

Effects of habitat fragmentation per se on decapods and fishes inhabiting seagrass meadows in the northern Gulf of Mexico

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ABSTRACT: The role of habitat fragmentation per se on ecological processes is incompletely understood in marine environments. Previous work in fragmented habitats has concentrated on growth of bivalve species, faunal abundances and predation of tethered crabs. Unlike other studies, in the present study we measured abundances of decapods and fishes and estimated secondary production from *in situ* sampling of multiple sized, naturally occurring seagrass beds and artificial seagrass units (ASUs). In 2 locations (*Thalassia testudinum* meadows in Big Lagoon, Florida, and *Halodule wrightii* meadows in Grand Bay, Alabama), we sampled 7 to 10 seagrass patches ranging in size from <1 to >100 m² at 2 mo intervals between June and October 2001. We also sampled 10 replicate ASUs of 2 shapes (stellate and circular) and 2 sizes (0.2036 and 0.0487 m²) that were colonized for 4 wk at both locations in June, August and October. Our results indicated that patch size, patch shape, intra-patch location, and degree of isolation can each influence macrofaunal community structure and secondary production estimates; however, their overall impact was inconsistent. Our data suggest that the effects of habitat fragmentation are location-, time- and species-specific, and that fragmentation at this scale may have little impact on faunal assemblages of seagrass meadows.

KEY WORDS: *Halodule wrightii* · Artificial seagrass units · Secondary production · *Thalassia testudinum* · Abundance

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INTRODUCTION

Habitat fragmentation per se, or fragmentation without loss of area, is a common occurrence in many terrestrial (reviews by Andr n 1994, Bender et al. 1998, Debinski & Holt 2000) and marine (Fonseca & Bell 1998) environments, and can lead to a reduction in patch size, an increase in patch perimeter inter-patch distance and in perimeter:area ratio, as well as an overall alteration of patch configuration (Trzcinski 1999, Villard et al. 1999). Typically, marine habitats are comprised of discrete patches of varying size. Often, a seagrass meadow is a mosaic of vegetated patches interspersed with patches of unvegetated substrate (Larkum & den Hartog 1989, Robbins & Bell 1994, Bell et al. 1995). Although seagrass cover may approach 100% in some areas, numerous

natural disturbances such as waves and episodic storms prevent continuous seagrass coverage (reviewed by Fonseca et al. 1998). In addition, human-induced seagrass loss resulting from activities such as dredging, eutrophication, disease, and damage from boating has increased dramatically in recent decades (Orth et al. 1984, Duarte 1995, Sargent et al. 1995). Existing submerged aquatic vegetation (SAV) habitats have been reduced in size and increasingly fragmented, increasing the likelihood that seagrass-associated macrofauna may be susceptible to these changes.

In perhaps the earliest paper available on this topic, McNeill & Fairweather (1993) found conflicting results between experiments with natural SAV and artificial seagrass units (ASU) that were both employed to test whether a single large or several small plots of the

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same total area (the SLOSS argument: see Ovaskainen [2002] and Peintinger et al. [2003] for debate) supported more species of benthic invertebrates and fishes. In natural SAV, several small beds supported significantly more species than a single large bed, while the results of the ASU experiments were equivocal. A study that compared bivalve abundances at the edges and in the interiors of seagrass beds (Bologna 1998, Bologna & Heck 2000) found greater macroinvertebrate abundance and secondary production at SAV bed edges than in bed interiors, even though plant biomass and shoot density (which are usually reported to be positively correlated with animal abundance) were lower at the edges than in the interiors. In addition, changing patch dynamics may influence (albeit inconsistently) many ecological processes including community structure (Bell et al. 2001), predation (Irlandi 1997, Hovel & Lipcius 2002), colonization (Eggleston et al. 1998, 1999) and settlement (Bologna & Heck 2000). To date, the only conclusion that can be drawn from recent habitat fragmentation research is that much more remains to be done to understand the effects of habitat size and shape as they influence biotic interactions in seagrass dominated habitats.

We know from a variety of studies in different types of environments that the ratios of 'edge' to interior (i.e. perimeter to area ratios, P:A) can determine rates of exchange of nutrients, food and organisms between habitats (see review by Polis et al. 1997). Unlike terrestrial literature, there is little available information that addresses how patch size, shape, inter-patch distance, or position within the patch influence the structure and function of seagrass beds or other marine habitats

(Turner et al. 1999), and that which does exist has not produced consistent results. We do know that seagrass patch dynamics can influence many ecological processes; however, it is unknown if fragmentation negatively influences the productivity of seagrass-associated fauna. It is important to understand these processes to allow prediction of the effects of fragmentation before they occur and how they will affect the recovery process if habitats begin to coalesce.

The specific objective of this project was to use a combination of natural and artificial seagrass beds representing a wide range of seagrass patch configurations to determine if variation in seagrass bed size, shape, location within a bed and degree of isolation influences the abundance, composition and secondary production of decapod crustaceans and finfishes in turtlegrass *Thalassia testudinum* and shoalgrass *Halodule wrightii* meadows.

MATERIALS AND METHODS

Natural seagrass patches. In both Big Lagoon, Florida (30° 25' N, 87° 18' W), and Grand Bay, Alabama (30° 23' N, 88° 19' W) (Fig. 1), we chose between 7 and 10 seagrass patches that were similar in depth and plant density to represent a gradient in patch size, shape and isolation. In Big Lagoon, these patches were monospecific stands of *Thalassia testudinum* located along the northern and southern shorelines of the lagoon that varied in size from <1 to 2265 m². In Grand Bay, we chose monospecific stands of *Halodule wrightii* along the eastern and northern shoreline of the bay that varied from <1 to 190 m². Because truly monospecific stands of seagrasses are rare in the northern Gulf of Mexico, we operationally defined a monospecific bed as any seagrass bed that consisted of at least 85% of a single species of seagrass. In Big Lagoon, *T. testudinum* beds were often mixed with the faster growing species, *H. wrightii*. In Grand Bay, *H. wrightii* is the dominant seagrass; however, during the spring and early summer small stands of widgeon-grass *Ruppia maritima* were present. These stands of *R. maritima* often die back as salinity increases throughout the summer (Stutes 2000).

We estimated the dimensions and perimeter of each seagrass patch using a 'Roll-a-tape™' measuring wheel. Because patches are often approximately elliptical, we measured the major and

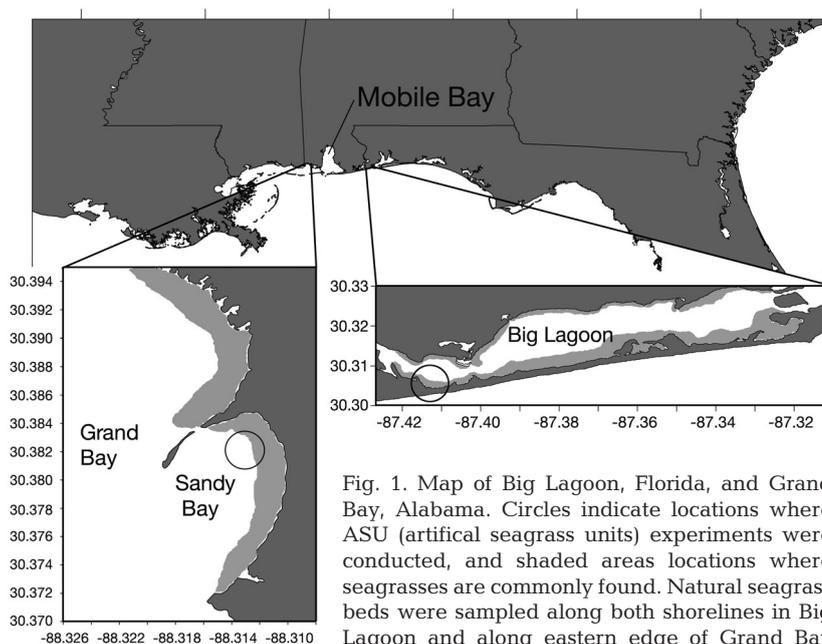


Fig. 1. Map of Big Lagoon, Florida, and Grand Bay, Alabama. Circles indicate locations where ASU (artificial seagrass units) experiments were conducted, and shaded areas locations where seagrasses are commonly found. Natural seagrass beds were sampled along both shorelines in Big Lagoon and along eastern edge of Grand Bay

