

ABSTRACT

DARCY, MEAGHAN CHRISTIAN. Influence of habitat corridors on dispersal success, predation induced mortality, and colonization of estuarine macrofauna in seagrass. (Under the direction of David B. Eggleston.)

A habitat corridor is a landscape feature that is hypothesized to promote dispersal between habitat patches that would otherwise be isolated, and promote population persistence. Habitat corridors have not been widely explored in marine and estuarine systems. We used artificial seagrass units (ASUs) placed on unstructured sediment in Middle Marsh and Drum Shoals, Back and Bogue Sounds, North Carolina to create seagrass patches (1m^2 and 4m^2) separated by bare sediment or connected by additional ASUs, which made up a habitat corridor. We assessed the interactive effects of habitat corridor (presence or absence) and interpatch distance (5m or 10m), as well as the ratio of corridor width to patch width upon dispersal of grass shrimp, *Palaemonetes* sp., and bay scallops, *Argopecten irradians* in seagrass. We conducted mark-recapture experiments where marked grass shrimp or bay scallops were placed in one patch from each treatment (donor patch). Regardless of the presence of a habitat corridor, interpatch distance, or ratio of corridor width to patch width, dispersal between seagrass patches for grass shrimp and bay scallops did not significantly vary. There was, however, a significant site effect with the number of scallops successfully dispersing between seagrass patches significantly higher at Drum Shoals than at Middle Marsh. The small spatial scales of this study and the perception of a homogeneous environment may explain the lack of a dispersal response by grass shrimp. Site-specific differences in bay scallop dispersal may have been due to varying flow at the two study sites. Tethering experiments were conducted concurrently with dispersal experiments to assess the interactive effects of

habitat corridor and interpatch distance, as well as perimeter to area ratio, on predation-induced mortality of bay scallops. Habitat corridor, interpatch distance or perimeter to area ratio did not significantly influence predation-induced mortality of scallops; however, there was a significant site by interpatch distance interaction. Predation rates were greater in patches separated by 10m at Middle Marsh than at Drum Shoals, whereas predation was greater in patches separated by 5m at Drum Shoals than at Middle Marsh. The lack of predation response to habitat corridors may have been due to a prey refuge in size (the scallops used in this study were relatively large, 35mm-50mm), or relatively low replication ($N = 5$) or another biotic or environmental factor not measured during this study. Colonization experiments were conducted to assess the interactive effects of habitat corridor and interpatch distance upon the colonization of estuarine macrofauna in seagrass. Neither mean density nor species diversity of estuarine macrofauna, nor mean density of individual taxonomic groups was significantly influenced by the presence of habitat corridors or by interpatch distance. Mean densities of slow-, intermediate-, and rapid-level dispersers were also not significantly influenced by the presence of habitat corridors or interpatch distance. The lack of community-level response may be explained by the interaction of hydrodynamics and its influence on the perception of a homogeneous or heterogeneous environment by dispersing organisms. Although habitat corridors may promote animal movement between habitat patches in terrestrial systems and for certain marine predators, the results from the present study do not confirm that habitat corridors are used by estuarine macrofauna for dispersal or colonization at relatively small spatial (10s of m) and temporal (hours to one month) scales. The coupled

effects of hydrodynamics and habitat use should be considered when investigating distribution and abundance patterns of organisms with different dispersal abilities.

KEYWORDS: habitat corridors, dispersal, predation, colonization, grass shrimp, bay scallops, estuarine macrofauna

**INFLUENCE OF HABITAT CORRIDORS ON DISPERSAL SUCCESS,
PREDATION INDUCED MORTALITY AND COLONIZATION OF ESTUARINE
MACROFAUNA IN SEAGRASS**

by

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DEDICATION

To my father, mother, and stepfather, for their endless support and encouragement.

Thank you.

BIOGRAPHY

Meaghan Christian Darcy was born on August 14, 1977 in Warwick, Rhode Island where she spent her childhood years. Meaghan graduated from high school in May of 1995 with hopes of becoming a doctor. When she entered Smith College the following fall she soon realized the road to medical school was not for her. After a marine ecology course, a semester in the Turks and Caicos Islands studying tropical marine ecology, and an internship at the NMFS Laboratory in Beaufort, NC, Meaghan decided she would dedicate her life to marine science. Meaghan graduated with a Bachelor of Arts degree from Smith College in May of 1999 and moved to the sunny, Florida Keys with the hopes of diving and fishing everyday and working a little here and there. While in the Florida Keys she worked with groups such as, The Nature Conservancy, Florida Marine Research Institute, Mote Marine Laboratory, and a group from Old Dominion University mainly working on projects studying queen conch and Caribbean spiny lobster. Through her colleagues in the Keys, Meaghan heard about a “hot shot” marine ecologist, Dr. Dave Eggleston, at North Carolina State University that would make a great graduate advisor. In the fall of 2001 she left Florida and entered the Master of Science program at North Carolina State University under the direction of Dr. Dave Eggleston.

While at North Carolina State University most of Meaghan’s time was spent thinking about habitat corridors in estuarine systems, however she also tried to embrace the southern culture and big university life. She bought a cowboy hat, started listening to country music, and went to a number of alt-country shows. She also went to as many tailgating parties and football games as she could, which she missed during her undergraduate years by going to an all women’s college. Some of Meaghan’s time was also spent weightlifting so that she could earn the bragging rights that she could curl more than Darren.

Meaghan has taken a position at Mote Marine Laboratory in Sarasota, Florida working at the Center for Fisheries Enhancement. She will specifically be working on a red snapper stock enhancement project in Mississippi and Sarasota, Florida.

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TABLE OF CONTENTS

	<u>PAGE</u>
LIST OF TABLES	vi
LIST OF FIGURES	vii
1. INTRODUCTION	1
2. MATERIALS AND METHODS	5
2.1 Study Sites	5
2.2 Artificial seagrass units	6
2.3 Experimental benthic landscapes	7
2.4 Dispersal of shrimp and scallops	8
2.5 Predation-induced mortality	11
2.6 Colonization by estuarine macrofauna	12
3. RESULTS	13
3.1 Dispersal of shrimp and bay scallops	13
3.2 Predation-induced mortality	14
3.3 Colonization by estuarine macrofauna	15
4. DISCUSSION	17
4.1 Patterns and possible mechanisms for grass shrimp dispersal	19
4.2 Patterns and mechanisms for bay scallop dispersal	19
4.3 Patterns and possible mechanisms for predation-induced mortality of bay scallops	20
4.4 Patterns and possible mechanisms for colonization by estuarine Macrofauna	23
4.5 General conclusions	25
5. LITERATURE CITED	28
6. APPENDIX	48

LIST OF TABLES

	<u>PAGE</u>
1. Effects of site, habitat corridor, and interpatch distance on bay scallop dispersal to receiver patches	34
2. Effects of site and the ratio of corridor width to patch width on dispersal of bay scallops	34
3. Effects of site, corridor, and interpatch distance on relative predation rates of bay scallops	34
4. Effects of site and the ratio of perimeter to area on relative predation rates on bay scallops	35
5. Effects of habitat corridor and interpatch distance on mean density of estuarine macrofauna colonizing ASUs	35
6. Effect of connected treatments and isolated treatment separated by 5m compared to isolated treatment separated by 10m on mean density of estuarine macrofauna colonizing ASUs	35
7. Effects of habitat corridor and interpatch distance on species diversity	35
8. Effect of connected treatments and isolated treatment separated by 5m compared to isolated treatment separated by 10m on mean density of gastropods colonizing ASUs	36
9. Effect of connected treatments and isolated treatment separated by 5m compared to isolated treatment separated by 10m on mean density of amphipods colonizing ASUs	36
10. Effect of connected treatments and isolated treatment separated by 5m compared to isolated treatment separated by 10m on mean density of polychaetes colonizing ASUs	36
11. Effect of connected treatments and isolated treatment separated by 5m compared to isolated treatment separated by 10m on mean density of bivalves colonizing ASUs	37
12. Effects of habitat corridor and interpatch distance on mean density of slow dispersers	37
13. Effects of habitat corridor and interpatch distance on mean densities of mid-level dispersers	37
14. Effects of habitat corridor and interpatch distance on mean densities of rapid dispersers	38
15. Effect of connected treatments and isolated treatment separated by 5m compared to isolated treatment separated by 10m on mean density of slow dispersers colonizing ASUs	38

LIST OF FIGURES

	<u>PAGE</u>
1. Map of study sites	39
2. Schematic of experimental design to test the effects of habitat corridor and interpatch distance on dispersal and relative predation rates of grass shrimp and bay scallops and colonization of estuarine macrofauna in ASUs	40
3. Schematic of experimental design to test the effects of the ratio of corridor to patch width on dispersal and relative predation rates of grass shrimp and bay scallops	41
4. Schematic of experimental design to test the effects of perimeter to area ratio on predation induced mortality of bay scallops	42
5. Mean number of scallops that successfully moved to a receiver patch	43
6. Mean relative predation rates on bay scallops, site and interpatch distance Interaction	44
7. Mean density of estuarine macrofauna colonization of ASUs	45
8. Mean densities of gastropods, amphipods, polychaetes, and bivalves colonizing ASUs	46
9. Mean densities of slow, intermediate, and rapid dispersers colonizing ASUs	47

Introduction

In marine and estuarine systems, the concept of habitat corridors has not been widely explored. Habitat corridors in terrestrial ecology have been defined as linear habitats connecting two or more larger blocks of habitat which are proposed to enhance or maintain viability of populations within habitat patches by promoting movement between patches (Beier and Noss, 1998). Perceived benefits of habitat corridors include increased movement between patches providing a source of immigrants alleviating population extinction and inbreeding, increased cover from predators, and alternative refuge from large disturbances (Noss, 1987; Beier and Noss, 1988; Haddad, 1999).

Considerable debate surrounds the perceived benefits of habitat corridors and, until recently, there has been little empirical evidence supporting their benefits. Movement has been greater between patches in the presence of a corridor than without a corridor for butterfly species, *Juonia coenia* and *Euptoieta claudia* (Haddad, 1999; Haddad and Baum, 1999; Tewksbury et al., 2002), field mice, *Microtus pennsylvanicus* (Coffman, 2001) and *Peromyscus leucopus* (Fahrig and Merriam, 1985; Merriam and Lanoue, 1990; Henein and Merriam, 1990), as well as for pollen and seeds carried by insect and bird movement (Tewksbury et al., 2002). Field surveys of Bahman's sparrow, *Aimophila aestivalis*, a relatively limited disperser, demonstrated that colonization of habitat patches connected by corridors was greater than in isolated patches (Dunning et al., 1995). These investigations suggest that habitat fragmentation can affect a variety of organisms with different dispersal abilities and that corridors may provide essential pathways for movement and colonization.

One hypothesized mechanism underlying increased survival of dispersing organisms in patches connected by habitat corridors includes increased immigration rates into patches, leading to increased species richness or diversity, increased population sizes of a particular species alleviating population extinction (rescue effect), and reduction of inbred populations (Noss, 1987). The positive response to habitat corridors may also be explained by increased protection from predators during dispersal (Noss, 1987).

