

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

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Abstract The response of the eastern oyster *C. virginica* to the presence of the oyster drill *Urosalpinx cinerea* was examined from July to September 2011. Several aspects of oyster growth were measured, including wet weight, shell weight, and dorsal shell area for oysters collected near Groton, Connecticut (41.32036 N, -72.06330 W). Wet weight and shell weight growth were significantly higher in the presence of the predator *U. cinerea*, while tissue weight showed no difference from the control. The control group showed more shell area growth and a much lower ratio of shell weight growth to shell area growth. Differences in shell weight to area ratio indicated that *C. virginica* dramatically shifted from lateral shell growth to shell thickening in the presence of *U. cinerea*. This inducible defense has not been previously shown for *C. virginica* and could play an important role in the predator–prey interaction between these two species.

Introduction

Inducible defenses in response to predation occur in a variety of taxa, including terrestrial plants (Karban and Myers 1989), marine seaweeds (Van Alstyne 1988; Cronin and Hay 1996), and benthic invertebrates (e.g., Harvell 1986; Lively et al. 1986). In most gastropods and bivalves, the shell is the primary defense mechanism and is often modified to defend against predators (Vermeij 1982; Palmer

1985; Appleton and Palmer 1988; Leonard et al. 1999; Trussell and Etter 2001). Graus (1974) found that shell thickness decreased with increasing latitude due to elevated CaCO₃ deposition rate and higher number of predators in tropical ecosystems. In the intertidal zone of the eastern United States the invasive green crab *Carcinus maenas* has induced thicker shells in multiple prey species including the whelk *Nucella lapillus* (Vermeij 1982; Trussell et al. 2003), the blue mussel *Mytilus edulis* (Leonard et al. 1999), and the snail *Littorina obtusata* (Trussell and Etter 2001). In sand flats of the southeast US, *Busycon* whelks induce changes in the shell growth of the clam *Mercenaria mercenaria* (Nakaoka 2000). These prey species display phenotypic plasticity in that individuals are able to alter their shell growth patterns, in some cases within a couple of months (Leonard et al. 1999; Trussell and Etter 2001).

While several studies have focused on inducible shell defenses, few have examined the response to drilling predators and none have tested the shell plasticity of oysters. The eastern oyster *C. virginica* is common in intertidal and shallow subtidal zones along the north-west Atlantic coast and plays a large part in estuarine ecosystems (Dame 1972). It has great commercial importance in the eastern United States and Canada, where it is farmed as far north as the Gulf of Saint Lawrence in Canada (Singh and Zouros 1978). Eastern U.S. populations have become genetically differentiated between estuaries including the Delaware River, James River, and Long Island Sound, where they grow to different sizes (Dittman 1998). Oyster growth and shell morphology is more variable than most bivalves, since their axes of growth are not well-defined (Palmer and Carriker 1979). The shells of oyster have high phenotypic plasticity, as they can alter shell growth patterns based on substrate, temperature, current, turbidity, and pollution, among other factors (Palmer and Carriker 1979; Polson

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et al. 2009). While growth varies with location and environmental conditions, *C. virginica* displays continuous growth throughout its life and size is closely tied to fitness (Singh and Zouros 1978).

A major predator of *C. virginica* is the oyster drill *Urosalpinx cinerea*, which can have a dramatic effect on oyster populations. In 1894, *U. cinerea* destroyed 90% of *C. virginica* at oyster farms in Hampton Roads, Virginia, and resulted in one million dollars of damage to oysters in Long Island Sound (Federighi 1931). The oyster drill has recently invaded both Europe and the west coast of North America and shown the ability to consume other oyster species found in these locations (Buhle and Ruesink 2009; Faasse and Lighthart 2009). While *U. cinerea* prefers to prey on oysters, it also consumes blue mussels (*M. edulis*), slipper limpets (*Crepidula fornicata*), barnacles (*Balanus balanoides*), and bivalves (*Argopecten irradians*, *Mya arenaria*) (Hanks 1957; Carriker 1969; Franz 1971; Pratt 1974; Ordzie and Garofalo 1980). The oyster drill feeds preferentially on smaller oysters and those with thinner shells, although it can drill adult oysters (Federighi 1931; Buhle and Ruesink 2009). The boring process is largely chemical and is facilitated by the application of viscid acid from the accessory boring organ (Carriker 1969). It can take *U. cinerea* up to 6 days to drill an adult oyster, but by focusing primarily on smaller individuals, one drill can consume up to 200 oysters per year (Federighi 1931).

