

## Do habitat corridors influence animal dispersal and colonization in estuarine systems?

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### Abstract

Studies investigating animal response to habitat in marine systems have mainly focused on habitat preference and complexity. This study is one of the first to investigate the affect of benthic habitat corridors and their characteristics on dispersal and colonization by estuarine macrofauna. In this study, mark-recapture field experiments using artificial seagrass units (ASUs) assessed the effects of seagrass corridors, interpatch distance (5 m vs. 10 m), and the ratio of corridor width to patch width (0.5 m:1 m vs. 0.25 m:1 m) on dispersal of two benthic organisms: the highly mobile grass shrimp, *Palaemonetes* sp., and the less mobile bay scallop, *Argopecten irradians*, in two estuarine systems in southeastern North Carolina (NC). The presence of a seagrass corridor, interpatch distance, and corridor width to patch width ratios did not significantly affect shrimp or scallop dispersal to receiver patches. Bay scallop dispersal to receiver patches was significantly higher at one site (Drum Shoals) with relatively high flow, compared to a second site (Middle Marsh) with lower flow. We then examined colonization of estuarine macrofauna to seagrass patches with and without corridors to determine which, if any, taxonomic groups respond positively to corridors at scales of 10 m and over 1 month. Colonization of estuarine macrofauna to seagrass patches was enhanced in the presence of corridors at a relatively large interpatch distance (10 m), which was statistically significant for relatively slow moving polychaete worms. Thus, although benthic habitat corridors may facilitate dispersal of relatively slow moving estuarine animals between otherwise isolated seagrass patches, several common seagrass fauna such as grass shrimp and bay scallops apparently use water currents to rapidly disperse across the seagrass/sand landscape.

### Introduction

In estuarine and marine systems, the concept of benthic habitat corridors has not been widely explored. The importance of habitat corridors in terrestrial systems, however, has been well

documented theoretically and empirically (Fahrig and Merriam 1985; Henein and Merriam 1990; Merriam and Lanoue 1990; Haddad 1999a, 1999b; Haddad and Baum 1999; Tewksbury et al. 2002). Movement of butterfly species (Haddad 1999a, 1999b; Haddad and Baum 1999), small mammals

(Fahrig and Merriam 1985; Merriam and Lanoue 1990; Coffman et al. 2001), as well as pollen and seeds (Tewksbury et al. 2002) was greater between patches in the presence of a habitat corridor than in the absence of a corridor. One hypothesized mechanism underlying increased densities of dispersing organisms in patches connected by habitat corridors includes increased immigration rates into patches through guided movement by habitat corridors leading to increased species richness and/or diversity, increased population sizes of a particular species alleviating population extinction (rescue effect), and reduction of inbred populations (Noss 1987). Increased densities of mobile organisms in patches connected by habitat corridors may also be explained by increased habitat complexity between patches providing protection from predators during dispersal (Noss 1987).

Although theoretical and empirical studies imply that habitat corridors provide connectivity and increase dispersal and colonization, there is little empirical evidence defining physical parameters such as optimal corridor length and width (Andreassen 1996). One common suggestion is that corridor parameters should be estimated based on the movement capabilities and the home range of the target species (Noss 1987; Harrison 1992; Haddad personal communication); however, disagreement about corridor parameters is evident. Noss (1987) suggests that corridors should be as wide as possible creating one large area out of two smaller areas. Although the "wider the better" idea is suggested often, Andreassen (1996) found root voles using corridors of intermediate width more so than wider or narrower corridors. Wider corridors may convolute movement within the corridor, potentially hindering linear dispersal between patches due to the absence of physical orientation cues guiding movement (Andreassen 1996). Narrower corridors have larger perimeter to area ratios, which may cause edge focused predators to concentrate foraging activity along the edge of corridors, decreasing their use by dispersing organisms (Ferguson 2000). The lack of consensus about optimal corridor parameters makes it difficult to determine the most effective lengths and widths of habitat corridors and indicates the need for such investigations.

Connectivity between populations in marine systems is assumed to occur primarily through passive and active behavioral dispersal via hydro-

dynamic currents (Caselle and Warner 1996; Palmer et al. 1996; Roberts 1997; Cowen et al. 2000; Blackmon and Eggleston 2001; Reynolds and Eggleston 2004), which calls into question whether benthic habitat corridors facilitate interpatch movement and colonization in marine systems. Recruitment to marine habitats is dependent on the life stage and community type (e.g., benthic or pelagic) of the organism. Most marine organisms have a complex life history with larval and early juvenile stages exhibiting planktonic dispersal over large spatial scales via hydrodynamic currents and limited swimming abilities. Juvenile and adult recruitment is often reliant on the reception of chemical and oratory cues from settlement habitat (Qian 1999; Berntson et al. 2000; Boxshall 2000). For example, reef noise is a settlement cue used by coral reef fish when recruiting to coral reefs (Tolimieri et al. 2004). Also, bay scallops are thought to use cues from seagrass when swimming away from predators in bare substrates towards the protection of seagrass beds (Hamilton and Koch 1996). Benthic habitat corridors may affect colonization of habitat patches by increasing the total area of the seagrass (i.e., increasing potential chemical and physical cues associated with the habitat), and increasing the probability of encountering seagrass habitat. Once seagrass is encountered it may act as a "drift-fence", intercepting dispersing individuals from the water column and surrounding matrix and directing them towards patches connected by corridors (Haddad and Baum 1999).

Studies of landscape ecology issues in marine systems have focused mainly on the relationship between patch size and number, as well as their spatial distribution on growth, movement rates, and colonization by bay scallops, *Argopecten irradians* (Irlandi et al. 1995, 1999; Irlandi 1997); grass shrimp, *Palaemonetes* sp.; juvenile blue crabs, *Callinectes sapidus*, as well as other seagrass associated species (Eggleston et al. 1998, 1999), and kelp holdfast communities (Goodsell and Connell 2002). Few studies have been conducted in the marine environment to specifically test the efficacy of benthic habitat corridors (Micheli and Peterson 1999; Brooks and Bell 2001). Results from several studies suggest that some marine organisms are likely to use benthic habitat corridors for movement (Irlandi and Crawford 1997; Micheli and Peterson 1999; Brooks and Bell 2001;

Goodsell and Connell 2002). For example, species diversity within kelp holdfast communities was greater when patches were either numerous or proximate than when patches were few or distant (Goodsell and Connell 2002), and abundance of pinfish, *Lagodon rhomboides*, was greater in salt marsh areas associated with seagrass than in isolated marshes (Irlandi and Crawford 1997). In addition, blue crab predation rates on clams were greatest on oyster reefs adjacent to seagrass and salt marshes (Micheli and Peterson 1999).

