Habitat Preferences and Predation of the Softshell Clam, *Mya arenaria*, in the Lower Chesapeake Bay

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Habitat Preferences and Predation of the Soft-Shell Clam, *Mya arenaria*, in the Lower Chesapeake Bay

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

by

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ABSTRACT

Soft-shell clams (*Mya arenaria*), once abundant, are currently in decline in the Chesapeake Bay, nearing disappearance from some areas in the lower Chesapeake Bay. Proposed explanations for these regional declines include residual effects of Tropical Storm Agnes (1972) and intense pressures from predators. This study was designed to examine the potential for restoring declining populations of *M. arenaria* in the Lynnhaven river system through transplanting juvenile clams. We used Manipulative field experiments to determine the survival and growth of transplanted juvenile *M. arenaria* in replicate plots at two locations: Broad Bay and Pleasure House Creek. We also utilized various substrate types (sand, gravel, oyster shell) and predator exclusion techniques (caged vs. open plots) to examine changes in *M. arenaria* survival and growth. At the conclusion of the study, survival of transplanted clams and abundance of ambient bivalves were both significantly higher in caged plots as compared to open plots, indicating a significant contribution of predation to clam mortality. High mortality rates were observed in all caged and open plots, suggesting that environmental conditions also contributed to mortality. In addition, the most abundant ambient bivalves were *Aligena elevata*, a bivalve that lives commensally with a polychaete, and *Tagelus plebeius*, a deep-dwelling bivalve. These two species appear to have developed mechanisms to survive in the face of predation pressures and were the species most suited to the Lynnhaven River System. Substrate type did not affect transplanted clam survival, though diversity of ambient clams was highest in gravel habitats. The results of this study indicate that future restoration efforts for *M. arenaria* in the Lynnhaven river system are likely to be most successful at establishing a resident population of *M. arenaria* if deeper,
cooler-water locations are used and significant predator-exclusion cages or substantial amounts of structural substrate are used.
INTRODUCTION

_Mya arenaria_, the soft-shell clam, is a critical component of benthic communities, influencing the ecological interactions throughout the Chesapeake Bay (Abraham and Dillon, 1986). The soft-shell clam serves as a prey species for numerous predators that are both commercially and recreationally important (Abraham and Dillon, 1986; Eggleston et al., 1992; Seitz et al., 2001), as well as supplying a substantial portion of the commercial clam fishery in the United States (Abraham and Dillon, 1986). _M. arenaria_ is a common, abundant species throughout the Chesapeake Bay (Eggleston et al., 1992; Seitz et al., 2005), but in recent years populations have been decreasing, especially in the lower regions of the Bay. Diminishing populations have been attributed to several factors including residual effects of tropical storms, predator-prey interactions, and commercial fishing pressures (Kennedy and Mihursky, 1971; Andrews, 1973; Seitz et al., 2001; Wheaton et al., 2008). The Lynnhaven River System provides an ideal location to study the effects of predators and substrate type on the survival of _M. arenaria_ in the Lower Chesapeake Bay due to historically abundant populations (Abraham and Dillon, 1986) that have been diminishing since 1972 (Andrews, 1973) and ecological conditions where soft-shell clams have survived in the past.

**Life History of the Soft-shell Clam**

A readily abundant commercial species along the Western Atlantic coast, _M. arenaria_ are distributed from the sub arctic regions to as far south as North Carolina (Abraham and Dillon, 1986; Maximovich and Guerassimova, 2003). Thin-shelled infaunal suspension-feeding clams, _M. arenaria_ (Mollusca: Bivalvia: Myacidae), engage in two spawning periods per year during mid-March through May and mid-October.
through November (Lucy, 1976). The timing of these spawning cycles is highly dependent on water temperature (Lucy, 1976), therefore any fluctuations in annual temperature averages play a crucial role in the timing of the soft-shell clam’s reproductive cycle.

Juvenile clams that have developed beyond the larval veliger stage temporarily secure themselves to the sediment using byssal threads, yet they continue to be motile until they reach about 12 mm in shell length (Abraham and Dillon, 1986). After juvenile clams exceed this size, they remain sessile, burrowing into the sediment (Abraham and Dillon, 1986). Because young *M. arenaria* are motile and more easily transported by wave action, distribution of juveniles is predominantly determined by local hydrodynamics (Lucy, 1976; Hunt and Mullineaux, 2002; St-Onge and Miron, 2007). As clams grow larger, their burial depth increases (Zaklan and Ydenberg, 1997), decreasing the effect of hydrodynamics on their distribution. Once the clams settle, a commercial size of 50 mm can be reached in about 1.5-2 years and peak reproductive maturity is reached after approximately five years (Abraham and Dillon, 1986). Adult *M. arenaria* can grow up to 150 mm in length and 80 mm or more in width, yet most commercial clams in the Chesapeake Bay are less than 100 mm in length (Wheaton et al., 2008). Growth rates of *Mya arenaria* are influenced by availability of sufficient phytoplankton (Abraham and Dillon, 1986), latitudinal distribution (Appeldoorn, 1983), clam density (Abraham and Dillon, 1986; Beal et al., 2001; Beal and Gayle Kraus, 2002), tidal height (Appeldoorn, 1983; Abraham and Dillon, 1986; Beal et al., 2001), spatial variation (Beal, 2006), temperature (Appeldoorn, 1983; Abraham and Dillon, 1986), and substrate type (Swan, 1952).
Soft-shell clams can persist across a wide range of environmental conditions, surviving in salinities ranging from 5 to 35 ppt, temperatures from 2 to 28°C, and dissolved oxygen levels from normoxic to hypoxic conditions (Kennedy and Mihursky, 1971; Abraham and Dillon, 1986; Taylor and Eggleston, 2000; Wheaton et al., 2008). Smaller clams are more tolerant of temperature fluctuations than larger adult clams but significantly less tolerant of lower salinities (Abraham and Dillon, 1986). Changes in the environmental conditions of an area can result in diminished abundances of *M. arenaria*. In 1972, low salinity, sedimentation, and increased temperatures in the Chesapeake Bay caused by Tropical Storm Agnes resulted in the death of 90% of clam populations in some areas, negatively impacting populations of *M. arenaria* across the Bay (Andrews, 1973; Abraham and Dillon, 1986). If environmental conditions became unsuitable for soft-shell clams, survival of *M. arenaria* could be impacted, potentially causing the disappearance of the species from some areas (Glick et al., 2007).