Conversely, the potential negative consequences of habitat corridors may include increased predation through the promotion of predator movement, as well as increased spread of disease, fire, and exotic species (Simberloff and Cox, 1987; Simberloff, 1992; Hess, 1994). Blue crabs used seagrass corridors as pathways to oyster reefs to prey on bivalves (Micheli and Peterson, 1999). Moreover, estuarine macro-invertebrate abundance was higher within isolated patches than patches connected with seagrass, due to reduced predation pressure (Micheli and Peterson, 1999). Hence, corridors may increase predation rates of macrofauna in connected patches. To determine the cost and benefits of habitat corridors, measurements focusing on movement, species abundance and diversity, and predation-induced mortality should be collected concurrently.

Organism dispersal ability needs to be considered when investigating the effects of spatial scale on their movement and colonization patterns within fragmented landscapes. The movement patterns of organisms at any spatial scale may be affected by the internal physiological state, age, or life history stage of an individual (Ims, 1995). The degree of mobility generally changes depending on these factors, therefore one would expect that organism mobility would determine the spatial scale at which an organism perceives and responds to the landscape. For example, small estuarine

macrofauna were more sensitive to habitat patchiness than larger macrofauna at scales of $< 4\text{m}^2$ (Eggleson et al., 1999). Also for species that dispersed over large distances (100s of m), distance between patches and overall spatial arrangement did not affect local population size (Fahrig and Paloheimo, 1988). Hence, marine organisms with different levels of dispersal ability should respond to spatial scales of patchiness or the presence of habitat corridors differently.

The spatial distribution of habitat patches can greatly impact the dispersal ability of marine organisms, colonization rates of habitat patches, and survival rates of animals moving through a habitat. Proximity and number of available habitat patches may promote movement and may increase abundance and species diversity in fragmented habitats. Species diversity within kelp holdfast communities was greater when patches were either numerous or proximate (Goodsell and Connell, 2002). Abundance of pinfish, *Lagodon rhomboides*, increased in salt marsh areas associated with seagrass beds compared to isolated marshes (Irlandi and Crawford, 1997). Increased foraging opportunities (Micheli and Peterson 1999) and reduced risk of predation (Irlandi et al., 1995) in structured versus non-structured habitat may explain the increased abundance of blue crabs and bay scallops found in patches within close proximity of one another.

Studies focusing on landscape ecology issues in marine systems have mainly focused on the relationship between patch size and interpatch distance on growth, movement rates, and colonization by marine organisms (Irlandi et al., 1995, 1999; Irlandi, 1997; Eggleson et al., 1998, 1999). Few studies have been conducted in the marine environment to test the efficacy of habitat corridors (but see Micheli and Peterson 1999, Brooks and Bell 2001). Blue crabs used seagrass corridors to move between oyster

reefs and salt marsh vegetation, and predation by blue crabs on prey species was greater in oyster reefs connected by seagrass than those separated by bare sediment (Micheli and Peterson, 1999). Faunal exchange in seagrass through mobile, drift algal corridors has been investigated and amphipod abundance was higher in clumps of drift algae that passed through seagrass beds compared to those that remained in bare sediment or seagrass beds (Elis, 1998; Brooks and Bell, 2001). The cumulative evidence (Irlandi et al., 1995, 1999; Irlandi, 1997; Micheli and Peterson, 1999) suggests that some marine organisms are likely to use corridors for movement. The purpose of this study was to determine whether estuarine macrofauna use habitat corridors in seagrass systems.

Seagrass beds are important nursery areas for a variety of invertebrate and fish species. Patterns of seagrass coverage in shallow marine environments range from continuous meadows of over 100m² to patches that are 1-10's m² (Fonseca and Bell, 1998). Seagrass is a naturally fragmented habitat, which is created and changed by tidal currents and wave action (Fonseca, 1992). However, anthropogenic effects such as scars from boat propellers, trawls, and dredging often destroy this habitat causing further fragmentation (Fonseca, 1992; Townsend and Fonseca, 1998). Increased damage to seagrass beds has led to worldwide programs of seagrass restoration (Fonseca, 1992; Kirkman, 1992). Information regarding the role of habitat corridors in facilitating organism movement between habitats is central to restoration plans. The patchy nature of seagrass beds naturally lends them to field tests of landscape ecological principles in the marine environment (Brooks and Bell, 2001).

The goal of this project was to assess the role of habitat corridors on organism dispersal success, predation-induced mortality rates, and colonization in an estuarine

environment. Specifically, we assessed the effects of 1) habitat corridor (presence or absence of connection), 2) interpatch distance (distance between seagrass patches), and 3) the ratio of corridor width to patch width on dispersal success of and relative predation rates on two estuarine species with varying dispersal abilities. Grass shrimp, *Palaemonetes* sp., represented a relatively rapid disperser (moved through areas measuring 0.56m² in 24 hours) and the bay scallop, *Argopecten irradians*, represented a relatively slow disperser (swam 4m in 45 minutes) (Howard, 1985; Winter and Hamilton, 1985). Dispersal between patches was measured directly through mark-recapture experiments and predation-induced mortality was assessed using tethering experiments. We also examined the effects of 4) habitat corridor and interpatch distance on short-term colonization of seagrass by estuarine macrofauna. Patterns of colonization were examined according to species, taxonomic group, and organism dispersal ability.

Methods

Study sites

This study was conducted at Middle Marsh, Back Sound, North Carolina and Drum Shoals, Bogue Sound, North Carolina (Figure 1). Experiments were conducted at Middle Marsh from 11 June to 11 July 2002, as well as 1-28 August 2002 in creeks with unstructured bottom surrounded by salt marsh, (primarily *Spartina alterniflora*) (see Eggleston et al., 1998, 1999; Elis, 1998 for a detailed description of study site). The subtidal areas surrounding Middle Marsh contained seagrass beds with two predominant species: *Zostera marina* and *Halodule wrightii*, as well as oyster reef (*Crassostrea virginica*) habitat (Eggleston et al, 1998, 1999). The closest seagrass bed to the experiments was approximately 20m away. During flood tide the flow in Middle Marsh

was in a northeast direction, and opposite during the ebb tide (Figure 1). The depth range was between 0.1m and 2.5m.

Experiments were conducted at Drum Shoals during 16-29 July 2002, in a channel along the eastern side of the shoal in unstructured, sandy habitat (Figure 1). Small seagrass patches ($<1\text{m}^2$) of *Zostera marina* were distributed sparsely throughout the shoal, however the dominant subtidal substrate was sand. The closest seagrass patch to the experiments was approximately 15m away. Flood and ebb tide flow moved in a north-south direction and the depth range was between 0.5m and 2.5m. Currents appeared to flow faster at Drum Shoals than Middle Marsh (personal observation).

Artificial seagrass units

This study utilized artificial seagrass units (ASUs) similar to those used by Eggleston et al. (1998, 1999) and Elis (1998). The ASUs were deployed within unvegetated sand flats and tidal creeks at the study sites to create a mosaic of isolated and connected patches. Frames measuring 0.25 m^2 (50 cm length x 50 cm width x 3 cm deep) were constructed with PVC pipe with 500 μm mesh lining the bottom. Each 0.25 m^2 ASU contained 300 blades of artificial seagrass (made of green, polypropylene ribbon), which is equivalent to natural densities (1200 m^2) in Middle Marsh (Elis, 1998). The ASUs were anchored at each corner to the bottom substrate using a J-shaped stake.

Using ASUs eliminated confounding factors such as patch shape, blade density and degree of epiphytism (Bell and Hicks 1991; Elis, 1998). The use of ASUs as an effective substitute for natural seagrass is well documented; ASUs are colonized by estuarine macrofauna in a manner similar to natural seagrass (Virnstein and Curran, 1986; Sogard, 1989; Elis, 1998).

Experimental benthic landscapes

A total of five experimental landscapes were used to test hypotheses concerning the influence of habitat corridors, interpatch distance, corridor width to patch width ratio and perimeter to area ratio on dispersal success and predation induced mortality. To test for the influence of habitat corridor and interpatch distance on dispersal success of shrimp and scallops, as well as predation induced mortality on scallops, the treatments had a standardized patch size (1m^2) and interpatch distance was varied (5m or 10m) (Figure 2). To test for corridor width to patch width ratio effects on dispersal, patch size was varied (1m^2 or 4m^2), as was interpatch distance (5m or 10m), yielding corridor width to patch width ratio measuring 0.5m:1m or 0.25m:1m (Figures 3). One patch was randomly chosen to be the donor patch, where marked animals were placed at the start of the experiment, and the other the receiver patch (Figures 2 and 3). The treatments were randomly placed in areas with unstructured bottom with approximately 15m-20m between each pair of donor and receiver patches.

To measure the response of predation-induced mortality to perimeter to area ratio the five experimental treatments were used (Figure 4). Perimeter to area ratio measured either 4m: 1m^2 or 2.69m: 1m^2 . To effectively reduce perimeter to area ratio the patch size of one treatment was increased 4m^2 (Figure 4).

Four experimental landscapes (Figure 2) were used to test hypotheses concerning the influence of habitat corridor and interpatch distance on colonization of seagrass by estuarine macrofauna. The size of each seagrass patch was standardized to 1m^2 . We manipulated connectivity between patches (presence or absence of a habitat corridor) and interpatch distance (5m and 10m). The manipulation of connectivity and interpatch

distance yielded four combinations of each factor (Figure 2) with three replicates. Each treatment was randomly placed along a 45m transect within the experimental creek, with 15m of separation between treatments.

Dispersal of shrimp and scallops

Mark-recapture experiments were conducted with shrimp and scallops during 4 June to 20 August 2002. The following null hypothesis was tested: dispersal success, defined as the number of marked individuals initially placed in a donor patch and found alive within the corresponding receiver patch, would not vary according to the presence or absence of a habitat corridor, corridor length, corridor width, or relative dispersal ability of the animals. This experiment was set up as in Figures 2 and 3 to test the influence of the habitat corridor, interpatch distance, and corridor width to patch width ratio on shrimp and scallop dispersal.

We chose two target species with different levels of dispersal ability. Grass shrimp, *Palaemonetes* sp., are highly mobile and cover short distances in a short period of time (Howard, 1985), and were designated as a rapid disperser. The bay scallops, *Argopecten irradians*, are more sedentary and were designated as a slow disperser. Mark-recapture experiments were carried out to measure dispersal of grass shrimp and bay scallops between seagrass patches. Grass shrimp were collected from marsh creeks using sweep nets and a beam trawl. Live animals were transported to a laboratory at the nearby North Carolina State University's Center for Marine Science and Technology, Morehead City, North Carolina, in coolers filled with aerated seawater on the day of capture. Grass shrimp were batch marked using vital stains, neutral red or methylene blue, which are effective methods for marking crustaceans (Howard, 1985; Etherington et

al., 2003). Grass shrimp were placed in aerated tanks of water mixed with either neutral red (concentration 1.43 g/l) or methylene blue (0.12g/l) stain where they remained for twelve hours (Perkins-Visser et al., 1996; Etherington et al. 2003). Mortality associated with these staining techniques is negligible (Howard, 1985; Etherington et al., 2003). Retention for neutral red stain in crustacean tissue is approximately seven molts (Howard, 1985; Perkins-Visser et al., 1996), whereas methylene blue stain is retained for greater than 24 hours (Etherington et al., 2003).

