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

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8           Running head: Caged oysters still get scared

9

**10 Abstract**

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

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

**31 Introduction:**

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

42           Although commonly overlooked in empirical studies and predator-prey models, both  
43 consumptive and non-consumptive predator-prey interactions are influenced by a variety of  
44 factors that may impact the magnitude, direction, and even presence of consumptive and non-  
45 consumptive effects differently. For example, use of complex habitats can reduce the  
46 consumptive effects of predators on prey, but non-consumptive interactions may still extend to  
47 these environments (Grabowski et al. 2005). Likewise, environmental conditions such as water  
48 temperature, pH, and salinity can influence predation rates (Whetstone & Eversole 1981, Held &  
49 Harley 2009). These conditions may also affect NCE by influencing the movement and  
50 detection of cues that trigger predator responses (Smee et al. 2008, Dixson et al. 2010, Kimbro  
51 2011, Kimbro et al. 2014), thus changing the perceived risk of predation. Differences in the  
52 responses of non-consumptive and consumptive effects to changing environmental factors may  
53 have major impacts on how predator-prey interactions and communities ultimately respond to  
54 environmental change.

55 Two major forms of variation that may influence consumptive and non-consumptive  
56 effects in different ways include variation in the allocation of biomass among predators (e.g.,  
57 several small vs few large predators) and the spacing of predators throughout a community.  
58 Predator body size can physically limit the ability of individual predators to consume prey or  
59 impact overall consumption (Paine 1976, Eurich et al. 2014). Predator density should also be  
60 positively correlated with consumption, with larger predator populations requiring more prey for  
61 survival. The impacts of size and abundance on non-consumptive interactions, however, are less  
62 clear. While some prey species may respond more strongly to predator cues when the prey are  
63 small (Selden et al. 2009, Johnson & Smee 2012), responding to predator size would require prey  
64 to discern predation risk based on external cues. Although evidence suggests prey may be able  
65 to identify and respond to different predators (Freeman 2007, Robinson et al. 2014) and prey  
66 may visually inspect predators to determine risk (Lima & Dill 1990), prey that evaluate risk  
67 through the use of chemical and auditory cues may or may not actually be able to distinguish the  
68 differing levels of risk posed by predators that differ in size (Chivers et al. 2001, Kusch et al.  
69 2004). Similarly, prey may (Van Buskirk & Arioli 2002) or may not (Gosnell & Gaines 2012)  
70 be able to determine and respond to predator density based on cues. Even within a single  
71 species, some defensive traits may show threshold responses and others may not (Van Buskirk &  
72 Arioli 2002). The inability to detect or respond to various sizes or densities of predators may  
73 lead to differences in the relative impacts of consumptive and non-consumptive effects as the  
74 size or abundance of predators change. For example, mud crabs have been shown to exhibit the  
75 same predator-induced behavior in the presence of one large blue crab and several small blue  
76 crabs even though small blue crabs pose minimal predation risk (Hill & Weissburg 2013). Since  
77 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

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

110 Focusing on responses of oysters to predators also allowed us to consider the importance  
111 of non-consumptive interactions in a real-world management context. Hundreds of years of  
112 overfishing combined with coastal development and environmental degradation have caused an  
113 85% loss of reefs globally (Beck et al. 2011), leading to efforts to rear oysters for future use in  
114 both restoration and food production. Off-bottom culture of oysters in floating cages is an  
115 increasingly common practice that is thought to benefit aquaculturists by increasing growth rates  
116 and reducing losses to predation compared to oysters grown without cages or bottom-caged  
117 oysters (Leonhardt 2013, Walton et al. 2013). Although predations mortality is a common  
118 concern for reared organisms that may be reduced by caging oysters (Griffin et al. 2000),  
119 potential NCE of predators are often not considered by these programs. This is true in the use of  
120 floating cages for oyster aquaculture despite the fact that large predators are commonly found on  
121 the cages (e.g., blue crabs), smaller predators such as mud crabs and drilling mollusks are still  
122 occasionally found in the cages, and that predators may also be in the general area of the cages.