**Substrate Type Facilitates Survival**

Within areas with the appropriate physical parameters, substrate type can influence the distribution and abundances of soft-shell clams (Abraham and Dillon, 1986). Found throughout intertidal areas (Beal, 2006), *M. arenaria* persist primarily in sand and mud substrates (Abraham and Dillon, 1986), with higher abundances observed in sand substrates (Seitz et al., 2001). In some cases, growth rates can be impacted by sediment type, with higher growth rates observed in sand substrates than in mud-gravel-shell mixtures (Swan, 1952). Additionally, substrate compositions with more structure (such as gravel or shell hash) have been demonstrated to provide bivalves with refuge against predators (Sponaugle and Lawton, 1990; Skilleter, 1994; Seitz et al., 2001).
**Predator-Prey Interactions**

In the Chesapeake Bay, the dominant predators of the soft-shell clam are the blue crab, *Callinectes sapidus*, and demersal fishes (de Goeij et al., 2001; Seitz et al., 2001). Crabs unearth clams from the sediment and consume the entire clam, leading to the easy identification of clams consumed by crabs from the shell damage inflicted (Beal, 2006). Siphon nipping by demersal fish results in shorter clam siphons, causing the clams’ burial depth to decrease, thereby exposing the bivalves to increased predation by probing predators (i.e., crabs) (de Goeij et al., 2001). Predation is a critical regulator of bivalve populations, often serving as the driving force of mortality (Eggleston et al., 1992; Beal et al., 2001; Bourque et al., 2001; de Goeij et al., 2001; Whitlow et al., 2003; Hunt, 2004; Flynn and Smee, 2010).

Despite intense predation pressure, populations of soft-shell clams persist throughout the Chesapeake Bay, especially in sandy habitats (Eggleston et al., 1992; Seitz et al., 2006). Refuge provides bivalve populations the ability to survive in the face of predation pressures and can result from low densities causing lower encounter rates (Seitz et al., 2001), structural protection by substrate (Skilleter, 1994), and increased burial depth (Zaklan and Ydenberg, 1997; Whitlow et al., 2003; Flynn and Smee, 2010). Predator exclusion cages have been used to successfully reduce mortality of bivalves (Flach, 2003; Hunt, 2004; Beal, 2006), indicating that predation has a significant impact on the survival of bivalves.

**Objectives**

The goal of this study is to investigate the influence of predation and substrate type on the survival and growth of *M. arenaria* and density and diversity of other
bivalves in the Lynnhaven river system in the lower Chesapeake Bay. We used three substrate treatments (sand, gravel, and oyster shell) to observe the potential refuge from predators afforded to bivalves by increased substrate structure. We examined the effects of predation on soft-shell clam mortality in three different substrates using predator exclusion techniques at two different locations within the Lynnhaven river system. In addition to examining the survival and growth of soft-shell clams, we examined ambient bivalve density, biomass, and diversity under varying predation, substrate type, and location regimes. We aimed to discern which bivalve species thrive under the environmental conditions present in the Lynnhaven river system. Using soft-shell clam predation and ambient bivalve community information, we sought to identify the causes of diminished *M. arenaria* abundances and assess the potential for restoration of this species to the Lynnhaven River System.

METHODS

*Site Selection*

Three locations in the Lynnhaven River System, Virginia Beach, Virginia, were chosen for the field study: (1) Broad Bay (36°54.204N, 76°03.465W), (2) Linkhorn Bay (36°53.311N, 76°00.859W), and (3) Pleasure House Creek (36°53.836N, 76°06.035W)(Fig. 1). Sites were selected for present physical conditions, including temperature and salinity, and habitats that have historically been conducive to thriving populations of soft-shell clams (Abraham and Dillon, 1986). In addition, these sites were selected for their unique hydrodynamics as predicted in a hydrodynamic model of the Lynnhaven River System, such that a large fraction of larvae spawned at each of our chosen locations will remain in the system to replenish the population (Lipcius et al.,
Survival Study

*Mya arenaria* were collected from flow-through tanks at the Virginia Institute of Marine Science from June 12, 2009, through June 21, 2009. Individuals were held in outdoor flow-through tanks that circulated water from the York River (25-27°C and 21-22‰). Prior to deployment, shells of individuals were dried with a towel, marked with a unique number using permanent markers, and initial length and width were recorded.

