Foraging and Reproductive Ecology of Intertidal Gastropods

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Foraging and Reproductive Ecology of Intertidal Gastropods

A thesis submitted in partial fulfillment of the requirement
for the degree of Bachelor of Science in Biology from
The College of William and Mary

By
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Abstract

Gastropods are a diverse and abundant class of molluscs found in all of the world’s oceans. In this thesis, I explore how predation affects two ecologically similar species of marine gastropods performing two essential activities: foraging and reproduction. First, I examined whether the Atlantic oyster drill, *Urosalpinx cinerea*, a common predator in the mid-Atlantic adjusted its foraging behavior in the presence of predatory crabs. I found that oyster drills do not reduce the number of oysters consumed nor do they alter the location in which they drill through an oyster shell in the presence of blue crabs. However, oyster drills did preferentially drill through the dorsal right quadrant of oyster shells. Preferential drilling of oyster shells is a novel result that contradicts prior claims in the literature. Second, I investigated whether the oviposition strategy of the dogwhelk, *Nucella lapillus*, acts to reduce predation and desiccation mortality. Here, as in previous work, I found that egg capsules themselves provide little direct protection against predators. However, the clustering of egg capsules in large groups does provide a significant benefit by reducing predation relative to uniformly spaced egg capsules. Similarly, it appears that encapsulation alone is an ineffective means of preventing desiccation-induced mortality in the embryos. However, clustering of capsules significantly reduced mortality due to desiccation. Overall, clustering increased survival of egg capsules and the increase in survival was roughly proportional to cluster size. Taken together, these two experiments suggest that predators may influence oviposition but not foraging in intertidal gastropods.
Introduction

Two fundamental processes that all living organisms must complete are energy acquisition and reproduction (McKay 1991; Koshland 2002). Natural selection can act to maximize the efficiency of these processes resulting in increased fitness (Pianka 1976; Pyke et al. 1977). One important selective force in the life history of most organisms is predation, the threat of which can strongly influence how prey species accomplish these two goals (Lima and Dill 1990; Schmitz et al 1997; Ripple and Bescheta 2004).

Predators structure ecosystems in both direct and indirect ways. A direct impact is when one species, through its own actions, influences a characteristic of a second species. An indirect impact is when one species' influence on a second species is dependent upon and transmitted through a third or more intermediate species (Abrams 1995). The study of direct and indirect impacts in ecology has long been focused on the density-mediated effects that predators have on their prey (Abrams 1995; Luttbeg et al. 2003).

A density-mediated direct influence (DMDI) is the direct impact of one species causing a change in the abundance of a second species (Creel and Christianson 2008). One well known example of a DMDI occurs when killer whales reduce the population of otters through predation (Estes et al. 1998). A density-mediated indirect influence (DMII) is the indirect cascading impact on a third species caused by a DMDI (Abrams 1996; Schmitz 1998). Using the previous DMDI as an example, the decrease in the population of otters leads to an increase in the population of sea urchins that in turn causes a decline in the abundance of kelp (Estes et al. 1998). However, predators often impact more than just the density of their prey items. Recently, focus has started to shift to examine the nonconsumptive effects --i.e. trait mediated influences--which predators exert on the organisms around them (Abrams 1995; Abrams et al. 1996; Luttbeg et al. 2003;
Werner and Peacor 2003). Trait mediated direct influences (TMDI) are the changes in prey behavior, morphology, and life history that are caused by the nonconsumptive effects of another species (Bolker et al. 2003). These TMDI’s can then cause indirect effects on either the density or traits of a third species, which are defined as trait mediated indirect influences (TMII). In several systems it has been found that these TMII’s have significant influences in structuring communities and that these effects are often greater than the density-mediated influences (Huang and Sih 1991; Wissinger and McGrady 1993; Grabowski 2004; Ripple and Beschta 2004). For example, isopod survival increases in the presence of green sunfish. This interaction is mediated through an intermediate predator, salamander larvae, who are a prey item to the sunfish yet is a predator of isopods (Huang and Sih 1991).

TMI’s and DMI’s are both common among intermediate consumers living in complex food webs. For intermediate consumers, foraging for resources often exposes them to increased risk of predation (Werner and Hall 1988). In complex food webs intermediate consumers must strike a balance between energy acquisition, reproduction and avoidance of predators. TMI’s are one way that prey respond to predators in order to minimize predation.

A common TMI is a shift in the foraging behavior of a prey species in the presence of a predator. This is a ubiquitous example found in both terrestrial and marine systems. For example, elk will shift their feeding habitat from high food abundance mesic to low abundance xeric upland steppe habitat in the presence of predatory wolves (Ripple et al. 2001). This shift reduces the threat of predation but also reduces their access to food. Similarly, grasshoppers decreased the average distance moved and the amount they consumed in the presence of a predatory spider (Schmitz et al. 1997). While common in terrestrial habitats, it has been suggested that TMI’s are more common in aquatic systems due to the fact that water born cues can be easily detected by
organisms (Tollrian and Harvell 1999). For example, dugongs will shift their foraging habitat from shallow (high quality) to deep (low quality) seagrass beds in the presence of tiger sharks (Wirsing et al. 2007). This shift allows dugongs more space in which they can maneuver to avoid predatory sharks but reduces their food intake (Heithaus et al., 2009). Among marine invertebrates, the best studied cases of TMIs are found in gastropods. In one well known example, the gastropod *Nucella lapillus* reduces its consumption and the location in which it feeds on barnacles in the presence of a predatory crab (Trussell et al. 2003).

Marine gastropods are globally abundant intermediate predators and are important members of coastal communities. My study uses two ecologically similar species to examine how predation influences gastropods. The Atlantic oyster drill, *Urosalpinx cinerea*, is an intertidal and subtidal marine snail that is native to the coast of North America from Florida to Nova Scotia (Franz 1971). *U. cinerea* has also become a successful invasive species along the west coast of the United States and Europe, having been established in Great Britain since 1920 (Orton 1930; Faasse and Lighthart 2009). The dog whelk, *Nucella lapillus*, is a marine snail that inhabits the lower intertidal and shallow subtidal of rocky shores on both sides of the North Atlantic (Crothers 1985).