The relative dispersal ability of an organism should be considered when investigating the effects of habitat corridors on their movement and colonization patterns. Degree of mobility generally changes depending on the physiological state, age, or life history stage of an individual (Ims 1995). Thus, organism mobility should determine the spatial scale at which an organism perceives and responds to the landscape. For example, small estuarine macrofauna (e.g., 500  $\mu\text{m}$ –2 mm) were more sensitive to seagrass and oyster bed patchiness than larger macrofauna (e.g., >2 mm) at scales < 4 m<sup>2</sup> (Eggleston et al. 1999). Also for field mice, *Peromyscus leucopus*, who easily disperse over large distances (100 s of m), distance between patches and overall spatial arrangement did not affect local population size (Fahrig and Paloheimo 1988). Hence, organisms with different levels of mobility should be expected to respond to the presence of habitat corridors differently.

An initial mark-recapture experiment examined the influence of benthic habitat corridors and corridor features on the dispersal success of organisms with different dispersal abilities: a relatively mobile disperser, the grass shrimp, *Palaeomonetes* sp., and a relatively slow disperser, the bay scallop, *Argopecten irradians*. Given the general lack of response of grass shrimp and bay scallops to the presence or absence of benthic habitat corridors, we then conducted a colonization study to see if densities of particular estuarine faunal colonizers would increase in patches connected with a benthic habitat corridor. The specific questions addressed were:

(i) Does the presence of a benthic habitat corridor increase dispersal between patches by estuarine macrofauna, regardless of interpatch distance, corridor width to patch width ratio, or organism dispersal ability?

(ii) Does the presence of a benthic habitat corridor increase colonization of patches by estuarine macrofauna (i.e., increase mean density), regardless of interpatch distance, taxonomic group or dispersal ability?

## Methods

This study was conducted at Middle Marsh, Back Sound, NC (34°41' N, 76°36' W) and Drum Shoals, Bogue Sound, NC (34°43' N, 76°46' W; Figure 1). Experiments were conducted at Middle Marsh from 4 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 dominated by *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 20 m away. During flood tide the flow in Middle Marsh was in a northeast direction, and opposite during ebb tide (Figure 1). The depth range was between 0.1 m and 2.5 m.

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 m<sup>2</sup>) of *Zostera marina* were distributed sparsely throughout the shoal; the dominant subtidal substrate was sand. The closest seagrass patch to the experiments was approximately 15 m away. Flood and ebb tide flow moved in a north–south direction and the depth range was between 0.5 m and 2.5 m. Peak spring flood-tide current speeds were higher at Drum Shoal ( $\bar{x}$  = 0.40 m s<sup>-1</sup>) than Middle Marsh ( $\bar{x}$  = 0.25 m s<sup>-1</sup>) (D.Eggleston unpublished data).

### Experimental benthic landscapes

We used seagrass as the experimental habitat because it is often naturally fragmented making it an ideal habitat to use in studies addressing the role of patchiness on benthic organism movement

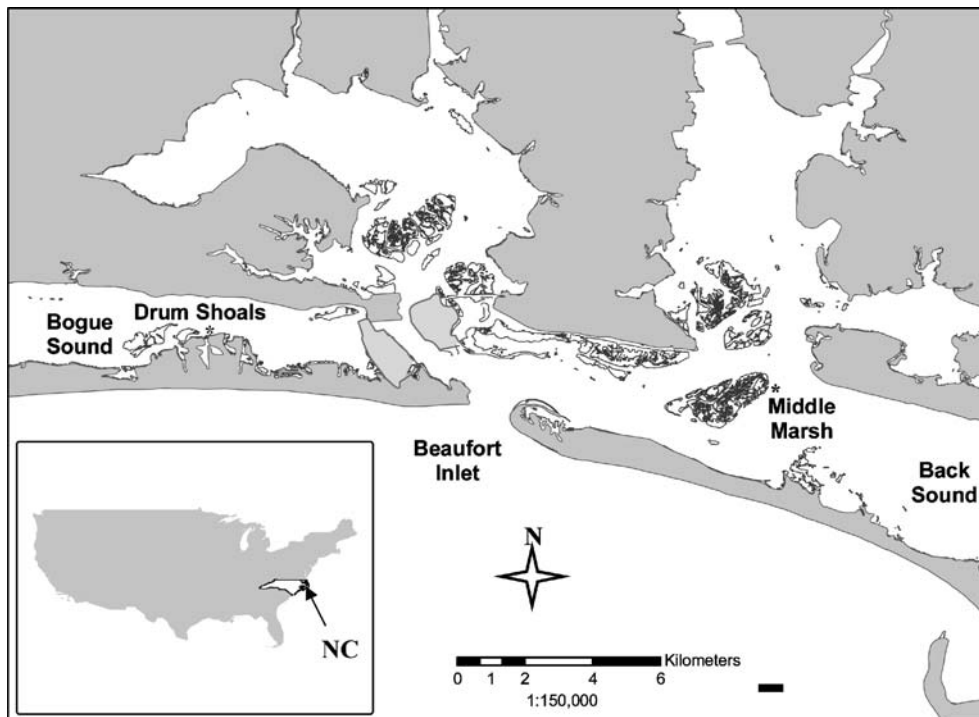


Figure 1. Study Sites, Middle Marsh in Back Sound, NC (34°41' N, 76°36' W) and Drum Shoals in Bogue Sound, NC (34°43' N, 76°46' W).

(Robbins and Bell 1994). This study used artificial seagrass units (ASUs) similar to those used by Eggleston et al. (1998, 1999) and Elis (1998) to simulate natural seagrass. The ASUs were deployed within unvegetated sand flats and tidal creeks at the study sites to create a mosaic of isolated and connected patches. ASUs were made of a 0.25 m<sup>2</sup> PVC frame with 500 µm mesh lining the bottom and contained 300 blades of artificial seagrass (made of green, polypropylene ribbon), which is equivalent to natural densities (1200 m<sup>2</sup>) in Middle Marsh (Elis 1998). The ASUs were anchored at each corner and to the seafloor using J-shaped stakes.

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 and they are colonized by estuarine macrofauna in a manner similar to natural seagrass (Virnstein and Curran 1986; Sogard 1989; Elis 1998).

A total of five experimental landscapes were used (Figures 2 and 3). To test for the influence of

benthic habitat corridor presence and interpatch distance on dispersal success of shrimp and scallops, the treatments had a standardized patch size (1 m<sup>2</sup>), with both connectivity (presence or absence of a 0.5 m, benthic habitat corridor) and interpatch distance (5 m or 10 m) manipulated (Figure 2). To test for corridor width to patch width ratio effects on animal dispersal, patch size was varied (1 m<sup>2</sup> or 4 m<sup>2</sup>) yielding corridor width to patch width ratios measuring 0.5 m:1 m or 0.25 m:1 m (Figure 3). One patch was randomly chosen to be a donor patch, where marked animals were placed at the start of dispersal experiments, and the other was a receiver patch (Figures 2 and 3). The treatments were randomly placed in areas with unstructured bottom with approximately 15–20 m between each pair of donor and receiver patches.