minor axes of each patch for use in area determinations. When beds were not elliptical, each bed was broken into several representative geometrical shapes and measurements were obtained to determine the area of each shape. The perimeter of each patch was determined by following the sand–seagrass interface using the measuring wheel. Inter-patch distance, or distance to the nearest seagrass patch (referred to as ‘nearest neighbor’), was also measured using the measuring wheel. Patches were sampled at each location in June, August and October 2001. Because of inclement weather and poor visibility, it was necessary to sample Grand Bay during both August and September 2001 to obtain at least 7 patches. These samples were combined and treated as a single sample period labeled August 2001.

Organisms were sampled using a suction sampling technique that has been slightly modified from that of Orth & von Montfrans (1987). Briefly, this sampling method employed a 1.6 m tall PVC cylinder with an internal diameter of 50 cm that was haphazardly placed in either the edge or the interior of the seagrass habitat and pushed firmly into the substrate. We defined the ‘edge’ as the vegetated area within 1 m of the sand–seagrass interface and ‘interior’ as more >1 m from any sand–seagrass interface. Although this distance may not be appropriate for all species, it was identified as relevant in seagrass systems during several previous studies by Bell et al. (2001) and Hovel et al. (2002). The contents of the cylinder were evacuated for 30 s with a gasoline-powered suction dredge (see illustration in Orth & van Montfrans 1987) and passed through a 0.5 mm mesh collection bag. The contents of the bag were stored on ice, transported back to the Dauphin Island Sea Laboratory, and frozen for further analysis. At the time of suction sampling, above ground seagrass biomass samples were collected by harvesting all shoots from two 0.01 m² quadrats in each patch within the vicinity of the suction dredge sample. We also measured water temperature and salinity during each sampling effort for use in general habitat descriptions and for potential help in understanding unusual events.

Suction samples were thawed and sorted into the following major taxonomic groups: juvenile blue crabs *Callinectes sapidus*, shrimps (Palemonidae, Hippolytidae, Penaeidae), fishes (Gobiidae, *Symphurus* spp., Ophichthidae, Syngnathidae) and mud crabs (Xanthidae) (Big Lagoon only). Because of the likelihood of large-scale movements among patches, adult blue crabs (≥80 mm carapace width) and large penaeids (≥40 mm total length, TL) were not included in this analysis.

Above ground seagrass and epiphyte biomasses were determined by gently removing all epiphytes from a haphazardly collected subset (≥5 turtlegrass

leaves or ≥10 shoalgrass leaves) of the seagrass leaves using a razor blade. The clean seagrass leaves and the removed epiphytes were collected and placed into 2 separate pans. All remaining unscraped seagrass leaves were carefully rinsed and placed into a third weighing pan. These pans were placed into a drying oven (80°C) for at least 24 h and then weighed to the nearest 0.0001 g. The samples were subsequently placed into a muffle furnace (500°C) for 5 h and reweighed in order to calculate the ash free dry weight (AFDW). Total above ground biomass (AFDW) and epiphyte loads (AFDW) were calculated by determining the percentage of epiphytes present in the subsample and applying this value to the remaining unscraped leaves.

Secondary production estimates were calculated for total decapods (crabs plus caridean shrimps), caridean shrimps, and crabs (juvenile blue plus mud). In addition, separate estimates were calculated for juvenile blue crabs and mud crabs in Big Lagoon. Secondary production estimates were obtained by first determining the dry biomass (DW) of each sample to the nearest 0.0001 g. This was done by drying each sample at 80°C to a constant weight. After the dry weight was measured, we determined the ash weight (AW) of the crabs and fishes by ashing them at 500°C for 5 h. After ashing, the samples were placed in desiccators and allowed to cool prior to reweighing. AFDW was calculated as DW minus AW. Because of the low inorganic content of shrimp, AFDW was calculated as DW × 0.9 (Waters 1977). We estimated secondary production using the equation provided by Robertson (1979): $\log P/B = 0.66 - 0.726 \log L$, where P = annual production (g AFDW m⁻² yr⁻¹), B = mean annual biomass (g AFDW m⁻²) and L = lifespan in years. Because reliable estimates of lifespans are required for the application of this equation, and these are difficult to ascertain with confidence for invertebrates, we used both the longest and shortest lifespans published to provide a range of secondary production estimates. This method has been previously used by Valentine & Heck (1993) and by Heck et al. (1995) to estimate ranges of secondary production in SAV habitats in Florida and in New England.

Data resulting from each of the 3 collection dates were analyzed using a stepwise multiple linear regression procedure (SPSS 2000). For abundances, separate analyses were calculated for total decapods, shrimps, fishes, juvenile blue crabs and mud crabs. For secondary production estimates, analyses were calculated for total decapods, caridean shrimps, crabs, juvenile blue crabs and mud crabs. Independent variables for all analyses were P:A ratio, nearest neighbor distance, above ground seagrass biomass, and epiphyte biomass. In addition, we conducted an additional linear

regression analysis where area was the only independent variable. Densities were transformed using a $\log_{10}(x + 1)$ transformation to satisfy the normality and homogeneity of variance assumptions of the linear regression model; however, in the few instances where the assumptions were not met, we feel that the robustness of this procedure ensures that results are reliable.

Differences between edges and interiors of seagrass patches were examined using 2-tailed *t*-tests for each dependent variable. When needed to meet the assumptions of the test, the data were transformed using a $\log_{10}(x + 1)$ transformation. Environmental parameters for each sampling location were monitored to ensure similarities among patches.

Artificial seagrass units. Because of the possibility of covariance between structural complexity and area at the smallest naturally occurring patch sizes, 10 replicate ASUs were deployed in June, August and October 2001 at each of the study locations. We must note that the June sampling occurred on July 2 (Big Lagoon) and 9 and is referenced as such in the figures and tables. These ASUs varied in both size (large and small) and shape (stellate and circular), thus also varying in area and P:A ratios (Bologna & Heck 1999, 2000). In Table 1, the differences in area and P:A are shown for 2 different-sized ASUs of each shape. We used 1.9 cm black Vexar mesh as a substrate to which artificial seagrass leaves were attached; 5 mm wide, smooth finish, green polypropylene ribbon was used to simulate *Thalassia testudinum* leaves, and 2.5 mm wide ribbon was used to simulate *Halodule wrightii* leaves. Shoot density was 2400 leaves m^{-2} for *T. testudinum* and 10 000 leaves m^{-2} for *H. wrightii*, mid ranges of field-measured values during 1997 and 1998 at the field sites (Stutes 2000, K. L. Heck & J. F. Valentine unpubl.). ASUs were placed on barren sand (Big Lagoon) and sand/mud (Grand Bay) flats, 5 m apart and at least 5 m from any living seagrass, and allowed to undergo colonization for 4 wk, after which time they were sampled with the suction-dredging technique described in the foregoing subsection. Because of the relatively small size of the ASUs, only a single suction sample was collected from each, using a shape-specific suction appliance that encompassed the entire ASU (no discrimination between edge

and interior), the ASU was sampled for a minimum of 1 min. To ensure that all macrofaunal organisms had been removed, a small dip net was passed through any seawater remaining within the suction appliance.

