Eastern oysters *Crassostrea virginica* deter crab predators by altering their morphology in response to crab cues

Elizabeth M. Robinson[1,4], Jessica Lunt[1], Christopher D. Marshall[2,3], Delbert L. Smee[1,*]

[1]Department of Life Sciences, Texas A&M University – Corpus Christi, 6300 Ocean Drive, Unit 5800, Corpus Christi, Texas 78412, USA

[2]Department of Marine Biology, Texas A&M University, Galveston, Texas 77553, USA

[3]Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77840, USA

[4]*Present address:* Department of Oceanography and Coastal Science, 1209 Energy, Coast & Environment Building, Louisiana State University, Baton Rouge, Louisiana 70803, USA

ABSTRACT: Many prey species alter their behavior and/or morphology in response to exudates from predators and injured con- or heterospecifics to alleviate predation risk. Yet, few studies have assessed the effectiveness of risk aversion in prey in terms of decreasing mortality. Recent studies have shown that eastern oysters *Crassostrea virginica* produce heavier shells in the presence of predators, but the benefits of this morphological change have not been evaluated. We performed an indoor laboratory experiment and exposed newly settled oysters to chemical cues from 2 common predators: blue crabs *Callinectes sapidus* and Atlantic mud crabs *Panopeus herbstii*. After 8 wk, we compared shell diameter, shell mass, shell breaking force, and susceptibility to predation between juvenile oysters in these predator treatments to those in controls without predators. Oyster shell diameter and mass were significantly greater in blue crab treatments than in controls, and mud crabs and controls were not significantly different in these parameters. Yet, in both mud crab and blue crab treatments, oysters produced shells that required more force to crush as measured with a hand-held force transducer. Oysters reared in the presence of blue and mud crabs were less susceptible to predation than those maintained in no-predator controls in feeding assays performed after the 8 wk induction. Although oysters reacted differently to mud crabs and blue crabs, changing their shell morphology was an effective deterrent against predators. Future studies are needed to determine the long-term effects of induced responses to predators on oyster growth, fitness, and reef formation.

KEY WORDS: Predator–prey interaction · Non-consumptive effects · Indirect interaction · Predator avoidance · Blue crab · *Callinectes sapidus* · Mud crab · *Panopeus herbstii*

INTRODUCTION

In response to threats from predation, prey have evolved a variety of mechanisms that allow them to reduce their risk of being consumed (reviewed by Kats & Dill 1998) including reducing their feeding activity (Saiz et al. 2003, Smee & Weissburg 2006a, Naddafi et al. 2007), burrowing more deeply (Griffiths & Richardson 2006, Flynn & Smee 2010), selecting different habitats (Turner & Mittelbach 1990), changing their life history (Crowl & Covich 1990, Fraser & Gilliam 1992), or adopting a morphology that makes them more predator-resistant (Harvell 1990, Leonard et al. 1999, Trussell & Smith 2000, Turner & Montgomery 2003, Relyea 2004). Altering morphology to reduce the risk of predation is a com-

*Corresponding author: lee.smee@tamucc.edu

mon strategy adopted by immobile or slow-moving species that are less able to flee (Leonard et al. 1999, Nakaoka 2000, Freeman & Byers 2006, Turner 2008). Although avoidance behaviors and morphological changes can be effective and necessary predator deterrents (Nakaoka 2000, Powers & Kittinger 2002, Smee & Weissburg 2006a, Flynn & Smee 2010), they are often costly to prey, resulting in reductions in growth and fecundity (Peterson 1986, Relyea & Werner 1999, Nakaoka 2000, Large & Smee 2013).

To minimize costs associated with predator avoidance, many prey species employ plastic responses that are initiated when predators pose significant risk of injury or death (Kats & Dill 1998, Hay 2009, Ferrari et al. 2010). Chemical cues provide reliable information regarding predator presence and intentions and are commonly used by prey to detect and evaluate predation risk (Kats & Dill 1998, Brown et al. 2000, Hay 2009, Ferrari et al. 2010). While predators may conceal visual or mechanical signals, it is unlikely that they are able to avoid releasing metabolites as they perform physiological functions (Brown et al. 2000). Additionally, many prey detect chemicals from injured conspecifics or heterospecifics that are released when they are being consumed and clearly indicate that predators are nearby (Kats & Dill 1998, Schoeppner & Relyea 2005, Turner 2008).