Bay scallops were collected by hand, using mask and snorkel, from Oscar Shoal, Back Sound, North Carolina. Live animals were transported in damp mesh bags and were transferred to raceways filled with seawater upon arrival at the laboratory. Bay scallops were marked using a stripe of colored nail polish on the upper valve (the darker colored valve) of each scallop and were painted one of five colors associated with the five treatments. Painting the shells of snails or bivalves is an effective marking technique and the mark remains on the shell for several weeks (Eggleston, 1988).

Experiments involving grass shrimp or bay scallops were carried out separately to minimize interspecific interactions between focal individuals. Inglis and Underwood (1992) recommend seeding experimental habitat patches with densities that are an order of magnitude greater than natural densities to promote density-dependent movement, however this was not realistic for this study because of the number of shrimp and scallops that would be needed in combination with the temporal scale of the experiments.

Densities of marked individuals released in a donor patch were species dependent and were two times the natural density found in Middle Marsh. Approximately 300 and 1200 grass shrimp, or 62 and 248 bay scallops were placed within small (1m^2) and large (4m^2)

donor patches, respectively. The total number of marked animals for each treatment was allocated evenly and placed within the individual ASUs that made up a given donor patch (Figure 2 and 3). The organisms were placed within an ASU and held in place with an inverted 0.25 m² box sieve for 15 minutes to allow for acclimation (Elis, 1998; Blackmon and Eggleston, 2001). After acclimation, removal of the box sieve allowed the marked individuals to move freely. Howard (1985) determined that mobile epifauna such as Palaemonid shrimp and gastropds were able to move through areas of 0.56m² within approximately 1-2 days, therefore recapture attempts for grass shrimp and bay scallops were initially conducted 24 hours and 4 days after release, respectively.

Four ASUs from the receiver patches from each treatment were sampled on recapture days for grass shrimp. Recapture involved placing a box sieve over each 0.25 m² ASU. This allows for easy removal of ASUs from the water. This technique is successful at capturing highly mobile species, such as pinfish, *Logodon rhomboides*, as well as less mobile species (Eggleston et al., 1998, 1999; Elis, 1998). The collected ASUs were placed within separate plastic bags for transport to shore-based facilities for preliminary sorting. The contents of the ASUs were sieved with a 500µm screen and marked individuals were identified immediately. After sorting, all samples were preserved in 70% ethanol (Elis, 1998). Due to easy detectibility of scallops within the ASUs, each ASU was collected and the number of bay scallops was noted immediately during collections.

The response variable was the number of marked bay scallops that successfully dispersed from a donor patch to the corresponding receiver patch (Figure 2). The interactive effects of the presence or absence of habitat corridors, interpatch distance, and

site on successful dispersal between seagrass patches were analyzed using a three way ANOVA model with site (Middle Marsh and Drum Shoal), habitat corridor (presence or absence), and interpatch distance (5m and 10m) as factors. The effect of the ratio of corridor width to patch width on the total number of marked bay scallops within a receiver patch was analyzed with a two-way ANOVA with site (Middle Marsh and Drum Shoals) and corridor width to patch width ratio (0.5m:1m and 0.25m:1m) as the main factors. All analyses were preceded by Levene's test for homogeneity of variance. Response variables were transformed by $\log_{10}(x+1)$ when variances were heterogeneous. If variances were heterogeneous after transformation, then hypotheses were rejected at alpha levels below the p-value at which variances were significantly heterogeneous (Underwood, 1981).

Predation-induced mortality of scallops

Tethering experiments were conducted concurrently with the dispersal experiments to test the following null hypotheses: 1) predation-induced mortality of bay scallops will not vary according to the presence or absence of habitat corridors or corridor length, and 2) predation-induced mortality will not vary according to perimeter to area ratio. These hypotheses were addressed to determine if habitat corridors are used to enhance predation by focusing predatory movement between patches or whether increasing perimeter to area ratios with greater isolation between patches allow for greater predation. Information on predation-induced mortality would presumably help understand distribution and abundance patterns identified in the mark-recapture experiments for scallops. Tethering was accomplished by affixing 10-pound test monofilament line with cyanoacrylate glue to the shell of bay scallops (Heck and Thoman, 1981; Heck and

Wilson, 1987; Pile et al., 1996; Kneib and Scheele, 2000; Hovell and Lipcius, 2001).

The other end of the monofilament line was connected to a brass swivel clip, which was clipped to a J-shaped metal stake that acted as an anchor.

The organisms were tethered at two randomly chosen corners of the donor and receiver patches, as well as two randomly chosen locations along the edge of the corridor and within the bare sediment of the isolated treatments. One animal was tethered at each location. The tethered animals were checked every twenty-four hours for the duration of the 4-day experiment and mortality was recorded. To test hypotheses concerning the influence of habitat corridor and interpatch distance experiments were set up as in Figure 2, whereas to test hypotheses concerning perimeter to area ratio experiments were set up as in Figure 4.

The interactive effects of the presence or absence of habitat corridor and interpatch distance on the relative rates of predation-induced mortality per 24 hours on bay scallops were analyzed with a two-way ANOVA model with habitat corridor (presence or absence) and interpatch distance (5m and 10m) as factors. A one-way ANOVA was also used to test the effect of perimeter to area ratio (4m:1m² and 2.69m: 1m²) on scallop mortality.

Colonization by estuarine macrofauna

Given the general lack of response of scallops and shrimp to the experimental treatments (see below), we assessed the effects of corridors on colonization by estuarine organisms to help discern what species or taxonomic groups of species might respond to the presence or absence of habitat corridors at the spatial scales (5-10m) examined in the mark-recapture experiments. Four experimental seagrass configurations (Figure 2) were

set out in a creek within the Middle Marsh creek system during rising tide on 29 July 2002 to test the following null hypothesis: mean densities and number of species of seagrass associated organisms, regardless of taxonomic or mobility group, will not differ in isolated patches and patches connected by a corridor. ASUs were left for one month to allow for colonization before removal.

On 28 August 2002 during rising tide, two randomly selected ASUs from each patch and corridor were retrieved (Figure 2). The ASUs were retrieved simultaneously by quickly placing 0.25m^2 box sieves, which were lined with $500\mu\text{m}$ mesh, around the edges of the ASU (as described above). The contents of the ASU were sieved with a $500\mu\text{m}$ box sieve and preserved in a 70% ethanol solution. All organisms were identified to species in the laboratory. The individual species were assigned to specific taxonomic and dispersal groups. The dispersal groups were categorized as slow, intermediate or rapid dispersers based on dispersal estimates over space and time. The interactive effects of habitat corridors (presence or absence) and interpatch distance (5m and 10m) on the mean density of estuarine macrofauna and mean densities of species within taxonomic and dispersal groups colonizing the ASUs as well as diversity of colonizers per 0.25m^2 were examined with a two-way ANOVA model.

Results

Dispersal of shrimp and bay scallops

A total of 2400 grass shrimp were marked and released into the experimental ASUs. When no grass shrimp were recaptured after 24 hours, we conducted a pilot study to assess shrimp recapture success at shorter distances between patches and a shorter release time. We established two 1m^2 patches connected by a 1m corridor and two 1m^2 patches separated by 1m. One hundred stained grass shrimp were placed in a 1m^2 ASU patch of

each treatment and left to disperse. After one hour, we sampled the ASUs and again recaptured zero marked grass shrimp. Since the stains used to mark the shrimp lasted 24 hours in laboratory trials and the ASU retrieval technique effectively captures grass shrimp (Eggleston et al., 1998), we concluded that grass shrimp exhibit extremely rapid dispersal (<1hr) at spatial scales greater than tens of meters.

On average, only 0.44% (SE = 0.27%) and 0.72% (SE = 0.23%) of total number of scallops placed into treatments with and without a habitat corridor, respectively, dispersed to the matching receiver patch. Approximately 33% (SE = 6.36%) and 42% (SE = 6.52%) marked scallops placed in ASUs with and without a habitat corridor, respectively, remained within the donor patch. Approximately 5% scallops placed into treatments with a habitat corridor moved into the corridor. A large percentage of marked scallops were missing from the experimental treatments indicating that the scallops either emigrated from the experimental treatments or experienced mortality. The percentage of missing scallops placed into treatments with corridors was equal to 61% and the percentage missing in treatments without corridors was equal to 57%.

The number of scallops that successfully dispersed to corresponding receiver patches did not vary according to the presence of habitat corridors or to interpatch distance (Table 1). There was, however, a significant site effect (Table 1), with the number of scallops successfully dispersing to a receiver patch significantly higher at Drum Shoals than at Middle Marsh (Figure 5). No interaction effects were significant (Table 1). The number of scallops that successfully moved to an associated receiver patch did not vary according to the ratio of corridor width to patch width (Table 2).

Predation-induced mortality of scallops

Relative predation rates did not vary with site, the presence of a habitat corridor, or interpatch distance; however, there was a significant site x interpatch distance interaction effect (Table 3). Relative predation rates on scallops were greater in treatments with a long interpatch distance (10m) at Middle Marsh than at Drum Shoal, whereas relative predation rates on scallops in treatments with relatively short interpatch distances were higher at Drum Shoal than Middle Marsh (Figure 6).

Relative predation rates on bay scallops did not vary according to the ratio of perimeter to area (Table 4). The relative predation rates on scallops were approximately equal, with 0.11 (SE = 0.021) and 0.095 (SE = 0.038) scallops eaten per 24 hours, for treatments with 4m : 1m² and 2.69m : 1m² perimeter to area ratios, respectively.

Colonization by estuarine macrofauna

A total of 19,379 individuals, consisting of 98 species from 12 taxonomic groups colonized the ASUs over one month, including 15 amphipods, 20 bivalves, 16 shrimp, 12 polychaetes, 13 gastropods, 8 crabs, 6 fish, 4 isopods, and 1 species each of copepod, ostracod, tanaid, and sea cucumber (Appendix Table 1). The samples were dominated by two gastropod species, *Crepidula fornicata* (32% of total abundance) and *Bittium varium* (28%), followed by amphipod species, *Melita nitida* (4.5%), *Ampithoe longimana* (4.5%), and *Corophium ascherium* (3.7%) and polychaete species, *Lumbrinerius tenuis* (3.1%), *Sabellaria vulgaris* (3.7%), and *Nereis succinea* (1.9%).

There was no statistically significant effect of the presence of habitat corridors or interpatch distance on the mean density of organisms colonizing ASUs and there was no significant interaction effect (Table 5). However, a pattern was observed where mean

density of estuarine macrofauna colonizing the ASUs was greater in patches connected by a corridor (5m and 10m) and in isolated treatments separated by 5m than isolated treatments separated by 10m (Figure 7). This pattern led us to compare the mean densities of organisms colonizing the connected treatments with 5m and 10m corridors and the isolated treatment separated by 5m with the isolated treatment separated by 10m using a one-way ANOVA with treatment as the main factor. The comparison was statistically significant, with significantly greater mean densities within treatments connected by 5m and 10m corridors and isolated patches separated by 5m than mean densities in patches separated by 10m (Table 6). There was no statistically significant effect of habitat corridor or interpatch distance on the number of species colonizing ASUs (Table 7). None of the interaction effects were significant (Table 7).

