

**The Role of Habitat Fragmentation in the  
Structure and Function of Seagrass Ecosystems  
in the Northern Gulf of Mexico**

Matthew W. Johnson,  
University of South Alabama

Final Report 2003-2004  
Mississippi-Alabama Sea Grant Consortium Fellowship Award



MASGP-04-049

Mississippi-Alabama Sea Grant Consortium

Project Number: E/O-16

Program Year: 2004

Grant Number: Other sources



This publication was supported by the Mississippi-Alabama Sea Grant Consortium and The University of Southern Alabama. The views expressed herein do not necessarily reflect the views of any of those organizations.

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**Matthew W. Johnson**

University of South Alabama  
Department of Marine Sciences  
Dauphin Island Sea Lab  
101 Bienville Blvd.  
Dauphin Island, AL 36528

## Abstract

The role of changes in patch size and shape (habitat fragmentation) on ecological processes of seagrass meadows is poorly understood. Most research to date has resulted in equivocal findings that are confined to a general description of community structure. In the handful of studies where ecological processes, such as predation, have been examined, experiments have been confined to organisms that are sessile or are easily tethered. We used a mesocosm approach to examine the role that habitat fragmentation and trophic structure plays on predation and habitat selection. Our experimental "ecosystem" consisted of juvenile red drum (*Sciaenops ocellatus*) (RD), juvenile pinfish (*Lagodon rhomboides*) (PF), and grass shrimp (*Palaemonetes* sp.) (GS), members of a food web common in the northern Gulf of Mexico. In this food web, red drum was our tertiary predator, pinfish were both prey items for red drum and predators of grass shrimp, and grass shrimp were prey for both red drum and pinfish. We used 4 different artificial seagrass habitats that varied by size and shape to eliminate any co-variation between patch size and seagrass density. GS predation was measured in each habitat when PF, RD, and PF+RD were present. PF predation was measured when RD and RD+GS were present. In addition, habitat selection by each of these three species was measured individually, and in the presence of every other combination of these three species (GS, PF, RD, GS+PF, GS+RD, PF+RD, GS+PF+RD). Results suggest that neither predation nor habitat selection were consistently impacted by changes in patch characteristics (size, shape, and P/A ratios) or the number of trophic levels. For grass shrimp, there was a negative relationship between patch size and predation rates, but only in the GS+PF+RD treatment. This, in turn, may be influencing the selection of larger habitats by grass shrimp. Pinfish predation indicated no significant relationship between patch characteristics and trophic structure, but did have a positive response in the PF and GS+PF+RD treatments. There were no significant relationships between patch size, shape, or trophic structure and habitat selection by red drum. We believe that habitat fragmentation may be important in structuring communities through predation and habitat selection; however, our data suggests that responses to patch characteristics are inconsistent and that trophic structure may be much more influential than previously believed.

## **Introduction**

During the past century, the critical role that seagrasses play in the marine environment has been well documented; however, despite their importance, seagrass populations continue to decline worldwide due to a myriad of natural and anthropogenic factors (Orth et al., 1984; Valentine, 1991; Walker and McComb, 1992; Durako, 1994; Onuf, 1994; Duarte, 1995; Short and Wyllie-Echeverria, 1996; Holmquist, 1997; Reusch, 1998; Koch and Gust, 1999; Stumpf et al., 1999; Eckrich and Holmquist, 2000; Beck et al., 2001). The result of these losses is the fragmentation of once continuous seagrass beds into smaller functional units (Fonseca and Bell, 1998; Seddon et al., 2000). This fragmentation can shift seagrass patch size and shape, ultimately altering the perimeter: area (P/A) ratio (i.e. the amount "edge" present), which in turn, may impact faunal abundance, biological interactions, and water flow (Fonseca et al., 1982; Keough, 1984; Irlandi, 1997; Bologna and Heck, 2000; Caley et al., 2001). Of the few studies examining these trends, there is little agreement on the exact consequences of shifts in patch size and/or shape on seagrass associated animals (see Eggleston et al., 1999; Bell et al., 2001).

