2010

Exploring the Potential for Bay Scallop Restoration in the Lynnhaven River Sub-Estuary of Chesapeake Bay

Ana Liza Hernandez Cordero
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Exploring the Potential for Bay Scallop, *Argopecten irradians concentricus*, Restoration in the Lynnhaven River Sub-estuary of Chesapeake Bay

A Thesis
Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science

by
Ana Liza Hernández Cordero
2010
APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Science

Ana L. Hernández Cordero

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DEDICATION

This thesis is dedicated to my beloved parents, L. Roberto Hernández Hernández and Lorena Cordero Hernández. My success is as much theirs as it is mine. Without their sacrifices, unconditional love, support, strength, and prayers, this achievement would have never become a reality. My father has pushed me and has never let me give up from the time I learned how to read. My mother has shown me love like only a mother can. Her wise words have helped shape me into the person I have become. My parents are my inspiration and I owe them everything. Los amo.
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ABSTRACT

Until the 1930s, bay scallop populations persisted in the seaside lagoons of Chesapeake Bay. Their decline is attributed to overexploitation, habitat loss, degraded water quality, and recruitment limitations. Individual bay scallops still exist in the lower Bay, though no restoration efforts have been attempted. This study was designed to examine the survival and growth of transplanted southern bay scallops, *Argopecten irradians concentricus*, within the Lynnhaven River sub-estuary. Scallop survival was significantly higher in *Zostera marina* (97.8 %) and *Gracilaria* spp. (90.0 %) than in rubble and oyster shell. Scallop growth differed significantly by location (0.76-1.22 mm/week), though not by substrate type.

We used a mesocosm experiment to assess the survival of several scallop size classes as a function of female blue crab, *Callinectes sapidus*, predation as it varied by habitat type (oyster shell, sand, macroalgae) and predator size (>140 mm, ≤140 mm carapace width). Scallop survival was significantly lower in the large predator treatment (F = 11.67, p = 0.001), and significantly higher in the oyster shell treatment than in the other substrates (F = 3.29, p = 0.044).

We also conducted a small-scale tethering experiment designed to assess the effects of predation on juvenile scallops (< 30 mm SH) in the field. We observed a significant effect of location (two-way ANOVA: F = 3.71, p = 0.020), which also emerged as the strongest predictor of survival (using Akaike’s Information Criterion; AIC). In a large-scale field tethering experiment, we detected a significant interaction between location and habitat (GLM, F = 5.79, p < 0.001), and the model including the interaction term emerged as the strongest predictor of scallop survival (AIC).

Based on our results, we conclude that bay scallops are able to survive and grow in the absence of predators in the Lynnhaven River. Scallop seed planting in structured substrates, such as oyster shell and *Gracilaria* spp., that offer protection against predation, will likely increase the potential for establishment of bay scallop populations. With the results presented herein, we are encouraged that scallop restoration within Chesapeake Bay is feasible.
CHAPTER 1

Substrate effects on the survival and growth of the Bay Scallop, *Argopecten irradians concentricus* (Say 1822), in the Lynnhaven River, Virginia
ABSTRACT

Populations of bay scallops (*Argopecten irradians*) persisted in the seaside lagoons of Chesapeake Bay until the 1930s, after which they experienced dramatic declines. Efforts to re-establish bay scallop populations in the seaside lagoons of the Chesapeake Bay have been initiated, but no restoration efforts on the bayside have been attempted. In recent years, low and sporadic abundances of bay scallops have been observed in the lower bayside areas of the Chesapeake Bay. This study was designed to examine the survival and growth of the southern bay scallop, *Argopecten irradians concentricus*, in different vegetated and non-vegetated substrates in the Lynnhaven River sub-estuary of the Chesapeake Bay, Virginia, while considering the feasibility for bay scallop re-establishment. Manipulative field experiments were conducted over six weeks, and we evaluated the survival and size increase of transplanted, caged adult scallops in various substrate types (*Zostera marina* L., *Gracilaria* spp., oyster shell, and rubble) at three locations (Linkhorn Bay, Broad Bay, Pleasure House Creek) within the Lynnhaven River system. After 3 weeks, there was a significant difference in scallop survival among substrates (two-way ANOVA); it was highest in the *Z. marina* habitat, followed by *Gracilaria* spp., averaging 97.8 % and 90.0 %, respectively, and survival in rubble and oyster shell was lowest. Cumulative scallop size increase differed significantly by location, though not substrate type, where it was significantly greater at Pleasure House Creek (1.22 mm/week) and Broad Bay (1.09 mm/week) than at Linkhorn Bay (0.76 mm/week). Our examination of bay scallop survival and size increase of transplanted adult scallops into the Lynnhaven River revealed that they are still able to survive and grow in the absence of predators. With the results presented herein we are encouraged that scallop restoration within Chesapeake Bay is feasible.
INTRODUCTION

1.1 Current Status of the Bay Scallop

The current state of global fisheries has prompted worldwide interest in the preservation, restoration, and conservation of commercially and recreationally important species. In the case of the Chesapeake Bay blue crab fishery, baywide reductions from 1992 to 2000 were estimated to be approximately 70% as compared to the previous decade (Lipcius and Stockhausen 2002). The case of the blue crab fishery is representative of the greater trend observed in all of the northeastern U.S. near-shore fisheries, with U.S. near-shore fisheries being defined by the National Marine Fisheries Service (NMFS; 1999) to be “those coastal and estuarine species found in the 0-3 nautical mile zone of the coastal state waters.”

The bay scallop, *Argopecten irradians*, fishery is no exception to the global trends towards decline. The bay scallop is particularly sensitive to environmental perturbations and has suffered tremendous losses in population abundances; the cause of the decline is a product of the synergistic interaction of multiple stressors including: habitat degradation, overharvesting, and harmful algal blooms (NMFS 1999, Greenawalt-Boswell et al. 2007). However, beginning in the 1930s, the loss of essential habitat for the bay scallop in the Virginia coastal bays is recognized as one the leading contributors to their population decline (Orth et al. 2006, Orth et al. 2010). In recent years, low and sporadic abundances of bay scallops have been observed in the lower bayside areas of the Chesapeake Bay (P. Freeman, pers. comm.), even though their primary habitat, *Zostera marina* L. (Belding 1910, Thayer and Stuart 1974, Garcia-Esquivel and Bricelj 1993,
Irlandi et al. 1999), has been absent since the 1930s (Orth and Moore 1984, Fonseca and Uhrin 2009).

Seagrass beds, particularly those consisting of eelgrass (*Zostera marina* L.), serve as the optimal nursery habitat, in part because they provide significant refuge from benthic predators (Ambrose and Irlandi 1992, Pohle et al. 1991) as well as protection from siltation associated with the bottom (Castagna 1975, Thayer and Stuart 1974). In spite of this, bay scallops have also been abundant in natural habitats devoid of eelgrass (Marshall 1947, Marshall 1960) and are known to attach to other substrates, such as small branching algal species, shells, rocks, or sessile animals (Ingersoll 1886, Marshall 1960, Thayer and Stuart 1974, Smith et al. 1988). Preference for structured habitats may be a function of size. In a previous mesocosm experiment, young bay scallops (<15 mm SH) equally preferred cobble, algal, and eelgrass habitats, all of which were selected over sand habitats; however, older bay scallops (> 25 mm SH) had no preference among cobble, algal, eelgrass, and sand habitats (Chintala et al. 2005).

With the current fluctuations in seagrass, we should consider the use of alternative substrates for the establishment of bay scallops. This study was designed to assess the survival and growth of transplanted southern adult bay scallops, *Argopecten irradians concentricus*, in the Lynnhaven River sub-estuary of the Chesapeake Bay. Specifically, we sought to (1) assess the effect of habitat quality upon the scallop’s growth and survival by using various substrates (i.e. eelgrass, macroalgae, oyster shell, and rubble) and, (2) to assess the spatial variation in scallop growth and survival by replicating enclosures at three locations (Broad Bay, Linkhorn Bay, and Pleasure House Creek).
1.2 Distribution and Fishery

Three subspecies of *Argopecten irradians* are commonly distinguished according to geographical distribution (Fay et al. 1983) and shell morphology (Clarke 1965, Waller 1969). These subspecies include: (1) *A.i. irradians* extending from Cape Cod to the mid-Atlantic region, (2) *A.i. concentricus* extending from the mid-Atlantic region to the Atlantic coast of Florida, and (3) *A.i. amplicostatus*, which extends farther into the Gulf of Mexico (Clarke 1965, Wilbur and Gaffney 1997).

Bay scallops have long supported commercial and recreational fisheries (Fay et al. 1983, Greenawalt-Boswell et al. 2007) dating as far back as 1858 (Ingersoll 1886). Beginning in the 1930s, significant decreases in bay scallop abundances along the eastern coast of the U.S. were observed in conjunction with the decimation of eelgrass beds (McHugh 1989, Dreyer and Castle 1941) resulting from eelgrass-wasting disease, eutrophication, and damage from the Storm King hurricane (Renn 1936, Castagna and Duggan 1971, Arnold et al. 1998, Goldberg et al. 2000, R. Lipcius, unpublished data). Recent declines in harvests may be attributed to recruitment limitation (Peterson and Summerson 1992, Peterson et al. 1996), which has been exacerbated by overharvesting, degraded water quality, habitat loss, coastal development, and the occurrence of harmful algal blooms (Arnold et al. 1998, Marelli et al. 1999, NMFS 1999, Arnold 2001, Tettelbach et al. 2002, Fegley et al. 2009).

1.3 Life History

*A.i. concentricus*, the subspecies of focus in this study, is a simultaneous protandrous hermaphrodite that fully matures and spawns at approximately one year of
age (Fay et al. 1983, Minchin 2003, Blake and Shumway 2006). During the course of its life, the southern bay scallop undergoes a single primary spawning event, which commences during the late fall in conjunction with decreasing water temperature (Gutsell 1930, Sastry 1963, Barber and Blake 1983, Arnold et al. 2005, Blake and Shumway 2006). However, in North Carolina, scallop undergo two spawning events, one in the spring and one in the fall, though it is predominately the fall spawn that survives to maturity (Bishop et al. 2006). Furthermore, a successful spawning event is also linked to the availability of an adequate food supply prior to and during gonad growth and development, which is essential for invoking oocyte growth (Sastry 1966, Sastry and Blake 1971).

