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SHORT COMMUNICATION

NURSERY EXPOSURE OF OYSTER SPAT TO DIFFERENT PREDATORS STRENGTHENS OYSTER SHELLS[§]

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INTRODUCTION

Inducible defenses are common in many organisms and allow potential prey to balance reducing predation risk with critical life history processes such as growth and reproduction (Kats and Dill 1998, Cronin 2001, Weissburg et al. 2014). Bivalves are preyed upon by a suite of predators and many can modify their behaviors (e.g., feeding or burrowing, Smee and Weissburg 2006, Flynn and Smee 2010) or morphology (e.g., shell size or shape, Leonard et al. 1999, Nakaoka 2000, Scherer et al. 2016) to reduce predation risk. For example, reduced feeding can help hard clams (*Mercenaria mercenaria*) avoid detection by potential predators (Smee and Weissburg 2006) while soft-shell clams (*Mya arenaria*) burrow deeper when green crabs (*Carcinus maenas*) are nearby, making it harder for crabs to capture them (Flynn and Smee 2010). Morphological changes include shell strengthening by the Eastern oyster (*Crassostrea virginica*) (Lord and Whitlatch 2012, Robinson et al. 2014) and increasing both shell thickness and byssal thread production by blue mussels (*Mytilus edulis*; Leonard et al. 1999).

Eastern oysters, hereafter referred to as oysters, are ecologically and economically important, providing a host of benefits such as shoreline protection, water filtration, and habitat creation (Grabowski and Peterson 2007). Additionally, oysters are an important commercial fishery and are a critical part of the economy and culture of local communities surrounding the Gulf of Mexico (GOM; Posadas 2017). Yet, oyster reefs are one of the most degraded marine habitats, with ~85% of oyster habitats lost worldwide (Beck et al. 2011). The GOM has experienced significant declines in the oyster fishery accompanied by loss of benefits oysters provide (zu Ermgassen et al. 2013), and there is considerable interest in restoring oysters to recover these ecological, economic, and cultural benefits. However, it is not uncommon for reef restoration efforts to fail (Mann and Powell 2007, La Peyre et al. 2014) as predators are a common source of mortality in juvenile oysters (Bisker and Castagna 1987), and yearly age-specific mortality rates can exceed 70% in some locations (Mann and Powell 2007). The purpose of this study was to ascertain if oyster susceptibility to predation

could be decreased by artificially inducing defenses while in an aquaculture production facility.

Oysters are known to increase shell hardness in response to blue crab (*Callinectes sapidus*) and mud crab (*Panopeus herbstii*) exudates (Newell et al. 2007, Robinson et al. 2014, Scherer et al. 2016, Scherer and Smee 2017), which makes them less susceptible to mud crab predators (Robinson et al. 2014). However, it is not well understood which predators induce the strongest defense in flow-through systems or how these defenses improve survival among different predators (Combs et al. 2019). Here, we tested oyster morphological responses to exudates from oyster drills (*Stramonita haemastoma*), a species believed by farmers to be the predominant predator of oysters in the northern GOM (Grice and Walton 2017), and compared their response to blue crab exudates when raised in a nursery. Then, oysters were used in laboratory feeding assays with both blue crabs and oyster drills to determine how changes in shell characteristics influenced survival among these different predators. Oysters exposed to exudates from both oyster drills and blue crabs produced stronger shells than those in controls without predator exudates. Oysters from control treatments were consumed more often than those reared with predators, indicating that shell induction effectively reduces predation risk from both oyster drill and crab predators.

MATERIALS AND METHODS

Nursery rearing

Oyster larvae were allowed to settle onto 2.5 cm x 2.5 cm granite tiles at the Auburn University Shellfish Laboratory on Dauphin Island, AL in May 2020. Following settlement and metamorphosis into spat, oysters were placed into a flow-through unfiltered seawater system at the Dauphin Island Sea Lab which pumped water directly from Mobile Bay and maintained natural abiotic water conditions. Oyster spat were exposed to predation risk from either oyster drills, blue crabs, or a control of no predators in 12 flow through mesocosms (2.0 m diameter, water depth = 0.4 m) with water flow ~20 L/min. Within each tank, oyster spat were held in 5 plastic cages (64

