

Habitat complexity and predator size mediate interactions between intraguild blue crab predators and mud crab prey in oyster reefs

Jennifer M. Hill^{1,2,*}, Marc J. Weissburg¹

¹Georgia Institute of Technology, 310 Ferst Drive, Atlanta, Georgia 30332, USA

²Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528, USA

ABSTRACT: The prevalence of inherently unstable intraguild (IG) predation in natural systems suggests that many biotic and abiotic factors, including habitat complexity and population size structure, affect interactions between IG predators and prey. We investigated the role of shared oyster resource use (*Crassostrea virginica*), predator size, and habitat complexity (i.e. sand, shell hash, and simulated oyster clusters) in mediating the interactions of IG predators, the blue crabs *Callinectes sapidus*, and IG prey, the mud crabs *Panopeus herbstii*, in oyster reef communities. In mesocosms, mud crabs consumed the shared oyster resource at higher rates than did blue crabs. Constructed oyster reef clusters in mesocosms reduced blue crab predation on mud crabs, suggesting increasing habitat complexity provides mud crabs with a more effective refuge from IG predators. Survival of mud crabs in less complex habitats depended on predator size; small blue crabs were not able to consume mud crabs in any habitat type. The refuge effects of oyster reefs were confirmed in the field using mud crabs tethered in sand, shell hash, and oyster clusters. These experiments demonstrate the importance of habitat complexity and body size in mediating intraguild interactions between blue crabs and mud crabs on oyster reefs; they also elucidate the impacts of these predators in oyster reef communities.

KEY WORDS: Intraguild predation · Body size · Tethering · *Callinectes sapidus* · *Panopeus herbstii* · Oyster reef

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Intraguild predation (IGP) entails predation between species that also share a common prey (Polis et al. 1989, Polis & Holt 1992, Holt & Polis 1997). In its simplest form, IGP involves 3 species: an intraguild (IG) predator that consumes an IG prey, and a common resource for which both species compete. Theoretical treatments often predict that IGP should be uncommon in nature; in particular, IG prey that must compete for shared resources and can be eaten by their potential competitors likely will be driven to extinction (Polis et al. 1989, Polis & Holt 1992, Mylius et al. 2001). Nonetheless, IGP is wide-

spread in nature despite its theoretical instability (Polis et al. 1989, Polis & Holt 1992, Arim & Marquet 2004).

The prevalence of IGP in natural environments is likely linked to habitat features and aspects of predator and prey population structure that can mediate interactions between IG predators and prey (Griffen & Byers 2006a,b, Janssen et al. 2007, Rudolf & Armstrong 2008). For instance, habitat complexity can serve as a refuge from predation for a multitude of organisms (Heck & Thoman 1981, Crowder & Cooper 1982, Diehl 1992, Persson & Eklöv 1995). These refuge effects result from reduced predator foraging efficiency through either increased predator hand-

*Email: jhill@disl.org

ling time or reduced prey encounters in complex habitats (Crowder & Cooper 1982, Lipcius & Hines 1986, Eklöv & Diehl 1994, Persson & Eklöv 1995, Seitz et al. 2001, Ferner et al. 2009). Similarly, habitat complexity influences IGP interactions in various systems (Finke & Denno 2002, Janssen et al. 2007, Griffen & Byers 2006a, Schmidt & Rypstra 2010). A meta-analysis of multiple IG predation studies demonstrated that increased habitat complexity decreased predation rates of IG predators on IG prey (Janssen et al. 2007). Thus, habitat complexity mediates interactions between IG predators and IG prey by providing IG prey a refuge.

Ontogenetic changes in body size may modify the roles of IG predators and IG prey by affecting trophic structure and competitive outcomes (Crumrine 2005, van de Wolfshaar et al. 2006, Rudolf & Armstrong 2008). Animal body size often dictates predator traits, including prey identity and consumption rates (Werner & Gilliam 1984, Cohen et al. 1993). Further, body size can influence an animal's ability to compete with both conspecifics and heterospecifics (Menge 1972, Wissinger 1992). Thus, the body size of IG predators and IG prey may facilitate IGP in nature by reducing the efficacy of IG predators or increasing the competitive abilities of IG prey.

Predator size and habitat complexity can interact to influence prey survivorship as predator body size can dictate the efficiency of predator interactions (Babbitt & Tanner 1998, Fernandez 1999, Lewis & Eby 2002, Sarty et al. 2006) and the survival of IG prey and their shared resource (Griffen & Byers 2006a,b) within habitat structure. For instance, body size alters a predator's ability to penetrate environments that differ in rugosity and provides an avenue for predator coexistence (McDonald 1982, Sarty et al. 2006). Larger predators often are inhibited by complex habitat structure and small interstitial spaces, whereas smaller predators still may access prey. For example, the small size of the xanthid crab *Eurypanopeus depressus* allows it to occupy interstitial spaces within complex oyster reef structure, which allows *E. depressus* to coexist with the larger xanthid *Panopeus herbstii*, despite diet overlap and a narrow habitat range (McDonald 1982, Meyer 1994). Although smaller consumers may have greater prey access due to their small body size, smaller consumers are typically less efficient than larger consumers in cases of gape- or crush-limited predation. Consequently, IG consumer foraging success may depend upon the interactions between predator size, habitat structure, and prey size.

We sought to investigate mechanisms of body size and habitat complexity that mediate interactions of IG predators and prey in oyster reef communities. Oyster reefs provide a variety of ecological services (Newell 2004) and serve as a habitat for species such as crab predators and bivalves that feed at different trophic levels (Wells 1961, Glancy et al. 2003, Stunz et al. 2010). We chose to investigate an IG predator, the blue crab *Callinectes sapidus*, and its IG prey, the mud crab *Panopeus herbstii*. Blue crabs and mud crabs are both important predators in oyster reef communities (Micheli 1997), and prey on bivalve species including clams and juvenile oysters (<30 mm; *Crassostrea virginica*; Seed 1980, Whetstone & Eversole 1981, Bisker & Castagna 1987, Eggleston 1990a, Fitz & Weigert 1991, Ebersole & Kennedy 1995, Micheli 1997, Grabowski et al. 2008, O'Connor et al. 2008). In addition, blue crabs prey on mud crabs and oysters in mesocosms (Grabowski et al. 2008), and xanthid and other non-portunid crabs and bivalves compose 11 to 43% and <10 to 35% of blue crab diets in the field, respectively (Laughlin 1982, Fitz & Weigert 1991). Thus, blue crabs, mud crabs, and oysters (along with other bivalve species) make up an IGP system.