*A. i. concentricus* exhibits planktotrophic development (Arnold et al. 1998, Cragg 2006) and its larval stage lasts about two weeks (Sastry 1965). During this stage, the distribution and eventual recruitment is determined primarily by the hydrodynamics of the estuary (Eckman 1987). Larvae metamorphose into juveniles (≥ 190 μm), a stage that is characterized by the appearance of the post-veliger dissonconch shell (Fay et al. 1983). The prodissococonchs settle onto a suitable substrate, typically attaching to seagrass blades, until they reach approximately 30 mm shell height (SH), at which point they unattach from the substrate, settle to the bottom and mature. Growth during the winter months is slow (Blake and Shumway 2006) and likely a function of decreased metabolism and food availability during these months. However, by the early spring 20-25 mm SH scallops can be found on suitable substrates (Barber and Blake 1983). By summer and early winter scallops reach > 50 mm SH. The average longevity of a bay
scallop is 12 to 18 months (Fay et al. 1983, Peterson and Summerson 1992), though in rare cases up to 26 to 30 months (Belding 1910).

1.4 Preferred Habitat

As its name implies, the bay scallop commonly exists in protected coastal bays, sounds, estuaries, and the inshore sides of barrier islands (Brand 2006). Within these areas, the populations are frequently found in association with submerged aquatic vegetation, which makes up their primary habitat (Belding 1910, Thayer and Stuart 1974, Garcia-Esquivel and Bricelj 1993, Irlandi et al. 1999). It is generally maintained that bay scallop larvae and young juveniles require structured nursery habitats for an increased chance of survival (Ingersoll 1886, Fay et al. 1983).

1.5 Restoration Efforts

Due to the declines of scallop abundances, efforts to restore populations have been made, particularly in the coastal waters of Florida (Arnold et al. 2005). Studies on the rearing of bay scallops in hatcheries and nurseries for natural population enhancements have also been conducted (Castagna and Duggan 1971, Castagna 1975, Widman and Rhodes 1991). Aquaculture of the bay scallop has been successful in China, where broodstock was introduced from the United States. Scallop production from Chinese aquaculture is high and exceeded 50,000 tons live weight in 1988 (Guo et al. 1999).

Locally, efforts to re-establish bay scallop populations in the seaside lagoons of the Chesapeake Bay have been initiated via experiments designed to inform upcoming restoration efforts (M. Luckenbach, pers. comm.). On the bayside of Chesapeake Bay
there has been no attempt at restoration, though in recent years, low and sporadic
abundances of bay scallops have been observed in the lower bayside areas of the
Chesapeake Bay (P. Freeman, pers. comm.).
MATERIALS AND METHODS

2.1 Scallop Collection and Transplantation

Scallops ranging from 27.7 to 54.6 mm SH were collected from the Middle Marsh in Back Sound near Beaufort, North Carolina, USA (34°41.940 N, 76°35.741 W; Fig. 1), and were transported in moist burlap sacks in coolers with ice packs to the Virginia Institute of Marine Science (VIMS), in Gloucester Point, Virginia, USA (37°14.891 N, 76°30.030 W). The transportation method was chosen based on results from Peterson et al. (1996), which indicated that handling mortality was greatly reduced using this method. In North Carolina, scallops were collected in highly saline water (32 psu). Upon arrival, the scallops were gradually adjusted to local salinities of approximately 20 psu. Salinities were dropped at a rate of about 2 psu per day. Once the scallops had adapted to local salinities, they were translocated to enclosures at our three study locations in the Lynnhaven River system.

2.2 Site Selection

The Lynnhaven River system is the southern-most system in Chesapeake Bay, located within the City of Virginia Beach, Virginia. It consists of four main water bodies: Broad Bay, Linkhorn Bay, and the Eastern and Western Branches. This study was conducted at three sites: Broad Bay, Linkhorn Bay, and Pleasure House Creek (Fig. 2). These locations were chosen based on the following criteria: (1) seagrass beds existed historically, (2) environmental conditions appeared suitable for bay scallop growth and survival, and (3) hydrodynamic conditions were predicted to be retentive of larvae, as indicated by a hydrodynamic model of the Lynnhaven River system. In the model, a large
fraction of oyster larvae spawned in the system, and particularly those larvae spawned in Broad Bay, Linkhorn Bay, and Pleasure House Creek were likely to remain in the system and provide larval replenishment to new populations (Lipcius et al. 2008). In contrast, larvae spawned at other locations in the Lynnhaven River system were more likely to be advected from the system and were not likely to subsidize the oyster metapopulation.

2.3 Experimental Design, Technical Approach, & Statistical Analyses

Manipulative field experiments using predator-exclusive enclosures were conducted at the three locations. Enclosures were constructed using thirty-two-gallon, cylindrical, Rubbermaid Brute plastic containers, with one container enveloped within another. Six equally spaced 12.7 cm x 35.6 cm sections were cut out and removed along the sides of both the outer and inner containers and replaced with 0.64 cm mesh to allow for water flow through the enclosures. In addition, a 30 cm in diameter, circular mesh panel was created on the lid to maximize light penetration into the enclosures (Fig. 3).

Each individual enclosure was randomly assigned one of four substrate treatments: *Zostera marina* L., *Gracilaria* spp., oyster shell, or rubble. At the time of deployment, there were no known existing seagrass beds within the Lynnhaven River system. Therefore, eelgrass was collected at Allen’s Island in the York River and was transplanted to the enclosures. *Gracilaria* spp., a branching macroalgae that is abundant in Lynnhaven, was collected on site and translocated to the enclosures. Oyster shell and rubble were also acquired from Lynnhaven and placed within randomly assigned enclosures.
At each location, there were three blocks of four enclosures (one enclosure with each substrate treatment), for a total of 36 enclosures. All enclosures were deployed within the shallow sub-tidal zone such that water depth ranged from 1-2 m, and the lids of the enclosures were slightly exposed at low tide. The blocks were placed approximately 80 m apart, and within each block, enclosures were spaced approximately 3 m apart from one another (Fig. 4). In addition, three replicates of two sets of controls, an environmental and a handling control, were established in Middle Marsh, North Carolina, and maintained for the duration of the experiment.

Adult scallops were placed in enclosures at natural densities. Natural densities of approximately 25/m² were inferred from published studies (Cooper and Marshall 1963, Duggan 1973, Castagna 1975, Peterson et al. 1996), and our own field observations in North Carolina. Consequently, scallops were transferred to enclosures (0.25 m²) at 10 adult scallops per enclosure and were divided into two subgroups: (1) five scallops 30-40 mm SH and (2) five scallops 41-50 mm SH. The control enclosures in North Carolina were also populated with 10 scallops per enclosure, five from each subgroup.

In Lynnhaven, scallops were deployed on 27 June 2008 and survival and size increase were monitored weekly from 3 July 2008 to 7 August 2008 by quantifying dead scallops and measuring both height and width of every scallop. Only those data collected through 17 July 2008 were used for analysis due to heavy cage fouling at the Linkhorn Bay site after this date, which precluded accurate interpretation of the results. Scallops were not individually marked, thus it was not possible to determine individual growth rates; however, we were able to estimate mean growth of scallops for each enclosure.
Water quality parameters (dissolved oxygen, temperature, and salinity) were also observed weekly. The enclosures in Lynnhaven were scrubbed weekly to reduce fouling and to ensure that adequate water flow was maintained within each enclosure. In North Carolina controls, scallop survival was determined after 13 weeks (17 June 2008 to 18 September 2008). In North Carolina, enclosures were scrubbed periodically. Several scallops that remained at the end of the experiment were left in Lynnhaven over the winter to determine whether they could survive the winter.

Akaike’s Information Criterion (AIC), which allows for the comparison of multiple working hypotheses, was used to better ascertain which factor or factors had the most influence on survival and size increase (Anderson 2008). Location, substrate, and habitat type were all hypothesized to have an effect. Overall, five hypotheses (models) were derived and analyzed using binary logistic regressions in the case of survival, and least-squares regressions for growth. From these analyses, we used the parameter estimates from each corresponding model to calculate the AIC values associated with each model, which represented a different combination of variables that described the observed differences in survival and size increase (Table 1). Using AIC, in cases involving small sample sizes, a second-order bias AIC correction (AICc) calculation is necessary. For survival, AICc values were calculated for each of our five models using the log-likelihood values obtained from the corresponding binary logistic regression using the following equation:

\[
AICc = -2 \log(L(\hat{\theta})) + 2k + \frac{2k(k + 1)}{n - k - 1}
\]
where \(-2\log(L(\hat{\theta}))\) is equal to the log of the maximum likelihood value obtained from the binary logistic regressions, \(k\) is the number of estimable parameters in the approximating model, and \(n\) is the sample size. For growth, AICc values were calculated for each of our five models using the residual sum of squares (RSS) obtained from the corresponding least-squares regressions using the following equation:

\[
AICc = n \times \ln(\hat{\sigma}^2) + 2k + \frac{2k(k + 1)}{n - k - 1}
\]

where \(\ln(\hat{\sigma}^2)\) is equal to the residual sum of squares (RSS) divided by the sample size \(n\) and \(k\) is the number of estimable parameters in the approximating model. \(\Delta AICc\) values were calculated for each model to rank the various models from most probable to least (i.e., low to high AIC values) using the following equation:

\[
\Delta AICc = AICc_i - AICc_{\text{min}}
\]

where \(AICc_i\) are the values for each of the \(i\) models and \(AICc_{\text{min}}\) is the lowest AICc value of all the models. In calculating these values, the best model is defined as having \(\Delta AICc = 0\). Model probabilities \((w_i)\), which indicate the relative probability that the model is the best among the whole set of candidate models, were calculated for each model using the following equation:

\[
w_i = \frac{e^{-\frac{1}{2} \Delta_i}}{\sum_{r=1}^{R} e^{-\frac{1}{2} \Delta_r}}
\]
where $\Delta_i$ is equal to the $\Delta AICc$ values calculated in the previous equation and $R$ is the number of models in the pool of candidate models. The model probabilities, also known as Akaike weights, sum to one and can be used to directly compare the weight of evidence for one model over another.