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

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



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

## 160 **Materials and Methods:**

### 161 **General experiment protocol**

162 We conducted two studies to determine if the growth of oysters was influenced by the  
163 density and abundance of crown conchs and to determine the range of these effects. We carried  
164 out these experiments in waters offshore of the Florida State University Coastal and Marine  
165 Laboratory (FSUCML, St. Teresa, Florida) between April and July 2014. Water temperature at  
166 the study site for these months ranged from 17.3 to 30 °C, with an average temperature of 25.24  
167 °C, and salinity varied from 21.3 to 31.5 ppt, with a mean reading of 27.96 ppt (data collected  
168 daily by staff at the FSUCML). Oysters and predators were housed in cages constructed of 3.2

169 mm diamond plastic mesh cut to 30.5 cm x 45.7 cm pieces and used to construct semi-rigid  
170 cages that measured 9 cm tall, 37 cm long, and 18 cm deep. Single cages (or the top cage for  
171 cages that were connected together) were attached to two 25 cm floats, allowing the cages and  
172 oysters to remain in the top 40 cm of the water column. Both the cage design and location were  
173 motivated by common techniques used in off-bottom oyster aquaculture. Oysters used in all  
174 experiments were triploid seed purchased from a local hatchery. A random sample of 90 oysters  
175 measured prior to the experiment had a mean shell height (umbo to ventral shell margin) of  
176 18.36 mm, ranging from 12.35 mm to 23.55 mm (interquartile range: 17.35 to 19.55 mm).  
177 Conchs were collected from oyster reefs adjacent to the Florida State University Coastal and  
178 Marine Laboratory (FSUCML).

179         Since accurately measuring the shell height and thus growth of oysters can be difficult  
180 (Johnson & Smee 2012), we employed several methods to consider the effects of predators on  
181 growth and development. A subset of oysters was marked at the beginning of the experiment by  
182 filing a small triangular notch in the middle of their beak using an xx-slim taper file (Appendix  
183 1). This method, which allows one to measure the percent growth and daily specific growth rate  
184 of individual organisms by taking both initial and growth measurements, has previously been  
185 used for oysters and other mollusks (Robinson et al. 2007, Gosnell & Gaines 2012). Daily  
186 specific growth was calculated for shell height following equations used for area by Carroll and  
187 Finelli (2015). Although past work has demonstrated an increased frequency of notching does  
188 not impact growth or mortality (Ford 1986), concerns that the method may impact growth still  
189 exist (Gosling 2003) and the method is not commonly used in NCE studies in oysters. For this  
190 reason, we compared final shell height, mass, and mortality in notched and unmarked oysters.  
191 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<sup>2</sup>) 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 mm shell  
212 height, average biomass: 15.603 g) conch, 3 small (average total biomass: 44.805 g) conchs, 1  
213 large (>70 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

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

225 Oysters were placed in the water on 01-Apr-2014, and predators were added a week later.  
226 The experiment lasted until 5-Jun-2014 for a total of 58 days of predator exposure. To reduce  
227 fouling on the cages, which can lead to reduced oyster growth and mortality, we followed  
228 standard aquaculture practice and removed all cages from the water for 24 hours once per week.  
229 When fouling increased later in the summer months, we also lightly scrubbed the cages prior to  
230 removal from the water. Conchs were also checked for escape or mortality weekly and replaced  
231 as needed. Oysters in the cages with conchs were not replaced during the experiment in order to  
232 limit differences among cages in the amount of potential alarm cues or chemicals released during  
233 oyster consumption. However, oysters remained alive in most of the cages containing conchs,  
234 including cages associated with each treatment, suggesting conchs were not generally food  
235 limited. Past work suggested impacts of conchs on caged oyster mortality are low (Hathaway  
236 1958), possibly due to difficulty conchs have in handling oysters that are not connected to a  
237 substrate. At the conclusion of the experiment, oysters were measured for final shell height,

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

$$242 \quad \frac{\ln(\text{final shell height}) - \ln(\text{initial shell height})}{\text{Number of days exposure}}$$

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

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

261 **Range of non-consumptive effects**

262 We used a similar experimental design to consider the potential distance at which  
263 predators may impact oyster growth. Four rows of five PVC pylons were deployed parallel to  
264 the shore. Pylons were spaced out by 0.5 m, meaning each row measured 2 meters long (cages at  
265 0, 0.5, 1.0, 1.5, and 2.0 meters). Each row was at least 3 meters from all other rows. We added  
266 10 notched and 10 unnotched oysters to floating cages attached to each of these pylons. Separate  
267 floating cage containing 3 large (<70 mm total height) conchs were added to one end of each row  
268 (Appendix 3b, c). To ensure any differences in growth were not due to local circulation or other  
269 factors, predators were added to the alternating ends of adjacent rows.

270 Oyster cages were placed in the water on 08-Apr-2014, and predator cages were added on  
271 10-Apr-2014. Cages were maintained as noted above. Oysters were removed from the water on  
272 14-Jul-2014 after 96 days.