#### *Mark-recapture experiments to measure dispersal of shrimp and scallops*

Mark-recapture experiments were conducted from 4 June to 20 August 2002 (Middle Marsh: 4

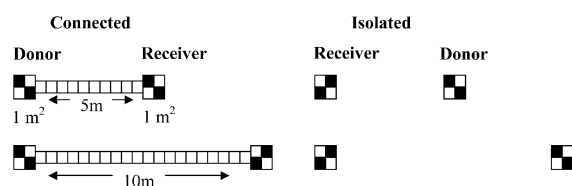


Figure 2. Schematic of experimental design used to test the effects of the presence or absence of habitat corridors and interpatch distance on dispersal of grass shrimp and bay scallops, and colonization of estuarine macrofauna. Each square represents one 0.25 m<sup>2</sup> artificial seagrass unit (ASU). Each mark-recapture trial was replicated six times (4 replicates of each treatment at Middle Marsh and 2 replicates of each treatment at Drum Shoals) over a 2.5 month period, and each treatment was randomly interspersed throughout the study site. 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. During the colonization study, three replicates of each treatment were randomly distributed throughout Middle Marsh. Darkened boxes represent a randomly chosen ASU for sampling during the colonization study.

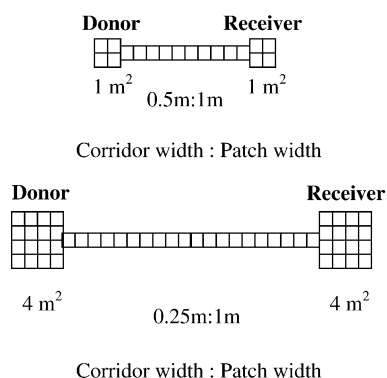


Figure 3. Schematic of experimental design used to test the effect of corridor to patch width ratio on animal dispersal. Each square represents an individual 0.25 m<sup>2</sup> ASU. The two habitat configurations were used at Middle Marsh and Drum Shoals with four and two replicates (a total of 6 replicates over a 2.5 month period), respectively. 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.

June-11 July 2002 and 30 July – 20 August and Drum Shoals: 16–29 July 2002). We chose two target species with different levels of dispersal ability. Grass shrimp, *Palaemonetes* sp., which are highly mobile (Howard 1985), were designated as

rapid dispersers. The bay scallop, *Argopecten irradians*, is more sedentary than grass shrimp and was designated as a slow disperser. Although grass shrimp and bay scallops are occasionally found in unvegetated habitat, they are commonly found in seagrass habitat (Eggleston et al. 1998; Irlandi et al. 1999). Grass shrimp densities are often greater in habitats with high structural complexity such as, vegetated habitats, where conspecific interaction and risk of predation is lower and food resources are abundant (Jordan et al. 2000). Bay scallops on barren sediment substrate will orient themselves and continuously swim towards seagrass patches, clearly demonstrating their preference for seagrass habitat (Hamilton and Koch 1996). We hypothesized that scallops would use benthic habitat corridors for dispersal with greater frequency than grass shrimp. Grass shrimp were collected from marsh creeks using sweep nets and a beam trawl and transported to a laboratory at the nearby NC State University's Center for Marine Science and Technology located in Morehead City, NC, using coolers filled with aerated seawater on the day of capture. Grass shrimp were batch marked using vital stains, either neutral red or methylene blue, which are effective methods for marking crustaceans (Howard 1985; Etherington and Eggleston 2003). Grass shrimp were placed in aerated tanks of water mixed with either neutral red (concentration 1.43 g/l) or methylene blue (0.12 g/l) stain where they remained for 12 h (Perkins-Visser et al. 1996; Etherington et al. 2003). Mortality associated with these staining techniques is negligible (Howard 1985; Etherington and Eggleston 2003). Also, observations of stained and unstained grass shrimp prior to transport to the field site indicated that behavior and health between the two groups was similar (personal observation). 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 h (Etherington and Eggleston 2003). Two stain colors were used to measure movement between treatments (i.e., shrimp were released into seagrass treatments according to color, alternating between red and blue).

Bay scallops (35–60 mm) were collected by hand, using mask and snorkel, from Oscar Shoal, Back Sound, NC. Live animals were transported in damp mesh bags and were transferred to race-

ways filled with seawater upon arrival at the laboratory. Bay scallops were marked using a stripe of colored nail polish on the upper 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 months (Eggleston 1989).

Field experiments with grass shrimp and bay scallops were carried out separately during a 2.5 month period to eliminate interspecific interactions. Densities of marked grass shrimp and bay scallops released in a donor patch were double the natural density found in Middle Marsh to facilitate density-dependent movement (Inglis and Underwood 1992). Approximately 300 grass shrimp  $m^{-2}$  or 62 bay scallops  $m^{-2}$  were placed within donor patches. 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 (Figures 2 and 3). The organisms were placed within an ASU and held in place with an inverted  $0.25 m^2$  box sieve for 15 min to allow for acclimation (Elis 1998; Blackmon and Eggleston 2001). Mobile epifauna such as Palaemonid shrimp and gastropods are capable of moving through seagrass patches with areas equal to  $0.56 m^2$  within approximately 1–2 days (Howard 1985), therefore recapture attempts for grass shrimp and bay scallops in this study were conducted initially 24 h and 4 days after release, respectively.

Grass shrimp were recaptured by simultaneously placing  $0.25 m^2$  box sieves over four ASUs making up the receiver patches from each treatment, regardless of receiver patch size. 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). Bay scallops were recaptured similarly; however, all ASUs were collected from each treatment. Differences in the number of ASUs collected during the experiments using grass shrimp and bay scallops were due to behavioral differences (i.e., relatively high and low dispersal abilities) between the target species. Grass shrimp are highly mobile; therefore, ASU collection was dependent on the number of personnel available and box sieves. The bay scallops remained motionless and hidden under the artificial seagrass blades during recapture attempts; therefore, all

ASUs could be collected (personal observation). The collected ASUs were placed within separate plastic bags and transported to shore-based facilities. The contents of the ASUs were sieved with a  $500 \mu m$  screen and marked individuals were identified immediately. All samples were preserved in 70% ethanol (Elis 1998). The number of bay scallops within a given ASU was noted at the time of collection.

The interactive effects of the presence or absence of benthic habitat corridors, interpatch distance, and site on the number of marked bay scallops that successfully dispersed from a donor to a corresponding receiver patch was analyzed using a three-factor ANOVA model with site (Middle Marsh and Drum Shoal), benthic habitat corridor (presence or absence), and interpatch distance (5 m and 10 m) 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-factor ANOVA with site (Middle Marsh and Drum Shoals) and corridor width to patch width ratio (0.5 m:1 m and 0.25 m:1 m) 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). Grass shrimp response to benthic habitat corridors, interpatch distance, and corridor width to patch width ratios was not analyzed statistically due to zero recaptures.

