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NONCONSUMPTIVE EFFECTS OF CRUSTACEANS AND AN ECHINODERM ON SPAT OF THE EASTERN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN, 1791)

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ABSTRACT Predation by crustaceans and echinoderms is a significant driver of mortality for sessile invertebrates in near-shore marine ecosystems. As a response, shellfish growers use predator exclusion cages to grow their product. Oysters grown in these cages and clams in and under nets have been observed to exhibit thinner, brittle shells, which is not optimal for market, nor for those being grown for restoration purposes. Here, the nonconsumptive predator effects of several native and nonnative predators on shell morphology of *Crassostrea virginica* oyster spat. Juvenile (1–3 mm) seed oysters were exposed separately to chemical cues of five different predators and one nonpredator crab were investigated and compared with control (no exposure) spat. Significant effects of predator presence on the total wet weight (g) of the spat was demonstrated, with the highest increase for spat exposed to black-fingered mud crabs (*Panopeus*, 1.70 mg d⁻¹) and the biggest decreases for spat exposed to the European green crabs (*Carcinus maenas*—1.34 mg d⁻¹) and the sea stars (*Asterias rubens*—1.47 mg d⁻¹). Changes to oyster length (mm) and shell density (crushing resistance) were not significant. Implications for aquaculturists and wild bivalve populations are that growth could be negatively affected by the lack of predators on these important organisms.

KEY WORDS: *Crassostrea virginica*, oysters, spat, crabs, shell growth, shell strength, *Asterias rubens*

INTRODUCTION

As global demand for seafood increases, commercial aquaculture has emerged as one solution to meet this demand. Today, aquaculture has reached parity as a main method of production of the world seafood supply (Naylor et al. 2021, FAO 2022), and will likely be more important as global catch fisheries continue to decline. Oysters are mass-farmed globally with China leading the world in oyster production at approximately 12 million produced per year (FAO 2022). There are several common issues impacting aquaculture producers, with predation on smaller oysters a major cause of mortality during the growing season (Mann et al. 2009, Getchis 2014). Current methods of oyster aquaculture during smaller life stages include natural maturation and the use of oyster cages to prevent predation (Jory et al. 1984, Malavé et al. 2012). To prevent the smaller oysters from being eaten by local predators, there have been attempts to use artificial maturation cages.

Growing oysters at high numbers is a multistep process, and there are typically three main steps: hatchery production, nursery, and natural development (grow-out). Hatchery production consists of spawning broodstock and growing to early stage juveniles (spat) and continuing the grow-out process with cultured algae. Once the oysters become seed stocks (length of ≥ 1 mm), they can be put in spat bags or upwellers until they are large enough to go into predator exclusion cages and are left to grow in the ocean (Hansen & Gosselin 2013, Getchis 2014, Davis et al. 2021). Some growers have noted that this growing practice results in products with weaker/more brittle shells (M. Gilman, pers. obs.) and to counter this, oysters have to be removed and tumbled in a metal drum to encourage shell buildup.

Predation is among the most common causes of mortality in many organisms (Krebs et al. 2001, Barclay & Leighton 2022)

and, as a consequence, animals have evolved a variety of predator-avoidance adaptations. Specific adaptations include physical defenses that make an organism unpalatable or difficult to handle (Riessen 1992, Benard 2004, Bollache et al. 2006, Jermacz et al. 2020). Motile molluscs have been found to recognize the nearby occurrence of crabs and other shell-crushing predators through chemical cues, then move to habitats that provide refuges from predators (McCarthy & Fisher 2000, Turner & Montgomery 2003). Sessile molluscs rely on morphological adaptations to withstand predation. These can include developing a thicker shell (Smith & Jennings 2000, Freeman 2007, Newell et al. 2007, Fässler & Kaiser 2008) or changing byssus strength and shell length to the presence of predators (Leonard et al. 1999, Hirsch et al. 2014). The appearance of heavily calcified opercula and shells as a passive form of predator-avoidance is a well-documented phenomenon in both extant and extinct molluscs (Vermeij 1983, Vermeij & Williams 2007).