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

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

282 **Results:**

283 *Predator surveys*

284 Surveys conducted between two days at the FSUCML yielded over 100 crown conchs  
285 (2.79/quadrat, mean shell height 53.1 mm), while surveys around Wakulla beach yielded only  
286 seven crown conchs (0.128/quadrat, mean shell height 59.1 mm)). Conch sizes ranged from 31.3  
287 to 79.5 mm (Fig. 2). Our size data was similar to earlier studies in the region (Bowling 1994).

### 288 *Biomass experiment*

289 Oyster survival was high during the experiment (>89%), and oysters that died during the  
290 experiment were removed from all analyses. Linear models indicated no significant difference in  
291 initial oyster size among treatments ( $F_4 = 1.234$ ,  $p = 0.298$ ) or cages ( $F_{19}=1.528$ ,  $p = 0.0841$ ).  
292 Predator treatments had a substantial but not significant impact on final oyster shell height ( $\chi^2_4 =$   
293  $8.977$ ,  $p = 0.062$ ) and percent dry mass in tissue ( $\chi^2_4 = 8.853$ ,  $p = 0.065$ ). For the examined  
294 contrasts, significant negative impacts on final shell height were only noted based on predator  
295 presence, with predator density having a substantial but not significant effect. Shell height was  
296 not impacted by the size or biomass of predators (Table 1, Fig. 3). Percent dry mass in tissue did  
297 not differ among any of the planned contrasts.

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

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

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

### 310 *Range of non-consumptive effects*

311 Minimal mortality was also observed in the range experiment, with only 1 out of 400  
 312 oysters dying. Linear models again indicated no significant difference in initial oyster size based  
 313 on distance from predators ( $F_{176} = 1.9577$ ,  $p = 0.164$ ) or cages ( $F_{19} = 1.0467$ ,  $p = 0.4117$ ). The  
 314 only measured trait that was significantly impacted by distance from predator was dry tissue  
 315 mass, with dry tissue mass increasing with distance (coefficient = 0.043,  $\chi^2_1 = 0.4644$ ,  $p = 0.029$ );  
 316 all other traits were not impacted (shell height: coefficient = -0.943,  $\chi^2_1 = 2.42$ ,  $p = 0.1174$ ; shell  
 317 growth: coefficient = -0.136,  $\chi^2_1 = 0.024$ ,  $p = 0.880$ ; mass: coefficient = -1.597,  $\chi^2_1 = 1.440$ ,  $p$   
 318 = 0.230; shell thickness index: coefficient = 0.030,  $\chi^2_1 = 0.183$ ,  $p = 0.669$ ; daily growth rate:  
 319 coefficient =  $3.05 \times 10^{-4}$ ,  $\chi^2_1 = 0.545$ ,  $p = 0.461$ ; dry mass of shells: coefficient = -0.488,  $\chi^2_1 =$   
 320 .3471,  $p = 0.558$ ; percent of dry mass in tissue: coefficient = -0.009,  $\chi^2_1 = 0.231$ ,  $p = 0.631$ ).

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

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

### 325 **Discussion**

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



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

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

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

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

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

381         An alternative explanation for our results may focus on the fact that oysters were caged  
382 for a longer period of time in the range experiment and thus may have reached a size refuge from  
383 which point growth was not impacted by predator presence. However, although oysters have  
384 demonstrated size-dependent responses to predatory mud crabs (oysters that are ~2 mm in shell  
385 height respond to these predators, while those 10 – 15 mm in shell height do not (Johnson &  
386 Smee 2012)) and the additional 38 days of growth for the range experiment led to a change in  
387 mean final shell height among the experiments from 33.8 to 49.86 mm, crown conchs typically  
388 feed on and may prefer oysters that are larger than those from our study (Garland & Kimbro  
389 2015). A third possibility is that the range of impact is greater than 2 meters and all oysters were  
390 impacted similarly by the predator cages, but this seems unlikely given that we observed  
391 differences in growth in the first experiment with various treatment cages spread 3 m apart. The  
392 cage design used in the first experiment also may have allowed conchs to physically contact  
393 oysters with their proboscis, but given the small mesh size employed and two cage layers  
394 existing between predators and prey, in addition to the consistent movement of oysters by waves,  
395 we believe physical contact between the predators and prey was likely extremely limited. It  
396 should also be noted that while our treatments allowed us to control long-term, consistent  
397 exposure to predators, individual differences in growth may be due to the presence of other

