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Evidence of a Divergent Growth Response in the Pacific Oyster, *Magallana Gigas*, When Exposed to Native and Invasive Crab Chemical Cues

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Abstract

Marine invertebrates exhibit a variety of plastic morphological defenses in response to predator chemical cues. Typically, bivalves increase shell mass and strength in order to mitigate predation risk. However, invasive species may give off unfamiliar chemical cues, rendering native prey unable to detect and respond to foreign predators. Nevertheless, some native prey may adapt to recognize foreign predators over relatively short time scales (i.e. decades). The Pacific oyster, *Magallana gigas*, was introduced into Barkley Sound in 1937 and has experienced predation from native predators for nearly 80 years. Little is known about its defence capabilities and how it responds to the invasive European green crab, *Carcinus maenas*, with which it has coexisted for less than a decade. This offers a unique opportunity to study short-term evolution of defence mechanisms in response to predators over multiple time scales. We conducted a laboratory experiment to test if shell growth of juvenile *M. gigas* would be influenced by chemical effluent from native red rock crabs, *Cancer productus*, and invasive European green crabs, *Carcinus maenas*. Our results suggest that oysters grown in the presence of red rock crabs produce heavier shells than oysters grown in the presence of green crabs and controls, although this was not statistically significant. Shell weight increase in response to red rock crabs suggests that Pacific oysters may have had time to evolve a response to red rock crabs, but not yet for invasive European green crabs.

Keywords — Phenotypic Plasticity, Predation Cues, Morphological Defenses, Invasive Species

1. Introduction

Intertidal and sublittoral predators drive an immense variety of defence responses in marine prey populations [1]. In the presence of predators, prey can modulate their behavior, life history or morphology in order to mitigate predation risk [2, 3, 4]. However, these defense mechanisms are energetically costly, and often trade-off with reductions in growth and fecundity. [2, 5, 6]. Consequently, many prey species reduce these costs by exhibiting plastic responses that are only upregulated in the presence of a predator [6].

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Sessile or slow-moving organisms like some bivalve species are widely known to alter their morphology in order to alleviate predation risk [3, 6, 7, 8]. Some prey species can detect chemical cues given off by their predators' physiological functions, such as waste excretion, [9], allowing them to adapt their phenotype to decrease the risk of predation [10]. For example, Côté [11] concluded that bivalve mussels increase byssal thread production in the presence of a predator in order to increase dislodgement force, and therefore predator handling time. Additionally, Freeman and Byers [12] found that mussels increase their shell thickness in the presence of a native predator.

Introduction of invasive species can alter predator composition, and has therefore been found to shift community dynamics [13]. Antipredatory responses of native prey to invasive species tend to vary with geographical location and the length of time that the prey and predator have coexisted [13]. Increases in predator composition also increase the variation in which prey plastically alter their morphology in response to predation risk [12]. For example, Freeman and Byers [12] found that the recent crab invader, *Hemigrapsus sanguineus*, did not induce shell thickening in naïve mussel populations from the West Atlantic. However, populations of mussels that had already coexisted with *H. sanguineus* for more than 15 years were able to demonstrate a shell thickening response [12]. In contrast, both the naïve and familiarized mussel populations thickened their shells in the presence of *Carcinus maenas*, a well-established invader [12]. This suggests that prey species are capable of evolving their plastic responses over relatively short time-scales (i.e. decades) to defend against invasive predators.

The European green crab (*Carcinus maenas*) was first observed on the West Coast of North America in San Francisco Bay, CA, in 1989 [14], and has invaded British Columbia waters over the past 15 years. Because of their recent introduction, *C. maenas* may not be recognized by native prey species [15]. This decapod crustacean feeds on a variety of prey, including many bivalve species [16]. *C. maenas* are extremely tolerant to fluctuating temperature, as they can survive in water temperatures ranging from 0°C to above 30°C, [17, 18], and are euryhaline to 4 ppt as adults, and up to 17 ppt as larvae [19]. *C. maenas* thrive in open sand, mudflats, shell, cobble, and algae beds [20]. The physiological tolerance of *C. maenas* facilitates their ability to successfully invade diverse environments, subsequently altering ecological structure at several levels. [21]. For example, *C. maenas* invasion into Maine, USA, coincided with an extensive decline in soft shell clam beds [21]. Since C. maenas influence the abundance and dynamics of bivalve communities in the Atlantic [22], we would like to investigate if bivalves can adapt and respond defensively to the recently invasive *C. maenas* in Eastern Pacific communities.