Dogwhelks and oyster drills are both carnivorous gastropods that attack their prey by drilling through their shell with their radula. *N. lapillus* feeds primarily on small mussels and barnacles (Crothers 1985) while *U. cinerea*’s primary food sources are oyster spat from the Eastern Oyster, *Crassostrea virginica*, mussels (*Mytilus edulis*) and barnacles (Cole 1942; Carriker 1955). *U. cinerea* is an extremely important predator of oysters and is estimated to consume 40-70% of oyster spat each year (Nelson 1931; Galtsoff et al 1937; Cole 1942). *U. cinerea* is considered a major pest in aquaculture and extremely hard to exclude (Jory et al.
1984). The yearly damage done by *U. cinerea* is estimated at several million dollars yearly (Nelson 1931; Hancock 1954)

Little is known of *U. cinerea*’s predators other than it is preyed upon by the gastropod *Fasciolaria hunteria* (Wells 1958). However, *U. cinerea* are commonly found on oyster reefs reaching densities close to 50 drills per square meter (Mackenzie 1961). One potential predator, the blue crab, *Callinectes sapidus*, is widely distributed along the eastern coast of North America reaching densities as high as 2 m\(^{-2}\) (Lipcius et al. 2004). *C. sapidus* are generalist feeders with strong claws that are able to prey upon many mollusks, including several gastropod species (e.g. *Littorina irrata*, *Rapana venosa*, *Illyanassa obsoleta*; Tagatz 1968; Hamilton 1976; Laughlin 1982; Hsueh et al. 1992; Harding 2003). Several potential prey species have been known to exhibit altered behaviors in the presence of *C. sapidus*. For example, the hard shell clam *Mercenaria mercenaria* will retract their siphons and tightly close their valves in the presence of blue crabs scent (Smee and Weissburg 2008). Amphipods will climb up available structures in order to escape blue crabs (Martin et al. 1989). The periwinkle *Littoraria irrata* will climb higher on stalks of marsh grass in order to escape *C. sapidus* (Damiani 2005).

It has been observed that several gastropods will reduce their rate of feeding in the presence of a predator, including *Nucella lapillus* (Trussell et al. 2003). The relatively simple system of top predator, intermediate predator, and oyster has previously been used to study direct and indirect influences. For example, oyster toad fish decrease oyster consumption by mud crabs and 95% of this decreased consumption can be attributed to TMII’s (Grabowski 2004). Similarly, stone crabs, *Menippe adina*, were found to decrease the individual consumption rates of the southern oyster drill, *Stramonita haemastoma*, on the oyster *C. virginica* (Fodrie et al.
2008). Due to their high densities, trophic positions and broad overlap in species ranges, I predicted that there would be TMII’s between *C. sapidus* and *U. cinerea*.

Another method that many organisms use to reduce the threat of predation is aggregation. There are several possible mechanisms by which aggregations may be beneficial, but I will focus on only two: the selfish herd theory and the attack abatement hypothesis. The selfish herd theory states that individuals will form aggregations in the presence of a predator as a form of cover, with individuals trying to be closer to the center, where there is greater protection (Hamilton 1971). The attack abatement hypothesis is composed of two effects that work together. The first effect is the avoidance effect under which a predator is less likely to find a single group rather than one out of many individuals spread out (Turner and Pitcher 1985). The avoidance effect works in conjunction with the dilution effect, and states that a predator is less likely to eat a given individual when it is surrounded by an increasing number of individuals (Turner and Pitcher 1985).

Most of the research on animal aggregations has focused on adults; however, observations of several species have suggested that clustering of eggs is also a beneficial survival strategy (Doody et al. 2009). For example, it has been shown in ladybird beetles (*Adalia bipucanta* and *Coccinella septempunctata*) that predation was 14% higher for individual eggs versus eggs in a cluster (Agarwala and Dixon 1993). It has also been observed that clustering, combined with habitat selection, has a strong effect in reducing predation on eggs in the predatory mite *Iphiseius degenerans* (Faraji et al. 2002). In vertebrates, eggs of the frog *Rana temporaria* in the center of an egg mass have lower rates of leech predation than eggs on the outside (Hakansson and Loman 2004).
*N. lapillus* and *U. cinerea* have similar reproductive patterns. *U. cinerea* deposits benthic developing egg capsules in clusters from which each capsule produces, on average, 30 fully developed juveniles (Cole 1942). Similarly, *N. lapillus* deposits small benthic egg capsules approximately 10 mm high and 3 mm in diameter (Feare 1970; Costello and Henley, 1971; Crothers 1985). Each egg capsule will contain approximately 1000 eggs, however, the vast majority of these are nurse eggs that will not develop. Instead, the nurse eggs condense into a yolk column that serves as food for 12-36 embryos that will emerge as fully developed juveniles after 2-4 months (Feare 1970; Crothers 1985; Costello and Henley, 1971). In a sister species of *N. lapillus*, *Nucella lamellosa*, adult females will often lay their egg capsules in clusters with additional females depositing egg capsules within the same cluster. These clusters can grow quite large and comprise over 400 individual egg cases (Spight 1974). *N. lapillus* also deposits egg capsules in clusters with more than 1000 capsules in a single cluster (JD Allen unpub.). In *N. lapillus*, egg capsules have been shown to experience very high rates of predation and the capsule itself provides little protection against most predators (JD Allen unpub.).

Many gastropod egg capsules, including those of *N. lapillus*, have been shown to offer little resistance to water flow or desiccation (Carriker 1955; Spight 1975; Pechenik 1978). Clustering has also been shown to reduce desiccation. In some amphibian and insect species clustered eggs have a greater rate of survival when the climate conditions promote water loss (Clark and Faeth, 1998). As an intertidal snail with a long development time in benthic egg capsules, *N. lapillus* is a good model system for testing how clustering mediates the risks of desiccation and predation.