Bivalves readily utilize chemical exudates that emanate from predators and from injured conspecifics to evaluate predation risk (Caro & Castilla 2004, Cheung et al. 2004, Smee & Weissburg 2006b). They respond to risk by increasing their burrowing depth (Griffiths & Richardson 2006, Flynn & Smee 2010), reducing their feeding behavior (Smee & Weissburg 2006a,b, Naddafi et al. 2007), and increasing their shell thickness (Trussell & Smith 2000, Caro & Castilla 2004, Freeman & Byers 2006). Additionally, mussels produce additional byssal threads to increase the force needed to dislodge them from substrates (Coté 1995, Leonard et al. 1999, Shin et al. 2009) and increase abductor muscle mass to deter prying predators (Freeman & Byers 2006). Morphological changes in shell thickness are a trade-off with soft tissue mass and gonad size, and thus increasing shell thickness may lower bivalve fecundity (Peterson 1986).

Eastern oysters *Crassostrea virginica* are both economically and ecologically important (Grabowski & Peterson 2007), and predation on oyster spat is a significant source of oyster mortality (Newell et al. 2000). Like other bivalves, eastern oysters are heavily preyed upon by a suite of predators including fish, crabs, and gastropods (Brown et al. 2003, Newell et al. 2007, Lord & Whitlatch 2012), and their vulnera-

bility to consumers is inversely related to body size (Newell et al. 2000, Johnson & Smee 2012). Three recent studies have shown that oysters react to gastropod and crustacean predators by producing thicker, heavier shells (Newell et al. 2007, Johnson & Smee 2012, Lord & Whitlatch 2012) and in doing so, produce less soft tissue (Johnson & Smee 2012, but see Lord & Whitlatch 2012). Here, we sought to build upon these studies by assessing how growth and shell morphology of newly settled oysters, the size class most vulnerable to crab predation, was influenced by 2 common predatory crabs: blue crabs *Callinectes sapidus* and Atlantic mud crabs *Panopeus herbstii*. Specifically, our goal was to test the potential benefits of induced shell thickening to oysters when responding to these predators by measuring growth as well as changes in shell strength and susceptibility to crab predation. Our results indicated that in the presence of both predators, oysters grew shells that required more force to crush and resultantly were afforded greater protection from crab predators.

MATERIALS AND METHODS

Design

The induction study was conducted in indoor tanks at Texas A&M University – Corpus Christi from June to August 2012. We used 30 opaque, polyethylene tanks (31 × 42 × 32 cm deep), each supplied with 37 l of artificial seawater (Instant Ocean™) maintained at a salinity of 20 and aerated. Air and water temperature was kept between 22 and 25°C. Oysters used for the experiment were purchased from the Auburn University Shellfish Laboratory as larvae and settled onto sun-bleached oyster shells in a large outdoor tank. These larvae were specifically bred from multiple adult lines to produce high genetic diversity. After settling, oysters were fed Kent Marine Phyto-Plex© daily for 1 wk prior to transfer into the smaller tanks for use in experiments. Three oyster shells, each containing 10 to 15 newly settled oysters, were sealed into a vexar pouch (mesh size 1 cm^2 openings) and placed in each tank. Oyster spat were ~2 mm at the beginning of the experiment, and oyster mortality was minimal during the experiment (~10% lost) and not qualitatively different between treatments.

The 30 tanks were randomly assigned to 1 of 3 experimental treatments: control (no crabs), mud crabs, and blue crabs (n = 10 per treatment for 30 total; 4 tanks were compromised during the experiment, viz. 1 control, 1 mud crab, and 2 blue crab tanks; thus, the

final total n = 26). Each mud crab treatment contained 3 mud crabs with carapace widths between 31 and 53 mm, while each blue crab treatment contained 1 blue crab with a carapace width between 91 and 137 mm. Crabs were collected from local oyster reefs and are representative of the sizes and sexes common in the local area. We elected to use 3 mud crabs and a single blue crab for 2 reasons. First, mud crabs are more abundant than blue crabs in local oyster reefs (D.L. Smee unpubl. data), and second, we wanted to provide a similar quantity of predator cue, and the biomass of 3 mud crabs was similar to that of a single adult blue crab. We used a mixture of male and female crabs in the experiment, but crab gender was not recorded or used as a factor in the experiment. Only crabs at the intermolt stage that were actively feeding were used in experiments, and no crabs molted during the study.