Square frames measuring 0.50 m² were constructed of PVC piping (¾” and 1”) and cages were constructed of ¼” galvanized mesh and measured 0.5 m x 0.5 m x 0.25 m with no bottom (Fig. 2). Two substrate treatments, (1) oyster shell and (2) gravel, were prepared for application in plots at the field sites, along with the natural sand substrates present at the locations. Oyster shell was obtained from discarded whole oyster shells at the Virginia Institute of Marine Science. Pea gravel was purchased from a local hardware store.

Plots, consisting of frames, mesh cages, and *M. arenaria* were deployed at shallow depths (1-2 m) on July 7, 2009, and July 8, 2009, at the three locations. At each location (Pleasure House Creek, Linkhorn Bay, Broad Bay), replicate blocks of six plots with pairs of caged and open plots with one of three substrate treatments (sand, gravel, and oyster shell) were established. Substrate treatments were randomly assigned (Fig. 3). Frames were first inserted into the sediment using stakes to secure them for the duration of the study. Substrates were then applied to each plot, providing a loose covering of oyster shell (1250 mL) and gravel (700 mL) to the assigned plots. Sand plots were left
with the ambient substrate type which remained relatively consistent across the three locations.

After applying substrates, six individually marked clams, a moderate density (Seitz et al. 2001), were carefully planted into the sediment with the siphon upwards. The individuals were spaced relatively evenly throughout the plot. Cages were then applied to all plots to allow the clams to acclimate to the plots and burrow into the sediment sufficiently. After the acclimation period, determined to be 24 hours by previous studies (Eggleston et al., 1992; Seitz et al., 2001), the acclimation cages were removed from half of the plots, (the assigned “open” treatment plots) to expose the clams to predators, but cages were left on the “caged” plots for the duration of the experiment.

All original plots remained at Pleasure House Creek and Broad Bay for 48 days from deployment dates until the collection dates: August 24, 2009 and August 25, 2009 respectively. The Linkhorn Bay plots were damaged within the first week of the study, therefore we did not collect or analyze those plots. An additional block of plot replicates was deployed at both Pleasure House Creek and Broad Bay, for a total of twelve additional plots, on July 29, 2009, and July 30, 2009, to compensate for the eliminated replicates and increase the sample size of the study. The additional plots remained at the locations for 28 days from their deployment to the collection dates. Survival data were standardized to proportional mortality per day, assuming that predation was constant across the experimental period, to account for differences in experimental duration among plots.

Suction sampling was used to collect the contents of each plot at the conclusion of the study. A suction pump was used to suction the contents of each plot up to about 40
cm deep in the sediment and contents were filtered into a 1-mm mesh bag. Sediment samples were taken adjacent to each plot to examine the sediment grain size present at each location (due to time limitations, sediment grain-size samples were not processed). All fish, crabs, and snails were returned to the area from which they were collected; the carapace widths of any present blue crabs, a major predator of soft-shell clams (Lucy, 1976; Abraham and Dillon, 1986; Eggleston et al., 1992; Seitz et al., 2001), were recorded. The remaining contents of the mesh bag were then rinsed on a 1-mm sieve, separated into plastic bags, placed on ice immediately, and later stored in freezers at the Virginia Institute of Marine Science for subsequent processing. Processing included sorting samples for marked *M. arenaria*, ambient bivalves, and blue crabs. Marked *M. arenaria* were identified by their number if possible, length was recorded for both live clams and recovered shells if shell was intact, and biomass was obtained for all live individuals collected. Ambient clams were identified to species, length was recorded for each individual, and biomass was obtained for size classes of individuals specific to each species. Carapace width was recorded for any blue crabs, but no adult crabs were found in the samples during processing.

At the midpoint of the study, predators in the area were surveyed to assess predation pressure on the benthic community, especially *Mya arenaria*. Two trawls were conducted at each of the three study locations in the Lynnhaven River System: one trawl with the current and one against the current. Each trawl lasted for two minutes at a constant speed for approximately 100 m. The trawl net was emptied into a fish tote, all predators, primarily fish and crabs, were enumerated, and predators were measured for later analyses.
After collection and processing, all datasets were analyzed for homogeneity of variance and normality; transformations of data were conducted if necessary. Survival (arcsine square root transformed proportional mortality per day) and growth of *M. arenaria* were analyzed using three-way ANOVAs to examine effects of location, substrate treatment, and caging treatment (i.e., predation). Ambient clam abundance was analyzed using a three-way ANOVA to examine effects of location, substrate treatment, and predation. Shannon Diversity Index (log e) was calculated for each plot and a three-way ANOVA was run to compare the effects of location, substrate type, and predation on diversity and biomass of ambient bivalve species.