My study hypothesized that the risk of predation is an important factor in structuring the foraging and reproductive ecology of marine gastropods. Specifically, I hypothesized that (1) *U.*
**cinerea** will exhibit reduced rates of feeding and altered feeding location in the presence of *C. sapidus*. I also hypothesized that (2) *N. lapillus* egg capsules will experience reduced rates of predation and desiccation when they are members of large clusters compared to small clusters or individually. These hypotheses were tested using a combination of field and laboratory experiments. Experiments using *N. lapillus* were conducted during the summer of 2010 at Bowdoin College's Coastal Studies Center on Orr's Island, Maine. During the fall of 2010, experiments were conducted on *U. cinerea* at the Virginia Institute of Marine Science's Eastern Shore Laboratory in Wachapreague, Virginia

**Methods**

**Urosalpinx cinerea**

To determine if oyster drills’ feeding behavior was affected by the odor of a blue crab, I conducted an experiment at the Virginia Institute of Marine Science’s Eastern Shore Laboratory (ESL) in Wachapreague, VA for 5 weeks from October 15\(^{th}\) 2010 to November 21\(^{st}\), 2010, in a flow through sea water system. Populations of oysters, oyster drills and blue crabs are all found locally in the waters surrounding the field station. Oyster drills (30-40 mm) were obtained from an oyster reef off the coast of Wachapreague, VA (37°61’ N, 75°69’ W). Oysters (25-45 mm) were obtained from the Virginia Institute of Marine Sciences’ oyster hatchery in Gloucester Point, VA (37°25’ N, 76°50’ W). The oysters used were triploid and were approximately 4 months old at the start of the experiment. Blue crabs (9-12 cm in carapace width) were collected locally from crab pots in the waters around Wachapreague.
After collection, all animals were brought back to the ESL and placed in containers in flowing sea water. Two sizes of containers were used: 2.8L containers either contained a blue crab or were empty and 2.0L containers contained 10 oysters and 5 oyster drills. Each experimental unit was composed of two connected containers: one 2.8L container and one 2.0L container containing oyster drills and oysters. Experimental units were placed in two sea tables (2.44 m x 56 cm x 20 cm) with each sea table containing 10 experimental units. Each sea table was fitted with a central PVC pipe (2.5 cm diameter) that was capped on the end and had 5 pairs of holes drilled in it spaced 40 cm apart. Plastic tubing (14 mm diameter) connected the central PVC pipe to the 2.8L container and the 2.8L container to the 2.0L container. Seawater flowed freely from the PVC pipe into the 2.8L container (which was empty or held a blue crab) and then drained into the 2.0L container holding oyster drills and oysters and finally drained into the sea table (Figure 1). Containers were submerged ¾ of the way in the sea table in order to maintain ambient sea water temperature, yet to also make sure that no water would flow back into the containers from the sea table and potentially contaminate treatments. The blue crabs, oysters and oyster drills were randomly assigned to each experimental unit. There were 10 replicates for the no crab treatment and 10 replicates for the crab treatment for a total of 20 experimental units. Experimental units were arranged in alternating pairs along each sea table so no containers of the same treatment were next to each other and to control for potential differences in flow along the pipe (Figure 2). A HOBO data logger (Onset®, TidBit v2 Water Temperature Data Logger) was placed in each sea table and set to record the temperature every 5 minutes to the closest thousandth of a degree Celsius. During the first week of the experiment no containers were exposed to the crab treatment in order to establish a baseline and to verify that all drills were feeding. The number of oysters eaten was recorded every 7 days and the oysters that were eaten
were replaced. All oysters were randomly assigned to each container. Crabs were placed in the containers after the first week on October, 23rd, 2010. Every other day crabs were monitored to see if they were alive and fed a cracked mussel (*Geukensia demissa*) once a week. A cracked mussel was also placed in the no crab treatment to control for effects of crushed mussels on oyster drill behavior. If found dead, crabs were replaced, however, as the weather cooled, the accessibility of crabs decreased and thus some of the crab treatments switched to no crab treatments.

The shells of the eaten oysters were collected each week and brought back to the laboratory. The size of the oysters eaten was recorded each week and the location of the hole drilled in each shell was recorded. To do this, each shell was divided into 4 regions: the dorsal half of the right shell, the ventral half of the right shell, the dorsal half of the left shell or the ventral half of the left shell (Figure 3).

*Nucella lapillus*

*N. lapillus* adults were collected in early June, 2010 from several sites throughout southern Maine: Orr’s Island (43°79' N, 69°95' W), Bailey’s Island (43°73' N, 69°99' W), the Rockland breakwater (44°12' N, 69°08' W), and Basin Point (43°74' N, 70°04' W). Following collection, all snails were immediately brought back to the Bowdoin College Coastal Studies Center, placed in unfiltered flowing sea water and provided with barnacle covered rocks as a food source. After two weeks, adults formed reproductive aggregations and females deposited egg capsules on the sides of the tank where they were housed. All egg capsules used in this experiment were laid in the laboratory, which ensured that all eggs were exposed to similar levels of predation and desiccation stress throughout their development. It also ensured that no
embryos would hatch from egg capsules during the course of the experiments due to their long pre-hatching period of up 2 - 4 months (Costello and Henley, 1971).

**Laboratory predation experiment**

Laboratory predation experiments were conducted to determine whether common crustacean predators consume *N. lapillus* egg capsules. Egg capsules were glued onto small rocks in a 3 x 3 grid with one centimeter separating egg capsules from one another. Egg capsules were glued using Krazy Glue® gel, which in previous studies has been shown to be effective in cementing the reproductive stages of marine invertebrates without deterring predators (Allen and McAlister, 2008; Dixon and Allen, 2010). All rocks used were of approximately the same size and color, and were 8 cm long by 8 cm wide by 1 cm thick. Rocks with egg capsules were placed in mesh cages (2 mm x 2 mm mesh size) approximately 12 x 25 x 15 cm in size, which were subsequently placed in flowing sea water. The mesh cages allowed the flowing sea water to enter and exit the cages freely. The rocks in each cage were then exposed to one of five treatments: one green crab (*Carcinus maenus*: 30-65 mm carapace width), one juvenile lobster (*Homarus americanus*: 20-35 mm carapace length), one rock crab (*Cancer borealis*: 40-75 mm carapace width), one hermit crab (*Pagurus longicarpus*: 20-30 mm shell length), or no predator for a control treatment. These predator species and sizes are commonly found overlapping in with *N. lapillus* capsules. Each day the number of egg capsules remaining was recorded, with each trial lasting four days. Trials were run for four days during four different weeks over the course of the summer (June 15th-19th, July 5th-9th, July 12th-16th, and July 27th-31st). While the composition of predators used varied from run to run depending on availability, there were always control treatments. There were 11 replicates of the green crab treatment, 9 replicates of the lobster
treatment, 13 replicates of the hermit crab treatment, 9 replicates of the rock crab treatment and 15 replicates for the control treatment.