Because of the relatively small amount of marine studies examining the roles of patch size and shape, initial research efforts relied heavily on the concept of the species-area relationship. However, earlier studies indicated that larger areas did not necessarily support more species in marine environments (Salm, 1989; McNeill and Fairweather, 1993). More specifically, McNeill and Fairweather (1993) found that several small grass beds often contained more total species than a single large grass bed of similar area. They also found that artificial seagrass units (ASUs) could contain more animal species

in several small units than in a single large unit. Additional work on the effects of seagrass patch size and shape by Bologna and Heck (2000) concluded that bivalve settlement was positively correlated with seagrass patch perimeter, while Irlandi et al. (1999) noted that scallop (*Argopecten irradians concentricus*) survival showed no correlation with the amount of perimeter. In each case, differential responses by predators were believed to be one control mechanism at work. When several trophic levels were examined, grass shrimp (*Palaemonetes* sp.) were found more frequently in smaller ASUs (increased perimeter), while, blue crabs (*Callinectes sapidus*) had higher abundances in larger ASUs (decreased perimeter). This inverse relationship may be due to post settlement predation by grass shrimp on blue crab megalopae (Eggleston et al., 1998). Finally, habitat fragmentation has been shown to have differential effects on juvenile blue crab survival depending on season, patch isolation, and shoot density; however, there was no relationship between blue crab survival and patch size (Hovel and Lipcius, 2002). These complex and variable results indicate that the consequences of fragmentation in marine habitats may be more complicated than previously expected.

The objectives for this study are to determine if habitat fragmentation (as measured by variation in patch size and shape) and trophic structure influence habitat selection or predation among three trophic levels of a food web common in the Northern Gulf of Mexico.

## **Methods**

To determine if patch size, shape, and trophic structure influences predation rates, we used a large flow-through mesocosm system consisting of 10, 1m<sup>3</sup> tanks approximately 182 x 46 x 46 cm in size. These experiments were carried at the Auburn

Shellfish Laboratory, located at the Dauphin Island Sea Lab (DISL), Dauphin Island, AL, USA. Seawater for these experiments was pumped from the Gulf of Mexico, along the south shore of the DISL. For our predation experiments, a single ASU was placed in the center of each tank and weighted down using, six-4oz. lead weights. ASUs varied by size (large (0.2036 m<sup>2</sup>) or small (0.0487 m<sup>2</sup>)) and shape (stellate or circular) (Table 1). For this experiment, we used juvenile red drum (*Sciaenops ocellatus*), juvenile pinfish (*Lagodon rhomboides*), and grass shrimp (*Palaemonetes* sp.). Each of these species are common in seagrass habitats though out the Gulf of Mexico and the southern Atlantic (Hoese and Moore, 1977; Williams, 1984; Swingle, 1990; Stunz et al., 1999). 150 juvenile red drum were purchased from a commercial supplier (The Fish Farm, Bacliff, TX) and ranged in size between 30 and 50 cm standard length, with a mean length  $\pm$  S.D. of  $39.9 \pm 4.7$  cm. Pinfish were collected by otter trawl from Big Lagoon, FL and ranged in size between 5.9 and 10.4 cm standard length, with a mean  $\pm$  S.D. of  $8.0 \pm 0.9$  cm. Adult grass shrimp were collected using a beam plankton trawl from Heron Bay marsh, Alabama Port, AL and were all in excess of one centimeter carapace length.

Red drum (RD), pinfish (PF), and grass shrimp (GS) were each stocked at 1, 6, and 486 animals/m<sup>2</sup>, well within reported ambient densities for seagrass meadows (Stunz et al., 1999; Johnson and Heck, 2003). Each trial lasted for a period of 24hrs and consisted of one of four combinations of animals. RD+PF, RD+GS, PF+GS, RF+PF+GS, and both ASU and animal configurations were randomly assigned to tanks and days to decrease the likelihood of artifacts. In addition, pinfish and grass shrimp were only used for a single trial; however, red drum were used twice. We ensured that all predators started at a similar satiation level by starving the red drum and pinfish for 24

hrs prior to each trial. Finally, prey items were stocked first and allowed for acclimate for several minutes before the introduction of a predator. At the conclusion of each trial, tanks were drained, animals enumerated and a new trial was initiated. A total of 10 replicates were conducted for each possible combination of animals and ASUs.

