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Colonization and Predation in Isolated Seagrass Beds: An Experimental Assessment From the Northern Gulf of Mexico

MATTHEW W. JOHNSON AND KENNETH L. HECK, JR.

We tested the effects of habitat fragmentation on the structure (community composition and biomass) and function (predation rates as assessed by tethering) of circular artificial seagrass units (ASUs) located in an area removed from the influence of immigrants from established seagrass meadows. ASUs varied by size (0.1–10 m²), perimeter, and perimeter:area ratios (P/A). Blue crabs and hermit crabs accounted for the greatest number of individuals and biomass present on the ASUs, but amphipods, shrimps, fishes, and gastropods were also present. We detected few significant relationships between abundance or biomass and patch size, perimeter, or P/A ratios. In tethering experiments, there were no significant differences in mortality among the different sized ASUs in any of the three tethering locations, but there was significantly less pinfish mortality in the ASU center as compared to the patch edge and unstructured sand habitats. Our results suggest that although community composition may be dissimilar to areas with established seagrass meadows, the ecological responses to habitat fragmentation remain constant. These data can provide a better understanding of faunal assemblages that can be expected for restored seagrass beds in areas without established seagrass populations.

Habitat fragmentation occurs when large contiguous habitats are broken into small discrete habitats with increasing isolation among patches (Bender et al., 1998). This process can include an overall loss of habitat as well as changes in patch shape, size, isolation, and edge (Andr n, 1994; Fahrig, 1997). The effects of patch configuration on organisms in terrestrial environments have been examined extensively. However, results from terrestrial studies have been inconsistent with respect to effects on faunal species richness and abundance (Debinski and Holt, 2000). In a review by Debinski and Holt (2000), results of experiments examining arthropod abundance agreed with the theoretical expectations of the effects due to habitat fragmentation (e.g., a positive relationship between patch size and species richness was detected); however, highly mobile birds and mammals, early-successional plants, long-lived species, and generalist predators did not respond in the hypothesized manner. Similarly, studies in marine ecosystems indicate that the response of seagrass macrofaunal community structure (e.g., abundance) and function (e.g., growth and survival) to habitat fragmentation are not consistent, preventing generalized conclusions about fragmentation.

For example, neither abundance, survival, nor growth of marine crustaceans (Eggleston et al., 1998, 1999; Bell et al., 2001; Hovel and Lipcius, 2001; Hovel et al., 2002; Hovel, 2003), shellfish (Irlandi, 1994, 1996, 1997; Bologna and Heck,

1999, 2000; Irlandi et al., 1999), or finfish (McNeill and Fairweather, 1993; Ault and Johnson, 1998; Caley et al., 2001) have responded consistently to changes in patch size, shape, and arrangement. In addition, predator-prey relationships (Orth and van Montfrans, 2002; Hovel, 2003; Laurel et al., 2003; Johnson and Heck, 2006a, 2006b) and faunal colonization rates can vary with patch size and shape (Eggleston et al., 1998; Bologna and Heck, 2000; Bell et al., 2001). For example, no significant relationship was found between seagrass area and predation on blue crabs (*Callinectes sapidus*) (Hovel and Lipcius, 2001, 2002; Hovel, 2003), grass shrimps (*Palaemonetes* spp.), or pinfish (*Lagodon rhomboides*) (Johnson and Heck, 2006b), but Laurel et al. (2003) demonstrated that predation on age-0 cod (*Gadus* spp.) was inversely related to seagrass patch size, presumably due to a decrease in the number of predators in smaller patches. Additionally, it has been demonstrated that patch area can influence abundance and secondary production (Eggleston et al., 1999; Bell et al., 2001; Johnson and Heck, 2006a). In North Carolina, seagrass patch size was negatively related to grass shrimp abundance (*Palaemonetes* spp.), positively related to blue crab megalopae abundance, but unrelated to blue crab juvenile abundances (Eggleston et al., 1998). Overall, these studies suggest that regardless of the measure of community structure or function, the responses of organisms to habitat fragmentation are species-, location-, and time-specific.

Despite increasing acknowledgment of the importance of seagrasses, and efforts to preserve them (Fonseca et al., 1982; Kenworthy et al., 1982; Heck et al., 1997; Granata et al., 2001), seagrass acreage globally has declined since the 1950s (Orth et al., 2006), resulting in changes in seagrass meadow patch dynamics. This decrease in acreage can be attributed to both natural (e.g., storms and wave action) and anthropogenic causes (Durako, 1994; Dawes et al., 1997; Fonseca and Bell, 1998; Creed and Amado-Filho, 1999; Kirkman and Kirkman, 2000; Bell et al., 2002; Duarte, 2002). Such habitat losses, coupled with the increase in edge that follows, may be a double-edged sword: increased edge can enhance the settlement of some species (Eggleston et al., 1999; Bologna and Heck, 2000), but it may come with a reduction in the overall amount of habitat available as shelter from predation. Habitat fragmentation per se, or fragmentation without habitat loss, can also increase the amount of edge a predator may utilize (Peterson et al., 2001), potentially leading to changes in postsettlement mortality rates for many seagrass-associated organisms.