Field Experiment

To determine the effect of clustering of egg capsules on survival, capsules were glued to rocks in three different distributions: one cluster of 100 capsules, two clusters of 50 capsules with each cluster spaced 10 cm apart, and 100 individual capsules spaced one centimeter apart in a 10 x 10 array. One replicate of each distribution was glued onto each rock for a total of 300 egg capsules per rock total. Each distribution was separated by 15 cm. The order in which the distributions were glued onto the rocks and which capsule was assigned to each distribution was randomized. All rocks were of approximately the same size: 80 cm long by 40 wide by 4 cm thick. On July 1, 2010 five rocks were deployed in the intertidal zone at the mean low tide line. Six days later on July 7th an additional five rocks were placed higher in the intertidal zone. These rocks were placed one meter directly up slope from the rocks deployed on July 1st. Every seven days the number of egg capsules discolored, the number of capsules clipped, and the number of capsules missing were recorded for each distribution type on each rock. Capsules that are discolored is an accurate proxy for determining desiccation mortality (Feare 1970; Costello and Henley 1971). The experiment continued through August 6, 2010.

Statistics

Analysis of all data were completed in SPSS version 18. All data from the N. lapillus experiments were presented as percentages and were arcsin squareroot transformed to conform to normality assumptions of 1-way and 2-way repeated measures ANOVA’s. All results are presented as mean ± standard error. I set the level of significance at p=0.005
Results

Urosalpinx cinerea

Temperature

Over the course of the 5 week experiment, temperature ranged from 8.94 C to 23.09 C. Linear, logarithmic, quadratic, power, and exponential regressions were run comparing the mean, minimum and the maximum temperatures to the number of oysters that were drilled each week. While all regressions were significant (p < 0.001) the linear regressions had the highest adjusted r square. The linear regression using the mean temperature was the best predictor of the number of oysters drilled (adjusted r squared=0.636, 1-way ANOVA, F_{1}=173.866, p < 0.001).

Quantity of Oysters Drilled

Oyster drills were observed to display maximal feeding during weeks one (3.8 oysters per container ± 0.2; Mean± SE) and two (4.4 ± 0.4; Mean± SE) when the average temperatures were the highest (16.35 C and 18.13 C) (Figure 4). During week three consumption fell to 1.7± 0.3 oysters per container as the average temperature fell to 14.48 C. Week four (0.5 ± 0.1; Mean± SE) and week five (0.8 ± 0.1; Mean± SE ) displayed minimal feeding rates as mean temperature dropped to 11.31 C and 12.03 C.

The number of oysters drilled was analyzed only using data from week two and week three because these were the only weeks where there were equal quantities of crab and no crab treatments for the duration of the week. The oysters consumed in each container were pooled between the two weeks and analyzed using a 2-way ANOVA with crab and location as fixed effects. Fewer oysters were consumed in the crab treatment (5.5 ± 0.7; Mean± SE) than in the no
crab treatment (6.6 ± 0.7; Mean± SE). However, there was no effect of crab treatment 
\((F_{1,13}=1.844, \ p = 0.198)\), or location in the sea table \((F_{4,13}=0.625, \ p = 0.653)\) on the number of 
oysters consumed.

**Drill Hole Location Experiment**

While the total number of oysters consumed did not differ in the presence of blue crabs it 
was possible that the location in which they drilled had been altered. Location of the drill hole 
data was analyzed using Chi-Square tests that analyzed if the distribution observed was 
significantly different from an even distribution. Using a 2 x 4 contingency table I found that the 
locations of drill holes were not different in the crab and no crab treatments \(\text{Pearson Chi-Square,}
\ p = 0.237\). However, I found that 51% of drill holes were in the dorsal right quadrant. Therefore,
a separate analysis was conducted to see if oyster drills displayed a preference for drilling 
through any one quadrant of the oysters shell. Using location data from weeks 2 and 3 pooled 
across all treatments, I found that drill holes were not evenly distributed in each quadrant \(\text{Chi-}
\text{Square; } p < 0.001\; \text{; Figure 5). Further analysis using pair wise comparisons of each quadrant}
showed that there were significantly more drill holes in the dorsal right quadrant than any other 
quadrant \(\text{Chi-Square; } p = 0.001\; \text{; Figure 6). The ventral left quadrant contained the second most}
drill holes with 24%. The ventral left quadrant had significantly more drill holes than the dorsal 
left quadrant \(\text{Chi-Square; } p = 0.008\) but not compared to the ventral right quadrant \(\text{Chi-Square;}
\ p = 0.149\). The ventral right quadrant contained 16% of drill holes but did not contain 
significantly more than the dorsal left which only contained 10% of all samples.

**Nucella lapillus**

**Laboratory Predation Trials**
There was a significant effect of predator type (1-way ANOVA, $F_{4} = 19.473, p < 0.001$) on the number of capsules eaten (Figure 7). Lobsters consumed the most capsules overall, ranging between 56% and 100% ($85 \pm 11\%$; Mean $\pm$ SE). Based on a Bonferroni post hoc test, lobsters ate significantly more capsules than all other treatments ($p < 0.001$) other than rock crabs ($p = 0.465$). Rock crabs were the second largest consumers of egg capsules, consuming an average of $56 \pm 15\%$ of capsules. Rock crabs ate significantly more capsules than hermit crabs or the no predator treatments ($p < 0.001, p < 0.001$) however they were not significantly different from green crabs ($p > 0.9$). Green crabs ate significantly fewer capsules ($38 \pm 11\%$) than lobsters ($p = 0.011$), and significantly more than the hermit crabs ($p < 0.001$) and the controls ($p < 0.001$). Hermit crab consumption ($8 \pm 1\%$) was not significantly different from the control treatment ($p > 0.9$) although no egg capsules were ever disturbed in the no predator treatment. It was observed in these lab trials that instead of simply clipping the capsules to get to the contents, lobsters, rock crabs and green crabs would often rip the capsule completely off the rock when they consumed them.

