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**Caged oysters still get scared: Predator presence and density influence
growth in oysters, but only at very close ranges**

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Running head: Caged oysters still get scared

Abstract

Two common forms of variation that may influence consumptive and non-consumptive effects differently are how the biomass of predators is allocated among individual predators (e.g., several small vs few large predators) and how predators are spaced throughout a community. We analyzed how varying the presence, biomass (density, size, and total biomass), and distance to crown conchs (*Melongena corona*) impacted growth in eastern oysters (*Crassostrea virginica*) grown in field conditions. The presence of predators decreased growth (new shell added and mass) and increased shell thickness in a 58-day experiment. Although these effects were more pronounced as predator density increased, total predator biomass and predator size had limited impact on the strength of non-consumptive effects. The allocation of total oyster mass between shell and tissue was also not impacted by predator treatments. Results from a 96-day study examining the range of these effects indicated that they may exist only over short distances or change as oysters grow, as oysters at varying distances from a caged predator showed no differences in growth traits. These results show that non-consumptive interactions in oyster reef communities may be highly non-linear in regards to predator community structure and exposure distance and indicate these factors may be important in determining the impact of non-consumptive effects in other communities. Our growth data also show that non-consumptive effects may have major impacts on oyster growth under normal aquaculture conditions and suggest that these effects may need to be considered in management efforts.

Key words: non-consumptive effects, predator-prey interactions, oyster reef ecology, predator biomass, *Crassostrea virginica*

Introduction:

The relationship between predators and their prey, and the impact these relationships have on ecological communities, has been and remains a dominant theme in ecology. Over the past decade a growing amount of attention has been directed toward the non-consumptive aspects of these interactions (Peckarsky et al. 2008). Non-consumptive effects (NCE) are characterized by changes in prey activity, behavior, morphology, and development in response to predator presence or cues (Orrock et al. 2008). Their impacts on prey and community dynamics can be as strong as or stronger than consumptive effects in many systems (Preisser et al. 2005). For these reasons, understanding how NCE operate along multiple environmental gradients and in conjunction with other interactions is essential to understanding how predators influence natural communities.

Although commonly overlooked in empirical studies and predator-prey models, both consumptive and non-consumptive predator-prey interactions are influenced by a variety of factors that may impact the magnitude, direction, and even presence of consumptive and non-consumptive effects differently. For example, use of complex habitats can reduce the consumptive effects of predators on prey, but non-consumptive interactions may still extend to these environments (Grabowski et al. 2005). Likewise, environmental conditions such as water temperature, pH, and salinity can influence predation rates (Whetstone & Eversole 1981, Held & Harley 2009). These conditions may also affect NCE by influencing the movement and detection of cues that trigger predator responses (Smee et al. 2008, Dixon et al. 2010, Kimbro 2011, Kimbro et al. 2014), thus changing the perceived risk of predation. Differences in the responses of non-consumptive and consumptive effects to changing environmental factors may have major impacts on how predator-prey interactions and communities ultimately respond to environmental change.

Two major forms of variation that may influence consumptive and non-consumptive effects in different ways include variation in the allocation of biomass among predators (e.g., several small vs few large predators) and the spacing of predators throughout a community. Predator body size can physically limit the ability of individual predators to consume prey or impact overall consumption (Paine 1976, Eurich et al. 2014). Predator density should also be positively correlated with consumption, with larger predator populations requiring more prey for survival. The impacts of size and abundance on non-consumptive interactions, however, are less clear. While some prey species may respond more strongly to predator cues when the prey are small (Selden et al. 2009, Johnson & Smee 2012), responding to predator size would require prey to discern predation risk based on external cues. Although evidence suggests prey may be able to identify and respond to different predators (Freeman 2007, Robinson et al. 2014) and prey may visually inspect predators to determine risk (Lima & Dill 1990), prey that evaluate risk through the use of chemical and auditory cues may or may not actually be able to distinguish the differing levels of risk posed by predators that differ in size (Chivers et al. 2001, Kusch et al. 2004). Similarly, prey may (Van Buskirk & Arioli 2002) or may not (Gosnell & Gaines 2012) be able to determine and respond to predator density based on cues. Even within a single species, some defensive traits may show threshold responses and others may not (Van Buskirk & Arioli 2002). The inability to detect or respond to various sizes or densities of predators may lead to differences in the relative impacts of consumptive and non-consumptive effects as the size or abundance of predators change. For example, mud crabs have been shown to exhibit the same predator-induced behavior in the presence of one large blue crab and several small blue crabs even though small blue crabs pose minimal predation risk (Hill & Weissburg 2013). Since NCE usually reduce prey growth or other traits in order to reduce predation rates, the inability of

78 prey to accurately perceive risk based on predator size or density could lead to increased costs
79 associated with NCE.