Previous studies have reached differing conclusions about the impacts of blue crabs and mud crabs on oyster prey. These differences potentially stem from size-specific effects of blue crab predators that have not been systematically evaluated. For instance, O'Connor et al. (2008) suggest blue crabs are the primary consumers of oysters compared with mud crabs, where blue crabs (30 to 70 mm carapace width; CW) consumed approximately 60% of oysters (<20 mm wide) and mud crabs (10 to 20 mm CW) consumed only 25%. However, Grabowski et al. (2008) suggest mud crabs (26.6 ± 1.0 mm CW) are the dominant oyster consumers, accounting for 40% of the oysters eaten in their study, relative to blue crabs (130 mm CW) which only consumed 15%. Furthermore, oyster mortality rates differed between studies in treatments of blue crabs and mud crabs, which suggests that blue crab body size affects oyster predation rates, interactions with habitat structure, or interactions with mud crabs. None of these studies compared oyster predation rates between different sizes of blue crabs and mud crabs, or examined the effects of blue crab predator size and habitat complexity on mud crab predation rates.

There is ample evidence that oyster reef habitat complexity increases survival of invertebrates (Micheli & Peterson 1999, Grabowski 2004, Hughes

& Grabowski 2006, Grabowski et al. 2008). However, increased habitat complexity of oyster reefs also may attract predators, including blue crabs, whelks, and demersal fishes (Langellotto & Denno 2006, Stunz et al. 2010). Furthermore, as oysters filter large volumes of water and release chemical cues, they may further facilitate predator aggregation by attracting predators that utilize odor-mediated foraging. For instance, blue crabs and knobbed whelks track oyster chemical cues emanating from reefs, resulting in higher predation rates on clams adjacent to oyster reefs (Wilson & Weissburg 2012). Despite these potential effects, the importance of oyster reef structure in mediating prey survival has rarely been demonstrated in the field and, to our knowledge, has only been demonstrated for bivalve species (Micheli & Peterson 1999, Wilson & Weissburg 2012) and porcelain crabs (*Petrolisthes armatus*; Hollebone & Hay 2008).

The goals of this study were to investigate the interactive effects of body size and structural complexity in mediating IGP interactions between blue crabs and mud crabs. Specifically, we sought to: (1) determine which predator, mud crabs, large blue crabs, or medium blue crabs, is the greater consumer of oysters; (2) investigate the roles of body size and habitat type on the predation success of blue crabs on mud crabs; and (3) to confirm the habitat effects in field environments.

MATERIALS AND METHODS

Animal collection and maintenance

Experiments were performed at the Skidaway Institute of Oceanography (SkIO), Skidaway Island, Georgia, USA. Blue crabs and mud crabs were collected from Wassaw Sound and its associated tributaries. Blue crabs were collected using commercial crab pots and a seine net. Mud crabs were collected by hand from loose oyster reef. Oysters *Crassostrea virginica* (10 to 20 mm in length) were obtained from Bay Shellfish (Tampa, FL). 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 starved 24 h prior to experiments. Mud crabs were maintained on a clam diet and were starved for 24 h prior to oyster consumption experiments and fed prior to blue crab predation experiments to limit cannibalism.

Use of a shared resource by mud crabs and blue crabs

We defined the best consumer as the predator that could reduce the abundance of the shared prey to the lowest abundance in the absence of the other predator. This measurement is often used as a proxy for competitive ability in IGP models (Polis & Holt 1992, Holt & Polis 1997). We then compared predation on oysters in laboratory mesocosms between mud crabs (25 to 45 mm CW) and 2 size classes of blue crab predators (>100 mm CW; 60 to 80 mm CW). Two size classes of blue crab predators were used as blue crab body size may affect handling time (Bisker & Castagna 1987, Eggleston 1990b) and their ability to access oyster prey. Large mud crabs were used, since, similar to blue crabs, their foraging abilities might be impeded by reef structure.

Predation on oysters by each predator was examined in mesocosms (0.7 m × 0.4 m × 0.3 m) containing approximately 2.5 cm of sand and artificial oyster reef that mimicked the complex structure of oyster reef habitat. Artificial reef (Fig. 1) was used to control for placement of live oysters within reefs and was constructed by gluing 10 oyster shells (obtained from natural shell banks) to create similar small clusters (approximately 4 to 6 cm in diameter). A total of 13 clusters were used to build artificial reefs (~25 cm in diameter). Seven of these artificial clusters had 3 juve-

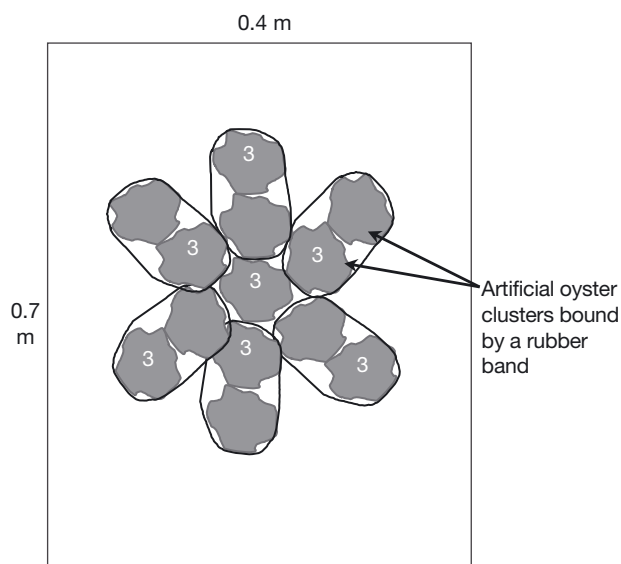


Fig. 1. Diagram of artificial oyster reef used in oyster predation experiments. Two oyster *Crassostrea virginica* clusters composed of glued oyster shells were joined together by rubber bands. These clusters were then arranged to create an oyster reef structure. Oyster clusters (indicated with the number 3) each had 3 juvenile oysters glued to the cluster