Most fragmentation experiments have been conducted in close proximity to established seagrass meadows. Because many seagrass macrofaunal organisms are known to migrate in and out of seagrass habitats on short time scales (Howard, 1985; Virnstein and Curran, 1986), this proximity allows for rapid colonization (hours to days) of patches by immigrants from adjacent seagrass beds (Stoner and Lewis, 1985; Virnstein and Curran, 1986). Experiments conducted in this manner allow for evaluation of ecological process as seagrass patches are fragmented within the matrix of a larger seagrass meadow; however, from a restoration point of view, this type of design does not allow for the evaluation of changes in structure and function that will occur with the reestablishment of seagrasses in locations removed from established seagrass meadows. In perhaps the only experiment that tested colonization at distances relatively far removed (8 km) from potential immigrant sources, Sogard (1989) found that colonization of artificial seagrass units (ASUs) was rapid, but that ASU settlers were mostly juvenile and adult organisms immigrating from adjacent nonseagrass habitats. The similarity in species composition between the ASUs far removed and those close to natural seagrass beds was generally low (< 50%), suggesting that communities reestablished at a distance from natural seagrass beds may initially be dissimilar from other seagrass communities. Ultimately, this variation in structure may result in the function of restored

seagrass communities being different from established seagrass meadows.

We evaluated changes in the structure and function of fragmented ASUs by placing them on an unstructured sand flat, far removed (~10 km) from naturally occurring seagrasses. We tested the effects of patch size, perimeter, and perimeter:area ratios (P/A) on epifaunal and macrofaunal colonization of ASUs. As a measure of ecosystem function, we estimated relative predation rates on fishes located within these same ASUs. We also tested if mortality and the amount of time it took for predation to occur were similar along ASU edges vs within ASU interiors and in vegetated vs nonvegetated areas. By conducting this experiment away from other seagrass meadows, immigration from adjacent seagrass meadows was minimized, allowing for a more realistic assessment of the ecology of recently restored seagrass habitats in locations that no longer have viable seagrass populations.

METHODS

Colonization.—Work was conducted during the summers of 2003 and 2004 on a sand flat located on the north side of Dauphin Island, AL, (Fig. 1) using ASUs to mimic patches of the seagrass *Thalassia testudinum*. ASUs were constructed by attaching 5-mm-wide green polypropylene ribbon to Vexar™ mesh circles (ASU sizes: 0.1, 0.25, 0.5, 1.0, 2.5, 5.0, and 10.0 m²). ASUs have been used successfully in numerous prior studies (Bell et al., 1985; Sogard, 1989; Sogard and Able, 1994; Johnson and Heck, 2006b) and are known to be rapidly colonized (hours to days) by waterborne settlers and immigrants (Bell and Devlin, 1983; Leber, 1985; Stoner and Lewis, 1985; Sogard, 1989). Simulated seagrass density was 1,500 leaves m⁻², well within the range of regional *T. testudinum* densities (Spitzer et al., 2000). Two replicates of each ASU were staked to the substrate approximately 10 m apart and the mesh was worked into the sand until buried. All ASUs were parallel to the shoreline in a layout that was randomized prior to deployment. Mean low water in this area was between 30 and 65 cm, but during these trials depth ranged between 55 and 90 cm with a tidal range of approximately 0.5 m.

ASUs were deployed during July of 2003, allowed to be colonized for 4 wk, and sampled monthly during Aug., Sept., and Oct. This time period was chosen because pilot experiments conducted in the same location indicated that there was ample colonization of ASUs by planktonic and immigrant settlers during these months (mean density > ~200 organisms m⁻²)

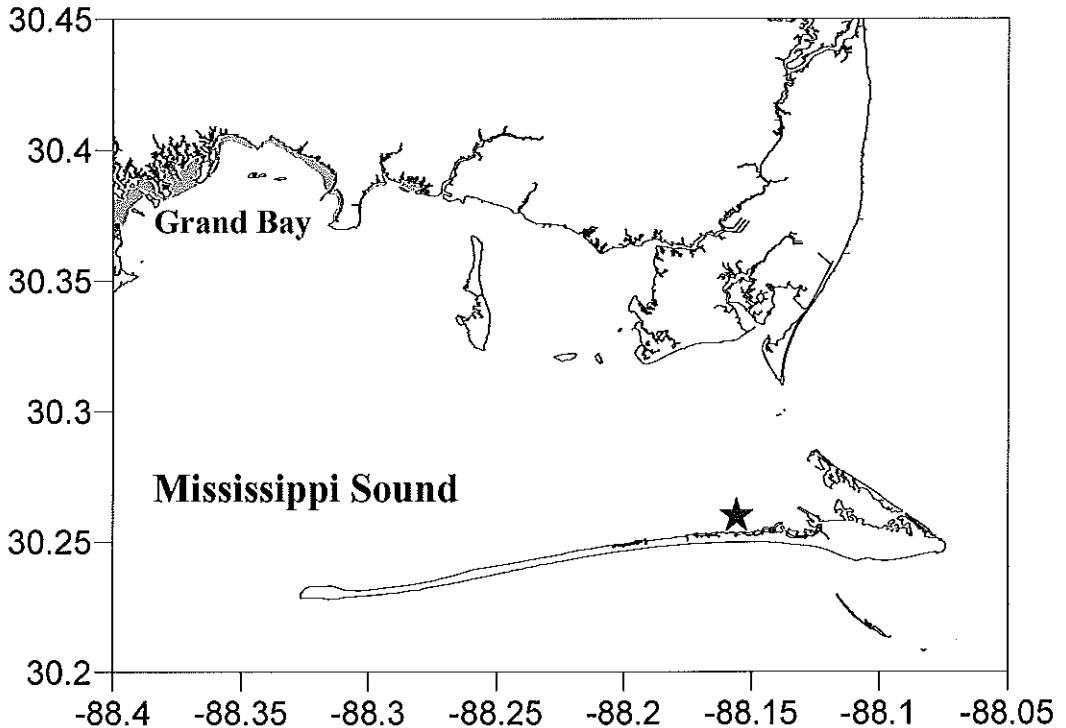


Fig. 1. Map of location where experiments were conducted during 2003 and 2004. Experimental site is indicated by the star symbol along the northern shoreline of Dauphin Island, AL. The shaded areas near Grand Bay represent the closest seagrass beds (*Halodule wrightii*) to the experiments.