Additionally, survival and size increase at three weeks of exposure were analyzed using two-way ANOVAs to determine the magnitude of the main effects of location and/or substrate type. A Student-Neuman-Keuls (SNK) post-hoc comparison test was used to determine where the differences occurred.
RESULTS

3.1 Survival

Substrate and habitat type (vegetated vs. unvegetated) had the greatest influence on scallop survival, as indicated by the AICc model comparison, where models $g_2$ (substrate type alone) and $g_5$ (habitat type alone; Table 1), emerged as the best-fit models with model probabilities of 0.32 and 0.30, respectively (Table 2). In general, models with $w_j \geq 0.20$ were considered likely models (Anderson 2008).

After three weeks, survival of caged scallops differed significantly by substrate treatment, though there was no significant difference among locations, and there was no significant interaction between these two variables (two-way ANOVA: Table 3). Survival was highest in the *Z. marina* habitat, followed by *Gracilaria* spp., averaging 97.8 % and 90.0 %, respectively (Fig. 5). There was significantly higher survival in the *Z. marina* treatment as compared to the rubble and oyster shell treatments (SNK, $p \leq 0.009$), though not compared to the *Gracilaria* spp. treatment (SNK $p = 0.107$; Fig. 5). A similar response in survival according to habitat type, defined as vegetated (*Gracilaria* spp. and *Z. marina*) and non-vegetated (rubble and oyster shell), was observed. For the two scallop size classes examined, there was a significant difference in survival by substrate, though not by location, and there were no significant interactions between the two or among the three variables (three-way ANOVA, Table 4). Salinity and temperature were similar among the three locations and overall averaged 22.1‰ and 27.5°C, respectively.

No general caging or environmental effects were observed in the control cages in North Carolina—most of the scallops survived except in two cages with extenuating
circumstances. Moreover, some enclosures contained more than the initial 10 scallops, indicating that enclosures had acquired recruits. Two of the six enclosures, however, had nearly 100 % mortality of the scallops; one of these enclosures was heavily fouled, had low water-flow, and was hypoxic, while the other enclosure experienced high predation on scallops as indicated by seven large predators that were found inside. A large break in the mesh had allowed three >100 mm carapace-length rock crabs and four very large oyster toadfish to enter the enclosure and prey on the scallops, as evidenced by shattered scallop shell fragments along the bottom of the enclosure.

3.2 Size Increase

Location was the primary factor influencing the rate of scallop size increase, as model g₄, including only location, was the best model and had strong support with a probability of 0.71 (AIC; Table 5). Location and vegetation type were also important to scallop size increase, as model g₃, including those variables had a probability of 0.24.

Cumulative scallop size increase differed significantly by location, though not substrate type, and there was no significant interaction of the two variables (two-way ANOVA: Table 6). Scallop size increase was significantly higher at Pleasure House Creek (1.22 mm/week) and Broad Bay (1.09 mm/week) than at Linkhorn Bay (0.76 mm/week; SNK test, p < 0.001; Fig 6).
DISCUSSION

The bay scallop was able to survive and grow in the Lynnhaven River tributary of the Chesapeake Bay and there were some differences according to habitat and location. Differences in adult scallop survival were apparent only among habitat substrate treatments and not locations. Overall survival was high, with highest survival in *Z. marina* (97.8 %), closely followed by that in the macroalgae *Gracilaria* spp. (90.0 %). Conversely, survival was lowest in the unvegetated habitats rubble (75.6 %) and oyster shell (78.9 %).

Numerous studies have been conducted under the well-established notion that eelgrass is the bay scallops’ preferred habitat (Pohle et al. 1991, Ambrose and Irlandi 1992, García-Esquível and Bricelj 1993, Irlandi et al. 1995, Bologna and Heck 1999, Irlandi et al. 1999). Although previous work has recognized the scallop’s ability to utilize a variety of substrates (Ingersoll 1886, Marshall 1947, Marshall 1960, Thayer and Stuart 1974), few have examined the direct effects of various substrates on bay scallop survival (Carroll et al. 2010) or growth, or effects on other scallop species (Bourgeois et al. 2006, Pacheco and Stotz 2006). Our findings resemble those from mesocosm experiments with bay scallops where habitat preferences were seen in juvenile scallops; however, differences were not seen in adult bay scallops; there was no significant difference in habitat preference among sand, cobble, eelgrass, and *Codium* (macroalgae) treatments for > 25 mm SH scallops (Chintala et al. 2005). Although in our study we did not focus on habitat preference by size class, rather habitat effects on survival, we found significant
differences in survival according to substrate treatments, which may have been driven by the smaller size class.

Our high survival of bay scallops in the *Gracilaria* spp. treatment, with survival similar to that in *Z. marina*, suggests that this substrate may provide similar ecological benefits to scallops as *Z. marina*. Eelgrass is thought to be a more important habitat for juvenile and larval stages of the bay scallop than for the adult phase; it provides an elevated surface for the larvae to attach and escape predators and sediment burial (Thayer and Stuart 1974, Castagna 1975). We suggest that for adult scallops, eelgrass as well as macroalgae serve as an important habitat for scallops, by not only providing a refuge from predators, as a result of the heterogeneous and protective nature of structured habitats, but also because of effects on food delivery for these suspension feeders. We suggest that *Gracilaria* spp. may provide the bay scallop with similar ecological benefits as eelgrass as a result of its large size, complex structure, and adaptability to environmental stressors (Thomsen et al. 2009). Increased rates of scallop survival in vegetated habitats were confirmed by the AIC model results, which indicated that both substrate type and its nature (vegetated vs. non-vegetated) were the most probable explanatory variables for the observed trends in scallop survival.

Eelgrass meadows are recognized as enhancing food resources for numerous benthic invertebrates (Orth 1973, Stoner 1980, Orth et al. 1984), including scallops, because they are able to alter the surrounding physical environment and create a depositional pool of organic matter, which becomes available to filter-feeding organisms for growth and survival (Eckman 1987, Cahalan et al. 1989). In addition, increased
survival in vegetated habitats may arise from the complex structure serving to elevate the scallops off of the bottom enough to avoid clogging of gills with suspended sediment.

Our translocated scallops appeared to grow well in the Lynnhaven River system, with mean scallop size increases of 0.76 to 1.22 mm/week. Unlike survival, differences in relative size increases did not appear to be a function of habitat treatment, but rather location. Growth was significantly lower at Linkhorn Bay (0.76 mm/week) than at Pleasure House Creek (1.22 mm/week) and Broad Bay (1.09 mm/week). Furthermore, AIC model results suggested that location was the primary variable influencing scallop size increase in addition to habitat type (vegetated vs. non-vegetated) also influenced size increase.

We hypothesize that the observed differences in size increase by location were related to changes in water flow among sites, as water flow has been documented to affect scallop growth (Kirby-Smith 1972, Eckman 1987, Cahalan et al. 1989, Eckman et al. 1989, Arsenault et al. 1997). Water velocity was not specifically quantified for any of the locations; however, we observed differences in water flow as well as differences in fouling of the mesh on cages in the field during scallop monitoring. Linkhorn Bay had low and inadequate water flow, allowed development of fouling organisms on cage mesh, and consequently was not capable of sustaining normal scallop growth rates. Without sufficient water flow, there would be insufficient delivery of food to these suspension feeders as well as a decreased rate of water exchange (Kirby-Smith 1972). It is possible that slightly lower growth rates at the Broad Bay location, as compared to those in Pleasure House Creek, may be attributed to its characteristic strong current conditions,
which may have adverse affects on scallop growth when optimal feeding current velocities are exceeded (Bricelj and Shumway 1991, Wildish and Saulnier 1993, Bourgeois et al. 2006). Pleasure House Creek tends to have high currents, which apparently supported scallop growth while not inhibiting it.

Our examination of bay scallop survival and size increase of transplanted adult scallops into an environment that once supported sustainable populations of this species revealed that they are still able to survive and grow in the absence of predators. Initial concerns revolving around the salinity barrier the scallops would have to overcome, as well as questions regarding scallop survival in the absence of seagrass, were addressed and neither issue appeared to be a barrier to successful scallop restoration. The notion that bay scallops can successfully survive and grow in alternative habitats, such as macroalgae, gives promise to the idea of restoring bay scallop populations in the Lynnhaven River sub-estuary, where seagrass is currently negligible; however, this would require taking into account the physiological, hydrodynamic, and environmental aspects of various locations. Other potential deterrents, such as predation pressure and recruitment limitation, which are known to affect the success of restoration and enhancement, must be taken into consideration when further exploring the potential for bay scallop restoration. The next step in assessing the feasibility of scallop restoration within Chesapeake Bay, in locations devoid of seagrass, will involve a quantitative assessment of predation on scallops in various available substrates. Ongoing studies on predator-prey interactions between blue crabs and bay scallops (Hernández Cordero et al., in prep.), both in the field and in the laboratory, will shed light on these issues. With
the results presented herein documenting survival and growth of caged scallops in the Lynnhaven River system, we are encouraged that scallop restoration within Chesapeake Bay is feasible.
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larval stages of the bay scallop, *Aequipecten irradians concentricus* Say, reared in


Sastry, A.N., Blake, N.J. 1971. Regulation of gonad development in the bay scallop,

versus recently transplanted eelgrass, *Zostera marina*, for the bay scallop,

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and ecological role of the non-native macroalga *Gracilaria vermiculophylla* in

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with emphasis on the tertiary and quaternary species of eastern North America.


Wilbur, A.E., Gaffney, P.M. 1997. A genetic basis for geographic variation in shell
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105.

82.
Table 1. The five models \((g_i)\) developed to describe the observed difference in scallop survival. If a \(\beta\) is present in a particular column, then that variable was included in that model. Number of parameters in each model is denoted by \(k\).