Despite the frequent co-occurrence of *C. virginica* and *Urosalpinx cinerea*, little is known about the non-lethal interactions between these species. The goal of this study was to assess the impact of predation stress on the growth patterns of *C. virginica* by measuring several aspects of *C. virginica* growth with and without the presence of *U. cinerea*. Changes in shell thickness or the energy allocation between shell growth and tissue growth could affect the susceptibility of *C. virginica* to predation. The eastern oyster has not been shown to have inducible defenses, but given the preference of *U. cinerea* for thin-shelled oysters, a shell-thickening response could serve as an effective defense. Therefore, we hypothesized that *C. virginica* exposed to *U. cinerea* for an extended period would produce thicker shells. Since *N. lapillus* and *Littorina littorea* have both been shown to produce thicker shells at the expense of linear shell growth (Trussell et al. 2003), we also hypothesized that shell thickening in *C. virginica* would result in reduced lateral shell growth.

Materials and methods

Crassostrea virginica were collected ($N = 80$) intertidally and subtidally between Jupiter Point and Bluff Point in Groton, Connecticut, USA (41.32036 N, -72.06330 W).

U. cinerea were collected ($N = 56$) in the intertidal zone less than one kilometer from Avery Point, Groton, Connecticut. Both species were collected on June 25, 2011 and were held in flowing seawater tables for 10 days in the University of Connecticut Avery Point Rankin Laboratory prior to the start of the experiment. Epibionts were removed, and oysters were individually labeled with Hallprint® shellfish tags super-glued to the side of the shells. Oysters were 3–8 cm in length, with a mean length of 5.5 cm, wet weight of 24.4 grams, and dry shell weight of 15.7 grams.

Several aspects of shell size were measured for *C. virginica* and *U. cinerea* on July 2 and 3, 2011 and again at the end of the experiment on September 4 and 5, 2011. Wet weight was measured on an electronic balance to the nearest 0.01 g after specimens were patted dry with paper towels. Immersed weight was also measured in order to estimate shell weight, using methods described by Palmer (1982). A tray was suspended in a bucket of water from the electronic balance, and then specimens were placed in this tray to measure immersed weight to 0.01 g. In order to estimate shell weight, 20 specimens of each species were sacrificed, tissue was dissected out, and then shells were patted dry with paper towels and weighed. Afterward, shells were placed in a muffle furnace at 500°C for two hours to remove any remaining organic material and moisture. Dry weight of the shells was then measured and two regressions were plotted, describing the relationships of both dry shell weight ($DSW = 1.443 * \text{immersed weight}$, $r^2 = 0.994$) and wet shell weight ($WSW = 2.071 * \text{immersed weight}$, $r^2 = 0.992$) to immersed shell weight. Coefficients of determination were similar to those described by Palmer (1982) who detailed this immersed weight method. The wet shell weight regression equation was used to estimate wet shell weight from immersed weight for all specimens before and after the experiment. Wet shell weight was used because oyster total wet weight (shell + tissue) was measured, so wet shell weight allowed for the calculation of tissue growth. In addition to these measurements, photos were also taken of the dorsal side of the oysters before and after the experiment, allowing for the digital measurement of shell area in ImageJ® image analysis software.

The experimental units were 12 large round (2.25 m diameter, 1 m tall) mesocosms with flow-through seawater outside of the Rankin Laboratory. Since the tanks were constantly supplied with raw seawater pumped out of Long Island Sound, oysters were not given additional food. Because chemical predator cues were being tested, six mesocosms were randomly assigned to have predators (*U. cinerea*) and six were used as controls. Oysters were kept in small (12 cm diameter, 20 cm tall) cylindrical plastic containers with both ends cut out and replaced with 4-mm plastic mesh. The predation treatment included four

U. cinerea inside a smaller plastic cylinder with mesh ends within the prey container. Since this smaller cylinder took up approximately 40% of the space in the container, predator treatments included three oysters per container and controls included five oysters per container. This kept *C. virginica* density constant between treatments, accounting for the smaller volume and ensuring that oysters were not space-limited in the containers. Predators were supplied with two live *C. virginica* within the predator cage to feed on each week, so that neither control nor predator treatments exceeded five oysters per container. Two containers were placed in each of the mesocosms for a total of 12 containers for both the predator and control treatments.