(M. Johnson, unpubl.). Organisms were sampled by firmly placing a 1.6-m-tall polyvinyl chloride cylinder with an internal diameter of 30 cm (area = 0.07 m²) into the sediment and removing the contents for 1 min using a modified suction sampling technique (Orth and van Montfrans, 1987). For the 0.1-, 0.25-, 0.5-, and 1.0-m² ASUs, a single haphazardly located suction sample was collected from each. For the 2.5-m² ASUs, a single sample was taken from the center of the unit and at a haphazardly selected location along the edge that varied with each sample. For the 5.0- and 10.0-m² ASUs, we sampled at a haphazardly selected locations in both the interior portion of the patch and along the edge of the ASU. As a result of this sampling technique, most of the blades on the 0.1- and 0.25-m² ASUs and the blades in the very center of the 2.5-m² ASUs were defaunated. In addition, this technique also disturbed the underlying sand and often removed epiphytic growth. Thus, our results were not independent through time and should be interpreted cautiously. However, the rapid colonization of ASUs evident in previous studies (Sogard, 1989; Virnstein and Curran, 1986) suggests that 4 wk was long enough to obtain presampling organism abundance and diversity.

After each collection, any holes created as a result of suctioning were filled and the ASUs were reworked into the sediment to cover any exposed infaunal organisms or ASU mesh.

Because several prior studies identified seagrass patch edges up to 1 m as being biologically relevant (although not appropriate for all species) (Bell et al., 2001; Hovel et al., 2002; Johnson and Heck, 2006a), we defined the edge as the area extending 0.75 m into the ASU from the sand-ASU interface. This allowed us to test for edge effects on all the ASUs with an area greater than 2.5 m using the same suction sample cylinder. Organisms were collected in a 0.5-mm mesh bag, placed on ice for transportation to the lab, and stored frozen for further analysis. During sample processing, each sample was sorted into the following major taxonomic groups: crabs, fishes, shrimps, amphipods, and gastropods (Table 1). Crabs, fishes, and most of the shrimps were furthered classified to the species level. For the grass shrimps, amphipods, and gastropods, classification was taken to the family or genus level. Although this coarse classification may mask some species-specific responses, broader functional responses were likely to be identified.

TABLE 1. List of organisms and faunal designations collected from artificial seagrass units. All groups represented here are considered to be nonsessile, mobile organisms.

Organisms	Faunal designation
Crabs	
<i>Clibanarius vittatus</i>	Epifauna
<i>Callinectes sapidus</i>	Epifauna
Fishes	
<i>Symphurus plagiusa</i>	Epifauna
<i>Myrophis punctatus</i>	Infafauna
Shrimps	
<i>Palaemonetes</i> sp.	Leaf fauna
<i>Farfantepenaeus aztecus</i>	Epifauna
<i>Litopenaeus setiferus</i>	Epifauna
<i>Alpheus heterochaelis</i>	Infafauna
Amphipods	
<i>Gammarus</i> sp.	Leaf fauna
Gastropods	
<i>Nassarius</i> sp.	Leaf fauna
<i>Mitrella</i>	Leaf fauna
Muricidae	Epifauna/infafauna
<i>Neritina usnea</i>	Leaf fauna
<i>Anachis</i> sp.	Leaf fauna

For biomass measurements, we dried each group to a constant weight at 80°C and determined the dry biomass (DW) to the nearest 0.0001 g. We determined the ash weight (AW) for all but shrimps and amphipods by ashing each sample at 500°C for 5 hr, then placing the samples in desiccators and allowing them to cool prior to reweighing. Ash-free dry weight (AFDW) was calculated as $DW - AW$. Because of the low inorganic content of shrimps and amphipods, AFDW was calculated as $DW \times 0.9$ (Waters 1977).

To measure community diversity, we calculated the expected number of taxa present (ET) in any given sample from our raw data using the rarefaction technique described by Sanders (1968), Hurlbert (1971), and Heck et al. (1975). Rarefaction is useful because it allows for the comparison of an expected number of taxa in samples that vary over a wide range of individuals (Clarke and Warwick, 2001). Because only a few organisms were collected in several of the samples, we conducted three separate rarefaction analyses where sample size was set at five, 10, and 15 individuals. This analysis was conducted using the software package PRIMER V 5.2.6 (2000).

To increase the strength of our analysis, we pooled the three sample dates into a single data

set. Again, we must note that because of the potential defaunation of the smaller ASUs, these samples may not be independent through time and should be interpreted cautiously. This combined data set was used in single-variable linear regressions (SPSS 2000) for each taxonomic group, total organisms, and estimated taxa with patch area, perimeter, or P/A ratio. To meet the assumptions of the regression models, the data set was transformed using a $\log_{10}(x + 1)$ transformation. Because patch area, perimeter, and P/A ratios can covary, each variable was examined independently. P/A ratio is a measurement that may reduce the possibility of correlation between area, perimeter, and other unmeasured variables and can be independent of either area or perimeter. We must note that this ratio cannot be back-transformed to obtain either perimeter or area (Schumaker, 1996). As a result, information pertaining to both patch area and perimeter can be lost, but the possibility of correlation among variables is reduced. P/A ratios have been used in other similar experiments at this scale (Johnson and Heck, 2006a, 2006b). In addition, we examined scatter plots of each data set for nonlinear trends. When a possible nonlinear pattern was identified, we tested the appropriate nonlinear models for each of the independent variables. For within-patch location, we used a t-test to examine any differences between abundance at the patch edge and the center.

ASUs were allowed to remain in place during the winter of 2003–04; however, a 5.0- and a 10.0-m² ASU were destroyed during this period and not replaced. In addition, a 0.25-m² ASU was also destroyed several days prior to the initiation of the 2004 tethering experiment (see below). To ensure that each ASU experienced an equivalent amount of colonization, these ASUs were not replaced.