[§]The first author conducted this research as part of the Dauphin Island Sea Lab's Research Experience for Undergraduates in the coastal and nearshore marine science program.

x 23 x 14 cm), and each cage contained 65 tiles with oyster spat (325 tiles per tank, 4,380 total tiles). The number of oyster spat per tile varied greatly from 0–50, and we elected to maintain this variation to mimic natural settlement and reef restoration practices. Cages were suspended above the substrate to reduce sediment build-up. Tanks were drained daily, and oysters rinsed to remove sediment. Four tanks contained adult blue crabs (6 crabs per tank in 3 cages that partitioned individuals apart), 4 tanks contained oyster drills, (30 per tank, caged in 3 groups of 10), and 4 control tanks without predators. Predator cages were distributed evenly along the tank edges. Crabs and oyster drills were fed recently shucked oyster tissue 3 times per week (6, ~5.0 cm oysters were used per tank). Crabs and oyster drills were replaced during the experiment as needed due to mortality. Oyster cages were rotated daily within their respective tank to prevent tank placement artifacts.

Shell morphology measurements

After 4 weeks, 2 tiles from each cage were haphazardly selected and 2 oysters from each tile were measured (4 oyster spat/cage, 20 oysters/tank; 80 oysters/cue treatment). At this size, oysters are roughly round, and shell diameter was measured to the nearest hundredth of a mm using digital calipers from the umbo to the outer shell edge. We then quantified the force needed to break each oyster shell using a penetrometer (Kistler force sensor 9203 and a Kistler charge amplifier 5995). A small blunt probe was placed centrally to be equidistant from the shell edges and perpendicular to shell surface. Gentle and consistent pressure was applied until the shell cracked, and the maximum force (N) needed to break the shell recorded, which is a standard proxy for shell hardness (Robinson et al. 2014). Because larger individuals have a stronger shell as a byproduct of their size, we divided shell crushing force by shell diameter to produce a size-standardized metric of shell strength (i.e., standardized crushing force). Care was taken to avoid measuring oysters surrounded by cohorts to ensure shell growth or shape was not limited by space.

We compared standardized oyster shell strength among those grown with blue crabs, oyster drills, and controls using ANOVA with predator treatment as a fixed factor and tank as a random factor. Tukey's multiple comparison test was used to determine pairwise differences in shell strength. Oyster shell length was analyzed similarly. All statistical analyses were conducted in R version 4.0.0 (R Core Development Team 2020).

Predator choice experiment

To ascertain if oyster shell changes were effective at reducing predation risk, we also performed laboratory feeding assays using oyster drills and blue crabs, 2 common predators of newly settled oysters in Alabama. We thinned oysters so that 10 spat were present on each tile. Feeding assays consisted of 3 oyster tiles, each containing 10 oyster spat, from each of the predator treatments (blue crab exposed, oyster drill exposed, control). Tiles were placed in a plastic bucket measuring 20 cm diameter and containing 2L of ambient seawater to a depth of 7 cm (30 spat total/bucket). Ten buckets received either a single oyster drill (size [mean \pm sd] = 3.2 \pm 0.5 cm), a single juvenile blue crab

(5.1 \pm 1.5 cm), or no predator to control for mortality due to environmental stress (30 buckets). Predators were starved for 48 h prior to commencing the experiment to standardize hunger levels (Hill and Weissburg 2013). The number of oysters alive was checked daily between 0830 – 1030 and between 1630 – 1830 for one week. A second experimental trial was completed using the same setup immediately after the conclusion of the first. All predators were only used once.

We performed a mixed-effects Cox proportional hazards model (i.e., survival analysis) to test whether oyster survival was governed by the fixed-effects predator species presence and cue exposure treatment. Holding bucket nested in experimental trial were treated as mixed-effects to account for non-independence among oysters exposed to the same individual predator.