<table>
<thead>
<tr>
<th>Model Parameters ((g))</th>
<th>(\beta_0)</th>
<th>(\beta_1)</th>
<th>(\beta_2)</th>
<th>(\beta_3)</th>
<th>(\beta_4)</th>
<th>(\beta_5)</th>
<th>(\beta_6)</th>
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<tr>
<td>((Z) &amp; (LB))</td>
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<td>(\beta_2)</td>
<td>(\beta_3)</td>
<td>(\beta_4)</td>
<td>(\beta_5)</td>
<td>(\beta_6)</td>
</tr>
<tr>
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<td>(\beta_2)</td>
<td>(\beta_3)</td>
<td>(\beta_4)</td>
<td>(\beta_5)</td>
<td>(\beta_6)</td>
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</tr>
<tr>
<td>(\beta_0)</td>
<td>(\beta_1)</td>
<td>(\beta_2)</td>
<td>(\beta_3)</td>
<td>(\beta_4)</td>
<td>(\beta_5)</td>
<td>(\beta_6)</td>
<td></td>
</tr>
<tr>
<td>(\beta_0)</td>
<td>(\beta_1)</td>
<td>(\beta_2)</td>
<td>(\beta_3)</td>
<td>(\beta_4)</td>
<td>(\beta_5)</td>
<td>(\beta_6)</td>
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<tr>
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<td>(\beta_3)</td>
<td>(\beta_4)</td>
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<td>(\beta_6)</td>
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Table 2. Results from AICc calculations, in descending order, for scallop survival based on the models designed to describe the observed differences in survival (see table 1).

<table>
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<tr>
<th>Model</th>
<th>Log-Likelihood</th>
<th>K</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>wi</th>
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<tr>
<td>$g_2$</td>
<td>-135.29</td>
<td>5</td>
<td>282.58</td>
<td>0.00</td>
<td>0.32</td>
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<tr>
<td>(Substrate)</td>
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<td></td>
</tr>
<tr>
<td>$g_5$</td>
<td>-137.99</td>
<td>3</td>
<td>282.72</td>
<td>0.14</td>
<td>0.30</td>
</tr>
<tr>
<td>(Veg)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$g_1$</td>
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<td>7</td>
<td>283.63</td>
<td>1.05</td>
<td>0.19</td>
</tr>
<tr>
<td>(Global)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$g_3$</td>
<td>-135.84</td>
<td>5</td>
<td>283.68</td>
<td>1.10</td>
<td>0.19</td>
</tr>
<tr>
<td>(Location)</td>
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<td></td>
</tr>
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<td>$g_4$</td>
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<td>4</td>
<td>303.71</td>
<td>21.13</td>
<td>0.00</td>
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<tr>
<td>(Loc &amp; Veg)</td>
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Table 3. Analysis of variance for scallop survival (arcsine-transformed) by two factors: (I) substrate treatment, and (II) location.

<table>
<thead>
<tr>
<th>Source</th>
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<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
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<td>Location</td>
<td>2</td>
<td>0.226</td>
<td>0.113</td>
<td>1.14</td>
<td>0.337</td>
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<tr>
<td>Substrate</td>
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<td>1.763</td>
<td>0.588</td>
<td>5.93</td>
<td>0.004</td>
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<td>0.902</td>
<td>0.150</td>
<td>1.52</td>
<td>0.215</td>
</tr>
<tr>
<td>Error</td>
<td>24</td>
<td>2.380</td>
<td>0.099</td>
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<td></td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>5.270</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Analysis of variance for scallop survival by three factors: (I) size class, (II) substrate treatment, and (III) location.

<table>
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<tr>
<th>Source</th>
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<th>MS</th>
<th>F</th>
<th>p</th>
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</thead>
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<tr>
<td>Size class (SC)</td>
<td>1</td>
<td>1.149</td>
<td>1.149</td>
<td>8.26</td>
<td>0.006</td>
</tr>
<tr>
<td>Location (Loc)</td>
<td>2</td>
<td>0.342</td>
<td>0.171</td>
<td>1.23</td>
<td>0.302</td>
</tr>
<tr>
<td>SC * Loc</td>
<td>2</td>
<td>0.137</td>
<td>0.069</td>
<td>0.49</td>
<td>0.614</td>
</tr>
<tr>
<td>Substrate (Sub)</td>
<td>3</td>
<td>2.742</td>
<td>0.914</td>
<td>6.57</td>
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<tr>
<td>SC * Sub</td>
<td>3</td>
<td>0.615</td>
<td>0.205</td>
<td>1.47</td>
<td>0.234</td>
</tr>
<tr>
<td>Loc * Sub</td>
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<td>1.337</td>
<td>0.223</td>
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<td>0.167</td>
</tr>
<tr>
<td>SC * Loc * Sub</td>
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<td>0.026</td>
<td>0.19</td>
<td>0.979</td>
</tr>
<tr>
<td>Error</td>
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<td>6.677</td>
<td>0.139</td>
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<tr>
<td>Total</td>
<td>71</td>
<td>13.154</td>
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Table 5. Results from AICc calculations, in descending order, for scallop size increase based on the models designed to describe the observed differences in growth.

<table>
<thead>
<tr>
<th>Model</th>
<th>RSS</th>
<th>$\sigma^2$</th>
<th>K</th>
<th>AICc</th>
<th>$\Delta$AIC</th>
<th>$w_i$</th>
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<tbody>
<tr>
<td>$g_4$ (Location)</td>
<td>16.44</td>
<td>0.46</td>
<td>4</td>
<td>-19.06</td>
<td>0.00</td>
<td>0.71</td>
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<tr>
<td>$g_3$ (Loc &amp; Veg)</td>
<td>16.49</td>
<td>0.46</td>
<td>5</td>
<td>-16.90</td>
<td>2.15</td>
<td>0.24</td>
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<td>$g_1$ (Global)</td>
<td>16.04</td>
<td>0.45</td>
<td>7</td>
<td>-13.82</td>
<td>5.24</td>
<td>0.05</td>
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<td>$g_2$ (Substrate)</td>
<td>29.28</td>
<td>0.81</td>
<td>5</td>
<td>3.76</td>
<td>22.82</td>
<td>0.00</td>
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<tr>
<td>$g_5$ (Veg)</td>
<td>29.68</td>
<td>0.82</td>
<td>3</td>
<td>0.18</td>
<td>19.23</td>
<td>0.00</td>
</tr>
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</table>
Table 6. Analysis of variance for scallop size increase by two factors: (I) substrate treatment, and (II) location.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
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<th>p</th>
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<tbody>
<tr>
<td>Location</td>
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<td>13.241</td>
<td>6.621</td>
<td>11.23</td>
<td>0.000</td>
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<td>0.454</td>
<td>0.151</td>
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</tr>
<tr>
<td>Interaction</td>
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<td>1.886</td>
<td>0.314</td>
<td>0.53</td>
<td>0.778</td>
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<tr>
<td>Error</td>
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<td>0.590</td>
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</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>29.734</td>
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</tbody>
</table>
Figure 1. Map of the Beaufort-Morehead City, NC region illustrating the scallop collection site in the Middle Marsh (34°41.940 N, 76°35.741 W) (indicated by the star)
Figure 2. Map of the sites of field experiments (stars) in the Lynnhaven River system within three locations: (1) Pleasure House Creek (PHC), (2) Broad Bay (BB), and (3) Linkhorn Bay (LB).
Figure 3. Schematic of cage (55.9 cm diameter x 69.2 cm height). Arrow indicates the section that was placed below the sediment-water interface. Gray indicates mesh panels for water flow.
Figure 4. Diagram of caged field blocks that were present at each location. Each circle represents an individual enclosure that contained one of the four randomly assigned substrates: *Gracilaria* spp. (G), *Zostera marina* L. (SG), Rubble (R), and Oyster Shell (OS). Arrows and measurements indicate distances between enclosure and blocks.
Figure 5. Patterns of survival of caged scallops for each substrate type at each of the three locations. Bars show mean cumulative survival and error bars are one SE. Significant differences at $\alpha = 0.05$ as determined by a two-way ANOVA and SNK are indicated by different letters above the bars.
Figure 6. Patterns of cumulative size increase of caged scallops over three weeks for each location (Linkhorn Bay (LHB), Broad Bay (BB), Pleasure House Creek (PHC)) with pooled substrate treatments. Bars show mean cumulative size increase and error bars are one SE. Significant differences at $\alpha = 0.05$ as determined by a two-way ANOVA and SNK are indicated by different letters above the bars.
Chapter 2

Blue Crab, *Callinectes sapidus*, predation on the Bay Scallop, *Argopecten irradians concentricus* (Say 1822): mesocosm and field experiments in the Lynnhaven River, Virginia
ABSTRACT

Predation by crabs and other benthic predators in estuarine systems is an important source of natural mortality for a variety of benthic organisms. We assessed predation on bay scallops (Argopecten irradians concentricus) in mesocosm and field experiments. In laboratory mesocosm experiments, we assessed the survival of bay scallops Argopecten irradians concentricus of various sizes (10-20 mm, 21-30 mm, 31-40 mm, and 41-50 mm shell height; SH) as a function of female blue crab Callinectes sapidus predation as it varied among treatments of habitat type (oyster shell, sand, macroalgae) and predator size (>140 mm, ≤ 140 mm carapace width). A balanced two-by-three factorial experimental design was used to evaluate the probability of scallop survival. There was a significant difference in the proportion of scallops surviving by habitat treatment and predator size (two-way ANOVA). Large female crabs exerted greater predation pressure on scallops of all size categories compared to smaller females (F = 11.67, p = 0.001), whereas oyster shell habitat provided the highest degree of structural refuge from crab predation (F = 3.29, p = 0.044). Differences in predation as a function of predator size may be attributed to differences in claw strength and crushing capabilities of the two predator size groups. Differences in survival among habitats may be a function of increasing habitat complexity and structural refuge. A series of field-tethering experiments (one small-scale and one large-scale) designed to assess the survival of tethered juvenile scallops (< 30 mm SH) in the Lynnhaven River sub-estuary of the Chesapeake Bay demonstrated significant effects of location within the sub-estuary, habitat, and/or their interaction depending on the scale of the experiment. Two-way ANOVAs and an information theoretic approach (Akaike’s Information Criterion analysis; AIC) were used for the analysis of the data. For the small-scale experiment, there was a significant effect of location (two-way ANOVA: F = 3.71, p = 0.020), which also emerged as the strongest predictor of survival (AIC). In the large-scale experiment, the interaction between the two variables (location and habitat) was significant (GLM, F = 5.79, p < 0.001) and also a strong predictor of scallop survival (AIC). Survival was significantly higher in Gracilaria spp. treatment (SNK, p ≤ 0.007) and at Alanton’s Cove (SNK, p ≤ 0.04). Overall, survival was not very high under all circumstances, which could present complications in restoring sustainable scallop populations to the area. However, a proper combination of efforts, such as seed planting in structured substrates that offer protection against predation, such as oyster shell and Gracilaria spp., will likely increase the success of restoration efforts.
INTRODUCTION