Previous research has demonstrated nonconsumptive effects of some predators on shellfish physiology. Eastern oysters, *Crassostrea virginica*, for example, exposed to blue crabs, *Callinectes sapidus*, had significantly higher shell diameters, mass, and breaking force than those not exposed to predators (Peterson 1986, Johnson & Smee 2014, Robinson et al. 2014). Similarly, significant differences in surface area were reported in individuals of *C. virginica* exposed to cues from blue crab predators, though no differences in crushing force resistance or weight were found (Scherer et al. 2017). As reviewed by Mizuta and Wikfors (2019), it is widely understood that bottom-planted oysters grow much thicker shells over similar time periods as opposed to cage-grown. Additionally, some farmers use practices whereby the oysters are cage-grown until they are less predator-prone (approximately 5 cm) and then bottom-planted on suitable habitat to grow thicker and stronger to market size. With the growth of aquaculture in waters with unsuitable substrate for bottom-planting, a larger number of growers use cage aquaculture for the duration of the life

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of the oyster, as opposed to just the predator-prone life history stages. It is also highly regarded that bottom-planted oysters have much higher natural mortality rates as opposed to cage-grown oysters and part of that is due to higher exposure to predatory species (Kennedy et al. 1996).

Reported differences in oyster responses to different predator species indicate that more studies are needed to explore a wider variety of predator species, as some of the responses might be species-specific. The goal of this study was to fill gaps in research surrounding the effects of predators on oyster growth. If the introduction of predator cues can assist in making oysters grow faster and thicker shells on a consistent basis, this method could be used to inform current oyster aquaculture methods. There is a paucity of literature describing which predators can be introduced in a safe manner to help grow oysters.

MATERIALS AND METHODS

Animal Maintenance

This experiment measured the potential impact that blue crabs (*Callinectes sapidus*), the invasive Asian shore crabs (*Hemigrapsus sanguineus*), spider crabs (*Libinia emarginata*), black-fingered mud crabs (Panopeid—one of five genera in Long Island Sound), green crabs (*Carcinus maenas*), and the common sea star (*Asterias rubens*) have on oyster spat measured as shell length, weight, and crushing resistance. Crabs were obtained from the Indian River Shellfish Farm in Madison, CT. Spat (approximately 1 mm) of the eastern oyster (*Crassostrea virginica*) were obtained from Martha's Vineyard Shellfish group in Martha's Vineyard, MA. All experimental animals were maintained in separate recirculating aquaria at 16°C. Crabs and sea stars were fed oysters in the recirculating aquaria, and never in the experimental chamber to prevent cues from predation of conspecifics from affecting the results. Oyster spat were fed a combination of live algae (*Tetraselmis chui*, *Pavlova lutheri*, *Nannochloropsis* spp.) at a maintenance ratio (10^4 cells mL⁻¹; Helm et al. 2004).

Experimental Procedure

To measure the responses of spat of the eastern oyster (*Crassostrea virginica*) to the presence of predators, animals were separately exposed to waterborne cues from five species of crabs and one sea star. There were seven treatments conducted, six experimental and one control, for a total of 37 trials ($n = 5-6$ per treatment). All predatory animals were placed in separate static aquaria with crushed coral and 1- μ M filtered seawater (FSW) for 18–24 h prior to exposing the oysters to the experimental water treatment. This process ensures that the seawater is saturated with waterborne cues from each predator species. Each of the experimental treatments consisted of seawater collected from one of the aquaria that held each of the crabs/sea stars: *Callinectes sapidus*/Panopeid/*Asterias rubens*/*Libinia emarginata* (native oyster predators) or *Hemigrapsus sanguineus*/*Carcinus maenas* (invasive oyster predators). Oysters were maintained at $17.0 \pm 1.5^\circ\text{C}$. The experiment was run for 5 wk, and oysters were fed daily with a mixture of live algae (*Tetraselmis chui*, *Pavlova lutheri*, *Nannochloropsis* spp.) at a concentration of 10^4 cells mL⁻¹ in a 1:1 ratio by biovolume.

There were 5–6 experimental chambers per treatment, and each chamber contained 10 individual oyster spat. Animals were exposed to the experimental water with predator cues three

times per week during water changes, and fed daily. Oysters were blotted and weighed, and images taken for length measurements at the beginning and end of the 5-wk experimental trial. ImageJ was used to measure the starting and final lengths of the oysters, using a linear scale from the hinge to the longest part of the shell. At the end of the experiment, a force gauge was used to measure the crushing strength of the oyster shells. Crushing force was calculated for five oysters per replicate and then averaged for each replicate. Statistical tests performed were an Analysis of Variance (ANOVA) on oyster lengths, wet weight, and crushing strength with an alpha-value of 0.05. RStudio (R Core Team 2021) was used for data analyses.