RESULTS

*Soft-shell Clam Survival*

*Mya arenaria* transplanted at Broad Bay and Pleasure House Creek had an initial size distribution ranging from 13.3-28.3 mm shell length with an average shell length of 18.33 mm (SE ± 0.1629; Fig. 4). At the end of the study, mean total percentage mortality was high at 85.19% (SE ± 4.03) ranging from a minimum of 16.67% to a maximum of 100%. Mean proportional mortality per day was 0.022 d\(^{-1}\) (SE ± 0.001) ranging from a minimum of 0.006 d\(^{-1}\) to a maximum of 0.038 d\(^{-1}\) in each plot.

Analysis of variance was run using the arcsine square-root transformed proportional mortality per day for transplanted *M. arenaria*. There was no significant difference in mean proportional mortality of transplanted *M. arenaria* per day by location (Broad Bay vs. Pleasure House Creek; Fig. 5), or substrate type (sand, gravel, oyster shell; Fig. 6); however caging treatments yielded higher survival than open treatments
(Fig. 7), and this was a significant difference (3-way ANOVA, Table 1). There were no significant interactions among the main factors.

Soft-shell Clam Growth

Surviving clams grew during the course of the experiment, size frequency of recovered clams was composed of larger individuals than those deployed (Fig. 8), and average final shell length for recovered *Mya arenaria* from the transplanting survival study was 29.29 mm (SE ± 0.85) with a minimum length of 19.30 mm and a maximum length of 42.80 mm. Mean growth of surviving *Mya arenaria* was 0.315 mm/day (SE ± 0.027) with the lowest growth rate at 0.171 mm/day and the highest growth rate at 0.498 mm/day, gaining an average of 10.13 mm (SE ± 0.701) of shell length over the course of the experiment (1-2 months). There were no significant differences in growth by location or substrate type and no interactions between these factors. There were higher growth rates of transplanted *M. arenaria* in open plots than in caged treatments, and this difference was marginally significant (Fig. 9; Table 2).

Densities of Ambient Bivalves

Ambient bivalve species collected from plots at the culmination of the field study were identified, measured, and analyzed to characterize the benthic community present at the study locations. Ambient bivalve species collected included *Aligena elevata*, *Tagelus plebeius*, *Gemma gemma*, *Mercenaria mercenaria*, *Mulinia lateralis*, *Macoma mitchelli*, *Anadara ovalis*, *Macoma balthica*, *Ensis directus*, *Mya arenaria*, and *Lyonsia hyalina*. *A. elevata* and *T. plebeius* were the two most abundant species in the study across both locations and all plots (Fig. 10). Of the two most abundant species, *A. elevata* had significantly higher density per square meter at Broad Bay than at Pleasure House Creek.
(Fig. 11: ANOVA: $F_{1, 24} = 31.99$, $P < 0.0005$), and *T. plebeius* had significantly higher density per square meter at Pleasure House Creek than at Broad Bay (Fig. 11: ANOVA: $F_{1, 24} = 24.74$, $P < 0.0005$). Broad Bay had significantly higher overall density of ambient bivalves than Pleasure House Creek (Table 3). There was no significant difference in bivalve density among sand, gravel, and oyster shell substrate treatments (Fig. 12: ANOVA: $F_{2, 31} = 0.40$, $P = 0.676$). Ambient bivalve density was significantly higher in caged plots than in plots left open to predators (Fig. 13: ANOVA: $F_{1, 31} = 12.30$, $P = 0.001$).

Shannon Diversity Indices ($\log_e$) were calculated for each plot in the study. The mean diversity index was 1.177 (SE $\pm 0.052$) with a minimum value of 0.319 and maximum value of 1.721. The highest diversity of ambient clams was observed in plots with gravel substrate, as determined by an ANOVA of the Shannon diversity index by location, substrate treatment, and predator exclusion (Table 4, Fig. 14). Location and predator exclusion did not significantly affect the diversity indices. There was a significantly higher diversity index in gravel substrates than in sand substrates (ANOVA: $F_{2, 31} = 4.06$, $P = 0.027$). Oyster shell substrates did not have a significantly different diversity index from either of the other two substrates.

The majority of the ambient bivalves collected were less than 25 mm in shell length (Fig. 15). Mean shell length for all ambient bivalves was 8.309 mm (SE $\pm 0.301$) with the smallest bivalve size of 1.2 mm (*G. gemma, T. plebeius, and M. mercenaria*) and the largest clam size of 95.80 mm (*M. mercenaria*).
Biomass of Ambient Bivalves

Ash-free dry weight (AFDW) in grams per square meter was calculated for each plot to quantify biomass of ambient bivalves. The average biomass across all plots was 23.33 g AFDW/m² (SE ± 3.69). Average biomass at Broad Bay was significantly higher than average biomass at Pleasure House Creek (Table 5, Fig. 16: ANOVA: F_{2,31} = 7.98, P = 0.008). However, there was no significant influence of substrate type or caging treatment on mean biomass (Table 5).