Tethering experiment.—During the summer of 2004, pinfish (*Lagodon rhomboides*) were collected from Big Lagoon, FL, using an otter trawl. They averaged 4.3 ± 0.6 cm standard length (SL), and were held in a recirculating seawater system for at least 48 hr prior to use. In the field, pinfish were tethered in place by placing a small snap swivel through the lower lip of each fish that was tied to a 0.5-m-long monofilament tether attached to a 15-cm-long aluminum stake pushed into the substrate. In a pilot study conducted on site ($n = 12$), we found that this technique had 100% survivorship during 8 hr, the duration of our trials. Tethered pinfish were placed in the center of each ASU and in the unstructured sandy substrate (referred to as sand) approxi-

mately 1 m from each ASU. For the 0.1-, 0.25-, and 0.5-m² ASUs, the tether length allowed fish access to both sand and ASU habitats; however, no pinfish were ever observed outside the seagrass. Fish in larger ASUs (2.5, 5.0, and 10.0 m²) were also tethered along the edge of each ASU giving them access to both seagrass and sand habitats. Trials were conducted for a period of 8 hr and each trial was initiated between 0800 and 1200 hr. To aid in the recovery of pinfish, tethers were placed along the northernmost ASU margin. Because our trials were not conducted regularly (only when conditions were ideal), we feel that the probability of predators associating tethering location with food availability was very low.

After deployment, tethers were checked for losses three times during the 8-hr trials (every 2.6 hr) and pinfish were recorded as either missing or alive. Trials were discarded when there was a noticeable increase in wave energy, a drop in water levels below 0.25 m at the shallowest ASU, or the death of a pinfish due to causes other than predation (e.g., entanglement). Potential pinfish predators include southern flounder (*Paralichthys lethostigma*), inshore lizardfish (*Synodus foetens*), red drum (*Sciaenops ocellatus*), spotted sea trout (*Cynoscion nebulosus*), and blue crab (*Callinectes sapidus*). We conducted a total of 10 successful trials over a period of 2.5 mo, resulting in 20 replicates of the 0.1-, 0.5-, 1.0-, and 2.5-m² ASUs and 10 replicates of the 0.25-, 5.0-, and 10.0-m² ASUs.

We examined differences in pinfish mortality between sand, edge, and center positions using a binary logistic regression procedure (Minitab® v. 13) and the time that it took for mortality to occur using a nonparametric Moods median test. We compared each ASU size individually, then combined data from all the ASUs and compared the three positions. To test whether patch characteristics influenced mortality, we again utilized a logistic regression procedure to determine if there was a significant relationship between log₁₀ area, log₁₀ perimeter, or P/A ratios and pinfish mortality. This technique has been used successfully by Hovel (2003) and Laurel et al. (2003) in similar experiments. Tethering experiments are useful for measuring the relative predation intensity among habitats, but there are certain artifacts inherent in these experiments (Curran and Able, 1998; Aronson et al., 2001; Haywood et al., 2003). As such, these results may not be an accurate measure of actual predation rates (Peterson and Black, 1994; McGuinness, 1997; Curran and Able, 1998; Kneib and Scheele, 2000).

To test whether patch characteristics can allow prediction of the amount of time that it takes for

attacks by predators to occur, we used linear regression with log₁₀ (x + 1) transformed data. For the models, the time it took for mortality to occur was the dependent variable and log₁₀ area, log₁₀ perimeter, or P/A ratio were independent variables. In a few instances, our data violated the homogeneity of variance assumption of the model; however, infrequency of this problem and the robustness this technique against this type of violation (Box, 1954) did not warrant further nonparametric analyses. To examine if the overall mortality rate between sampling times varied by location, we used a repeated measures analysis of variance in which sand, patch edge, and patch center were the independent variables and pinfish mortality was our repeated measure (Davis, 2002).

RESULTS

Colonization.—During 2003 we collected a total of 14 different species representing five groups from our ASUs (Table 1). Thinstripe hermit crabs (*Clibanarius vittatus*) and blue crabs (*Callinectes sapidus*) were the most abundant organisms collected (Fig. 2). Mean hermit crab densities declined monthly, but mean blue crab abundance increased from Aug. to Sept. and then declined between Sept. and Oct. Amphipods (primarily *Gammarus* sp.) were the next most common taxa collected, with mean abundances that increased between Aug. and Oct. (Fig. 2). Amphipods were collected on each size ASU at some point during the experiment; however, density varied considerably with ASU size. For gastropods, mean abundance increased from Aug. to Sept., but declined by Oct. (Fig. 2). The most commonly collected gastropods belonged to the genus *Nassarius* and the family Muricidae. *Anachis* sp., *Neritina usnea*, and *Mitrella* sp. were also collected, but abundances were less than 1/3 those of the more commonly collected gastropods.