Since the mesocosms were outdoors, the experimental organisms were exposed to natural light cycles and temperature fluctuations over the course of the experiment. The experiment ran for a period of 2 months from July 4 to September 4, 2011. Temperatures in 3 tanks of each treatment were elevated by immersion heaters (for an unrelated experiment) and were recorded with temperature probes connected to a computer but did not vary more than an average of one degree between tanks over the course of the experiment. Containers rested on the bottom of each of the mesocosms and were kept clear of fouling algae by *Littorina littorea* snails that grazed freely within the mesocosms.

Once measurements were made after the end of the experiment, a one-way ANOVA compared differences between containers and tanks within each treatment. Two-sample *T* tests (two-tailed) were run in Minitab® to compare differences in total growth, shell growth, shell area growth, and tissue growth between treatments.

Results

Comparisons of oyster wet shell weight growth showed no significant difference (Two-sample *t* test, $t_{78} = 0.19$, $P = 0.84$) between heated and non-heated tanks. An ANOVA comparing growth between all mesocosms of the same treatment revealed highly non-significant differences in shell growth within control treatments (ANOVA, $F_{(5,46)} = 0.30$, $P = 0.83$) and within predator treatments (ANOVA, $F_{(5,28)} = 0.80$, $P = 0.50$). Because of the lack of differences within treatments, data from all tanks were pooled to allow for a more powerful comparison of the effect of predation on *C. virginica* growth. Underwood (1997) suggested that data from nested designs such as this can safely and effectively be pooled when the null hypothesis cannot be rejected even with an alpha critical value of 0.25. Since *P*-values within treatments for the current experiment were found to exceed 0.50, we pooled the data from the different tanks within each treatment. Eleven oysters died during the 2-month period of the experiment, two from the predator

treatment (5.6%), and nine from the control treatment (15%). An additional 7 oysters from the control group were not included in the analysis because of data outliers (greater than three standard deviations from mean) due to very small changes in area over the course of the experiment, which resulted in extraordinarily high weight/area ratios that skewed the means. Therefore, for all analyses, the sample size for the predator treatment was 34 and for the control treatment was 46. Significant differences were found between oysters in predator and control treatments in terms of shell weight growth and shell thickness, as well as total wet weight growth over the course of the experiment.

Oysters exposed to *U. cinerea* predation stress increased their wet weight significantly more than the controls, with a predator treatment mean increase of 1.137 g (4.67% of initial weight) and control mean of 0.787 g (3.22%) (Two-sample *t* test, $t_{78} = 2.03$, $P = 0.046$) (Fig. 1). This increase was almost exclusively due to a significantly greater increase in wet shell weight for *C. virginica* exposed to predators ($X \pm SE = 0.818 \pm 0.140$ g, $N = 34$, 3.90% increase) than the control ($X \pm SE = 0.399 \pm 0.086$ g, $N = 46$, 1.90%) (Two-sample *t* test, $t_{78} = 2.67$, $P = 0.009$) (Fig. 1). Wet shell weight was used because it was measured in the same manner as total wet weight and thus could be directly used to calculate wet tissue weight. The difference in dry shell weight between predator (mean = 0.570, 3.64% increase) and control (mean = 0.278, 1.78%) treatments was also highly significant ($t_{78} = 2.67$, $P = 0.009$). There was no significant difference in tissue (non-shell) growth between the two treatments over the experimental period (control mean = 0.388 g, predation mean = 0.319 g, $P = 0.50$).

