

Eastern Oysters *Crassostrea virginica* Produce Plastic Morphological Defenses in Response to Crab Predators Despite Resource Limitation

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Abstract. Many prey react to predation risk by altering their phenotype to reduce their chances of being consumed but incur reductions in growth and fecundity when reacting to predators. To determine when to produce defenses, prey collect information and evaluate the costs and benefits of defense induction. Resource availability can affect prey ability and willingness to incur defense costs. When resources are scarce, defenses may suffer disproportionate decreases in energy allocation if defenses would further reduce prey access to resources or if resources are needed to maintain metabolic functions. We tested the effects of predation risk and resource availability on plastic defenses in eastern oysters *Crassostrea virginica* and present novel findings that oysters continued to produce defended shells in response to predators when resources were limited, even though they grew smaller, lighter shells when deprived of food in control conditions. Predation risk affected all three tested shell metrics (area, weight, and strength), but food availability did not. Although low food levels often limit expression of predator defenses, predator cues caused oysters to build shells that were larger and heavier, with a similar trend for shell strength, in treatments with both low and high food levels, suggesting that predation is an important pressure in this system. The differences between predator and control treatments were greater under conditions of low food availability, and thus, resource availability may influence interpretations of plastic responses to predators.

Introduction

Many prey alter their behavior (Relyea, 2002; Large *et al.*, 2012; reviewed in Lima and Dill, 1990), morphology (Lively,

1986; Schoeppner and Relyea, 2005; Chivers *et al.*, 2007), or life history (Covich and Crowl, 1990; Fraser and Gilliam, 1992; Li and Jackson, 2005) in response to predation risk to reduce their chances of being consumed. Such changes can incur costs to prey if energy is allocated away from processes such as growth or fecundity (as with production of defensive structures or chemicals; Baldwin, 1998) or if defending prey sacrifice opportunities to acquire additional resources (as with behavioral reductions in activity or foraging; Ovadia and Schmitz, 2002; Smee and Weissburg, 2006b). Thus, prey must balance the need to defend against predation with support for other life processes such as growth and reproduction. Using plastic or inducible defenses allows prey to limit defense expression to situations where predation risk is high and to minimize defenses and associated costs when risk is low (Harvell, 1990).

To determine when to produce plastic defenses, prey must assess the costs and benefits of defense induction (Houston *et al.*, 1993; Lima and Bedneckoff, 1999); and prey continuously collect information on a variety of factors to monitor predation risk. For example, many species possess elaborate systems of risk analysis that incorporate information on predator species (Smee and Weissburg, 2006a; Bourdeau, 2009; Robinson *et al.*, 2014), predator diet (Scherer and Smee, 2016), and predator cue concentration (which can be a proxy for predator proximity, density, or size; Turner and Montgomery, 2003; Hill and Weissburg, 2013, 2014), as well as their own susceptibility (prey size [Marcus and Brown, 2003; Scherer *et al.*, 2016], alternate defenses [Chivers *et al.*, 2007; Wolfe *et al.*, 2016], and safety in numbers [Brown *et al.*, 2006; Ferrari *et al.*, 2010]).

In addition to factors indicating predation risk, changes in resource availability can influence the relative costs, in relation to an organism's overall energy budget, of performing various biological functions including defense induction. Processes such as growth and maintenance require baseline amounts

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of energy investment for survival, and below this energy threshold, other processes would have to be sacrificed (Cronin, 2001). Several studies have demonstrated that the intensity of prey defenses is lower or the threshold for defense induction is higher when resources are limited (Brown and Cowan, 2000; Ferrari *et al.*, 2010). For example, many fish species reduce behavioral defenses in response to predation cues after food deprivation (Smith, 1981; Brown and Smith, 1996), and a single day without food is often sufficient to reduce responses (Godin and Crossman, 1994; Brown and Cowan, 2000). Brown and Smith (1996) suggested that fish may increase vigilance responses and be more sensitive to visual predation cues under these conditions to compensate for reduced responses. If resource and predator conditions suggest low chances of survival in the long term, prey may even prioritize reproduction to increase the chances of producing offspring before death (Fraser and Gilliam, 1992). These considerations would reduce the proportion of energy available for defense, and an overall reduction of energy would make every unit of energy more valuable. Therefore, under conditions of scarcity, defenses may suffer disproportionate decreases in energy allocation, especially if defenses would further reduce prey access to resources (Brown and Cowan, 2000; Ferrari *et al.*, 2010; but for theories regarding alternative strategies, see Cronin, 2001).