Predator Survey

Species collected during our predator survey include: silver perch (*Bairdiella chrysura*), spot (*Leiostomus xanthurus*), blue crab (*Callinectes sapidus*), black sea bass (*Centropristis striata*), oyster toad (*Opsanus tau*), pigfish (*Orthopristis chrysoptera*), summer flounder (*Paralichthys dentatus*), pinfish (*Diplodus holbrooki*), diamondback terrapin (*Malaclemys terrapin*), pipefish (*Syngnathus sp.*), bay anchovy (*Anchoa mitchillia*), killifish (*Fundulus sp.*), blennies (*Chasmodes sp.*, *Hypsoblennius sp.*), and gobies (*Gobiosoma sp.*). Many of the predators that prey on mollusks were abundant at both locations (Fig. 17). The most abundant predators across locations were silver perch, spot, and blue crab, but silver perch were only present at Pleasure House Creek.

Environmental Conditions

Temperatures were recorded at the start of the study on July 29, 2009, and July 30, 2009, ranged from 27.0-29.6°C. Temperatures during the course of the experiment were likely higher than those recorded at the beginning. Salinity recorded at the beginning of the study ranged from 18-21 ppt. Sediment samples taken at Pleasure House
Creek exhibited finer sediments than observed at Broad Bay. Sediment samples will be analyzed for grain size in future studies.
DISCUSSION

In this study, the soft-shell clam *Mya arenaria* experienced high rates of mortality in the Lynnhaven River System in comparison to other studies (Seitz et al., 2001). Few individuals survived the duration of the experiment, yet survivors were able to grow. While some transplanted soft-shell clams grew, the greater prevalence of other ambient bivalve species indicates that the Lynnhaven River System may now be more conducive to survival of other bivalves than to survival of the soft-shell clam. Predator-prey interactions between the blue crab, *Callinectes sapidus*, and *M. arenaria* have been suggested to play a significant role in the survival of *M. arenaria* in various habitats (Eggleston et al. 1992) in addition to substrate type (Sponaugle and Lawton, 1990; Skilleter, 1994), clam density (Eggleston et al., 1992; Beal et al., 2001; Seitz et al., 2001), burial depth (Zaklan and Ydenberg, 1997; Flynn and Smee, 2010), extreme weather events (Andrews, 1973), and physical conditions including temperature and salinity (Kennedy and Mihursky, 1971; Abraham and Dillon, 1986). Both predation and environmental conditions likely played a role in mortalities in the Lynnhaven system.

*Mya arenaria*

In previous studies, mortality rates for juveniles are higher than those for adult *M. arenaria* (Brousseau, 1978; Hunt and Mullineaux, 2002), yet mortalities in this study were higher than expected mortality rates (Seitz et al., 2001), even for juvenile soft-shell clams (Ayers, 1956; Brousseau and Baglivo, 1991). Because no difference in mortality rate was observed between our two study locations, we were able to compare the responses to substrate and predator treatments across locations. Despite evidence that substrate plays a significant role in the survival of soft-shell clams (Sponaugle and
Lawton, 1990; Skilleter, 1994), in our study, mortality did not differ by substrate type, indicating that there was no difference in the refuge from predation afforded to *M. arenaria* between the gravel or oyster shell substrate in the Lynnhaven River System. Therefore, among the factors that we investigated, the presence or absence of predators is a significant factor influencing the mortality of the transplanted *M. arenaria*.

Clam mortality rates in plots with cages that eliminated predation by blue crabs were significantly lower than that in plots left open to predation, elucidating the importance of pressures from predators on the survival of the soft-shell clam as examined in previous studies (Eggleston et al., 1992; Beal and Gayle Kraus, 2002). Additionally, demersal fish have been known to consume the exposed end of the soft-shell clam’s siphon, which can reduce the burial depth of the soft-shell clam (de Goeij et al., 2001), thereby reducing the ability of individuals to use increased burial depth as a refuge from predators (Zaklan and Ydenberg, 1997; Whitlow et al., 2003; Flynn and Smee, 2010). Insufficient burial depth caused by this siphon nipping could also have contributed to the increased *M. arenaria* mortality in this study due to predation, as siphon-nipping fish were collected at our locations. Because burial depth increases with shell length (Zaklan and Ydenberg, 1997), the juvenile clams used in this study might not have been able to bury deep enough to escape predators.

Higher predation on juvenile clams explains the significantly higher mortality in the open plots compared to caged plots, yet mortality remained rather high in the caged plots as well, with an average of 74% total mortality at the culmination of the study. These generally high mortality rates across the entire study (all plot types) must be due to an external variable rather than to the variables tested in the study. Temperature is the
most likely cause of the high mortalities observed in this study because temperature is extremely important for survival, growth, and reproduction of the soft-shell clam (Abraham and Dillon, 1986). Moreover, the temperature levels in the Chesapeake Bay have the potential to approach lethal levels (~30°C) for soft-shell clams in the summer months (Lucy, 1976). During the course of this study, temperatures at the study locations were recorded at 29°C in early July, approaching the lethal limit (Kennedy and Mihursky, 1971). In addition, all of the plots were in shallow water, which tends to experience high water temperatures. The Lynnhaven River System is situated near the southern limit of the soft-shell clam’s distribution, therefore as global climate change continues to increase the water temperatures throughout the Chesapeake Bay (Hayhoe et al., 2007), the soft-shell clam could have limited survival in the lower Chesapeake Bay due to the temperatures exceeding inhabitable levels (Glick et al., 2007).

