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Organism responses to habitat fragmentation and diversity: Habitat colonization by estuarine macrofauna

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Abstract

Ecologists increasingly recognize that their choice of spatial scales may influence greatly their interpretation of ecological systems, and that small changes in the patchiness of habitat resources can produce abrupt, sometimes dramatic shifts in distribution and abundance patterns of a species. Moreover, identification of scale- and habitat-dependent ecological patterns are central to management efforts aimed at predicting the response of organisms to the increasing threat of habitat fragmentation. We used habitat plots containing artificial seagrass, oyster shell, and a mixture of seagrass and shell, placed on unstructured seafloor for 14 days in Back Sound, North Carolina, USA to examine the interactive effects of patch size, habitat diversity and experimental site on colonization by assemblages of estuarine macrofauna. We tested three a priori predictions of the general hypothesis that macrofaunal colonization is scale- and habitat-dependent: (1) colonization (per unit area) will be higher in small patches than in large ones; (2) small macrofauna will show a stronger response to habitat patchiness at a given scale than large macrofauna; and (3) colonization by estuarine macrofauna will be higher in habitat plots containing a mixture of seagrass and oyster shell compared to monotypic plots. Macrofauna responded to habitat patchiness in a complex manner that varied according to habitat type, experimental site, species, taxon, functional group, and animal body size (small: 500 μm–2 mm; large: >2 mm). Of the five out of seven response variables where we observed a significant patch size effect, grass shrimp (*Palaemonidae* sp.) and small, mobile crustaceans (i.e., amphipods and isopods) were the only taxonomic or functional groups whose densities were higher in small (0.25 m^2) than large (1 m^2) patches, as predicted. Moreover, there was a disproportionate reduction in macrofaunal abundance and diversity in small patches of oyster shell compared to seagrass and mixed habitat treatments; this pattern was significant for both the total density and numbers of small species but not for large macrofauna. The total density and number of macrofaunal species

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was not higher in the mixed habitat treatment compared to seagrass or oyster shell. Our study demonstrates that an organism's response to habitat patchiness is dependent upon species, taxa, functional group, and animal body size, and that an organism's response is further modified by habitat type. The patterns observed in this study highlight the importance of scale- and habitat-dependent responses by mobile organisms to complex benthic habitats, and, because of the disproportionate reduction in faunal density and diversity in small versus large patches of oyster shell, heightens concern over the negative impacts to biodiversity through large-scale fragmentation of subtidal oyster reefs in certain regions.

Keywords: Colonization; *Crassostrea virginica*; Fragmentation; Marine benthos; Grass shrimp; Habitat selection; Palaemonidae; Patchiness; Recruitment; *Zostera marina*

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1. Introduction

A fundamental issue in ecology is the detection of scale-dependent organism distribution and abundance patterns and identification of the processes underlying these patterns (Kareiva, 1987; Doak et al., 1992; Levin, 1992; Gascon and Travis, 1992; Dunning et al., 1995; Gustafson and Gardner, 1996, and references therein). Experimentalists increasingly recognize that their choice of spatial scales may influence greatly their interpretation of ecological systems (O'Neill, 1989; Kotliar and Wiens, 1990; Gascon and Travis, 1992; Schneider, 1994; Farnsworth and Ellison, 1996; Fonseca, 1996; Hewitt et al., 1996; Thrush et al., 1996, and references therein). Moreover, small changes in the spatial patterning of habitat resources can produce abrupt, sometimes dramatic shifts in distribution and abundance patterns of species (Allen and Starr, 1982; Pulliam, 1988; Kolasa, 1989; Andren, 1994; Robbins and Bell, 1994; With and Crist, 1995). Such threshold responses by organisms to changes in habitat heterogeneity bolster the perception that the processes controlling community formation and persistence operate at different spatial and temporal scales (Menge and Olson, 1990), and underscore the need to examine how distribution and abundance patterns of animals vary according to spatial scale and habitat type. Moreover, identification of scale- and habitat-dependent ecological patterns are central to management efforts aimed at predicting the response of organisms to the increasing threat of habitat fragmentation (Gascon and Travis, 1992; Dunning et al., 1995; With and Crist, 1995; Gustafson and Gardner, 1996, and references therein). The overall goal of this study was to quantify how colonization of habitat plots by assemblages of estuarine macrofauna varied according to patch size, habitat diversity, and experimental site.

In nearshore coastal marine environments, complex benthic habitats such as seagrass and oyster reefs possess a suite of spatial and ecological characteristics that make them amenable to assessing the effects of habitat patchiness on animal abundance (Robbins and Bell, 1994; Bell et al., 1995; Fonseca, 1996; Eggleston et al., 1998). For example, seagrass habitats range from monospecific beds that extend over several km to fragmented patches (<0.25 m^2). Similarly, oyster reefs range in size from small, fragmented intertidal reefs of less than 1 m^2, to continuous subtidal reefs over 1 km in length. For estuarine macrofauna (e.g., postlarval and early juvenile stages of shrimp and crabs, amphipods, polychaetes, bivalves, gastropods, etc.), the spacing of seagrass and oyster shell among unstructured, soft-bottom habitat is relatively large (1–100 m) compared to their body size (0.5–10 mm). Thus, mosaics of sediment, seagrass and oyster reefs may directly or indirectly impact populations through a variety of mechanisms such as alteration of predator (e.g., shrimp, fish) distribution, abundance, and foraging behavior (e.g., Leber, 1985; Main, 1987; Bell and Hicks, 1991; Irlandi, 1994; Irlandi et al., 1995), modifications of water flow which may passively entrain or deposit settlement stages (Eckman, 1983; Bell et al., 1995), accumulation of secondary structure such as drift algae and detrital salt marsh grass (Reidenbaugh and Banta, 1980; Kulcycki et al., 1981; Holmquist, 1994; Bell et al., 1995), and changes in animal behavior (review by Heck and Crowder, 1991). Moreover, organisms differ greatly in those morphological, physiological, and behavioral characteristics that influence the way in which habitat heterogeneity is perceived (Hart and Horwitz, 1991). Thus, recruitment success of marine benthic species in complex habitats may be scale- and body size-dependent.

1.1. Predictions

Recent studies in seagrass systems suggest that many small seagrass patches may increase the overall probability of encounter by larvae or other immigrants, thereby increasing overall colonization of the patch, compared to larger patches (e.g., Bell et al., 1987; Sogard, 1989; Worthington et al., 1992; McNeill and Fairweather, 1993; Eggleston et al., 1998, but see Bell et al., 1995 for an example of disproportionately high algal accumulation rates on large versus small patches). Increased recruitment of barnacles into small versus large habitat patches has also been observed in rocky shore habitats (Paine and Levin, 1981; Keough, 1984; Sousa, 1984, but see Kim and DeWreede, 1996, for an example of high barnacle densities in intermediate and large size patches; and Underwood and Skilleter, 1996, for an example where the diameter of pools in rocky shore habitats had little influence on organism colonization). The hypothesized mechanism for the scale-dependent patterns observed in rocky shore habitats was similar to that posed for seagrass; increased probability of interception of larvae by the patch edge in small versus large patches (Paine and Levin, 1981; Sousa, 1984). Similarly, Smith and Brumsickle (1989) proposed that postlarval immigration by benthic infauna is higher in small patches of disturbed soft-bottom areas than large patches. Thus, small patches should contain higher densities and numbers of species than large patches.

Large areas are more likely to contain more habitat types than small areas (Rosenzweig, 1995, and references therein). For large areas, species richness is additive in that potential species occurring in a patch containing a group of habitats is the union of the species lists for each habitat type occurring alone (Hart and Horwitz, 1991). Alternatively, certain species may require a group of habitats (e.g., for feeding, reproduction), such that those species only occur in areas with mixed habitat types (Hart and Horwitz, 1991). Thus, habitat plots consisting of a mixture of seagrass and oyster shell should contain higher densities and numbers of species than monotypic plots of seagrass or oyster shell.

The smallest scale at which an organism responds to patch structure is its ‘grain’

(Kotliar and Wiens, 1990). At a given spatial scale, small organisms will generally have smaller grain than large organisms because small organisms do not functionally perceive a mosaic of habitat patches as a single patch, whereas large organisms do (Kotliar and Wiens, 1990; Gunther, 1992). Thus, the abundance and diversity of relatively small macrofauna should change in a significant manner to varying patch size more often than the abundance and diversity of large macrofauna. We emphasize that many of the predictions described above will hold only if abundance patterns are maintained after settlement from the plankton or post-settlement immigration.

In this study we examined the main and interactive effects of patch size, habitat diversity and experimental site on short-term colonization of habitat plots by shallow-water, estuarine macrofauna. Patterns of colonization were examined according to species, functional groups, taxa, and body size. By use of experimental habitat plots, we were able to separate variability among habitat patch sizes and unconfound differences due to habitat characteristics (e.g., seagrass shoot density, shell volume, alternative microhabitats) with habitat area, as well as manipulate habitat diversity. Numerous studies of the relationship between community structure and habitat heterogeneity have lumped species into groups defined by anatomy, morphology and other ecological attributes. This ‘functional group’ approach has proven to be a useful tool in a variety of community-level studies (terrestrial: Wilson and Roxburgh, 1994; wetlands: Ellison and Bedford, 1995; freshwater: Poff and Allan, 1995; and marine: Steneck and Dethier, 1994, and references therein). Specifically, we addressed four main questions. (1) Is macrofaunal abundance higher in small versus large patches, as predicted by the increased probability of intercepting larvae and immigrants by the patch edge in small versus large patches (i.e., increased perimeter:area ratio) (e.g., Paine and Levin, 1981; Sousa, 1984; McNeill and Fairweather, 1993)? (2) Do relatively small macrofauna have a lower grain than large macrofauna (i.e., is there a significant patch size by body size interaction effect?) (e.g., Kotliar and Wiens, 1990)? (3) Are patch size effects upon macrofauna dependent upon habitat type (i.e., is there a significant patch size by habitat interaction?) (4) Does a mixture of habitat types contain higher densities and numbers of species than monotypic habitats (e.g., Hart and Horwitz, 1991)?