Predation by crabs in estuarine systems is an important source of natural mortality for a variety of benthic organisms, particularly during the larval and juvenile phases (Jensen and Jensen 1985, Juanes 1992, Strieb 1995). Numerous studies have demonstrated the crab’s ability to regulate bivalve population dynamics and community structure (Virnstein 1977, Holland et al. 1980, Arnold 1984). Bivalve prey can coexist alongside their predators with a reduced risk of mortality if (1) they reach a partial or total size refuge at adult sizes, (2) exist in a habitat inaccessible to predators, or (3) develop heavy shell morphology (Blundon and Kennedy 1982a, 1982b). Increased habitat complexity also provides spatial refuge from predators, particularly during the early stages of bivalve development (Arnold 1984, Talman et al. 2004).

The blue crab, *Callinectes sapidus* (Rathbun), is an ecologically and commercially important large epibenthic predator found along the eastern seaboard of North America (Hill et al. 1989, Eggleston 1992). In Chesapeake Bay, the blue crab is one of the dominant predators, reaching high abundances with vigorous foraging activity from late spring through autumn (Lipcius and Hines 1986, Eggleston 1992, Moody 1994). Blue crabs consume fish, crabs, detritus, shrimp, aquatic plants, conspecifics, and mollusks (Hill et al. 1989, Lipcius et al. 2007); however, bivalve mollusks form a major fraction of their diet (Laughlin 1982, Hines et al. 1990, Seitz et al. 2001).

Three subspecies of bay scallops, *Argopecten irradians*, are commonly distinguished according to geographical distribution (Fay et al. 1983) and shell morphology (Clarke 1965, Waller 1969). They include: (1) *A.i. irradians* extending from
Cape Cod to the mid-Atlantic region, (2) *A. i. concentricus* extending from the mid-Atlantic region to the Atlantic coast of Florida, and (3) *A. i. amplicostatus*, which extends farther into the Gulf of Mexico (Clarke 1965, Wilbur and Gaffney 1997).

Beginning in the 1930s, significant decreases in southern bay scallop, *A. i. concentricus*, abundances were observed in Virginia in conjunction with the decimation of eelgrass beds (McHugh 1989, Dreyer and Castle 1941) resulting from eelgrass-wasting disease, eutrophication, and damage from the storm king hurricane (Renn 1936, Castagna and Duggan 1971, Arnold et al. 1998, Goldberg et al. 2000, R. Lipcius, unpublished data). Recent declines in harvests may be attributed to recruitment limitation (Peterson and Summerson 1992, Peterson et al. 1996), which has been exacerbated by overharvesting, degraded water quality, habitat loss, coastal development, and the occurrence of harmful algal blooms (Arnold et al. 1998, Marelli et al. 1999, NMFS 1999, Arnold 2001, Tettelbach et al. 2002, Fegley et al. 2009). Efforts to re-establish bay scallop populations in the seaside lagoons of the Chesapeake Bay have been initiated via experiments designed to inform upcoming restoration efforts (M. Luckenbach, pers. comm.), although no experiments or restoration efforts on the bayside have been attempted. In recent years, sporadic abundances of bay scallops have been observed in the lower bayside areas of the Chesapeake Bay (P. Freeman, pers. comm.).

Bay scallops are simultaneous protandrous hermaphrodites with an average life span of 12 to 18 months (Fay et al. 1983, Peterson and Summerson 1992), though in rare cases may reach up to 26 to 30 months (Belding 1910). Within their southern range, they undergo a single primary spawning event, which commences during the late fall in
conjunction with decreasing water temperature, increased food availability, and minimal risk of predatory mortality (Gutsell 1930, Sastry 1963, Barber and Blake 1983, Arnold et al. 2005, Blake and Shumway 2006). It is generally maintained that bay scallop larvae and young juveniles require structured nursery habitats for increased chances of survival (Ingersoll 1886, Fay et al. 1983).

Seagrass beds, particularly those consisting of eelgrass (*Zostera marina* L.), serve as the preferred nursery habitat for bay scallops, in part, because they provide significant refuge from benthic predators (Pohle et al. 1991, Ambrose and Irlandi 1992) as well as protection from siltation associated with the bottom (Thayer and Stuart 1974, Castagna 1975). In spite of this, bay scallop populations are also abundant in natural habitats devoid of eelgrass (Marshall 1947, Marshall 1960) and are known to attach to other substrates, such as small branching algal species, shells, rocks, or sessile animals (Ingersoll 1886, Marshall 1960, Thayer and Stuart 1974, Smith et al. 1988). Preference for structured habitats may be a function of size. In a previous mesocosm experiment, young bay scallops (<15 mm shell height; SH) equally preferred cobble, algal, and eelgrass habitats, all of which were selected over sand habitats; older bay scallops (> 25 mm SH) had no preference among cobble, algal, eelgrass, and sand habitats (Chintala et al. 2005).

The present study assessed predation on bay scallops (*Argopecten irradians concentricus*) in mesocosm and field experiments. In mesocosm experiments, we quantified the impacts of female blue crab predation on juvenile and adult bay scallops (10-19 mm, 20-29 mm, 30-39 mm, 40-49 mm shell height; SH) as it varied among
treatments of habitat type (oyster shell, sand, *Gracilaria* spp.) and predator size (> 140 mm, ≤ 140 mm carapace width; CW). In the field, we examined predation by conducting two field experiments (small-scale and large-scale) using scallop tethering at various locations and habitats within the Lynnhaven River sub-estuary of the Chesapeake Bay, Virginia (Figure 3).
MATERIALS AND METHODS

2.1. Mesocosm Experiments

2.1.1. Experimental Design and Technical Approach

Scallops ranging from 12.3 to 44.7 mm SH were obtained from an 18 m x 29 m shore-side mesocosm pond at the UNC Institute of Marine Sciences (IMS) in Morehead City, NC (34°43.354 N, 76°45.146 W). They were transported in moist burlap sacks in coolers with ice packs to the Virginia Institute of Marine Science (VIMS), in Gloucester Point, Virginia, USA (37° 14.891 N, 76°30.030 W). The transportation method was chosen based on results from Peterson et al. (1996), which indicated that handling mortality was greatly reduced using this method. Upon arrival, the scallops were gradually adjusted to local salinities over one week. Female blue crabs ranging from 112.0 to 167.7 mm CW were obtained from the annual VIMS Blue Crab winter dredge survey. Only female crabs were used in this experiment to avoid sex-related biases in feeding behavior and cheliped morphology (Eggleston 1990b, Barbeau and Scheibling 1994, Nadeau and Cliche 1998).

Mesocosm experiments were conducted to examine the effect of predator size, prey size, and habitat complexity on the survivorship of bay scallops. The experiments were conducted in seven 69.9 x 40.6 cm circular tanks (155.7 liters). We used a 2 x 3 balanced factorial experimental design where each tank represented a single data point (Fig. 1). Six tanks included one of the three habitat treatments (oyster shell, sand, Gracilaria spp.), one of the two predator sizes (large: >140 mm CW; small: ≤ 140 mm CW) and a total of eight scallops (two from each size class: 10-19 mm, 20-29 mm, 30-39
mm, 40-49 mm shell height; SH). The seventh tank was used to control for handling
mortality; therefore, it did not include a predator or habitat treatment.

Crabs were acclimated and starved for 48 hours prior to each trial to standardize
hunger levels. To maintain sampling independence, each crab was used only once. We
conducted a total of 11 feeding trials (N = 66) each lasting 24 hours. Water temperature
of the experimental and holding tanks was maintained at 20.0°C to ensure normal blue
crab feeding activity. The numbers of scallops eaten were recorded following each
experimental trial.

2.1.2. Statistical Analyses

Scallop survival data was analyzed using a two-way analysis of variance
(ANOVA) to determine the effects of habitat type and predator size. To meet
assumptions of normality and homogeneity of variance, the survival data were arcsine
transformed. Multiple comparisons were performed with a Student-Neuman-Keuls
(SNK) test. Prey-size preference was analyzed using a general multivariate analysis of
variance (MANOVA).

2.2. Field Experiments: Small-Scale

2.2.1. Site Selection

The Lynnhaven River system is the southern-most system in Chesapeake Bay,
located within the City of Virginia Beach, Virginia. It consists of four main water bodies:
Broad Bay, Linkhorn Bay, and the Eastern and Western Branches of the Lynnhaven
River. This study was conducted at four locations in the Lynnhaven River system: Broad
Bay, Pleasure House Creek, First Landing State Park, and Linkhorn Bay (Fig. 2). In
addition to the blue crab, potential predators of scallops in Lynnhaven include: oyster toadfish, flounder, mud crabs, and whelks.

2.2.2. Predation Mortality

We used tethering experiments to test for differences in mortality of juvenile bay scallops among three habitat types and four locations. The three habitats included oyster shell, *Gracilaria* spp., and sand, which were artificially created in 1 m x 1 m plots approximately six meters from shore and three meters apart 24 hours prior to scallop deployment. Mean water depth ranged from 1-1.5 m at MLW. Each plot generally included two tethered scallops, but most sand plots included only one tethered scallop. Survival estimates were based on the mean survival of scallops per plot.