Oyster spat were exposed to these 3 treatments for 8 wk. For the first 3 wk, oysters were fed 3 drops of Kent Marine PhytoPlex© every other day. Oyster growth was slow, so we increased feeding for the remaining 5 wk to 10 drops daily. This level of food resulted in some accumulation of particles in each tank, suggesting that oysters were not food limited. Crabs were fed 3 adult oysters (6–8 cm length) within the experimental tanks once a week to provide cues from predators actively feeding on conspecifics. We ensured that each mud crab received 1 oyster and each blue crab 3 oysters so that all predator treatments had a similar amount of injured oyster cues. After crab feedings, the water in each tank was replaced with newly made artificial seawater at the same temperature and salinity. After 8 wk, we measured the shell diameter, shell mass, force needed to break the shell, and susceptibility to predation among oysters reared in the 3 treatments (i.e. mud crab, blue crab, control).

Shell diameter and mass

Spat shell diameter was recorded prior to measuring shell breaking force. Measurements of shell diameter were performed to the nearest 0.1 mm using digital calipers. At the size measured, oysters did not have elongated shells, and diameter was an appropriate measure of size. We measured all spat on a single oyster shell in each tank and used the mean for each tank as our replicate. Oyster diameter was compared among treatments using a 1-way ANOVA with predator treatment as a fixed factor. Tukey's post hoc analysis was used for pairwise comparisons between means (Sokal & Rohlf 1995).

To assess differences in shell mass, 3 oyster spat from each tank (1 from each shell) were collected. Each oyster was carefully lifted off of the shell to which it was attached, placed in a metal tin, and dried for 48 h at 90°C. At the size used, only the top valve was measured because the bottom valve was very small and difficult to remove without breaking. Oyster spat were small at the conclusion of the experiment, and separating soft tissue from shell was difficult and imprecise. Further, more than 99.5% of wet mass and all measurable dry mass were attributed to shell. In preliminary studies, when soft tissue was removed from 15 oyster spat, it weighed less than 0.0001 g. Thus, we refer to changes in shell mass even though we measured tissue and shell mass together since soft tissue represented much less than 0.5% of the final dry mass. Mass of oyster shells were compared between treatments using a 1-way ANOVA with predator treatment as a fixed factor, and Tukey's post hoc analysis was used for pairwise comparison between means (Sokal & Rohlf 1995).

Shell breaking force

The force required to break each shell was measured using a Kistler FSH 9312A piezoelectric force transducer (following Herrel et al. 1999, 2001). Signals from the transducer were amplified by a hand-held charge amplifier (Kistler FSH 5995) and recorded. A small blunt probe (1 mm diameter) that mimicked a tubercle (i.e. molariform tooth) present on a crab claw was fabricated for our prey hardness tests. We selected a single, large oyster shell from each treatment and measured shell breaking force by crushing spat that were still attached to the larger shell. We crushed at least 5 but not more than 10 spat on each shell. The probe was consistently placed centrally to be equal distance from the shell edges and perpendicular to the surface for all oyster spat tested. We applied gentle and consistent pressure on all specimens until structural failure of the oyster spat shell occurred. Treatments were tested in the blind so that the person using the instrument was unaware to which treatment the oyster shell being crushed belonged. We recorded the maximum force needed to break the shell as our measurement of prey hardness, which is an appropriate proxy for shell strength.

The mean force in Newtons (N) needed to crush each individual oyster was recorded, and a mean for all individuals measured per tank was calculated and used as the unit of replication. Shell breaking force was compared between predator treatments

using a 1-way ANOVA with predator treatment as a fixed factor. Tukey's post hoc analysis was used for pairwise comparisons between means (Sokal & Rohlf 1995).