2. Materials and methods

2.1. Study site

The experiment was conducted on May 4–15, 1995 at two shallow subtidal sites (East, West) within Middle Marsh, in Back Sound, North Carolina, USA (Fig. 1). Water depth at the sites ranged from 0.1–0.4 m at low tide to 1.2–1.5 m at high tide. Water temperature and salinity during the experiment averaged 25°C and 35 ppt. Salinities are high throughout the year because of relatively low riverine input and high tidal flushing through Beaufort Inlet (Fig. 1). The experiment was conducted on unstructured bottom within two small coves surrounded by *Spartina alterniflora* marshes. The closest seagrass bed was located approximately 20 m and 10 m away at the East and West sites, respectively. Sediment at the East site was primarily sandy mud with 20.1% silt–clay

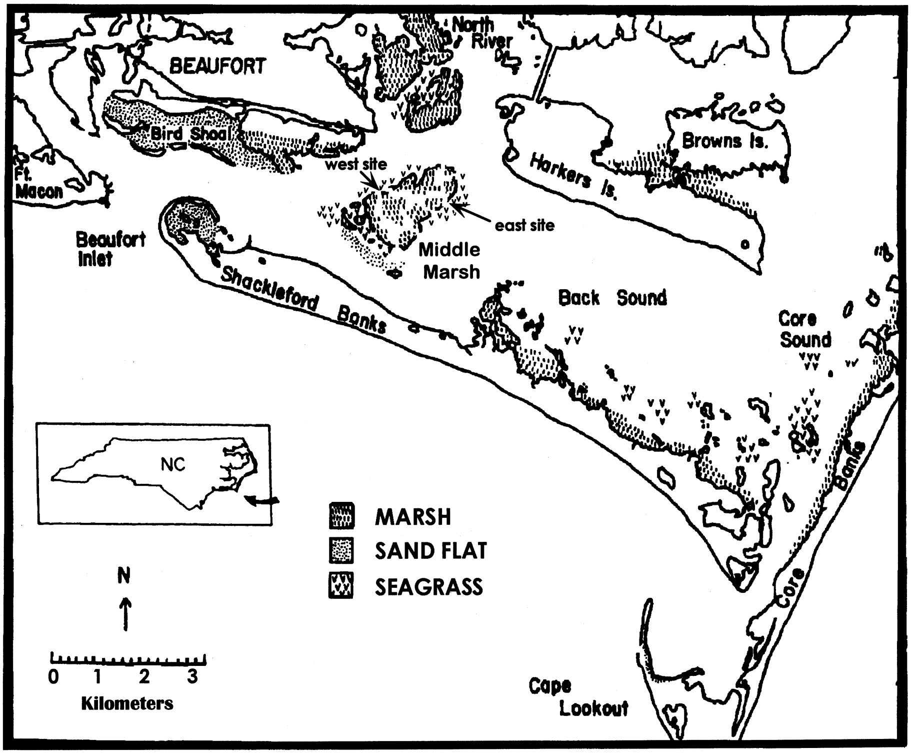

Fig. 1. Study sites in Middle Marsh, Back Sound, North Carolina, USA.

and 79.9% very fine sands; sediment at the West site was primarily muddy sand with 7.4% silt–clay and 92.6% very fine sands. Middle Marsh typifies the Albemarle-Pamlico estuarine system and is characterized by extensive seagrass (primarily *Zostera marina* and *Halodule wrightii*), marsh creek, and oyster (*Crassostrea virginica*) habitats.

2.2. Artificial settlement plots

The most direct means of testing the effects of habitat fragmentation on biota is by comparing the density of a given species (or number of species per unit area), as measured from samples of equal size, within increasingly larger habitat patches or segments (Coleman et al., 1982; Haila, 1983; Kelly et al., 1989; Hart and Horwitz, 1991; McGarigal and McComb, 1995, and references therein). In this study, we assessed the interactive effects of habitat diversity, patch size, and experimental site on small (between 500 μm and ca. 2 mm) and large (> 2 mm) macrofauna with artificial seagrass, trays filled with oyster shell, or a mixture of both within one plot. The a posteriori size distribution of macrofauna was bimodal and appeared to divide naturally after sieving and measuring into two groups depending upon body size: (1) small (500 μm–2 mm), which consisted primarily of polychaetes, bivalves, gastropods, amphipods and isopods; and (2) large ($>$ ca. 2 mm), which consisted of fish, crabs and shrimp (see Appendix A for the complete list of species). Although there was overlap for a given species or taxonomic group between size categories (e.g., polychaetes >2 mm), the average sizes conformed to our small and large size-classes. The small size-class, in particular, encompassed a wide range of organism mobility from relatively sessile bivalves, to highly mobile amphipods and isopods. Thus, each broad size category was further divided into functional or taxonomic groups to better reflect organism mobility, which, in turn, could influence organism response to habitat patchiness (e.g., Hewitt et al., 1996).

Artificial seagrass plots were constructed of green plastic ribbon (Equality Specialty, Chicago, IL, USA) tied to 0.25 m^2 squares of black plastic mesh (Vexar) with a mesh size of 25 mm. Each shoot consisted of two blades, 30 cm in height and 5 mm wide, with a total shoot density of 2704 m^{-2}. Natural densities of patchily distributed seagrass in this area during October range from 2651 to 2917 m^{-2} (Irlandi 1994). Under each seagrass plot was a tray of 500 μm-mesh supported by a 0.25 m^2 plastic frame (50 cm length $\times$ 50 cm width) of 12 mm PVC-pipe. Seagrass plots were anchored to the bottom by pushing a 'J-shaped' metal stake into the sediment on each corner of a plot.

Oyster-shell plots were constructed by filling a 500 μm mesh-lined 0.25 m^2 plastic tray with 19 l of air-dried oyster shell. The substrate surface in these trays stood 5 cm above the surrounding sediment surface. Although the use of dead oyster shells does not represent the complex architecture of natural intertidal reefs (e.g., Wells, 1961), the oyster shells do mimic low vertical profile subtidal reefs found throughout the East and Gulf coasts of North America, and are characteristic of sites disturbed by dredging and disposal (Mann et al., 1991; Rothschild et al., 1994).

2.3. Experimental procedure and design

The experiment was timed to correspond with high abundances of fish and invertebrates in Back Sound during the late spring and early summer (Ross and Epperly, 1985). Experimental habitat plots were placed on the bottom during low tide at the end of the new moon, spring tide series in May, and retrieved 12 days later during low tide at the end of the full moon, spring tide series.

We assessed the direct and interactive effects of patch size (small: 0.25 m^2; large: 1 m^2), habitat diversity (oyster shell, seagrass, mixture of both), and experimental site ('East' vs. 'West'; Fig. 1) on short-term (14 days) macrofaunal colonization. Our choice of patch sizes was based on the size distribution of natural patches in the area, which are sometimes skewed greatly towards patches that are <4 m^2 (Irlandi, 1994; Eggleston, in press), and ease of deployment. A similar patch size distribution has been identified in *Z. marina* beds in Denmark (Olesen and Sand-Jensen, 1994). We also have good evidence for habitat- and species-specific responses by grass shrimp (*Palaemonetes* sp.) and early juvenile blue crabs (*Callinectes sapidus*) to habitat patchiness at this scale (Posey and Hines, 1991; Eggleston et al., 1998). At each site, replicate treatments ($N=3$) were randomly assigned to positions along three 70 m transect lines. Thus, a total of 18 small (0.25 m^2) and 18 large (1 m^2) habitat plots were deployed. To minimize disturbance of plots during retrieval, and to help ensure statistical independence, all plots were located 3 m apart. For the large (1 m^2), mixed habitat treatment, which contained two 0.25 m^2

seagrass and two oyster shell plots, we subsampled a single seagrass and oyster shell plot and averaged the contents. Trays were retrieved by quickly placing a 0.25 m^2 box sieve with 500 μm mesh around the edges of a tray, and lifting the tray out of the water. This approach was presumably effective at retrieving both sessile and mobile macrofauna since large, highly mobile blue crabs (< 16 cm carapace width; CW) and pinfish, *Lagodon rhomboides* (< 12 cm total length; TL) were effectively captured with this technique. For the large, mixed habitat treatment, the two trays (seagrass and oyster shell) were simultaneously retrieved to avoid disturbing the other plot. Water depth during tray retrieval was typically 0.1–0.5 m. Upon retrieval, individual trays were placed into plastic bags with an identification tag; the contents of a tray were then sieved with a 500 μm screen, and organisms preserved in 10% formaldehyde solution for later enumeration. All organisms were identified to species in the laboratory.

2.4. Statistical analyses

The interactive effects of patch size, habitat diversity, and experimental site on macrofaunal abundance and diversity (per 0.25 m^2) were analysed using seven separate response variables representing different taxonomic or functional groupings of organisms. These were: (1) total numbers of large (> 2 mm) individuals; (2) total numbers of small (500 μm–2 mm) individuals; (3) total numbers of large species; (4) total numbers of small species; (5) total numbers of Palaemonid shrimp (*Palaemonetes pugio*, *P. vulgaris*, *P. intermedius*); (6) total numbers of hippolytid shrimp (*Tozeuma carolinense*); and (7) total numbers of small, mobile crustaceans (represented by amphipods and isopods). Palaemonid shrimp, hippolytid shrimp, and small, mobile crustaceans were the dominant faunal groups collected (see Section 3). We pooled all three species of palaemonid shrimp (*P. pugio*, *P. vulgaris*, *P. intermedius*) because our previous results indicated that these species respond in a similar manner to patch size (Eggleston et al., 1998). Although large meiofauna such as amphipods and isopods were probably undersampled by the 500 μm-mesh, we include this functional group too make relative comparisons across experimental treatments.