nile oysters (1 of each size class, length: 15 to 16 mm, 16 to 17 mm, 17 to 18 mm) glued to its face with cyanoacrylate glue (21 oysters total). Mud crab and blue crab size classes used in our experiment (25 to 45 mm and 60 to 140 mm CW, respectively) have been shown to successfully feed on oysters between 15 and 20 mm in length (Bisker & Castagna 1987, Eggleston 1990a). Artificial clusters with oysters were then secured to a second oyster cluster with rubber bands and placed around a center oyster cluster to create an artificial reef (Fig. 1). Artificial oyster clusters were arranged so that live juvenile oysters faced both into and out of the reef in order to control for edge effects. We monitored the number of oysters consumed by each type of predator every 24 h for 72 h. Five replicates were run at 1 time in 2 experimental runs, a total of 10 replicates for each crab species and size class. Preliminary data analysis showed that run (time) did not significantly affect oyster predation; consequently, all data from runs were pooled. Since data could not be transformed to meet assumptions of normality, the number of oysters eaten at the completion of the experiment was examined by a 1-way nonparametric Kruskal-Wallis (K-W) test for the effects of predator type (large blue crab, medium blue crab, mud crab). We excluded any replicate in which the predator died or molted.

Blue crab predation on mud crabs mediated by body size and habitat

We performed a 3 × 3 factorial experiment in a randomized block design in which we manipulated blue crab predator size (>100 mm, 60 to 80 mm, and 40 to 60 mm CW) and habitat complexity (oyster reef, shell hash, and sand) in order to examine their effects on mud crab survivorship. The habitats were constructed in laboratory mesocosms that consisted of covered outdoor fiberglass tanks (0.62 × 0.50 × 0.27 m) supplied with flow-through seawater. All mesocosms contained approximately 2.5 cm of sand, which was the lowest habitat complexity used in experiments (sand only). Oyster reef and shell hash habitats were constructed on top of sand substrates. Shell hash habitats were constructed by scattering approximately 2 l of oyster shell hash (obtained from natural shell banks) in the center of mesocosms. Oyster reef habitats consisted of artificial oyster clusters (similar to previous experiment) that were bundled with rubber bands to build a reef in the center of mesocosms (~35 cm in diameter; 27 clusters per tank). These artificial reefs allowed us to maintain a homogenous reef structure across tanks.

Ten mud crabs (similar to natural size distributions: seven 15 to 20 mm CW, two 20 to 25 mm CW, one 25 to 30 mm CW; Lee & Kneib 1994) were added to mesocosms containing each habitat type and allowed to acclimate overnight. One of 3 blue crab size classes was then assigned randomly to each habitat type and placed in mesocosms. Blue crabs foraged on mud crabs for approximately 18 h, encompassing both the evening and overnight periods when both species are most active (Clark et al. 1999, Grabowski 2004). No-predator controls consisting of 10 mud crabs in sand habitats were performed simultaneously with predation trials to determine mud crab background mortality. Preliminary experiments documented that habitat type did not influence background mortality in the absence of predators; <3% of mud crabs died regardless of habitat type (data not shown). The number of mud crabs surviving was recorded at the conclusion of the experiment. Replicates were excluded if the blue crab died or molted. Two replicates of each treatment were performed simultaneously due to limited tank space. This was repeated for 3 experimental runs, totaling 6 replicates of each treatment. Due to molting and deaths, respectively, we performed another experimental run consisting of only 40 to 60 mm and >100 mm CW blue crabs. The distribution of surviving mud crabs was non-normal despite a variety of transformations. Thus, mud crab survivorship was analyzed by generalized linear model (GLM) based on a Poisson distribution, typically used for count data (Quinn & Keough 2002). We tested for the effects of habitat and predator size, and survivorship was modeled with and without overdispersion parameters. Although both models fit based on goodness-of-fit statistics ($p > 0.90$) and yielded similar statistical conclusions, a Poisson distribution without overdispersion was chosen because of smaller residuals.

Investigating oyster habitat refuge effects in the field

In order to examine mud crab survival in differing field habitat types, we assessed predation rates on tethered mud crabs in intertidal sand/mud, shell hash, and oyster reef habitats. Predation rates measured by tethering animals often are difficult to interpret, as tethers can restrict escape behaviors that limit predation (Zimmer-Faust et al. 1994, Aronson & Heck 1995). However, mud crabs typically rely on their cryptic nature and foraging abilities within refuge habitats for predator defense (J. M. Hill pers.

obs.), suggesting restrictions on mobility may be relatively benign. Further, although tethers restrict mobility, they will do so in all habitat types. For instance, although tethers in bare habitats prevented access to structure, crabs in oyster reefs were also prevented from accessing deep and small interstitial reef spaces (J. M. Hill pers. obs.), suggesting tethering may be an accurate measure of relative predation for this species in each habitat. Despite potential artifacts, many previous studies have used this methodology (Micheli & Peterson 1999, Hollebone & Hay 2008). The tethering experiment was performed at 2 different sites in Wassaw Sound, Georgia, Priest's Landing (PL) and Dead Man's Hammock (DMH), to confirm that our observations can be generalized to different areas within the marsh. Both sites are characterized by patches of loose and fixed oyster reef, interspersed with shell hash and sand/mud habitat. Mud crabs, as well as a suite of potential mud crab predators including blue crabs and demersal fishes, are common to both locations (J. M. Hill pers. obs.).