The Pacific oyster (*Magallana gigas*) is native to the western Pacific, ranging from Russia to China, and into Southeast Asia [23, 24] but has been widely introduced, for commercial use, across the globe [25]. *M. gigas* was first introduced to Puget Sound in 1902, and Barkley Sound (the site of our study) in 1937, [25], and is now Canada's second most valuable commercial shellfish species (after mussels). *M. gigas* represented 59% of total oyster production in British Columbia in 2013, with an estimated economic contribution of $ 12.4 million [26]. On the West Coast of North America, *Metacarcinus magister* (Dungeness crab), *Metacarcinus gracilis* (graceful rock crab), and *Cancer productus* (red rock crab) are the primary predators of *M. gigas* [25]. As such, *M. gigas* has had

a longer evolutionary history of exposure (80 years) to native crab predators than the recently invasive *C. maenas*. Despite the importance of crab predation on *M. gigas*, little is known about its defence capabilities and responses to *C. maenas*.

Recent studies on the eastern oyster, *Crassostrea virginica*, have found that oysters increase shell thickness, mass and strength but produce less soft tissue in the presence of predators [7, 27, 28]. Furthermore, Robinson et al, [6], found that recently settled eastern oysters raised in the presence of crab predators produced thicker, wider and stronger shells and were less susceptible to predation by crabs. These findings suggest that oyster prey have the ability to appropriately allocate energy stores in order to successfully defend against more familiar predators.

Continual invasion of *C. maenas* into British Columbia prompts our investigation of plastic defence responses by *M. gigas*. In this study, we examine how growth in juvenile *M. gigas* is impacted when raised in the presence of two crab predators: the native *C. productus*, and the invasive *C. maenas*. We predict that *M. gigas* will increase shell weight when exposed to the red rock crab *C. productus*, to mitigate predation risk from a more familiar predator. We predict no such changes when oysters are exposed to the invasive predator, *C. maenas*, relative to controls. Results from this study could aid in management of wild and farmed oyster beds in the face of permanently settling invasive *C. maenas*. Furthermore, understanding the timescale associated with predator response evolution has far reaching implications in invasion ecology, beyond the organisms studied here.

2. Materials and Methods

2.1. Experimental Organisms

We collected male *C. maenas* by hand and crab trap from Effingham Inlet (N49°5'45.449", W125°11'54.882") on October 17, 2015. We collected male *C. productus* by crab trap from Bamfield Inlet (N48°49'2.15", W125°8'42.843") and Grappler Inlet (N48°49'53.667", W125°7'5.41") on October 25, 2015, and November 8, 2015, respectively. All collection sites are situated within Barkley Sound, British Columbia (Figure 1). We obtained three-month-old hatchery raised *M. gigas* from NOVA Harvest Ltd. (an aquaculture facility). Oysters ranged from 0.001 to 0.029 g in shell weight (0.896 - 13.94 mm shell length), which is within the limits of green crab predation (up to 60mm) and red rock crab predation (who eat seed and juvenile oysters) [29, 30]. We housed all organisms at the Bamfield Marine Sciences Centre where laboratory experiments were conducted.

We fed juvenile *M. gigas* 1 g of oyster spat formula (Innovative Aquaculture Products Ltd) per 200 mL of seawater. Spat formula contained the microalgae *Phaeodactylum tricornutum*, *Chaetocerus-B*, and *Nannochloropsis oculata*. We fed oysters every morning and evening throughout the experiment. We fed crabs chopped *Mytilus californianus* every three days until satiation. We also provided control aquaria with chopped mussel to control for any effects of mussel effluent on oyster growth. Lastly, we cleaned all aquaria, including controls, every fourth day after substantial feeding time. Oyster growth is most efficient in water ranging from 15-18°C (JP Hastey, NOVA Harvest aquaculture. Email. 10 Nov 2015. pers. comm.). Therefore, in each sea table, we used an 11.5cm deep heated water bath around all experimental aquaria. We warmed water

using 100 watt Theo Hydor aquarium heaters set to 18°C. We limited water flow to a twice daily flush of 13 minutes each, as incoming seawater was approximately 12°C, and would not be able to sustain maximal oyster growth. We recorded temperature in aquaria twice daily before seawater flushing in the morning (08:00hrs), and after seawater flushing in the evening (19:00hrs) to ensure temperature did not act as a confounding variable.