80 Besides distinguishing between a single large predator and several small predators, prey
81 may be exposed to cues from predators at varying distances or threat levels (Turner &
82 Montgomery 2003, Cresswell et al. 2010). For example, while consumptive interactions and the
83 event of a predator actively pursuing a prey item require close contact, cues may emanate out
84 from a predator to prey that are out of its reach or search area, leading prey to overestimate risk.
85 Predator proximity and size are also related, as cues from a near small predator may also be
86 similar in concentration (chemical cues) or intensity (sound) to those from a larger predator at a
87 distance (or dilute cues from multiple distant predators may be similar to those from fewer
88 nearby threats (Ferrari et al. 2006)). For these reasons, understanding how NCE are influenced
89 by biomass allocation and distance to predators, along with the interactions between these
90 factors, is critical in determining how non-consumptive interactions affect communities and
91 relate to consumptive effects. The inability to differentiate threat levels may explain the non-
92 linear relationships that have been observed between predator density and non-consumptive
93 responses and may enable small groups of predators (in size or number) to continually influence
94 prey in ways far beyond what actual consumption would suggest. Alternatively, if prey can
95 detect differences in the size, density, and distance of predators and accurately assess risk, the
96 overall effects of predators on communities may be very different.

97 Unfortunately, limitations on space and the inability to replicate variation in water
98 movement and water quality parameters means that recreating realistic variation in predator
99 biomass and proximity (and associated impacts on cue production and detection) may be
100 extremely difficult in lab settings. For this reason, we assessed the ability of prey to perceive

variation in predator presence, size, density, biomass, and distance through a set of field-based mesocosm experiments focused on eastern oysters (*Crassostrea virginica*). Bivalves and other mollusks may (Johnson & Smee 2012, as suggested by differential response to predation risk by large and small oysters) or may not (Gosnell & Gaines 2012) demonstrate graded responses to predation risk, and oyster reefs and other foundational bivalve communities in general have proved useful systems for assessing NCE (Grabowski et al. 2005, Freeman 2007, Gosnell & Gaines 2012, Hughes et al. 2012). Past work on NCE in oyster reefs has shown that small oysters grow more slowly in the presence of some predators (Johnson & Smee 2012) and may vary shell thickness due to predator presence (Garland 2014, Johnson & Smee 2014).

Focusing on responses of oysters to predators also allowed us to consider the importance of non-consumptive interactions in a real-world management context. Hundreds of years of overfishing combined with coastal development and environmental degradation have caused an 85% loss of reefs globally (Beck et al. 2011), leading to efforts to rear oysters for future use in both restoration and food production. Off-bottom culture of oysters in floating cages is an increasingly common practice that is thought to benefit aquaculturists by increasing growth rates and reducing losses to predation compared to oysters grown without cages or bottom-caged oysters (Leonhardt 2013, Walton et al. 2013). Although predations mortality is a common concern for reared organisms that may be reduced by caging oysters (Griffin et al. 2000), potential NCE of predators are often not considered by these programs. This is true in the use of floating cages for oyster aquaculture despite the fact that large predators are commonly found on the cages (e.g., blue crabs), smaller predators such as mud crabs and drilling mollusks are still occasionally found in the cages, and that predators may also be in the general area of the cages.

Considering the non-consumptive interactions between cultured oysters and potential predators may be important for several reasons. Oysters exposed to predator cues may grow more slowly, meaning these interactions could impact aquaculture projects even without obvious impacts of consumption. Oysters exposed to predators may also develop traits that may or may not be desired by managers. Lab studies such as Freeman's (2007) work with mussels and Robinson et al.'s (2014) work with oysters have demonstrated that exposure to predator cues can induce bivalves to change their shell and tissue morphology. Bivalves may increase shell thickness to lower the success of predators that break shells or increase muscular tissue used to keep shells closed in response to predators that pry open shells; alternatively, responses may not be species-specific or seem counter-intuitive (Garland 2014). These changes in morphology may reduce future susceptibility to predation (a potential benefit for oysters destined to be used to rebuild reefs) (Robinson et al. 2014) but also may change the amount of consumable tissue oysters produce or overall growth rate (a potential negative consequence in oysters cultured for human consumption). For these reasons, we carried out our experiments using procedures commonly employed by aquaculture and conservation groups to rear oysters. This design also allowed us to determine if non-consumptive interactions were noticeable in an environment characterized by natural variation in water movement, temperature, and other factors and in a setting where predators may realistically be caged next to prey for a number of weeks.