We examined mud crab survival by tethering 30 (20 to 25 mm CW) mud crabs in each of 3 differing habitat types: oyster reef, shell hash, and bare habitats. This mud crab size class was rarely consumed in our mesocosm trials, due, in part, to its low proportional abundance. However, since interactions of body size and structure can influence vulnerability (Babbitt & Tanner 1998, Fernandez 1999, Sarty et al. 2006), we used this intermediate size class to assess the survivorship of mud crabs in field habitats. Tethers consisted of monofilament line (~25 cm, 10 lb test [~4.5 kg]) that was tied around mud crabs between the chelipeds and legs and secured to the top of the carapace with cyanoacrylate glue. The other end of the tether was secured to a landscaping stake. Each stake was numbered and labeled with orange flagging tape to track individual survival. Tethered mud crabs were maintained overnight in flow-through seawater tanks for a minimum of 12 h where <3% died or escaped their tethers. Mud crabs were then transported into the field in coolers where they were secured in the substrate in each habitat type. Stakes were secured amongst loose shell in shell hash habitats and in sand/mud within 3 to 5 cm of oyster reef for reef habitats. Each tethered animal was approximately 1 to 2 m apart and was marked with a survey flag for ease of retrieval. Once secured, mud crabs used cryptic strategies almost immediately by either burying in the mud or hiding within the reef or shells. Although tethers restricted mobility in each habitat type, they rarely

became tangled in habitat structure (<5%). Tethers were monitored for the presence or absence of mud crabs at 24 h. Tethers that were missing were excluded from analysis. Tethering experiments were performed when the 12 h low tide period occurred at night to limit access of visual terrestrial predators such as birds. The number of mud crabs remaining and absent in each habitat type at each site was analyzed by a nominal logistic regression for the effects of habitat and site using likelihood ratio tests. Lack-of-fit statistics were run to assess the model fit.

RESULTS

Use of a shared resource by mud crabs and blue crabs

Blue crabs and mud crabs differed significantly in their ability to consume juvenile oysters (Fig. 2; K-W, $H = 17.16$, $df = 2$, $p < 0.001$). Mud crabs consumed approximately 15 oysters on average and typically foraged equally in the reef interior and at the edges (data not shown). However, neither size class of blue crabs was a significant consumer of oysters, consuming on average only 1 oyster during the experimental period, or <2% d^{-1} (Fig. 2).

Blue crab predation on mud crabs mediated by body size and habitat

Mud crab survivorship was significantly affected by both predator size (Fig. 3; GLM, $\chi^2 = 56.07$, $p < 0.001$) and habitat type (GLM, $X^2 = 45.50$, $p < 0.001$), but these 2 factors interacted to determine the effect magnitude (Predator size \times Habitat; GLM, $\chi^2 = 56.90$, $p < 0.001$). Large blue crabs (>100 mm CW) were efficient predators of mud crabs, consuming almost all mud crabs in sand habitats (Fig. 3). However, in the presence of large blue crab predators, mud crab survivorship increased with habitat complexity, reaching a maximum of almost 90% in reef habitats. Medium-sized blue crabs (60 to 80 mm CW) were inefficient predators relative to large blue crabs; approximately 6 to 7 mud crabs out of 10 survived experimental trials in both the sand and shell hash habitat types. Reef habitats again tended to increase the survivorship of mud crabs in the presence of medium-sized blue crabs. Small blue crabs did not prey on mud crabs in any habitat type, with on average 90% of mud crabs surviving (Fig. 3).

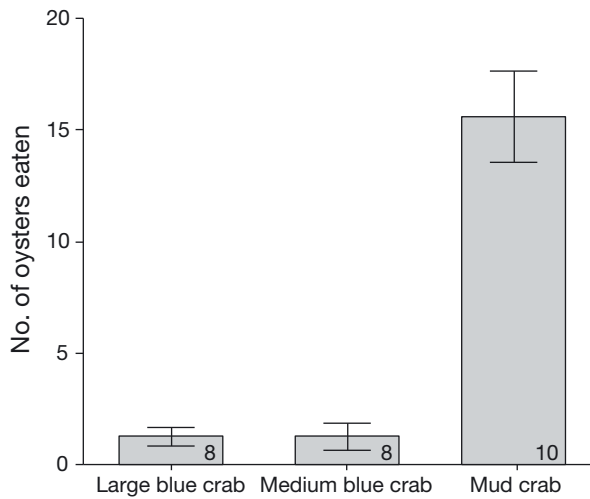


Fig. 2. Predation on oysters *Crassostrea virginica* (mean ± SE) by differing predators (blue crabs *Callinectes sapidus*, mud crabs *Panopeus herbstii*). The number of replicates is denoted by numbers at the base of graph bars; 21 oysters were secured to reefs in each mesocosm. Large: >100 mm CW; medium: 60 to 80 mm CW

The mud crab size classes consumed by all blue crabs in each habitat were generally in proportion to their abundance, in which the smallest mud crabs (15 to 20 mm) were typically consumed most often. Medium and large mud crabs often survived most predator treatments, even in low habitat complexity environments (except sand–large blue crab treatments), but these size classes were also the lowest in abundance (data not shown).

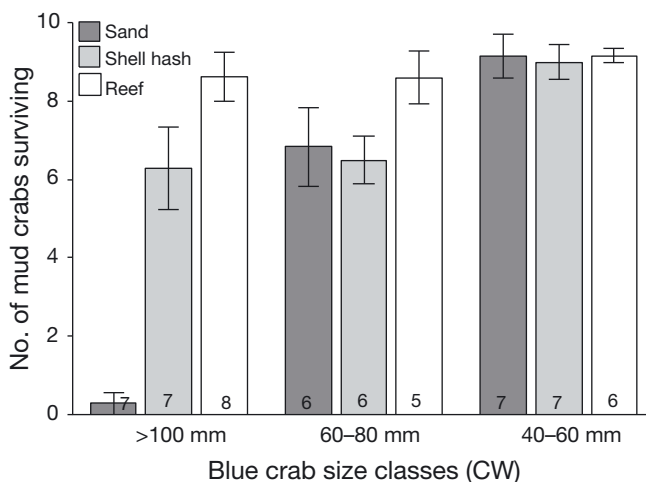


Fig. 3. *Callinectes sapidus*, *Panopeus herbstii*. The effects of blue crab body size and habitat type on mud crab survivorship (mean ± SE) in laboratory mesocosms. A total of 10 mud crabs were placed in each mesocosm. The number of replicates is denoted by numbers at the base of graph bars