#### *Colonization field study*

Given the general lack of response of bay scallops and grass shrimp to the presence or absence of benthic habitat corridors (Figure 2), we assessed the effects of benthic habitat corridors on colonization by estuarine organisms to help discern what species or taxonomic groups might respond to the presence or absence of benthic habitat corridors at the spatial scales (5–10 m) examined in the mark-recapture experiments. Four experimental seagrass configurations (Figure 2) were set out at Middle Marsh during rising tide on 29 July 2002. On 28 August 2002 during rising tide, within each replicate treatment 4 ASUs were collected (two

randomly selected ASUs from each patch) (Figure 2). The ASUs were retrieved simultaneously with a box sieve, transported to the lab, sieved and preserved as described above. All organisms were identified to species in the laboratory and the individual species were assigned to specific taxonomic groups. A two-factor ANOVA model with corridor (presence vs. absence) and interpatch distance (5 m vs. 10 m) as the main factors was used to assess the effects of these factors on the following response variables: (1) mean density of all estuarine macrofauna, (2) mean density of individual taxonomic groups, and (3) the number of species within specific taxonomic groups colonizing the seagrass patches. Pairwise contrasts tested the differences in the mean density of estuarine macrofauna and mean density of species within specific taxonomic groups colonizing seagrass patches among treatments with either a 5 m or 10 m benthic habitat corridor, or separated by 5 m with no corridor compared to the treatment with seagrass patches separated by 10 m with no corridor.

## 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 h, we conducted a pilot study to assess shrimp recapture success at shorter distances between patches and a reduced recapture time. We established two 1 m<sup>2</sup> patches connected by a 1 m corridor and two 1 m<sup>2</sup> patches separated by 1 m. One hundred stained grass shrimp were placed in a 1 m<sup>2</sup> ASU patch of each treatment and left to disperse. After 1 h, we

Table 1. Percentage of bay scallops found at specific locations within treatments and missing scallops due to emigration or mortality. Values in parentheses represent standard error

Location	Treatment	
	Corridor present	Corridor absent
Receiver patch	0.44% (0.27%)	0.72% (0.23%)
Donor patch	33% (6.36%)	42% (6.52%)
Corridor	5% (1.33%)	NA
Missing	61% (6.50%)	57% (7.25%)

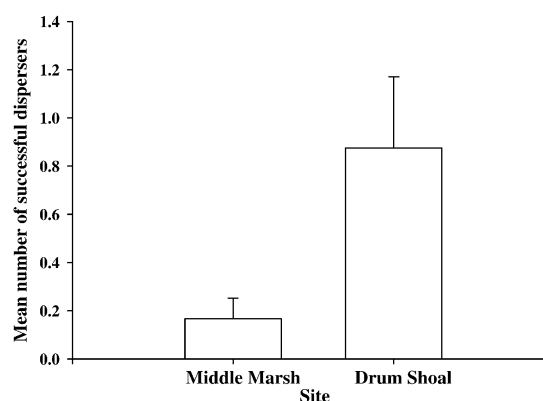


Figure 4. Mean number ( $\bar{x} + SE$ ) of bay scallops that successfully dispersed to a receiver patch for a given treatment (with or without a habitat corridor, interpatch distance of 5 m and 10 m, and site).  $N = 4$  and  $N = 2$  at Middle Marsh and Drum Shoals, respectively.

sampled the ASUs and again recaptured zero marked grass shrimp. Since the stains used to mark the shrimp lasted 24 h 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 (<1 h) at spatial scales greater than tens of meters.

Table 1 summarizes the bay scallop dispersal data. The number of scallops that successfully dispersed to corresponding receiver patches did not vary according to the presence of benthic habitat corridors or interpatch distance (Three-factor ANOVA; corridor:  $F_{1,16} = 0.58$ ,  $p = 0.73$ , interpatch distance:  $F_{1,16} = 2.53$ ,  $p = 0.19$ ). There was, however, a significant site effect ( $F_{1,16} = 7.83$ ,  $p = 0.01$ ), with the number of scallops successfully dispersing to a receiver patch significantly higher at Drum Shoals than at Middle Marsh (Figure 4). No interaction effects were significant (all  $p > 0.05$ ). The number of scallops that successfully moved to an associated receiver patch did not vary according to the site or ratio of corridor width to patch width (Two-factor ANOVA; site:  $F_{1,9} = 1.12$ ,  $p = 0.33$ , corridor:  $F_{1,9} = 1.61$ ,  $p = 0.25$ ).

### *Colonization by estuarine macrofauna*

A total of 19,379 individuals, consisting of 98 species from 12 taxonomic groups colonized the

ASUs over 1 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%).

The mean density of estuarine macrofauna colonizing seagrass patches did not significantly vary according to presence of benthic habitat corridors or interpatch distance (Table 2). The mean density of estuarine macrofauna colonizing the ASUs; however, was significantly greater in isolated seagrass patches separated by 5 m than isolated seagrass patches separated by 10 m (Table 2, Figure 5). The number of species colonizing seagrass patches did not vary according to the presence of benthic habitat corridors or interpatch distance (Two-factor ANOVA; corridor:  $F_{1,8} = 0.01$ ,  $p = 0.94$ , interpatch distance:  $F_{1,8} = 0.23$ ,  $p = 0.64$ , corridor  $\times$  interpatch distance interaction:  $F_{1,8} = 0.84$ ,  $p = 0.39$ ).

Ninety-six percent of the individuals colonizing ASUs fell into the following five taxonomic categories: gastropods (61.5%), amphipods (18%), polychaetes (10.3%), shrimp (4.2%), and bivalves (2.9%). Colonization of seagrass patches by species within the abovementioned taxonomic groups was not significantly influenced by the presence of a benthic habitat corridor or interpatch distance (Table 3). A significant interaction, however, between corridor and interpatch distance was

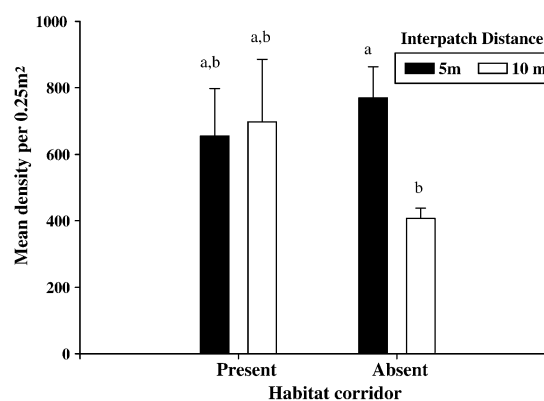


Figure 5. Effects of habitat corridor (presence or absence) and interpatch distance (5 m or 10 m) on mean densities ( $\bar{x} + SE$ ) of estuarine macrofauna colonizing ASUs.  $N = 3$ .

found for polychaetes, with significantly more polychaetes colonizing seagrass patches connected by benthic habitat corridors regardless of interpatch distance, and colonizing seagrass patches isolated by 5 m than patches isolated by 10 m (Tables 3 and 4, Figure 6). The mean density of gastropods colonizing seagrass patches isolated by 5 m was significantly greater than in seagrass patches isolated by 10 m (Table 4, Figure 6). The mean density of amphipods and bivalves was also greater in patches connected by a benthic habitat corridor and patches isolated by 5 m than in the isolated treatments separated by 10 m, however this was not significant (Table 4, Figure 6).