2.2. Experimental Design

Our experiment consisted of two treatments and a control designed to test the effects of, 1, *C. maenas* chemical effluent cues on *M. gigas* growth, and, 2, *C. productus* chemical effluent cues on *M. gigas* growth. We designed our control to assess juvenile oyster growth in the absence of any crab. We placed a small, perforated container housing 10 *M. gigas* in a 7 L aquarium that contained an individual *C. maenas*, or *C. productus* (treatments), or an aquarium with no crab (control).

We arranged aquaria in a complete randomized block design within sea tables. Each block consisted of four replicates of each predator treatment and four controls (no predator), totaling to 12 containers per sea table. We used three sea tables, for a total of 3 blocks, containing 4 sets of each treatment per block.

We weighed crabs with a Yamato Accu-Weigh SPC-5005 electronic scale to ensure all individuals were similar in weight. *C. productus* individuals ranged from 92 - 182 grams in weight, and *C. maenas* individuals ranged from 90 - 142 grams in weight. We acclimated crabs to aquaria for 24 hours before trials began.

We selected three hundred and sixty juvenile oysters for the experimental trial. We measured oyster length using Mastercraft 58-6800-4 digital calipers (accuracy = 0.01 mm). We measured length from the umbo (hinge line) of the oyster to the tip of the longest frill. We measured oyster wet weight and shell weight to the nearest 1 mg using the Mettler BasBal BB240 electronic scale, as adapted from Palmer [31]. This non-destructive technique allowed us to obtain initial and final measurements of wet weights and shell weights of the same oysters. The scale rested on a wooden scaffold that allowed for suspension of a weighing dish from underside of the scale. The weighing dish was immersed in a container of seawater and tared to compensate for the weight of the dish. This allowed us to measure oysters while they were immersed in seawater. We placed an individual oyster in the dish; assuming the density of seawater is equal to the density of the oyster tissue [31], and the scale measured the weight of the shell alone. First, we took wet weight measurements using the standard platform on the scale. Next, we measured the immersed weight of the same oyster to obtain the shell weight. We calculated tissue weight by subtracting shell weight from the total wet weight of each oyster. Afterwards, we placed ten oysters in one of thirty-six perforated containers. These containers allowed for effluent flow, but deterred direct crab predation. Lastly, we placed containers in aquaria attached to an air stone.

We ran the experimental trial for 22 days. At the end of the exposure, we removed juvenile oysters from aquaria and measured them using the same methods as described above for their final length, wet weight, shell weight, and tissue weight. One *C. productus* moulted, and one *C. maenas* escaped and was promptly replaced with a new individual during our experiment. We do not believe this affected the amount of chemical cues

oysters experienced and these replicates were included in our analysis.

2.3. Statistical Analysis

We considered the mean of each group of ten oysters a replicate. For each treatment, we calculated mean shell length, shell weight, wet weight and tissue weight. We took the differences by subtracting initial values from final values, and calculated unitless proportions (i.e. growth change) by subtracting mean initial weight from mean final weight and dividing by mean final weight.

Many of the differences we calculated for total wet weight, tissue weight, and shell length were negative, suggesting that growth decreased. We suspect that wet weight measurements were confounded by water weight between frills of the oyster shells, so we omitted wet weight data in our analysis. We also omitted length measurements from our analysis, as we postulate that negative values are indicative of human error. Shell weight of oysters was the most accurate measurement in our study (Dr. R. Palmer, Conversation. 29 Nov 2015. pers. comm.), so we used only shell weight data in our analysis.