We conducted experiments to determine how size and density of, and distance from, the predatory crown conch, *Melongena corona*, impacted non-consumptive interactions between the predator and its oyster prey. *Melongena corona* are part of a larger *Melongena* species complex of carnivorous gastropods that can be found intertidally in the United States from Alabama to the Atlantic coast of Florida (Hayes 2003). The species typically inhabit shallow protected intertidal

sites and feed on a variety of bivalves, gastropods, and horseshoe crabs (Hayes 2003), in addition to acting as scavengers. Crown conchs feed on oysters by inserting their proboscis between the shell valves (as opposed to drilling) (Bowling 1994), and the presence of conchs has been shown to have variable effects on shell thickness in oysters (Garland 2014, Garland & Kimbro 2015). Recent work has suggested that predation by conchs is an increasing cause of mortality for oysters in the region, potentially due to reduced freshwater flow (Florida Sea Grant 2013, Garland & Kimbro 2015). Conchs are negatively impacted by freshwater and also have a larger impact on stressed oyster populations (Hathaway & Woodburn 1961). Focusing on the impacts of crown conchs thus allowed us to consider a predator-prey interaction that may be particularly relevant for on-going conservation work (Hayes 2003). Considering non-consumptive interactions among these predators and their oyster prey may be important to understanding how reefs may change as human- and naturally-induced changes occur in water input, temperature, and salinity, especially as increasing predator abundances may alter the relative strength of consumptive and non-consumptive effects.

Materials and Methods:

General experiment protocol

We conducted two studies to determine if the growth of oysters was influenced by the density and abundance of crown conchs and to determine the range of these effects. We carried out these experiments in waters offshore of the Florida State University Coastal and Marine Laboratory (FSUCML, St. Teresa, Florida) between April and July 2014. Water temperature at the study site for these months ranged from 17.3 to 30 °C, with an average temperature of 25.24 °C, and salinity varied from 21.3 to 31.5 ppt, with a mean reading of 27.96 ppt (data collected daily by staff at the FSUCML). Oysters and predators were housed in cages constructed of 3.2

mm diamond plastic mesh cut to 30.5 cm x 45.7 cm pieces and used to construct semi-rigid cages that measured 9 cm tall, 37 cm long, and 18 cm deep. Single cages (or the top cage for cages that were connected together) were attached to two 25 cm floats, allowing the cages and oysters to remain in the top 40 cm of the water column. Both the cage design and location were motivated by common techniques used in off-bottom oyster aquaculture. Oysters used in all experiments were triploid seed purchased from a local hatchery. A random sample of 90 oysters measured prior to the experiment had a mean shell height (umbo to ventral shell margin) of 18.36 mm, ranging from 12.35 mm to 23.55 mm (interquartile range: 17.35 to 19.55 mm). Conchs were collected from oyster reefs adjacent to the Florida State University Coastal and Marine Laboratory (FSUCML).

Since accurately measuring the shell height and thus growth of oysters can be difficult (Johnson & Smee 2012), we employed several methods to consider the effects of predators on growth and development. A subset of oysters was marked at the beginning of the experiment by filing a small triangular notch in the middle of their beak using an xx-slim taper file (Appendix 1). This method, which allows one to measure the percent growth and daily specific growth rate of individual organisms by taking both initial and growth measurements, has previously been used for oysters and other mollusks (Robinson et al. 2007, Gosnell & Gaines 2012). Daily specific growth was calculated for shell height following equations used for area by Carroll and Finelli (2015). Although past work has demonstrated an increased frequency of notching does not impact growth or mortality (Ford 1986), concerns that the method may impact growth still exist (Gosling 2003) and the method is not commonly used in NCE studies in oysters. For this reason, we compared final shell height, mass, and mortality in notched and unmarked oysters. Besides changes in shell height, we also measured the final total mass of each oyster and

192 separate weights for shell and tissue. We then dried tissue and shell for 24 hours in a 70 C
193 drying oven to obtain weights of dry shell and dry tissue.

194 All analyses were conducted in R (R Core Team 2014). Data were manipulated and
195 plotted using the reshape (Wickham 2007) and ggplot2 (Wickham 2009 2) packages.
196 Geographic data were provided by Natural Earth and read using the rgdal (Bivand et al. 2015)
197 library.

198 **Impact of conch density, size, and biomass on oyster growth**

199 In the first study, we explored how the size and density of crown conchs impacted oyster
200 growth. To determine appropriate ranges for conch density and natural size variation, we
201 sampled reefs adjacent to the Florida State University Coastal and Marine Laboratory
202 (FSUCML) as well as reefs southeast of Wakulla Beach (See Fig. 1) to determine natural
203 variation. Sites were sampled at low tide to ensure all areas of oyster coverage, including sites
204 that remained covered at low tide by less than 0.3 meter of water, could be included.

205 Approximately every 5 m along the entire length of each exposed reef during low tide a quadrat
206 (1 m^2) was haphazardly placed in regards to the width of the reef; reefs varied in width from 1 to
207 5 meters wide. Care was taken to collect every crown conch within each quadrat. Using a
208 Vernier caliper, the height (measured as the distance from the apex of the shell to the tip of the
209 siphonal canal) of each conch shell was measured and recorded. Both oyster coverage and
210 whether or not the area within the quadrat was submerged was also recorded.