RESULTS

Change in Oyster Spat Size

Change in the shell length (cm) of oyster spat did not differ significantly between treatments (Table 1: ANOVA, $F_{6,33} = 1.664$, $P > 0.05$). Oyster spat exposed to sea star had a change in length of 0.018 ± 0.02 cm, oysters exposed to the mud crabs had a change in length of 0.023 ± 0.03 cm, and the green crabs had a change in length of 0.026 ± 0.03 cm. The oyster spat under the control (FSW) conditions had a change in length of 0.068 ± 0.05 cm, oysters exposed to the spider crabs *Libinia emarginata* had a change in length of 0.08 ± 0.01 cm, and the hemigrapsid crab *H. sanguineus* had a change in length of 0.046 ± 0.03 cm, and those exposed to the blue crab *Callinectes sapidus* had a change in length of 0.034 ± 0.024 cm. Calculations of changes in the area of the oyster spat (data not shown) yielded a similar result. Daily changes in length (mm d^{-1}) were not different for spat exposed to the different experimental conditions (Table 2).

Change in Wet Weight

Change in the whole wet weight of oyster spat varied significantly depending on the experimental exposure (Fig. 1: ANOVA, $F_{6,33} = 4.03$, $P < 0.05$). On average, there was no mass change observed for the control oysters (0 ± 0.05 g SD) or oysters

TABLE 1.
Final crushing densities, measured as resistance force (N), and final length (mm) of oyster spat exposed to waterborne cues from different predator species.

Predator exposure	Crushing resistance (N)	Final length (mm)
Control (FSW)	19.7 (± 10.1)	3.37 (± 0.01)
<i>Callinectes sapidus</i> (blue crab)	16.5 (± 7.51)	3.47 (± 0.16)
<i>Panopeus</i> spp. (black-fingered mud crabs)	11.5 (± 3.81)	3.50 (± 0.22)
<i>Asterias rubens</i> (Common sea star)	19.8 (± 3.59)	29.3 (± 0.19)
<i>Carcinus maenas</i> (European green crabs)	19.4 (± 3.62)	27.5 (± 0.31)
<i>Hemigrapsus sanguineus</i> (Asian shore crab)	17.8 (± 11.2)	3.32 (± 0.12)
<i>Libinia emarginata</i> (Spider crab)	21.5 (± 11.6)	3.47 (± 0.20)

Data shown as mean (\pm SD), $n = 5-6$.

TABLE 2.
Daily average changes in the length (mm) and weight (mg) of oyster spat under the different experimental conditions.

Predator exposure	Length change (mm d ⁻¹)	Weight change (mg d ⁻¹)
Control (FSW)	0.20	-0.011
<i>Callinectes sapidus</i> (blue crab)	0.10	-0.45
<i>Panopeus</i> spp. (black-fingered mud crabs)	0.07	1.70
<i>Asterias rubens</i> (Common sea star)	0.05	-1.47
<i>Carcinus maenas</i> (European green crabs)	0.07	-1.34
<i>Hemigrapsus sanguineus</i> (Asian shore crab)	0.13	0.43
<i>Libinia emarginata</i> (Spider crab)	0.08	0.96

Data shown as mean, $n = 6$.

exposed to *Callinectes sapidus* (0 ± 0.05 g SD). Oysters exposed to *Asterias rubens* (-0.05 ± 0.01 g SD) and *Carcinus maenas* (-0.048 ± 0.02 g SD) showed the largest decrease in weight. Oysters exposed to *Hemigrapsus sanguineus* (0.014 ± 0.05 g SD), *Libinia emarginata* crabs (0.035 ± 0.05 g SD), and Panopeid crabs (0.06 ± 0.07 g SD) had the largest increase in weight.

Crushing Density

The ability of oyster spat to withstand crushing pressure (measured in Newtons) was not significantly different between treatments (Table 1: ANOVA, $F_{6,33} = 0.813$, $P > 0.05$). Oyster spat exposed to Panopeid crabs had the lowest crushing density (11.5 ± 3.81 N), whereas those exposed to *Libinia emarginata* had the highest crushing density (21.5 ± 11.6). No relationship was found between crushing density and final weight ($P > 0.05$), or between crushing density and final shell height ($P > 0.05$).

DISCUSSION

This work investigated the effects of the presence of predator and nonpredator cues on the morphology of *Crassostrea virginica* oyster spat. Generally, a significant effect of predator species on oyster shell wet mass was elicited. Primarily, oysters exposed to cues from Panopeid crabs had a higher mass, whereas those exposed to cues from *Carcinus maenas* crabs and *Asterias rubens* sea stars weighed significantly less. No such effect was found for oyster shell length or crushing density based on predator treatment. These findings indicate differences in responses by oyster spat to waterborne cues from predator species, and are consistent with previous findings (Robinson et al. 2014, Scherer et al. 2017).