Predation assay

Feeding assays were conducted to assess how changes in oyster shell morphology would influence oyster survival using adult mud crabs (40–50 mm carapace width, n = 8). Crabs for the study were inter-molt crabs and actively feeding. Mud crabs were collected from the field and acclimated in laboratory aquaria for 7 d prior to predation assays. On Day 1 after collection, each mud crab was fed oyster tissue until satiation and then starved for 6 d until use in feeding assays to standardize hunger level. We placed a single, large oyster shell with oyster spat from each treatment into a 1.0 l plastic container along with a single mud crab (40–50 mm carapace width, n = 8). We removed oysters manually so that only 5 oysters were present on each shell. Thus, the mud crab could forage on oysters grown in controls, mud crab treatments, or blue crab treatments. Artificial, aerated seawater with the same salinity and temperature was used in each container. Mud crabs were able to forage on the oysters for 48 h. After 48 h, oyster shells were removed and the remaining oyster spat were counted. The number of oysters alive that had been grown in controls, mud crab treatments, and blue crabs treatments was compared using a Kruskal-Wallis test. Pairwise comparisons were made using a Wilcoxon test. We used both male and female crabs for this assay to represent ecological relevant predatory encounters. To determine whether male and female crabs forage differently on oyster spat, we performed a separate feeding assay. We compared foraging rates on oyster spat grown in controls between male and female crabs using the same protocol. All statistical analyses were performed using JMP™ version 10. Blue crabs were unwilling to consume oysters smaller than 5 mm in diameter in preliminary assays and were not used in this part of the study.

RESULTS

Shell diameter and mass

Mean oyster shell diameter was 4.2 mm in blue crab treatments, 3.4 mm in mud crab treatments, and 2.7 mm in controls, and was significantly different among treatments ($F_{2, 23}$ = 8.4, p < 0.01, Fig. 1a). Significant pairwise differences in shell diameter were found between oysters in blue crab treatments and controls, but mud crab treatments were not significantly different from either blue crab treatments or controls using Tukey's post hoc test.

Oysters exposed to blue crabs produced significantly heavier shells (0.0032 g) than those in mud crab (0.0017 g) and control (0.0016 g) treatments ($F_{2, 23}$ = 4.42, p < 0.05, Fig. 1b). Significant differences in shell mass were not found between oysters in mud crab treatments versus those in controls, but mass of oyster shells in blue crab treatments was twice that of those in controls when compared using Tukey's post hoc test.

Shell breaking force

Shell breaking force was significantly greater among oysters grown in blue crab (4.4 N) and mud crab treatments (3.3 N) as compared to control (2.3 N) treatments ($F_{2, 23}$ = 14.3, p < 0. 001, Fig. 2). Post hoc analysis indicated that oysters produced a shell that required more force to break when reared in tanks with mud crabs as compared to controls, even though the mass and diameter of their shells was not statistically different from controls. The shell breaking force was also significantly greater in the blue crab treatment as compared to both mud crab treatments and controls.
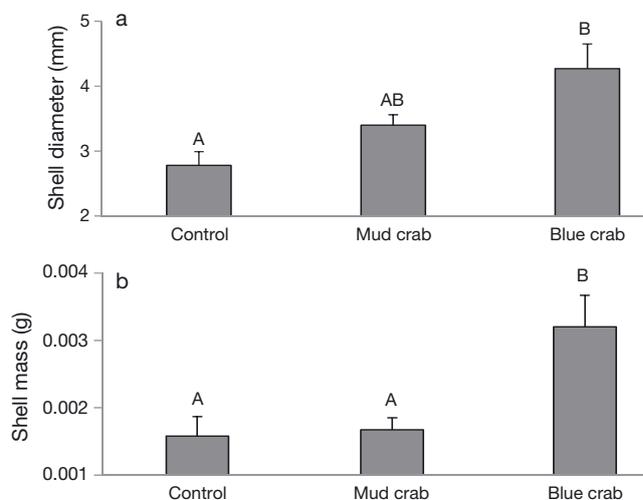