## Discussion

This study is one of the first attempts to specifically investigate the influence of benthic habitat

Table 2. Analysis of variance (2-factor model) determining the influence of habitat corridor (presence or absence) and interpatch distance (5 m and 10 m) on mean density of all organisms colonizing ASUs. Mean density was  $\log_{10}(x + 1)$  transformed to meet assumptions of normality and homogeneity.

Source of variation	df	MS	F	p
<b>Main effects</b>				
Corridor	1	0.011	0.61	0.45
Distance	1	0.049	2.67	0.14
Corridor $\times$ Distance	1	0.062	3.38	0.10
Error	8	0.018		
<b>Paired contrasts</b>				
Corridor, 10 m $\times$ no corridor, 10 m	1	0.063	3.43	0.10
Corridor, 5 m $\times$ no corridor, 10 m	1	0.054	2.92	0.13
No corridor, 5 m $\times$ no corridor, 10 m	1	0.112	6.03	0.04



Table 3. ANOVA model results determining the influence of benthic habitat corridors and interpatch distance on colonization of seagrass patches by different taxonomic groups.

Source of variation	df	MS	F	p
<b>Polychaetes</b>				
Corridor (C)	1	0.221	5.03	0.05
Interpatch distance (ID)	1	0.198	4.52	0.06
C×ID	1	0.222	5.06	0.05
Error	8	0.044		
<b>Gastropods</b>				
C	1	0.007	0.48	0.51
ID	1	0.056	3.71	0.09
C×ID	1	0.040	2.65	0.14
Error	8	0.151		
<b>Bivalves</b>				
C	1	0.000	0.00	0.97
ID	1	0.307	2.92	0.13
C×ID	1	0.090	1.01	0.34
Error	8	0.247		
<b>Amphipods</b>				
C	1	0.244	0.27	0.62
ID	1	0.072	0.81	0.39
C×ID	1	0.190	2.13	0.18
Error	8	0.089		
<b>Shrimp</b>				
C	1	0.345	0.52	0.49
ID	1	0.128	0.19	0.67
C×ID	1	0.004	0.06	0.82
Error	8	0.066		

corridors on dispersal and colonization of estuarine macrofauna. We incorporated and tested much of the existing corridor theory, such as the presence/absence of corridors and corridor features (length and width) and their influence on organisms with different dispersal abilities. Unlike many terrestrial studies resulting in a higher densities of species in and dispersal between patches connected by habitat corridors, this study demonstrated that seagrass habitat corridors (presence or absence), interpatch distance, and the ratio of corridor width to patch width did not influence dispersal of highly mobile grass shrimp, or mobile bay scallops between seagrass patches. We did, however, demonstrate that patch colonization by estuarine macrofauna over one month is enhanced by corridors when patches are relatively far apart (10 m), this trend was strongest for relatively slow moving taxonomic groups such as gastropods and polychaetes. Species diversity of colonizers was not influenced by benthic habitat corridors.

### Corridor Effects on Dispersal

Grass shrimp are a highly mobile species and within seagrass beds can have a complete turnover of individuals within 24 h in areas measuring as small as 0.56 m<sup>2</sup> (Howard 1985; this study). Hence, our recapture schedule of grass shrimp seemed appropriate to maximize movement between seagrass patches. All of our recapture attempts, however, resulted in zero grass shrimp suggesting that the presence of a benthic 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 10 s of meters and over 24 h. Shrimp dispersal over the entire life history can range from 1 m–1000's of kilometers (Gillanders et al. 2003). Perhaps because of their large dispersal range and ability to quickly disperse, grass shrimp were able to traverse unvegetated sand areas between ASUs and natural seagrass patches, which was a distance of at least 20 m in our study sites. The spatial scale over which an organism responds to habitat patchiness is defined, in part, by an animal's grain, the smallest scale at which an organism responds to patch structure by perceptually differentiating among a number of patches (Kotliar and Weins 1990). An animal's perception of habitat can be determined by its physiological state and behavioral attributes such as, its life stage and dispersal ability. An organism that does not respond to habitat patchiness at relatively small scales perceives its environment as homogeneous (i.e., one contiguous patch of habitat), therefore its grain is at a larger scale (Kolasa 1989). The lack of response of marked grass shrimp to benthic habitat corridors in our field experiments indicates that they apparently perceive seagrass patches separated by 10–20 m as homogenous; therefore, dispersal is not hindered while dispersing between habitat patches negating the benefit of benthic habitat corridors (e.g., Kotliar and Weins 1990).

Bay scallops represented a slow disperser, relative to grass shrimp, and have evolved the capacity to swim over short, horizontal distances by clapping their valves together while water is siphoned and forced out of the mantle cavity, which propels them (Peterson et al. 1982; Winter and Hamilton 1985; Powers and Peterson 2000). Bay scallop movement can be in response to a predator stim-