Confirming oyster habitat refuge in the field

Increasing habitat complexity in natural environments significantly enhanced the survival of tethered mud crabs at each field site (Fig. 4; habitat; likelihood ratio $\chi^2 = 14.69$, $p = 0.006$). Lack-of-fit tests confirmed that the regression model fit habitat and site parameters and confirmed that habitat × site interaction terms were unnecessary ($\chi^2 = 1.40$, $p = 0.496$). Only 40% of mud crabs were recovered in sand habitats at PL, followed by 60 and 80% in shell hash and reef habitats, respectively (Fig. 4A). Less than 40% of mud crabs were recovered from sand habitats at DMH in contrast to 65% recovered from both shell hash and reef habitat types (Fig. 4B). However, the 2 sites were not significantly different (likelihood ratio $\chi^2 = 0.99$, $p = 0.319$). Missing mud crabs were likely a result of predation, as few mud crabs died or escaped their tethers in the laboratory. On average, 95% of all tethers were recovered from habitats at each site.

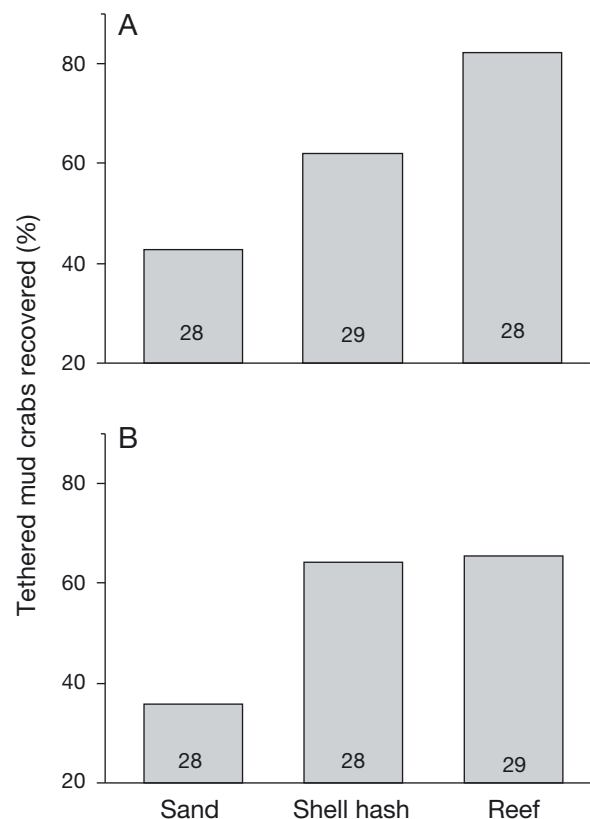


Fig. 4. *Panopeus herbstii*. Percent of tethered mud crabs recovered in differing field habitats at (A) Priest's Landing and (B) Dead Man's Hammock. The sample size (total number of tethers recovered, with or without mud crabs) is denoted by numbers at the base of graph bars. Missing tethers were excluded from the analysis

DISCUSSION

Blue crabs and mud crabs comprise an IGP system that is present in estuarine systems on the Atlantic and Gulf coasts. Our results suggest that resource use, habitat complexity, and predator size may mediate interactions between these IG predators in which: (1) mud crabs are better consumers for oyster prey in complex habitats, (2) habitat complexity provided by oyster reefs offers mud crabs a refuge from predation, and (3) only large blue crabs are efficient predators on mud crabs.

Mud crabs consistently consumed more oysters than blue crabs, suggesting mud crabs are the dominant consumer of shared oyster prey (Fig. 2). Further, mud crabs typically consumed oysters similarly on the reef interior and at the reef edges, suggesting they are not inhibited by reef structure. Mud crabs are ideal predators on oyster reefs because their body size and chelae morphology allows them to penetrate spaces within oyster reef structure and crush attached oysters (McDonald 1982), and several previous studies have documented high oyster predation rates by mud crabs (Grabowski & Kimbro 2005, Grabowski et al. 2008, Toscano & Griffen 2012). The oyster predation rates we observed with 1 large mud crab are higher than per capita predation rates reported in other studies that use multiple mud crabs at natural densities (Grabowski et al. 2008, O'Connor et al. 2008). This higher rate may be due to the large sizes of mud crabs we used, but is more likely because conspecific interference at natural mud crab densities lowers predation rates (Grabowski & Powers 2004). Blue crabs are generalists that feed on a variety of estuarine prey and have a larger habitat range than mud crabs (Hines et al. 1987, Meise & Stehlik 2003). Consequently, blue crabs are less adapted to oyster reef foraging. The greater capacity of mud crabs to exploit oysters within reef structure may stabilize blue crab–mud crab interactions (Polis et al. 1989; but see Grabowski et al. 2008, O'Connor et al. 2008 for additive combinations).

Although the low oyster consumption by blue crabs in this study (<2% consumed d^{-1}) is consistent with a stable IGP system, previous studies have documented higher predation rates, which suggests blue crabs may effectively compete with mud crabs for oyster prey. For instance, small to medium blue crabs (30 to 70 mm) can consume oysters at a rate of 60% d^{-1} (O'Connor et al. 2008). Large blue crabs have documented rates from 4.6% d^{-1} in complex habitats (Grabowski et al. 2008) to 30 to 80% d^{-1} (Eggleston 1990a). High predation rates in previous studies may

reflect differences in methodology that may allow greater access to oysters. Many previous experiments have used oysters settled on or glued to loose oyster shell (Eggleston 1990a,b, Grabowski et al. 2008) or tethered oysters (O'Connor et al. 2008) to assess oyster predation. Oysters in our experimental design were attached to a fixed vertical oyster reef structure. Further, oysters within our reef were glued flat on the face of oyster shells, which can decrease blue crab foraging success (Eggleston 1990a). Thus, the structural complexity and placement of oysters in reefs may have resulted in the extremely low predation rates observed. Although carefully constructed reefs composed of 3-dimensional aggregates also result in structural complexity that reduces oyster predation (Grabowski et al. 2008), our method of gluing oysters onto oyster reef mimics may have further diminished the effects of foraging blue crab predators. Since loose shell, shell aggregates, and fixed structures are all common settlement locations for oysters, more investigations may be required to determine the full impact of blue crabs on oyster mortality.