Ninety-six percent of the individuals fell in the following five categories: gastropods (61.5%), amphipods (18%), polychaetes (10.3%), shrimp (4.2%), and bivalves (2.9%). The mean density of individuals falling in these groups was analyzed with a two-way ANOVA model to determine the effects of habitat corridor (presence or absence) and interpatch distance (5m and 10m) on colonization by a particular taxonomic group. All ANOVAs were carried out separately for each taxonomic group. No statistically significant effect for habitat corridor or interpatch distance was found (all $p > 0.05$); however, amphipods, gastropods, polychaetes, and bivalves exhibited a pattern where mean density was greater in patches connected by a corridor (5m and 10m) and in isolated treatments separated by 5m than isolated treatments separated by 10m (Figure 8). This pattern led us to compare the mean densities of amphipods, gastropods, polychaetes, and bivalves colonizing the patches of the two connected treatments with 5m and 10m

corridors and isolated patches separated by 5m with the isolated patches separated by 10m using a one-way ANOVA with treatment as the main factor. The comparisons were carried out separately for each taxonomic group. The comparison was not statistically significant for amphipods, polychaetes, or bivalves (Tables 9, 10, 11, Figures 7b, c, d). The mean densities of gastropods within the patches of the two connected treatments with 5m and 10m corridors and isolated patches separated by 5m, however, were significantly greater than in the isolated patches separated by 10m (Table 8, Figures 8a).

There was no statistically significant effect of habitat corridor or interpatch distance on the mean densities of individuals with varying assumed dispersal abilities (slow, intermediate, and rapid) colonizing ASUs (Tables 12, 13, 14). Interaction effects were not statistically significant (Table 12, 13, 14). Slow dispersers included gastropods, bivalves, and polychaetes, intermediate dispersers included amphipods, copepods, isopods, ostracods, and tanaids, and rapid dispersers included shrimp and crabs. Slow and intermediate-level dispersers exhibited a pattern where mean density was greater in patches connected by a corridor (5m and 10m) and in isolated treatments separated by 5m, than isolated treatments separated by 10m (Figure 9a, b). This pattern led us to compare the mean densities of slow and intermediate-level dispersers colonizing the patches of the two connected treatments connected by 5m and 10m corridors and the isolated patches separated by 5m with the mean densities within the isolated patches separated by 10m. Comparisons were carried out separately for each dispersal group. The mean densities of slow dispersers within the connected patches with 5m and 10m corridors and the isolated patches separated by 5m was significantly higher than in

isolated patches separated by 10m (Table 15), however the comparison was not significant for intermediate-level dispersers ($p > 0.05$).

Discussion

This study is one of the first attempts to specifically investigate the influence of habitat corridors at a small spatial scale in estuarine systems. We incorporated and tested much of the existing corridor theory, such as the presence/absence of corridors, corridor length and width, perimeter to area ratio, and organism dispersal ability. Unlike many of the terrestrial studies resulting in a positive response to habitat corridors, this study demonstrated that seagrass habitat corridors (presence or absence), interpatch distance, and the ratio of corridor width and patch width did not influence grass shrimp or bay scallop dispersal between patches, or predation induced mortality of bay scallops. We also demonstrated that habitat corridors and interpatch distance did not influence the number of species or the mean density of estuarine macrofauna colonizing artificial seagrass patches. However, overall mean density and mean densities of certain taxonomic groups (amphipods, gastropods, and polychaetes), as well as animals with relatively slow dispersal abilities were significantly influenced by the presence of corridors when patches were isolated by a large distance (10m).

The results from the present study do not confirm that habitat corridors are widely used by estuarine macrofauna for dispersal or colonization at relatively small spatial (10s of m) and temporal (hours to months) scales. Unlike terrestrial systems, the marine environment is three-dimensional increasing the complex nature of organism dispersal. We therefore need to consider the unique nature of the marine environment when

investigating dispersal and colonization by marine organisms in response to landscape features.

Patterns and possible mechanisms for grass shrimp dispersal

Grass shrimp are a highly mobile species and within seagrass beds can have a complete turnover of individuals in areas measuring as small as 0.56m^2 in 24 hours (Howard, 1985; this study). Hence, our recapture schedule of grass shrimp seemed appropriate to maximize movement between seagrass patches. Our recapture attempts, however, resulted in zero grass shrimp suggesting that the presence of a habitat corridor, interpatch distance, and the ratio of corridor to patch width do not influence grass shrimp dispersal between seagrass patches at a scale of 10s of m and over 24 hours. Shrimp dispersal over the entire life history can range from 1m – 1000's of kilometers (Gillanders et al., 2003). Perhaps because of their large dispersal range, grass shrimp did not respond to the presence or absence of habitat corridors or corridor features in this study.

Patterns and mechanisms for bay scallop dispersal

Bay scallops have evolved the capacity to swim over short, horizontal distances (Peterson et al., 1982; Powers and Peterson, 2000). They clap their valves together while water is siphoned and forced out of the mantle cavity, which propels the scallop (Peterson et al., 1982; Winter and Hamilton, 1985). Bay scallop movement can be in response to a predator stimulus (Peterson et al., 1982; Winter and Hamilton, 1985), chemical and visual cues from seagrass beds (Hamilton and Koch, 1996), and the interaction of density dependent dispersal with increasing flow (Powers and Peterson, 2000). Scallops placed in bare sand swam approximately 4m in 45 minutes, in a series of repeated bursts,

towards perceived seagrass (Winter and Hamilton, 1985). Thus, the spatial scale and timing of recapture for this experiment also seemed reasonable. Although bay scallop dispersal was not influenced by the presence of habitat corridors, interpatch distance, or the ratio of corridor to patch width, it did vary according to study site; with higher dispersal at Drum Shoals than Middle Marsh. Site-specific differences in dispersal may have been due to differing flow.

Although not quantified, the flow at Drum Shoals appeared stronger than the flow at Middle Marsh (personal observation). Also, the orientation of the treatments at Middle Marsh was perpendicular to the current, whereas the treatments at Drum Shoal ran more parallel with the current. Scallop movement parallel with current flow at Drum Shoals may have facilitated bay scallop dispersal at this site leading to a significant site effect on scallop dispersal success to receiver patches. Densities of marked scallops in this study were double those of natural populations in Back Sound, NC, but were similar to the densities used in a study conducted by Powers and Peterson (2000), which induced density-dependent movement in high flow areas. Thus, it was somewhat surprising to observe relatively little movement of scallops in this study (0.08 - 0.55 scallops/day). The generally limited movement of scallops observed in this study may have been due to relatively low flow at both sites since our experimental scallop densities were similar to those of Powers and Peterson (2000), which elicited density-dependent emigration in their study.

Patterns and possible mechanisms for predation-induced mortality of bay scallops

Relative rates of predation-induced mortality were measured by tethering scallops within and adjacent to the ASUs. Although behavioral artifacts can be produced and

higher rates of predation are sometimes observed when implementing tethering techniques (Peterson and Black, 1994; Kellison et al., 2000; 2003), tethering is considered a powerful technique for measuring relative rates of predation as a function of experimental treatments. Tethering bias is minimal for organisms exhibiting anti-predator behaviors that do not rely on rapid escape (Heck and Wilson, 1987). Although bay scallops sometimes swim to avoid predators, they also rely on camouflage to blend into their seagrass environment (Winter and Hamilton, 1985). Because of their limited mobility and cryptic nature, scallops seem appropriate for the application of tethering to measure relative predation rates.

One negative aspect of habitat fragmentation is that the perimeter to area ratio of a habitat patch increases as a patch becomes smaller leading to an increased risk of predation for organisms inhabiting a particular habitat patch (Andrén, 1992). Therefore, assuming that predators respond to edge for hunting purposes and their prey items use edge for foraging increased predation-induced mortality is expected in areas where perimeter to area ratio is large. Examples where predation rates were greater in smaller than larger patch sizes include bird nests (Andrén, 1992), bivalves (Irlandi et al., 1995; Irlandi, 1997), and juvenile cod (Laurel et al., 2003). As perimeter to area ratio increases, more of the central habitat is closer to the edge making prey items more accessible to predators (Andrén, 1992).

The treatments used to determine the effects of habitat corridor and interpatch distance on predation in this study (Figure 2) had equal perimeter to area ratios (4m : 1m²), which may explain why predation-induced mortality was not significantly influenced by the presence of a habitat corridor and interpatch distance. The treatment

with the larger patch size used to test the effects of the ratio between corridor width and patch width (Figure 3) had a relatively low perimeter to area ratio ($2.69\text{m} : 1\text{m}^2$) compared to the other corridor treatments (Figure 2). Predation-induced mortality of scallops, however, was not significantly influenced by perimeter to area ratio in this study. The lack of a predation response was most likely due to the relatively large size of scallops used in this study (35-50mm shell height), which may have provided a relative refuge in size from local predators.

Predation is often controlled by prey availability and accessibility (ie., size) of the prey items. A number of bivalve species experience a relative refuge in size (Hughes and Seed, 1981; Eggleston, 1990; Juanes, 1992; Smith and Jennings, 2000 and references within). For example, mussels, *Modiolus demissa* with lengths $> 25\text{mm}$ and oysters, *Crassostrea virginica*, of approximately 45-50mm shell heights experienced a prey refuge from blue crab predators (Hughes and Seed, 1981; Eggleston, 1990). The shell heights used during the tethering experiments were relatively large (35-50mm) and potentially above the size of which local predators, other than cownose rays (*Rhinopterus bonasus*), can prey on them (Juanes, 1992 and references within).

Although predation-induced mortality of scallops in this study was not significantly influenced by habitat corridors, interpatch distance, or site, there was a significant interaction effect on predation rates between interpatch distance and site. Predation rates were greater in patches separated by 10m at Middle Marsh than at Drum Shoals, whereas predation was greater in patches separated by 5m at Drum Shoals than at Middle Marsh. One possible explanation for the interpatch distance by site effect involves predator-specific foraging efficiency under varying flow regimes. Higher flow regimes

significantly reduced predation on scallops and hard clams, *Mercenaria mercenaria*, by blue crabs due to turbulent mixing and dilution of odor plumes and increased predation on scallops by whelks (Powers and Kittinger, 2002). Whelks rely also rely on chemical cues to find prey but often bury when searching therefore their use of chemoreception may not be inhibited in high flow areas allowing for predation success (Powers and Kittinger, 2002). Higher predation-induced mortality in treatments with longer interpatch distance at Middle Marsh may be due to predators, such as blue crabs, who more effectively perceive prey items using chemical cues under relatively low flow to locate prey items (Powers and Kittinger, 2002). Conversely, higher predation-induced mortality of scallops at Drum Shoals in treatments with shorter interpatch distance may be due to relatively high flow at this site, thereby increasing mortality due to predators that chemical reception abilities are not affected by turbulent mixing, such as predatory whelks (Powers and Kittinger, 2002). Although this explanation for the interaction effect between interpatch distance and site of predation-induced mortality of scallops is highly speculative, it does highlight the need to experimentally investigate how flow mediates species-specific predator foraging success in marine systems in general, and the crab, whelk, and scallop predator-prey system likely operating in this study.