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

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

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

421 experiment. These changes could have major impacts on growth rates for both natural and  
422 aquacultured oysters. Although growth rate varies widely based on size, temperature, and other  
423 factors, rates of ~8 mm/month change in shell height were the maximum average growth rates  
424 observed in recent studies of off-bottom culture methods in the Northern Gulf of Mexico  
425 (Leonhardt 2013, for oysters beginning in the 40-50 mm range), which closely matched our  
426 results for the biomass experiment. Similarly, recent summaries of growth in the region suggest  
427 initial growth rates may approach 10 mm/month for newly settled spat (Florida Fish and Wildlife  
428 Commission 2013). If we assume 10 mm/month is a high estimate for monthly growth rate, our  
429 changes in growth suggest exposure to predators could reduce growth between 8 and 18%.  
430 Losses in oyster mass would similarly impact the production of fishermen and shucking houses  
431 relying on wild or planted bottom-cultured oysters. While our combined studies suggest that  
432 predators may impact oyster growth only when they are extremely close, this is the scenario that  
433 exists when predators rest in or on cages as we observed on both our study cages and at local  
434 aquaculture sites or when conchs invade local reefs. Many aquaculture designs also house  
435 multiple cages together, similar to the design we used in our first experiment, meaning a predator  
436 invading one cage may cause NCE in oysters in adjacent cages until they are removed.  
437 Obviously the extent of impact will depend on both the actual exposure time and how long NCE  
438 last when predators leave a cage, but this suggests that aquaculture operations should at least  
439 consider the influence of predators and potentially attempt to avoid areas near natural reefs that  
440 may harbor large predator populations. Sampling predator densities and occurrences at  
441 aquaculture sites would also be useful in understanding the impacts of NCE on aquaculture  
442 operations. While predator presence only slows growth with minimal impacts on mortality,  
443 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.

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

472 In conclusion, the results from our two studies add to the growing literature on how non-  
473 consumptive effects are influenced by common variation in predator communities and suggest  
474 that size- and density-specific responses for both predators and prey should be considered but  
475 may not always exist. Changes in the risk prey perceive may be impacted differentially by  
476 predator presence, size, density, and biomass, and these factors may need to be explored  
477 independently to understand what cues prey are using and how the size- and density-structure of  
478 predator populations impacts cue production. Recent work on identifying chemical cues  
479 suggests methods for pursuing these research questions (Decho et al. 1998, Ferrer & Zimmer  
480 2007). Studies building upon this work could focus on changes in non-consumptive interactions  
481 throughout biological development and may wish to consider how impacts of biomass and range  
482 differ among predators. Past results suggest some responses may be predator specific, possibly  
483 due to attack mode or change in predation risk based on density and size (Freeman 2007,  
484 Johnson & Smee 2012, Robinson et al. 2014). For example, crabs and fish may be faster than  
485 conch predators, and thus prey may be selected to respond to their presence at a greater distance  
486 (and thus be more responsive to biomass) using behavioral responses, while the threat of conchs  
487 and their speed may dictate responding to nearby threats only. The relative mobility of predators  
488 may also be important, and crown conchs have been shown to have limited site mobility and  
489 remain in a small area of oyster reefs for months at a time (Hathaway 1958). Future studies

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

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654

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 presence (absent vs. present)				Impact of predator size (large vs. small)				Impact of predator density (multiple vs. single)		Impact of predator biomass	
	$\chi^2_4$	$p$	Coefficient	$z(p)$	Coefficient	$z(p)$	Coefficient	$z(p)$	Coefficient	$\chi^2_4(p)$		
Shell height (mm)	8.977	0.062	1.207	<b>(0.005)</b>	0.747	(0.177)	-1.070	(0.053)	-0.004	(0.325)		
Shell growth (mm)	21.058	<b>&lt;0.001</b>	1.623	<b>(0.001)</b>	1.140	(0.089)	-1.597	<b>(0.017)</b>	-0.007	(0.127)		
Daily specific growth rate (ln(mm)/day)	11.577	<b>0.021</b>	.003	<b>(0.020)</b>	0.0005	(0.333)	-0.0015	(0.065)	$10^{-6}$	(0.156)		
Mass (whole, intact oysters) (g)	22.367	<b>&lt;0.001</b>	.7705	<b>1)</b>	0.002	(0.994)	-0.592	)	-0.007	(1.00)		