Fig. 1. *Crassostrea virginica.* Mean + SE (a) shell diameter, (b) shell mass of oysters reared in the presence of blue crabs, mud crabs, or no-predator controls. Letters denote significant pairwise differences based upon Tukey's post hoc test (n = 9, 9, 8 for control, mud crab, and blue crab treatments, respectively, p < 0.05)
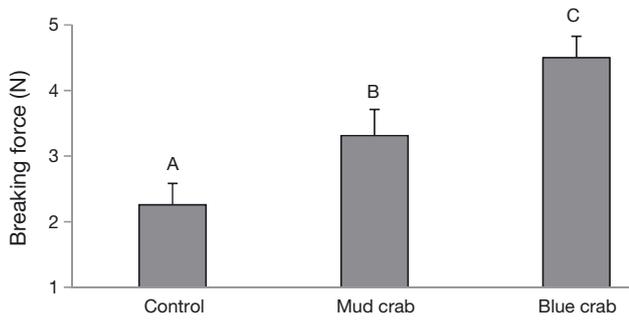
Fig. 2. *Crassostrea virginica*. Mean + SE force (N) needed to crush shells of oysters reared in the presence of blue crabs, mud crabs, or no-predator controls. Letters denote significant pairwise differences based upon Tukey's post hoc test (n = 9, 9, 8 for control, mud crab, and blue crab treatments, respectively, p < 0.001)

Predation assay

When exposed to mud crab predators in feeding assays, oyster mortality was significantly less among those reared in mud crab and blue crab treatments as compared to controls (χ^2 = 9.86, df = 2, p < 0.01, Fig. 3). Statistical differences in survivorship were not found between oysters grown in the presence of blue crabs versus mud crabs in post hoc analysis. Predation on oyster spat was not significantly different between male and female crab controls (χ^2 = 1.51, df = 1, p = 0.22).

DISCUSSION

Ecologists have long reasoned that, by reacting to predators, prey increase survival, but that responding to predators incurs costs such as a loss of foraging time, growth, and/or fecundity (Kats & Dill 1998, Relyea & Werner 1999, Relyea & Mills 2001). Few studies have assessed whether prey responses to predators indeed reduce predation risk and increase
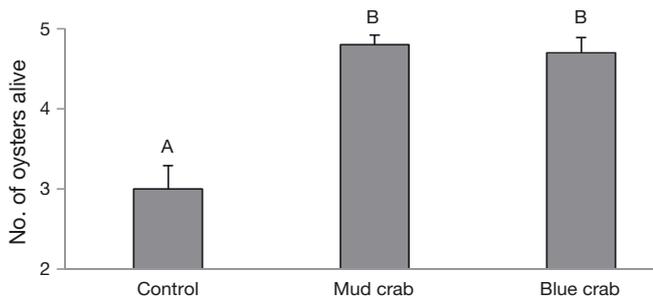

Fig. 3. *Crassostrea virginica*. Mean + SE number of oysters grown in the presence of blue crabs, mud crabs, or no-predator controls that were alive after a 48 h feeding assay with mud crab predators. Letters denote significant pairwise differences based on Tukey's post hoc test

survival (but see Turner et al. 2000, Smee & Weissburg 2006a, Flynn & Smee 2010). Our results complement those of earlier studies showing that oyster morphology changes in response to cues indicative of predation risk (Newell et al. 2007, Lord & Whitlatch 2012) and builds upon this work by testing the benefits of morphological changes. Our study provides the first evidence that by altering their morphology in response to predator cues, oysters can reduce predation risk.

In aquatic systems, nonconsumptive effects of predators on prey most commonly result from prey detecting chemical cues indicative of predation risk (Chivers & Smith 1998, Kats & Dill 1998, Preisser et al. 2005, Large & Smee 2010). We presented oyster spat with chemical cues from 2 ubiquitous predators consuming conspecifics and found that the presence of predation risk cues influenced oyster growth. Oysters grew significantly more laterally (i.e. larger diameter) and produced heavier shells that required more force to break in response to blue crabs, a pattern also noted by Newell et al. (2007). Oyster diameter and shell mass were not significantly different in mud crab treatments and controls. Yet, significantly more force was required to break oyster shells grown in mud crab treatments compared to controls. In control treatments, the force needed to break oyster shells was 30% lower than the force required to break oysters in mud crab treatments, and almost 50% less than oysters in blue crab treatments.