However, because prey must balance many conflicting demands simultaneously, it is often difficult to predict which they will prioritize in given situations. In contrast to the fish studies above, several studies in amphibians have noted no change in response to risk when resources are low (Horat and Semlitsch, 1994; Whitman and Mathis, 2000; Maerz *et al.*, 2001), even after a one-month resource deprivation period (Adler, 1968). Amphibians have high metabolic efficiency, which may provide a unique mechanism to maintain defenses in low-resource conditions (Maerz *et al.*, 2001). In addition, two species of snails produce defended shell morphology under conditions of risk and intensify this defensive response under conditions of low resources (Appleton and Palmer, 1988; Bourdeau, 2010). Bourdeau (2010) characterized the mechanism of this response in the marine snail *Nucella lamellosa* (Gmelin, 1791). When exposed to crabs, these snails grow thicker shells that are effective in deterring predators, but they also develop this morphology in treatments without predators when deprived of food. Furthermore, when predators are present, snails also exhibit a behavioral defense in the form of reduced foraging. Thus, defended morphology in *N. lamellosa* is the indirect result of reduced foraging, which is compounded under conditions of resource limitation (Bourdeau, 2010).

We tested the effects of predation risk and resource availability on plastic defenses in the eastern oyster *Crassostrea virginica* (Gmelin, 1791). Oysters increase the weight and strength of their shells in response to exudates from predators (Newell *et al.*, 2007; Johnson and Smee, 2012; Lord and Whitlatch, 2012; Robinson *et al.*, 2014; Scherer *et al.*, 2016) to re-

duce their risk of predation (Robinson *et al.*, 2014). But the effect of resource availability on plastic defenses in bivalves has received little empirical testing, and it is unknown how changes in food availability influence this response. We investigated whether reductions in food impair fortification of oyster shells in the presence and absence of predators. Under control conditions (without predators), oyster shells were smaller and weaker when food was scarce, consistent with the assumption that shells are costly to produce. Despite this, when predators were present, oysters built larger, heavier shells to reduce risk regardless of food level.

Materials and Methods

Study organisms

Oyster larvae were acquired from the Auburn University Shellfish Laboratory at the Dauphin Island Sea Lab, Dauphin Island, Alabama. Oysters, hereafter referred to as oyster spat (~1-mm initial diameter), were settled onto sun-bleached oyster shells before initiation of the experiment. Settlement occurred in 90-l pools containing clean dead shell that is ideal for settlement. Circulation and aeration within the pools were maintained with two circulation pumps placed to create a circular current. Tarpaulins were used to protect the surface of the pools and to block light, encouraging settlement (Baker and Mann, 1998). After 3 d, oysters were provided with ~115 ml of PhytoPlex phytoplankton (KENT Marine, Franklin, WI) per pool per day for 3 wk until spat reached ~1 mm in diameter.

Treatment exposures

After settlement, oysters were reared in 32 opaque tanks under treatment conditions for 8 wk, which is sufficient for expression of morphological defenses in this species (Scherer *et al.*, 2016). The experiment consisted of a 2 × 2 factorial design with 2 levels of predation risk (present, absent) and 2 levels of food availability (low, high). Eight replicates of each predation risk and food level combination were performed. Tanks assigned to the predation risk treatment contained three Atlantic mud crabs *Panopeus herbstii* H. Milne Edwards, 1834 (carapace width: 36–52 mm). Oysters were protected from crab predators with a plastic mesh covering (1-cm² openings). High-resource-availability tanks received 10 ml of PhytoPlex phytoplankton daily, and low-resource tanks received 5 ml. Quantities were chosen based on previous studies that suggested that 5 ml limited oyster growth rates (Robinson *et al.*, 2014) and that oyster consumption of PhytoPlex was saturated at 10 ml (Scherer, 2017).

Tanks were aerated and contained 20 liters of artificial seawater made using Instant Ocean Sea Salt (Blacksburg, VA) and maintained at a salinity of 20 ppt. Each tank contained 2 shells with at least 10 spat per shell, and spat were thinned as needed during the experiment to prevent competition for

Table 1*Test statistics for comparisons of oyster spat shell metrics*

Metric	Factor						Denominator df
	Food availability		Predation treatment		Interaction		
	<i>t</i> -ratio	<i>P</i> -value	<i>t</i> -ratio	<i>P</i> -value	<i>t</i> -ratio	<i>P</i> -value	
Shell area	-1.04	0.31	-2.51	0.02**	-1.51	0.14	28
Shell weight	-0.83	0.41	-2.53	0.02**	-0.71	0.48	28.5
Shell crushing force	-1.49	0.15	-1.97	0.06*	-0.66	0.51	28

df, degree of freedom.