Each response variable was analyzed with a separate three-way ANOVA model with Site (East, West), Habitat type (oyster shell, seagrass, mixture), and Patch size (small, large) as factors. Heteroscedastic variances were corrected with a $\log(x + 1)$ transformation. Differences between means were revealed with either a protected, lower-level ANOVA, or a Tukey's multiple comparison test. Additional multivariate analyses (Warwick, 1993) of the seven response variables did not provide additional insight into community-level interactions. For brevity, the results of MANOVA were not included in Section 3.

3. Results

3.1. General description of faunal assemblages

We identified 171 species from 32 taxonomic groups on all of the experimental habitat plots (Appendix A). Numerically, assemblages of small macrofauna (500 μm–2 mm) were dominated by amphipods ($\bar{x} = 2743$ individuals m^{-2}), bivalves ($\bar{x} = 304$ individuals m^{-2}), polychaetes ($\bar{x} = 251$ individuals m^{-2}) and gastropods ($\bar{x} = 165$ individuals m^{-2}). These groups were also the most speciose; led by polychaetes (52 species), gastropods (29 species), amphipods (28 species), and bivalves (24 species) (Appendix A). The most abundant polychaete species were *Streblospio benedicti* (29% of the total number of polychaetes), *Exogone dispar* (9%), *Driloneris magna* (8%), and *Dorvillea sociabilis* (7%). Gastropods were dominated by *Crepidula fornicata* (31%), followed by *Mitrella lunata* (21%), *Pyramidella crenulata* (12%), and *Bittium varium* (4%). The most abundant amphipod species was *Corophium acherusicum* (41%), followed by *Micropotopus raneyi* (8%) and *Ampithoe longimana* (7%). Bivalves were dominated by three species: *Macoma tenta* (31%), *Mactra fragilis* (28%), and *Papyridae soleniformis* (20%).

Large macrofaunal assemblages (>2 mm) were numerically dominated by hyppolytid ($\bar{x} = 46.8$ individuals m^{-2}) and palaemonid shrimp ($\bar{x} = 34$ individuals m^{-2}), followed by xanthid crabs ($\bar{x} = 18$ individuals m^{-2}). The only species of hyppolytid shrimp was *Tozeuma carolinense*, whereas the most abundant species of palaemonid shrimp were *Palaemonetes intermedius* (56%) and *P. vulgaris* (48%). *Panopeus herbstii* was the most common species of xanthid crab (79% of xanthid crabs) and *Callinectes sapidus* was the most common species of portunid crab (75% of portunid crabs). *Lagodon rhomboides* was the most common species of fish (89%).

3.2. Interactive effects of patch size, habitat type, and experimental site on colonization by large and small macrofauna

Patterns of recruitment for macrofauna at spatial scales of 0.25–1 m^2 varied according to experimental site, patch size, habitat type, and body size. Densities of small and large macrofauna were highest at the West and East sites, respectively. Small macrofauna had lower grain (i.e., showed a stronger response to patch size) than large macrofauna, and all macrofauna had lower grain in oyster shell than seagrass or mixed habitats. Contrary to our expectations, the mixed habitat treatment did not contain the highest density or numbers of species.

3.2.1. Total density

The density of large macrofauna varied significantly according to Site (three-way ANOVA; Site: $F = 15.9$; $df = 1{,}22$; $p = 0.001$), but not Habitat type (seagrass, oyster shell, mixed) or Patch size (small, large) (three-way ANOVA; $df = 1{,}22$; all $p > 0.13$). The statistical power to detect significant patch size and habitat type main effects ranged from adequate (80%) to marginal (60%), respectively. None of the interaction effects were significant (all $p > 0.29$). The mean density of large macrofauna was significantly higher at the East site than at the West (Fig. 2a and Fig. 2b; lower-level ANOVA). Total densities at the East site averaged from 23 to 52, whereas total densities at the West site averaged from only 5 to 25 (Fig. 2a and Fig. 2b).

The average density of small macrofauna was one to two orders-of-magnitude higher than for large macrofauna (Fig. 2). The mean density ($\log(x + 1)$ transformed) of small

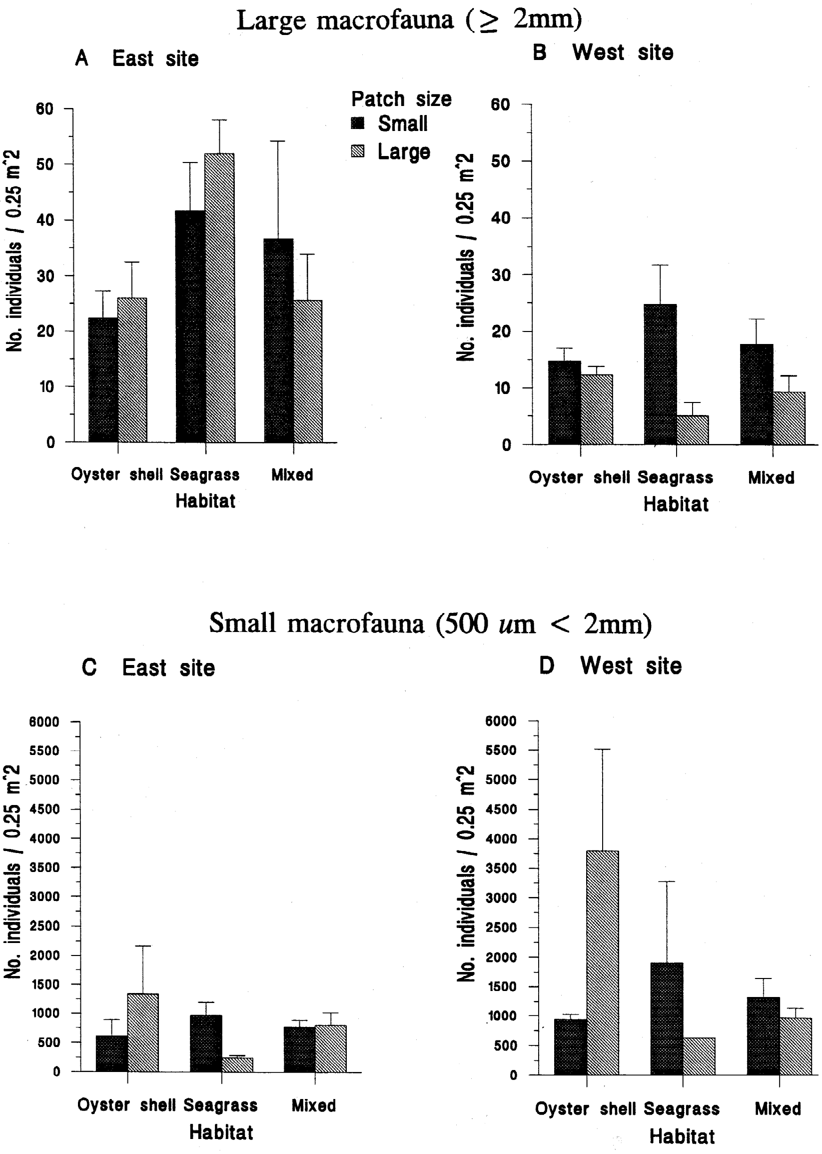

Fig. 2. Effects of Site (East, West), Patch size (small, large) and Habitat type (oyster shell, seagrass, mixture of seagrass and oyster shell) on the mean density (+ S.E.) of large (A,B) and small (C,D) estuarine macrofauna colonizing artificial habitat plots. Note different scales on y-axes. See text for significance levels.

macrofauna varied significantly according to Site (three-way ANOVA; Site: $F = 5.2$, $df = 1{,}23$, $p = 0.033$), and was significantly higher at the West site than the East (Fig. 2c and Fig. 2d: lower-level ANOVA). This site-specific pattern was opposite to that observed for large macrofauna (Fig. 2). Although the Patch size and Habitat type main effects were non-significant (all $p > 0.38$), there was a significant Patch size by Habitat type interaction effect ($F = 4.13$, $df = 2{,}22$, $p = 0.028$). None of the other interaction effects were significant (all $p > 0.5$). The interaction effect was due to significantly higher densities of small macrofauna in large patches of oyster shell than in either seagrass or mixed habitats, and no difference in mean densities of small macrofauna between habitat types in small patches (Fig. 2c, Fig. 2d; Tukey's multiple comparisons test).

3.2.2. Numbers of species

The patterns observed for the numbers of small and large macrofaunal species tended to mirror those observed for the density of small macrofauna. The abundance of large macrofaunal species varied significantly according to Site (three-way ANOVA; Site: $F = 11.74$, $df = 1{,}22$, $p = 0.002$), but not Patch size or Habitat type (all $p > 0.09$). There were significantly higher numbers of large macrofaunal species at the East site than the West (Fig. 3a, Fig. 3b; lower-level ANOVA). There was also a significant Patch size by Habitat type interaction effect (three-way ANOVA; $F = 8.73$, $df = 2{,}22$, $p = 0.002$). None of the other interaction effects were significant (all $p > 0.16$). The interaction effect was due to significantly lower numbers of macrofaunal species in small oyster patches compared to seagrass or mixed habitats, and no difference in species abundance between habitat types in large patches (Fig. 3a, Fig. 3b; Tukey's multiple comparisons test).