Patterns and possible mechanisms for colonization by estuarine macrofauna

Habitat corridors and interpatch distance did not significantly influence mean density and number of species of estuarine macrofauna colonizing ASUs over one month in this study. A proposed benefit of habitat corridors is that they provide a source of immigrants to patches where inhabitant populations would otherwise go extinct if the patches were fragmented, or to a patch that was not located in a position within the landscape to

initially receive dispersing organisms (Beier and Noss, 1988; Haddad, 1999). This implies that patches connected by corridors should have greater mean densities of organisms and species than in isolated patches, assuming patches undergo turnover over time and the surrounding matrix is relatively inhospitable for movement.

The hydrodynamics of the marine realm likely facilitates movement by organisms between isolated patches negating any benefit of a habitat corridor at relatively small spatial scales. For example, early juvenile blue crabs exhibit planktonic, post-larval dispersal over relatively large spatial scales (50 km) and under a variety of environmental conditions in Pamlico Sound, NC (Etherington and Eggleston, 2003). Brown shrimp, *Penaeus aztecus*, and pink shrimp, *Penaeus duorarum*, also move over spatial scales of 10s to 100s of meters when moving between juvenile and adult habitats (Gillanders et al., 2003). Water flow can lessen the degree of isolation between habitat patches by facilitating movement over potentially inhospitable habitat, effectively increasing the dispersal range and thereby increasing perception of habitat homogeneity of a particular organism. A better understanding of how hydrodynamics influence dispersal should provide insight into how an organism's perception of habitat heterogeneity varies with spatial scale (Palmer et al., 1996).

The ASUs in this study were colonized by a wide variety of organisms including amphipods, bivalves, crabs, gastropods, isopods, polychaetes, tanaids, and shrimp. Amphipods, bivalves, gastropods (statistically significant), and polychaetes showed an affinity for seagrass patches connected by a corridor and isolated seagrass patches that were within a relatively short distance (5m) of one another. This pattern of abundance indicates that relatively slow to intermediate-level dispersers may benefit from the

addition of a habitat corridor for movement, and that they may perceive isolated patches with greater than 5m separation as heterogeneous. Hypotheses regarding organism perception of spatial heterogeneity based on dispersal ability as applied to distribution and movement patterns within a landscape requires further testing.

General conclusions

The lack of importance of habitat corridors to estuarine macrofauna at relatively small scales in time and space as demonstrated in this study does not appear to hold at larger spatial scales. For example, numerous marine organisms exhibit ontogenetic habitat shifts from nursery areas to adult habitats (Gillanders et al., 2003). During different life history stages dispersal ability of a particular organism will vary, therefore their response to habitat will likely vary accordingly. Seagrass habitat structure varies at the local and landscape scale from 1m - 1000s of m, which may influence movement and predation, and shape community structure (Robbins and Bell, 1994). Determining how life history stage influences the scale of dispersal and habitat use of a particular organism will indicate an appropriate scale for sampling animal populations when questioning their response to landscape features and whether patterns exhibited at a one scale are observed at multiple scales (Robbins and Bell, 1994). Population persistence of species that exhibit ontogenetic habitat shifts relies on the presence of habitat for foraging and protection, and the ability of organisms to move between habitats successfully (Gillanders et al., 2003). Habitat corridors may provide connections between nursery and adult habitats at the scale of an entire estuary, thus ensuring persistence of the population (Beck et al., 2001). Therefore, studies investigating the influence of habitat corridors in

marine systems should focus on relatively large-scale movements at relatively large spatial scales (eg., rivers, estuaries).

The weak community-level response of estuarine macrofauna to habitat corridors in this study may have also been due to the time scale of the colonization experiment. Colonization of artificial seagrass by estuarine macrofauna is similar to colonization of natural seagrass with peak total abundance and species richness occurring within 4-8 days (Virnstein and Curran, 1986; Sogard, 1989). Elis (1998), however, found that total abundance and species diversity was greater after 4 months than after one or two months, but the greater colonization was associated with peak recruitment of shrimp and crab species. Also, in seagrass beds, crustaceans and gastropods exhibited high turnover rates, with 50% replacement of shrimp in 3 hours (Howard, 1985). Therefore, the timing of recruitment pulses and organism turnover rates should be considered when investigating the effects of landscape structures such as habitat corridors on total abundance, abundance of specific species, and species diversity in seagrass systems.

The results from this study suggest that habitat corridors do not strongly influence dispersal, predation-induced mortality, or colonization of estuarine macrofauna at relatively small scales in space (10m's) and time (1hr - 1month). This weak response is likely due to the ease of organism dispersal via currents. In terrestrial systems, the majority of dispersal is an active process, whereas in marine systems dispersal can be passive or assisted by currents indicating that habitat corridors may not be as influential to animal movement in marine environments as they appear in some terrestrial systems (Robbins and Bell, 1994; Fahrig and Merriam, 1985; Merriam and Lanoue, 1990; Henein and Merriam, 1990; Dunning et al., 1995; Haddad, 1999; Haddad and Baum, 1999;

Coffman, 2001; Tewksbury et al., 2002;). Many larval invertebrates, however, are competent swimmers and respond to habitat characteristics, whether chemical or physical, by investigating and actively settling during settlement or choosing to swim away (Qian, 1999; Berntson et al., 2000; Boxshall, 2000). Our research has led us to identify several components of marine landscape ecology that need further study. In particular, understanding the interaction between hydrodynamics, animal dispersal, habitat structure, and landscape structure will be essential in understanding how populations distribute themselves in subtidal areas, as well as determining appropriate spatial scales to test patch dynamics in marine systems (Robbins and Bell, 1994).

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Table 1: Effects of site (Middle Marsh and Drum Shoals, connection (presence or absence of habitat corridor), interpatch distance (5m and 10m) on dispersal of marked bay scallops (*Argopecten irradians*) to receiver ASU patches. Total number of successful dispersers was $\log_{10}(x+1)$ transformed. N = 4 for Middle Marsh, N = 2 for Drum Shoal. NS > 0.05; * p < 0.05.

Three-way ANOVA			
Source of variation	df	MS	F
Site (A)	1	0.171	7.83*
Corridor (B)	1	0.013	0.58 NS
Distance (C)	1	0.055	2.53 NS
A x B	1	0.010	0.47 NS
A x C	1	0.001	0.06 NS
B x C	1	0.034	1.56 NS
A x B x C	1	0.00	0.00 NS
Error	16	0.022	

Table 2: Effects of site (Middle Marsh and Drum Shoals) and corridor width to patch width ratio (0.5m:1m and 0.25m:1m) on dispersal of marked bay scallops (*Argopecten irradians*). Total number of successful dispersers was $\log_{10}(x+1)$ transformed. N = 4 for Middle Marsh, N = 2 for Drum Shoal. NS > 0.05.

Two-way ANOVA			
Source of variation	df	MS	F
Site (A)	1	0.023	1.12 NS
Width (B)	1	0.034	1.61 NS
A x B	1	0.025	1.18 NS
Error	6	0.021	

Table 3: Effects of site (Middle Marsh and Drum Shoals), corridor (presence or absence of habitat corridor), and interpatch distance (5m and 10m) on relative predation rates of bay scallops (*Argopecten irradians*). Relative predation rates were $\log_{10}(x+1)$ transformed. N=5. NS > 0.05, * p<0.05.

Three-way ANOVA			
Source of variation	df	MS	F
Site (A)	1	0.0004	0.15 NS
Corridor (B)	1	0.0009	0.03 NS
Distance (C)	1	0.0013	0.48 NS
A x B	1	0.0003	0.12 NS
A x C	1	0.0163	5.80*
B x C	1	0.0001	0.33 NS
A x B x C	1	0.0004	0.15 NS
Error	12	0.0028	

Table 4: Effects of perimeter to area ratio (4m:1m² and 2.5m:1m²) on relative predation rates on bay scallops (*Argopecten irradians*). Relative predation rates were log₁₀(x+1) transformed. N = 4. NS > 0.05.

One-way ANOVA			
Source of variation	df	MS	F
Perimeter to Area Ratio	1	0.0001	0.10 NS
Error	6	0.0005	

Table 5: Effects of habitat corridor (presence or absence) and interpatch distance (5m and 10m) on the mean density of all organisms colonizing ASUs. Mean density was log₁₀(x+1) transformed. NS > 0.05. ** 0.05 < p < 0.07.

Two-way ANOVA			
Source of variation	df	MS	F
Corridor (A)	1	0.0167	1.07 NS
Distance (B)	1	0.0397	2.55 NS
A x B	1	0.0745	4.79 NS**
Error	8	0.0155	

Table 6: Effect of treatment (four combinations of the presence or absence of corridor and interpatch distance (Figure 2)) on mean density of organisms colonizing ASUs. Contrast equals a comparison of treatments connected by corridors with interpatch distances equal to 5m and 10m as well as isolated patches with an interpatch distance equal to 5m to isolated patches separated by 10m interpatch distance. Mean density was log₁₀(x+1) transformed. NS > 0.05, * p < 0.05.

One-way ANOVA			
Source of variation	df	MS	F
Treatment	3	0.087	3.49*
Contrast	1	0.223	8.95*
Error	18	0.025	

Table 7: Effects of habitat corridor (presence or absence) and interpatch distance (5m and 10m) on species diversity within the ASUs. Species diversity was log₁₀(x+1) transformed. NS > 0.05.

Two-way ANOVA			
Source of variation	df	MS	F
Corridor (A)	1	0.75	0.01 NS
Distance (B)	1	12	0.23 NS
A x B	1	40.3	0.77 NS
Error	8	52.27	

Table 8: Effect of treatment (four combinations of the presence or absence of corridor and interpatch distance (Figure 2)) on mean density of gastropods colonizing ASUs. Contrast equals a comparison of treatments connected by corridors with interpatch distances equal to 5m and 10m as well as isolated patches with an interpatch distance equal to 5m to isolated patches separated by 10m interpatch distance. Mean density was $\log_{10}(x+1)$ transformed. NS > 0.05, * p < 0.05.

One-way ANOVA			
Source of variation	df	MS	F
Treatment	3	0.068	1.86 NS
Contrast	1	0.164	4.48*
Error	18	0.037	

Table 9: Effect of treatment (four combinations of the presence or absence of corridor and interpatch distance (Figure 2)) on mean density of amphipods colonizing ASUs. Contrast equals a comparison of treatments connected by corridors with interpatch distances equal to 5m and 10m as well as isolated patches with an interpatch distance equal to 5m to isolated patches separated by 10m interpatch distance. Mean density was $\log_{10}(x+1)$ transformed. NS > 0.05.