* Fixed factor significant at $\alpha = 0.1$.** Fixed factor significant at $\alpha = 0.05$.

space. Predators were fed ~0.6 g of refrigerated oyster tissue in the experimental tanks once per week, and tissue was divided into 3 pieces to reduce antagonistic interactions between predators. Water changes were carried out weekly following predator feeding to remove waste and prevent the buildup of cues over the course of the experiment.

Data collection

Five oysters from each tank were measured for shell diameter and crushing force after the 8-wk exposure period. At this size (5.05 ± 0.06 mm), oysters had not begun to elongate, and only one measurement of shell diameter was made to the nearest tenth of a millimeter. Diameter was then used to calculate shell area using the formula of a circle ($A = \pi r^2$). Shell compression force was measured using a Kistler 5995 charge amplifier and a Kistler 9203 force sensor (Amherst, NY) (*sensu* Robinson *et al.*, 2014) with settings of sensitivity 47.8 and range 50. A small blunt probe (1-mm diameter) was consistently placed centrally to be equidistant from the shell's 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 spat's shell occurred, and we then recorded the maximum force needed to break the shell, which is a measure of shell strength (Zuschin *et al.*, 2001). Shell mass was measured on an additional 5 oysters by removing the top valve of the spat from their substrate and drying it at 38 °C for 48 h. We then weighed the shell on an electric balance to the nearest 0.001 g. Measured masses contained both shell and soft tissue, but ~99% of the total mass was shell at this point in development (Robinson *et al.*, 2014).

Statistical analysis

All analysis was completed in JMP Pro, version 12 (SAS, Cary, NC). Shell area, weight, and crushing force were compared between treatments using both a three-way mixed ANOVA model, with predation level and food availability as fixed factors and tank as a random factor, and a two-way factorial ANOVA model, with predation level and food availability as

fixed factors and oyster values averaged across tanks. Model results were qualitatively identical, and those of the three-way mixed model are presented here. Results were considered significant at $\alpha = 0.05$, but results significant at $\alpha = 0.1$ are also discussed.

Results

Predator treatment was significant for shell area and weight (area $P = 0.02$, weight $P = 0.02$; Table 1; Figs. 1, 2), indicating that oysters constructed larger, heavier shells when predators were present; but food level (area $P = 0.31$, weight $P = 0.41$; Table 1) and the interaction of predation and food level (area $P = 0.14$, weight $P = 0.48$; Table 1) were not significant. Shell crushing force demonstrated a similar pattern, although predation treatment was significant at $\alpha = 0.1$ (predation $P = 0.06$, food level $P = 0.15$, interaction $P = 0.5$; Table 1; Fig. 3).

Discussion

Under conditions of limited resources, prey may be unable to acquire sufficient resources to manufacture defenses or may acquire sufficient energy but sacrifice defenses to prioritize growth and reproduction (Brown and Cowan, 2000; Cronin,

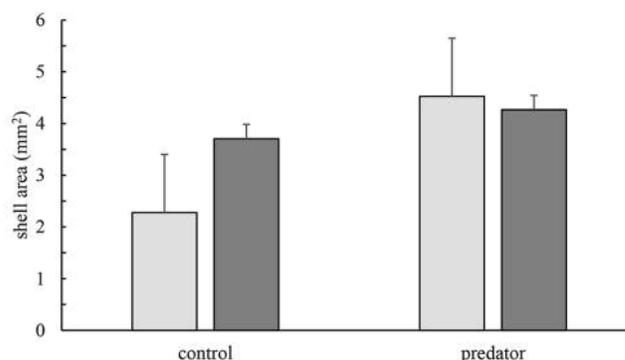


Figure 1. Mean oyster shell area (\pm SE) in control and predator treatments with low (light gray) and high (dark gray) food availability.

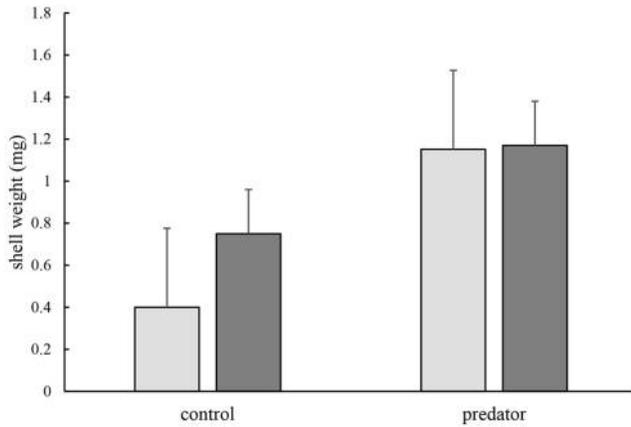


Figure 2. Mean oyster shell weight (\pm SE) in control and predator treatments with low (light gray) and high (dark gray) food availability.