Juvenile bay scallops ranging between 13.1 and 25.9 mm SH (20.1 ± 0.3 mm) were tethered by gluing a 20-cm-long monofilament fishing line to the umbo area of the upper valve. This area was cleaned and thoroughly dried prior to gluing to facilitate attachment. The tethered scallops were held in an outdoor flow-through seawater tank for 48 hours prior to deployment to ensure the tether was securely attached.

The tethered scallops were transported to the study locations in petri dishes (10 scallops per dish) lined with wet paper towels placed inside a cooler with moist burlap and ice packs on 16 September 2009. This technique enhanced scallop survival during transportation by reducing the risk of valve opening and, thus, gill desiccation. In the field, the free end of the fishing line (tether) was tied to a metal plant stake. For the plots that contained two scallops per plot, the stakes were inserted at diagonally opposite ends of the quadrat to ensure no chance of scallop entanglement.
Tethered scallops were left at each study location for 4 hours and 15 minutes at which point their status was recorded and the experiment was terminated. In a pilot study conducted two weeks prior, we estimated that tethered scallop survival in the field was approximately 50% after 4 hours and 15 minutes using sand treatments only.

Additionally, on 9 September 2009, trawl data was collected at each location to compare relative predator abundances. For this, we used a 2 m-wide, 4.9 m-long otter-trawl net, with a 0.95 cm mesh size, to sample along the shoreline. The trawl net was pulled behind the boat for two consecutive minutes at 11 rpms. This was done twice, once with the current and once against the current. All species collected were identified, measured to the nearest millimeter (total length), counted, and recorded.

2.2.3. Statistical Analyses

Survival of tethered scallops was predicted to be a function of location, habitat, and their interaction. Akaike’s Information Criterion (AIC), which allows for the comparison of multiple working hypotheses, was used to determine which factor or factors were the strongest predictors of survival among the variables examined (Anderson 2008). Overall, four hypotheses (models) were derived and analyzed using binary logistic regressions and ranked according to how well the model fit the data using AIC. Each model represented a different combination of variables that described the observed differences in survival (Table 1). Using AIC, in cases involving small sample sizes, a second-order bias AIC correction (AICc) calculation is necessary. AICc was calculated for each of our four models using the log-likelihood values obtained from the corresponding binary logistic regression using the following equation:
\[ AICc = -2 \log(L(\hat{\theta})) + 2k + \frac{2k(k + 1)}{n - k - 1} \]

where \( \log(L(\hat{\theta})) \) is equal to the log of the maximum likelihood value obtained from the binary logistic regressions, \( k \) is the number of estimable parameters in the approximating model, and \( n \) is the sample size. \( \Delta AICc \) values were calculated for each model to rank the various models from most probable to least (i.e., low to high AIC values) using the following equation:

\[ \Delta AICc = AICc_i - AICc_{\min} \]

where \( AICc_i \) are the values for each of the \( i \) models and \( AICc_{\min} \) is the lowest AICc value of all the models. In calculating these values, the best model is defined as having \( \Delta AICc = 0 \). Model probabilities (\( w_i \)), which indicate the probability that the model is the best among the whole set of candidate models, were calculated for each model using the following equation:

\[ w_i = \frac{e^{-\frac{1}{2} \Delta_i}}{\sum_{r=1}^{R} e^{-\frac{1}{2} \Delta_r}} \]

where \( \Delta_i \) is equal to the \( \Delta AICc \) values calculated in the previous equation and \( R \) is the number of models in the pool of candidate models. The model probabilities, also known as Akaike weights, sum to one and can be used to directly compare the weight of evidence for one model over another.

Scallop survival was also analyzed using two-way ANOVAs on square-root-
transformed data to determine if there was an interaction effect as well as to gage the magnitude of the effects of location and/or habitat type. A Student-Neuman-Keuls (SNK) post-hoc comparison test was used to determine where the differences occurred.

2.3. Field Experiments: Large-Scale

2.3.1. Site Selection

This study was conducted at three locations within the Lynnhaven River system: Broad Bay, Alanton’s Cove, and Pleasure House Creek (Fig. 3). As in the previous experiment, we aimed to test for differences in mortality of juvenile bay scallops among three habitat types. In this case we were interested in minimizing the confounding effect of creating artificial plots of structured habitat that might attract predators seeking refuge or favorable foraging areas. Therefore, our study locations were chosen based on the natural availability of large and established *Gracilaria* spp. beds, oyster reefs, and sand habitats all within the same vicinity, where predator abundances would remain similar within a location and through time.

2.3.2. Predation Mortality

Juvenile bay scallops ranging between 12.6 and 30.9 mm SH (19.5 ± 0.3 mm) were tethered in the same manner as the scallops used for the small-scale field study. The tethered scallops were held in an outdoor flow-through seawater tank for 48 hours prior to deployment.

On 28 October 2009, the tethered scallops were transported to the study locations in petri dishes (10 scallops per dish) lined with wet paper towels placed inside a cooler with moist burlap and ice packs to enhance species survival, similar to procedures in the
prior experiment. In the field, the free end of the fishing line (tether) was tied to a swivel attached to a cable tie that was attached to a ~1 m tall PVC pole. The cable tie was clasped around a hole drilled into the PVC pole about 30 cm from the bottom. The pole was then inserted into the sediment to where the point of scallop attachment was about 2 cm off the sediment surface. This was done to mimic the natural setting of the scallops on the sediment surface and to allow for complete range of motion within the length of the tether.

At Pleasure House Creek and Broad Bay, 20 tethered scallops were haphazardly placed per habitat treatment for a total of 60 tethered scallops per location. Each PVC stake was placed at least 2 m apart from its closest neighbor. Due to time limitations, only 10 scallops per habitat treatment were placed at Alanton’s Cove. Since this experiment was conducted in late October when predator foraging was reaching a minimum, the tethered scallops were left out in the field for 48 hours and monitored every 24 hours.

To control for potential mortality associated with tethering and transportation, an additional 20 scallops were tethered and placed in 244 x 91 cm outdoor flow-through seawater tanks without predators, along with another 20 untethered scallops 48 hours prior to the experiment. All scallops, experimental and control, were treated equally with regard to the transportation procedure. They were placed in the petri dishes (10 scallops per dish) lined with wet paper towels placed inside a cooler with moist burlap and ice packs. After two hours the scallops were removed from the cooler and the free ends of the lines of the 20 tethered scallops were attached to the sides of the experimental tanks (5 tanks, 4 scallops/tank) about 2 cm off the bottom. Untethered scallops were also placed
in a separate experimental tank for the duration of the experiment. No scallops from the tanks were ever found dead, missing, or unattached verifying that handling had no effect on survivorship and that tethers were securely attached.

Tethering is considered the simplest and least time-consuming method for measuring predation potential (Aronson and Heck 1995). However, results must be interpreted cautiously since they may not represent true measurements of natural mortality. To assess the potential artifacts associated with tethering, we conducted another series of experiments in the lab where tethered and untethered scallops were held in 69.9 x 40.6 cm circular tanks including one of the three habitats (Gracilaria spp., oyster shell, sand) and a predator (blue crab). Experiments lasted 48 hours and were monitored every 24 hours. The tanks were maintained at 20° C to ensure normal feeding activity and also to mimic the ambient environmental conditions observed and recorded during the field tethering experiments.

2.3.3. Statistical Analyses

Survival of tethered scallops was predicted to be a function of location, habitat, and their interaction. We used AIC to determine which factor or factors were the strongest predictors of survival among the variables examined. We derived four hypotheses (models), each representing a different combination of the variables, which were analyzed using binary logistic regressions (Table 2). AICc and model probability values were calculated for each model to determine which candidate model best fit the data.

Scallop survival was also analyzed using two-way ANOVAs on untransformed
data to determine if there was an interaction effect, as well as to gage the magnitude of
the location and/or habitat type effects. A Student-Neuman-Keuls (SNK) post-hoc
comparison test was used to determine where the differences occurred.
RESULTS

3.1 Mesocosm Experiment

The proportion of scallops surviving varied significantly by habitat and predator size; there was no significant interaction between these two variables (two-way ANOVA: Table 3). Survival was highest in the oyster shell habitat (0.61) and lower in both the _Gracilaria_ spp. and sand treatments (0.41 and 0.42, respectively; Student-Neuman-Keuls; Fig. 4). Survival was also significantly higher with smaller predators (Fig. 5).

Large and small blue crabs showed preference for scallops ≤ 30 mm SH as well as a significant effect of habitat treatment; no interaction between the two variables was observed (MANOVA: Table 4). For both predator treatments, in the sand and _Gracilaria_ spp. treatments, we observed significantly lower survival of the ≤ 30 mm SH scallops compared to larger (> 30 mm SH) scallops (Figs. 6a, b). Conversely, we saw no significant difference in scallop survival by size class in the oyster shell treatment for both predator sizes (Figs. 6a, b). Overall, survival was highest in the oyster shell treatment for all scallop size classes for both predator size treatments (Fig. 4), though as would be expected, overall scallop survival was lower for the large predator size treatment (Fig. 5).

3.2 Field Experiment: Small-scale

Location emerged as the strongest predictor of scallop survival, as indicated by the AICc model comparison (Table 5). In general, models with \( w_I \geq 0.10 \) were considered likely models (Anderson 2008). After exposure to predators (4 hours and 15 mins), survival of tethered scallops differed significantly by location, though not by habitat, and
there was no significant interaction between the variables observed (two-way ANOVA: Table 6). Survival was highest at Broad Bay, followed by Linkhorn Bay, and lowest at Pleasure House Creek and First Landing State Park (Fig. 7). Post-hoc multiple comparisons indicated significant differences in survival between Broad Bay and Pleasure House Creek (SNK, \( p = 0.043 \)), Broad Bay and First Landing State Park (SNK, \( p = 0.042 \)), though not between Broad Bay and Linkhorn Bay (SNK, \( p = 0.468 \)). All other pair-wise comparisons were non-significant (SNK, \( p \geq 0.084 \)).