211 Using these data, we decided to focus on five predator treatments: 1 small ($<50 \text{ mm}$ shell
212 height, average biomass: 15.603 g) conch, 3 small (average total biomass: 44.805 g) conchs, 1
213 large ($>70 \text{ mm}$, average biomass: 99.48125) conch, 3 large conchs (average total biomass:
214 185.42 g), and a no-conch control. This design allowed us to consider impacts of predator size

(large vs small), density, and biomass on oyster growth; a length-weight graph of conch data is also provided (Appendix 2). Ten notched and 10 unnotched oysters were added to 20 floating cages that were subsequently attached to PVC pylons set in the local bay. Pylons were approximately 3 meters long and were set in the sandy bottoms so that approximately 2 m extended above the water. Pylons were set in deep enough water so that all cages would remain submerged during normal tidal phases. All pylons were at least 3 meters apart. A second cage (without floats) was attached to the bottom of each oyster cage (Appendix 3a). Predators were introduced into these cages (except for the no-predator treatment). All bottom cages were also supplied with 5 oysters for predator consumption. A total of four replicate cages were constructed for each treatment (for a total of 20 cages).

Oysters were placed in the water on 01-Apr-2014, and predators were added a week later. The experiment lasted until 5-Jun-2014 for a total of 58 days of predator exposure. To reduce fouling on the cages, which can lead to reduced oyster growth and mortality, we followed standard aquaculture practice and removed all cages from the water for 24 hours once per week. When fouling increased later in the summer months, we also lightly scrubbed the cages prior to removal from the water. Conchs were also checked for escape or mortality weekly and replaced as needed. Oysters in the cages with conchs were not replaced during the experiment in order to limit differences among cages in the amount of potential alarm cues or chemicals released during oyster consumption. However, oysters remained alive in most of the cages containing conchs, including cages associated with each treatment, suggesting conchs were not generally food limited. Past work suggested impacts of conchs on caged oyster mortality are low (Hathaway 1958), possibly due to difficulty conchs have in handling oysters that are not connected to a substrate. At the conclusion of the experiment, oysters were measured for final shell height,

changes in shell height (or *shell growth*, for filed oysters) and mass with tissue preparation carried out as noted above. Initial shell height was estimated by subtracting shell growth from final shell height, and we used this initial shell height to calculate a daily specific growth rate for filed oysters (calculated as

$$\frac{\ln(\text{final shell height}) - \ln(\text{initial shell height})}{\text{Number of days exposure}}$$

). We also calculated a shell thickness index for all oysters by dividing final shell height by oyster mass.

Initial shell heights for filed oysters were regressed against treatment and cage to determine if significant variation existed among treatments in initial oyster size. The impacts of treatment on oyster traits were analyzed in two ways. The overall effects of treatments (factors) were analyzed using linear mixed effect models to account for the potential for oysters in the same cage to have similar growth patterns (Zuur 2009). Impact of fixed factors was determined by comparing nested models using likelihood ratio tests in R using the lme4 and car packages (Fox & Weisburg 2011, Bates et al. 2012 4). If significant differences existed among treatments, planned post-hoc orthogonal contrasts focused on differences based on predator a) presence (i.e., all treatments containing predators vs control), b) density (i.e., three predators vs one predator), and c) size (i.e., large predators vs small predators) were carried out in the multcomp package (Hothorn et al. 2008). The impact of total predator biomass on traits was also considered in a separate model by regressing traits and mean predator biomass (average of predator masses in each set of cages at beginning and end of experiment). The impact of filing on oyster traits was also considered by including a variable to account for filed status into models comparing the final shell heights and masses of oysters; a similar binomial model was also employed to determine if filing influenced oyster mortality.

Range of non-consumptive effects

We used a similar experimental design to consider the potential distance at which predators may impact oyster growth. Four rows of five PVC pylons were deployed parallel to the shore. Pylons were spaced out by 0.5 m, meaning each row measured 2 meters long (cages at 0, 0.5, 1.0, 1.5, and 2.0 meters). Each row was at least 3 meters from all other rows. We added 10 notched and 10 unnotched oysters to floating cages attached to each of these pylons. Separate floating cage containing 3 large (<70 mm total height) conchs were added to one end of each row (Appendix 3b, c). To ensure any differences in growth were not due to local circulation or other factors, predators were added to the alternating ends of adjacent rows.

Oyster cages were placed in the water on 08-Apr-2014, and predator cages were added on 10-Apr-2014. Cages were maintained as noted above. Oysters were removed from the water on 14-Jul-2014 after 96 days.

At the conclusion of the experiment, we again measured for final shell height, shell growth, and mass, and tissue preparation was carried out as noted above. We also calculated an initial shell height and daily specific growth rate for filed oysters and a shell thickness index for all oysters.

To analyze the data, we used a linear mixed-effects model to regress distance from predators against oyster traits. Random effects were included to consider similarities within cages and rows of the experiment. We also again considered the impact of filing oysters by including a variable to account for filed status into models focusing on changes in shell height and mass.