Generally, spat exposed to predator and the nonpredator spider crab cues were smaller than control spat by the end of the experiment. The smallest spat after the 6-wk exposure were those exposed to the Panopeid mud crab and sea stars. This finding is revealing, as historically, that these are two of the major predators for juvenile oysters (Flimlin & Beal 1993). The daily growth rate for the control oysters in this study (0.20 mm d⁻¹) is comparable to growth rates reported in other studies (Newell et al. 2007, Grizzle et al. 2017). This was higher than those

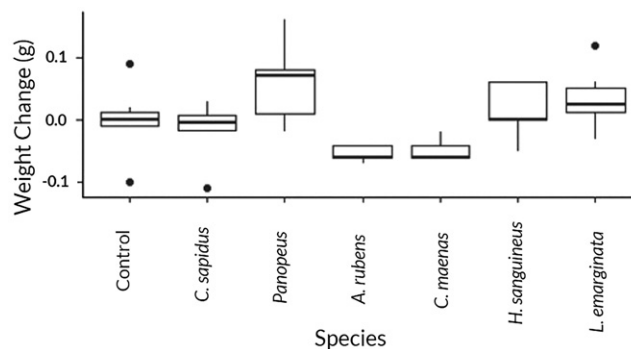


Figure 1. Changes in wet weight (g) of oyster spat exposed to the different predator cues. There were significant differences in weight change of the oysters during the experimental period [ANOVA, $F(6, 33) = 4.03$, $P < 0.05$, $n = 5-6$]. The biggest change observed was in oysters exposed to cues from sea star and green crab predators (Tukey HSD, $P < 0.05$).

reported by Munroe et al. (2017), where the authors followed several cohorts of spat settling on clam shells in the field, and measured growth and mortality. In that study, oyster spat took an average of 243 days to reach 20 mm shell length, for a corresponding growth rate of 0.082 mm per day.

In a laboratory study, Robinson et al. (2014) tested the effects of chemical cues from predator crabs feeding on conspecifics on oyster growth, and found that shell diameters were significantly larger in oysters exposed to *Callinectes sapidus* crabs, versus those exposed to Panopeid mud crab and the control (no predator cues). There was a similar effect of predator cues on the shell-breaking force (crushing resistance). Other studies examining nonlethal predator effects on molluscs have also found cues from consumed conspecifics have a significant effect on physiology (Bourdeau 2010, Daleo et al. 2012, Scherer et al. 2017). In the data presented previously, crabs were never fed in the same tanks as the treatment water was collected from. This ensured that cues from conspecifics (i.e., dead oysters) were not interfering with cues from the crab exudates or other chemosensory cues. This may have resulted in a weaker response, and which might explain why we did not see a significant effect of the predator exposure on length.

Significant variability in the morphological responses of the oyster spat between experimental treatments were also found in this study. For example, the observed mass changes in animals exposed to the different predator cues did not correspond to changes in oyster spat length. The oyster spat exposed to Panopeid mud crabs, for one, were heavier than the control (no predator) oyster spat, but not larger. These animals also had some of the lowest crushing densities when exposed to predator cues, so a thicker shell did not always correspond to a stronger shell. The change in weight found in this study for spat exposed to Panopeid mud crabs was on par with that found by Scherer and Smees (2017). That study reported oysters exposed to Atlantic mud crabs, *Panopeus herbstii*, showed significant increase in shell mass and area compared with control treatment oysters. They reported an average of 0.8 mg (0.008 g SD) in shell weight for control animals, and 1.12 mg (0.011 g SD) for the oyster spat exposed to crab cues.

No consistent trends in shell-crushing density between control and predator exposure treatments were found in this study. A study by Scherer et al. (2017) exposed oysters for 16 wk

to crabs fed either live or aged oysters (to simulate predatory versus scavenger crabs), and found shell strength was highest in treatments exposed to predatory crabs, followed by scavenging crabs, and finally the control treatment. They found, however, that there was no difference in oyster wet mass between the treatments. Since the current study was limited to 6 wk, it is possible that a longer time span is needed to detect differences in shell morphology. It would also be useful to examine the crushing density and growth of spat that have been exposed to predator cues and then outplanted to determine latent effects, if any. Second, one key difference in experimental design between our work and other reports was the inclusion of crushed coral in the aquaria to provide sources of calcite/aragonite for shell-building. This inclusion mimics what oyster growers might see in the wild, and may promote shell-building in the presence of predators.