**Field Trials**

There was a significant effect of cluster size (2-way repeated measures ANOVA, $F_{2,85} = 19.991, p < 0.001$) but not of tidal height (2-way repeated measures ANOVA, $F_{2,7} = 0.642, P=0.445$) nor the interaction between treatment and tidal height (2-way repeated measures ANOVA, $F_{2,85} = 1.041, p = 0.358$) on the number of capsules missing. Clusters of 100 and clusters of 50 did not have significantly different numbers of missing capsules (Bonferonni post-hoc test; $p > 0.9$), however both had significantly fewer capsules missing than the 100 uniformly spaced capsules (Bonferonni post-hoc test; $p<0.001$ and $p<0.001$; Figure 8). There was also a
significant effect of cluster size (2-way ANOVA, $F_{2,109} = 9.148, p<0.001$) but not of tidal height (2-way repeated measures ANOVA, $F_{2,7} = 1.156, p=3.14$) on the number of capsules that were clipped. Clusters of 100 and clusters of 50 were not significantly different (Bonferroni post-hoc test; $p = 0.265$) but both had significantly fewer capsules clipped than the 100 uniformly distributed capsules (Bonferroni post-hoc test; $p = 0.038$ and $p < 0.001$ respectively; Figure 9). There was also a significant interaction between treatment and tidal height (2-way repeated measures ANOVA, $F_{2,109} = 5.300, p = 0.006$) on the number of capsules clipped. This interaction was driven by clusters of 50 and 100 uniformly spaced capsules, which had greater numbers of capsules clipped at the high tidal height compared to the low tidal height. However, clusters of 100 had approximately equal number of capsules clipped at the low and high tidal height.

Mortality due to predation was defined as the number of capsules missing plus the number of capsules eaten. This assumption was well supported because predators in lab experiments would commonly completely rip egg capsules off the rock on which they were glued. Also, we never observed glued capsules to fall off of rocks without predation. There was a significant effect of cluster size (2-way repeated measures ANOVA, $F_{2,84} = 25.120, p < 0.001$) but not tidal height (2-way repeated measures ANOVA, $F_{1,7} = 0.737, p = 0.445$) on the number of capsules eaten ($26\pm 3\%$; Mean$\pm$ SE). Clusters of 100 ($27\pm 7\%$; Mean$\pm$ SE) were not clipped significantly less than clusters of 50 ($26\pm 3\%$; Mean$\pm$ SE; Bonferroni post-hoc test; $p > 0.9$). However, both types of clusters had significantly fewer capsules eaten than the 100 uniformly distributed capsules ($51\pm 7\%$; Mean$\pm$ SE; Bonferroni post-hoc test; $p < 0.001$ and $p < 0.001$; Figure 10). However, there was a significant interaction between treatment and tidal height (2-way repeated measures ANOVA, $F_{2,84} = 3.963, p < 0.023$). This interaction was driven by
clusters of 50 and 100 uniformly spaced capsules, which had greater numbers of capsules eaten at the high tidal height. Due to the fact that predation is a combination of the number of missing and clipped capsules, the interaction between treatment and tidal height was caused by the clipped component of predation.

Desiccation mortality was evaluated in two different ways. First, I counted the number of capsules that were discolored and had succumbed to desiccation mortality on each rock. There was a significant effect of cluster size (2-way repeated measures ANOVA, $F_{2,74} = 8.315, p = 0.001$) but not tidal height (2-way repeated measures ANOVA, $F_{1,7} = 0.119, p = 0.739$) on the number of capsules desiccated. The interaction between treatment and tidal height was also not significant (2-way repeated measures ANOVA, $F_{2,74} = 0.784, p = 0.460$). Clusters of 50 had significantly higher numbers of capsules desiccated than clusters of 100 (Bonferonni post-hoc test; $p = 0.037$) but not 100 uniformly distributed capsules (Bonferonni post-hoc test; $p = 0.374$) (Figure 11). Clusters of 100 did have significantly fewer capsules discolored than the 100 uniformly distributed capsules (Bonferonni post-hoc test; $p = 0.044$). However, this method of determining desiccation mortality was skewed due to the fact that the 100 uniformly distributed capsules had higher rates of predation mortality and thus there were fewer remaining capsules to be discolored.

In order to avoid this constraint, I divided the number of capsules desiccated by 100 minus the number that had succumbed to predation. This provided the percent of the capsules desiccated that were available to be desiccated, which provides a better index of how cluster size affects desiccation mortality. There was a significant effect of cluster size (2-way repeated measures ANOVA, $F_{2,78} = 16.508, p < 0.001$) but not tidal height (2-way repeated measures
ANOVA, $F_{1,7} = 1.826, p = 0.214$) or the interaction between treatment and tidal height (2-way repeated measures ANOVA, $F_{2,78} = 1.264, p = 0.288$) on the percent of available capsules desiccated. The desiccation mortality for clusters of 100 was $31 \pm 4\%$ (Mean ± SE) and was determined to be significantly lower than the 100 uniformly distributed capsules ($74 \pm 8\%$; Mean ± SE, Bonferonni post-hoc test; $p < 0.001$) and lower than clusters of 50 ($66 \pm 5\%$; Mean ± SE, Bonferonni post-hoc test; $p = 0.013$)(Figure 12). Clusters of 50 also had significantly lower rates of desiccation than the 100 uniformly distributed capsules (Bonferonni post-hoc test; $p = 0.019$).

Survivorship was determined by subtracting the number of capsules missing, clipped and discolored from 100. There was a significant effect of cluster size (2-way repeated measures ANOVA, $F_{2,63} = 35.056, p < 0.001$) but not of tidal height (2-way repeated measures ANOVA, $F_{1,7} = 1.207, p = 0.304$) on the number of capsules remaining. There was also a significant interaction between tidal height and treatment (2-way repeated measures ANOVA, $F_{2,63} = 5.491, p = 0.006$) on the number of capsules remaining. All treatments had low levels of survival over the 5 weeks they were deployed. Clusters of 100 had the highest rates of survival ($41 \pm 4\%$; Mean ± SE), followed by clusters of 50 which had medium rates of survival ($24 \pm 4\%$; Mean ± SE), while the 100 uniformly spaced capsules has the lowest rates of survival ($14 \pm 4\%$; Mean ± SE). Clusters of 100 did not significantly differ from clusters of 50 (Bonferonni post-hoc test; $p = 0.105$). Yet both clusters of 100 and clusters of 50 had significantly higher survival rates than the 100 uniformly spaced capsules (Bonferonni post-hoc test; $p < 0.001$ and $p < 0.001$; Figure 13). As discussed previously this was caused by clusters of 50 and the 100 uniformly spaced capsules having greater numbers of capsules clipped at the high tidal height which decreased survivorship.
The mean percent of capsules suffering predation across all treatments was 35% ± 4% (Mean ± SE). The average number of capsules that succumbed to desiccation across as treatments was 38% ± 3% (Mean ± SE). Thus desiccation mortality and predation mortality are approximately equal threats to the survival of egg capsules in the intertidal zone.