Results:

Predator surveys

Surveys conducted between two days at the FSUCML yielded over 100 crown conchs (2.79/quadrat, mean shell height 53.1 mm), while surveys around Wakulla beach yielded only seven crown conchs (0.128/quadrat, mean shell height 59.1 mm)). Conch sizes ranged from 31.3 to 79.5 mm (Fig. 2). Our size data was similar to earlier studies in the region (Bowling 1994).

Biomass experiment

Oyster survival was high during the experiment (>89%), and oysters that died during the experiment were removed from all analyses. Linear models indicated no significant difference in initial oyster size among treatments ($F_4 = 1.234$, $p = 0.298$) or cages ($F_{19}=1.528$, $p = 0.0841$). Predator treatments had a substantial but not significant impact on final oyster shell height ($\chi^2_4 = 8.977$, $p = 0.062$) and percent dry mass in tissue ($\chi^2_4 = 8.853$, $p = 0.065$). For the examined contrasts, significant negative impacts on final shell height were only noted based on predator presence, with predator density having a substantial but not significant effect. Shell height was not impacted by the size or biomass of predators (Table 1, Fig. 3). Percent dry mass in tissue did not differ among any of the planned contrasts.

All other examined traits (shell growth (calculated by measuring difference between filed mark and shell edge, Appendix 1), daily specific growth rate, shell thickness index, total mass, shell dry mass, and tissue dry mass) differed significantly among treatments. Planned contrasts indicated the presence of predators negatively impacted all traits except for shell thickness, which predator presence significantly increased. Increases in predator density led to significant decreases in shell growth, mass, dry tissue mass, and dry shell mass while significantly increasing shell thickness; predator density also had substantial but insignificant negative effects on shell height and daily growth rate. All other planned contrasts were insignificant, indicating

predator size had no impacts (Table 1, Fig. 3). Higher total predator biomass led to significant increases in shell thickness indices and significant decreases in shell and tissue dry mass.

There was no noticeable effect of filing the shell on height, mass, or mortality (results from these models: $\chi^2_1 = 0.032$, $p = 0.857$; $\chi^2_1 = 0.0365$, $p = 1$; $\chi^2_1 = 0.8441$, $p = 0.358$).

Range of non-consumptive effects

Minimal mortality was also observed in the range experiment, with only 1 out of 400 oysters dying. Linear models again indicated no significant difference in initial oyster size based on distance from predators ($F_{176} = 1.9577$, $p = 0.164$) or cages ($F_{19} = 1.0467$, $p = 0.4117$). The only measured trait that was significantly impacted by distance from predator was dry tissue mass, with dry tissue mass increasing with distance (coefficient = 0.043, $\chi^2_1 = 0.4644$, $p = 0.029$); all other traits were not impacted (shell height: coefficient = -0.943, $\chi^2_1 = 2.42$, $p = 0.1174$; shell growth: coefficient = -0.136, $\chi^2_1 = 0.024$, $p = 0.880$; mass: coefficient = -1.597, $\chi^2_1 = 1.440$, $p = 0.230$; shell thickness index: coefficient = 0.030, $\chi^2_1 = 0.183$, $p = 0.669$; daily growth rate: coefficient = 3.05×10^{-4} , $\chi^2_1 = 0.545$, $p = 0.461$; dry mass of shells: coefficient = -0.488, $\chi^2_1 = 0.3471$, $p = 0.558$; percent of dry mass in tissue: coefficient = -0.009, $\chi^2_1 = 0.231$, $p = 0.631$).

However, oysters did grow throughout the experiment. Analysis of notches indicated an average shell growth of 36.26 mm across the experiment, with an average final shell height of 49.86 mm.

Filing of oysters was again found not to impact height ($\chi^2_1 = 1.721$, $p = 0.190$) or mass ($\chi^2_1 = 1.651$, $p = 0.120$); mortality was not analyzed since only one individual died.

Discussion

These two studies examined how the NCE of predatory crown conchs on oyster growth varied based on **a)** total predator biomass and how it was apportioned among individuals and **b)** the proximity of prey to predators. In the study focusing on biomass, planned post-hoc contrasts

showed that predator presence had significant effects on all measures of oyster growth but did not impact allocation of mass between shell and body tissue. The presence of predators led to decreases in all measures of growth except for shell thickness, suggesting the primary effect of predators was a decrease in growth. Changes in shell thickness due to predator presence has been observed in oysters and other bivalves (Freeman 2007, Johnson & Smee 2012), but past work on oysters and crown conchs have shown mixed impacts on shell thickness (Garland 2014, Garland & Kimbro 2015). Increasing shell thickness is also more commonly associated with a response to drilling predators as opposed to those that open bivalves. Increases in predator density had significant (five traits) and near significant (two traits) effects on oyster traits, decreasing growth while increasing shell thickness, while predator size did not significantly impact any traits and total predator biomass significantly increased shell thickness and decreased dry tissue mass. Though not all relationships were statistically significant, it is notable that increases in density and biomass had negative impacts on all traits except shell thickness, while predator size had mixed impacts on measured growth traits.