Prey may respond to predation threats by increasing growth rates (and delaying reproduction) to reach a size refuge (Crowl & Covich 1990) or by altering their morphology to deter predator attacks (Trussell & Smith 2000, Relyea 2004). Our results suggest that oysters may possess the ability to increase growth rates and alter shell composition depending upon the predator encountered. In our study, oyster spat reacted differently to blue crabs than to mud crabs, but in both predator treatments, oysters grew shells that required more force to break and that were more resistant to predators. In blue crab treatments, oysters grew larger, heavier shells while in mud crab treatments the shells were strengthened without an increase in shell diameter or weight as compared to controls. Thus, in response to blue crabs, oysters increased their growth rate, but in response to mud crabs, altered their shell to increase breaking force. Although shell strength was increased in both predator treatments, the relative increase in strength was much greater in response to mud crabs per shell size. Changes in life history versus modifications in morphology have different

costs and benefits, and more work is required to determine the mechanism(s) oysters employ in response to predators and the trade-offs involved.

Cues from injured conspecifics are commonly used by prey to evaluate predation risk (Turner 2008, Large & Smee 2010, Large et al. 2012). We fed similar amounts of oyster tissue to predators to ensure that they released cues indicative of oyster predation and to prevent differences in the amount of injured conspecific cues from biasing our results. Despite using similar amounts of oyster tissue in all predator treatments, oysters responded differently to blue crabs than to mud crabs, suggesting that oysters perceive these predators differently. Previously, eastern oysters were found to react differently to estuarine mud crabs *Rhithropanopeus harrisii* than blue crabs (Newell et al. 2007). In response to both *R. harrisii* and blue crabs, oysters produced shells that required more compression force to break, but did so via different mechanisms (Newell et al. 2007). In response to *R. harrisii*, oysters produced more organic content in their shells than they did in response to blue crabs, perhaps to make their shells more pliable and resistant to fracturing (Newell et al. 2007) or to help heal their shells after nonlethal attacks (Prezant et al. 2006). In response to blue crabs, oysters grew denser, harder shells by adding inorganic material to the shells (Newell et al. 2007). Thus, oysters may respond to predators by either hardening their shells or making them more pliable, depending upon the type of predator encountered, and either strategy may increase compression force needed to break the shell and thereby offer protection against predators. Our results mirror those of Newell et al. (2007) in that we saw different responses to mud and blue crabs that were both effective predator deterrents, but we were unable to measure organic content of our shells due to the small size of oysters at the conclusion of the experiment.

Prey size often affects vulnerability to consumers (Wong et al. 2010), and crabs prey more heavily on smaller bivalves possibly because they require less energy to open (Nakaoka 2000, Johnson & Smee 2012) and are less likely to cause injury to crab claws (Juanes 1992). We therefore elected to focus on oyster spat for this experiment because they are readily consumed by many organisms, including mud crabs (Newell et al. 2000, Johnson & Smee 2012). Our results suggest that oyster spat detect and respond to predation risk by altering their morphology, that they can perceive differences in predator species, and that their responses to predators can increase survival even when they are small (<5 mm).

Changes in morphology that increase predator resistance may occur passively in some species (Bourdeau 2010). For example, the carnivorous marine snail *Nucella lamellosa* reduces feeding in response to predators, which causes a reduction in somatic growth and a thickening of the shell. For *N. lamellosa*, shell thickening does not result from a diversion of resources and was not considered to be more energetically costly than food deprivation (Bourdeau 2010). In contrast, *N. lapillus*, an Atlantic congener, increased shell thickness in response to crab predators even though they consumed similar numbers of barnacles in predator treatments and controls (Large et al. 2012). Thus, unlike *N. lamellosa*, *N. lapillus* allocated energy to shell growth at an expense of tissue growth, and the morphological changes were not due to starvation. Oysters grow less soft tissue in the presence of mud crabs, which alters the ratio of shell to tissue and causes a relatively thicker shell. Although we did not measure food consumption by oysters during the experiment, we did find that in blue crab treatments spat grew the largest, heaviest, and strongest shells. In our study, shell accounted for more than 99.5% of total oyster dry weight, and thus differences observed in the final weight resulted from differences in the amount of shell growth. It seems unlikely that a reduction in food intake would cause an increase in shell growth, and we hypothesize that oysters are actively allocating resources to shell growth in this treatment. However, additional studies are needed to assess how food availability and intake influences the costs, benefits, and resulting morphological changes that occur in oysters in response to predators. These studies should assess energy allocation to somatic growth and shell growth in response to predators and the effectiveness of these changes in reducing predation.