We completed graphing and analysis in 'RStudio' version 0.98.1087 (R version 3.0.2 GUI 1.62 Snow Leopard build) using the 'nlme' package (Pinheiro et al., 2015). We analyzed mean proportional growth of shell weight for each treatment using a mixed effects analysis of variance (ANOVA), blocked by sea table as a random effect to account for within sea table growth variation. We performed this analysis using a linear mixed effects model (lme) fit by restricted maximum likelihood (REML). Finally, we performed an ANOVA on temperature from the three sea tables used in our experiment, and found that temperature did not significantly differ between sea tables over the course of the experimental exposure time (ANOVA; DF=1, SS=0.82, MS=0.82, f-value=1.02, p=0.317).

3. Results

Over the 22-day experimental predator exposure, shell weights in both treatments and the control increased significantly relative to initial values (DF=1, denDF=21, f-value=39.08, p<0.0001)

Results indicated that *M. gigas* grown in the presence of *C. productus* had a higher mean proportional shell weight increase (0.525 ± 0.094) relative to *C. maenas* (0.354 ± 0.092) and controls (0.444 ± 0.088). However, we found no statistically significant differences in *M. gigas* growth between treatments (Blocked ANOVA; DF=2, denDF=21, f-value=1.66, p=0.215, Figure 2).

In all treatments, large *M. gigas* had similar proportional shell growth relative to initial size, whereas small *M. gigas* appeared to have greater differences between treatments, indicated by the converging treatment lines in Figure 3. Smaller *M. gigas* had a higher mean proportional shell weight growth in the *C. productus* treatment, than in the *C. maenas* treatment, or control (Figure 3). However, smaller *M. gigas* in the *C. maenas* treatment had a lower mean proportional shell weight growth than the control (Figure 3).

4. Discussion

4.1. Effect of Treatment

The purpose of our study was to determine whether or not *M. gigas* could recognize novel predator cues from the invasive *C. maenas*, compared to that of *C. productus*, which has co-existed with *M. gigas* for nearly 70 more years [25]. Although we did not find a significantly different effect between native and invasive crab treatments, the heavier shell mass produced by oysters grown in the presence of *C. productus* suggests a biologically relevant trend. Below, we consider our results in light of our predictions and their implications for responses of sessile organisms to familiar and unfamiliar chemical cues.

Our results suggest that juvenile oysters may be able to increase shell weight depending on the crab predator the oyster is exposed to. Robinson et al [6] found that juvenile (<5mm) eastern oysters, *Crassostrea virginica*, increased shell mass and diameter significantly more when grown in the presence of native blue crab predators, compared to controls, providing evidence that *C. virginica* can plastically adopt morphological defences that protect themselves from crab predators. Our results compliment those of Robinson et al [6] demonstrating that juvenile *M. gigas* may adopt plastic defenses depending on predator familiarity. This may suggest that continual coexistence of the invasive *C. maenas* and *M. gigas* could lead to the evolution of predator cue recognition in decades to come.

Studies from the East Coast of North America have demonstrated that predator cue recognition to *C. maenas* has already evolved in areas where the crab first invaded. For example, Large and Smee [13] found that populations of dogwhelks in the Gulf of Maine produced heavier shells in areas where *C. maenas* were well established. Conversely, they found that dogwhelk populations unfamiliar with *C. maenas* did not produce heavier shells compared to controls [13]. Similarly, the whelk Nucella lapillus was found to increase shell thickness when familiar with *C. maenas*, although populations both familiar and unfamiliar to the invasive crab responded by reduced foraging [32]. These studies indicate that species may quickly evolve predator cue recognition and upregulate plastic morphological defence mechanisms in response to foreign predators given sufficient time to coexist. Our study sheds light on prey responses during early *C. maenas* invasion in the Eastern Pacific, suggesting that *M. gigas* has not yet evolved the required predator cue recognition to defend itself.

Numerous studies have found plastic defence responses in bivalves, including other oysters [8, 13, 33]. We therefore suggest that juvenile *M. gigas* does produce heavier shells in the presence of a familiar predator, but that our study failed to significantly detect these differences. Our study had a limited sample size and effect size, which led to higher variance and lower power between treatments. In addition, our study exposed oysters to crab predators for 3 weeks, whereas most studies on morphological plasticity in molluscs range from approximately 6-8 weeks [28, 34]. Therefore, our study may not have had sufficient power to resolve differences between treatments.