RESULTS AND DISCUSSION

Oyster spat shells were significantly harder when reared with predators compared to those grown in control tanks without predators ($F_{2,9} = 14.81$, $p = 0.001$, Figure 1A), consistent with previous findings (Robinson et al. 2014). Additionally, oyster spat were 15% larger in blue crab treatments than controls while those exposed to oyster drills were 5% larger than controls ($F_{2,9} = 3.75$, $p = 0.065$, Figure 1B). Shell hardness of oysters

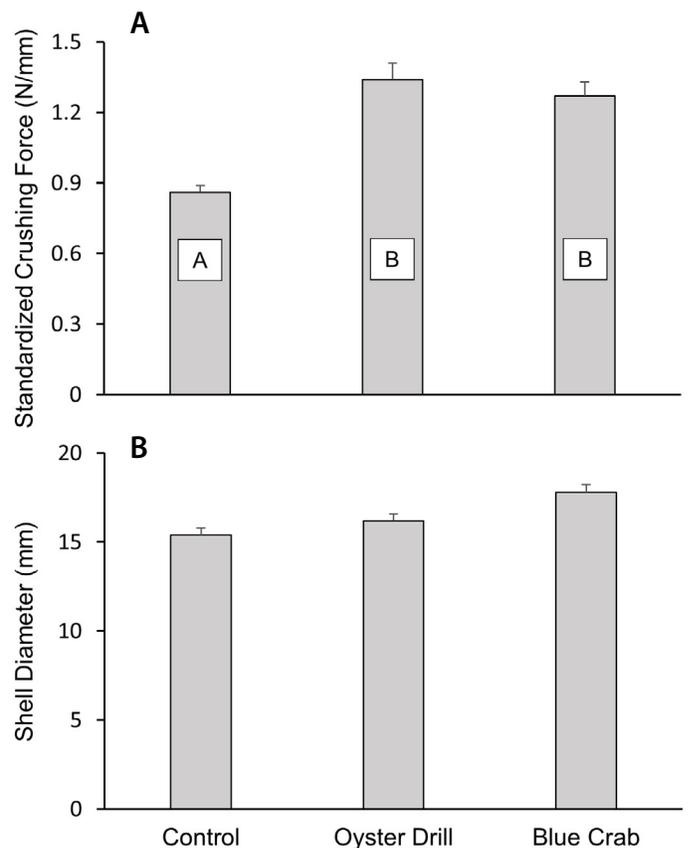


FIGURE 1. Oyster spat shell characteristics when reared with either blue crabs, oyster drills, or no predators (control). A. Mean + se oyster shell hardness standardized by shell diameter (N/mm). B. Mean + se shell diameter (mm). Letters denote significant pairwise differences from Tukey's post-hoc tests ($n = 80$, $p < 0.05$).

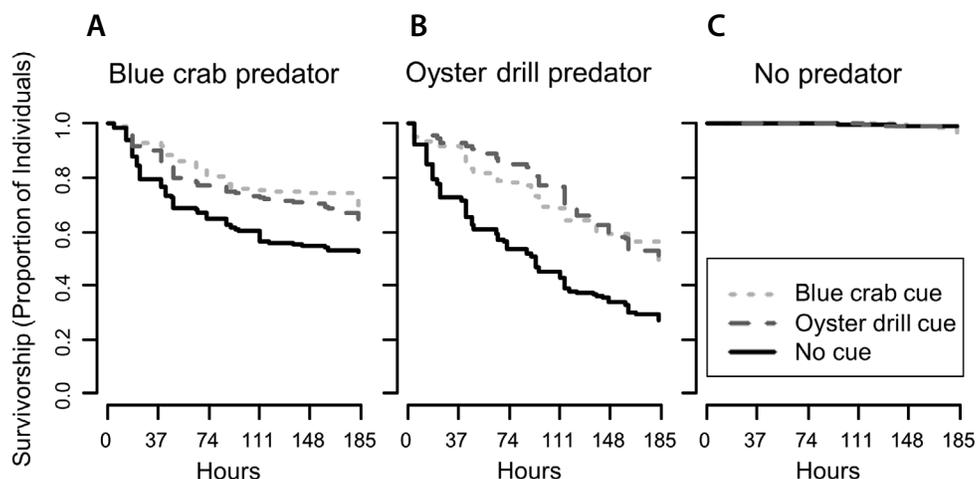


FIGURE 2. Survivorship curve of the proportion of individual oysters (*Crassostrea virginica*; $n = 200$ per treatment) which survived over time (h). A. Presence of blue crab (*Callinectes sapidus*) predators. B. Presence of oyster drill (*Stramonita haemastoma*) predators. C. No predators (controls). Lines denote prior oyster exposure to different predator cues (blue crab, oyster drill, or no predator cues; $n = 20$ per treatment). Both predator treatments had higher survival than controls, $p < 0.05$.

was not significantly affected by the specific predator species used to provide cues.