One-way ANOVA			
Source of variation	df	MS	F
Treatment	3	0.196	0.62 NS
Contrast	1	0.341	1.08 NS
Error	18	0.315	

Table 10: Effect of treatment (four combinations of the presence or absence of corridor and interpatch distance (Figure 2)) on mean density of polychaetes colonizing ASUs. Contrast equals a comparison of treatments connected by corridors with interpatch distances equal to 5m and 10m as well as isolated patches with an interpatch distance equal to 5m to isolated patches separated by 10m interpatch distance. Mean density was $\log_{10}(x+1)$ transformed. NS > 0.05.

One-way ANOVA			
Source of variation	df	MS	F
Treatment	3	0.0067	0.27 NS
Contrast	1	0.00006	0.00 NS
Error	18	0.0259	

Table 11: Effect of treatment (four combinations of the presence or absence of corridor and interpatch distance (Figure 2)) on mean density of bivalves colonizing ASUs. Contrast equals a comparison of treatments connected by corridors with interpatch distances equal to 5m and 10m as well as isolated patches with an interpatch distance equal to 5m to isolated patches separated by 10m interpatch distance. Mean density was $\log_{10}(x+1)$ transformed. NS > 0.05, ** 0.05 < p < 0.07.

One-way ANOVA			
Source of variation	df	MS	F
Treatment	3	0.134	1.12 NS
Contrast	1	0.266	2.21 **
Error	18	0.120	

Table 12: Effects of habitat corridor (presence or absence) and interpatch distance (5m and 10m) on the mean density of estuarine macrofauna with relatively slow dispersal abilities (eg., gastropods, bivalves, polychaetes) colonizing ASUs. Mean density was $\log_{10}(x+1)$ transformed. NS > 0.05.

Two-way ANOVA			
Source of variation	df	MS	F
Corridor (A)	1	0.0181	1.23 NS
Distance (B)	1	0.0642	4.37 NS
A x B	1	0.0517	3.52 NS
Error	8	0.0147	

Table 13: Effects of habitat corridor (presence or absence) and interpatch distance (5m and 10m) on the mean density of estuarine macrofauna with mid-level dispersal abilities (eg., amphipods, copepods, isopods, ostracods, and taniads) colonizing ASUs. Mean density was $\log_{10}(x+1)$ transformed. NS > 0.05.

Two-way ANOVA			
Source of variation	df	MS	F
Corridor (A)	1	0.0343	0.41 NS
Distance (B)	1	0.0844	1.05 NS
A x B	1	0.2029	2.53 NS
Error	8	0.0802	

Table 14: Effects of habitat corridor (presence or absence) and interpatch distance (5m and 10m) on the mean density of estuarine macrofauna with rapid dispersal abilities (eg., shrimp and crabs) colonizing ASUs. Mean density was $\log_{10}(x+1)$ transformed. NS > 0.05.

Two-way ANOVA			
Source of variation	<i>df</i>	MS	F
Corridor (A)	1	0.0427	0.74 NS
Distance (B)	1	0.0108	0.19 NS
A x B	1	0.0049	0.08 NS
Error	8	0.0574	

Table 15: Effect of treatment (four combinations of the presence or absence of corridor and interpatch distance (Figure 2)) on mean density of slow dispersers colonizing ASUs. Contrast equals a comparison of treatments connected by corridors with interpatch distances equal to 5m and 10m as well as isolated patches with an interpatch distance equal to 5m to isolated patches separated by 10m interpatch distance. Mean density was $\log_{10}(x+1)$ transformed. NS > 0.05. * $p < 0.05$

One-way ANOVA			
Source of variation	<i>df</i>	MS	F
Treatment	3	41422.9	2.20 NS
Contrast	1	115770.1	6.16*
Error	18	18795.5	

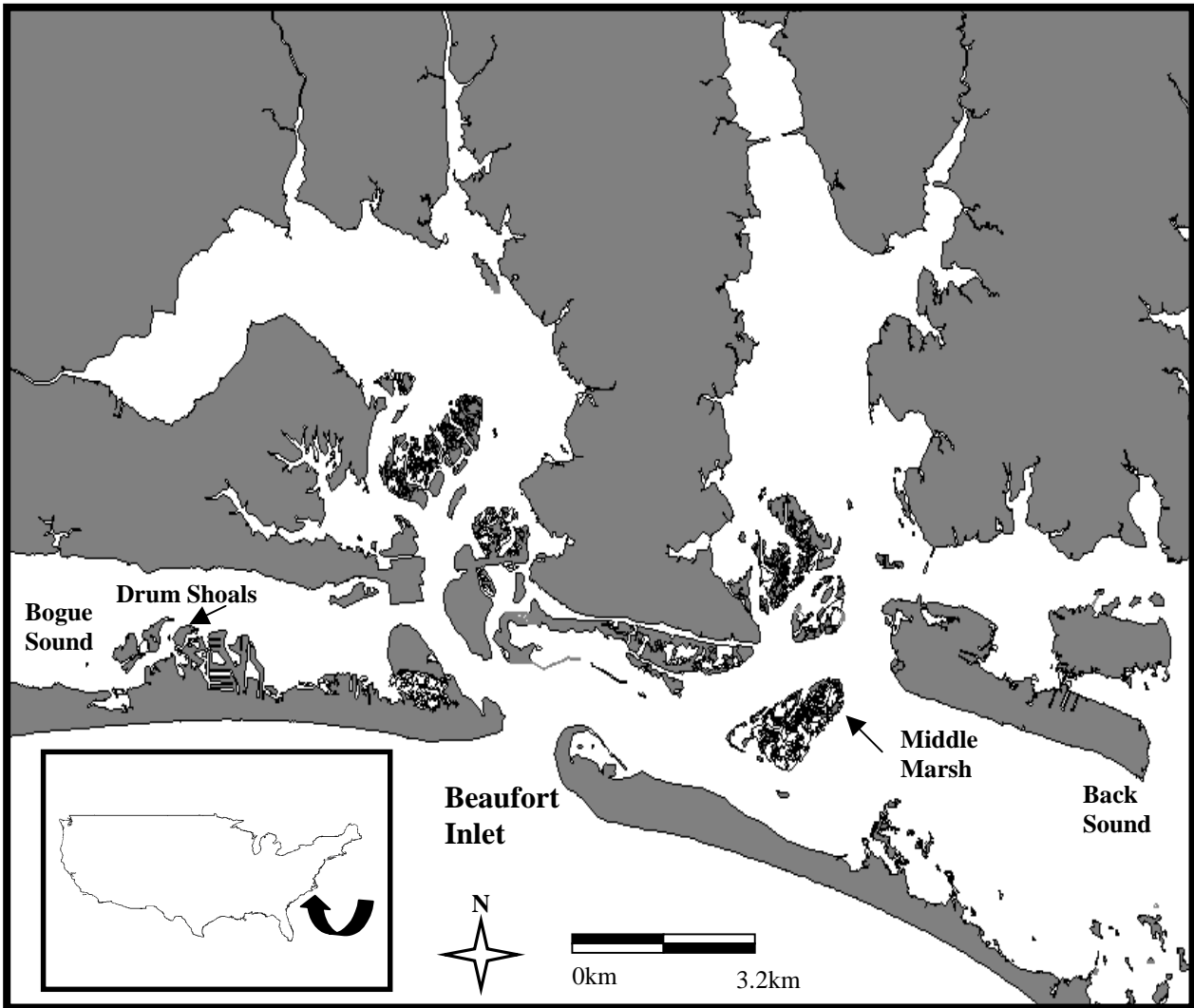


Figure 1: Study Sites, Middle Marsh in Back Sound, NC and Drum Shoals in Bogue Sound, NC.

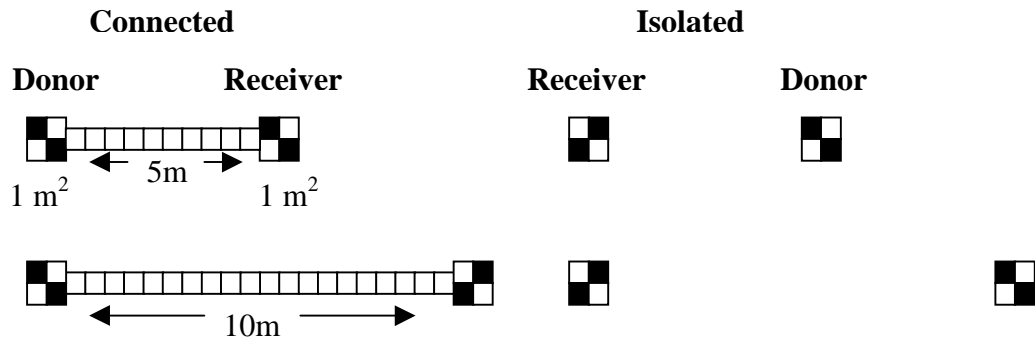


Figure 2: Schematic of experimental design used to test the main and interactive effects of the presence or absence of habitat corridors and interpatch distance. Each square represents one 0.25m² artificial seagrass unit (ASU). All replicates (N=6) of each treatment were randomly dispersed throughout the study site creek systems were carried out over time for the dispersal experiments. All replicates (N=3) of each treatment were randomly distributed throughout the study site creek simultaneously during the colonization experiments. Donor patches were randomly chosen and represented the patch where marked animals were initially released. Receiver patches were associated with a particular donor patch and represented the patch where recapture attempts occurred. Darkened boxes represent a randomly chosen ASU for sampling during colonization experiments.

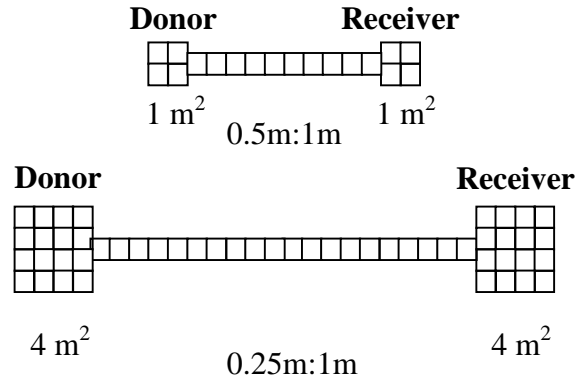
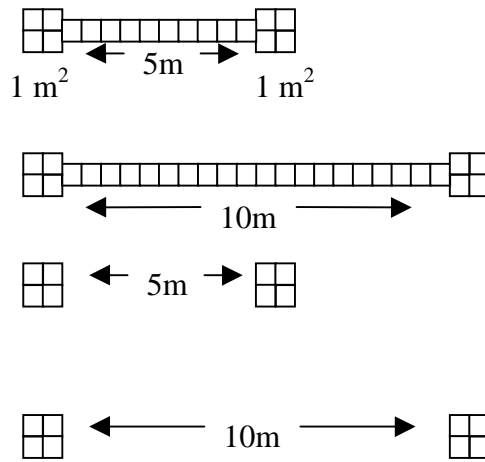


Figure 3: Schematic of experimental design used to test the main effect of corridor width :patch width ratio. Each square represents an individual 0.25m² ASU. All replicates (N=7 and 4) of each treatment were randomly dispersed throughout the creek system and replicated over time for dispersal experiments. Ratio values represent the corridor width to patch width ratio for each treatment. Donor patches were randomly chosen and represented the patch where marked animals were initially released. Receiver patches were associated with a particular donor patch and represented the patch where recapture attempts occurred.