Statistical analysis was completed using a 2-way analysis of covariance (ANCOVA) to examine the relationship between size/shape and mortality. Due to the failure of the mortality data to fit the assumptions of ANCOVA, the data was transformed using a  $\log(x+1)$  transformation. Because of unanticipated temperature changes during the course of the experiment, we used temperature as a covariate. To examine the relationship between mortality and perimeter, area, perimeter + area, and perimeter:area ratios, we utilized stepwise linear regression techniques (SPSS, version 11.0).

Regressions were carried out for each animal for the entire data set, as well as under each arrangement of possible predator/prey items. Finally, we examined how the presence of a prey item or the presence of a predator influences mortality using an ANCOVA with mortality being the dependent variable, trophic structure as independent variable, and temperature as a covariate. All relationships were considered significant at the  $p < 0.05$  level.

To examine the effects of patch shape, patch size, and trophic structure on habitat selection, we used a large, 10 tank mesocosm set up similar to the previous experiment; however, during this experiment, tanks were held stagnant during the 24 hr. trial with a single air stone hanging in the middle along the western edge of the tank. Each tank was 2.3 x 0.45 x 1 m in size and had drains with stoppers at each end of the tank. In addition, each tank had a small "track" located in the center of each tank that allowed a 3 mm PVC



divider to be placed, dividing the tank in two equal sections. Prior to every trial, each tank was filled to a depth of 45 cm with fresh seawater. We conducted 10 trials of each combination of ASUs and organisms (Table 1) along with 5 controls with only a single species present, for a total of 330 trials. ASUs were held in place using six- 4oz lead weights. Each trial lasted 24 hours and animals and ASU layout was completely randomized for day, treatment, and “in tank” ASU configuration.

Similar to the previous experiment, we used red drum, pinfish, and grass shrimp to represent a common Gulf of Mexico food web. Thirty five red drum used during our previous predation experiment were retained for this experiment. These fish had a mean  $\pm$  S.D. standard length of  $43.3 \pm 2.7$  cm. In addition, mean  $\pm$  S.D. pinfish standard length was  $4.3 \pm 0.6$  cm and all grass shrimp were adults in excess of 1 cm carapace length. All animals were captured in the previously described manner. Red drum, pinfish, and grass shrimp were stocked at a density of 1, 6, and 1500 organisms/m<sup>2</sup>, respectively. To reduce the possibility of intra-tank predation, all animals were fed to satiation prior to the initiation of each trial.

Statistical analysis of the impact of trophic level on habitat preference was carried out using a method adopted from Peterson and Renaud (1989). Because two habitats in the same tank are not independent and have correlated error rates, comparing these habitats *per se* does not meet the independence assumption of ANOVA; however, the (Peterson and Renaud, 1989) method results in a single value that satisfies this assumption. This method measures the change in preference by comparing the difference in organism density between habitats under multiple trophic levels to differences under control situations. To facilitate comparison between habitats, organism densities were

reported on a per m<sup>2</sup> basis. In addition, habitat preference data was transformed to meet the normality and variance assumptions using a  $x = 2 \arcsin \sqrt{p}$  transformation. Using an ANOVA approach, we made all pair-wise comparisons of habitat preference for each species under each habitat configuration and every trophic level configuration. We also used a stepwise regression analysis to examine the relationship between perimeter, area, perimeter + area, and perimeter:area ratios for the habitat preferences of grass shrimp and pinfish when exposed to different trophic levels.

For red drum treatments, our use of a single red drum in any given treatment resulted in data that did not meet the assumptions of ANOVA testing. Because further transformations failed to resolve the problem, we made all pair-wise comparisons of trophic levels for each ASU combination using a Mann-Whitney U nonparametric test. In lieu of using a stepwise linear regression to examine the relationship between perimeter, area, and P/A ratios, we used a Kruskal-Wallis nonparametric test. All relationships were considered significant at the  $p < 0.05$  level.

## Results

In the predation experiments, mean mortality for pinfish ranged between 0% and 11% (Figure 1) and grass shrimp mortality ranged between 3% and 25% (Figure 1). Patch size and patch shape played a minor role in the amount of mortality experienced by pinfish when in the presence of a red drum predator or when both predator and prey were present. Our ASU shaped as a large circle was the only ASU to have predation occur under both trophic scenarios (Figure 1). Our analyses indicated that whether the data were handled as a whole (combined all trophic levels), or individually (separate trophic levels), none of our ANCOVA results comparing patch size and shape were significant.