Oyster reefs are both economically and ecologically important (Grabowski & Peterson 2007), but have declined by ~85% worldwide (Beck et al. 2011). Understanding factors that influence the growth and fecundity of individual oysters and of oyster populations will provide useful information that may help the management, conservation, and restoration of this species. Future studies that assess the mechanisms involved in oyster plasticity and the exact costs of reacting to predators in terms of both growth and fecundity are likely to provide key insights into oyster reef ecology.

LITERATURE CITED

Beck MW, Brumbaugh RD, Airoldi L, Carranza A and others (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61: 107–116

Bourdeau PE (2010) An inducible morphological defence is a passive by-product of behaviour in a marine snail. Proc R Soc Lond B Biol Sci 277:455–462

Brown GE, Paige JA, Godin JGJ (2000) Chemically mediated predator inspection behaviour in the absence of predator visual cues by a characin fish. Anim Behav 60: 315–321

Brown KM, Peterson GW, Banks PD, Lezina B, Ramcharan C, McDonough M (2003) Olfactory deterrents to black drum predation on oyster leases. J Shellfish Res 22: 589–595

Caro AU, Castilla JC (2004) Predator-inducible defences and local intrapopulation variability of the intertidal mussel Semimytilus algosus in central Chile. Mar Ecol Prog Ser 276:115–123

Cheung SG, Lam S, Gao QF, Mak KK, Shin PKS (2004) Induced anti-predator responses of the green mussel, Perna viridis (L.), on exposure to the predatory gastropod, Thais clavigera Küster, and the swimming crab, Thalamita danae Stimpson. Mar Biol 144:675–684

Chivers DP, Smith RJF (1998) Chemical alarm signaling in aquatic predator-prey systems: a review and prospectus. Ecoscience 5:338–352

Côté IM (1995) Effects of predatory crab effluent on byssus production in mussels. J Exp Mar Biol Ecol 188:233–241

Crowl TA, Covich AP (1990) Predator-induced life history shifts in a fresh-water snail. Science 247:949–951

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

Flynn AM, Smee DL (2010) Behavioral plasticity of the soft-shell clam, Mya arenaria (L.), in the presence of predators increases survival in the field. J Exp Mar Biol Ecol 383:32–38

Fraser DF, Gilliam JF (1992) Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. Ecology 73:959–970

Freeman AS, Byers JE (2006) Divergent induced responses to an invasive predator in marine mussel populations. Science 313:831–833

Grabowski JH, Peterson CH (2007) Restoring oyster reefs to recover ecosystem services. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) Ecosystem engineers—plants to protists. Elsevier, Salt Lake City, UT, p 281–298

Griffiths C, Richardson C (2006) Chemically induced predator avoidance behaviour in the burrowing bivalve Macoma balthica. J Exp Mar Biol Ecol 331:91–98

Harvell CD (1990) The ecology and evolution of inducible defenses. Q R Biol 65: 323–340

Hay ME (2009) Marine chemical ecology: chemical signals and cues structure marine populations, communities, and ecosystems. Annu Rev Mar Sci 1:193–212

Herrel A, Spithoven L, Van Damme R, De Vree F (1999) Sexual dimorphism of head size in Gallotia galloti: testing the niche divergence hypothesis by functional analyses. Funct Ecol 13:289–297

Herrel A, Van Damme R, Vanhooydonck B, De Vree F (2001) The implications of bite performance for diet in two species of lacertid lizards. Can J Zool 79:662–670

Johnson KD, Smee DL (2012) Size matters for risk assessment and resource allocation in bivalves. Mar Ecol Prog Ser 462:103–110

Juanes F (1992) Why do decapod crustaceans prefer small-sized molluscan prey? Mar Ecol Prog Ser 87:239–249