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

657

658

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

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

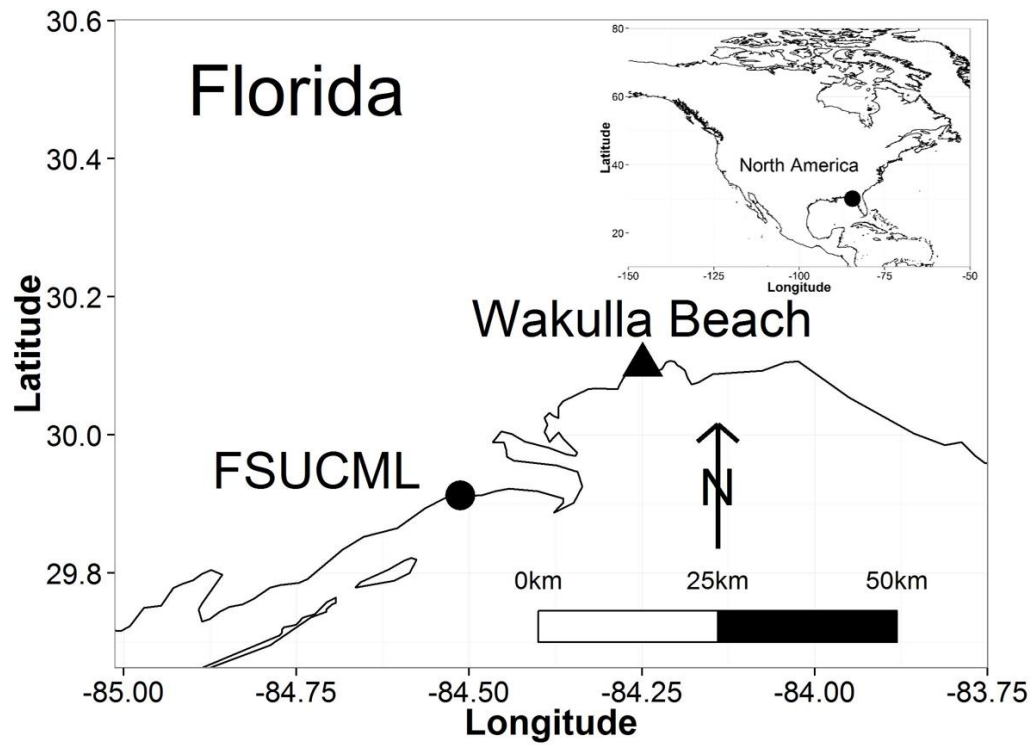
663 Figure 3: Impact of predator treatments on oyster traits. Points represent mean responses for  
664 each group, and lines indicates 95% confidence intervals.

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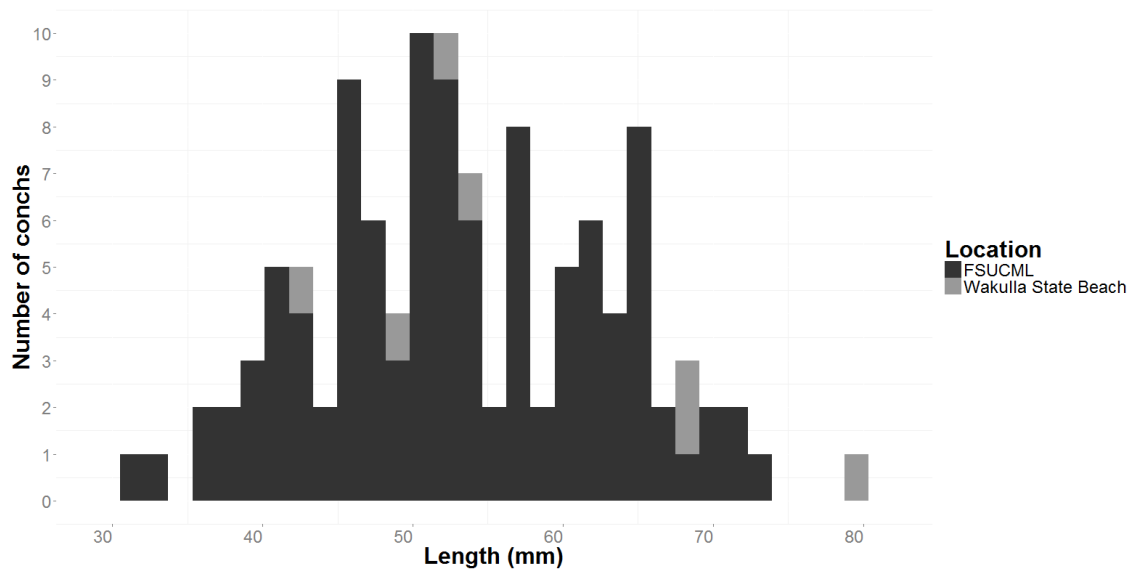
667 Figure 1