2001; Preisser *et al.*, 2009; Ferrari *et al.*, 2010). This could manifest as a reduction in defense intensity under all conditions of risk or as an increase in the threshold of risk intensity required for defense induction. Although prey defenses may remain unchanged (Adler, 1968; Horat and Semlitsch, 1994; Whitman and Mathis, 2000; Maerz *et al.*, 2001) or even intensify (Appleton and Palmer, 1988; Bourdeau, 2010) under conditions of limited resources, prey defense expression is often reduced when resource availability is low (Ferrari *et al.*, 2010). However, in this study, predator cues caused oysters to build shells that were equally large and heavy in treatments with both low and high food levels, even though oysters grew less in low food treatments without predator cues.

Although not significant at $\alpha = 0.05$ ($P = 0.058$), shell crushing force demonstrated a trend consistent with the other shell metrics tested in this study and with previous work in this system (Robinson *et al.*, 2014; Scherer and Smee, 2016; Scherer *et al.*, 2016). This is likely a conservative estimate of oyster defensive responses compared to responses under natural conditions for several reasons. First, meta-analysis of research on the effects of resources on plastic prey responses found that studies that use dynamic resource populations, as seen under natural conditions and unlike the static resources provided here, produce stronger negative nonconsumptive predator effects (Preisser *et al.*, 2009). Second, it is possible that the length of this study was insufficient to allow complete defense induction and that a longer exposure time would have produced significant changes in shell crushing force. Previous results demonstrate that eight weeks can be sufficient for induction in this size class under identical laboratory conditions (Scherer *et al.*, 2016). However, oyster growth under these conditions (without flowing seawater) is slower than in the field (Scherer, 2017), likely because of lower temperatures, quantities of shell minerals, and resource diversity (S. Rikard, Auburn University, pers. comm.). Finally, crabs were fed refrigerated oyster tissue, which induces weaker defensive responses than crabs fed freshly shucked tissue (Scherer

et al., 2017). Given these factors, we believe our crushing force results represent a conservative estimate of a biologically significant defensive response that would have become statistically significant with dynamic resources, additional time, and/or stronger risk cues.

Our results contrast with those seen for the marine snail *Nucella lamellosa*, a second species of mollusc that possesses plastic morphological defenses. For both snails and oysters, predator presence induces the construction of a fortified shell that is resistant to predation (Bourdeau, 2010; Robinson *et al.*, 2014; Scherer *et al.*, 2016). In *N. lamellosa*, this fortified morphology is also produced under conditions of reduced food availability, even in the absence of predators, demonstrating that shell fortification in response to predation results from passive changes in shell structure when snails behaviorally defend against predators through reduced foraging (Bourdeau, 2010). In contrast, oysters displayed reduced shell production when resources were limited, suggesting that a different process is responsible for shell fortification in this species.

Defended oyster morphology results from increases in calcium carbonate (Scherer, 2017), which is energetically inexpensive to produce (Frieder *et al.*, 2017). Although it contributes somewhat to shell strength (Avery and Etter, 2006; Lombardi *et al.*, 2013), calcium carbonate is likely more valuable for its quick production (Carter, 1980; Lee *et al.*, 2011), speeding growth (*i.e.*, shell area and weight) and reducing the time necessary to reach a size refuge while balancing energy costs (Avery and Etter, 2006). In contrast, preliminary evidence suggests that, under higher conditions of risk, oysters may also increase organic shell material (Scherer, 2017), which is more energetically costly (Lee *et al.*, 2016) but which maximizes shell strength (Taylon and Kennedy, 1969; Zuschin *et al.*, 2001; Avery and Etter, 2006; Lee *et al.*, 2011). Under this hypothesis, shell strength will be significantly different from controls above a certain threshold of risk only when defense benefits outweigh additional costs. That our results for shell strength were not significant at a more restrictive α ($\alpha = 0.05$) may suggest that, un-