Despite the low recovery rates of marked *M. arenaria*, trends were identifiable among the measured growth rates. Individuals recovered from open plots tended to exhibit higher growth rates than individuals collected from caged plots. In previous studies, exclusion of predators using rigid mesh that is elevated off the sediment, similar to the cages used in this experiment, tends to increase the growth and survival of individual clams (Beal and Gayle Kraus, 2002), therefore it is unlikely that the cages themselves directly caused the trend of lower growth rates in caged plots. It is possible that fouling of cages by various algae could have contributed to lower water flow through the cages, which may have decreased food availability for the transplanted *M. arenaria*, potentially causing the decrease in growth rates, but this hypothesis has not been tested.
Ambient bivalve populations

Few ambient *M. arenaria* were collected from the plots used in this study, yet other bivalve species were recovered in high densities at both locations. The significantly higher densities of *Aligena elevata* and *Tagelus plebeius* at Broad Bay and Pleasure House Creek, respectively, indicate that the environmental conditions in the Lynnhaven River System are conducive to survival of other bivalve species. *Aligena elevata* lives commensally with the polychaete *Clemenella torquata*, residing at the base of the polychaete’s burrow in sandy sediments like those present in Broad Bay (Sanders et al., 1962; Gage, 1968; Lawless, 2008). This lifestyle allows *A. elevata* to survive at depths that it would not normally be found, facilitating increased survival of a small bivalve that would be easily consumed by predators if residing at the surface of the sediment (Gage, 1968). The sandy-mud sediment at Pleasure House Creek is slightly less rigid than the sand substrate at Broad Bay, potentially allowing easier access to shallow-dwelling infauna by predators (Seitz et al., 2001), or reducing densities of the commensal polychaete and explaining the decrease in the presence of *A. elevata*.* T. plebeius* tends to be abundant in sediments composed of sand mixed with silt and clay (Holland and Dean, 1977). Additionally, *T. plebeius* are deep burrowers and are able to escape predators by burrowing deeper into the softer sediments, accounting for their increased densities at Pleasure House Creek where sediments were finer (Holland and Dean, 1977). These bivalve adaptations, commensalism and deep burrowing, that *A. elevata* and *T. plebeius* have acquired are likely what allows them to persist at higher densities than other ambient clam species. Additionally, higher densities of ambient bivalves were found in caged plots as compared to open plots at both locations, demonstrating the significant
influence of predators on the survival of ambient bivalves in Lynnhaven River System, similar to patterns observed for survival of transplanted *Mya arenaria*.

While all ambient species collected during the study were found at both locations, Broad Bay exhibited larger total biomass than Pleasure House Creek. This is potentially due to the higher sand content in the sediment at Broad Bay than the finer sediment found at Pleasure House Creek. The finer sediments could clog a bivalve’s filter-feeding apparatus, preventing effective filtration of the bivalves, which may limit the growth and survival of bivalves. Water flow rates could also be higher at Broad Bay because of the wider expanse of the bay at that location, facilitating greater growth and survival; however, flow rates were not quantified in this study. Despite the greater biomass of ambient bivalves at Broad Bay, diversity of ambient bivalves as established by Shannon indices differed significantly by substrate but not by location. Gravel substrates had significantly higher diversity than sand substrates, while oyster shell substrates were not significantly different from either of the other two treatments. Higher diversity in gravel plots could be indicative of the use of gravel substrate as a refuge from predation (Skilleter, 1994), creating multiple niches for different types of bivalves and protecting a larger diversity of bivalves than oyster shell or sand substrates, which may only enable the persistence of a few well-adapted species. Oyster shell would have been expected to provide some refuge for bivalves also, yet there was no difference between bivalve diversity in oyster shell as compared to the other substrate treatments, potentially due to insufficient volume of oyster shell used for our substrate treatment. In future studies, varied volumes of oyster shell or gravel could be used to induce a more significant response of bivalves to substrate treatment.
**Predator-prey interactions**

Surveys of predators returned numerous species that could potentially impact the bivalve populations in the Lynnhaven River System; the dominant species collected were the silver perch (*Bairdiella chrysura*), spot (*Leiostomus xanthurus*), and blue crab (*Callinectes sapidus*). Silver perch were only collected at Pleasure House Creek, and were therefore not likely to be the main predator influencing survival of bivalves across the Lynnhaven River System (because significant predation on bivalves occurred at both locations). Blue crabs and spot, however, are readily abundant throughout the Chesapeake Bay and are known predators of bivalves, suggesting that these two predators contributed to mortality of local bivalve populations, similar to other systems (Eggleston et al., 1992; de Goeij et al., 2001; Seitz et al., 2001).

