, 1999). Within predator species, predation threat can change based on life history stage (i.e. juvenile/adult, moulting, hibernation), time of year when predators are most abundant or most active and/or location (Basille, Fortin, Dussault, Ouellet, & Courtois, 2012; Griffen, Toscano, & Gatto, 2012; Lipcius & Herrnkind, 1982; Sheriff, Krebs, & Boonstra, 2011; Yen, 1983). Differences in threat-specific behaviours are important because they can greatly influence community structure by altering foraging behaviour and fitness of prey (Ferrari, Wisenden, & Chivers, 2010; Kats & Dill, 1998; Stankowich & Blumstein, 2005), which can indirectly affect the survival of the prey's resource (often called trait-mediated indirect interactions, or nonconsumptive effects: Abrams, 2007; Preisser, Bolnick, & Benard, 2005; Werner & Peacor, 2003). Therefore, understanding how prey assess predator threat is essential to predict outcomes for prey survival and cascading indirect effects.

Predator body size is an intraspecific trait often associated with greater predatory threat and frequently determines where predators feed, as well as their feeding rates and diet choices (Cohen, Pimm, Yodzis, & Saldana, 1993; Werner & Gilliam, 1984). Furthermore, size-based predator traits lead to numerous cascading

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indirect interactions in communities (Dodson, 1970; Rudolf, 2006; Werner & Gilliam, 1984). However, despite its importance in predicting predator–prey outcomes, the role of predator body size in threat assessment and its propensity to propagate indirect effects are still understudied, especially in aquatic communities and for nonvisual modalities. According to the threat-sensitive predator avoidance hypothesis (Helfman, 1989), prey will respond to predators with antipredator behaviours that match predator threat levels. Thus, if increasing predator size is indicative of greater threat, prey should display greater antipredator responses to larger predators, and this would translate into stronger cascading effects on prey resources.

In many aquatic communities, the perception of predator threat often is determined by chemical cues emanating from predators or crushed conspecifics (Kats & Dill, 1998) since the transmission of acoustic or visual cues is more limited (Dusenberry, 1992). Predator body size may also be chemically perceived through differing cues (Kusch, Mirza, & Chivers, 2004) or through greater cue release (i.e. concentration; Chivers, Mirza, Bryer, & Kiesecker, 2001; Pettersson, Nilsson, & Bronmark, 2000) from larger predators. For example, Kusch et al. (2004) found that minnows responded to sympatric small pike predators more than they did to allopatric large pike predators, suggesting that differing cues were responsible for size-based perception. In contrast, Chivers et al. (2001) and Pettersson et al. (2000) found that prey fishes avoided large, but not small, fish predators, suggesting concentration-dependent responses. Importantly, the manner in which size is chemically communicated (i.e. either quantitatively or qualitatively) may cause differing behavioural responses and indirect effects on prey resources depending on predator population size structure and/or predator density. For instance, if the perception of size is concentration based, small predators at high densities may elicit behavioural responses and indirect effects similar to those of a single large predator. In contrast, if prey respond to qualitative differences in predator chemical cues, then predators will cause size-specific behavioural effects and indirect effects regardless of predator density. Thus, the perception of size will not only have consequences for antipredator behaviour, but also for numerous cascading interactions that affect community structure.

In systems where predator body size dictates the trophic level where predators feed (i.e. intraguild predation systems or systems containing predators that shift their diet during maturation), diet cues may be beneficial in determining the threat of oncoming predators. Predator diet often affects a prey's evaluation of threat, and diets including conspecifics often result in the greatest antipredator responses as a result of qualitative differences in predator diet cues (Chivers & Mirza, 2001a, 2001b; Ferrari et al., 2010; Schoeppner & Relyea, 2005; Smee & Weissburg, 2006; Turner, 2008). Some prey species show antipredator responses to predators fed a diet of heterospecific prey, but these responses can often decrease with increasing phylogenetic distance of prey in the predator's diet (Schoeppner & Relyea, 2005). However, diet-dependent antipredator behaviours are not ubiquitous (Chivers & Mirza, 2001a, 2001b). Furthermore, similar to studies on chemically mediated body size, studies examining behavioural responses of prey to diet cues of predators often have not examined whether differences in prey behaviour result in differing indirect (cascading) effects. As the magnitude and direction of antipredator behaviour may vary based on predator traits such as size and diet, indirect effects on prey resources may also vary based on predator threat assessment. Yet, how changes in behaviour directly translate into indirect interactions is often inferred but not directly tested.

As predator size and diet may affect predator threat assessment and indirect interactions, we had multiple objectives in our study. Our goals were to (1) investigate the role of predator size and biomass (i.e. cue concentration) in chemically mediated threat perception, (2) examine whether predator diet influences the threat response and (3) determine whether differences in antipredator behaviour due to predator size and diet also translate into indirect effects on prey resources.

METHODS

Model System

To examine the influence of predator biomass and diet in predator threat assessment and the resulting indirect effects, we chose an intraguild predation system consisting of both adult and juvenile blue crabs, *Callinectes sapidus*, the mud crab *Panopeus herbstii*, and their shared oyster prey, *Crassostrea virginica*. This system is ideal for examining size-based interactions because blue crabs are generalist predators, predation by crabs is crush limited (i.e. larger body sizes have greater crush strength), prey size scales with predator body size, and size classes co-occur. The blue crab, which is the top predator in this system, is an important predator and scavenger of estuarine environments (Micheli, 1997) and has been shown to prey on a variety of bivalve and crustacean species (Eggleston, 1990a, 1990b; Fitz & Weigert, 1991; Micheli, 1997). The intermediate prey, mud crabs, are small cryptic xanthid crab predators found in both oyster reef and salt marsh habitats. Mud crabs occupy the interstices of oyster beds at high densities (Hollebone & Hay, 2007; Lee & Kneib, 1994) and prey on a number of bivalve species (Bisker & Castagna, 1987; Seed, 1980). Xanthid and other nonportunid crabs make up approximately 43% of the diet of blue crab (Fitz & Weigert, 1991). Furthermore, risk of predation to mud crabs varies as a function of blue crab predator size; large adult blue crabs (>100 mm carapace width; CW) are voracious predators on mud crabs in laboratory mesocosms, whereas small juvenile blue crabs (40–60 mm CW) rarely present a threat to mud crabs greater than 15 mm CW (Hill & Weissburg, 2013b). Thus, according to the threat-sensitive predator avoidance hypothesis (Helfman, 1989), mud crabs should show stronger antipredator responses to larger blue crabs. A priori, this also suggests that blue crab body size may propagate differing indirect effects.

Animal Collection and Maintenance

All experiments were performed at the Skidaway Institute of Oceanography (SkIO), Skidaway Island, Georgia, U.S.A. over summer months in multiple years from 2008 to 2010. Both blue crabs and mud crabs were collected from Wassaw Sound and associated tributaries with permits from the Georgia Department of Natural Resources. Blue crabs were collected by commercial crab pot and seine net. Mud crabs were collected by hand from loose oyster reef. Hatchery-reared oysters (10–15 mm in length) were obtained from Bay Shellfish (Tampa, FL, U.S.A.). All animals were maintained in covered outdoor flow-through sea water tanks ($0.62 \times 0.50 \times 0.27$ m) at the 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. Blue crabs were not used in experiments if they were premoult. No ovigerous female crabs were utilized in experiments. Animals were held no longer than 2 months and all animals were released into an estuary adjacent to SkIO following the experiments.

Investigating How Prey Encode Size-based Threat

To examine the ability of prey to distinguish predator body size via chemical cues, we monitored mud crabs foraging on oysters in