Sample processing and secondary production estimates were done in a manner similar to that for natural seagrass beds; however, grouping for density and secondary production estimates varied slightly. Groupings for density values were: total decapods; total fishes; total crabs; juvenile blue crabs; mud crabs; juvenile penaeids (≤ 40 mm); caridean shrimps. Groupings for production values were: total decapods (total crabs plus total shrimps); total crabs (juvenile blue plus mud); total shrimps (small penaeid plus caridean); total fishes (Gobiidae, *Symphurus* spp., Ophichthidae, Syn-gnathidae). In addition, because of the large amount of time required to process samples from Big Lagoon in June 2001, a haphazardly chosen subset of ASUs (Table 2) from each remaining sample date was randomly selected and processed in lieu of processing all 10 replicates.

The lifespan estimate for secondary production of the fish group was derived for the numerically dominant fish (*Gobiosoma robustum*: 84.4% of total). Since no reliable estimates exist for this species, lifespan estimates were obtained for *G. bosci*, a species with identical life history that is often confused with *G. robustum*. Because *G. bosci* is considered to be an annual species (Peterson et al. 2003), we used 1.5 and 0.5 yr as our high and low lifespan estimates, respectively.

Abundance and secondary production data from the ASU experiments were analyzed using a 2-way ANOVA with patch size (large and small) and patch shape (stellate and circular) as factors. In addition, we examined each sample date separately. Post-hoc analyses were carried out using Fisher's least significant difference (LSD) test. All densities were transformed using a $\log_{10}(x + 1)$ transformation to meet the normality and homogeneity of variance assumptions of the ANOVA model; however, in the few instances where the assumptions were not met, the robustness of this procedure ensures that the results are reliable. In addition, we used linear regression techniques (SPSS stepwise process) to examine the relationship between perimeter:area ratios and organism abundance and production.

Table 1. Dimensions of ASUs deployed in Big Lagoon, Florida, and Grand Bay, Alabama, in 2001. ASUs differed in size (large/small) and shape (stellate/circular)

	Large		Small	
	Stellate	Circular	Stellate	Circular
Area (m^2), A	0.2036	0.2036	0.0487	0.0487
Perimeter (m), P	3.265	1.6	1.6	0.7825
P:A ratio	16.04	7.86	32.85	16.07

Table 2. Sample sizes for ASU experiment for Big Lagoon and Grand Bay during 2001. L: large; S: small patches

Big Lagoon			Grand Bay		
Date	Stellate	Circular	Date	Stellate	Circular
Jul 2	10 L, 10 S	10 L, 10 S	Jul 9	5 L, 5 S	5 L, 5 S
Aug 29	5 L, 8 S	6 S, 6 S	Aug 30	5 L, 5 S	5 L, 5 S
Oct 24	5 L, 5 S	5 S, 6 S	Aug 30	5 L, 4 S	5 L, 5 S

RESULTS

Physical environment

Water temperatures at Big Lagoon during the experiment ranged between 19 and 32.5°C (NOAA data: available at http://co-ops.nos.noaa.gov/data_retrieve.shtml). October was the coolest month with temperatures averaging 20.8°C, while June and August had mean temperatures of 29.6 and 30.0°C, respectively. Salinity during the experiment ranged between 23 and 35. Salinity in June and August ranged between 23 and 29, while salinity in October averaged 34.8.

Water temperatures at Grand Bay ranged between 20 and 31°C during the summer/fall of 2001. As expected, mean temperatures decreased between July and October and remained seasonable for that time period (NOAA data). Salinity during the experiment ranged between 10 and 31. During June 2001, mean salinity was 12, while in August and October mean salinities were 23 and 28, respectively.

Natural seagrass patches

Big Lagoon

Distributional patterns indicated minimal monthly variation, with all taxa occurring during each sample period. In addition, all species were collected over the entire range of sizes of seagrass beds sampled (Fig. 2). Blue crabs and mud crabs were collected in 42 and 70% of the suction samples, respectively; while caridean and penaeid shrimps were present in 94 and 39% of the samples collected, respectively. Penaeid shrimps did exhibit a seasonal density increase of approximately 25% between the sample periods. Gobies (primarily *Gobiosoma robustum*) were the numerically dominant species collected, comprising 71% of the total fish abundance, and were present in 39% of the samples. The remaining 29% of the fishes collected consisted of blackcheek tonguefish *Symphurus plagiatus* (13%), speckled worm eels *Myrophis punctatus* (7%) and pipefishes *Syngnathus* spp. (9%). Total fish densities ranged between 0 and 82 fishes m^{-2} (Fig. 2).

Low lifespan estimates of productivity of all decapods combined ranged between 0.04 and 14.7 g AFDW $m^{-2} yr^{-1}$ for natural seagrass beds in Big Lagoon. High lifespan estimates ranged between 0.02 and 6.8 g AFDW $m^{-2} yr^{-1}$. Caridean shrimps represented the largest amount of decapod production in Big Lagoon; in 81% of the samples collected, they accounted for more than half the biomass production. Maximum estimated caridean shrimp production was 8.2 g AFDW $m^{-2} yr^{-1}$ (low lifespan estimate), minimum

estimated production 0.03 g AFDW $m^{-2} yr^{-1}$ (high lifespan estimate). When mud crabs were present, they comprised the next most productive group, with low lifespan estimates ranging between 0.006 and 13.4 g AFDW $m^{-2} yr^{-1}$ and high lifespan estimates ranging between 0.003 and 6.01g AFDW $m^{-2} yr^{-1}$. Blue crabs were the least common decapod and represented the smallest amount of annual production in Big Lagoon. Estimated annual productivities of blue crabs ranged between 0.02 and 3.5 for low lifespans, and between 0.002 and 6.1 g AFDW $m^{-2} yr^{-1}$ for high lifespan estimates.

Stepwise multiple linear regression analysis revealed little of the relationships between organism densities and perimeter:area ratio, distance to nearest neighbor, above ground seagrass biomass and epi-

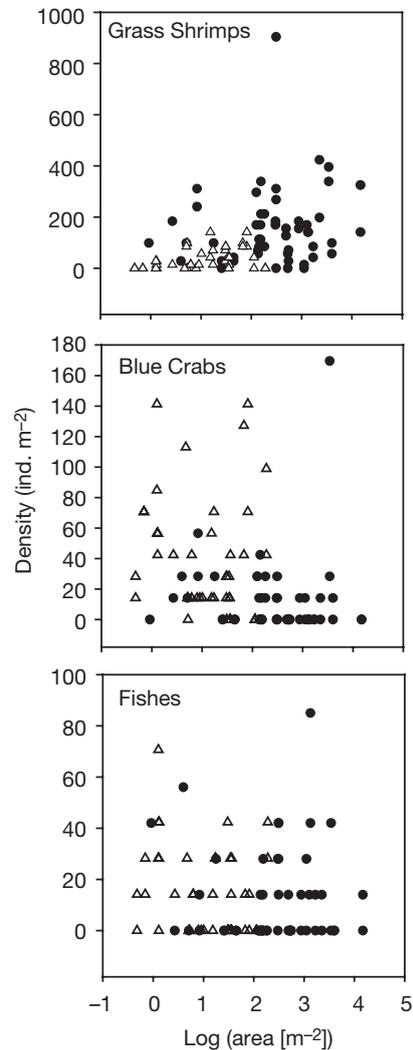


Fig. 2. Densities of grass shrimps, blue crabs, and total fishes within different-sized patches in (●) *Thalassia testudinum* beds in Big Lagoon and (△) *Halodule wrightii* beds in Grand Bay between June and October 2001

phyte biomass. No multiple regression models were significant for data collected in Big Lagoon, nor were there any significant relationships between secondary production estimates and any independent variables. The only significant regressions resulting from this procedure were simple linear regressions between fish density and distance to nearest neighbor, and between mud crab densities and perimeter:area ratios (Fig. 3). Our regression analysis between patch area and both abundance and production resulted in a single significant relationship with mud crab density ($F_{1,50} = 12.16$, $p = 0.001$). The resulting relationship was positive and could be described by the relationship $\log_{10}(\text{ind. m}^{-2}) = 0.19 + 0.35 \times \log_{10}(\text{area})$, $r^2 = 0.20$.