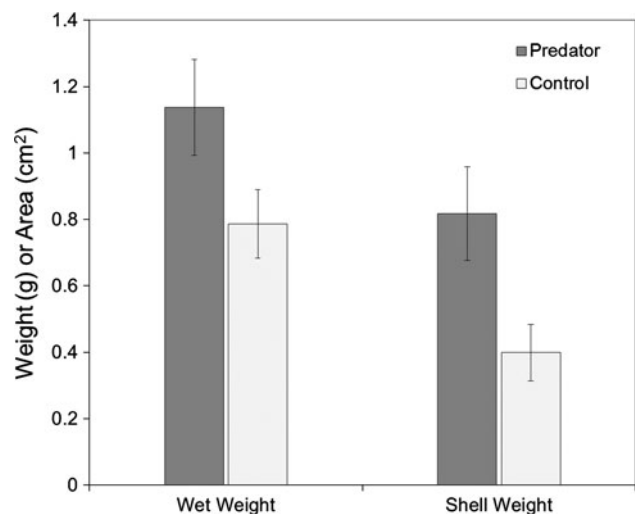


Fig. 1 Comparison of wet weight and wet shell weight gain over a period of 2 months between *C. virginica* in the control treatment and those exposed to the predator *U. cinerea*. Both wet weight and wet shell weight growth were significantly higher when oysters were exposed to predation (\pm SE bars)

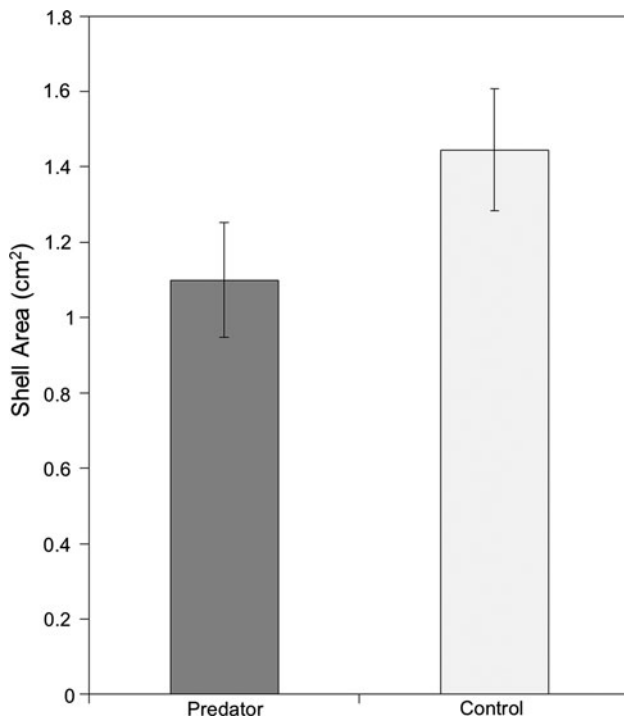


Fig. 2 Comparison of dorsal shell area growth over a period of 2 months between *C. virginica* in the control treatment and those exposed to the predator *U. cinerea*. Oysters in the absence of *U. cinerea* grew more in terms of dorsal shell area but not significantly more ($P = 0.11$) (\pm SE bars)

Despite the greater shell weight gain in the predator treatment, oysters in the control group displayed more lateral areal shell growth of the dorsal side of the shell (predator mean = 1.10 cm^2 , control mean = 1.44 cm^2), but this difference was not significant with a critical value of 0.05 (Two-sample t test, $t_{78} = 1.61$, $P = 0.11$) (Fig. 2). To estimate the amount of shell deposition allocated to thickening the shell, shell thickness was approximated as wet shell weight (g) per square centimeter of dorsal shell area. Figure 3 shows tenfold significant differences in shell thickness (ratio of shell weight growth to shell area growth) between control ($X \pm \text{SE} = 0.19 \pm 0.24 \text{ g/cm}^2$, $N = 46$) and predator ($X \pm \text{SE} = 1.91 \pm 0.71 \text{ g/cm}^2$, $N = 34$) treatments (Two-sample t test, $t_{78} = 2.57$, $P = 0.012$). Similar results were found with thickness estimated from the ratio of dry shell weight growth to shell area growth, with a control mean of 0.14 g/cm^2 and predator mean of 1.33 g/cm^2 (Two-sample t test, $t_{78} = 2.57$, $P = 0.012$). Variability shown in error bars of Fig. 3 was relatively high due to the inclusion of two variables: dorsal shell area and shell weight, but did not adversely affect the significance of the results.