**Discussion**

*Urosalpinx cinerea*

Oyster drills are extremely adept at detecting chemical cues in the water and have been shown to detect several different prey cues as well as cues from conspecifics (Blake 1960; Blake 1961; Pratt 1976; Ordzie and Garofalo 1980; Williams et al. 1983). In addition, gastropods are also known to sense and respond to predator cues (Alexander and Covich 1991; Trussell et al. 2003; Damiani 2005; Fodrie et al. 2009). However, there was no significant effect of the presence of a crab on the rates of feeding of oyster drills. This result was counter to my prediction that oyster drills would be able to sense a blue crab in proximity to them and reduce their foraging behavior to avoid exposure to predators. The fact that oyster drills do not reduce feeding in the presence of blue crabs suggests that oyster drills are not mediating an indirect interaction between blue crabs and oysters. One possible reason for this lack of a TMII is that oyster drills are heavily defended and protected from blue crab predation (Harding 2003). A second reason could be that blue crabs prefer to eat the oyster or other bivalve that the oyster drill is feeding on rather than the oyster drill itself (Tagatz 1968; Laughlin 1982; Ebersole and Kennedy 1995; Micheli 1995). If alternate prey are less defended, easier to eat, or contain more energy than oyster drills, then blue crabs might preferentially consume the bivalves and pass over the drill.
Alternatively, oyster drills may indeed respond to the threat of crab predation but the design of my experiments may have been inadequate to detect a response. For example, the 'no-crab' treatment may in fact be an 'ambient crab' treatment. My experiment used flowing sea water to provide food for the oysters, however, there are high densities of blue crabs in the waters surrounding the ESL in Wachapreague (personal observation). Therefore treatments might be more accurately described as elevated crab level (crab) versus background crab level (no crab). If true, then my experiment actually tested how oyster drills might react when a crab is in proximity to them. In addition, it is possible that oyster drills from Wachapreague and the waters along the mid Atlantic have become acclimated to blue crab presence over their life span. Oyster drills from locations without abundant blue crabs might react differently. The oyster drill's range extends further north than the blue crab's range (Cole 1942; DeRivera et al., 2005) and it would be possible to test hypotheses about acclimation to blue crab scent by using naive drills from the northern part of their range (e.g Maine).

It is also possible that the oyster drills used in this experiment have reached a size refuge from blue crab predation. At earlier life stages oyster drills might be greatly influenced by the threat of blue crab predation. However, once oyster drills reach a size refuge, the threat of predation from blue crabs may be relaxed allowing the drills to forage freely in the presence of crabs. In support of this alternative, previous research has shown that gastropods can reach size refuges where predation from blue crabs is minimal (Schindler et al. 1994; Harding 2003)

Results from a pilot study examining whether blue crabs eat oyster drills in the laboratory suggest that oyster drills are not a preferred prey item (personal observation). Qualitatively, crabs appeared uninterested in the oyster dills and did not appear to disturb them even after several
days in close contact. As suggested by Harding (2003) oyster drills have coevolved with blue crabs and their ornamented shell may be highly effective at deterring predation. Another possible scenario is that oyster drills might be chemically defended somehow; however there is no direct evidence to support this claim. Anecdotally, oyster drills placed in an aquarium with several predators including green crabs, rock crabs, and sea stars remained alive several months later. This suggests that they are infrequently preyed upon by common crustacean and echinoderm predators. In contrast, mud snails (*Ilyanassa obsoleta*) added to the same aquarium quickly fall victim to predation.

In addition to maintaining their foraging levels, oyster drills did not alter their feeding location in the presence of crabs. However, I found that oyster drills preferentially (over 50% of the time) drilled through the dorsal right quadrant of oyster shells. This is in contrast to previous research where it was found that oyster drills bore through the right and left valves equally (Harding et al. 2007). Unlike the current study, Harding et al. (2007) separated each valve into 9 regions and thus their location data have greater resolution. I found that when oyster drills bore through the dorsal right quadrant, the borehole was often located along a groove in the shell (Figure 6b). This groove might provide a better attachment site for the oyster drill or this section of the oyster shell might offer easier access to the soft tissue of the oyster because it is thinner (Galstoff 1964; Harding et al. 2007). The ventral sections of both valves were drilled in approximately equal amounts. However, the dorsal left quadrant was drilled significantly less frequently, possibly because this is the location where an oyster cements itself to the seafloor and is often the thickest part of an oyster's shell (Galstoff 1964). Caution should be used in interpreting bore location data because the orientation of oysters was not randomized when they were placed into containers, instead they were haphazardly placed. Haphazard placement
potentially skews my results because when oysters are dropped into water and sink, they often land on their left valve because it is heavier (Galstoff 1964). However, because there was only 3 cm of water in our containers, there may not have been sufficient distance for the oyster to orient with the left valve down.

I was unable to detect any trait mediated interactions between blue crabs and oyster drills; however, this does not mean they are not present. In nature, blue crabs might physically disturb the oyster drills feeding on oysters by knocking them off and thus reduce their feeding rates. In addition, my study only investigated feeding behavior as a response; however, many marine gastropods grow differently in the presence of predators (Trussell, 1996; Trussell and Smith 2007; Vaughn, 2007; Santoni and Allen in review). Thus, there are several untested potential influences from blue crabs on oyster drills’ growth rates, shell morphology or reproductive behavior.