Fish and shrimps were collected least often and at mean densities that changed little among sample periods (Fig. 2). Blackcheek tonguefish (*Symphurus plagiusa*) and speckled worm eel (*Myrophis punctatus*) were the only fish species collected. When present, fish density ranged from 14 to 28 fish m⁻². Grass shrimp (*Palaemonetes* sp.) were the most common shrimp collected, followed by penaeids (*Farfantepenaeus aztecus* and *Litopenaeus setiferus*) and snapping shrimps (*Alpheus heterochaelis*). Mean shrimp abundance varied minimally between Aug. and Sept., and values remained less than 5 shrimps m⁻² (Fig. 2). Mean total abundance increased between Aug. and Sept., but declined by Oct. (Fig. 2). Organisms were collected on every ASU

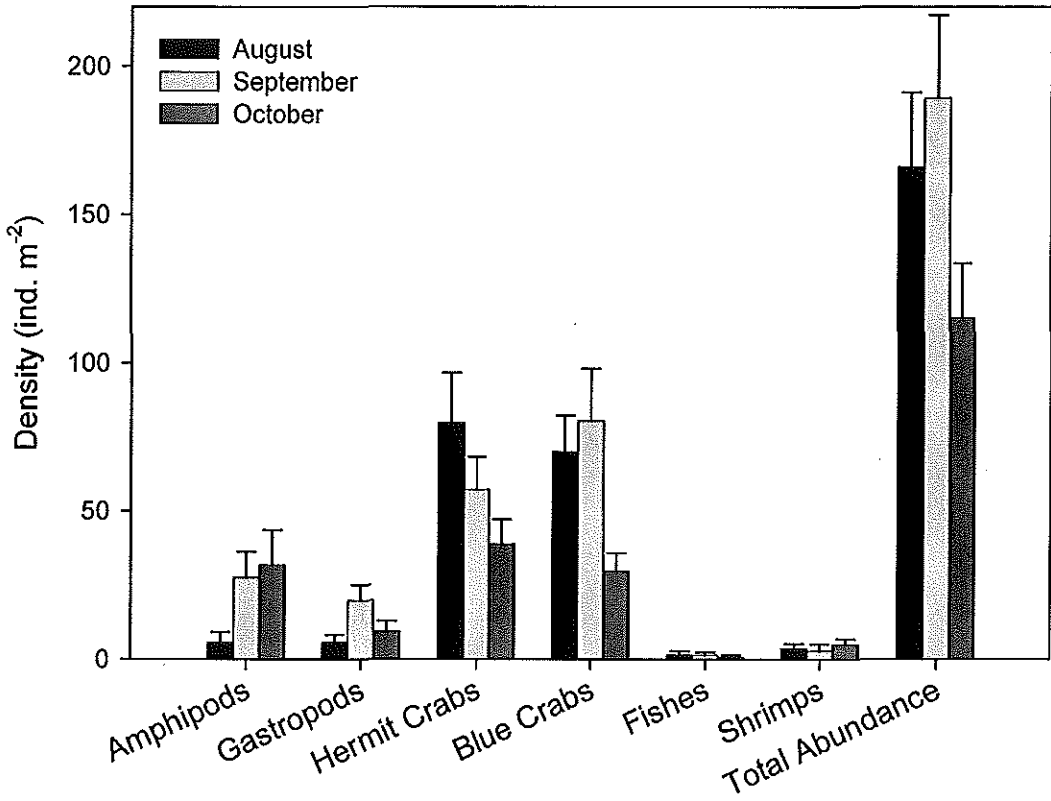


Fig. 2. Mean monthly abundance (\pm SE) during 2003 for organisms collected from all the artificial seagrass units (ASUs). These data represent all the ASU sizes combined into a single group.

with mean densities that ranged from 14.1 to 508.2 individuals m^{-2} . For the number of rarefaction ET in each ASU, there was a mean \pm SE of 2.3 ± 0.10 , 2.65 ± 0.12 , and 2.72 ± 0.13 taxa present in any given sample for sample sizes of five, 10, and 15 individuals, respectively. When the sample size was set at five and 10 individuals, the ET value increased steadily from Aug. to Oct.; however, when set at 15 individuals, the ET value increased between Aug. and Sept., but declined during Oct. The mean range for ET was between 1 and 4.9 taxa present for each ASU.

Linear regression analysis of abundances of each organism, total abundance, and estimated taxa did not result in any significant relationships with patch area, perimeter, or P/A ratios. In addition, subsequent analysis of density vs area, perimeter, and P/A ratio plots did not identify any nonlinear relationships for any of the independent variables. Finally, gastropods were the only organism to show any significant differences in abundance between patch interior and exterior ($t = 28.97$, $P = 0.014$). The exterior part of the ASUs had a greater mean abundance (0.72 ± 0.18 gastropods m^{-2}) than the interior (0.16 ± 0.11 gastropods m^{-2}).

Biomass.—The greatest amount of biomass on the ASUs was due to colonization by hermit crabs and blue crabs. Although density of blue crabs collected on the ASUs was higher, hermit crabs were typically larger, resulting in a greater biomass than any other taxa (Fig. 3). Hermit crab biomass declined between Aug. and Sept., but increased again by Oct. Blue crab biomass declined steadily across the three sample periods. For amphipods, gastropods, shrimps, and fishes, mean biomass was less than 0.02 g AFDW m^{-2} . Amphipod biomass peaked during Sept. whereas gastropod biomass was lowest during Sept. (Fig. 3). Shrimp biomass declined steadily between Aug. and Oct. and fish biomass increased over the sample period. Because hermit crabs alone were responsible for the largest amount of biomass, total biomass was similar to that of hermit crabs, with a substantial decline between Aug. and Sept., followed by a large increase by Oct. (Fig. 3).