The low oyster consumption by blue crabs suggest that the guild connection (i.e. shared oyster prey) between blue crabs and mud crabs is relatively weak. However, since blue crabs and mud crabs are generalists, many species may serve as the shared prey within the guild. The weak connection with shared oyster prey may result from geographical differences in predator preference that can depend on the local morphology of oysters, oyster reefs, and species assemblages. The morphology of oysters and oyster reefs varies geographically (Groue & Lester 1982, Dittman et al. 1998). Thus, previous experiments with higher blue crab predation rates on oysters may represent blue crab behaviors in other locations that differ in oyster morphology, reef structural complexity, or blue crab diet preferences. Additionally, prey assemblages in oyster reef communities likely vary geographically based on a number of biotic and abiotic factors. Thus, blue crab diets and prey preferences may reflect differences in prey diversity and evenness. For instance, previous studies on blue crab diets from Atlantic and Gulf coasts report different diet compositions for blue crab species. Fitz & Weigert (1991) have documented that bivalves make up <10% of blue crab diets in coastal Georgia, while Laughlin (1982) has documented that bivalves make up ~35% of blue crab diets on the Gulf coast of Florida. Differential predator preferences of mud crabs and blue crabs and the potential for local predator adaptation to oyster morphology suggest the consequences of local variation in reef structure

and species assemblage merits further inquiry in order to understand the trophic structure of oyster reef communities.

Previous studies on IGP have documented that increased habitat complexity can promote the survivorship of IG prey (Finke & Denno 2002, Griffen & Byers 2006a, Janssen et al. 2007, Schmidt & Rypstra 2010). Our results are consistent with this evidence as the structural complexity of oyster reefs provided refuge from blue crab predation in laboratory mesocosms. Importantly, the value of habitat complexity as a refuge habitat was dependent upon predator size (Fig. 3). The significant interaction between predator size and habitat type likely occurred because smaller predator size classes of 60 to 80 mm and 40 to 60 mm CW were generally less efficient predators regardless of habitat type. This lack of predation likely resulted from the inability of smaller predators to crush and consume mud crabs and because the behavior of mud crabs deterred smaller blue crab predators (J. M. Hill pers. obs.). When approached by a blue crab of any size, mud crabs used a classic mermaid spread display common to many decapods (Dingle 1983). This behavioral tactic was ineffective with large blue crabs; however, small blue crabs were often deterred by the display and retreated (J. M. Hill pers. obs.).

Whereas smaller blue crab predators consumed few mud crabs, independent of habitat complexity, large blue crabs (>100 mm CW) were significantly deterred by increased habitat complexity, as represented by both shell hash and oyster reefs (Fig. 3). The mud crab survivorship in oyster reef structure (90%) is only slightly less than that in no predator controls (97%), demonstrating that oyster reefs provide an effective refuge from large blue crab predation. Increased mud crab survivorship with increasing habitat complexity has been noted in response to toadfish predators (Grabowski 2004), suggesting that oyster reef provides a refuge for mud crabs from a variety of predators.

Although oyster reef structure provides a predation refuge, oyster reefs can also attract predators by emitting chemical attractants to foraging consumers (Wilson & Weissburg 2012). We confirmed the benefits of oyster reefs as a predation refuge in field tethering experiments, where more mud crabs generally survived in more complex habitats. Mud crabs were recovered from oyster reef habitats at a greater frequency than from shell hash and sand habitats at the PL site (Fig. 4A). The second field site, DMH, showed a slightly differing pattern, where shell hash and reef habitats resulted in similar mud crab survivorship

(Fig. 4B). Oyster reefs may not have conferred a greater benefit at this site, because reef clusters were relatively small and provided limited refuge space. However, despite slight differences in pattern, sites were not statistically different from one another.

Since all oyster reefs within Wassaw Sound are intertidal, with semi-diurnal tides, tethered mud crabs were exposed to a variety of potential predators. However, tethering periods were chosen when the 12 h low tide period occurred at night, which limited access of terrestrial visual predators such as birds. Aquatic predators that may have consumed tethered crabs included demersal fish, such as bonnethead sharks and red drum, and roaming crab predators, such as stone crabs and blue crabs. Although we cannot exclude fish as possible predators, preliminary experiments where fishing hooks were attached to mud crabs (similar to methods used by Fernandez et al. 1993) caught zero fish, and tethers and hooks always remained when mud crabs were consumed. In full field trials, <3% of tethers were missing, suggesting fish had not taken off with tethers. These observations suggest the bulk of the predation was from blue crabs, which are the most common crab predators at our sites.

In their entirety, our results suggest that blue crab body size and habitat structure impact the survival of mud crabs, which may cascade to oyster prey. For instance, large blue crabs may have a positive indirect effect on oyster survival by controlling mud crab populations, especially if mud crabs are encountered outside structured habitats (i.e. moving between or among reef patches). Although we did not test additive predator effects (Sih et al. 1998), Grabowski et al. (2008) support this hypothesis, where combinations of large blue crabs and mud crabs result in greater oyster survivorship (7 to 11% mortality rate) than do mud crabs alone (28 to 39%) when mud crabs were the dominant consumer. This risk reduction results from blue crab consumption of mud crabs (a density effect) as well as non-consumptive effects (Grabowski et al. 2008, Hill & Weissburg 2013). Since smaller blue crabs are not able to consume mud crabs in any habitat type, it is likely that the indirect effects of small blue crab predators on oyster prey will be mediated only by non-consumptive effects (interference or behavioral avoidance), and may produce differing oyster mortality compared to situations with large blue crabs. Results from O'Connor et al. (2008) support this hypothesis; additive combinations of blue crabs (30 to 70 mm CW) and mud crabs resulted in risk reductions in comparison with single blue crabs. However, even with risk reductions, oyster

mortality with additive combinations of the 2 consumers was still ~50%. This suggests that risk reductions with additive combinations of small to medium blue crabs are not as great as with large blue crabs. This is further supported by Hill & Weissburg (2013) where only chemical cues from large blue crabs, and not small blue crabs, reduce mud crab foraging and increase oyster survival. Consequently, the indirect effects of blue crabs on oyster prey are highly dependent upon blue crab predator size.