The numbers of small macrofaunal species was, on average, ten times higher than for large macrofauna (Fig. 3). The patterns for small macrofauna were similar to those just described for large macrofauna, with a significant Site main effect, and a significant Patch size by Habitat type interaction effect (three-way ANOVA; Site: $F = 8.21$, $df = 1{,}22$, $p = 0.009$; Patch size X Habitat type: $F = 4.23$, $df = 2{,}22$, $p = 0.028$). None of the other main or interaction effects were significant (all $p > 0.12$). There were significantly higher numbers of small macrofaunal species at the West site than the East, opposite the pattern observed for large macrofauna (Fig. 3). The interaction effect was due to significantly higher numbers of species in large oyster patches compared to seagrass and mixed habitats, and no difference between habitat types in small patches (Fig. 3c, Fig. 3d; Tukey's multiple comparisons test).

3.3. Functional group- and taxon-specific patterns

3.3.1. Large macrofauna, palaemonid shrimp

The density of palaemonid shrimp ($\log(x + 1)$ transformed) varied significantly according to Site, Habitat type, and Patch size (three-way ANOVA; Site: $F = 14.32$, $df = 1{,}19$, $p = 0.001$; Patch size: $F = 5.32$, $df = 1{,}19$, $p = 0.03$; Habitat type: $F = 8.64$, $df = 1{,}19$, $p = 0.002$). None of the interaction effects were significant (all $p > 0.23$). Shrimp densities were significantly higher at the East site than West (Fig. 4; lower-level ANOVA), higher in seagrass and mixed habitats compared to oyster shell (Fig. 4; Tukey's multiple comparison test), and higher in small than large patches (lower-level ANOVA; Fig. 4).

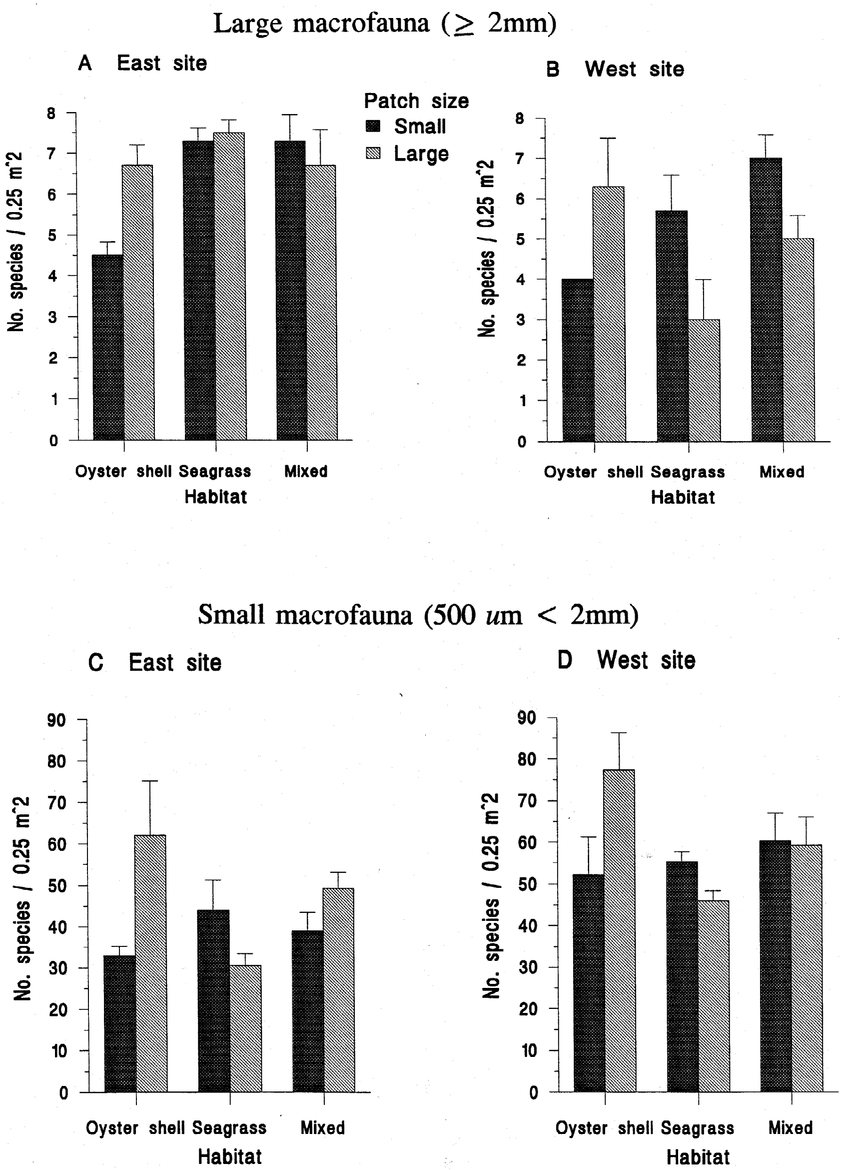

Fig. 3. Effects of Site (East, West), Patch size (small, large) and Habitat type (oyster shell, seagrass, mixture of seagrass and oyster shell) on the mean number (+ S.E.) of species of large (A,B) and small (C,D) estuarine macrofauna colonizing artificial habitat plots. Note different scales on *y*-axes. There was no variance associated with the mean for the small, oyster shell plot in (B). See text for significance levels.

3.3.2. Large macrofauna, hippolytid shrimp

The density of hippolytid shrimp varied significantly according to Site and Habitat type (three-way ANOVA; Site: $F = 29.2$, $df = 1,22$, $p = 0.001$; Habitat type: $F = 6.5$,

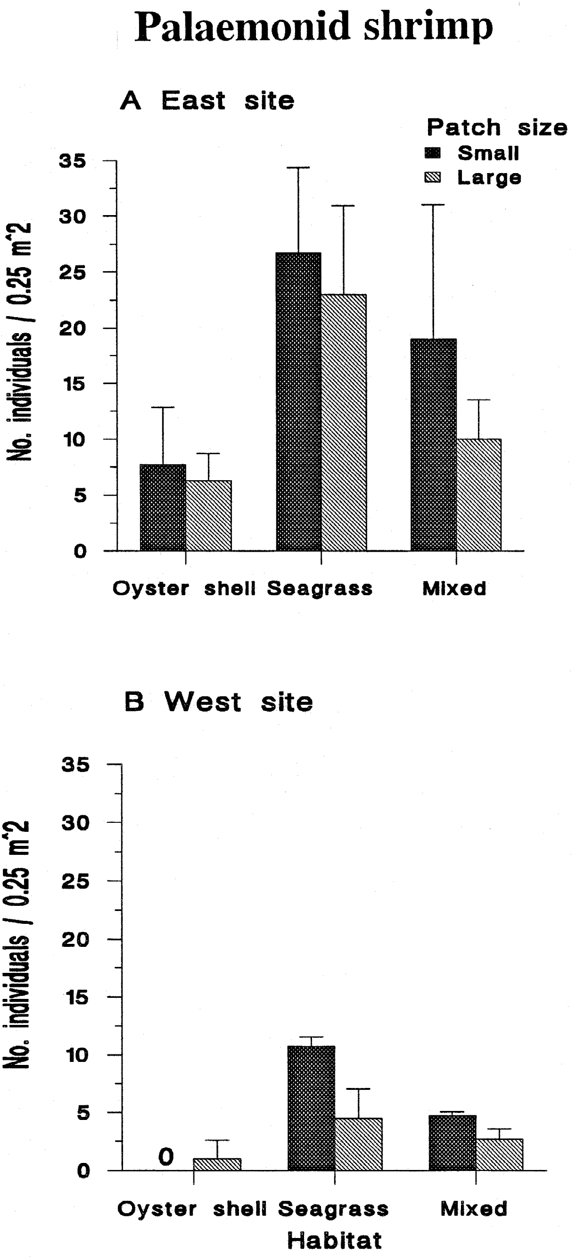

Fig. 4. Effects of Patch size (small, large) and Habitat type (oyster shell, seagrass, mixture of seagrass and oyster shell) on the mean density (+ S.E.) of palaemonid shrimp (*Palaemonetes pugio*, *P. vulgaris*, *P. intermedius*) inhabiting experimental habitat plots at the East site (A) and West site (B). See text for significance levels.

df = 2,22, $p = 0.006$). Statistical power for detecting a significant patch size effect was low (30%). None of the other main or interaction effects were significant (all $p > 0.18$). The Site main effect was due to significantly higher densities of hippolytid shrimp at the East than the West site (Fig. 5a; lower-level ANOVA). The habitat type effect was due to significantly higher densities of shrimp in seagrass than in either oyster shell or mixed habitats (Fig. 5; Tukey's multiple comparison test).