Linear regression analysis of organism biomass resulted in no significant models when regressed against patch area or perimeter. There was a significant positive relationship ($F_{1,58} = 5.15$, $P = 0.027$) present between gastropod biomass

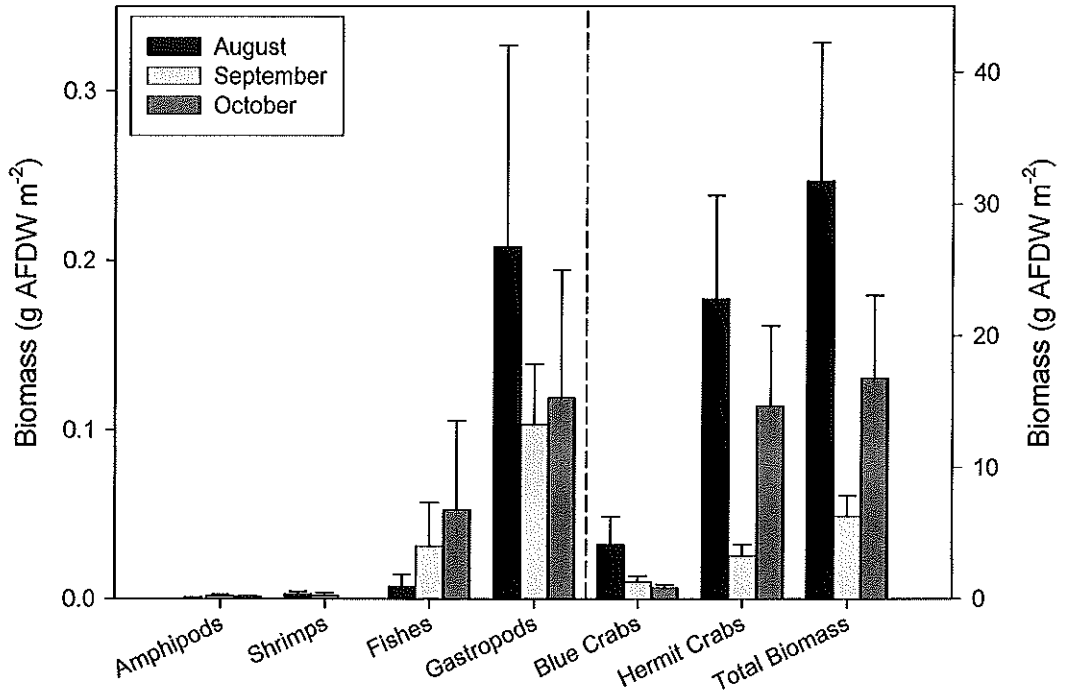


Fig. 3. Mean (\pm SE) biomass measurements for all organisms collected during 2003. The left axis represents amphipod, shrimp, gastropod, and fish measurements, and the right axis represents blue crab, hermit crab, and total biomass measurements.

and P/A ratios, but this regression model explained only 8% of the variation in the data. When the biomass for each organism was plotted against each of the independent variables, blue crab and fish plots suggested that a nonlinear analysis might be more appropriate. We tested these data using logarithmic, inverse, cubic, and quadratic models, but there were no significant relationships evident. Our estimates of biomass for each taxon showed that the patch interior was not significantly different from the patch edge.

Tethering.—After 8 hr, pinfish mortality was in excess of 70%, regardless of treatment or location. Fish tethered on the sand adjacent to each ASU had a mean mortality rate of $94 \pm 1.8\%$. Pinfish tethered near the 1- and 5-m² ASUs had the highest mortality at 100%, whereas mortality on the other five ASUs ranged between 89% and 95% (Fig. 4). Fish tethered along the edge or in the center of the ASUs had a mean mortality rate of $93 \pm 2.5\%$ and $80 \pm 2.0\%$, respectively. Mortality along the edge was greatest in the 5-m² ASU (100%), followed by the 2.5-m² (90%) and the 10-m² (88%) ASUs. For pinfish tethered within the center of the ASUs, mortality was the greatest on the 0.25-m² ASU (89%) and smallest on the 0.1-m² ASUs (71%).

Our logistic regression analysis did not indicate any significant differences in mortality among the seven ASUs in any of the three tethering locations; however, there was a significant difference in the mortality for fishes tethered in sand, along the edge, or in the center (parameter = 2.78, df = 1, $P = 0.005$, odds ratio = 1.99). These results were driven by the increased survival times in the patch center compared to the patch edge and the open-sand treatments (Fig. 4). Additionally, regression analysis of mortality vs log area, log perimeter, and P/A ratios resulted in no significant relationships in any of the three tethering locations (Table 2). Examination of time to mortality among the seven ASUs for each of the three tethering locations revealed no significant differences between the ASUs for fish tethered on the sand or along the ASU edge. Only when pinfish were tethered in the ASU center were there any significant differences ($\chi^2 = 12.81$, df = 6, $P = 0.046$) among ASUs. These results were influenced by the fact that it took 155 min longer for predation to occur in the 5.0-m² ASUs as compared to the 1.0-m² ASUs.

The amount of time that it took for mortality to occur did not vary significantly among the three habitats. Mortality occurred the fastest in the sand (223.0 ± 10.7 min), followed by the