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669 Figure 2

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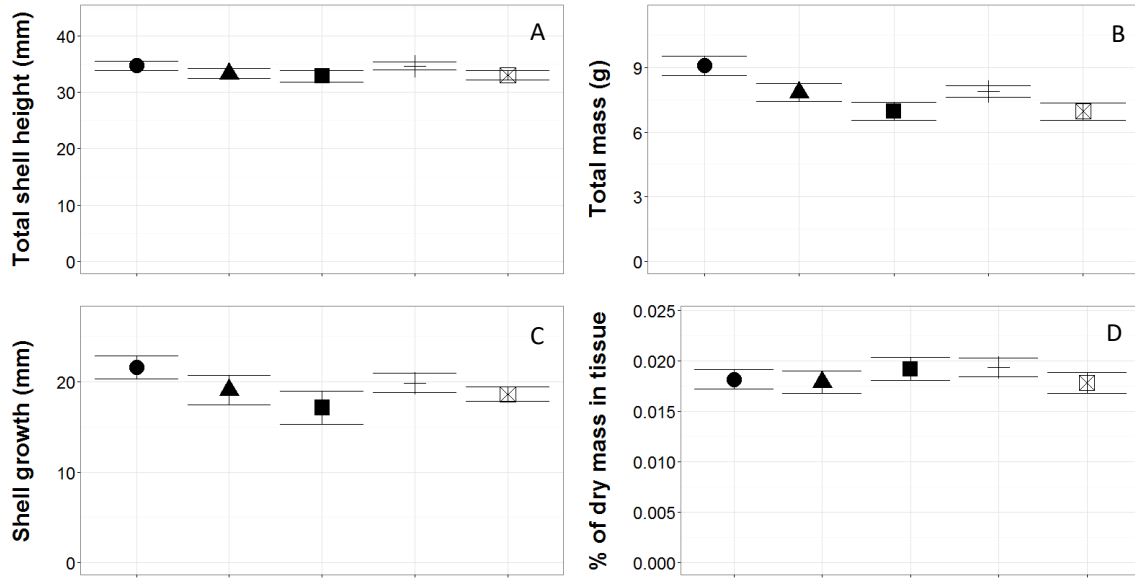


671 Figure 3

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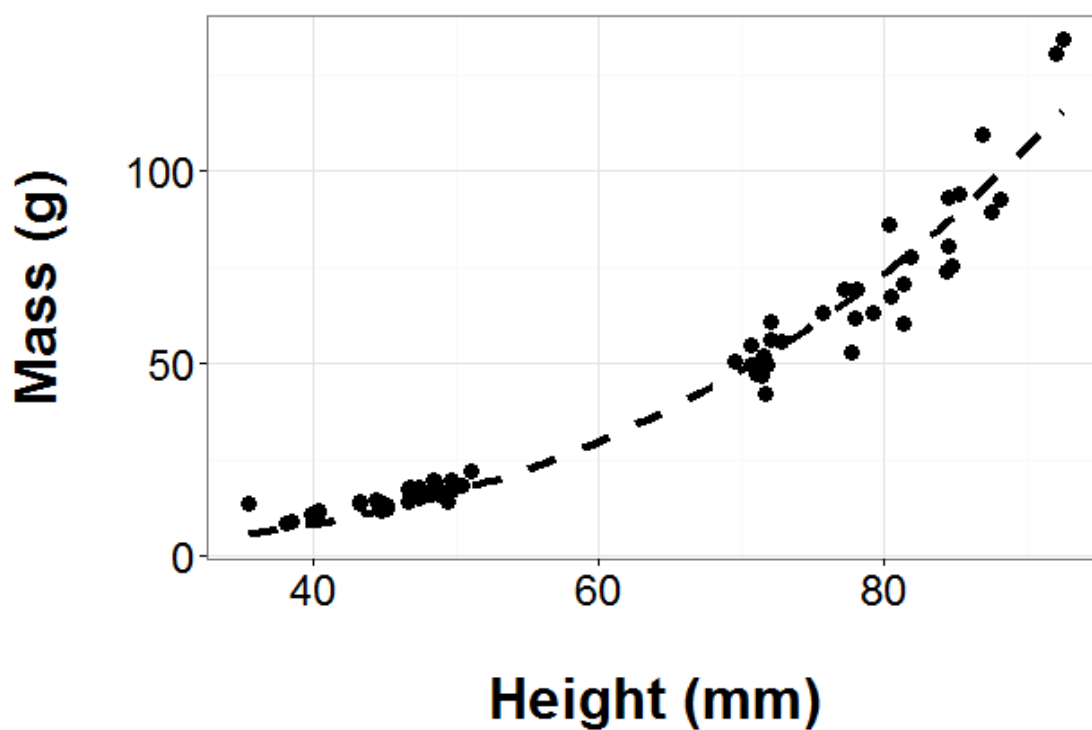
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680 Appendix 2: Mass-height relationship for whelks used in the biomass study. Comparison of  
681 models using AIC indicated a power law relationship fit the data better than a linear fit.