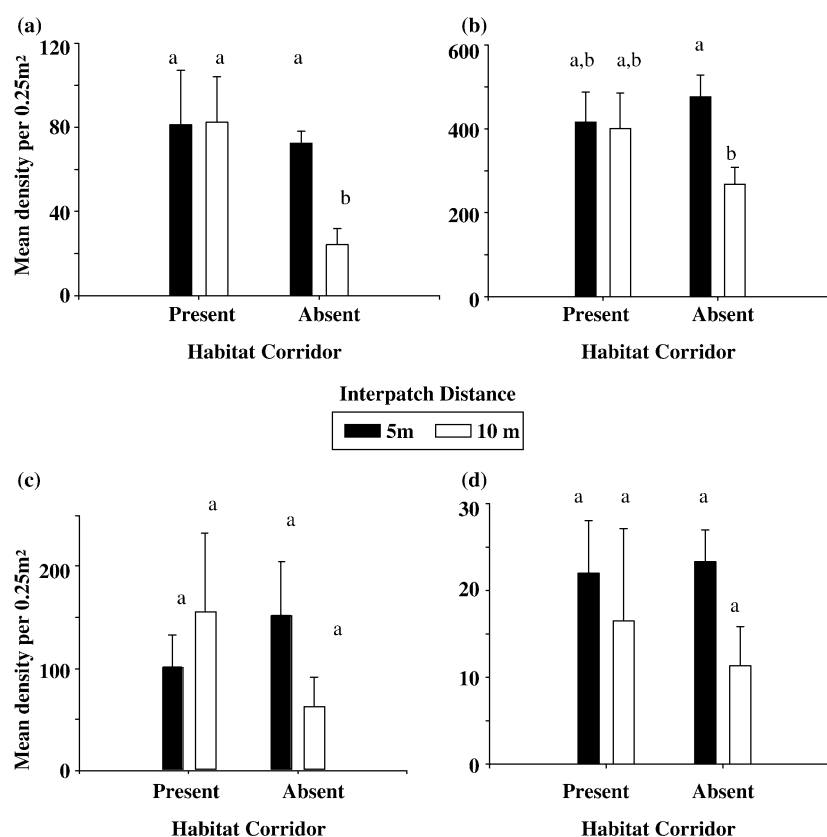


Figure 6. Effects of habitat corridor (presence or absence) and interpatch distance (5 m or 10 m) on mean densities ( $\bar{x} + SE$ ) of (a) polychaetes, (b) gastropods, (c) amphipods, and (d) bivalves per 0.25 m<sup>2</sup>.  $N = 3$ .

Table 4. ANOVA model paired contrast results listed by taxonomic group and hypothesis.

	df	MS	F	<i>p</i>
<b>Polychaetes</b>				
Corridor, 10 m > no corridor, 10 m	1, 8	0.444	10.09	0.01
Corridor, 5 m > no corridor, 10 m	1, 8	0.419	9.54	0.01
No corridor, 5 m > no corridor, 10 m	1, 8	0.421	9.57	0.01
<b>Gastropods</b>				
Corridor, 10 m > no corridor, 10 m	1, 8	0.041	2.70	0.14
Corridor, 5 m > no corridor, 10 m	1, 8	0.052	3.43	0.10
No corridor, 5 m > no corridor, 10 m	1, 8	0.095	6.32	0.04
<b>Bivalves</b>				
Corridor, 10 m > no corridor, 10 m	1, 8	0.005	0.04	0.84
Corridor, 5 m > no corridor, 10 m	1, 8	0.159	1.52	0.25
No corridor, 5 m > no corridor, 10 m	1, 8	0.204	1.94	0.20
<b>Amphipods</b>				
Corridor, 10 m > no corridor, 10 m	1, 8	0.175	1.97	0.19
Corridor, 5 m > no corridor, 10 m	1, 8	0.090	1.01	0.34
No corridor, 5 m > no corridor, 10 m	1, 8	0.247	2.78	0.13

ulus (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 current flow (Powers and Peterson 2000). Scallops placed in bare sand swam approximately 4 m in

45 min, in a series of repeated bursts, towards perceived seagrass (Winter and Hamilton 1985). Thus, the spatial scale (5–10 m) and timing of recapture (4d) for this experiment also seemed reasonable. Although bay scallop dispersal was not influenced by the presence of benthic 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 higher flow at Drum Shoals than Middle Marsh, which could have facilitated hydrodynamic transport while scallops were in the water column. 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. Also, the size range of scallops (35–60 mm) and current speeds at Drum Shoals ( $0.40 \text{ m s}^{-1}$ ) and at Middle Marsh ( $0.25 \text{ m s}^{-1}$ ) were similar to the size range (45–50 mm) current speeds ( $0.25 \text{ m s}^{-1}$ ) used by Powers and Peterson (2000), which facilitated density-dependent movement. Thus, it was somewhat surprising to observe relatively little movement of scallops in this study (0.08–0.55 scallops/day).

#### *Corridor Effects on Colonization*

Proposed benefits of habitat corridors are that they provide a source of immigrants to (1) otherwise isolated patches where inhabitant populations would go extinct if the patches were fragmented, or (2) a patch that was not located in a position within the landscape to initially receive dispersing organisms (Beier and Noss 1988; Haddad 1999). These proposed benefits imply 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. Corridors do not only function to regulate dispersal between larger patches of habitat, they also alter patch area and shape, which facilitates colonization by recruiting organisms. Corridors increase the total area of a patch and change patch shape, increasing the likelihood of coming into contact with a patch and may act as a drift-fence, intercepting individuals moving through the habitat and diverting them into patches increasing colonization of a particular patch (Haddad and Baum 1999; Tewksbury et al. 2002).

The hydrodynamics of the marine realm likely facilitates movement by organisms between isolated patches potentially negating any benefit of a benthic habitat corridor for dispersal at relatively small spatial scales. For example, early juvenile blue crabs exhibit planktonic, post-settlement 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 10–100 s of meters when moving between juvenile and adult habitats (Gillanders et al. 2003). Current and water flow can lessen the degree of isolation between habitat patches by facilitating movement over potentially inhospitable habitat, effectively increasing the dispersal range of a particular organism. Hence, marine organisms that use currents to aid movement can colonize habitat patches over a larger area than if they only used benthic habitat alone. Colonization of benthic habitats in marine systems is often dependent on invertebrate and fish species using chemical or physical cues from the habitat and conspecifics for settlement when dispersing in the water column (Qian 1999; Berntson et al. 2000; Boxshall 2000). The presence of a benthic habitat corridor increases patch area and changes patch shape and may increase the probability of marine organisms detecting settlement cues from preferred habitat that would otherwise be missed if the habitat was small in area and separated by large distances. Colonization, thereby, increases due to enhanced settlement cues from the larger area of habitat and the corridor diverts recruiting organisms into the larger patches (i.e., the corridor acts as a drift-fence) (Haddad and Baum 1999; Tewksbury et al. 2002).

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 and polychaetes showed an affinity for seagrass patches connected by a corridor and isolated seagrass patches that were within a relatively short distance (5 m) of one another. Polychaetes were significantly influenced by the presence of a connection when interpatch distance was 10 m. This pattern of abundance indicates that some relatively slow dispersers and organisms closely associated with the benthos during juvenile and adult life-stages (e.g., gastropods and polychaetes) may benefit from the addition of a benthic habitat corridor for initial recruitment and movement between patches with greater than 5 m separation. All colonizers recruited from the surrounding environment over the course of 1 month; therefore, the response to corridors is confounded between corridor and dispersal affects. The benthic habitat corridors used in this study increased the total area of the treatments connected by habitat corridors, which may have increased the encounter rate of these, treatments by recruiting organisms, compared to the treatments separated by bare substrate. The additional habitat provided by the corridors may have also acted as a drift-fence diverting the recruiting organisms to the corresponding patches, thereby increasing colonization of treatments with corridors. Also, there were significantly greater densities of gastropods and polychaetes colonizing patches separated by 5 m bare substrate than that in patches separated by 10 m of bare substrate for. Gastropods and polychaetes are truly benthic organisms once they recruit to benthic habitat; therefore, the results indicate that they are dispersal limited between seagrass patches at a spatial scale of 10 m. Hence, a habitat corridor may promote movement between patches connected by a benthic corridor, thereby increasing colonization by truly benthic organisms like gastropods and polychaetes.