Other IGP studies further support the importance of IG predator body size in mediating shared prey mortality (Crumrine 2005, Griffen & Byers 2006b). For instance, invasive crab species, *Carcinus maenas* and *Hemigrapsus sanguineus*, had redundant impacts on amphipod survivorship in substitutive predation experiments when each predator was of a similar body size. However, pairings of differing sized crab predators resulted in an increased chance of IGP and risk reduction for amphipod prey (Griffen & Byers 2006a). The interaction of predator size and habitat complexity is particularly important in oyster reef habitats, since current methods of oyster harvesting often reduce the structural complexity of reefs (Lenihan & Peterson 1998), which currently are declining due to over-harvesting (Beck et al. 2011). Further, many fisheries species that utilize oyster reefs, including blue crabs (Lipcius & Stockhausen 2002), have undergone shifts to smaller size classes due to the harvest of large adults. The changing habitat structure of oyster reef communities and anthropogenic impacts on predator body size suggest that the impacts of habitat complexity and body size may affect both future oyster restoration efforts and fisheries management.

In conclusion, variance in both habitat structure and predator body size mediates interactions between blue crab IG predators and mud crab IG prey. Mud crabs are the primary consumers of oysters and successfully use oyster reefs as a refuge from predation, as reef complexity often precludes blue crabs from accessing mud crabs and their shared oyster prey. Large blue crabs can positively impact oyster reef communities through top-down control of mud crab predators outside complex habitats or through non-consumptive effects. However, as blue crabs are generalists, it is possible that diverse predator diets may dampen the potential for trophic cascades within this system. Unfortunately, there are few data on crab preferences in oyster reef communities. However, many other papers (e.g. Grabowski et al. 2008, Hill & Weissburg 2013) demonstrate top-down trophic cascades mediated by both consumptive and

non-consumptive effects that are transmitted to oyster prey. Future research of oyster reef communities should consider interactions of body size, habitat type, and predator-prey preferences (i.e. trophic structure) that will help to further our knowledge about factors that control oyster survival in these ecologically and economically important communities.

Acknowledgements. We acknowledge M. Wilson, K. Schafer, and C. Yeager for their assistance in completing both the laboratory and field experiments. We also thank J. Byers, R. Lipcius, and 3 anonymous reviewers for editorial advice that significantly improved the manuscript. This research was funded by the National Science Foundation grant NSF-OCE No. 0424673 to M.J.W. and the NSF IGERT Fellowship in Aquatic Chemical Signaling.

LITERATURE CITED

- Arim M, Marquet PA (2004) Intraguild predation: a widespread interaction related to species biology. *Ecol Lett* 7: 557–564
- Aronson RB, Heck KL (1995) Tethering experiments and hypothesis testing in ecology. *Mar Ecol Prog Ser* 121: 307–309
- Babbitt KJ, Tanner GW (1998) Effects of cover and predator size on survival and development of *Rana utricularia* tadpoles. *Oecologia* 114:258–262
- Beck MW, Brumbaugh RD, Airoidi L, Carranza A and others (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* 61: 107–116
- Bisker R, Castagna M (1987) Predation on single spat oysters *Crassostrea virginica* (Gmelin) by blue crabs *Callinectes sapidus* and mud crabs *Panopeus herbstii*. *J Shellfish Res* 6:37–40
- Clark ME, Wolcott TG, Wolcott DL, Hines AH (1999) Foraging and agonistic activity co-occur in free-ranging blue crabs (*Callinectes sapidus*): observation of animals by ultrasonic telemetry. *J Exp Mar Biol Ecol* 233:143–160
- 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
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interactions between bluegills and their prey. *Ecology* 63:1802–1813
- Crumrine PW (2005) Size structure and substitutability in an odonate intraguild predation system. *Oecologia* 145: 132–139
- Diehl S (1992) Fish predation and the benthic community structure: the role of omnivory and habitat complexity. *Ecology* 73:1646–1661
- Dingle H (1983) Strategies of agonistic behavior in Crustacea. In: Rebach S, Dunham DW (eds) *Studies in adaptation: the behaviour of high Crustacea*. John Wiley & Sons, New York, NY, p 84–111
- Dittman DE, Ford SE, Haskin HH (1998) Growth patterns of oysters, *Crassostrea virginica*, from different estuaries. *Mar Biol* 132:461–469
- Ebersole EL, Kennedy VS (1995) Prey preferences of blue crabs *Callinectes sapidus* feeding on three bivalve species. *Mar Ecol Prog Ser* 118:167–177