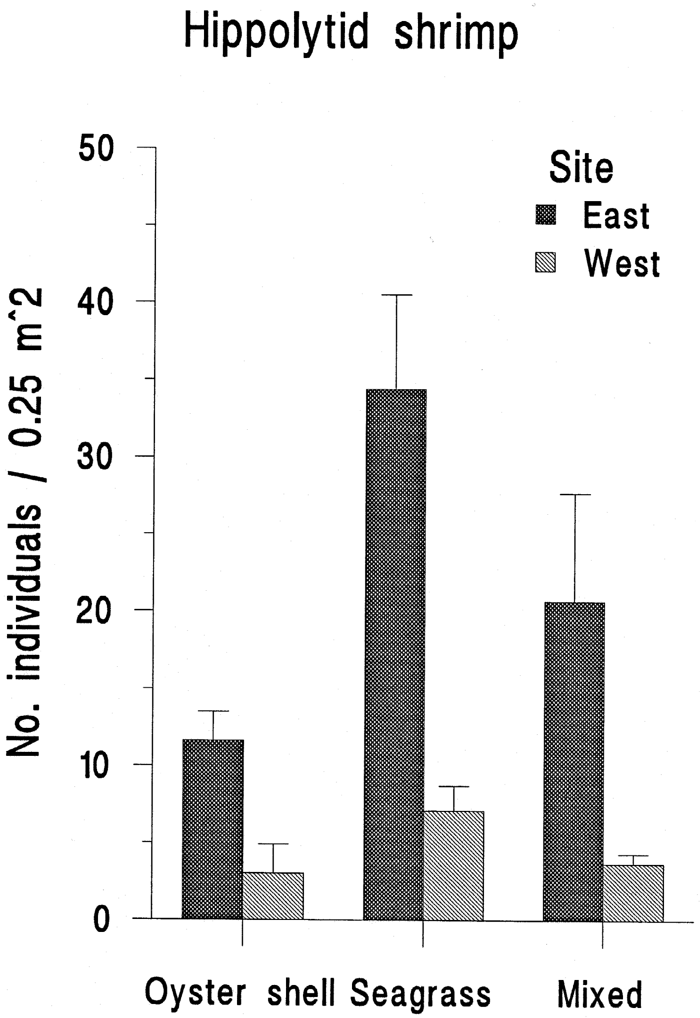

Fig. 5. Effects of Site (East, West) and Habitat type (oyster shell, seagrass, mixture of seagrass and oyster shell) on the mean density (+ S.E.) of hippolytid shrimp (*Tozeuma carolinense*). See text for significance levels.

3.3.3. Small macrofauna, small mobile crustaceans

The mean density ($\log(x+1)$ transformed) of small, mobile crustaceans did not vary with Patch size, Habitat type, or Site (three-way ANOVA; all $p > 0.13$). There was marginal statistical power (70%) to detect a significant habitat type main effect. Nevertheless, there was a significant Patch size by Habitat type interaction effect (three-way ANOVA; $F = 4.32$, $df = 2{,}22$, $p = 0.03$). None of the other interaction effects were significant (all $p > 0.48$). The interaction effect was due to significantly higher densities of small mobile crustaceans in large oyster patches than seagrass or mixed habitats, and no difference between habitat types in small patches (Fig. 6a; Tukey's multiple comparison test). None of the other interaction effects were significant (all $p > 0.08$).

4. Discussion

The data from our study of artificial habitat plots involving naturally recruited assemblages of 171 macrofaunal species and 10 000's of individuals, indicated that macrofauna responded to habitat patchiness in a complex manner that varied according to habitat type, experimental site, species, taxon, functional group, and animal body size. The key findings from this study were that: (1) the density of two of seven response groups (grass shrimp and small, mobile crustaceans) was higher in small than large patches as predicted; (2) there was a disproportionate reduction in macrofaunal abundance and diversity in small patches of oyster shell compared to seagrass and mixed habitat treatments; this pattern was significant for both the total density and numbers of species of small macrofauna, but not for large macrofauna; and (3) macrofaunal colonization was highly variable across seemingly similar sites located only 200 m apart.

A major direct impact of habitat fragmentation is the disruption of animal dispersal (Doak et al., 1992). This disruption in dispersal depends upon the scale of fragmentation relative to the mobility of the organism being studied (Hart and Horwitz, 1991; Doak et al., 1992). The spatial scale of fragmentation consists of two different scales: (1) the relative size of the habitat fragments (patches); and (2) the spatial scale at which these patches are arrayed (Doak et al., 1992). Unfortunately, there is little experimental evidence to permit the formulation of general models that predict an organism's response to habitat fragmentation at a given scale.

Our study focused on the 'habitat patchiness' component of scale (sensu Doak et al., 1992), and provides some of the first evidence that an organism's response to the spatial arrangement of habitats in a landscape, independent of the structural characteristics of the habitat, is dependent upon the joint effects of spatial scale, habitat type, and body size. The results from this study suggest that estuarine macrofauna respond to habitat heterogeneity at relatively small spatial scales (0.25–1 m^2), and that the high variability often observed in abundance patterns of estuarine macrofauna (e.g., Wells, 1961 Coen et al., 1981; Sogard, 1989; McNeill and Fairweather, 1993, and references therein) may be due, in part, to the scale of sampling. Variation in abundance between sites, however, appeared to overwhelm any variation associated with patch size. Thus, variation in

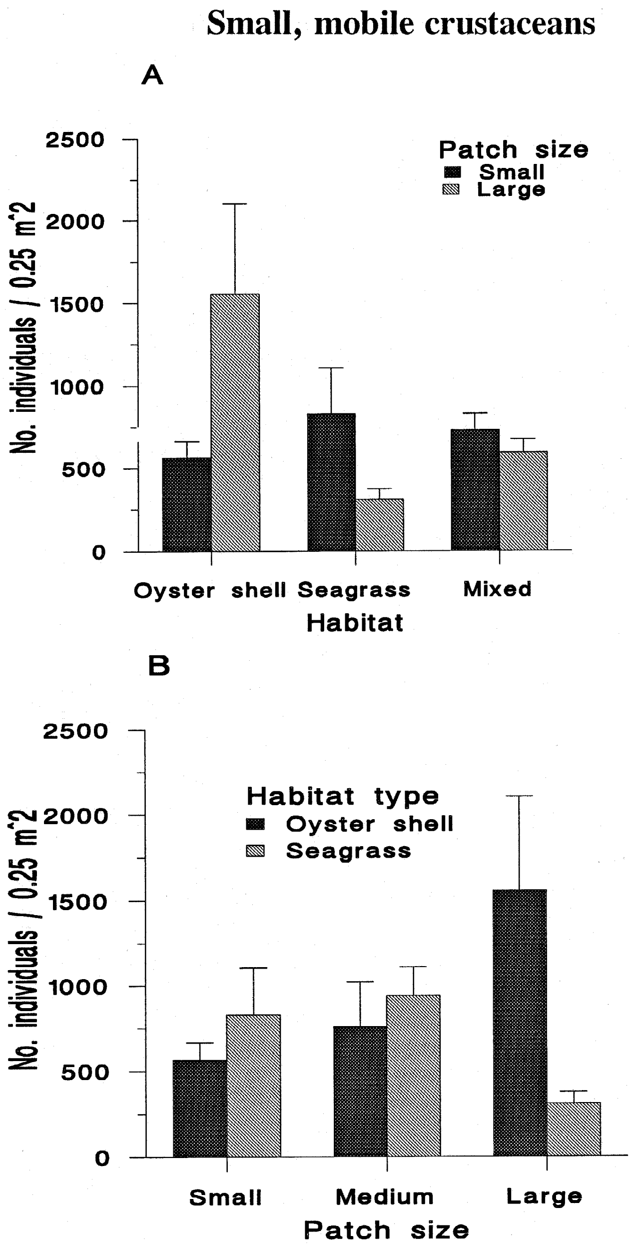

Fig. 6. Effects of Patch size (small, large) and Habitat type (oyster shell, seagrass, mixture of seagrass and oyster shell) (A), and Habitat type (seagrass, oyster shell) and patch size (small, medium, large) on the mean density (+ S.E.) of small, mobile crustaceans (i.e., amphipods and isopods) inhabiting experimental habitat plots. See text for significance levels.

abundance across large spatial scales (100–200 m) appears just as important, if not more so, than variation due to the small-scale (0.25–1 m^2) patchiness of specific habitats.

Although the mechanisms underlying the scale-dependent abundance and diversity patterns described in this study are unknown, the results suggest that certain species may be more ‘sensitive’ (i.e., smaller grain) to fragmentation of oyster shell than either seagrass or a mixture of both habitat types. We are aware of only one other study in which a species (or assemblage of species) appeared to be more sensitive to fragmentation in one habitat type versus another. For example, studies of metapopulation dynamics of the Bay checkerspot butterfly (*Euphydryas editha bayensis*) suggest that local extinction is more frequent in small patches of serpentine grass compared to native grass (Harrison et al., 1988). The apparent sensitivity of macrofauna to fragmentation in oyster shell observed in this study is particularly disturbing from a biodiversity and ecosystem conservation perspective, given that the majority of subtidal oyster habitats in western Atlantic estuaries have been severely fragmented (Seliger et al., 1985; Mann et al., 1991; Rothschild et al., 1994). These observations underscore the need to examine how distribution and abundance patterns of mobile animals covary with habitat type, spatial scale, and body size.

4.1. Potential experimental artifacts

There are no strict conventions regarding the spatial scale over which an organism’s response to habitat patchiness should be measured (Hart and Horwitz, 1991). Identification of the smallest scale at which an organism responds to patch structure (i.e., grain) provides a framework, based on scale, in which comparisons of relative patchiness between systems may be standardized (Kotliar and Wiens, 1990). The response of macrofauna to habitat patchiness and diversity in our study was examined at relatively small spatial scales (0.25–1 m^2) compared to more extensive seagrass and oyster reef systems. Since we chose to use artificial seagrass and shell-filled trays to avoid confounding habitat characteristics with patch size, we were constrained logistically to relatively small patch sizes (up to 1 m^2), compared to natural patch sizes. Nevertheless, the size distribution of natural seagrass and oyster patches is sometimes skewed towards patches <4 m^2 (Wells, 1961; Olesen and Sand-Jensen, 1994; Irlandi, 1997; Eggleston, in press).

The patterns of grass shrimp density with patch size observed in this study also appeared to be biologically realistic since similar patterns have been observed in natural seagrass patches and at larger scales of space and time (Elis, 1998; M. Fonseca, National Marine Fisheries Service (NMFS), Beaufort, NC, pers. comm.; E. Irlandi, University of Miami, pers. comm.). The value of artificial seagrass and oyster shell-filled trays has been demonstrated in numerous ecological studies (e.g., Barber et al., 1979; Eggleston, 1988; Bell et al., 1985, 1987, 1995; Virnstein and Curran, 1986; Sogard, 1989; Bell and Hicks, 1991; Eggleston and Armstrong, 1995; Irlandi, 1997; Eggleston et al., 1998).