Predator abundances varied by location: Broad Bay had the fewest potential scallop predators, followed by Pleasure House Creek, First Landing State Park, and finally, Linkhorn Bay (Table 7).

### 3.3 Field Experiment: Large-scale

The global model, which included all variables and interaction terms, emerged as the strongest predictor of scallop survival, as indicated by the AICc model comparison (Table 8). After 48 hours of predator exposure, survival of tethered scallops differed significantly by habitat, though not by location, and a significant interaction between the variables was observed (two-way ANOVA: Table 9). Survival was significantly high at Alanton’s Cove compared to Pleasure House Creek (SNK, \( p = 0.054 \)) and Broad Bay (SNK, \( p = 0.039 \)). There was no significant difference in survival between Pleasure House Creek and Broad Bay (SNK, \( p = 0.599 \); Fig. 8).

In the mesocosm study designed to address the artifacts associated with tethering, we saw no significant difference among the three habitat treatments for the tethered scallops. We did, however, find a difference in survival among the habitats for the
untethered scallops, though they were non-significant \( (p > 0.05) \). Patterns of survival show highest survival in oyster shell (0.5) and *Gracilaria* spp. (0.4) and lowest in sand (0.2).
DISCUSSION

Our study yielded important results regarding the natural mortality of juvenile bay scallops in both mesocosms as well as in the field in the Lynnhaven River tributary of the Chesapeake Bay. Mesocosm experiments demonstrated significant differences in scallop survival among habitat treatments and with respect to predator size. Proportional survival was highest in oyster shell and lowest in the macroalgae *Gracilaria* spp., where survival was similar to sand. Both large and small predators preferred the two smallest size classes (10-19 and 20-29 mm SH) in all habitat treatments, though the preference was less pronounced and statistically non-significant in the oyster shell treatment. This suggests that oyster shell habitat may provide all sizes of bay scallops with structural benefits associated with heterogeneous habitat, such as providing refuge from predation.

In our experiments, blue crabs showed selection for the smaller prey sizes. Predation on bivalves such as *Mercenaria mercenaria* (MacKenzie 1977, Arnold 1984), *Crassostrea virginica* (Bisker and Castagna 1987, Eggleston 1990a) and *Geukensia demissa* (Seed 1980, Seed 1982, Hughes and Seed 1981) by blue crabs has been well documented. In these studies, blue crabs preferred small prey in spite of their ability to consume larger prey. Observed preference for the smaller scallops (≤30 mm SH) by blue crabs may be explained by their relative ease with which they handle the smaller prey. Prey that are too large with substantial shell strength, measured as the force required to achieve fracture (Juanes 1992), will increase a crab’s handling time by requiring that they adopt techniques such as edge clipping and prying the valves apart (Seed and Hughes 1995, Aronhime and Brown 2009). Outright crushing of smaller prey is less time-
consuming, allowing feeding crabs to maximize their net rate of energy intake (Hughes and Seed 1981). Furthermore, a predator’s probability of suffering non-lethal injury, such as claw damage, increases with the shell strength of its prey (Juanes 1992) and likely influences observed patterns of preferred smaller bivalve prey.

Although we detected a clear preference for small scallops in both predator treatments (small and large), we also observed crabs preying on scallops of up to 49 mm SH. Blue crabs are one of the dominant predators in the Chesapeake Bay that are able to regulate bivalve population dynamics and community structure (Virmstein 1977, Holland et al. 1980, Arnold 1984). Therefore, a prey’s ability to obtain a spatial or size refuge from crab predation is important, possibly required, for maintaining a sustainable population. Our study showed increasing survival of scallops with an increase in size (shell length), which is related to shell strength. This increasing trend in survival with increasing scallop size may indicate a scallop’s ability to achieve a size refuge from blue crabs above our maximum experimental scallop size (49 mm SH). Our results also suggest that in the absence of seagrass, which provides juvenile scallops with a spatial refuge from predation, oyster shell habitat may provide an adequate habitat refuge, particularly for the smaller scallop sizes, through heterogeneity and inaccessibility.

In the small-scale field tethering experiment, differences in scallop survival varied significantly among location, though not habitat. We do not suggest that the differences in scallop survival among locations could be explained by the relative predator abundances found at each location. Although predator abundances were lowest at our Broad Bay location, which was the location with the significantly highest level of scallop
survival, the survival data for the remaining locations does not coincide with the relative predator abundances. The high abundances of potential predators in Linkhorn Bay and First Landing State Park appear to be driven by the high abundances of spot (*Leiostomus xanthurus*), which may not be a likely predator of bay scallops. Consequently, it may be that predator abundances do not vary enough to explain the observed differences in survival. However, it is still important to consider and direct scallop restoration in areas with fewer predators, such as in Broad Bay in the Lynnhaven River System.

It is likely then, that in creating the artificial plots for the small-scale study 24 hours prior to the beginning of the experiment, we attracted predators seeking refuge or favorable foraging areas. Therefore, we believe that the large-scale tethering study offers a more realistic account of rates of scallop predation. Since the habitats were well established, we would expect predator abundances not to fluctuate substantially as a function of habitat formation and prey addition.

Differences in scallop survival for the large-scale experiment varied significantly among habitats, though not locations, and there was a significant interaction between the two variables. Survival was highest for the *Gracilaria* spp. treatment and was low for both the sand and oyster shell treatments. Although a marginally significant difference was observed for location (*p* = 0.059), the trends was toward highest survival in Alanton’s Cove, followed by Pleasure House Creek, and then Broad Bay. The Alanton’s Cove location was particularly complex and unique, as compared to the other locations, in that the oyster reef mounds created elevation differences. This likely presented the
scallops with a greater advantage, which resulted in elevated survival levels, suggesting that complex habitats are advantageous to scallop survival.

The high survival of bay scallops in the *Gracilaria* spp. treatment suggests that this substrate may provide similar ecological benefits to scallops as *Z. marina*. Eelgrass is an important habitat for juvenile and larval stages of the bay scallop as it provides an elevated surface to which the larvae can attach and escape predators and burial by sediment (Thayer and Stuart 1974, Castagna 1975). Its benefits could also result from its large size, complex structure, and adaptability to environmental stressors (Thomsen et al. 2009). Conversely, the macroalgal blooms of *Gracilaria* spp. could also impose negative impacts to the ecosystem.

The emergence of dense canopies of various benthic macroalgal species, including *Gracilaria* spp., is a growing phenomenon along many of the world’s coastlines, primarily associated with human activity (Valiela et al. 1997). In 1995, Taylor et al. suggested that in coastal waters with high nutrient enrichment, we observe a conversion from seagrass to macroalgal habitats, which is commonly considered a degradation of coastal environments. After an expansive bloom of *Gracilaria* spp. the accumulation of the plant detritus may result in low oxygen and high sulfide conditions within the sediments (Martínez-Lüscher and Holmer, in press), having adverse effects on the benthic community. In the case of the Lynnhaven River system, expansive *Gracilaria* spp. mats that could impose such conditions have been observed in Alanton’s Cove, Linkhorn Bay, and within the shallow coves of Lynnhaven proper (R. Lipcius, pers. comm.).
Previous work has indicated that translocated scallops are able to survive and grow in the Lynnhaven River system, though the scallop’s ability to do so depends on location or habitat (Hernández Cordero et al., in prep.) Combined results from the research herein point to significant differences in survival of juvenile bay scallops, as a function of habitat complexity, predator abundance and size, and, potentially, location. We suggest that restoration be focused primarily on oyster shell habitats in locations with low large predator densities.

The establishment of bay scallop populations in Lynnhaven River may be more successful if previously used strategies are taken account. For example, in 2001, Arnold reported on a strategy that led to the successful restoration of bay scallops in the coastal lagoons of Florida. His strategy was to concentrate spawning scallops, thereby increasing fertilization success, larval supply, and the availability of competent recruits. In North Carolina Fegley et al. (2009) reported that maintaining high enough adult scallop densities promotes effective spawning (> 2 scallops/m², Peterson and Summerson 1992), even when cownose ray predation pressure is at its peak. High adult densities were maintained through the erection of protective stockades (10 m wide x 27 m long), which successfully inhibited high scallop mortality from predation.

The Lynnhaven River system is a fairly large system (~ 67 square miles in area and ~ 150 miles of shoreline), comparable in size to the study systems of the aforementioned studies. As such, we would benefit from employing similar strategies of restoration. It would also be to our advantage to time these efforts accordingly. From my work we saw that blue crabs preferentially feed on the smaller size classes (≤ 30 mm
SH). We also recognize that predation is highest in the summer months and that scallops spawn in the fall. Therefore, caging juvenile (~ 30 mm SH) scallops in concentrated stocks in the spring and allowing them to acclimate, grow and later spawn, would result in the availability of competent recruits. Moreover, placing these concentrated stocks near areas of structured habitat (e.g. oyster reefs) would provide the recruits with protective habitat, thus increasing their chances of survival.

The notion that bay scallops can successfully find refuge from predation in alternative habitats, such oyster shell, gives promise to the idea of restoring bay scallop populations in the Lynnhaven River sub-estuary, where seagrass is currently negligible. For successful restoration to take place, a thorough account of other potential deterrents to successful restoration, such as recruitment limitation and environmental stressors, must be taken into account.
LITERATURE CITED


Nadeau, M., Cliche, G. 1998. Predation of juvenile sea scallops (*Placopecten magellanicus*) by crabs (*Cancer irroratus* and *Hyas* sp.) and starfish (*Asterias*...


Table 1. The four models $(g_i)$ developed to describe the observed difference in scallop survival for the small-scale field tethering experiment. If a $\beta$ located in a particular column, then that variable was included in that model. Number of parameters in each model is denoted by $k$. 