Furthermore, we suspect that increased fouling by *C. maenas* on *M. gigas* (due to waste excretion) and unfamiliar predator cues could have led to smaller proportional growth. In contrast, control *M. gigas* were able to grow in an environment free of fouling,

potentially explaining the smaller proportional growth in the *C. maenas* treatment compared to controls.

4.2. Effect of Size

Smaller *M. gigas* grown in the presence of *C. productus* had higher mean proportional increases in shell weight, although this was not significantly different between treatments. Bivalve prey size can affect their vulnerability to crab predators [35]. Crabs will prey more heavily on smaller bivalves because they require less energy to open [28], and have a lower probability of causing claw injury [16]. Our findings suggest that juvenile *M. gigas* compensate for this by growing significantly faster when they are smaller in size. Johnson and Smee [28] found that smaller oysters grew significantly less tissue and more shell weight in the presence of a crab predator. Our findings prompt further investigation as to whether or not juvenile oysters are able to perceive differences in predator species.

Future studies should examine if plastic defence strategies in bivalves have consequences on survival rates [6, 33, 36]. Robinson et al [6] found that juvenile Eastern oysters grown in the presence of crab predators required a 30-50% increase in shell crushing force, and therefore higher survival rates. To further expand on our study, measuring shell crushing force would provide insight into the mechanism by which oysters increase their fitness given the crab predator encountered, as this has not yet been demonstrated in *M. gigas*. Furthermore, predation assays would determine if observed changes in shell mass have biologically relevant consequences on survival of juvenile *M. gigas*. Lastly, future studies should also assess whether the plastic growth morphology of bivalves could not only be governed by predator effluent, but also by effluent from conspecifics being preyed upon.

5. Conclusion

By testing the effects of chemical cues from invasive and native crab predators on a commercially important bivalve, we were able to assess short-term evolution of defence mechanisms in response to familiar and unfamiliar predators at known time intervals.

Bivalve aquaculture operations in the Eastern Pacific are commonly run in open environments where the organisms reared are exposed to predators [25]. Predation is of great concern to bivalve farmers [37], where *C. maenas* has been reported to predate upon juvenile oyster spat [38]. In the coming decades, *C. maenas* may be a significant pest for farmed and wild oyster beds. However, over a longer time scale, *M. gigas* may evolve predator cue recognition for *C. maenas* to increase fitness and survival.

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A. Figures

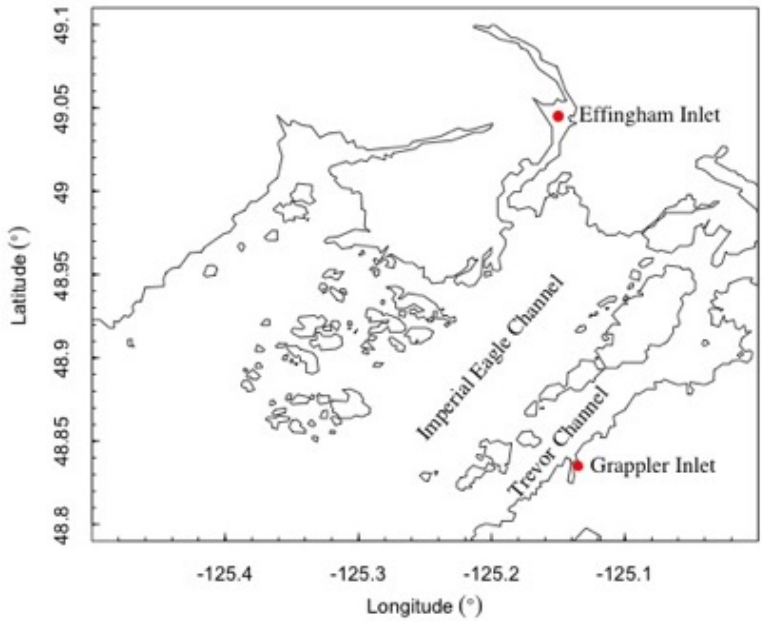

Figure 1: *Sites of green crab collection (Effingham Inlet - N49°5'45.449", W125°11'54.882"), and red rock crab collection (Grappler Inlet - N48°49'53.667", W125°7'5.41"), in Barkley Sound, British Columbia. Green crabs were collected from Effingham Inlet on October 17, 2015. Red rock crabs were collected from Grappler Inlet on October 25, 2015.*