Since allocation between shell and tissue did not change, it is possible the primary effect of conchs is to limit when oysters might open their shell and thus reduce growth. Change in shell thickness may be indications of direct responses to or impacts of predators, but the combined effects of reduced growth and changes in shape as oysters develop may have led our shell thickness index to pick up changes in growth and shape as well; this also suggests the need for future studies to incorporate direct measures of thickness and shape better than our current project. Other studies of oyster responses to conchs have found limited evidence for reductions in shell mass (Garland 2014) that have also been attributed to changes in feeding patterns. Work on other bivalves has also shown that predator presence can lead to reductions in gaping (Smee

& Weissburg 2006). Limiting gaping may decrease feeding success of conchs, but would also serve to reduce the amount of water filtered by oysters. Limiting gaping would also be a logical behavioral response when conchs are close, especially as conchs (Hathaway & Woodburn 1961) and other predatory gastropods (Ferner & Weissburg 2005, Smee & Weissburg 2006) have been shown to be able locate prey even in turbid conditions, suggesting predator cues may be highly indicative of future predation risk. This may be especially true for crown conchs, which show high site fidelity to very specific, small areas (Hathaway 1958). Accordingly we found the density of predators also impacted multiple oyster traits, with more predators leading to reduced growth and mass in both shell and tissue, while the size of predators and total biomass impacted fewer traits. Since the largest contrasts we noted were based on the presence of predators as opposed to changes in density, our results indicate that NCE may operate primarily as a step-response, with the simple presence of predators leading to major changes. These responses were most likely to be further modified by predator abundance as opposed to predator size or total biomass. Predator density could have a large impact on NCE if it increased the number of close encounters between oysters and conchs. For example, contact with excretions released by conch as they move across substrates may be important cues, and an increasing number of close “paths” would be expected when three conchs are present. Studies in other gastropods have also shown that mucus production does not scale linearly with size (Davies & Williams 1995) and that mucus constituents may play a role in chemical signaling (Kuanpradit et al. 2012).

Close encounters being important to the NCE of conchs on whelks could also explain the lack of difference in growth that we observed in the range experiment. While predator cages were housed beneath oyster cages in the biomass experiment, in the range study the predators were housed in a cage connected to the same pylon as the closest oysters (Appendix 3b). This

setup was used to ensure movement did not differ among the various cages, since housing the predators on the bottom of one cage would have added extra weight to one cage and potentially impacted movement. This difference, however, also meant that the closest oysters were actually further from the predators than all oysters in the biomass experiment. If the chemical signal used to predict predation was quickly diluted over space or degraded in the environment, even these small changes in distances could have led to a lack of NCE.

An alternative explanation for our results may focus on the fact that oysters were caged for a longer period of time in the range experiment and thus may have reached a size refuge from which point growth was not impacted by predator presence. However, although oysters have demonstrated size-dependent responses to predatory mud crabs (oysters that are ~2 mm in shell height respond to these predators, while those 10 – 15 mm in shell height do not (Johnson & Smee 2012)) and the additional 38 days of growth for the range experiment led to a change in mean final shell height among the experiments from 33.8 to 49.86 mm, crown conchs typically feed on and may prefer oysters that are larger than those from our study (Garland & Kimbro 2015). A third possibility is that the range of impact is greater than 2 meters and all oysters were impacted similarly by the predator cages, but this seems unlikely given that we observed differences in growth in the first experiment with various treatment cages spread 3 m apart. The cage design used in the first experiment also may have allowed conchs to physically contact oysters with their proboscis, but given the small mesh size employed and two cage layers existing between predators and prey, in addition to the consistent movement of oysters by waves, we believe physical contact between the predators and prey was likely extremely limited. It should also be noted that while our treatments allowed us to control long-term, consistent exposure to predators, individual differences in growth may be due to the presence of other

predators. For example, we have occasionally observed blue crabs (*Callinectes sapidus*) sitting on oyster cages in the bay and elsewhere along the coast, and small mud crabs (likely *Panopeus* sp.). However, it again seems unlikely this was a major difference between the two studies.

We consider it most likely that NCE between oysters and conchs do not occur over large distances and require concentrated chemical cues to initiate. However, the changes in growth we observed suggest that NCE of conchs on oysters may reduce growth on reefs especially since conchs are known to remain in small areas on reefs (Hathaway 1958). These results add to current work on the impacts of conchs on reefs and increase our overall understanding of how NCE may structure oyster reef communities. If conchs slow the growth of oysters by limiting their ability to filter water and feed, NCE may directly reduce the growth of reefs and lead to oysters that are less prepared to deal with other environmental stressors. This may be extremely important given the water issues facing the region and could greatly increase the impact of predatory conchs. Future studies may wish to more closely consider the range of these effects over very small scales to determine how far they extend from predators, the chemical identity of the cue used by oysters to estimate predation risk, and how NCE change throughout prey development and with predator exposure patterns (Trussell et al. 2011). This may be especially important in considering how prey respond to predators due to simultaneous variation in their own size and the perceived size or risk of predators.