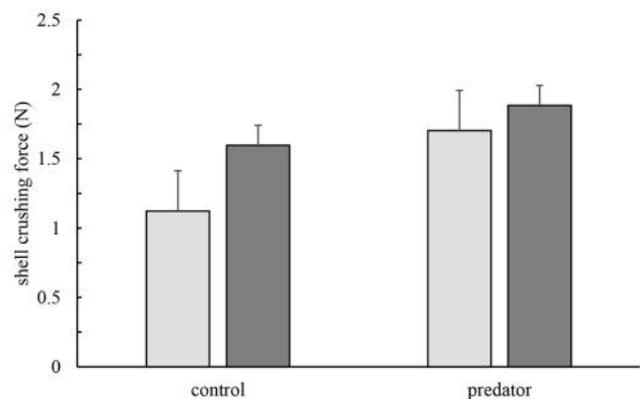


Figure 3. Mean oyster shell crushing force (\pm SE), a measure of shell strength, in control and predator treatments with low (light gray) and high (dark gray) food availability.

der our experimental conditions, predation risk was at or near an important threshold to justify additional defense costs. These results contribute to a young but growing literature on the mechanism responsible for morphological defenses in oysters. Additional research is required to develop our understanding of the complex factors influencing induced defenses in this species.

Phenotypic plasticity theory suggests that defenses should be costly to produce; otherwise organisms would always produce them, and they would not be plastic. Our results in control treatments suggest that this is true for oysters, since shell weight and strength were reduced when resources were limited. Yet if defenses are inexpensive to produce, as with additions of calcium carbonate, and/or if the threat that predators pose is sufficiently high, the threshold for employing defenses, even more costly strategies, may be low. It is possible that the prioritization of defenses under conditions of limited resources seen here is due to unrealistically elevated predator cue concentrations in mesocosm studies (Weissburg, 2000; Hill and Weissburg, 2013). However, mud crabs *Panopeus herbstii* can reach very high densities (Rodney and Paynter, 2006) and are known to exert strong predation pressure under conditions of mesopredator release (Grabowski and Powers, 2004; Grabowski and Kimbro, 2005; Lunt and Smee, 2014), suggesting that they can be an important source of predation pressure in oyster reef ecosystems. Furthermore, mud crabs are resident predators on oyster reefs, and their presence in a system is likely to represent a reliable indication of constant predation risk. We suggest that mud crabs represent an ecologically relevant source of pressure sufficient to justify the increased cost of defense induction, even under conditions of limited resources.

Costs of shell production are expected to increase under warmer, more acidic ocean conditions as shell dissolution increases and it becomes increasingly energetically expensive to maintain internal $p\text{CO}_2$ concentrations (Kroeker *et al.*, 2014). Studies have found that several species (Bibby *et al.*, 2007; Gazeau *et al.*, 2007; Gaylord *et al.*, 2011; Melatunan *et al.*, 2013; Coleman *et al.*, 2014; Mackenzie *et al.*, 2014), including oysters (Gazeau *et al.*, 2007; Amaral *et al.*, 2012), reduce calcification under conditions of ocean acidification. Higher costs of these morphological defenses could increase the costs of defense induction and present negative consequences for oysters under conditions of food limitation. If oysters continue to prioritize defenses, they would suffer further reductions in fecundity or body condition. Further, there are presumably baseline values of energy investment needed for these other processes, and, in extreme conditions, oyster defenses would have to be reduced or eliminated. That oysters prioritized defenses in this study suggests that defenses are important for prey survival and that their reduction could have serious consequences for oyster populations in the long term.

However, warmer ocean conditions and increased nutrient runoff are also expected to favor growth of algal species (Hallegraff, 1993; Paerl and Huisman, 2008). Growth and calci-

fication rates in mussels *Mytilus edulis* are maintained under predicted acidification levels if food availability remains high (Thomsen *et al.*, 2013). Whether this is true under conditions of predation risk has not been tested. For estuarine species, such as oysters, that are adapted to highly variable habitat conditions, this increased resource availability may ameliorate some of the negative consequences of climate change.

Nonconsumptive predator effects are influenced by a diverse array of factors and vary considerably among species and systems (Chivers and Smith, 1998; Weissburg *et al.*, 2014). Resource availability is known to alter patterns of defensive response in many prey species (Preisser *et al.*, 2009; Ferrari *et al.*, 2010), including gastropod molluscs. For oysters, and perhaps other bivalves, resource availability does not influence response pattern but may influence the apparent strength of nonconsumptive predator effects. Thus, resource levels should be carefully monitored and assessed in studies of phenotypic plasticity.

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