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<th>Oyster Shell</th>
<th>Broad Bay</th>
<th>First Landing Bay</th>
<th>Linkhorn Bay</th>
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<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. The four models (g_j) developed to describe the observed difference in scallop survival for the large-scale field tethering experiment. If a β located in a particular column, then that variable was included in that model. Number of parameters in each model is denoted by k.
<table>
<thead>
<tr>
<th>Model</th>
<th>Parameters</th>
<th>Pleasure House Creek &amp; Sand</th>
<th>Gracilaria</th>
<th>Oyster Shell</th>
<th>Broad Bay</th>
<th>Alanton's Cove</th>
<th>(G*BB)</th>
<th>(G*LB-AC)</th>
<th>(OS*BB)</th>
<th>(OS*LB-AC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$g_1$</td>
<td>10</td>
<td>(PHC) &amp; (S)</td>
<td>(G)</td>
<td>(OS)</td>
<td>(BB)</td>
<td>(LB-AC)</td>
<td>$\beta_0$</td>
<td>$\beta_1$</td>
<td>$\beta_2$</td>
<td>$\beta_3$</td>
</tr>
<tr>
<td>$g_2$</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_0$</td>
<td>$\beta_1$</td>
<td>$\beta_2$</td>
<td>$\beta_3$</td>
</tr>
<tr>
<td>$g_3$</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_0$</td>
<td>$\beta_1$</td>
<td>$\beta_2$</td>
<td>$\beta_3$</td>
</tr>
<tr>
<td>$g_4$</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_0$</td>
<td>$\beta_1$</td>
<td>$\beta_2$</td>
<td>$\beta_3$</td>
</tr>
</tbody>
</table>
**Table 3.** Analysis of variance of mesocosm experiments for scallop survival (arcsine-transformed) by two factors: (I) predator size, and (II) habitat type.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predator Size</td>
<td>1</td>
<td>1.031</td>
<td>1.031</td>
<td>11.67</td>
<td>0.001</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.581</td>
<td>0.291</td>
<td>3.29</td>
<td>0.004</td>
</tr>
<tr>
<td>Interaction</td>
<td>2</td>
<td>0.153</td>
<td>0.077</td>
<td>0.87</td>
<td>0.425</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td>5.304</td>
<td>0.088</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>65</td>
<td>7.070</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Multivariate analysis of variance (MANOVA) results of mesocosm experiment for scallop prey size-selection by two factors: (I) predator size, and (II) habitat type.

<table>
<thead>
<tr>
<th>Statistic</th>
<th>Value</th>
<th>F</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilks' lambda</td>
<td>0.779</td>
<td>4.191</td>
<td>4, 59</td>
<td>0.005</td>
</tr>
<tr>
<td>Lawley-Hotelling</td>
<td>0.284</td>
<td>4.191</td>
<td>4, 59</td>
<td>0.005</td>
</tr>
<tr>
<td>Pillai's</td>
<td>0.221</td>
<td>4.191</td>
<td>4, 59</td>
<td>0.005</td>
</tr>
</tbody>
</table>
Table 5. Results from AICc calculations, in descending order, for scallop survival of the small-scale field tethering experiment based on the models designed to describe the observed differences in survival (see table 1).

<table>
<thead>
<tr>
<th>Model</th>
<th>Log-Likelihood</th>
<th>k</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>$w_j$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$g_3$ (Location)</td>
<td>-39.269</td>
<td>5</td>
<td>89.967</td>
<td>0.000</td>
<td>0.915</td>
</tr>
<tr>
<td>$g_2$ (Loc &amp; Hab)</td>
<td>-39.070</td>
<td>7</td>
<td>94.940</td>
<td>4.973</td>
<td>0.076</td>
</tr>
<tr>
<td>$g_4$ (Habitat)</td>
<td>-45.243</td>
<td>4</td>
<td>99.416</td>
<td>9.450</td>
<td>0.008</td>
</tr>
<tr>
<td>$g_1$ (Global)</td>
<td>-33.432</td>
<td>13</td>
<td>103.570</td>
<td>13.603</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Table 6. Analysis of variance of the small-scale field tethering experiment for scallop survival by two factors: (I) habitat type, and (II) location.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.033</td>
<td>0.017</td>
<td>0.13</td>
<td>0.877</td>
</tr>
<tr>
<td>Location</td>
<td>3</td>
<td>1.303</td>
<td>0.464</td>
<td>3.71</td>
<td>0.020</td>
</tr>
<tr>
<td>Interaction</td>
<td>6</td>
<td>1.168</td>
<td>0.195</td>
<td>1.56</td>
<td>0.188</td>
</tr>
<tr>
<td>Error</td>
<td>36</td>
<td>3.438</td>
<td>0.095</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>47</td>
<td>5.453</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 7. Total number of benthic predators collected in trawls at the four locations used for the small-scale field tethering study.

<table>
<thead>
<tr>
<th>Species Name</th>
<th>Common Name</th>
<th>Broad Bay</th>
<th>Pleasure House Creek</th>
<th>First Landing State Park</th>
<th>Linkhorn Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bidyanus bidyanus</td>
<td>Silver Perch</td>
<td></td>
<td>1</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Callinectes sapidus</td>
<td>Blue Crab</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centropristis striata</td>
<td>Black Seabass</td>
<td></td>
<td></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Chilomycterus schoepfi</td>
<td>Spiny Burrfush</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Dorosoma cepedianum</td>
<td>Gizzard Shad</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eucinostomus argenteus</td>
<td>Spotfin Mojarra</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leiostomus xantharus</td>
<td>Spot</td>
<td>1</td>
<td></td>
<td>15</td>
<td>55</td>
</tr>
<tr>
<td>Lutjanus griseus</td>
<td>Grey Snapper</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mugil cephalus</td>
<td>Mullet</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Opsanus tau</td>
<td>Oyster Toadfish</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orthopristis chrysoptera</td>
<td>Pigfish</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paralichthys dentatus</td>
<td>Summer Flounder</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pogonias cromis</td>
<td>Black Drum</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sphoeroides maculatus</td>
<td>Northern Puffer</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

TOTAL NUMBER OF PREDATORS: 6  8  18  65
Table 8. Results from AICc calculations, in descending order, of the large-scale field tethering experiment for scallop survival based on the models designed to describe the observed differences in survival (see table 2).

<table>
<thead>
<tr>
<th>Model</th>
<th>Log-Likelihood</th>
<th>k</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>( w_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g_1 )</td>
<td>-80.950</td>
<td>10</td>
<td>183.483</td>
<td>0.000</td>
<td>0.997</td>
</tr>
<tr>
<td>(Global)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( g_2 )</td>
<td>-91.834</td>
<td>6</td>
<td>196.255</td>
<td>12.773</td>
<td>0.002</td>
</tr>
<tr>
<td>(Loc &amp; Hab)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( g_3 )</td>
<td>-98.658</td>
<td>4</td>
<td>196.986</td>
<td>13.503</td>
<td>0.001</td>
</tr>
<tr>
<td>(Habitat)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( g_3 )</td>
<td>-33.432</td>
<td>4</td>
<td>205.592</td>
<td>22.109</td>
<td>0.000</td>
</tr>
<tr>
<td>(Location)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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Table 9. Analysis of variance of the large-scale field tethering experiment for scallop survival by two factors: (I) location, and (II) habitat type, including the interaction between factors.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>2</td>
<td>1.117</td>
<td>0.558</td>
<td>2.890</td>
<td>0.059</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>3.160</td>
<td>0.654</td>
<td>3.380</td>
<td>0.037</td>
</tr>
<tr>
<td>Interaction</td>
<td>4</td>
<td>4.473</td>
<td>1.118</td>
<td>5.790</td>
<td>0.000</td>
</tr>
<tr>
<td>Error</td>
<td>141</td>
<td>27.250</td>
<td>0.193</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>149</td>
<td>36.000</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
**Figure 1.** 2x3 Factorial design of mesocosm experiments. Each circle represents an individual tank, containing one of two predator types (LG vs. SM) and one of three habitat treatments (OS vs. *Grac.* vs. Sand).
Figure 2. Map of field sites of small-scale tethering experiments (stars) in the Lynnhaven River system within four locations: (1) Pleasure House Creek (PHC), (2) Broad Bay (BB), (3) First Landing State Park (LB-FL), and (4) Linkhorn Bay (LBC).
Figure 3. Map of field sites of large-scale tethering experiments (stars) in the Lynnhaven River system within three locations: (1) Pleasure House Creek (PHC), (2) Broad Bay (BB), and (3) Alanton’s Cove (AC).
Figure 4. Patterns of scallop survival (± one SE) for each habitat treatment in mesocosm experiments. Bars show mean cumulative scallop survival and error bars are one SE. Significant differences at $\alpha = 0.05$ as determined by a two-way ANOVA and SNK are indicated by different letters above the bars.
Figure 5. Patterns of scallop survival (± one SE) for each predator size treatment in mesocosm experiments. Bars show mean cumulative scallop survival and error bars are one SE. Significant differences at $\alpha = 0.05$ as determined by a two-way ANOVA.
Figure 6. Scallop survival (± one SE) in mesocosm experiment by size class (mm shell length) for (A) Small predators, and (B) Large predators.
Figure 7. Small-scale field tethering experiment. Mean survival (± one SE) of tethered scallops by location (Pleasure House Creek (PHC); First Landing State Park (LB-FL); Linkhorn Bay (LBC); Broad Bay (BB)).
**Figure 8.** Large-scale field tethering experiment. Mean survival (± one SE) of tethered scallops by location (Broad Bay (BB); Pleasure House Creek (PHC); Alanton’s Cove (AC)). Significant differences at α = 0.05 as determined by a two-way ANOVA and SNK are indicated by different letters above the bars.
VITA

ANA LIZA HERNÁNDEZ CORDERO

Born in San José, Costa Rica on 25 October 1984 to L. Robert Hernández Hernández and Lorena Cordero Hernández. In December of 1990, her parents relocated to Independence, Kentucky, where she later graduated from Scott High School in 2002. She earned a B.S. in Biology and a B.A. in Geography from Northern Kentucky University in Highland Heights, Kentucky. She entered the Master of Science program at VIMS in the fall of 2007.