Colonization was also examined within a relatively short time frame (14 days). Nevertheless, previous studies examining colonization of recently defaunated seagrass by grass shrimp and amphipods found that densities reached an asymptote after 4 days and 7 days, respectively (Nelson, 1979; Stoner and Lewis, 1985; Sogard, 1989). Our longer experimental period (14 days) appeared adequate in terms of maximizing the density of mobile crustaceans in our artificial habitat plots, because soak time was beyond that presumably required for densities to reach an asymptote.

The role of small-scale experiments such as this is to aid in the design of future tests of hypotheses regarding patterns and processes of scale-dependence, and to link studies conducted at different scales (Thrush et al., 1997 and references therein). For example, large-scale correlative and manipulative studies could determine whether or not macrofaunal species diversity is reduced faster and to a greater degree in fragmented oyster habitats than in fragmented seagrass beds, as predicted from this small-scale study. Moreover, information on spatial distributions of functional or taxonomic groups of organisms identified at relatively small spatial scales can provide theories about movement and ecological processes operating at this scale, but also identify processes that generate larger ecological patterns (Dayton and Tegner, 1984; Smith and Brumsickle, 1989; Thrush et al., 1997, and references therein). For example, individual mobility and habitat/organism interactions often play a fundamental role in maintaining marine populations and communities on large habitat patches (Barry and Dayton, 1991; review by Thrush et al., 1997). Basic information on body size, feeding mode, and mobility has been used to predict successfully small-scale spatial arrangements of marine benthic species (Hewitt et al., 1996; this study). Such basic life history information is essential in predicting how species respond to environmental heterogeneities on different scales (Thrush et al., 1997).

4.2. Was faunal colonization higher in small versus large patches?

Of the five cases in which we observed a significant patch size effect, grass shrimp (*Palaemonetes* sp.) and small, mobile crustaceans (i.e., amphipods and isopods) were the only taxonomic or functional groups whose densities were higher in small than large patches. This was surprising given the general trend towards higher recruitment in small versus large patches in marine systems (e.g., Paine and Levin, 1981; Keough, 1984; Sousa, 1984; Bell et al., 1987; Sogard, 1989; Smith and Brumsickle, 1989; Worthington et al., 1992; McNeill and Fairweather, 1993; Robbins and Bell, 1994; Eggleston et al., 1998). Grass shrimp (*Palaemonetes* sp.) and amphipods are highly mobile species that migrate between subtidal seagrass beds, or between seagrass beds and salt marshes as the latter habitats are inundated during flooding tides (Nelson, 1979; Lewis and Stoner, 1983; Kneib and Wagner, 1994). The pattern for grass shrimp was consistent with our previous findings of increasing grass shrimp density with decreasing patch size (Eggleston et al., 1998). Several alternative explanations for this pattern seem plausible, and are discussed in Eggleston et al. (1998). Briefly, both grass shrimp and small, mobile crustaceans may be responding to an edge effect either as refuge, foraging, or both. For example, based upon changing perimeter:area ratios with patch size, as these crustaceans move between complex benthic habitats, they were two-times more likely to encounter one of our small patches (0.25 m^2) than our large patch (1 m^2). Similarly, if grass shrimp and small, mobile crustaceans were using the patch edge as a refuge from predators (Coen et al., 1981), and periodically foraging on benthic infauna in the surrounding soft-bottom habitat (Posey and Hines, 1991), then small patches would contain two-times the amount of foraging edge as our largest patch size. The relative importance of a foraging edge as opposed to a refuge edge in explaining the scale-dependent density patterns observed in this study remain to be determined experimentally. Several other alternative explanations would include predation being higher on grass shrimp and small, mobile crustaceans in large versus small patches, or predators perceiving large patches as foraging sites, causing prey to shift to smaller patches.

Given that the density of both grass shrimp and small, mobile crustaceans was higher in small versus large patches, we were surprised that the abundance of hippolytid shrimp did not vary in a similar manner. Hippolytid shrimp are common, mobile fauna within seagrass beds (e.g., Virnstein, 1987, and references therein), and we expected that they would be found in higher numbers in small versus large patches. However, hippolytid shrimp apparently use drift algae as a refuge from predators and for foraging (Dugan, 1983; Virnstein, 1987). Previous studies indicate that the accumulation of drift algae is higher in large patches of seagrass than in small patches of (Bell et al., 1995). Thus, the abundance of hippolytid shrimp may be more dependent upon the response of secondary structure such as drift algae to patch size, rather than to seagrass patch size itself.

4.3. Do relatively small macrofauna have lower grain than large macrofauna, and were patch size effects habitat-specific?

In general, small macrofauna were more sensitive to habitat patchiness than large macrofauna, and most macrofauna were more sensitive to patchiness in oyster shell than seagrass or mixed habitats. Although the number of large macrofaunal species residing in large patches was similar between habitat types, small patches of oyster shell contained fewer species than seagrass or mixed habitats. The total density of large macrofauna did not vary according to habitat type or patch size. Conversely, for small macrofauna, both the total density and number of species was significantly higher in large patches of oyster shell compared to large patches of either seagrass or mixed habitats. For small habitat patches, there was no difference in total density nor the number of small macrofaunal species between habitat types. The patterns observed for small macrofauna appeared to be driven primarily by small, mobile crustaceans such as amphipods and isopods. For example, the density of small, mobile crustaceans was significantly higher in large oyster patches than large seagrass or mixed habitat patches, similar to the general pattern observed for small macrofauna.

Several biotic mechanisms may explain the disproportionate reduction in macrofauna in small oyster habitats versus seagrass and mixed habitat plots. These possible mechanisms involve scale-dependent processes associated with the lower vertical relief of oyster shell versus seagrass habitats. Seagrass provides a high degree of architectural complexity because of its three-dimensional nature via vertical shoots (Heck and Crowder, 1991, and references therein). Because of this architectural complexity, survival rates of seagrass residents is often greater in seagrass than other unvegetated habitats (Heck and Crowder, 1991; Perkins-Visser et al., 1996, and references therein). Moreover, the three-dimensional nature of seagrass provides additional space within which shrimp can distribute themselves, thereby reducing inter- and intra-specific displacement from patches when densities are relatively high (Van Dolah, 1976; Coen et al., 1981). Conversely, the architectural complexity of oyster reefs results from the number, maximum sizes, shape, and size frequency of oysters (Eggleston, 1988). Although the architectural complexity of oyster reefs and individual shells can provide refuge to decapod crustaceans residing within the shell matrix (Fernandez et al., 1993; Eggleston and Armstrong, 1995), we are unaware of any studies that have directly compared survival or emigration between seagrass and oyster shell habitats. Thus, final conclusions regarding the role of scale-dependent biotic processes underlying interactions between animal body size, patch size, and habitat type on macrofaunal abundance remains to be determined experimentally. We eliminated physical disturbance (e.g., storm-induced sedimentation) as an explanation for these habitat- and scale-dependent patterns because we would have expected to see an even more pronounced reduction in macrofaunal abundance and diversity in small oyster patches for small macrofauna than that observed for large macrofauna—this was not the case.

4.4. Does a mixture of habitat types contain higher densities and numbers of species than monotypic habitats?

The total density and number of macrofaunal species was not higher in the mixed habitat treatment compared to seagrass or oyster shell as initially predicted. Nevertheless, this result was not surprising given that the species list for seagrass and oyster shell habitats were very similar (although abundances were different), such that combining these lists had no additive effect upon overall species richness. Of the seven response variables examined, three showed a clear pattern with respect to habitat type; the density of grass shrimp, large macrofauna, and species richness was generally higher in seagrass than oyster shell.

Information on the interdependence of shallow estuarine habitats such as seagrass and oyster reef habitats, as well as their relative importance as settlement and refuge sites, is critical for understanding population dynamics of numerous commercially and ecologically important estuarine-dependent species. This information is particularly important in areas lacking seagrass (e.g., southern North Carolina southward to Georgia, USA), where oyster reefs may represent the only structural refuge available. For example, grass shrimp and amphipods are generally associated with submerged aquatic vegetation and intertidal habitat containing emergent vegetation (Welsh, 1975; Nelson, 1979; Rozas and Hackney, 1984; Kneib and Wagner, 1994, and references therein). Nevertheless, Posey et al. (in press) found higher densities of grass shrimp and blue crabs in subtidal oyster reefs than in inundated salt marshes. Moreover, their laboratory habitat choice experiments indicated that in the presence of fish predators, grass shrimp actively chose oyster shell over low density seagrass (Posey et al., in press). The results from this study and others highlights the potential importance of oyster reefs as an alternative habitat for a wide variety of marine benthic invertebrates. Moreover, the scale-dependent distribution and abundance patterns observed in this study suggest numerous, explicit hypotheses, which await testing in natural habitats and at larger scales.