The noticeable impacts of predators on growth in our first study also suggest NCE may have ramifications for oyster aquaculture. For example, oysters reared in the presence of multiple predators (high density treatments) grew 1.75 mm less in regards shell height and 3.53 mm less shell in regards to shell growth than those grown in the absence of predators; oysters exposed to cues from multiple predators also added 2.12 grams less mass during the two month

experiment. These changes could have major impacts on growth rates for both natural and aquacultured oysters. Although growth rate varies widely based on size, temperature, and other factors, rates of ~8 mm/month change in shell height were the maximum average growth rates observed in recent studies of off-bottom culture methods in the Northern Gulf of Mexico (Leonhardt 2013, for oysters beginning in the 40-50 mm range), which closely matched our results for the biomass experiment. Similarly, recent summaries of growth in the region suggest initial growth rates may approach 10 mm/month for newly settled spat (Florida Fish and Wildlife Commission 2013). If we assume 10 mm/month is a high estimate for monthly growth rate, our changes in growth suggest exposure to predators could reduce growth between 8 and 18%. Losses in oyster mass would similarly impact the production of fishermen and shucking houses relying on wild or planted bottom-cultured oysters. While our combined studies suggest that predators may impact oyster growth only when they are extremely close, this is the scenario that exists when predators rest in or on cages as we observed on both our study cages and at local aquaculture sites or when conchs invade local reefs. Many aquaculture designs also house multiple cages together, similar to the design we used in our first experiment, meaning a predator invading one cage may cause NCE in oysters in adjacent cages until they are removed. Obviously the extent of impact will depend on both the actual exposure time and how long NCE last when predators leave a cage, but this suggests that aquaculture operations should at least consider the influence of predators and potentially attempt to avoid areas near natural reefs that may harbor large predator populations. Sampling predator densities and occurrences at aquaculture sites would also be useful in understanding the impacts of NCE on aquaculture operations. While predator presence only slows growth with minimal impacts on mortality, longer growth times lead to increased exposure to other concerns such as disease or loss of cages

444 due to storms in addition to delaying oyster production. alternatively, these effects could prove
445 useful in managing growth rates and future survival rates. Although work in other species (Jarvi
446 & Uglem 1993, Gaudioso et al. 2011), including other cultured bivalves (Brokordt et al. 2011,
447 Robinson et al. 2014), has shown that exposure to predator cues can induce traits that benefit
448 survival in released organisms, we generally did not note changes in traits that support this NCE
449 in oysters, especially given the noted issues with our shell thickness index and lack of difference
450 in allocation among tissues based on predator treatments. However, we did not carry out
451 predation trials following this work to fully assess if differences in predation rates existed based
452 on exposure.

453 The impact of NCE may also differ based on available resources and base metabolic
454 needs. For oysters in particular, NCE may differ between triploid oysters that do not produce
455 gametes (such as those used in this project) and diploid populations. Triploid oysters typically
456 grow faster than diploid oysters since energy is not expended on gamete productions, but this
457 could lead to NCE having a more noticeable effect if predator presence led to a decrease in
458 growth or a smaller effect if the larger availability of energy allows triploid oysters to continue
459 growing in predator presence. Differences in energy allocation may also lead to diploid and
460 triploid oysters employing different strategies for dealing with predation, with larger energy
461 stores encouraging hurried growth (Touchon et al. 2013) and limited energy availability instead
462 favoring the development of defensive phenotypes or behaviors (e.g., shell thickening,
463 reductions in gaping). These issues may be essential to considering how NCE will affect natural
464 and modified organisms.

465 These experiments also demonstrated that notching oyster shells to easily monitor and
466 measure oyster growth has no significant impact on measured morphological traits or mortality.

We suggest that this method can be used as an inexpensive, quick method of marking growth for oysters in studies of NCE and other areas where growth is important. Although not demonstrated here, use of sequential or systematic notches would enable growth to be measured over time and removes issues associated with the loss of tags or other markers used to identify organisms.