Perimeter: Area = 4m : 1m²



Perimeter : Area = 2.69m : 1m²

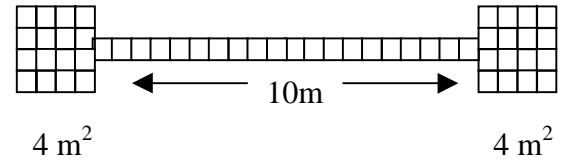


Figure 4: Schematic of experimental design to test the main effect of perimeter to area ratio on predation induced mortality. Each square represents an individual 0.25m² ASU. Two tethered scallops were placed in randomly chosen, opposing corners within each patch, one opposing side of the corridor, and within the bare substrate separating isolated patches.

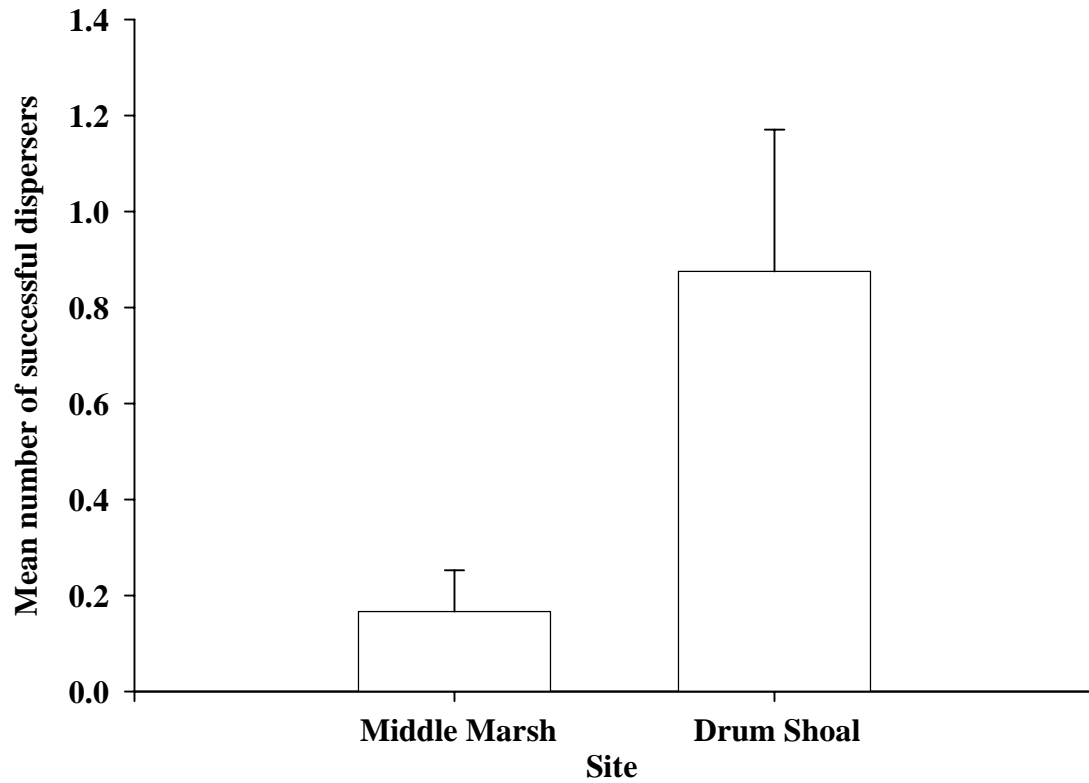


Figure 5: Mean number ($\bar{x} \pm SE$) of bay scallops that successfully dispersed to a receiver patch for a given treatment (with or without a habitat corridor, interpatch distance of 5m and 10m, and site). $N = 4$ and $N = 2$ at Middle Marsh and Drum Shoals, respectively. See Table 1 for results of statistical analysis.

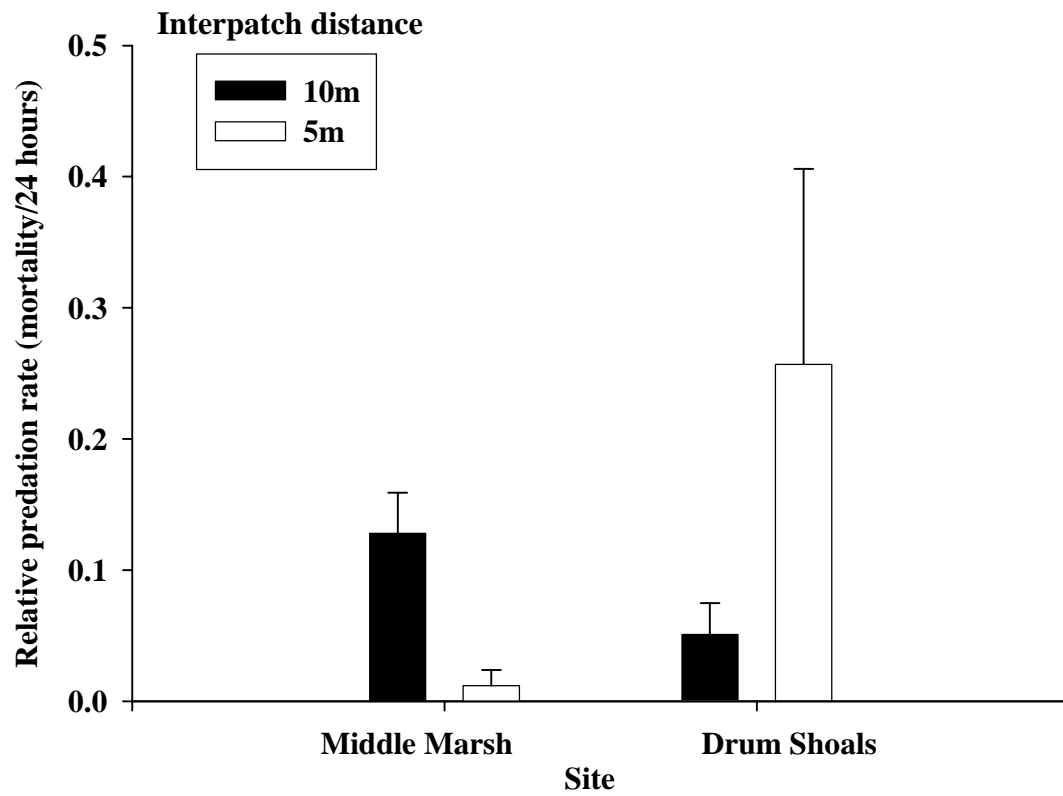


Figure 6: Mean relative predation rates (mortality/24 hours; $\bar{x} + SE$) on bay scallops as a function of interpatch distance and site (N=5). See Table 3 for results of statistical analysis.

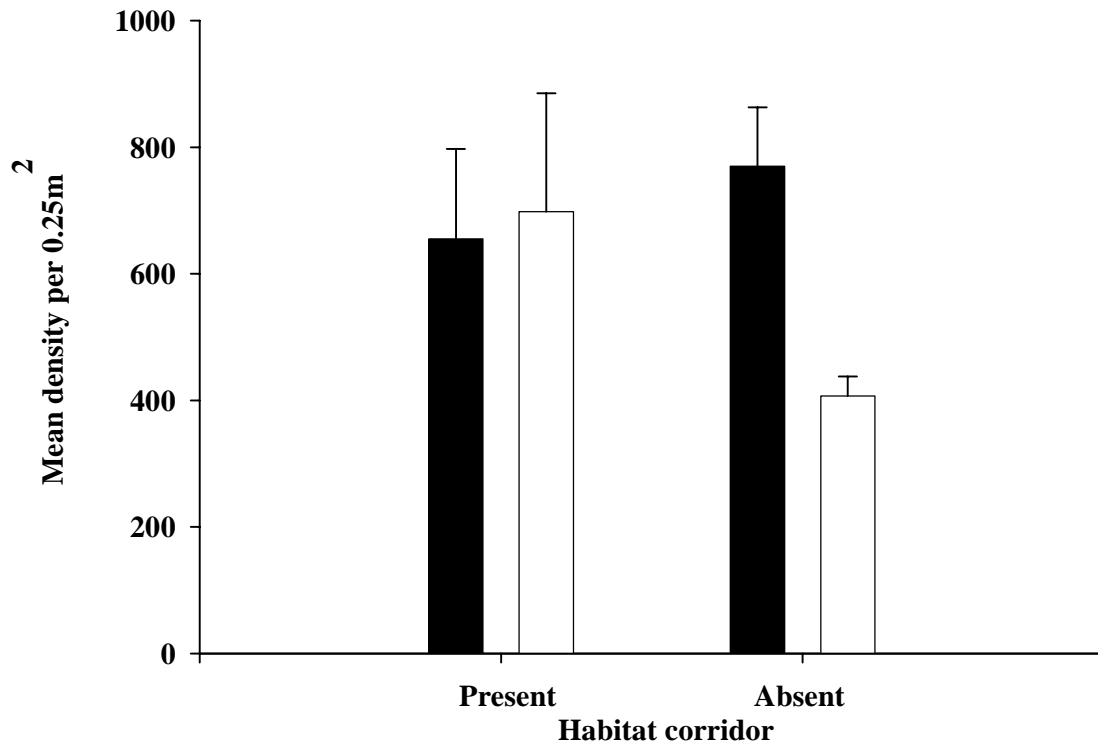


Figure 7: Effects of a habitat corridor (presence or absence) and interpatch distance (5m or 10m) on the mean density of estuarine macrofauna colonizing ($\bar{x} + SE$) ASUs. See Table 6 for results of statistical analysis.