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Appendix A

List of taxonomic groups and species collected from artificial recruitment plots in Middle Marsh, Back Sound, North Carolina, USA

Anemones	*Ewardsia* sp.
Ascidians	
Bivalves	*Anadara ovalis, Anadara transversa, Brachidontes exustus, Chione Pubera/cancellata, Chione grus, Crassunella lunutata, Dosinia elegans, Gemma gemma, Lyonsia hyalina, Macoma tenta, Mactra fragilis, Modiolus americanus, Mulinia lateralis, Musculus lateralis, Nucula proxima, Nuculana verrilliana, Papyridea soleniformis, Pseudamussium vitreus, Solemya velum, Tagelus divisus, Tagelus plebius, Tellina alternata, Tellina duplicatus, Tellina versicolor*
Bryozoans	
Chaetognaths	
Crustaceans	
Amphipoda	*Ampelisca abdita, Ampelisca vadorum, Ampelisca verrilli, Ampithoe longimana, Ampithoe valida, Batea catharinensis, Caprella equilibra, Caprella penatus, Corophium acherusicum, Corophium actum, Cymadusa compta, Elasmopus brasiliensis, Elasmo pus levis, Erichthonius brasiliensis, Gammarus mucronatus, Harpinia propinqua, Lembos smithia/unicornis, Lembos webesteri, Lysianopsis alba, Melita appendiculata, Melita nitida/dentata, Microprotopus raneyi, Paracaprella tenius, Paraphoxus spinosus, Rudilembiodes nageli, Stenothoe minuta, Trichophoxus epistomus*
Cirripedia	*Balanus amphitrite, Balanus eburneus*
Copepoda	*Calanoida, Cyclopoida, Harpacticoida*
Cumacea	
Decapoda	
Caridean shrimps	*Alpheus normanni, Palaemonetes intermedius, Palaemonetes pugio, Palaemonetes vulgaris, Tozeuma carolinense*

Portunid crabs	*Callinectes sapidus, Callinectes similis*
Xanthid crabs	*Hexapanopeus angustifrons, Neopanopeus sayi, Panopeus herbstii*
Isopoda	*Cyathura burbaneki, Cyathura polita, Edotea triloba, Erichonella attenuata, Jaera marina, Sphaeroma quadridentatum*
Tanaidacea	*Leptochelia rapax, Leptochelia savignyi*
Fish	*Gobionellus bolesoma, Gobionellus shuffeldti, Lagodon rhomboides*
Gastropods	*Acteon punctostriatus, Anachis avara, Anachis translirata, Betusa caridei, Bittium varium, Bursatella leachi, Busycon* sp., *Caecum puichellum, Cerithium floridanum, Chaetopleura apliculata, Crepidula fornicata, Crepidula maculosa, Elysia catula, Eupleura catula, Fiscus communis, Hydrobia minuta, Mangelia plicosa, Mitrella lunata, Nassarius vibrex, Odostomia bisuturalis, Odostomia impressa, Petricola pholadiformis, Polinices duplicatus*, Polycera hummi, Pyramidella crenulata, Retusa candei, Rissoina decussata Terebra dislocata, Turbonella interrupta*
Hydrozoans	
Insects	
Ant	
Arachnida	*Hydracarina tabanidae*
Ceratopogonidab	(‘No see ums’)
Chironomidae	(‘Non-biting midges’)
Coleoptera	
Collembola	
Hemioptera	
Hymenoptera	
Kinorhyncha	
Nematodes	*Amphiporus ocraceus, Micura rubra, Tetrastemma elegans*
Ophiuroids	*Ophioderma brevispinum*
Ostracods	
Phoronids	*Phoronis psammophila*
Polychaetes	
Ampharetidae	*Melinna maculata*
Amphictenidae (Pectinaridae)	*Cistena* (= *Pectinaria*) *gouldii*
Arabellidae	*Arabella iricolor, Drilonereis magna*
Capitellidae	*Capitella* sp. *capitella, Mediomastus californiensis, Notomastus hemipodus*
Chrysopetalidae	*Bhawamia goodei*
Cirratulidae	*Tharyx marioni*
Dorvilleidab	*Dorvillea sociabilis, Schistomeringos rudolphi*
Eunicidae	*Marphysa sanguinea*
Flabelligeridae	*Piromis eruca*

Glyceridab	*Glycera americana*
Goniadidae	*Goniada littorea*
Hesionidae	*Podarke obscura*
Lumbrineridae	*Lumbrinereis coccinea*
Maldanidae	*Axiothella mucosa, Clymenella forquata, Petaloproctus socialis*
Nephytidae	*Nephtys picta*
Nereidae	*Ceratonereis irritabilis, Nereis succinea, Nereis falsa, Platynereis dumerilii, Rulliernereis mexicana, Stenonineris martini*
Onuphidae	*Diapatra cuprea, Onuphis jenneri*
Ophelidae	*Armandia maculata*
Orbinidae	*Haploscolopis robustus*
Paraonidae	*Aricidea fragilis*
Phyllodocidae	*Eulalia sanguinea, Phyllodoce arenae, Phyllodoce fragilis*
Poecilochaetidae	*Poecilochaetus johnsoni*
Sabellidae	*Maglomma bioculatum, Sabella micro phthalma*
Serpulidae	*Hydroides dianthus*
Spionidae	*Malacoceros vanderhorsti, Spiophanes bombyx, Spiophanes setosa, Streblospio benedicti*
Spirorbidae	*Spirorbis borealis, Spirorbis spirullum*
Syllidae	*Brania clavata, Exogone dispar, Paraspionsyllis longicerrata, Sphaerosyllis labyrinthophila, Syllis cornuta*
Terebellidab	*Pista palmata, Polycirrus eximius*
Priapula	
Pycnogonids	*Anoplodactylus lenthus, Callipallene brevirostris, Tanystylum orbiculare*
Sipuncula	*Aspidusiphon parvulus*
Turbellarians	*Lactocestus* sp., *Stylochus* sp.

References

Allen, T.F.H., Starr, T.B., 1982. Hierarchy: Perspectives for Ecological Diversity, University of Chicago Press, Chicago.

Andren, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71, 355–366.

Barber, W.E., Greenwood, J.G., Crocos, P., 1979. Artificial seagrass: A new technique for sampling the community. Hydrobiologia 65, 135–140.

Barry, J.P., Dayton, P.K. 1991. Physical heterogeneity and the organisation of marine communities. In: Kolasa, K., Pickett, S.T.A. (Eds.), Ecological Heterogeneity, Springer-Verlag, New York, pp. 270–320.

Bell, J.D., Steffe, A.S., Westoby, M., 1985. Artificial seagrass: How useful is it for field experiments on fish and macroinvertebrates? J. Exp. Mar. Biol. Ecol. 90, 171–177.

Bell, J.D., Westoby, M., Steffe, A.S., 1987. Fish larvae settling in seagrass beds of different leaf density? J. Exp. Mar. Biol. Ecol. 111, 133–144.

Bell, S.S., Hicks, G.R.F., 1991. Marine landscapes and faunal recruitment: A field test with seagrasses and copepods. Mar. Ecol. Prog. Ser. 73, 61–68.

Bell, S.S., Hall, M.O., Robbins, B.D., 1995. Toward a landscape approach in seagrass beds: Using macroalgal accumulation to address questions of scale. Oecologia 104, 163–168.

Coen, L.D., Heck, Jr. K.L., Abele, L.G., 1981. Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62, 1484–1493.

Coleman, B.D., Mares, M.A., Willig, M.R., Hsieh, Y.-H., 1982. Randomness, area, and species richness. Ecology 63, 1121–1133.

Dayton, P.K., Tegner, M.J., 1984. The importance of scale in community ecology: A kelp forest example with terrestrial analogs. In: Price, P.W., Slobodchikoff, C.N., Gaud, W.S. (Eds.), A New Ecology: Novel Approaches to Interactive Systems, Wiley, New York, pp. 457–483.

Doak, D.F., Marino, P.C., Kareiva, P.M., 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: Implications for conservation. Theor. Pop. Biol. 41, 315–336.

Dugan, P.J., 1983. Seasonal and geographic distribution of seven decapod crustaceans in Apalachee Bay. Florida. Contr. Mar. Sci. 26, 65–79.

Dunning, Jr. J.B., Stewart, D.J., Danielson, B.J., Noon, B.R., Root, T.L., Lamberson, R.H., Stevens, E.E., 1995. Spatially explicit population models: Current forms and future uses. Ecol. Appl. 5, 3–11.

Eckman, J.E., 1983. Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr. 28, 241–257.

Eggleston, D.B., 1988. Predator–prey dynamics between the blue crab and juvenile oysters, M.A. Thesis, College of William and Mary, Williamsburg, VA, 222 p.

Eggleston, D.B., in press. Application of landscape ecological principles to oyster reef restoration. In: Luckenbach, M.W. (Ed.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches, Virginia Institute of Marine Science Press, Gloucester Point, VA, USA.

Eggleston, D.B., Armstrong, D.A., 1995. Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. Ecol. Monogr. 65, 193–216.

Eggleston, D.B., Etherington, L.L., 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.

Ellison, A.M., Bedford, B.L., 1995. Response of a wetland vascular plant community to disturbance: a simulation study. Ecol. Appl. 5, 109–123.

Elis, W.E., 1998. Scale-dependent effects of patch age and starting conditions on floral accumulation and faunal colonization in seagrass. M.S. thesis, North Carolina State University, Raleigh, NC, USA, 100pp.

Farnsworth, E.J., Ellison, A.M., 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. Ecol. Monogr. 66, 45–66.

Fernandez, M., Iribarne, O., Armstrong, D.A., 1993. Habitat selection by young-of-the-year Dungeness crab, *Cancer magister* Dana and predation risk in intertidal habitats. Mar. Ecol. Prog. Ser. 92, 171–177.

Fonseca, M.S., 1996. Scale dependence in the study of seagrass systems. In: Kuo, J., Phillips, R.C., Walker, D.I., Kirkman, H. (Eds), Seagrass Biology: Proc. Intl. Workshop, Rottnest Island, Western Australia, 25–29 January 1996, pp. 95–104.

Gascon, C., Travis, J., 1992. Does the scale of experimentation matter? A test with tadpoles and dragonflies. Ecology 73, 2237–2243.

Gunther, C-P., 1992. Dispersal of intertidal invertebrates: A strategy to react to disturbances of different scales. Neth. J. Sea. Res. 30, 45–56.