Discussion

The eastern oyster *C. virginica* showed a distinct response to predation stress induced by the oyster drill *Urosalpinx*

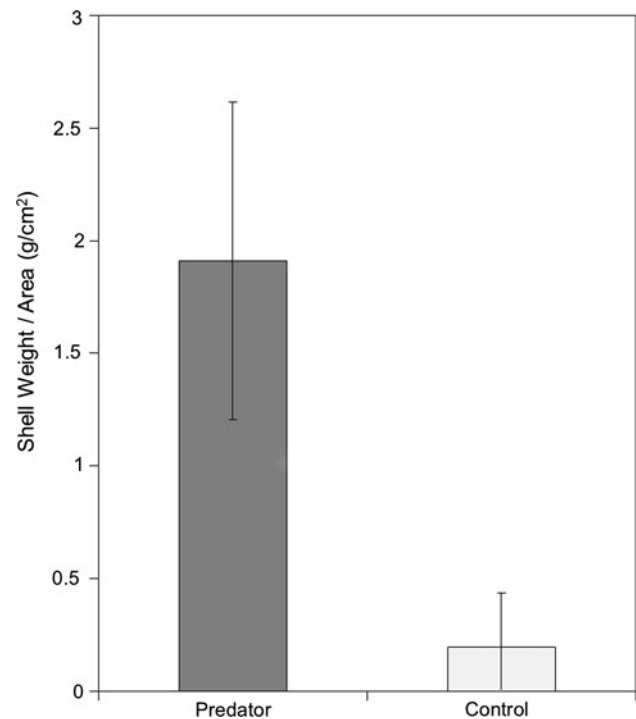


Fig. 3 Comparison of wet shell weight growth to shell area growth ratio between *C. virginica* in the control treatment and those exposed to the predator *U. cinerea*. Oysters in the presence of *U. cinerea* for 2 months showed a tenfold increase in this approximation of shell thickness and had a significantly higher wet shell weight growth to shell area growth ratio than oysters in the control group (\pm SE bars)

cinerea. The cue involved is likely chemical and not tactile, because predator and prey were kept spatially segregated within experimental containers. It is unknown whether the chemosensory response of *C. virginica* was due solely to the presence of *U. cinerea* or was related to attacks on oysters within the predator cages. The clam *M. mercenaria* changed shell growth patterns solely due to chemical cues of a *Busycon* whelk (not damaged conspecifics), so we predict that the response of *C. virginica* is also a result of chemical cues from the predator *U. cinerea* (Nakaoka 2000). The response to a chemical cue is similar to those described for crab predator stress induction on mussels (Leonard et al. 1999) and snails (Vermeij 1982; Palmer 1985; Trussell and Etter 2001).

The presence of the predatory whelk *U. cinerea* caused an increase in the wet weight growth of *C. virginica* (Fig. 1), but the difference between the predator treatment and the control was entirely explained by shell weight growth patterns (Fig. 1). Since there was no significant difference in tissue (non-shell) growth between predator and control treatments, it appears that the energy required to produce increased shell mass was not due to a change in allocation between shell and tissue growth. If this had been the case, increased shell weight would have been accompanied by a decrease in tissue growth during the 2-month span

of this study. However, it is possible that tissue growth could show different long-term patterns with regard to shell deposition, since body growth is limited by the size of the shell (Trussell and Etter 2001).

The higher rate of *C. virginica* shell weight growth (Fig. 1) in the predator treatment indicates that calcification rate was likely not a limiting factor. The fact that shell weight growth increased without a corresponding decrease in tissue weight growth rate could be due to several factors beyond the scope of this study, including increased feeding rate, increased metabolism, changes in allocation to reproductive tissue, or other physiological changes that could enhance shell deposition rate (McIntosh and Townsend 1996; Schmitz et al. 1997; Turner et al. 2000; Peacor and Werner 2001).