Mud crabs were the only organisms showing significant differences between the edge and interior of patches. The mean (\pm SE) number of mud crabs found

in the interior was 39.14 ± 7.6 crabs m^{-2} , which was significantly greater (Student's $t = 2.711$, $df = 50$, $p = 0.009$) than crab density in the edge (mean = 15.6 ± 3.5 crabs m^{-2}). Production estimates for both the high and low lifespan estimates of mud crabs were significantly higher (high: $t = 2.062$, $df = 50$, $p = 0.044$; low: $t = 2.091$, $df = 50$, $p = 0.042$) for the interior of the patches. High lifespan estimates of mean production were 0.59 ± 0.26 g AFDW $\text{m}^{-2} \text{yr}^{-1}$ and 0.09 ± 0.04 g AFDW $\text{m}^{-2} \text{yr}^{-1}$ for patch interiors and exteriors, respectively. The low lifespan estimates of mean production for the patch were 1.3 ± 0.57 g AFDW $\text{m}^{-2} \text{yr}^{-1}$ (interior) and 0.204 ± 0.08 g AFDW $\text{m}^{-2} \text{yr}^{-1}$ (exterior).

Grand Bay

Caridean and penaeid shrimps, juvenile blue crabs and fishes were present at each sample period and collected over the entire range of patch sizes (Fig. 2); however, densities showed little variation in the summer/fall of 2001. Blue crabs and caridean shrimps were present in 61 and 86% of the samples, respectively, and were the most abundant organisms collected. Penaeid shrimps and fishes were present in 45 and 54% of the samples collected, respectively. Gobies (primarily *Gobiosoma robustum*) comprised 45% of the total fishes collected, occurring in densities ranging between 0 and 42 m^{-2} . Blackcheek tonguefish *Symphurus plagiusa* (38%), speckled worm eels *Myrophis punctatus* (9%) and pipefish *Syngnathus* spp. (7%) were present at densities ranging between 0 and 28 ind. m^{-2} .

High lifespan estimates of annual productivity of all decapods combined ranged between 0.003 and 38.2 g AFDW $\text{m}^{-2} \text{yr}^{-1}$. Low lifespan estimates ranged between 0.006 and 83.5 g AFDW $\text{m}^{-2} \text{yr}^{-1}$. Caridean shrimps represented at least 75% of the total production in 43% of the samples, while crab production was at least 75% of the total production in 40% of samples. There was an overall increase in crab production and a decrease in shrimp production between June and October. The maximum estimated caridean shrimp production was 20.7 g AFDW $\text{m}^{-2} \text{yr}^{-1}$ (low lifespan estimate), while the minimum estimated production when shrimp were present was 0.14 g AFDW $\text{m}^{-2} \text{yr}^{-1}$ (high lifespan estimate). When crabs were present, they had high lifespan production estimates ranging between 0.0002 and 36.0 g AFDW $\text{m}^{-2} \text{yr}^{-1}$ and low lifespan estimates ranging between 0.0005 and 79.9 g AFDW $\text{m}^{-2} \text{yr}^{-1}$.

Stepwise multiple linear regression analyses indicated that the only significant relationships between abundance and any independent variable were

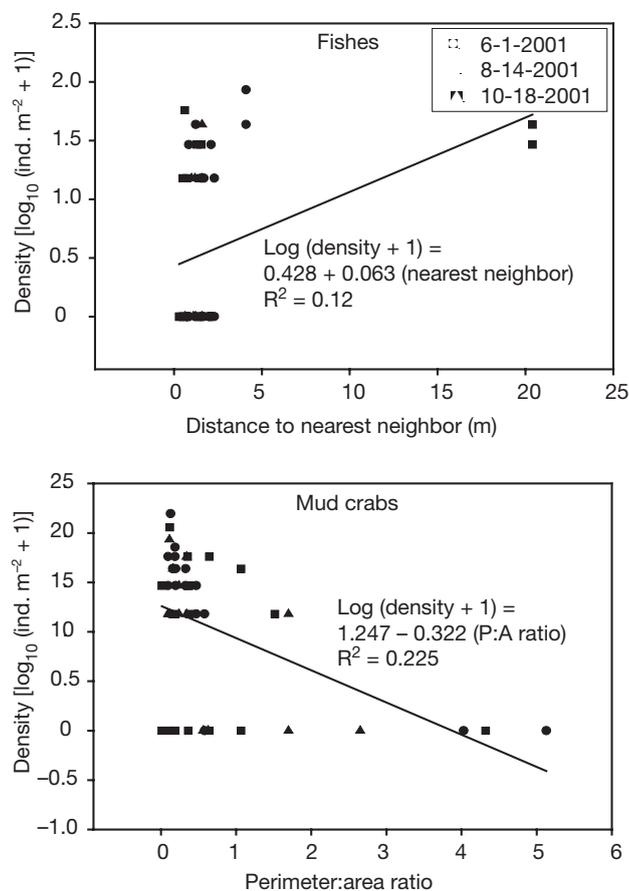


Fig. 3. Significant stepwise multiple linear regressions for Big Lagoon (*Thalassia testudinum*) meadows computed using organism density as dependent variable, and perimeter:area ratio, distance to nearest neighbor, above-ground seagrass biomass and epiphytic biomass as independent variables. Distance to nearest neighbor measured as shortest distance between 2 adjacent seagrass beds. Here and in subsequent figures, dates presented as mm-dd-yyyy

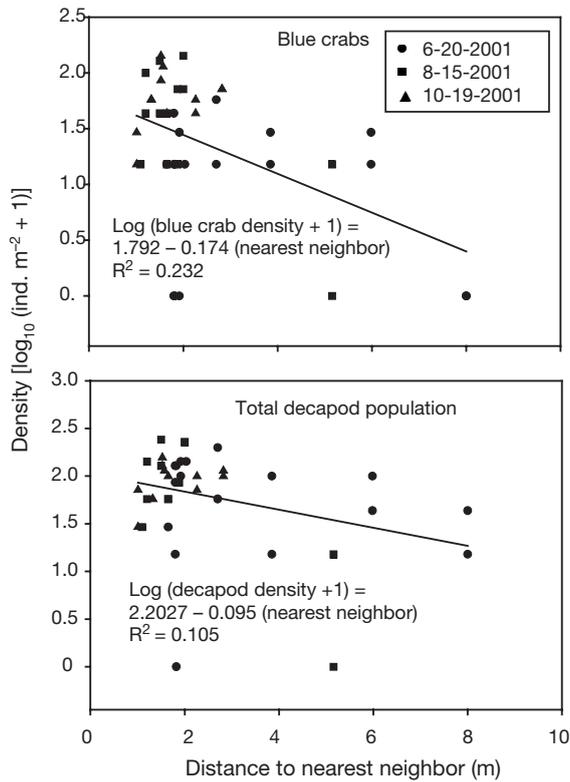


Fig. 4. Significant stepwise multiple linear regressions for Grand Bay. Details as in Fig. 3 legend

between both blue crab and total decapod densities and the distance a patch was located from its closest neighbor (Fig. 4). Secondary production estimates did not show significant relationships with any of the independent variables. Student's *t*-tests comparing abundances and secondary production within patch interiors versus exteriors found no significant differences for any of the dependent variables.