_Nucella lapillus_

In the lab, I found that _N. lapillus_ capsules are readily consumed by three out of four predators tested. These results suggest that the capsule itself provides little protection to the developing embryos inside, a finding in agreement with previous research on _N. lapillus_ (Dixon and Allen 2010). However, the capsules appear to offer some protection against hermit crabs. Hermit crabs rarely ate egg capsules, and the capsules that were eaten were neither ripped off the rock nor clipped, instead they appeared to be squeezed until they popped. However, since so few of the capsules were eaten in the hermit crab trials they were not significantly different from the no predator treatment. It is possible then that encapsulation is an effective strategy to protect against predation from small crustaceans, such as hermit crabs.
In the field, the arrangement of capsules appeared to be important in reducing predation. Clustering of capsules significantly reduced the number of capsules that were clipped and the number of capsules that were missing. In both of these categories, clusters of 100 were not significantly different from clusters of 50 but both were significantly different from the 100 uniformly distributed individuals. The fact that increasing cluster size does not increase survivorship implies that once a cluster reaches a threshold size, it gains the benefit of being in a cluster. One possible mechanism for this threshold response might be that when capsules are sufficiently clustered it is physically difficult for predators to single out and grab one capsule. A second mechanism, consistent with the selfish herd hypothesis (Hamilton 1971), is that predators consume the capsules on the fringes of the cluster first and slowly progress inward. The clipped capsules on the outside would insulate the capsules in the middle protecting them from being eaten. A third mechanism, consistent with the avoidance effect of the attack abatement hypothesis (Turner and Pitcher 1985) is that predators will be less likely to encounter the capsules in clusters relative to a more dispersed distribution. The avoidance effect is unlikely to be driving this result due to the fact that all the distributions were in close vicinity to each other on a single rock. Therefore it seems likely that if the predators found one distribution they would find them all. In the field it is possible that all of these mechanisms work together to produce increased survival of capsules in clusters.

A possible reason that clustering is effective is that none of the predators consumed large numbers of egg capsules at one time. Lobsters, the most voracious predators in the lab trials, never consumed all 9 capsules within 1 day. It is likely then that predators in the field will not consume entire clusters of capsules at a time. This agrees with the dilution effect of the attack abatement hypothesis (Turner and Pitcher 1985). Due to the fact that predators only consume a
few capsules at a time, as cluster size increases the probability that an individual capsule will be eaten decreases. However, if *N. lapillus* capsules were exposed to high predation rates from a predator that was attracted to and consumed entire clusters at a time it might be beneficial to have their capsules dispersed.

Defining mortality due to predation as the sum of the number of capsules missing and the number of capsules clipped was justified in several ways. In the lab trials, rock crabs, green crabs and lobsters ripped the capsules completely off the rocks when they consumed them. In the field it was occasionally observed that a capsule was missing yet the very base of the capsule was still glued to the rock. Ten months after the beginning of the experiment, rocks were examined and several clipped and desiccated capsules were still glued to the rocks despite a severe winter with heavy snow and ice scour. It can be assumed then that the Krazy glue® that held capsules to the rocks was not failing and leading to missing capsules. The field site where these rocks were deployed is also quite protected with little wave energy. Clusters of 100 and clusters of 50, both had significantly lower rates of missing and clipped capsules compared to 100 uniformly distributed capsules. The fact that the same pattern of loss is observed for capsules scored as missing and capsules that were clipped suggests that the same factor (predation) is causing this mortality.

The significant interaction of cluster type by tidal height on the number of capsules clipped is perplexing. One potential explanation for this result is that there are unique predators present at higher tidal heights that are more likely to clip capsules rather than completely pull them off the rock and are affected by cluster size in ways that predators lower in the intertidal are not. My results suggest that these hypothetical predators would preferentially attack individual
egg capsules or clusters of 50 while avoiding clusters of 100. My laboratory experiments only sampled four crustacean predators; however, there are several other types of predators in the rocky intertidal. One example might be predatory polychaetes which are known to be important in structuring marine communities (Ambrose 1984; Desroy et al 1998). A polychaete might prey on capsules high in the intertidal using their jaws to clip the capsules rather than pull them off the rocks. Further research should investigate how abundant predatory polychaetes such as _Lepidonotus squamatus, Nereis pelagic_ and _Harmothoe imbricata_ impact egg capsule survival (Ojeda and Dearborn 1989). The significance of the interaction between tidal height and cluster size on the number of capsules clipped is most likely driving the significance of the interaction between tidal height and cluster size in both the predation and remaining categories.

Previous research has demonstrated that encapsulation alone is not an effective means to prevent desiccation mortality (Pechenik 1978; 1984). In my study, the arrangement of capsules, however, does appear to be important. As cluster size increased, desiccation mortality decreased thus it appears that clustering is an effective means of reducing desiccation induced mortality. When capsules are clustered and exposed at high tides the capsules surrounding them might act as a buffer against physical stressors. For example, being closely packed could allow water to get trapped between the capsules keeping them cool and moist. If at high tide the capsules are exposed to direct sun light, being in a cluster would also reduce the surface area exposed to the sun. Thirdly, being in a tight cluster might reduce airflow within a cluster, minimizing water loss due to evaporation. An individual capsule would be at greater risk of all of these physical stressors compared to a capsule in a cluster. Increasing cluster size from 50 to 100 eggs
significantly reduces desiccation rates in a cluster. This is the expected result if there is greater buffering against environmental variables as the number of capsules increases.

If physical and biological factors are causing mortality, the capsules on the outside of clusters would be expected to experience edge effects and have higher rates of predation and desiccation mortality. While not quantified, some comments on edge effects are possible based on my qualitative observations. In general, outside edges of clusters had greater rates of predation and desiccation mortality, in agreement with the selfish herd hypothesis (Hamilton 1971) that clustering is beneficial to individuals in the center of aggregations. However, often there would be desiccated, eaten or missing capsules throughout the clusters. In my experiment the largest clusters only contained 100 capsules, which were approximately 3 cm in diameter; this small area may not provide adequate resolution to determine edge effects. In order to test this hypothesis cluster size would have to be greatly increased. When looking at large natural egg capsule deposits in the field it often appears that capsules in the middle of clusters experience lower rates of desiccation and predation. These observations should be rigorously tested in future field studies on *N. lapillus*.