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

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

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690 **A. Biomass experiment cage setup**

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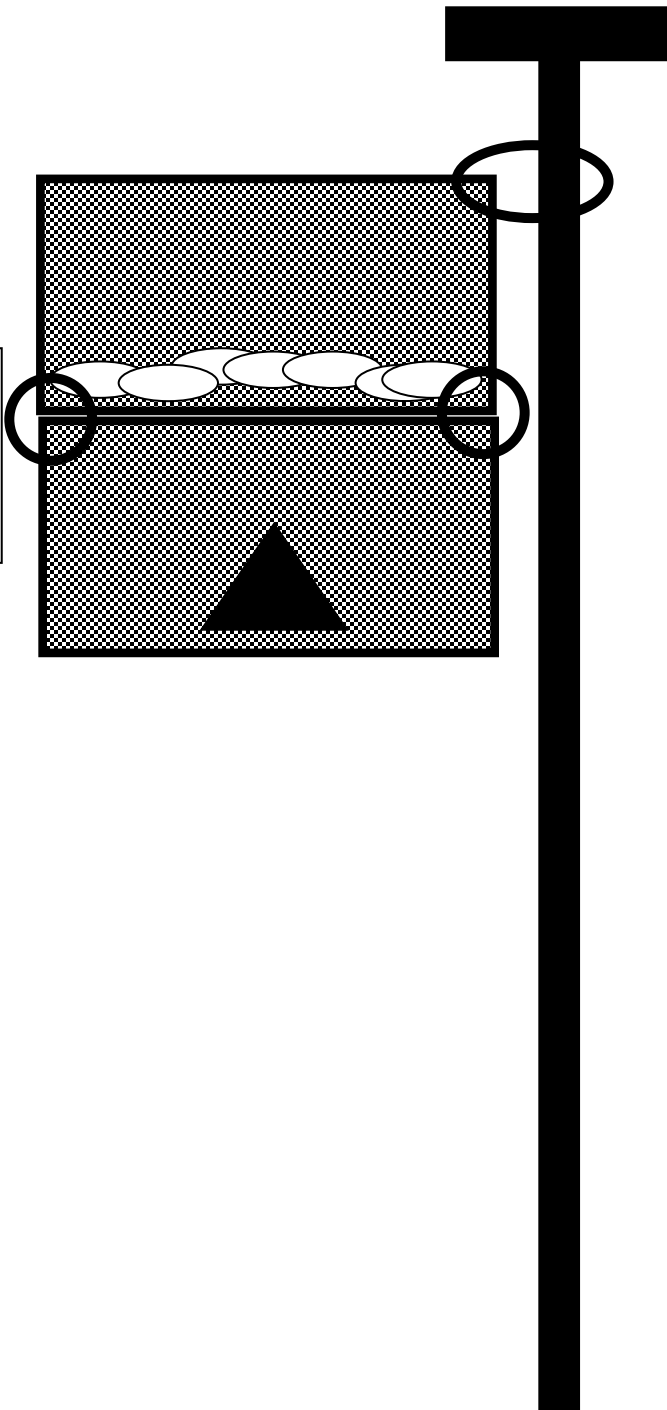
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696 Zip ties were  
697 used to connect  
698 cages and to  
699 connect cage  
unit to pylon



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713 **B. Range experiment cage setup**