Artificial seagrass units

Big Lagoon

During the June ASU sampling effort, fishes, primarily *Gobiosoma robustum*, were most abundant, followed by blue crabs, carideans, penaeids and mud crabs (Fig. 5). There were no significant density differences among the four different ASUs for any of the organisms captured (Fig. 5). In August, blue crabs, caridean shrimps, and fishes remained the most common groups. No mud crabs and only a single penaeid shrimp were collected during this period. Caridean shrimp abundance varied significantly with patch size, but not with patch shape (size: $F_{1,1} = 6.773$, $p = 0.016$;

shape: $F_{1,1} = 2.540$, $p = 0.125$) mean abundance (\pm SE) on the large and small ASUs was 68.8 ± 35 and $29.1 \pm 12.6 \text{ m}^{-2}$, respectively (Fig. 5). During October, caridean shrimp abundance surpassed that of fishes, and they became the most abundant group (Fig. 5). Blue crabs and fishes were also common during this period, and were present at densities similar to those in other collection periods. Penaeid shrimp densities increased by 387% during this period, while mud crabs were uncommon (~ 1.4 mud crabs m^{-2}) and were only present on large ASUs. As a result, mud crabs were significantly more abundant on large ASUs (size: $F_{1,1} = 6.836$, $p = 0.018$; shape: $F_{1,1} = 2.153$, $p = 0.161$). In addition, significantly more caridean shrimps (size: $F_{1,1} = 11.244$, $p = 0.004$; shape: $F_{1,1} = 1.632$, $p = 0.423$) and decapods (size: $F_{1,1} = 13.044$, $p = 0.002$; shape: $F_{1,1} = 0.147$, $p = 0.300$) were collected in the large than the small ASUs (Fig. 5).

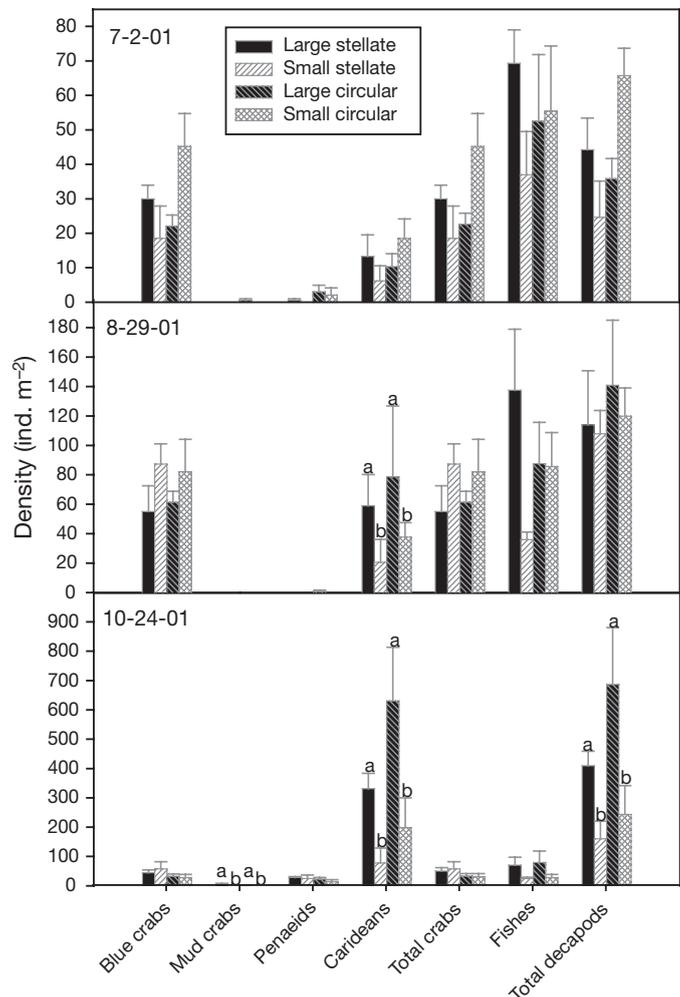


Fig. 5. Mean (+SE) densities of animals collected from artificial seagrass units (ASUs) in Big Lagoon. Significant ($p < 0.05$) differences and post-hoc groupings indicated by lowercase letters

High and low lifespan estimates of production were significantly greater in the large than the small ASUs for crabs (high and low size: $F_{1,1} = 7.842$, $p = 0.01$; shape: $F_{1,1} = 1.401$, $p = 0.245$) and fishes (high and low size: $F_{1,1} = 7.283$, $p = 0.014$; shape: $F_{1,1} = 2.233$, $p = 0.15$) (Table 3). For decapods, there were general increases in secondary production between June and October within each type of ASU, but changes were similar among the 4 ASU types. For fishes, production peaked in August and there were no similarities in trends temporally or among ASU types.

Table 3. Secondary production estimates (g AFDW m^{-2}) of crab and shrimp populations that colonized *Thalassia testudinum* artificial seagrass units in Big Lagoon, Florida, in 2001, with high and low estimates of lifespan. Superscripts indicate significant differences (2-way ANOVA, $p < 0.05$) and appropriate groupings. Crab lifespan estimates from Warner (1977), shrimp lifespan estimates from Bauer (1989), fish lifespan estimates from Peterson et al. (2003)

Organism, lifespan (yr)	Stellate		Circular	
	Large	Small	Large	Small
Jul 9				
Crabs				
3	0.15 ^a	0.03 ^b	0.13 ^a	0.11 ^b
1	0.34 ^a	0.06 ^b	0.29 ^a	0.25 ^b
Shrimps				
0.42	0.11	0.03	0.16	0.63
0.17	0.22	0.06	0.32	1.25
Decapods				
High	0.26	0.06	0.28	0.74
Low	0.56	0.12	0.61	1.50
Fishes				
1.5	0.54	0.50	0.35	1.38
0.5	1.24	1.15	0.81	3.17
Aug 29				
Crabs				
3	0.36	0.61	0.34	0.61
1	0.83	1.41	0.77	1.42
Shrimps				
0.42	3.72	0.01	1.12	0.71
0.17	7.39	0.26	2.22	1.41
Decapods				
High	4.08	0.74	1.45	1.32
Low	8.22	1.67	3.00	2.82
Fishes				
1.5	3.07 ^a	0.39 ^b	1.08 ^a	0.66 ^b
0.5	7.07 ^a	0.89 ^b	2.22 ^a	1.51 ^b
Oct 24				
Crabs				
3	0.66	0.32	0.18	0.13
1	1.52	0.73	0.42	0.29
Shrimps				
0.42	5.58	8.65	7.78	3.66
0.17	11.09	17.20	15.47	7.28
Decapods				
High	6.24	8.97	7.96	3.79
Low	12.61	17.93	15.88	7.57
Fishes				
1.5	0.18	0.66	0.42	0.12
0.5	0.42	1.53	0.96	0.27

Regression analysis of the relationship among perimeter:area ratios and organism density in the ASUs indicated that P:A ratios may exert some influence over decapod settlement and production. There was a negative relationship among P:A ratios and blue crab, caridean shrimp and total decapod densities, as well as crab production (Fig. 6). However, these results were not consistent among the 3 sample periods and only explained between 15 and 35% of the variance.