- Eggleston DB (1990a) Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: effects of prey density and size. *Bull Mar Sci* 46: 62–82
- Eggleston DB (1990b) Functional-responses of blue crabs *Callinectes sapidus* Rathbun feeding on juvenile oysters *Crassostrea virginica* (Gmelin): effects of predator sex and size, and prey size. *J Exp Mar Biol Ecol* 143:73–90
- Eklöv P, Diehl S (1994) Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* 98:344–353
- Fernandez M (1999) Cannibalism in Dungeness crab *Cancer magister*: effects of predator–prey size ratio, density, and habitat type. *Mar Ecol Prog Ser* 182:221–230
- Fernandez M, Iribarne O, Armstrong D (1993) Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. *Mar Ecol Prog Ser* 92:171–177
- 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
- Finke DL, Denno RF (2002) Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* 83:643–652
- 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
- Glancy TP, Frazer TK, Cichra CE, Lindberg WJ (2003) Comparative patterns of occupancy by decapod crustaceans in seagrass, oyster, and marsh edge habitats in a Northeast Gulf of Mexico estuary. *Estuaries* 26:1291–1301
- Grabowski JH (2004) Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004
- Grabowski JH, Kimbro DL (2005) Predator-avoidance behavior extends trophic cascades to refuge habitats. *Ecology* 86:1312–1319
- Grabowski JH, Powers SP (2004) Habitat complexity mitigates trophic transfer on oyster reefs. *Mar Ecol Prog Ser* 277:291–295
- Grabowski JH, Hughes AR, Kimbro DL (2008) Habitat complexity influences cascading effects of multiple predators. *Ecology* 89:3413–3422
- Griffen BD, Byers JE (2006a) Partitioning mechanisms of predator interference in different habitats. *Oecologia* 146:608–614
- Griffen BD, Byers JE (2006b) Intraguild predation reduces redundancy of predator species in multiple predator assemblage. *J Anim Ecol* 75:959–966
- Groue KJ, Lester LJ (1982) A morphological and genetic analysis of geographic variation among oysters in the Gulf of Mexico. *Veliger* 24:331–335
- Heck KL, Thoman TA (1981) Experiments on predator–prey interactions in vegetated aquatic habitats. *J Exp Mar Biol Ecol* 53:125–134
- Hill JM, Weissburg MJ (2013) Predator biomass determines the magnitude of non-consumptive effects (NCEs) in both laboratory and field environments. *Oecologia* 172: 79–91
- Hines AH, Lipcius RN, Haddon AM (1987) Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Mar Ecol Prog Ser* 36:55–64
- Hollebone AL, Hay ME (2008) An invasive crab alters interaction webs in a marine community. *Biol Invasions* 10: 347–358
- Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Am Nat* 149:745–764
- Hughes AR, Grabowski JH (2006) Habitat context influences predator interference interactions and the strength of resource partitioning. *Oecologia* 149:256–264
- Janssen A, Sabelis MW, Magalhaes S, Montserrat M, van der Hammen T (2007) Habitat structure affects intraguild predation. *Ecology* 88:2713–2719
- Langellotto GA, Denno RF (2006) Refuge from cannibalism in complex-structured habitats: implications for the accumulation of invertebrate predators. *Ecol Entomol* 31: 575–581
- Laughlin RA (1982) Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bull Mar Sci* 32:807–822
- 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
- Lenihan HS, Peterson CH (1998) How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol Appl* 8:128–140
- Lewis DB, Eby LA (2002) Spatially heterogeneous refugia and predation risk in intertidal salt marshes. *Oikos* 96: 119–129
- Lipcius RN, Hines AH (1986) Variable functional responses of a marine predator in dissimilar homogenous microhabitats. *Ecology* 67:1361–1371
- 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
- McDonald J (1982) Divergent life-history patterns in the co-occurring intertidal crabs *Panopeus herbstii* and *Eurypanopeus depressus*. *Mar Ecol Prog Ser* 8:173–180
- Meise CJ, Stehlik LL (2003) Habitat use, temporal abundance variability, and diet of blue crabs from a New Jersey estuarine system. *Estuaries Coasts* 26:731–745
- Menge BA (1972) Competition for food between two intertidal starfish species and its effect on body size and feeding. *Ecology* 53:635–644
- Meyer DL (1994) Habitat partitioning between xanthid crabs *Panopeus herbstii* and *Eurypanopeus depressus* on intertidal oyster reefs (*Crassostrea virginica*) in southeastern North Carolina. *Estuaries* 17:674–679
- Micheli F (1997) Effects of predator foraging behavior on patterns of prey mortality in marine soft bottoms. *Ecol Monogr* 67:203–224
- Micheli F, Peterson CH (1999) Estuarine vegetated habitats as corridors for predator movements. *Conserv Biol* 13: 869–881
- Mylius SD, Klumpers K, de Roos AM, Persson L (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am Nat* 158:259–276
- Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension feeding bivalve molluscs: a review. *J Shellfish Res* 23:51–61
- O'Connor NE, Grabowski JH, Ladwig LM, Bruno JF (2008) Simulated predator extinctions: predator identity affects survival and recruitment of oysters. *Ecology* 89:428–438
- Persson L, Eklöv P (1995) Prey refuges affecting interactions

- between piscivorous perch and juvenile perch and roach. *Ecology* 76:70–81
- Polis GA, Holt RD (1992) Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol Evol* 7: 151–154
- Polis GA, Meyers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge
- Rudolf VHW, Armstrong J (2008) Emergent impacts of cannibalism and size refuges in prey on intraguild predation systems. *Oecologia* 157:675–686
- Sarty M, Abbott KL, Lester PJ (2006) Habitat complexity facilitates coexistence in a tropical ant community. *Oecologia* 149:465–473
- Schmidt JM, Rypstra AL (2010) Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters. *Oecologia* 164:899–910
- 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
- Seitz RD, Lipcius RM, Hines AH, Eggleston DB (2001) Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology* 82:2435–2451
- Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13:350–355
- Stunz GW, Minello TJ, Rozas LP (2010) Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas. *Mar Ecol Prog Ser* 406:147–159
- Toscano BJ, Griffen BD (2012) Predatory crab size diversity and bivalve consumption in oyster reefs. *Mar Ecol Prog Ser* 445:65–74
- van de Wolfshaar KE, de Roos AM, Persson L (2006) Size-dependent interactions inhibit coexistence in intraguild predation systems with life-history omnivory. *Am Nat* 168:62–75
- Wells HW (1961) The fauna of oyster beds, with special reference to the salinity factor. *Ecol Monogr* 31:239–266
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size structured populations. *Annu Rev Ecol Syst* 15:393–425
- Whetstone JM, Eversole AG (1981) Effects of size and temperature on mud crab, *Panopeus herbstii*, predation on hard clams *Mercenaria mercenaria*. *Estuaries* 4:153–156
- Wilson ML, Weissburg MJ (2012) Biotic structure indirectly affects associated prey in a predator specific manner via changes in the sensory environment. *Oecologia* 171: 427–438
- Wissinger SA (1992) Niche overlap and the potential for competition and intraguild predation between size structured populations. *Ecology* 73:1431–1444
- Zimmer-Faust RK, Fielder DR, Heck KL, Coen LD, Morgan SG (1994) Effects of tethering on predatory escape by juvenile blue crabs. *Mar Ecol Prog Ser* 111:299–303

*Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA*

*Submitted: May 25, 2012; Accepted: April 24, 2013
Proofs received from author(s): July 11, 2013*