#### *General conclusions and scaling up*

The general lack of response by grass shrimp and bay scallops to benthic habitat corridors at rela-

tively small scales in space (10 m) and time (1 h–4 d) was 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. These differences in movement strategies suggest that benthic 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 et al. 2001; Tewksbury et al. 2002). Use of currents during dispersal can effectively increase the dispersal range of many fish and invertebrate species and allow for easy dispersal throughout a patchy landscape. Future studies addressing landscape ecology questions in marine systems should investigate water currents as potential corridors used for movement.

Benthic habitat corridors may play a role during juvenile recruitment to habitat in a patchy environment. Many early juvenile invertebrates and fish species respond to the chemical and physical attributes of habitats and use them for settlement cues (Qian 1999; Berntson et al. 2000; Boxshall 2000). The density of benthic estuarine macrofauna colonizing ASUs was increased in this study when benthic habitat corridors were present and ASUs were relatively far apart (10 m). Benthic habitat corridors increased the total area of treatments connected by habitat corridors and changed the shape of the patch, which may have increased encounter rates of treatments connected by benthic habitat corridors and acted as drift-fences increasing dispersal and colonization of our seagrass habitats. Area and shape affects were confounded in this study and determining which factor was more influential was beyond the scope of this study. If corridors function by increasing patch area, then colonization within a patch connected by a corridor would be identical to colonization in a patch that is increased in area by the size of the corridor without altering patch shape (Tewksbury et al. 2002). Therefore, future studies investigating landscape ecology issues in marine systems should isolate and test patch area and shape affects to truly determine how each interacts and regulates the function of habitat corridors.

Numerous marine organisms have complex life cycles and exhibit ontogenetic habitat shifts from nursery to adult habitats (Gillanders et al. 2003). Population persistence of species that exhibit ontogenetic habitat shifts relies on the presence of habitat for settlement cues, foraging, protection, and the ability of organisms to move between habitats successfully (Gillanders et al. 2003). Ontogenetic habitat shifts can occur over a large spatial scale such as, an entire estuary, and will depend on the community type (i.e., benthic or pelagic) and dispersal ability of a particular organism during different life history stages. Understanding how life history stage and community type 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 are exhibited at multiple scales (Robbins and Bell 1994). Therefore, studies investigating the influence of habitat

corridors in marine systems should focus on movement and colonization on a variety of spatial scales for a multitude of species and life history stages to understand how they effectively function to affect population persistence in marine systems.

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

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Fish	<i>Gobinellus bolesoma</i> , <i>Lagodon rhomboides</i> , <i>Leiostomus xanthurus</i> <i>Monacanthus setifer</i> , <i>Opanus tau</i>
Crabs	<i>Callinectes sapidus</i> , <i>Hexopanopeus angustiformis</i> , <i>Neonape sayi</i> , <i>Panopeus herbistii</i> , <i>Panopeus occidentalis</i>
Shrimp	<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>
Amphipod	<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>
Copepods	<i>Argulus</i> sp.
Isopods	<i>Edotea triloba</i> , <i>Erichsonella attenuata</i> , <i>Erichsonella truncata</i> , <i>Sphaeroma quadridentum</i>
Ostracod	<i>Ostracod</i> sp.
Tanaids	<i>Leptocheilia savignyi</i>
Bivalves	<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 tellinoides</i> , <i>Donax variabilis</i> , <i>Dosinia discus</i> , <i>Dosinia elegans</i> , <i>Macoma tenta</i> , <i>Mercenaria mercenaria</i> , <i>Modiolus americanus</i> , <i>Mulinia lateralis</i> , <i>Musculus lateralis</i> , <i>Nucula proxima</i> , <i>Tagelus divinus</i> , <i>Tellina versicolor</i> , <i>Ventricolaria rugatina</i>
Gastropods	<i>Anachis avara</i> , <i>Bittium varium</i> , <i>Cerithium</i> , <i>Chaetoplura apiculata</i> , <i>Crepidula</i> , <i>Hydrobia minuta</i> , <i>Littorina</i> sp., <i>Mitrella lunata</i> , <i>Polinices duplicatus</i> , <i>Pyramidella crenulata</i> , <i>Retusa candei</i> , <i>Turbonilla divinus</i> , <i>Turbonilla interrupta</i>
Polychaetes	<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 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>
Sea cucumber	<i>Sclerodactyla briareus</i>