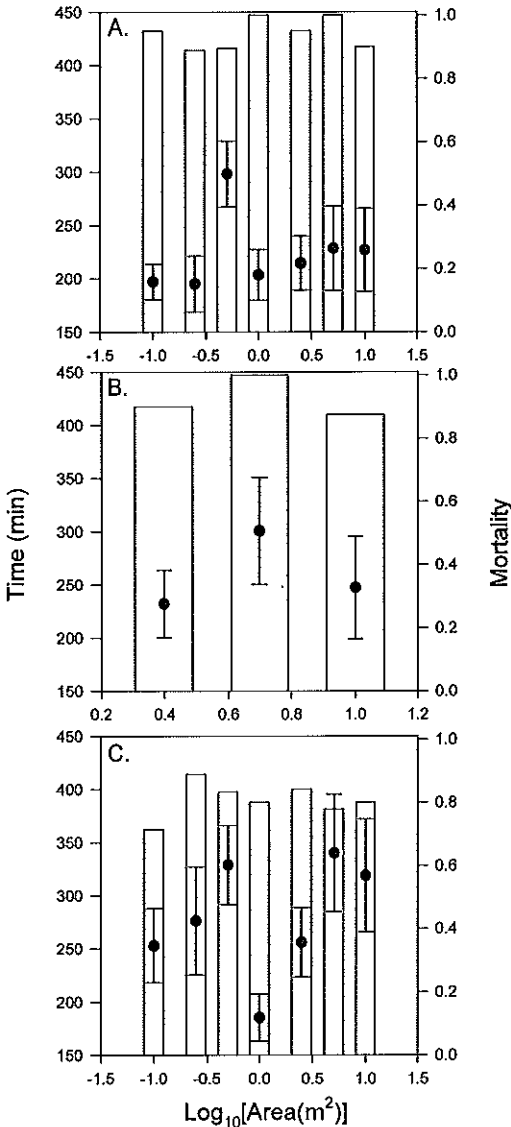


Fig. 4. Mean (\pm SE) length of time for pinfish mortality to occur (\bullet) and total pinfish mortality (bars) on artificial seagrass units (ASUs) during tethering experiment conducted in 2004. Panel A is for fishes tethered outside the ASUs, panel B is for fishes tethered along the edge of the ASUs, and panel C is for fishes tethered in the center of the ASUs.

patch edge (253.9 ± 23.4 min) and patch center (270.0 ± 14.9 min). For the ASU centers, mortality occurred in less than 200 min on the 1.0-m^2 ASU, between 250 and 277 min for the 0.1 -, 0.25 -, and 2.5-m^2 ASUs, and between 318 and 328 min for the 0.5 -, 5.0 -, and 10.0-m^2 ASUs (Fig. 4). Along the edge, survival was longest on the 5.0-m^2 habitats (300 min) and shortest on the 2.5 - and 10.0-m^2 ASUs (240 min). In the sand, mortality for all the ASUs, excluding the

0.5-m^2 ASUs, occurred between approximately 200 and 225 min. For the 0.5-m^2 ASUs, mortality occurred at a mean time of 298 min (Fig. 4). Linear regression examining the influence of patch size, perimeter, and P/A ratios on time resulted in no significant relationships in any of the three locations. Examination of the overall mortality rate among the tethering locations revealed no significant differences among them ($F_{2,27} = 1.13$; $P = 0.338$) (Table 2).

DISCUSSION

The use of ASUs enabled us to minimize the confounding effects of patch size and habitat quality (Hovel and Lipcius, 2001; Goodsell and Connell, 2002) and test only the effects of patch size and perimeter. We were able to detect only a few significant differences in abundance, biomass, or mortality that were related to patch size, perimeter, or P/A ratio. This suggests that for patches less than 10 m^2 , the patch characteristics investigated here may be of little consequence. We did confirm (like many others) that more structurally complex habitats provided increased refuge from predators (Ray and Stoner, 1994; Bernot and Whittinghill, 2003; Adams et al., 2004; Magoulick, 2004; Ryer et al., 2004), even in locations removed from habitats such as seagrass meadows that are known to concentrate predators (Micheli and Peterson, 1999). Our data also suggest that at this spatial scale patch edges may not concentrate predators or expose prey to higher predation rates as suggested by Micheli and Peterson (1999) and Bologna and Heck (2000). The increased abundance of gastropods on the patch exterior may be related to a lack of grazing competition with grass shrimp for epiphyte resources. Although it was not significant, the abundance of grass shrimp in the patch interior was twice that of the patch exterior.

Compared to other local studies (Johnson, 2006; Johnson and Heck, 2006a), the sites on Dauphin Island contained many fewer species at lower densities. For example, collections in Grand Bay, AL, (~ 10 km NW) and Big Lagoon, FL, (~ 30 km E) seagrass meadows had mean densities that ranged from 500 to 20,000 organisms m^{-2} and contained five to six different taxa (Johnson, 2006). At Dauphin Island, there were half the taxa present and abundances were between 0.5 and two orders of magnitude less than in Grand Bay or Big Lagoon. In these locations species composition was dominated by gastropods, amphipods, and grass shrimps, whereas on Dauphin Island, hermit crabs and blue crabs were the most commonly collected organisms. These results highlight the impor-

TABLE 2. Statistical results for tethering experiments. Panel A contains the results for the logistical regression analysis between tethering location patch descriptors. Panel B contains the repeated measures analysis of variance table where location (sand, edge, center) was the independent variable and mortality was our repeated measure.

A.					
Source	df	Parameter	P value	Odds ratio	
<i>Center</i>					
Area	1	-0.02	0.987	0.99	
Perimeter	1	-0.02	0.987	0.99	
P/A ratio	1	-0.11	0.915	0.99	
<i>Edge</i>					
Area	1	0.18	0.857	1.57	
Perimeter	1	0.18	0.857	2.45	
P/A ratio	1	-0.26	0.793	0.71	
<i>Sand</i>					
Area	1	0.31	0.758	1.23	
Perimeter	1	0.31	0.758	1.51	
P/A ratio	1	-0.3	0.763	0.97	
B.					
Source	Type III sum of squares	df	Mean square	F	P value
Location	0.47	2	0.23	1.13	0.34
Error	5.58	27	0.21		

tance of location in determining colonization rates of habitats (Sogard, 1989). In Grand Bay and Big Lagoon, natural seagrass beds were in close proximity (≤ 10 m) to the ASUs, increasing the odds of colonization by seagrass-associated animals. On Dauphin Island, the experiment was conducted on a sand flat with no seagrass as a source of colonization for many kilometers (Fig. 1). Historically, there was seagrass (*Halodule wrightii*) located in the general area (Vittor and Associates, 2003); however, surveys of the entire northern shoreline of Dauphin Island during 2003 and 2004 did not identify any living submerged aquatic vegetation (Byron and Heck, 2006). The results of this experiment do, however, support the conclusions of previous studies (Bell et al., 2001, 2002; Hovel, 2003; Johnson and Heck, 2006a) in confirming that at the 1-10-m² scale, we were not able to detect differences among treatments based on patch size, perimeter, and P/A ratios.