Grand Bay

Blue crabs, mud crabs, penaeid shrimps and caridean shrimps were all present during June 2001. Although not significantly different, caridean shrimp densities were greater on large ASUs, while blue crabs and mud crabs were collected in larger numbers on small ASUs (Fig. 7). Combined, total crab density was significantly different between the large and small ASUs (size: $F_{1,1} = 7.040$, $p = 0.017$; shape: $F_{1,1} = 0.192$, $p = 0.667$). Fishes collected at this time consisted of 70% *Gobiosoma robustum*, 17% blackcheek tonguefish, and 11% speckled worm eels and 2-way ANOVAs indicated no significant relationship between ASU size or shape and fish abundance. In August, there was an increase in the overall numbers of penaeid shrimps and blue crabs compared to June. Both organisms were more abundant on stellate than circular ASUs; however, penaeid shrimps comprised the only taxon that was significantly different (size: $F_{1,1} = 1.265$, $p = 0.277$; shape: $F_{1,1} = 4.737$, $p = 0.045$) (Fig. 7). October sampling resulted in few changes from the previous sampling date, but there was an overall increase in penaeid densities. No significant differences in abundances were detected during this period.

Secondary production estimates for crabs and decapods in June 2001 indicated that the largest amount of production in Grand Bay was due to penaeid and caridean shrimps (Table 4). For this date, large ASUs were responsible for significantly more (size: $F_{1,1} = 5.102$, $p = 0.038$; shape: $F_{1,1} = 0.00$, $p = 0.999$) production of decapods for the low lifespan estimate. Fish production, although not significantly different, was greater on small ASUs (Table 4). During August, shrimps were still responsible for more secondary production than crabs; however, there were no significant differences or general trends evident between patch size and patch shape for decapods. Fish secondary production, on the other hand, was significantly larger on stellate ASUs during June (high and low size: $F_{1,1} = 0.01$, $p = 0.92$; shape: $F_{1,1} = 5.580$, $p = 0.031$). In October, patch size played a larger role in crab and overall decapod production than in the other sample periods. Large ASUs showed significantly more crab production (high and low size: $F_{1,1} =$

10.051, $p = 0.006$; shape: $F_{1,1} = 0.028$, $p = 0.87$) and overall decapod production (high- size: $F_{1,1} = 5.427$, $p = 0.033$; shape: $F_{1,1} = 0.188$, $p = 0.671$; low size: $F_{1,1} = 11.812$, $p = 0.003$; shape: $F_{1,1} = 0.165$, $p = 0.69$) than the small ASUs (Table 4). In addition, shrimp secondary production was consistently higher in the large ASUs than

the small ASUs. Fish secondary production was greatest on the large stellate ASUs, but there was no significant or consistent pattern.

Regression analysis between perimeter:area ratios and animal density or secondary production estimates resulted in few significant relationships among vari-

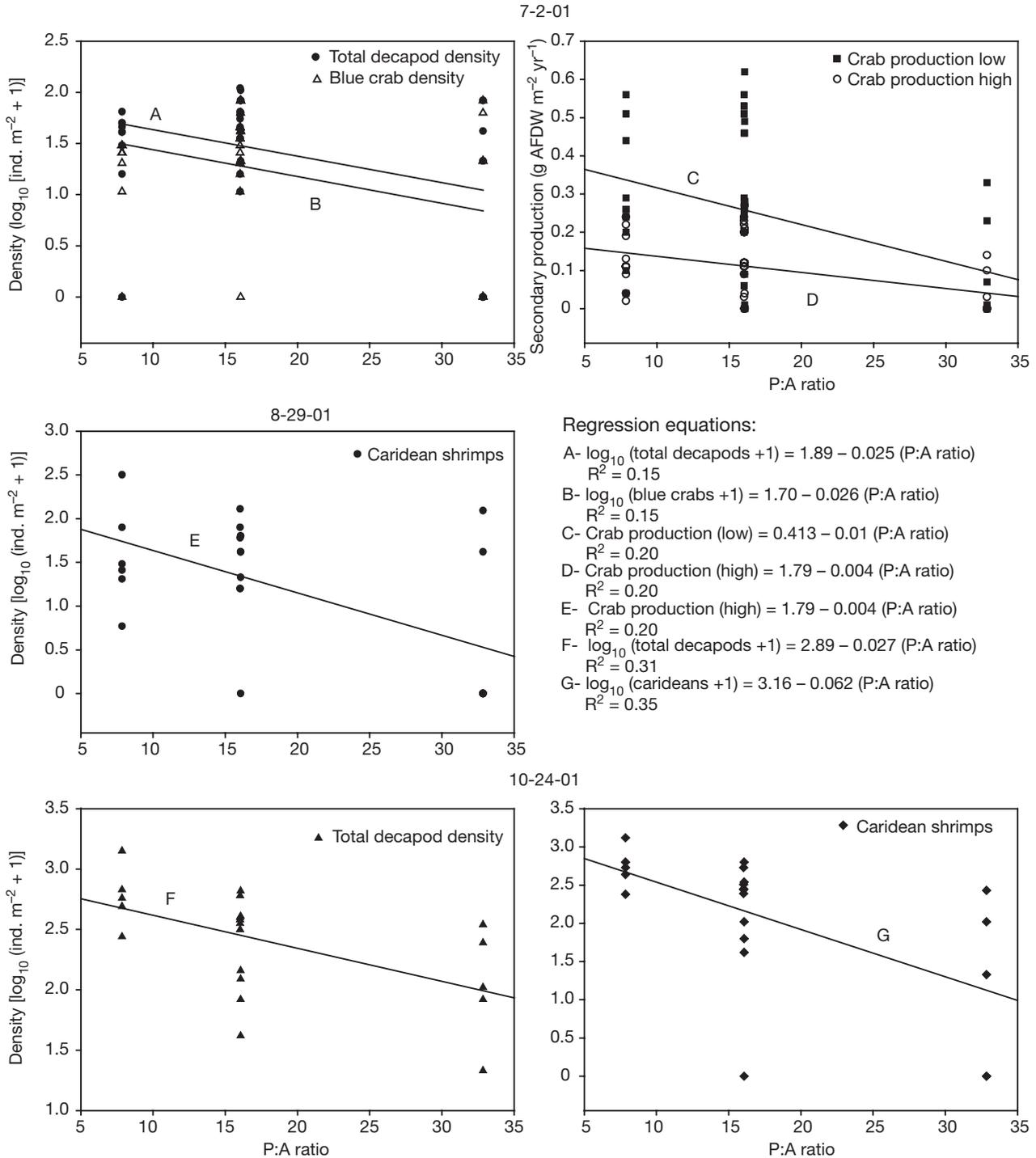


Fig. 6. Significant ($p < 0.05$) linear regressions for density and secondary production estimates versus perimeter:area (P:A) ratio for ASUs in Big Lagoon. For August 2001, caridean shrimp were only collected from 2 of the 8 small stellate ASUs (P:A = 32.85)