Greater lateral shell growth in the control treatment (Fig. 2) is most likely due to the switch to shell-thickening processes in the predator treatment due to the perceived threat of *U. cinerea* predation. Lateral shell growth in the absence of predators indicates that this is the typical summer growth pattern for *C. virginica*, which makes sense because lateral growth increases the volume of the oyster, unlike shell thickening. This increased internal size allows for greater tissue growth, higher feeding rates, and higher fecundity (Peters 1983; Sebens 1987; Arendt 1997).

Shell thickness was approximated from the ratio of shell weight to dorsal shell area. This is not a direct measure of thickness but does indicate the amount of shell material per unit area, since bivalve shells are deposited in accretionary layers shell density cannot be altered after layers are deposited. Therefore, higher shell weight growth (Fig. 1) and lower shell area growth (Fig. 2) in predator-exposed *C. virginica* indicated a clear increase in interior shell deposition or shell thickness. Even if there were a disparity in new shell deposit density between the two treatments, the ten-fold difference in shell weight growth to shell area growth ratio (Fig. 3) is so large that small density alterations would not impact the overarching shift from lateral shell growth to shell thickening. Given the two-month period of this study, it is unknown if *C. virginica* shell thickness would continue to increase with many months or years of exposure to *U. cinerea*, or if there is an optimization of shell thickness after which there is little benefit to continued thickening with regard to *U. cinerea* predation.

While the full extent and timing of *C. virginica* response to *U. cinerea* is unclear, it is clear that oyster inducible defenses allow it to produce thicker shells in response to the threat of predation by *U. cinerea*. As with other types of phenotypic plasticity and inducible defenses, the ability of *C. virginica* to only produce more shell and thicker shell in the presence of predators provides several potential energetic advantages (Vermeij 1982; Appleton and Palmer 1988; Leonard et al. 1999; Trussell and Etter 2001). By not

always producing thick shells, the eastern oyster may be able to put more energy into lateral shell growth (Fig. 2) that rapidly increases the size of the organism and thus has many ecological benefits such as increased feeding rate and reproduction (Peters 1983; Sebens 1987). Allocation of energy to processes other than shell thickening could allow for greater lateral shell growth directly or provide energy necessary for the growth of the mantle, which facilitates lateral shell extension (Ren and Ross 2001).

Since oysters did not grow as much in terms of shell weight in the absence of predators, they may also be able to allocate more energy toward tissue growth, reproduction, feeding, or other non-defensive energetic costs. Feeding rate could have other implications as well, as Bourdeau (2010) found that an inducible shell-thickening response in a marine snail (*Nucella lamellosa*) was actually a behavioral response that resulted in decreased feeding in the presence of predators. While oysters may alter feeding rates in response to the threat of predation, they do not need to move around to feed as snails do and feeding may not increase the threat of predation by a slow-moving drill (unlike snails with crab predation). Since *C. virginica* in this experiment displayed a response to a drilling predator, the most probable reason behind increased shell thickness is that it may decrease mortality rate in an environment with exposure to *U. cinerea*.

Since the presence of *U. cinerea* induced shell thickening and inhibited lateral shell growth, we predict that *C. virginica* populations in areas with high densities of *U. cinerea* would be smaller in terms of shell area than similar populations with few *U. cinerea*. Calcification rate changes with temperature as well and several mollusks have been shown to grow shell faster in warmer temperatures, so it is possible that the inducible defenses of *C. virginica* change with latitude (Graus 1974; Trussell and Etter 2001; Kawai 2009; Miyaji 2010). If this is the case, then environmental changes such as increased ocean temperatures or dissolved CO₂ levels could impact the shell production of *C. virginica* and facilitate (warming) or inhibit (CO₂) the ability of this oyster to produce thicker shells in response to the presence of predators such as *U. cinerea* (Dame 1972; Newell and Kofoed 1977; Gazeau et al. 2010; Thomsen and Melzner 2010). Recent invasion of Europe and western North America by *U. cinerea* highlights the importance of understanding prey response to this whelk, as multiple species of oysters will be exposed to this novel predation threat over the next several years as the distribution of *U. cinerea* spreads (Buhle and Ruesink 2009).

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