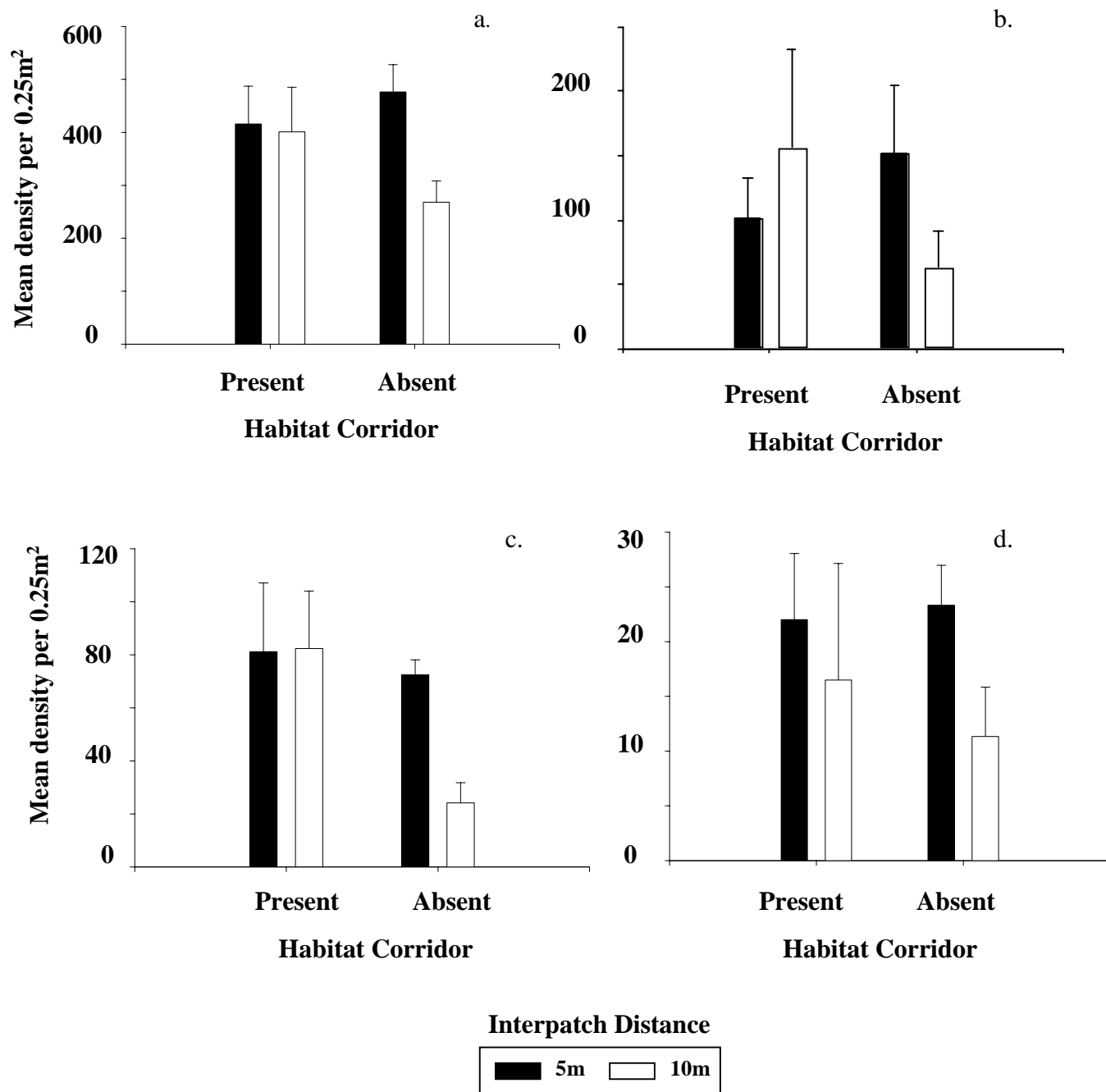


Figure 8: Effects of habitat corridor (presence or absence) and interpatch distance (5m or 10m) on colonization ($\bar{x} \pm SE$) by a.) gastropods, b.) amphipods, c.) polychaetes, and d.) bivalves per 0.25m². N = 3. See Tables 8, 9, 10, and 11 for results of statistical analysis.

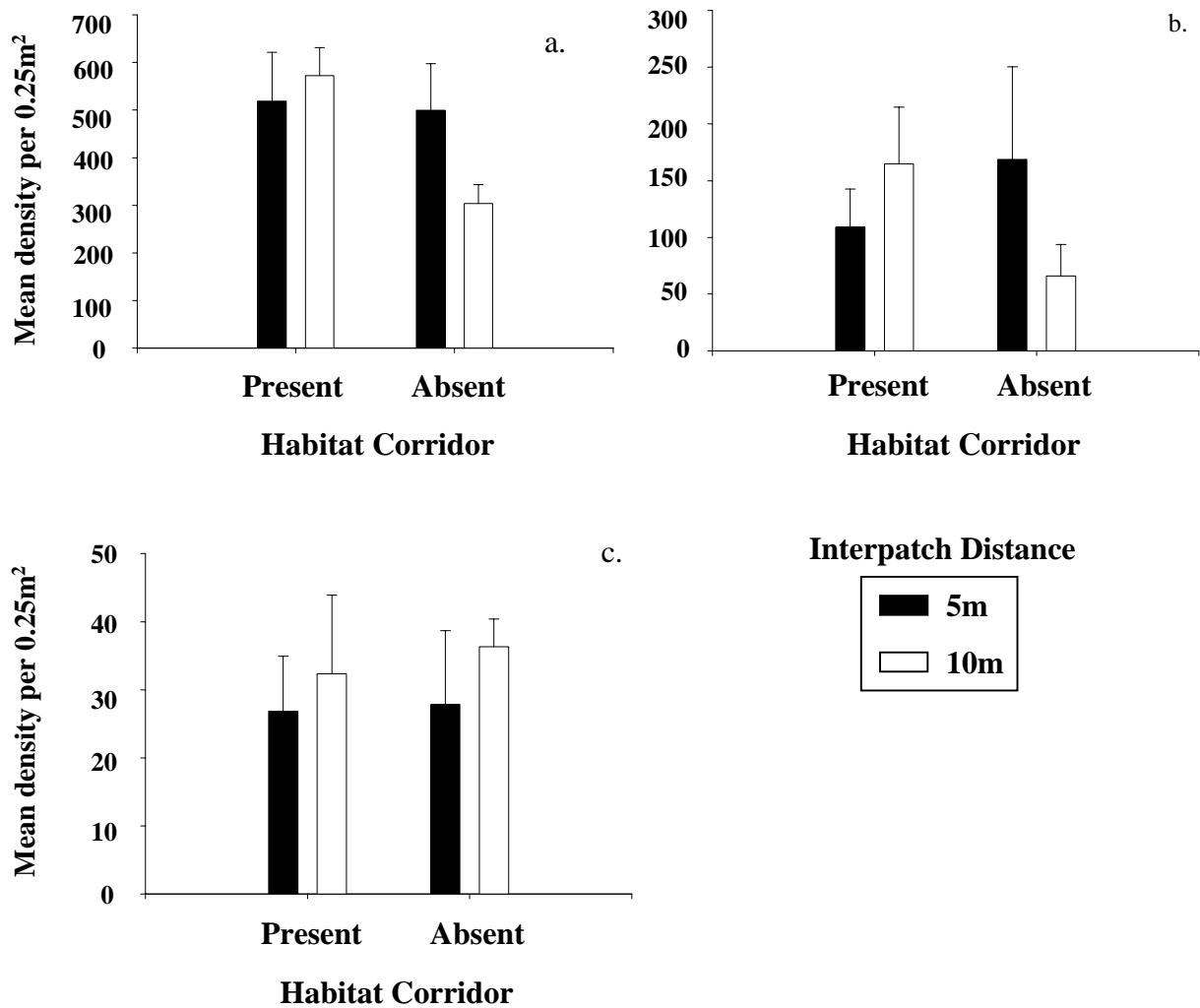


Figure 9: Effects of habitat corridor (presence or absence) and interpatch distance (5m or 10m) on colonization ($\bar{x} + SE$) by a.) slow dispersers, b.) intermediate dispersers, and c.) rapid dispersers per 0.25m² ASU for a given treatment (with or without a corridor and interpatch distance equal to 5m or 10m). N = 3.

APPENDIX

Appendix 1. List of taxonomic groups and species collected from artificial seagrass unit patches in Middle Marsh, Back Sound, North Carolina, USA.

<u>Amphipod</u>	<i>Ampithoe longimana</i> , <i>Corophium ascherium</i> , <i>Cymadusa compta</i> , <i>Gitanopsis</i> sp., <i>Lembos unicornis</i> , <i>Lysianopsis alga</i> , <i>Melita denata</i> , <i>Melita nitida</i> , <i>Paracaprella tenuis</i> , <i>Paraphoxus spinosus</i>
<u>Bivalves</u>	<i>Abra aequalis</i> , <i>Andara ovalis</i> , <i>Andara transversa</i> , <i>Argopecten irradians</i> , <i>Brachidontes exustus</i> , <i>Corbula nasuta</i> , <i>Crassostrea virginica</i> , <i>Cumingia</i> <i>tellinoides</i> , <i>Donax variabilis</i> , <i>Dosinia discus</i> , <i>Dosinia elegans</i> , <i>Macoma</i> <i>tenta</i> , <i>Mercenaria mercenaria</i> , <i>Modiolus americanus</i> , <i>Mulinia lateralis</i> , <i>Musculus lateralis</i> , <i>Nucula proxima</i> , <i>Tagelus divisus</i> , <i>Tellina versicolor</i> , <i>Ventricolaria rugatina</i>
<u>Copepods</u>	<i>Argulus</i> sp.
<u>Crabs</u>	<i>Callinectes sapidus</i> , <i>Hexopanopeus angustiformis</i> , <i>Neonape sayi</i> , <i>Panopeus herbistii</i> , <i>Panopeus occidentalis</i>
<u>Fish</u>	<i>Gobinellus bolesoma</i> , <i>Lagodon rhomboides</i> , <i>Leiostomus xanthurus</i> <i>Monacanthus setifer</i> , <i>Opanus tau</i>
<u>Gastropods</u>	<i>Anachis avara</i> , <i>Bittium varium</i> , <i>Cerithium</i> , <i>Chaetoplera apiculata</i> , <i>Crepidula</i> , <i>Hydrobia minuta</i> , <i>Littorina</i> sp., <i>Mitrella lunata</i> , <i>Polinices</i> <i>duplicatus</i> , <i>Pyramidella crenulata</i> , <i>Retusa candeii</i> , <i>Turbonilla divisus</i> , <i>Turbonilla interrupta</i>
<u>Isopods</u>	<i>Edotea triloba</i> , <i>Erichsonella attenuata</i> , <i>Erichsonella truncata</i> , <i>Sphaeroma</i> <i>quadridentum</i>
<u>Ostracod</u>	<i>Ostracod</i> sp.
<u>Polychaetes</u>	<i>Arabella mutans</i> , <i>Batea catharensis</i> , <i>Brania clavata</i> , <i>Hydroides dianthus</i> , <i>Lumbrinerius tenuis</i> , <i>Marphysa mortensenii</i> , <i>Nereis succinea</i> , <i>Pectenaria</i> <i>gouldii</i> , <i>Prinospii</i> , <i>Priomis gruce</i> , <i>Sabellaria vulgaris</i> , <i>Spirorbis borealis</i> , <i>Spirorbis spirillum</i> , <i>Streblospio benedictii</i>
<u>Sea cucumber</u>	<i>Sclerodactyla briareus</i>
<u>Shrimp</u>	<i>Alpheus heterochaelis</i> , <i>Alpheus normanii</i> , <i>Hippolyte pleuracanthus</i> <i>Hippolyte zostericola</i> , <i>Palaemonetes intermedius</i> , <i>Palaemonetes pugio</i> <i>Palaemonetes vulgaris</i> , <i>Perclimenes longicaudatus</i> , <i>Penaeus aztecus</i> <i>Penaeus duorarum</i> , <i>Penaeus vulgaris</i>
<u>Tanaids</u>	<i>Leptochelia savignyi</i>