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

Large SI, Smee DL (2010) Type and nature of cues used by Nucella lapillus to evaluate predation risk. J Exp Mar Biol Ecol 396:10–17

Large SI, Smee DL (2013) Biogeographic variation in behavioral and morphological responses to predation risk. Oecologia 171:961–969

Large SI, Torres P, Smee DL (2012) Behavior and morphology of Nucella lapillus influenced by predator type and predator diet. Aquat Biol 16:189–196

Leonard GH, Bertness MD, Yund PO (1999) Crab predation, waterborne cues, and inducible defenses in the blue mussel, Mytilus edulis. Ecology 80:1–14

Lord J, Whitlatch R (2012) Inducible defenses in the eastern oyster Crassostrea virginica Gmelin in response to the presence of the predatory oyster drill Urosalpinx cinerea Say in Long Island Sound. Mar Biol 159:1177–1182

Naddafi R, Eklov P, Pettersson K (2007) Non-lethal predator effects on the feeding rate and prey selection of the exotic zebra mussel Dreissena polymorpha. Oikos 116: 1289–1298

Nakaoka M (2000) Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. Ecology 81:1031–1045

Newell RE, Alspach GS, Kennedy VS, Jacobs D (2000) Mortality of newly metamorphosed eastern oysters (Crassostrea virginica) in mesohaline Chesapeake Bay. Mar Biol 136:665–676

Newell RE, Kennedy V, Shaw K (2007) Comparative vulnerability to predators, and induced defense responses, of eastern oysters Crassostrea virginica and non-native Crassostrea ariakensis oysters in Chesapeake Bay. Mar Biol 152:449–460

Peterson CH (1986) Quantitative allometry of gamete production by Mercenaria mercenaria into old age. Mar Ecol Prog Ser 29:93–97

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

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

Prezant RS, Chapman EJ, McDougall A (2006) In utero predator-induced responses in the viviparid snail Bellamya chinensis. Can J Zool 84:600–608

Relyea R (2004) Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. Ecology 85:172–179

Relyea RA, Mills N (2001) Predator-induced stress makes the pesticide carbaryl more deadly to gray treefrog tadpoles (*Hyla versicolor*). Proc Natl Acad Sci USA 98: 2491–2496

Relyea RA, Werner EE (1999) Quantifying the relationship between predator-induced behavior and growth performance in larval anurans. Ecology 80:2117–2124

Saiz E, Calbet A, Broglio E (2003) Effects of small-scale turbulence on copepods: the case of *Oithona davisae.* Limnol Oceanogr 48:1304–1311

Schoeppner NM, Relyea RA (2005) Damage, digestion, and defence: the roles of alarm cues and kairomones for inducing prey defenses. Ecol Lett 8:505–512

Shin PKS, Yang FY, Chiu MY, Cheung SG (2009) Cues from the predator crab *Thalamita danae* fed different prey can affect scope for growth in the prey mussel *Perna viridis.* Mar Freshw Behav Physiol 42:343–355

Smee DL, Weissburg MJ (2006a) Clamming up: environmental forces diminish the perceptive ability of bivalve prey. Ecology 87:1587–1598

Smee DL, Weissburg MJ (2006b) Hard clams (*Mercenaria mercenaria*) evaluate predation risk using chemical signals from predators and injured conspecifics. J Chem Ecol 32:605–619

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research. 3rd edn. WH Freeman, New York, NY

Trussell GC, Smith LD (2000) Induced defenses in response to an invading crab predator: an explanation of historical and geographic phenotypic change. Proc Natl Acad Sci USA 97:2123–2127

Turner A (2008) Predator diet and prey behaviour: freshwater snails discriminate among closely related prey in a predator's diet. Anim Behav 76:1211–1217

Turner A, Mittelbach G (1990) Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. Ecology 71:2241–2254

Turner AM, Montgomery SL (2003) Spatial and temporal scales of predator avoidance: experiments with fish and snails. Ecology 84:616–622

Turner AM, Bernot RJ, Boes CM (2000) Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. Oikos 88: 148–158

Wong MC, Peterson CH, Kay J (2010) Prey size selection and bottom type influence multiple predator effects in a crab–bivalve system. Mar Ecol Prog Ser 409: 143–156