In conclusion, the results from our two studies add to the growing literature on how non-consumptive effects are influenced by common variation in predator communities and suggest that size- and density-specific responses for both predators and prey should be considered but may not always exist. Changes in the risk prey perceive may be impacted differentially by predator presence, size, density, and biomass, and these factors may need to be explored independently to understand what cues prey are using and how the size- and density-structure of predator populations impacts cue production. Recent work on identifying chemical cues suggests methods for pursuing these research questions (Decho et al. 1998, Ferrer & Zimmer 2007). Studies building upon this work could focus on changes in non-consumptive interactions throughout biological development and may wish to consider how impacts of biomass and range differ among predators. Past results suggest some responses may be predator specific, possibly due to attack mode or change in predation risk based on density and size (Freeman 2007, Johnson & Smee 2012, Robinson et al. 2014). For example, crabs and fish may be faster than conch predators, and thus prey may be selected to respond to their presence at a greater distance (and thus be more responsive to biomass) using behavioral responses, while the threat of conchs and their speed may dictate responding to nearby threats only. The relative mobility of predators may also be important, and crown conchs have been shown to have limited site mobility and remain in a small area of oyster reefs for months at a time (Hathaway 1958). Future studies

should also consider how non-consumptive interactions change throughout biological development. Translating short-term measures, especially those gained in experimental settings, to real-world impacts remains the greatest challenge in determining the true importance of non-consumptive interactions. However, work in natural systems continues to suggest their importance (Berger 2007, Kuijper et al. 2013), and here we documented the existence of these effects in field conditions when oysters are close to predators and demonstrated their potential impact on aquaculture programs.

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655 Table 1: Impact of predator (crown conch) treatment on oyster traits. Significant relationships ($p < 0.05$) are in bold. Units for
656 coefficients are indicated next to the trait name. Contrast coefficients are scaled to represent difference among group averages.

Trait	Impact of predator					Impact of predator				
	Impact of predator		presence (absent vs.		Impact of predator size		density (multiple vs.		Impact of predator	
	treatment		present)		(large vs. small)		single)		biomass	
	χ^2_4	p	Coefficient	$z(p)$	Coefficient	$z(p)$	Coefficient	$z(p)$	Coefficient	$\chi^2_4(p)$
Shell height				3.167		1.351		-1.936		0.968
(mm)	8.977	0.062	1.207	(0.005)	0.747	(0.177)	-1.070	(0.053)	-0.004	(0.325)
Shell growth				3.492		1.342		-2.380		2.335
(mm)	21.058	<0.001	1.623	(0.001)	1.140	(0.089)	-1.597	(0.017)	-0.007	(0.127)
Daily specific										
growth rate				2.321		0.967		-1.846	-6.953 x	2.011
(ln(mm)/day)	11.577	0.021	.003	(0.020)	0.0005	(0.333)	-0.0015	(0.065)	10^{-6}	(0.156)
Mass (whole,				3.966				-		
intact oysters)				(<0.00		0.007		3.277(0.001		7.4847
(g)	22.367	<0.001	.7705	1)	0.002	(0.994)	-0.592	)	-0.007	(1.00)

Shell thickness				-2.094		0.260		2.102		4.097
index (mm/g)	7.5695	0.019	-0.773	(0.036)	0.071	(0.794)	0.569	(0.035)	0.004	(0.043)
				4.056		-		-		
Shell mass (dry)				(<0.00		0.586(0.55		3.446(<0.0		10.032
(g)	23.281	<0.001	0.585	1)	-0.123	8)	-0.7195	01)	-0.006	(0.002)
				3.375						
Tissue mass				(0<.00		-0.347		-2.303	-1.258 x	6.547
(dry) (g)	13.3887	0.008	0.1425	1)	-0.0021	(0.729)	-0.014	(0.021)	10 ⁻⁴	(0.011)
% dry mass in				0.502		0.303		0.605		
tissue	8.853	0.0325	0.001	(0.616)	1.96x10 ⁻⁴	(0.762)	3.91x10 ⁻⁴	(0.545)	4.008 x10 ⁻⁶	0.325

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658

Figure 1: Field studies and predator (crown conch) survey sites were located on the northern coast of the Gulf of Mexico in Florida. Inset displays study area position in larger context of North America.

Figure 2: Size distribution of crown conchs collected from the two survey sites.

Figure 3: Impact of predator treatments on oyster traits. Points represent mean responses for each group, and lines indicates 95% confidence intervals.

669 Figure 2

670

Figure 3

Treatment ● No predators ▲ Low density, small predators ■ High density, small predators □ Low density, large predators □ High density, large predators

675 Appendix 1: Picture of filed oyster shell. Yellow circle indicates spot where oyster was filed at
676 beginning of experiment.

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679

Appendix 2: Mass-height relationship for whelks used in the biomass study. Comparison of models using AIC indicated a power law relationship fit the data better than a linear fit.

$$\text{Mass (g)} = (7.867 \times 10^{-5}) * \text{Height (mm)}^{3.137}$$

Appendix 3: Diagram of cage designs. White ovals represent oysters measured during the study, and black triangles represent crown conchs. Not drawn to scale. *Biomass experiment cage setup* (A); *Range experiment cage setup* (B); *Range experiment pylon set-up* (C)

A. Biomass experiment cage setup

B. Range experiment cage setup

738

739 **C. Range experiment pylon set-up**

740