On the other hand, grass shrimp mortality occurred on every ASU, regardless of treatment (Figure 2). When a single predator was present, pinfish consumed more grass shrimp in the large circle, large stellate, and small stellate ASUs; however, these results were not significant. With all three trophic levels present, there was significantly more grass shrimp predation ( $df=1$ ,  $f=6.08$ ,  $p=0.019$ ) on the smaller habitats compared to the larger habitats. Predation on the small ASUs ranged between ~3% and ~10%, while on the larger ASUs, predation was between ~13% and 26%. When we examined the entire data set (all three trophic level data sets combined) for the influence of patch size and shape, there was a significant interaction between size and shape ( $df=1$ ,  $f=4.607$ ,  $p=0.034$ ), indicating that grass shrimp mortality was not consistently influenced by patch size or patch shape.

Stepwise regression analysis of perimeter, area, perimeter:area ratio, and perimeter + area, yielded few significant relationships, regardless of prey item or predators (Table 2). Pinfish, patch perimeter and area measurements were not significant whether there was a red drum predator or both a predator and grass shrimp present. In addition, when the data was examined without respect to trophic level, the results were still non-significant. On the other hand, area and P/A ratios did influence grass shrimp mortality when predation was due to multiple predators. These relationships each explained ~12% of the variance in the models; however, the relationship between area and mortality was slightly negative and the relationship with P/A ratios was slightly positive (Table 2). When the entire grass shrimp data set was combined, there were no significant relationships between any of the independent variables and mortality.

In our habitat preference experiments, there were no clearly discernable trends relating to patch shape and size. Grass shrimp, when tested alone, were more abundant in the smaller habitats than in the larger habitats in three of the four sets of experiments that contained both large and small habitats. However, when presented with the large stellate and small stellate habitats, grass shrimp were found at a higher density in the larger habitat (Figure 3). For grass shrimp, when a single predator was present, density in any given habitat ranged between 40% and 60%, and often the values are separated by less than the standard error of the analysis. For trials where grass shrimp were presented with two predators, grass shrimp were found in higher densities in larger habitats for the large stellate-small circle and the large circle-small circle treatments. In the trials with either two large or two small habitats, mean grass shrimp densities were higher in the stellate shapes. When confronted with predation, grass shrimp altered their habitat preference in 8 of 18 pair-wise comparisons (Table 3). However, in habitats where both ASUs were the same shape, there was no statistical change between grass shrimp alone and grass shrimp with predators. The only noteworthy result was that when confronted with two predators with habitats of varying size, there was a significant shift in habitat preference. This shift, however, was not consistent. The large stellate (65% to 35%)-small circle (35% to 65%) and the large stellate (28% to 62%)-small stellate (72% to 38%) treatments saw a shift in habitat preference, while the large circle-small stellate and large stellate-small stellate treatments saw preferences change from higher densities in the larger habitats to both habitats having approximately 50% of the animals.

Habitat selection by pinfish varied greatly depending on habitats present and the presence of other trophic levels (Figure 4). When presented with two habitats of the

same shape but varying in size, more pinfish were present in the larger habitats when unthreatened by predation. This trend continued for fish in the large circle-small circle treatment, but did not hold true in the large stellate-small stellate treatments after a predator or predator/prey was introduced. For treatments with same sized ASUs, mean  $\pm$  SE habitat preference hovered close to 50% regardless of the trophic structure; while habitat that varied by shape and size, with the introduction of a predator, habitat preference moved towards the larger habitats (Figure 4). Pair-wise comparisons of changes in habitat preference, as related to trophic structure, indicated statistical differences in three of 36 comparisons (Table 3). Each of the differences was in treatments where ASU size was the only varying parameter of habitat structure.

For red drum, habitat preference also varied based on habitat and trophic level (Figure 5). In habitats where ASUs varied by both size and shape (Figure 5 top row), red drum were found in the larger habitats. In habitats where shape was the only variable (Figure 5 middle row), red drum were found more often the circular ASUs. When presented with ASUs that varied by size (Figure 5 bottom row), red drum were not found in any particular habitat. Pair-wise comparisons indicated no statistical differences between red drum habitat preference and the number of trophic levels present (Table 3).