In feeding assays, 573 (out of 1,200) oysters died when predators were present, while only 7 (out of 600) oysters died in control containers with no predators (coef = 4.41, $Z_{10, 48.75} = 6.20$, $p < 0.001$, Figure 2), indicating that predators were actively consuming oysters and that oyster mortality was caused by predators. There was not a significant difference in consumption rate between the 2 predator species (coef = 0.57, $Z_{10, 48.75} = 1.17$, $p = 0.240$). Throughout the experiment, prior exposure to either blue crab or oyster drill predator cues significantly increased oyster survival compared to controls with no prior predator exposure (coef = -0.90 , $Z_{10, 48.75} = -7.88$, $p < 0.001$; coef = -0.89 , $Z_{10, 48.75} = -8.05$, $p < 0.001$, respectively). Spat exposed to blue crab cues had 58% higher survival than spat with no prior cue exposure while oyster drill cues increased spat survival by 39% over controls. However, the survival benefits provided by these 2 cue sources were not significantly different at the conclusion of the experiment (coef = -0.26 , $Z_{10, 48.75} = -1.34$, $p = 0.180$; Figure 2A,B). The interaction between predator species present and prior cue exposure treatment was above $\alpha = 0.05$ but likely ecologically relevant (coef = 0.46, $Z_{10, 48.75} = 1.83$, $p = 0.067$). Survival benefits from prior cue exposure were 12% greater for spat when in the presence of blue crabs than when oyster drills were present. During the first 72 h, the predator cue source which provided the greatest increase in survival for oysters corresponded to the predator currently consuming the oysters, but this trend did not last for the duration of the experiment (Figure 2A,B). This trend likely did not persist because predators were becoming limited in their prey options in this enclosed system. Field experiments are needed to test how prior cue exposure affects survival to a natural suite of predators. Further, we cannot ascertain if the increase in survival was due to predators handling oysters

and then being able to consume the weaker, control oysters or if predators could determine these differences outright and selected the control oysters. Additional experiments are also needed to tease out the survival mechanism(s).

Avoiding being consumed is critical for prey survival, and prey may adjust their behavior or morphology to reduce predation risk (Preisser et al. 2005, Weissburg et al. 2014, Scherer and Smee 2016). Yet, responding to predators, while necessary, can incur costs of lower growth and fecundity for prey (Relyea 2002, Miner et al. 2005). To minimize predator avoidance costs, many organisms use chemical cues to evaluate predation risk, and then limit responses to predators when risk of being consumed is high (Preisser et al. 2005, Weissburg et al. 2014, Scherer and Smee 2016). A growing body of literature suggests that while costly, changing morphology to deter predators can effectively increase survival (Smee and Weissburg 2006, Flynn and Smee 2010, Robinson et al. 2014). Our results indicate that oysters responded to both blue crabs and oyster drills, 2 common predators in the GOM, and increased their shell hardness to successfully deter both predators.

Oyster restoration is critical for reestablishing oyster reef habitat, and remote setting of spat-on-shell is often used for reef restoration and enhancement. Yet, many oyster restorations fail (La Peyre et al. 2014), in part due to high predation from crabs and oyster drills. Our findings may be useful for improving reef restoration efforts by modifying nursery techniques to produce stronger, tougher oysters that are more predator resistant. Within 4 weeks, oysters were harder and less susceptible to 2 common predators. Thus, using predator cues in hatcheries may increase the efficiency of restoration efforts by enabling more oysters to reach adulthood. Additional studies are needed to explore the feasibility of this technique and determine if changes in oyster morphology are similarly effective in enhancing survival in the field.

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