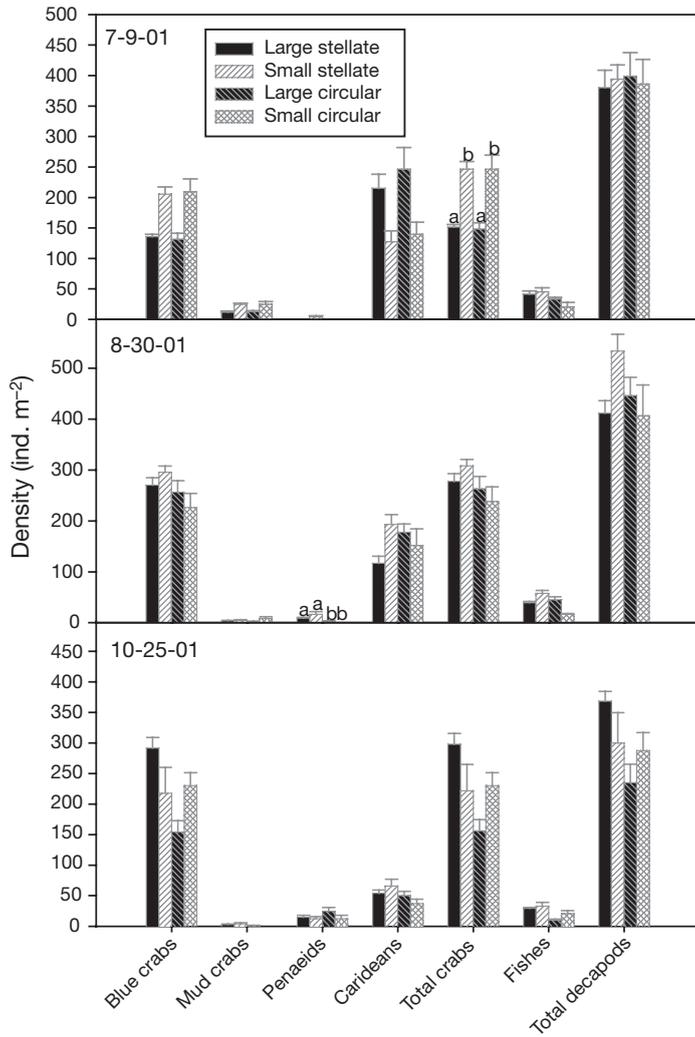


Fig. 7. Mean (+SE) densities of animals collected from artificial seagrass units in Grand Bay. Significant ($p < 0.05$) differences and post-hoc groupings indicated by lowercase letters

ables. During June, crab abundance had a significant positive relationship ($F_{1,18} = 4.48$, $p = 0.045$) with P:A ratios (Fig. 8). In August, there were no significant relationships between P:A ratios and any of the density or secondary production variables. For October, high and low lifespan estimates of crab secondary production (high and low $F_{1,18} = 4.911$, $p = 0.040$) and low lifespan estimates for total decapod secondary production ($F_{1,18} = 5.743$, $p = 0.028$) each had a significant negative relationship with P:A ratios.

DISCUSSION

Large-scale sampling efforts such as ours, across a range of naturally occurring seagrass patches in conjunction with ASU experiments, are rare, and studies

that have been done have failed to produce consistent conclusions regarding the role of habitat fragmentation (Irlandi 1997, Hovel & Lipcius 2001). This study is no exception: habitat fragmentation per se did influence abundances and secondary production estimates, but results were inconsistent and varied by species, location and date. In natural seagrass beds, the degree of isolation, area and perimeter:area ratios each had a minor influence on faunal distributions, while measures of seagrass biomass and epiphyte biomass played no significant role for decapods and fishes. In addition, linear regressions of secondary production estimates against these variables revealed in no significant relationships.

Table 4. Secondary production estimates (g AFDW m^{-2}) of crab and shrimp populations that colonized *Halodule wrightii* artificial seagrass units in Grand Bay, Alabama. Further details as for Table 3

Organism, lifespan (yr)	Stellate		Circular	
	Large	Small	Large	Small
Jul 9				
Crabs				
3	6.14	3.73	6.57	3.39
1	14.14	8.60	15.15	7.81
Shrimps				
0.42	21.50	13.35	22.94	11.71
0.17	42.75	26.54	45.62	23.28
Decapods				
High	48.89	30.27	52.19	26.67
Low	35.64 ^a	21.95 ^b	38.09 ^a	19.52 ^b
Fishes				
1.5	1.72	9.64	1.61	3.42
0.5	13.32	74.59	12.49	26.45
Aug 29				
Crabs				
3	6.91	9.09	6.80	5.89
1	15.94	20.96	15.68	13.57
Shrimps				
0.42	9.14	13.97	16.22	10.28
0.17	18.17	27.79	32.25	20.44
Decapods				
High	25.08	36.88	39.06	26.33
Low	25.07	34.93	31.90	23.85
Fishes				
1.5	1.65 ^a	2.50 ^a	1.13 ^b	0.16 ^b
0.5	12.78 ^a	19.34 ^a	8.72 ^b	1.21 ^b
Oct 24				
Crabs				
3	7.32 ^a	2.52 ^b	7.10 ^a	2.74 ^b
1	16.88 ^a	5.8 ^b	16.37 ^a	6.32 ^b
Shrimps				
0.42	8.57	5.59	11.97	3.97
0.17	17.04	11.12	23.80	7.90
Decapods				
High	24.36 ^a	13.64 ^b	30.90 ^a	10.64 ^b
Low	25.45 ^a	11.4 ^b	28.34 ^a	10.29 ^b
Fishes				
1.5	3.98	0.85	1.51	1.19
0.5	30.85	6.57	11.67	9.25

In general, distance between patches seemed to have the most influence on fish and blue crab densities in naturally occurring seagrass meadows. We propose that for blue crabs, increased isolation of seagrass patches may result in decreased densities by reducing the post-settlement movement of crabs both into and out of the seagrass patch. Because of increased predation risks when crossing unstructured seafloor among seagrass beds (Orth et al. 1984, Micheli & Peterson 1999), juvenile blue crabs may have little success in immigrating from larger source areas to the patch, or emigrating from the isolated patch to more suitable habitats. The coupling of these 2 processes may be responsible for the decreased abundances in isolated patches. Hovel & Lipcius (2002) found that, for blue crabs, increased mortality was more clearly related to both decreased shoot density in large isolated patches and increased conspecific predation in small isolated patches than to the degree of patch isolation. To our knowledge, ours is the first study to demonstrate instances of a relationship between degree of isolation and blue crab densities in the Gulf of Mexico.

In the present study, P:A ratios explained significant amounts of variation in some mud crab, blue crab and caridean densities as well as crab secondary production. Perimeter:area ratios are a useful, and underutilized, measure of habitat fragmentation that combine patch shape and size into a single metric. This metric can be utilized at both the landscape scale and patch scale, although, methodologies vary between the two. At the landscape scale, mean perimeter:area ratios are used (Schumaker 1996), but at the patch level we utilized individual patch measurements in our regression analyses. The P:A ratio is a unique measurement of patch characteristics that can reduce the possibility of correlation between area or perimeter and other unmeasured variables and can be independent of either area or perimeter. As a result, the new value is not able to be back-transformed to estimate perimeter or area (Schumaker 1996). Thus, some information pertaining to both patch area and perimeter are lost, but the possibility of correlation among variables is reduced. However, use of P:A ratios does not mean that patch quality or isolation can be ignored. It is critical that these also be included because they are important aspects of habitat fragmentation (Andr en 1994, Farhig 1997, Bender et al. 1998).