**Future Implications for Soft-shell Clams**

As a major commercial species for the Chesapeake Bay and other regions (Abraham and Dillon, 1986; Wheaton et al., 2008), the soft-shell clam necessitates appropriate fishery management and potentially restoration efforts to ensure the continued existence of both the industry and the species. Our assessment of the survival and growth of *M. arenaria* based on location, substrate type, and predator exclusion reveals that a significant effect on the continued decline of soft-shell clam populations in the Lynnhaven River System is predation. Residual effects of the population devastation caused by Tropical Storm Agnes (Andrews, 1973), rising temperatures due to the effects of global climate change (Glick et al., 2007), and intense reduction of soft-shell clam populations by predators, as indicated by the this study, all contribute to loss of soft-shell clams throughout the Chesapeake Bay. Because the interactions of these factors have
dramatic implications for the future of the soft-shell clam in the Chesapeake Bay, the importance of each factor must be carefully considered when approaching the management and restoration of this vital commercial species. Effective protection of the soft-shell clam in habitats with low predator exposure and appropriate temperature ranges could allow for the partial restoration of the species in those areas. Because the Lynnhaven River System experiences intense predation and warmer water temperature, particularly in shallow habitats, any attempts to restore the soft-shell clam to this area through transplanting juveniles, as in this study, would need to improve upon temperature and predation conditions. Despite the unsuitable conditions for soft-shell clam restoration in our study in the Lynnhaven River System, the results presented herein provide valuable information about the influence of predation, substrate type, and fluctuating temperatures on *M. arenaria* survival that can aid in improving restoration efforts in other areas of the Chesapeake Bay and the entire distribution of the soft-shell clam. Future efforts could potentially utilize deeper, cooler-water locations, hardy predator-exclusion cages, or substantial amounts of structural substrate to increase the likelihood of successful restoration and establishment of a resident population of *M. arenaria* in the Lower Chesapeake Bay.
ACKNOWLEDGMENTS

I would first like to thank my advisor, Rochelle Seitz, for welcoming me into her research lab when I was only a sophomore, and for guiding and motivating me through first an REU project and now this honors thesis. I will also be forever grateful to John Swaddle for agreeing to be my Honors Thesis Committee Chair, and then going above and beyond to become a second advisor. Without their unwavering support, endless time, and constant encouragement from the conception of the project to the final presentation, this project would certainly not have been possible. I would also like to thank Randy Chambers and Jonathan Allen for serving on my Honors Committee and for their assistance throughout this process.

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Finally, I would like to thank my family and friends who reminded me to breathe during the past four years and especially throughout this thesis. None of this would have been possible without their constant faith in me.
REFERENCES


Appeldoorn, R.S., 1983. Variation in the growth rate of Mya arenaria and its relationship to the environment as analyzed through principal components analysis and the omega parameter of the von Bertalanffy equation. Fishery Bulletin 81, 75-84.


APPENDIX I: TABLES

Table 1: Analysis of variance of proportional mortality per day of *Mya arenaria* from transplanting survival experiment in the Lynnhaven River System.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caging</td>
<td>1</td>
<td>0.0004303</td>
<td>0.0004303</td>
<td>6.88</td>
<td>0.013*</td>
</tr>
<tr>
<td>Substrate</td>
<td>2</td>
<td>0.0000217</td>
<td>0.0000108</td>
<td>0.17</td>
<td>0.842</td>
</tr>
<tr>
<td>Location</td>
<td>1</td>
<td>0.0000000</td>
<td>0.0000000</td>
<td>0.00</td>
<td>1.000</td>
</tr>
<tr>
<td>Error</td>
<td>31</td>
<td>0.0019381</td>
<td>0.0000625</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>0.0023901</td>
<td></td>
<td></td>
<td></td>
</tr>
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*Notes:* Factors included caging treatment (caged and open), substrate treatment (sand, gravel, and oyster shell), and location (Broad Bay and Pleasure House Creek).

*Significant influence on mortality.

Table 2: Analysis of variance of growth per day of *Mya arenaria* from transplanting survival experiment in the Lynnhaven River System.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>DF</th>
<th>Seq SS</th>
<th>Adj SS</th>
<th>Adj MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caging</td>
<td>1</td>
<td>0.037349</td>
<td>0.037349</td>
<td>0.037349</td>
<td>4.71</td>
<td>0.055</td>
</tr>
<tr>
<td>Substrate</td>
<td>2</td>
<td>0.030324</td>
<td>0.016841</td>
<td>0.008420</td>
<td>1.06</td>
<td>0.382</td>
</tr>
<tr>
<td>Location</td>
<td>1</td>
<td>0.001587</td>
<td>0.000662</td>
<td>0.000662</td>
<td>0.08</td>
<td>0.778</td>
</tr>
<tr>
<td>Error</td>
<td>10</td>
<td>0.079247</td>
<td>0.079247</td>
<td>0.007925</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>14</td>
<td>0.148507</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Notes:* Factors included caging treatment (caged and open), substrate treatment (sand, gravel, and oyster shell), and location (Broad Bay and Pleasure House Creek).

No significant interactions.
Table 3: Analysis of variance of densities of ambient clams per square meter in the Lynnhaven River System.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caging</td>
<td>1</td>
<td>222784</td>
<td>222784</td>
<td>12.30</td>
<td>0.001*</td>
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<tr>
<td>Substrate</td>
<td>2</td>
<td>14353</td>
<td>7176</td>
<td>0.40</td>
<td>0.676</td>
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<tr>
<td>Location</td>
<td>1</td>
<td>104114</td>
<td>104114</td>
<td>5.75</td>
<td>0.023*</td>
</tr>
<tr>
<td>Error</td>
<td>31</td>
<td>561622</td>
<td>18117</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>902873</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Factors included caging treatment (caged and open), substrate treatment (sand, gravel, and oyster shell), and location (Broad Bay and Pleasure House Creek). *Significant influence on density.