Significant differences in wet mass between spat exposed to the Panopeid mud crabs, a native predator, and the spat exposed to the green crab *Carcinus maenas*, an invasive predator was noted. Mud crab-exposed spat were generally smaller than those exposed to the green crab, but there was a lot of variability in the length of spat exposed to green crab. Oysters exposed to Asian shore crab, *Hemigrapsus sanguineus*, another invasive crab, and spider crabs, *Libinia emarginata*, a non-predator crab, were the most similar in response to the control spat. In fact, oysters exposed to the nonpredator *L. emarginata* spider crab had the largest gain in weight. Some of this can be explained by the prey naiveté hypothesis, particularly for newer invasive species (Newell et al. 2007, Grason 2010, Bible et al. 2017). The green crab, however, has been present for greater than 150 y, and studies have reported evidence of nonconsumptive effects of this predator on molluscs (Matassa & Trussell 2011, Coverdale et al. 2013). More work on these interactions is needed as the effects of some invasive crab species in temperate systems have been reported to be positive, such as aiding in marsh recovery (Coverdale et al. 2013), and regulating top-down effects of community interactions (Gosnell & Gaines 2012).

In terms of the potential impact of current aquaculture practices, the absence of predator cues does appear to result in larger oysters that have thinner shells at this developmental stage (spat). In many marine invertebrates, environmental effects in the larval and juvenile stage can carry over to adult stages as legacy effects (see Padilla & Miner 2006). If the effects of waterborne predator cues on the shell of oyster spat can carry over to adult stages remains to be studied. There is more evidence that the presence of predators can affect shell strength and size in adult oysters (Robinson et al. 2014, Scherer et al. 2017). There has been less work on the practical nonconsumptive responses of molluscs to the presence of predators in an aquaculture setting. One study examined the responses of blue mussels, *Mytilus edulis*, grown in suspension versus bottom cages that were exposed to predator cues (Christensen et al. 2012). Those workers reported significant, but different, physiological responses in the mussels in the presence of *Carcinus*

maenas crabs. The authors suggested the use of suspended aquaculture as a better alternative than bottom-planted cages for growing mussels for market in this region.

In terms of informing conservation efforts, hatchery-grown molluscs are used to enhance wild populations (Wilbur et al. 2005, Guest et al. 2008, Tettelbach et al. 2011, 2013, Steppe et al. 2016). In one study, northern abalone *Haliotis kamtschaticana* that were outplanted to enhance wild population numbers faced high mortality due to predation (Hansen & Gosselin 2013). Conversely, populations of the blue mussel *Mytilus edulis* exposed to predator cues developed a thicker shell, which resulted in a 48% increase in handling time by the crab *Carcinus maenas*, and a subsequent defense against future predation (Freeman 2007). Similarly, hatchery-grown bay scallops, *Argopecten irradians irradians*, outplanted directly on sea beds had higher mortalities, but less biofouling and higher growth rates than animals maintained in suspended bags (Tettelbach et al. 2011). Together with the results of this study, these findings indicate that molluscs grown in the absence of predators can exhibit maladaptations that can place a constraint to the restoration of wild populations.

Significant effects of predator presence on the total wet weight (g) of oyster spat was demonstrated in this study. Given the changes in shell length with some crab predator treatments, this work supports the previously demonstrated concept that shell accretion is affected by predator presence. This technique could be used by shellfish growers to thicken the otherwise brittle shells of cage-grown oysters. As noted by previous work, the shell thickening likely comes at the energetic cost of soft tissue biomass (Peterson 1986, Johnson & Smee 2014), but oysters can be moved from site to site or crab predator treatments can be removed when shells are thick enough for market. This potential application for aquaculture operators can be used to enhance the growth of specific parameters of bivalves in culture as compared with wild bivalve populations that experience more variable growth. Although more applied research needs to be done as to how to implement this strategy of exposing juvenile oysters to crabs and other predators to enhance particular growth characters effectively, there is potential for this technique to produce market bivalves with a thicker shell. An important outcome of our findings is that the species of predator in the exposure system matters, with the presence of some species resulting in significantly heavier shells than the control. These findings indicate that there are complex community dynamics and predator-prey interactions in this system that warrant further study.

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