To examine the role that perimeter and area have in influencing habitat preference, we combined each of the data sets for all three animals at each trophic level and examined them strictly on how they related to perimeter, area, P/A ratios, and perimeter + area (Figure 6). Our step-wise regression analysis resulted in multiple significant relationships for grass shrimp (Table 4). While in a treatment without predators, grass shrimp density often had a negative relationship with perimeter and area,

and a positive relationship with P/A ratios. These models explained 17%, 51%, and 35% of the variance in the data, respectively. When red drum were present, grass shrimp had a generally positive relationship with perimeter and area and a negative relationship with P/A ratios. However, for grass shrimp, examination of the entire data set as a whole did not result in any significant relationships in any of the models.

For our pinfish data set, regression analysis indicated significant, usually positive, relationships between perimeter and area when pinfish were held by themselves and also when both a predator and a prey items are present (Table 4). For P/A ratios, there was also a significant positive relationship with pinfish density when both grass shrimp and red drum were present. In addition, when the entire data set was combined, there was a significant negative relationship between P/A ratios and pinfish densities.

For red drum, our analysis of the role that patch shape and size plays on the habitat preference of red drum resulted in no significant relationships between habitat preference and perimeter, area, or P/A ratios (Table 4). In addition, there were no significant relationships in the RD+GS, RD+PF, or RD+PF+GS treatments between perimeter, area, or P/A ratios and habitat selection.

## **Discussion**

Habitat fragmentation is a complex issue that can be influenced by many environmental factors. In fragmented seagrass meadows, patch size, patch shape, habitat complexity, scale, and proximity to patch edge can each influence species interactions (Irlandi, 1996, 1997; Eggleston et al., 1998; Eggleston et al., 1999; Bell et al., 2001). In addition, under normal field conditions, patch size and habitat complexity often co-vary (Irlandi et al., 1995). Complex habitats can also support greater organism diversity,

abundances, and result in decreased predation (Heck and Orth, 1980; Bartholomew et al., 2000; Heck and Orth, in press), making discrimination of potential impacts of habitat fragmentation difficult. Our use of artificial seagrass units eliminated covariance between habitat complexity and patch characteristics and allowed us to discern the role that patch size and patch shape had on predation and habitat selection without undue influence from co-varying biotic factors. At the scale of our experiment ( $0.04\text{m}^2$ - $0.2\text{m}^2$ ), neither grass shrimp, pinfish, or red drum acted in a consistent manner in selecting habitats or engaging in predation while residing in habitats that varied by size and shape; however, the number of trophic levels in the experiment was much more influential than we expected. To date, these are the only experiments we are aware of to carry out this type experiment under controlled mesocosm conditions.

Regardless of habitat, pinfish mortality in this experiment was minimal; suggesting patch size and shape had little influence over predation of red drum on pinfish. Because predation did occur, we feel that our smallest ASU treatments were ample habitat to allow pinfish to successfully avoid predation by red drum rather than an artifact of red drum not actively feeding or a lack of suitable structure. Predation is often lower in complex habitats than on unstructured substrates (Hovel and Lipcius, 2001; Stunz and Minello, 2001; Adams et al., 2004; Talman et al., 2004); and that sometimes a threshold level of complexity may be required for effective protection from predators (Crowder and Cooper, 1979; Heck and Orth, 1980). In an unpublished pilot study we conducted, pinfish without ASU habitats were consumed in a matter of minutes, suggesting the complexity of our habitats was above any possible threshold. The only consistent predation by red drum on pinfish was within the large circular ASU habitats;

however, predation rates were very low ( $\bar{x} = 5\%$ ) and statistically non-significant from any other habitat. Linear regression analysis revealed no relevant relationships between perimeter and area, reinforcing a decreased influence of patch size and patch shape on predation rates of pinfish by red drum.