Table 4: Analysis of variance of the Shannon Diversity Index for ambient bivalves in the Lynnhaven River System.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
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<tr>
<td>Caging</td>
<td>1</td>
<td>0.05260</td>
<td>0.05260</td>
<td>0.63</td>
<td>0.434</td>
</tr>
<tr>
<td>Substrate</td>
<td>2</td>
<td>0.68048</td>
<td>0.34024</td>
<td>4.06</td>
<td>0.027*</td>
</tr>
<tr>
<td>Location</td>
<td>1</td>
<td>0.03224</td>
<td>0.03224</td>
<td>0.38</td>
<td>0.540</td>
</tr>
<tr>
<td>Error</td>
<td>31</td>
<td>2.59832</td>
<td>0.08382</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>3.36365</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Shannon Index was calculated for each plot based on ambient bivalve species abundance and richness. *Substrate type significantly influenced diversity index.

Table 5: Analysis of variance of Biomass (AFDW/m²) of ambient bivalves in the Lynnhaven River System.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caging</td>
<td>1</td>
<td>24.6</td>
<td>24.6</td>
<td>0.06</td>
<td>0.813</td>
</tr>
<tr>
<td>Substrate</td>
<td>2</td>
<td>392.9</td>
<td>196.4</td>
<td>0.46</td>
<td>0.638</td>
</tr>
<tr>
<td>Location</td>
<td>1</td>
<td>3433.4</td>
<td>3433.4</td>
<td>7.98</td>
<td>0.008*</td>
</tr>
<tr>
<td>Error</td>
<td>31</td>
<td>13335.7</td>
<td>430.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>17186.6</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Ash-free dry weight was measured for each species of clam in each plot. Total biomass per square meter was then calculated. *Significant influence on biomass.
Figure 1: Map of the Chesapeake Bay depicting the location of the Lynnhaven River Study area (black box) and the placement of the study locations (Broad Bay, Pleasure House Creek, and Linkhorn Bay) within the River System.
**Figure 2:** Schematic of the wire mesh cage and PVC frame design. All sides of cage were mesh wire. There was no cage bottom. The frame was constructed to connect two plots of the same substrate. “X” indicates stakes used to secure frames.

**Figure 3:** Experimental set up of plots at Broad Bay and Pleasure House Creek. Replicates 1 and 2 are the original plots and Replicate 3 is the additional plots. White plots represent sand substrate treatments, gray plots represent gravel substrate treatments, and black plots represent oyster shell substrate treatment. Cross-hatching represents caged plots.
Figure 4: Initial size frequency distribution of transplanted *Mya arenaria*.

Figure 5: *Mya arenaria* proportional mortality (d⁻¹) of all substrate and caging treatments at Broad Bay (BB) and Pleasure House Creek (PHC) in the Lynnhaven River System. Bars depict the mean proportional mortality per day. Error bars represent one SE.
Figure 6: *Mya arenaria* proportional mortality (d\(^{-1}\)) of all caging treatments at both study locations in the Lynnhaven River System. Bars depict the mean proportional mortality per day for sand, gravel, and oyster shell treatments. Error bars represent one SE.

Figure 7: Proportional mortality (d\(^{-1}\)) of *Mya arenaria* by caging treatment at study locations in the Lynnhaven River System. Bars depict the mean proportional mortality per day for caged and open plot treatments. Error bars represent one SE.
Figure 8: Final size frequency distribution of recovered *Mya arenaria*.

Figure 9: Transplanted *Mya arenaria* mean growth rate per day, where growth rates in caged plots were marginally lower than in open plots. Error bars represent one SE.
Figure 10: Total abundance of ambient bivalve species across both locations and all plot treatments. The most abundant species were *Tagelus plebeius* and *Aligena elevata*.

Figure 11: Average density per square meter of ambient bivalve species at Pleasure House Creek (PHC) and Broad Bay (BB) from all plots combined. Of the two most abundant species (Fig. 9), *T. plebeius* had significantly higher density at Pleasure House Creek and *A. elevata* had significantly higher density at Broad Bay, as indicated by asterisks.
Figure 12: Density per square meter of ambient bivalve species by substrate treatment: sand, gravel, and oyster shell.
Figure 13: (A) Average density per square meter of ambient bivalve species in caged and open plots at both study locations across all substrate treatments. (B) Average ambient bivalve densities in all caged plots and open plots at both study locations across all substrate treatments.
Figure 14: Mean Shannon Diversity Index by substrate type (sand, gravel, oyster shell).

Figure 15: Size frequency of all collected ambient bivalves by shell length (mm).
Figure 16: Average biomass per square meter of ambient bivalve species by location. Letters indicate a significant difference between biomass at Broad Bay and Pleasure House Creek.

Figure 17: Total abundance of species surveyed that are predators of bivalves at Broad Bay (BB) and Pleasure House Creek (PHC) in the Lynnhaven River.