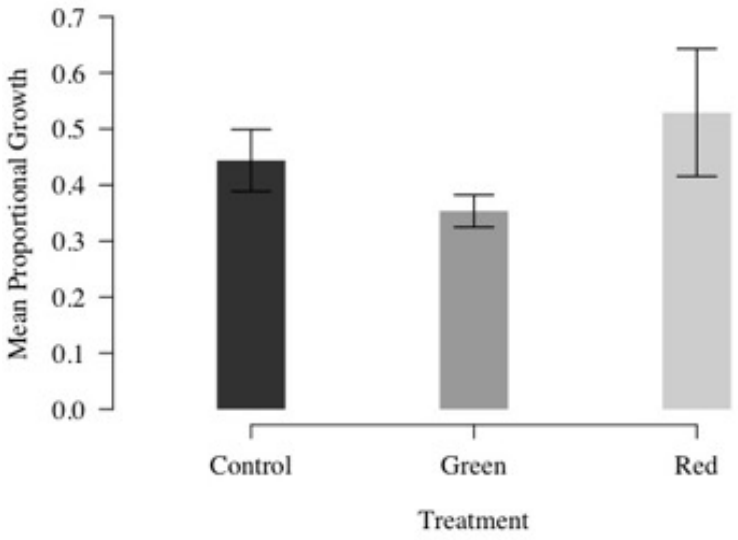

Figure 2: *Mean proportional growth of oysters exposed to green crabs* ($0.354 \pm 0.092; n = 12$)*, red rock crabs* ($0.525 \pm 0.094; n = 12$)*, and no crab predators* ($0.444 \pm 0.088; n = 12$)*. Data was collected on December 2 and 3, 2015.*

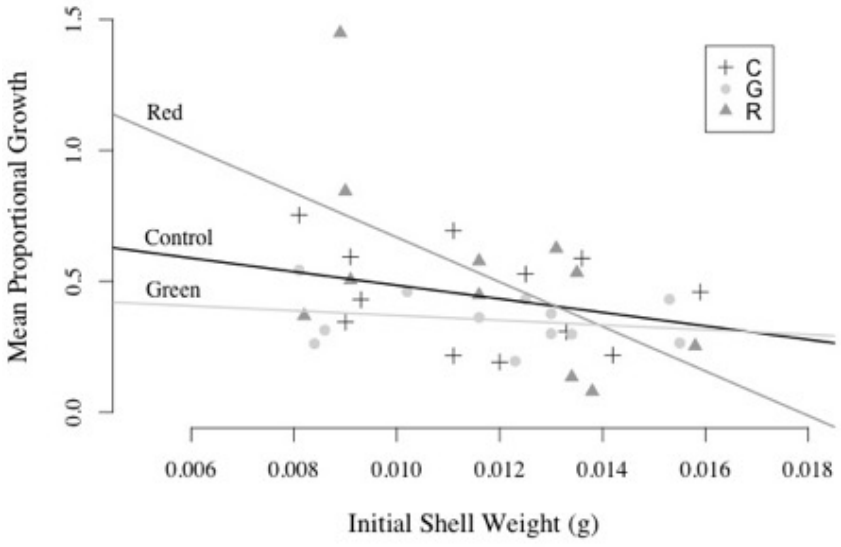

Figure 3: *Mean proportional growth in weight versus initial weight. Regression lines were fit using means of each treatment* ($n = 12$ *for each). Equations of the lines were calculated to be* $y = -85.215x + 1.521; (R^2 = 0.32)$ *for native crab treatments,* $y = -9.149x + 0.462; (R^2 = 0.05)$ *for invasive crab treatments, and* $y = -25.949x + 0.745; (R^2 = 0.11)$ *for controls.*