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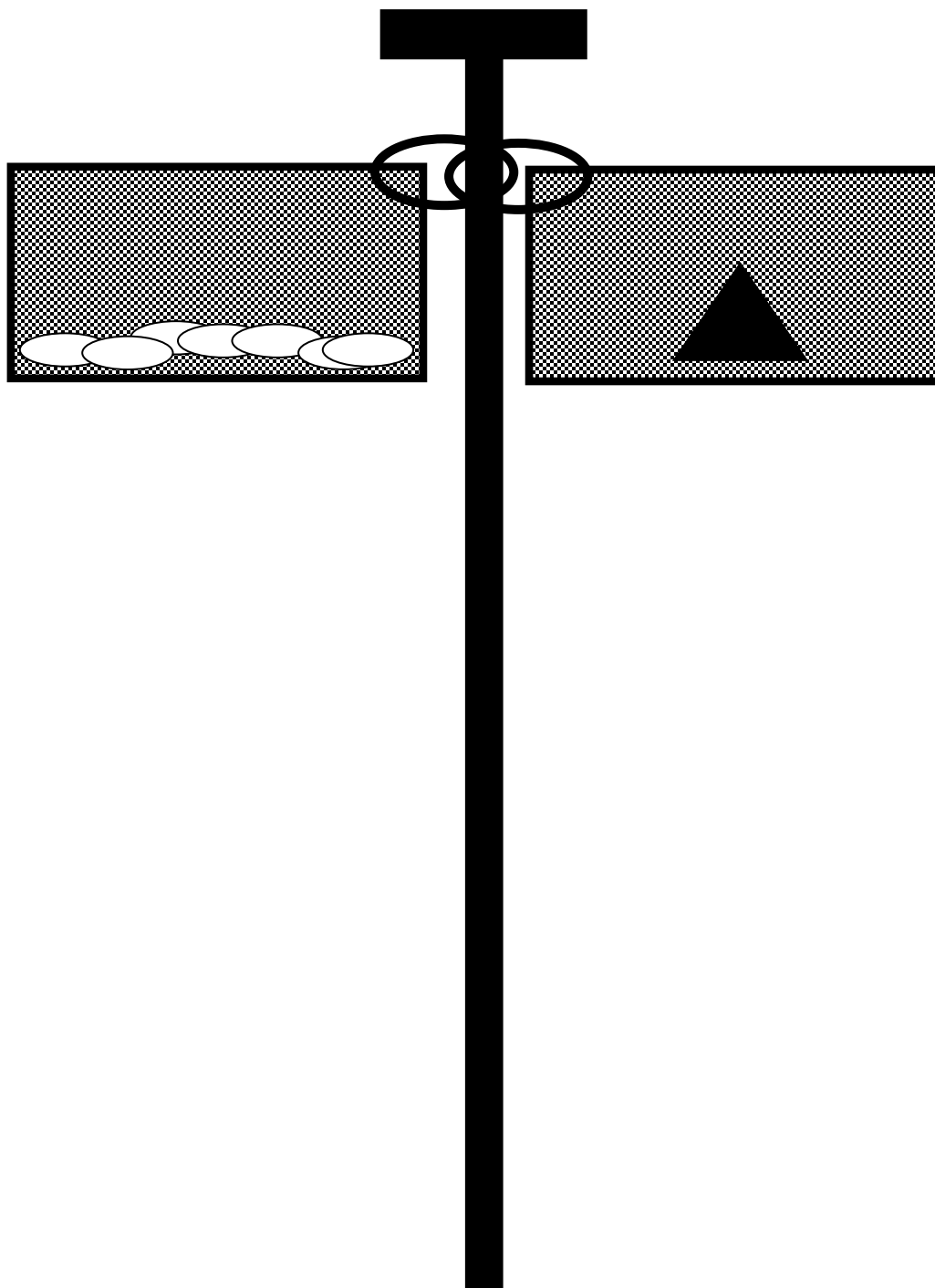
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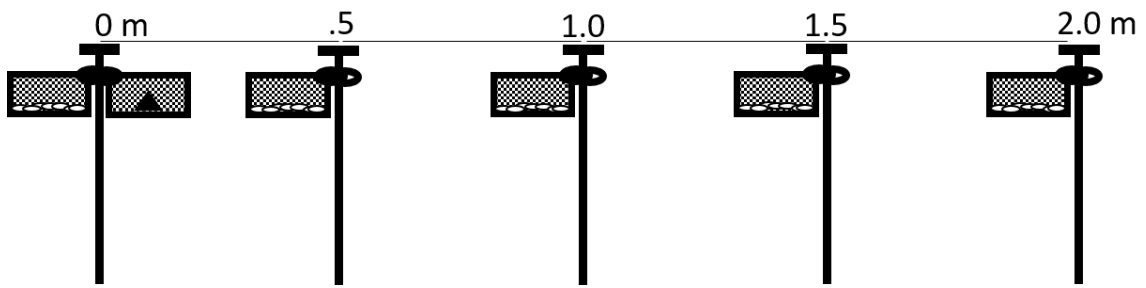
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739 **C. Range experiment pylon set-up**



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