Does the apparent lack of consistency among locations, species and sample periods suggest that habitat fragmentation per se is not structuring communities? Our data and analyses do suggest this, although the answer is not simple. Our analysis employed \log_{10} transformation of non-linear data in order to utilize linear regression techniques. Many terrestrial relationships resulting from habitat fragmentation have been

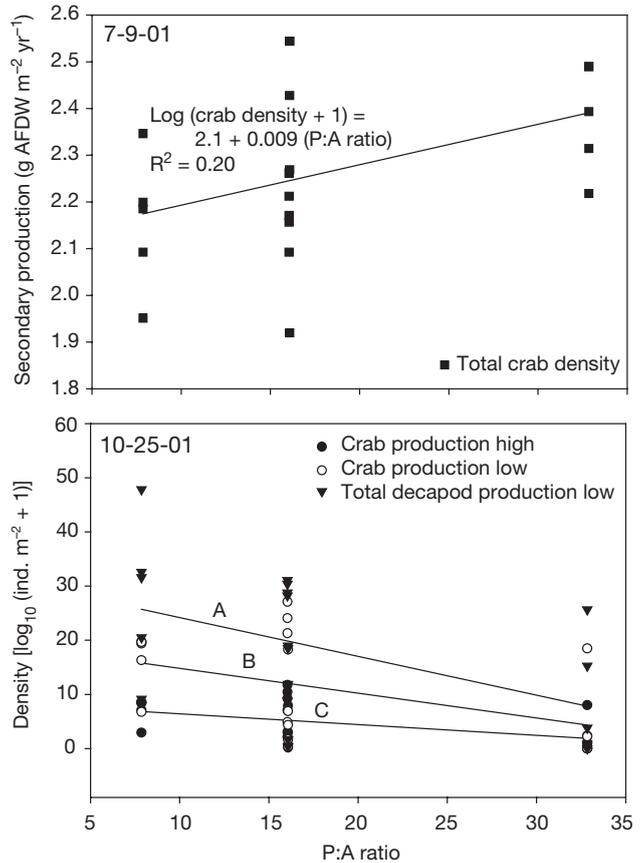


Fig. 8. Significant ($p < 0.05$) linear regressions for density and production estimates versus P:A ratios for ASUs in Grand Bay. Regression equations for October 25, 2001 = A: decapod production (low) = $31.3 - 0.72 \text{ P:A}$, $r^2 = 0.24$; B: crab production (low) = $19.4 - 0.458(\text{P:A ratio})$, $r^2 = 0.21$; C: crab production (high) = $8.41 - 0.20 \text{ P:A}$, $r^2 = 0.21$, where P:A = perimeter:area ratio

shown to be non-linear, usually in conjunction with a threshold level of patch size (With & Crist 1995). The significant linear relationships that resulted after the \log_{10} transformation does suggest that non-linear effects of fragmentation may be at work here; however, we felt it advisable to restrict analyses to simple analytical methods. In addition, we acknowledge that the scale of this study may have also influenced our conclusions (Stephens et al. 2004, Ribas et al. 2005). Habitat fragmentation is by definition a landscape issue, and we have utilized patch-level patterns to draw inferences. This means that although scaling up results is not uncommon, our results must be applied with caution until they can be verified on a landscape level. In a review, Andr en (1994) noted that although the mechanisms at work varied, models using individuals rather than local populations to examine the effects of habitat fragmentation on bird and mammals reached results similar to those of landscape-scale metapopulation models.

Despite these caveats, we believe that habitat fragmentation per se is not of critical importance within these seagrass meadows because of the nature of the organisms that inhabit them. Excluding some of the fishes, the organisms that we examined could all be considered habitat generalists that migrate to some extent, 2 traits that can reduce the impact of habitat fragmentation (Bender et al. 1998). An animal that is a habitat generalist does not discriminate between the edge of a patch and the interior (Andr en 1994). Mud crabs from Big Lagoon were the only species that were area-sensitive, and may be the only species of interest that could not be labeled a habitat generalist. More crabs were collected in the interior of a patch than the exterior and were found on larger ASUs more than on smaller ASUs. This may have been the result of an interaction between flow dynamics and the settlement of detritus on larger patches, a source of food for mud crabs (Williams 1984). According to Bell et al. (1995), smaller patches accumulate less drift algae than larger patches, and we suggest that a similar process with detrital material may have been at work here. In addition, as noted above, the ability to migrate is also common in these systems. Seagrasses in Big Lagoon and Grand Bay are ephemeral, dying back in the cold months and growing during the warm months (M. W. Johnson pers. obs.), resulting in most organisms migrating either offshore, to shallow tidal creeks, or to deeper bay waters.

The influence of patch size and patch shape on densities and secondary production was most obvious for decapods within ASUs and illustrates what may occur when mean patch size is reduced without loss of habitat. In Grand Bay, large patches had higher estimated secondary production for crabs, shrimps and combined decapods in June and October. In June, crab abundance was positively related to P:A ratio and more crabs were collected on smaller than larger ASUs. Increased recruitment to smaller habitats has been demonstrated in multiple types of habitats (Sousa 1984, Bell et al. 1987, Worthington et al. 1992, McNeill & Fairweather 1993, Thrush et al. 1996). In addition, conspecific predation by larger blue crabs can produce decreases in blue crab populations and may contribute to crab predation in ASUs (Hines et al. 1990, Mansour 1992, Moksnes et al. 1997). In Big Lagoon, secondary production estimates for large ASUs were higher for crabs in June and both shrimps and total decapods in August. Mean densities of blue crabs were higher for small ASUs in August, and caridean densities were larger for large ASUs in August and October. This suggests that, in Big Lagoon, either crabs do not respond to patch dynamics or that post-settlement processes (i.e. predation) are masking responses. Grass shrimp, however, may settle, migrate or grow faster on larger

ASUs. Caridean shrimp densities in seagrasses have been attributed to predator avoidance rather than increased food availability (Coen et al. 1981), suggesting that the increased amount of structure in larger ASUs may decrease predation rates on caridean shrimp (see Orth et al. 1984). In addition, caridean shrimps and blue crabs are highly mobile organisms whose distributions can vary daily (Howard 1985, Kneib & Wagner 1994). This leads us to believe that post-settlement processes have a major influence on abundance and secondary production estimates.

Comparisons with other habitat fragmentation studies must be made with caution. Impacts of habitat fragmentation may vary with the scale of the experiment (Stephens et al. 2004, Ribas et al. 2005), species of interest, and the terms used to describe patch size (e.g. large and small). Latitudinal patterns in habitat fragmentation may also exist and must be noted in any comparisons of multiple studies. Habitat-fragmentation in seagrass beds along the mid-Atlantic and Pacific coasts (Irlandi 1996, 1997, Eggleston et al. 1998, 1999, Irlandi et al. 1999, Hovel & Lipcius 2001, 2002, Hovel 2003) seems to have a stronger influence over organisms than in the Gulf of Mexico (Bologna & Heck 2000, Bell et al. 2001, 2002, present study). To be more specific, within the northern Gulf of Mexico, Bologna & Heck (2000) and the present study found more of an impact than studies carries out farther south (Bell et al. 2001, 2002). The exact reasons for this are unknown; however, in general there is an increase in tidal movement and decrease in trophic complexity with increasing latitude. More tidal movement may allow greater movement of organisms among patches and increase passive food delivery, thus increasing the importance of edge (Fonseca et al. 1982). Potentially, the impact of flow dynamics on settlement and recruitment may also increase with stronger tidal flow. It is possible that by decreasing the number of species within a system, the interaction between an organism and its habitat may also be altered. In a recent study, habitat preference by grass shrimp was influenced by the number of trophic levels within a mesocosm system (Johnson & Heck 2005). Much more effort is needed to understand the role that latitude (and longitude) play.

In conclusion, we have demonstrated that at the scale of this study, habitat fragmentation per se did not consistently influence densities of seagrass-associated decapods and fishes in Big Lagoon, Florida or Grand Bay, Alabama. However, the degree of isolation of a patch may exert some control over organism densities; also, as patches got smaller, P:A ratios seemed to increase in importance. Our study is unique because we found no significant covariation between patch size and above-ground biomass in naturally occurring seagrass beds. Combined with the ASU experiments, we

were able to examine the role of habitat fragmentation without confounding effects of habitat loss, a common by-product of habitat fragmentation (Andr n 1994, Fonseca & Bell 1998). In each study location, intrapatch location played a minor role in explaining the densities of decapods and fishes, suggesting that edge effects in marine systems may not play as extensive a role in determining the kind and abundance of organisms as suggested for terrestrial systems (Yahner 1988). Ultimately, habitat fragmentation may be most detrimental to seagrass-associated animals when it leads to large-scale losses of the area covered by seagrasses.

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