The lack of significant patterns in abundance, biomass, or community structure does little to clarify if the pre- and postsettlement processes at work around Dauphin Island are similar to other local seagrass ecosystems (Johnson, 2006; Johnson and Heck, 2006a). Unlike Dauphin Island, at Grand Bay and Big Lagoon there are extensive seagrass habitats that contain an ample supply of recruits for immigration and larval settlement. However, seagrass beds are also known to harbor more predators than unvegetated habitats

(Hines et al., 1990; Jordan et al., 1997; Micheli and Peterson, 1999). Thus, both postsettlement predation and presettlement supply of organisms may determine community structure in Grand Bay and Big Lagoon. Based on the relatively small amount of secondary production, the lack of obvious predators on amphipods and blue crabs, the abundance of blue crab megalopae, and the lack of significant adjacent structured habitats, we suggest that presettlement supply of recruits rather than postsettlement losses may be more important in the waters near Dauphin Island. Bell et al. (1985, 1987) reached similar conclusions from a series of experiments conducted on a subtidal flat, but Sogard (1989) demonstrated that immigration could also be a source of colonization on nonvegetated flats.

Results of our settlement/colonization experiments suggest that there were no measurable differences among treatments; however, regardless of habitat, there exists a substantial risk of predation for pinfish from piscivorous predators. The predators we observed were southern flounder (*Paralichthys lethostigma*) and inshore lizardfish (*Synodus foetens*), but red drum (*Sciaenops ocellatus*) and spotted sea trout (*Cynoscion nebulosus*) also frequent the area. Unlike Laurel et al. (2003), we did not estimate the relative abundance of predators that frequented each habitat, but each of the predators, except the southern flounder, are highly mobile, known to

be susceptible to noise, and are not considered "ambush" style predators. Because of these traits, along with the relatively shallow depths, moderate water visibility, and small ASU size, we felt that neither seining, visual observation, nor gillnetting would accurately estimate the abundance of predators. However, Laurel et al. (2003) found that predator densities for cod were similar in ASUs between 0.32 and 11 m², whereas Hovel and Lipcius (2001) found no correlation between patch size (0.25 to > 3,000 m²) and crab predation and Moksnes and Heck (2006) found no relationship between blue crab predation and presumed predator densities.

For our pinfish tethering experiments, patch area, perimeter, and P/A ratios did not have a detectable influence on mortality rate; however, the presence of artificial seagrass did result in a decrease in predation rates. At the patch edge, total mortality was similar to that of sand, but the amount of time that it took for mortality to occur was similar to the patch centers. Typically, patch edges are thought to create opportunities for increased interaction between predators and prey, resulting in greater predation rates along edges (Bologna and Heck, 1999; Micheli and Peterson, 1999; Peterson et al., 2001; Wellenreuther and Connell, 2002). Even at the small scale of this study, our data suggest that rather than being areas of increased predation, patch edges may act more as a transition zone with a graded response between the refuge of the patch center and the vulnerability of the sand. Effects of patch edge on predation rates may be more evident in areas with established seagrass and presumably more predators (Laurel et al., 2003).

We must address several caveats that pertain to this experiment. First, because of the low replication during this experiment, the power of our analyses was lower than that recommended to adequately protect against Type II errors (Sokal and Rohlf, 1981). Because our conclusions that variation in patch characteristics does not lead to measurable differences in macrofaunal community structure, combined with the agreement with most prior studies, we feel that the possibility of our conclusions being misled by a Type II error is minimal. Second, the scale of this experiment may be smaller than the grain of some of organisms that settled on the ASUs and many of the predators that frequented these habitats (Kotliar and Weins, 1990). Grain is defined as the scale at which an organism no longer functionally perceives heterogeneity in the environment and it differentiates patches in the environment as individual habitats (Kotliar and Weins, 1990). Is this case, our experimental

design may have been perceived as a single seagrass patch rather than a series of independent seagrass patches. If this is the case, the response to patch characteristics may vary to some extent if these patches were placed at greater distances apart.

Our conclusions suggest that when seagrass patches are far removed from seagrass beds, community composition may vary, but abundance, biomass, and predation all respond to habitat fragmentation in a manner similar to those ASUs where immigration from nearby seagrass meadows has an overriding impact. Thus, conclusions drawn from previous experiments conducted near established seagrass meadows may be applicable to more remote habitats. There are also implications of our data for seagrass restoration. For example, the expected outcome of identical restoration projects may depend on the habitats surrounding those projects and the amount of time since restoration has been completed. It has been demonstrated that restored marine habitats often require extensive amounts of time, a minimum of 3 yr and often greater than 10 yr, to become similar in function to naturally occurring habitats (Zedler, 2000; Evans and Short, 2005; Travis and Sheridan, 2006; Cardoso et al., 2007). Restoration of seagrasses and the communities that inhabit them may ultimately depend little on the size and perimeter of patches, but more on immigration, an ample supply of potential recruits, or other patch characteristics (Bell et al., 2001; Fonseca and Koehl, 2006; Montefalcone et al., 2007). As such, supply side dynamics must be considered as a covariate with which to design or evaluate newly restored habitats. The lack of influence by any single patch characteristic implies that design of successful restoration projects must rely on multiple factors that are unique to each location (Hovel, 2003). In the northern Gulf of Mexico, patch configuration may influence seagrass fauna (Johnson and Heck, 2006a), but seagrass characteristics such shoot density (Coen et al., 1981; Heck et al., 2001), areal extent within a landscape, and proximity to similar habitats are likely to be the most important factors influencing macrofaunal communities.

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