While there was no significant effect of tidal height on the number of capsules desiccated, there was a trend toward higher rates of desiccation at higher tidal heights. Rocks at the high tidal height were only 1 meter closer to shore from the low tidal height, and thus only elevated approximately 2 cm. The small change in tidal height means that at a maximum they would be exposed for approximately 15 minutes longer during low tide. My results show that even with small changes in tidal height there might be an effect on desiccation mortality. Thus
adult *N. lapillus* are likely to be under strong selective pressure for where they deposit their capsules.

Clustering increases survivorship, and appears to be an effective strategy to reduce mortality due to both desiccation and predation. While clustering may be a side effect of adult mating aggregations, the current study shows that it is also beneficial in and of itself. When looking at the entire 5 weeks that rocks were deployed, there were high rates of mortality. In a single treatment on a rock there could be 100 percent mortality. *N. lapillus* embryos can take up to 4 months to develop thus even small changes in mortality rates over the 5 weeks this experiment ran could be magnified over their entire development (Costello and Henley 1971). If the mortality rates per month were maintained over the four months that these capsules can develop, there would be approximately 2.8% survival for clusters of 100, 0.3% survival for clusters of 50, and 0.01% survival for individual capsules. However, there are possible downsides to clustering. When juveniles emerge from capsules they will be in close proximity to each other and thus there might be high competition for food in the immediate vicinity (Zajac et al 1989; Gosselin and Qian 1997; Hixon and Jones 2005).

The threat of predation can be important in structuring communities and organisms can respond to this threat on different temporal scales. Clustering appears to be a response to predation and desiccation on an evolutionary time scale. These snails most likely experience a fitness gain by laying egg capsules in clusters to reduce mortality. The threat of predation can also impact organisms on short time scales (Lima and Dill 1990; Schmitz et al 1997; Lima and Bednekoff 1999; Ripple and Bescheta 2004). I examined how the threat of predation from blue
crabs might induce altered behaviors of oyster drills on short time scales but did not find any evidence of predator induced changes in foraging.

Previous research has shown that there are high rates of mortality on egg capsules of *Nucella* species (Feare 1970; Spight 1974; Dixon and Allen 2010). Understanding the natural history of the rocky intertidal ecosystem provided the framework for me to predict that predation would be important in structuring *N. lapillus*’ reproductive ecology. However, I could not find any examples describing the predator-prey interactions between oyster drills and blue crabs. Thus because blue crabs are aggressive, generalist predators eating a wide variety of prey (Laughlin 1982), I assumed that blue crabs would be predators of oyster drills, however, this key assumption now appears false. Basic knowledge of the links between trophic levels in this system needs further study, and detailed food webs need to be published. Knowing the natural histories of the systems is fundamental to being able to predict basic and complex interactions between the organisms in a community (Heithaus et al. 2009).

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References


### Tables

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Table 1. ANOVA table displaying degrees of freedom, F values and P values from the *N. lapillus* field experiment. The percent discolored are the percent of the available capsules to be discolored that are discolored, while the number discolored are absolute number of capsules that were recorded. Significant p values are bolded.
Figure 1. A schematic of an experimental unit. Water flows into the treatment container which holds either a blue crab or is empty. Water then flows into the container holding oyster drills and oyster and then drains into the sea table. Arrows indicate water flow.
Figure 2. A schematic showing how the containers and treatments are set up in the sea tables. The box in the top left highlights one experimental unit. Two sea tables were used in this experiment.
Figure 3. (A) A drawing of an oyster drill taken from Galstoff (1964). The right shell is on top and the left shell is on bottom. The bar down the middle separates the dorsal (left) from ventral (right) portions of the oyster shell. (B) Picture of two oysters used in this experiment. The oyster on the left is oriented with the dorsal section to the right and it is resting on its left valve. The oyster on the right is oriented with the dorsal section to the right; however it is resting on its right valve. The right valve is thinner than the left valve and generally flatter.
Figure 4.
The bars represent the average number of oyster eaten per container by week. The average, minimum and maximum temperature is overlaid. There was a highly significant effect of temperature on the number of oysters bored. No containers in week one were exposed to crab cue, however, containers that were later exposed to crab cue were categorized as crab containers to demonstrate that they were not significantly different than the no crab containers.
Figure 5. The percentages of bore holes in each quadrant. Letters signify significance which was determined from chi square tests.
Figure 6. Picture of drilled juvenile oysters, red arrow points to location of drill hole. (A) A picture of the right valve. The anterior of the oyster is on the left while the dorsal section is on the right. (B) A picture taken from the anterior side of the oyster. Visible is a groove, which was a preferred location for the drills to bore through.
Figure 7. The averages of the number of capsules that were eaten in the lab predation trials. Letters signify significance.
Figure 8. The averages of the percentage of capsules that were missing by week. There was no significant interaction between tidal height and cluster type thus data from both tidal heights were pooled together. The 100 uniformly distributed capsules had significantly higher percentages of missing capsules.
Figure 9. Average percentage of capsules that were clipped by week. A) Both tidal heights were pooled together and data is shown. The 100 uniformly distributed capsules had significantly higher percentages of clipped capsules. Because there was a significant interaction between tidal height and cluster type the means from the low tidal height are shown in B and the rock means from the high tidal height are shown in C.
Figure 10. The averages of the percentage of capsules that succumbed to predation by week. A) Both tidal heights were pooled together and data are shown. The 100 uniformly distributed capsules had significantly higher rates of predation. Because there was a significant interaction between tidal height and cluster type the means from the low tidal height are shown in B and the rock means from the high tidal height are shown in C.
Figure 11. Average percentage of the capsules that were desiccated by week. There was no significant interaction between tidal height and cluster type thus data from both tidal heights were pooled together. The clusters of 100 had significantly lower percentages of capsules that were discolored.
Figure 12. Average percentage of the intact capsules that were desiccated by week. There was no significant interaction between tidal height and cluster type thus data from both tidal heights were pooled together. All treatments were significantly different. The clusters of 100 had significantly the lowest percentage of desiccated capsules. The 100 uniformly distributed capsules had significantly the highest percentage of desiccated capsules.
Figure 13. Average percentage of capsules that were remaining and still viable to produce juveniles by week. A) Both tidal heights were pooled together and data is shown. The 100 uniformly distributed capsules had significantly lower rates of survival. Because there was a significant interaction between tidal height and cluster type the means from the low tidal height are shown in B and the rock means from the high tidal height are shown in C.