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## References

- Andreassen H.P. 1996. Optimal width of movement corridors for root voles: not too narrow and not too wide. *J. Appl. Ecol.* 33: 63–70.
- Beier P. and Noss R.F. 1998. Do habitat corridors provide connectivity? *Conserv. Biol.* 12(6): 1241–1252.
- Bell S.S. and Hicks G.R.F. 1991. Marine landscapes and faunal recruitment: A field test with seagrasses and copepods. *Mar. Ecol. Prog. Ser.* 73(1): 61–68.
- Berntson K.M., Jonsson P.R., Jekholl M. and Gatenholm P. 2000. Analysis and behavioural rejection of micro-textured surfaces and implications for recruitment by the barnacle *Balanus improvius*. *J. Exp. Mar. Biol. Ecol.* 251: 59–83.
- Blackmon D.C. and Eggleston D.B. 2001. Factors influencing planktonic, post-settlement dispersal of early juvenile blue crabs (*Callinectes sapidus* Rathbun). *J. Exp. Mar. Biol. Ecol.* 257: 183–203.
- Boxshall A.J. 2000. The importance of flow and settlement cues to larvae of the abalone, *Haliotis rufescens* Swainson. *J. Exp. Mar. Biol. Ecol.* 254(2): 143–167.
- Brooks R.A. and Bell S.S. 2001. Mobile corridors in marine landscapes: enhancement of faunal exchange at seagrass/sand ecotones. *J. Exp. Mar. Biol. Ecol.* 264: 67–84.
- Caselle J.E. and Warner R.R. 1996. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* 77(8): 2488–2504.
- Coffman C.J., Nichols J.D. and Pollock K.H. 2001. Population dynamics of *Microtus pennsylvanicus* in corridor-linked patches. *Oikos* 93: 3–21.
- Cowen R.K., Lwiza, K.M.M., Sponaugle S., Paris C.B. and Olson D.B. 2000. Connectivity of marine populations: open or closed? *Science* 287: 857–859.
- Dunning J.B., Borgella R., Clements K. and Meffe G.K. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conserv. Biol.* 9(3): 542–550.
- Eggleston D.B. 1989. Use of a mark-recapture technique to assess crab-attributable mortality rates of subtidal juvenile oyster, *Crassostrea virginica*. *J. Shellfish Res.* 8(2): 475.
- Eggleston D.B., Etherington L.L. and Elis W.E. 1998. Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. *J. Exp. Mar. Biol. Ecol.* 223: 111–132.
- Eggleston D.B., Elis W.E., Etherington L.L., Dahlgren C.P. and Posey M.H. 1999. Organism response to habitat fragmentation and diversity: Habitat colonization by estuarine macrofauna. *J. Exp. Mar. Biol. Ecol.* 236: 107–132.
- Elis W.E. 1998. Scale dependent effects of patch age and starting conditions on floral accumulation and faunal colonization in seagrass. Masters of Science thesis. North Carolina State University, Raleigh, NC, pp. 102.
- Etherington L.L. and Eggleston D.B. 2003. Spatial dynamics of large-scale, multistage crab (*Callinectes sapidus*) dispersal: determinants and consequences for recruitment. *Can. J. Fish. Aquat. Sci.* 60: 873–887.
- Fahrig L. and Merriam G. 1985. Habitat patch connectivity and population survival. *Ecology* 66(6): 1762–1768.
- Fahrig L. and Paloheimo J. 1988. Effect of spatial scale arrangement of habitat patches on local population size. *Ecology* 69(2): 468–475.
- Ferguson S.H. 2000. Predator size and distance to edge: is bigger better? *Can. J. Zool.* 78: 713–720.
- Gillanders B.M., Able K.W., Brown J.A., Eggleston D.B. and Sheridan P.F. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Mar. Ecol. Prog. Ser.* 247: 281–295.
- Goodsell P.J. and Connell S.D. 2002. Can habitat loss be treated independently of habitat configuration? Implications for rare and common taxa in fragmented landscapes. *Mar. Ecol. Prog. Ser.* 239: 37–44.
- Haddad N.M. 1999. Corridor use predicted from behaviors at habitat boundaries. *Am. Nat.* 153(2): 215–227.
- Haddad N.M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecol. Appl.* 9(2): 612–622.
- Haddad N.M. and Baum K.A. 1999. An experimental test of corridor effects on butterfly densities. *Ecol. Appl.* 9(2): 623–633.
- Hamilton P.V. and Koch K.M. 1996. Orientation toward natural and artificial grassbeds by swimming bay scallops, *Argopecten irradians* (Lamarck, 1819). *J. Exp. Mar. Biol. Ecol.* 199: 79–88.
- Harrison R.L. 1992. Toward a theory of inter-refuge corridor design. *Conserv. Biol.* 6(2): 293–295.
- Henein K. and Merriam G. 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecol.* 4(2/3): 157–170.
- Howard R.K. 1985. Measurements of short-term turnover of epifauna within seagrass beds using an *in situ* staining method. *Mar. Ecol. Prog. Ser.* 22: 163–168.
- Ims R.A. 1995. Movement patterns related to spatial scale. In: Hansson L., Fahrig L. and Merriam G. (eds), *Mosaic Landscapes and Ecological Processes*. Chapman and Hall, London, pp. 85–109.
- Inglis G. and Underwood A.J. 1992. Comments on some designs proposed for experiments on the biological importance of corridors. *Conserv. Biol.* 6(4): 581–586.
- Irlandi E.A., Ambrose W.G. and Orlando B.A. 1995. Landscape ecology and the marine environment: how spatial configuration of seagrass habitat influences growth and survival of the bay scallop. *Oikos* 72(3): 307–313.
- Irlandi E.A. 1997. Seagrass patch size and survivorship of an infaunal bivalve. *Oikos* 78: 511–518.
- Irlandi E.A. and Crawford M.K. 1997. Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* 110: 222–230.
- Irlandi E.A., Orlando B.A. and Ambrose W.G. 1999. Influence of seagrass habitat patch size on growth and survival of juvenile bay scallops, *Argopecten irradians concentricus* (Say). *J. Exp. Mar. Biol. Ecol.* 235: 21–43.
- Jordan F., Babbitt K.J., McIvor C.C. and Miller S.J. 2000. Contrasting patterns of habitat use by prawns and crayfish in a headwater marsh of St. Johns River, Florida. *J. Crust. Biol.* 20(4): 769–776.
- Kotliar N.B. and Wiens J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253–260.

- Merriam G. and Lanoue A. 1990. Corridor use by small mammals: field measurement for three experimental types of *Peromyscus leucopus*. *Landscape Ecol.* 4(2/3): 123–131.
- Micheli F. and Peterson C.H. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conserv. Biol.* 13(4): 869–881.
- Noss R.F. 1987. Corridors in real landscapes: A reply to Simberloff and Cox. *Conserv. Biol.* 1(2): 159–164.
- Palmer M.A., Allan J.D. and Butman C.A. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trend. Ecol. Evol.* 11(8): 322–326.
- Perkins-Visser E., Wolcott T.G. and Wolcott D.L. 1996. Nursery role of seagrass beds: enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). *J. Exp. Mar. Biol. Ecol.* 198: 155–173.
- Peterson C.H., Ambrose W.G. and Hunt J.H. 1982. A field test of the swimming response of bay scallop (*Argopecten irradians*) to changing biological factors. *Bull. Mar. Sci.* 32(4): 939–944.
- Powers S.P. and Peterson C.H. 2000. Conditional density dependence: The flow trigger to expression of density-dependent emigration in bay scallops. *Limnol. Oceanogr.* 45(3): 727–732.
- Qian P.Y. 1999. Larval settlement of polychaetes. *Hydrobiologia* 402: 239–253.
- Reyns N.B. and Eggleston D.B. 2004. Environmentally-controlled, density-dependent secondary dispersal in a local estuarine crab population. *Oecologia* (in press).
- Robbins B.D. and Bell S.S. 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. *Trend. Ecol. Evol.* 9: 301–305.
- Roberts C.M. 1997. Connectivity and management of Caribbean coral reefs. *Science* 278: 1454–1457.
- Sogard S.M. 1989. Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. *J. Exp. Mar. Biol. Ecol.* 133: 15–37.
- Tewksbury J.J., Levey D.J., Haddad N.M., Sargent S., Orrock J.L., Weldon A., Danielson B.J., Brinkeroff J., Damschen E.I. and Townsend P. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc. Natl. Acad. Sci.* 99(20): 12923–12926.
- Tolimieri N., Haine O., Jeffs A., McCauley R., Montgomery J., 2004. Directional orientation of pomacentrid larvae to ambient reef scord. *Coral reefs* 23(2): 184–191.
- Underwood A.J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol.* 19: 513–605.
- Virnstein R.W. and Curran M.C. 1986. Colonization of Artificial seagrass versus time and distance from source. *Mar. Ecol. Prog. Ser.* 29: 279–288.
- Winter M.A. and Hamilton P.V. 1985. Factors influencing swimming in bay scallops, *Argopecten irradians* (Lamarck 1819). *J. Exp. Mar. Biol. Ecol.* 88: 227–242.