Gustafson, E.J., Gardner, R.H., 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77, 94–107.

Haila, Y., 1983. Land birds on northern islands: A sampling metaphor for insular colonization. Oikos 41, 334–351.

Harrison, S., Murphey, D.D., Ehrlich, P.R., 1988. Distribution of the Bay checkerspot butterfly, *Euphydryas editha bayensis*: Evidence for a metapopulation model. Am. Nat. 132, 360–382.

Hart, D.D., Horwitz, R.J., 1991. Habitat diversity and the species–area relationship: Alternative models and tests. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), Habitat Structure: The Physical Arrangement of Objects in Space, Chapman and Hall, New York, pp. 47–68.

Heck, K.L., Jr., Crowder, L.B., 1991. Habitat structure and predator–prey interactions in vegetated aquatic systems. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), Habitat Structure: The Physical Arrangement of Objects in Space, Chapman and Hall, New York, pp. 281–299.

Hewitt, J.E., Thrush, S.F., Cummings, V.J., Pridmore, R.D., 1996. Matching patterns with processes: Predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. Mar. Ecol. Prog. Ser. 135, 57–67.

Holmquist, J.G., 1994. Benthic macroalgae as a dispersal mechanism for fauna: Influences of a marine tumbleweed. J. Exp. Mar. Biol. Ecol. 180, 235–251.

Irlandi, E.A., 1994. Large- and small-scale effects of habitat structure on rates of predation: How percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. Oecologia 98, 176–183.

Irlandi, E.A., 1997. Seagrass patch size and survivorship of an infaunal bivalve. Oikos 78, 511–518.

Irlandi, E.A., Ambrose, Jr. W.G., 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, 307–313.

Kareiva, P.M., 1987. Habitat fragmentation and the stability of predator–prey interactions. Nature 321, 388–391.

Kelly, B.J., Wilson, J.B., Mark, A.F., 1989. Causes of the species–area relation: A study of islands in Lake Manapouri. New Zealand J. Ecol. 77, 1021–1028.

Keough, M.J., 1984. Effects of patch size on the abundance of sessile marine invertebrates. Ecology 65, 423–437.

Kim, J.H., DeWreede, R.E., 1996. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. Mar. Ecol. Prog. Ser. 133, 217–228.

Kneib, R.T., Wagner, S.L., 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. Mar. Ecol. Prog. Ser. 106, 227–238.

Kolasa, J., 1989. Ecological systems in hierarchical perspective: Breaks in community structure and other consequences. Ecology 70, 36–47.

Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos 59, 253–260.

Kulcycki, G.R., Virnstein, R.W., Nelson, W.G., 1981. The relationship between fish abundance and algal biomass in a seagrass-drift community. Estuar. Coast. Shelf Sci. 12, 341–347.

Leber, K.M., 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. Ecology 66, 1951–1964.

Levin, S.A., 1992. The problem of patterns and scale in ecology. Ecology 73, 1943–1967.

Lewis, F.G. III,, Stoner, A.W., 1983. Distribution of macrofauna within seagrass beds: An explanation for patterns of abundance. Bull. Mar. Sci. 33, 296–304.

Main, K.L., 1987. Predator avoidance in seagrass meadows: Prey behavior, microhabitat selection, and cryptic coloration. Ecology 68, 170–180.

Mann, R., Burreson, E.M., Baker, P.K., 1991. The decline of the Virginia oyster fishery in Chesapeake Bay: Considerations for introduction of a non-endemic species, *Crassostrea gigas* (Thunberg, 1793). J. Shellfish Res. 10, 379–388.

McGarigal, K., McComb, W.C., 1995. Relationship between landscape structure and breeding birds in the Oregon coast range. Ecol. Monogr. 45, 235–260.

McNeill, S.E., Fairweather, P.G., 1993. Single large or several small marine reserves? An experimental approach with seagrass fauna. J. Biogeogr. 20, 429–440.

Menge, B.A., Olson, A., 1990. Role of scale and environmental factors in the regulation of community structure. Trends Ecol. Evol. 5, 52–57.

Nelson, W.G., 1979. An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. J. Exp. Mar. Biol. Ecol. 39, 213–264.

Olesen, B., Sand-Jensen, K., 1994. Biomass-density patterns in the temperate seagrass *Zostera marina*. Mar. Ecol. Prog. Ser. 109, 283–291.

O'Neill, R.V., 1989. Perspectives in hierarchy and scale. In: Roughgarden, J., May, R.M., Levin, S.A. (Eds.), Perspectives in Ecological Theory, Princeton University Press, Princeton, NJ, pp. 140–156.

Paine, R.T., Levin, S.A., 1981. Intertidal landscapes: Disturbances and the dynamics of pattern. Ecol. Monogr. 51, 145–178.

Perkins-Visser, E., Wolcott, T.G., 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.

Poff, N.L., Allan, L.D., 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76, 606–627.

Posey, M.H., Hines, A.H., 1991. Complex predator–prey interactions within an estuarine benthic community. Ecology 72, 2155–2169.

Posey, M.H., Powell, C.M., Alphin, T.D., Townsend, E.C., in press. Oyster reefs as a habitat for fish and decapods. In: Luckenbach, M.W. (Ed.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches, Virginia Institute of Marine Science Press, Gloucester Point, VA, USA.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Nat. 132, 652–661.

Reidenbaugh, T.G., Banta, W.C., 1980. Origin and effects of *Spartina* wrack in a Virginia salt marsh. Gulf Res. Rep. 6, 393–401.

Robbins, B.D., Bell, S.S., 1994. Seagrass landscapes: A terrestrial approach to the marine subtidal environment. Trends Ecol. Evol. 9, 301–304.

Ross, S.W., Epperly, S.P., 1985. Utilization of shallow estuarine nursery areas by fishes in Pamlico Sound and adjacent tributaries, North Carolina. In: Yanez-Aranciba, A. (Ed.), Fish Community Ecology in Estuaries and Coastal Lagoons: Towards and Ecosystem Integration, UNAM Press, Mexico, pp. 207–232.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time, Cambridge University Press, Cambridge.

Rothschild, B.J., Ault, J.S., Goulletquer, P., Heral, M., 1994. Decline of the Chesapeake Bay oyster population: A century of habitat destruction and overfishing. Mar. Ecol. Prog. Ser. 111, 29–39.

Rozas, L.P., Hackney, C.T., 1984. Use of oligohaline marshes by fishes and macrofaunal crustaceans in North Carolina. Estuaries 7, 213–224.

Schneider, D.C., 1994. Quantitative ecology: spatial and temporal scaling. Academic Press, San Diego, California, USA.

Seliger, H.H., Boggs, J.A., Biggley, W.H., 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. Science 228, 70–73.

Smith, C.R., Brumsickle, S.J., 1989. The effect of patch size and substrate isolation on colonization modes and rate in an intertidal sediment. Limnol. Oceanogr. 34, 1263–1277.

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.

Sousa, W.P., 1984. Intertidal mosaics: Patch size, propagule availability, and spatially variable patterns of succession. Ecology 65, 1918–1935.

Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69, 476–498.

Stoner, A., Lewis, G.R., 1985. The influence of quantative and qualitative aspects of habitat complexity in tropical seagrass meadows. J. Exp. Mar. Biol. Ecol. 94, 19–40.

Thrush, S.F., Whitlach, R.B., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., Wilkinson, M.R., 1996. Scale-dependent recolonization: The role of sediment stability in a dynamic sandflat habitat. Ecology 77, 2472–2487.

Thrush, S.F., Schneider, D.C., Legendre, P., Whitlach, R.B., Dayton, P.K., Hewitt, J.E., Hines, A.H., Cummings, V.J., Lawrie, S.M., Grant, J., Prodmore, R.D., Turner, S.J., McArdle, B.H., 1997. Scaling-up from experiments to complex ecological systems: Where to next? J. Exp. Mar. Biol. Ecol. 216, 243–254.

Underwood, A.J., Skilleter, G.A., 1996. Effects of patch-size on the structure of assemblages of rock pools. J. Exp. Mar. Biol. Ecol. 197, 63–90.

Van Dolah, R.F., 1976. Interference competition as a mechanism of coexistence between the sympatric species of the grass shrimp *Palaemonetes* (Decapoda: Palaemonidae). J. Exp. Mar. Biol. Ecol. 25, 19–35.

Virnstein, R.W., 1987. Seagrass-associated invertebrate communities of the Southeastern US: A review. In: Durako, M.J., Phillips, R.C., Lewis, R.R., III (Eds.), Proc. Symp. on Subtropical–Tropical Seagrasses of the Southeastern United States 42, 89–116.

Virnstein, R.W., Curran, M.C., 1986. Colonization of artificial seagrass versus time and distance from source. Mar. Ecol. Prog. Ser. 29, 279–288.

Warwick, R.M., 1993. Environmental impact studies on marine communities: Pragmatical considerations. Australian Journal of Ecology 18, 63–80.

Wells, H.W., 1961. The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. 31, 239–266.

Welsh, B.L., 1975. The role of grass shrimp, *Palaemonetes pugio*, in a tidal marsh ecosystem. Ecology 56, 513–530.

Wilson, J.B., Roxburgh, S.H., 1994. A demonstration of guild-based assembly rules for a plant community, and determination of intrinsic guilds. Oikos 69, 267–276.

With, K.A., Crist, T.O., 1995. Critical thresholds in species' responses to landscape structure. Ecology 76, 2446–2459.

Worthington, D.G., Ferrell, D.J., McNeill, S.E., Bell, J.D., 1992. Effects of shoot density of seagrass on fish and decapods: Are they evident over large spatial scales. Mar. Biol. 112, 139–146.