Examining pinfish predation from the perspective of increasing habitat structure, there was a shift from predation within the large circular and small stellate habitats to predation within the large circular and large stellate habitats. This translates to a positive relationship between the amount of habitat and red drum predation rates upon pinfish; however, this trend was not identified as significant in our regression analysis of the complete predation data set (see Table 2). Our findings run concurrent to recent literature suggesting that predation is inversely related to the amount of habitat present within an environment (Crowder and Cooper, 1979; Heck and Orth, 1980; Nelson and Bonsdorff, 1990; Micheli, 1996; Hovel and Lipcius, 2001). We believe this positive relationship between predation and the amount of habitat may be an artifact of low predation rates. As such, these results must be interpreted cautiously.

Grass shrimp mortality rates also varied greatly depending on habitat; however, patch size was significantly greater in the smaller ASUs compared to the larger ASU. This occurred when pinfish and redfish were each present in the system; however, the impact of two predators on grass shrimp mortality was non-additive (Gonzalez and Tessier, 1997). In addition, when both predators were present, there was a significant negative relationship between area and grass shrimp mortality and a positive relationship between P/A ratios and grass shrimp mortality (Table 2). Albeit, the  $r^2$  values of these regressions were low ( $\sim 0.12$ ); however, the relationships were significant none the less.



This increase of grass shrimp predation in smaller habitats may be due to the influence of a predator (red drum) altering the behavior of the prey (pinfish), resulting in an increase in the amount of time spent by both pinfish and grass shrimp co-inhabiting a single habitat. Behavior modification of pinfish (Jordan F., 1996), as well as other predator/prey items within multiple trophic levels is not uncommon (Soluk, 1993; Gonzalez and Tessier, 1997; Peckarsky and McIntosh, 1998) and may very well be occurring under these conditions.

Results from our second set of experiments suggest that patch size and shape may play a role in habitat selection; however, we believe that trophic structure also plays an important part in determining habitat selection as it relates to different habitats, especially for lower trophic levels. Although not always significant, in each trial with two different sized ASUs, there is a marked change in habitat preference for grass shrimp once a potential predator is introduced (Figure 3, Table3). Without predator influence, perimeter, area, and P/A ratios explain 17, 51, and 35% of the variance in our regression models. Perimeter and area each have a negative relationship with grass shrimp density, while P/A ratios have a positive relationship. This runs concurrent to other studies examining grass shrimp (*Palaemonetes* and *Hippolytidae* spp.) colonization within other seagrass habitats (Eggleston et al., 1998; Eggleston et al., 1999), but in each of these studies the experiments were carried out within seagrass meadows and not under controlled mesocosm conditions. Our regression analysis of grass shrimp habitat selection with one and two additional trophic levels did, however, agree with the findings of these previous studies. When pinfish were added with the grass shrimp, there were no longer any significant relationships; however, when red drum alone and when both red

drum and pinfish were added, significant relationships became evident, positive for perimeter and area, and negative for P/A ratios.

For pinfish and red drum, the impact of patch size and shape was less than that of grass shrimp. In individual mesocosm treatments, neither pinfish nor red drum showed any appreciable shifts in habitat preference. After combining all mesocosm treatments, pinfish showed a significant positive relationship while in treatments without any other trophic level and when in treatments with both red drum and grass shrimp. Red drum, did not have any significant relationships relating to patch size or shape; however, like the grass shrimp treatments, trophic structure did influence pinfish behavior. The apparent decline in the importance of trophic structure and patch dynamics may be attributed to the shift in "grain" (Kotliar and Weins, 1990) from smaller to larger animals. That is, larger animals may view a mosaic of habitats as a single habitat, while smaller animals may see this same mosaic as collection of many smaller, unique habitats (Kotliar and Weins, 1990; Gunther, 1992). For red drum used in this experiment, the overall scale of the experiment was probably below the grain of these fish: that is, at this scale, red drum functionally perceived both small habitats as a single large habitat with two parts, thus the lack of any significant influence of patch size or shape. The primary role of red drum in the experiment was to act as a predation threat for lower trophic layers; as such, conclusions pertaining to red drum resulting from this data must be interpreted cautiously. Pinfish and grass shrimp, on the other hand, did respond, suggesting that the grain of these fish was correct for the scale of this experiment.

Predation within fragmented seagrass environments has concentrated on easily tethered or sessile organisms (i.e. bivalves and crabs). Irlandi (1999) noted that predation

on juvenile bay scallops (*Argopecten irradians concentricus*) in the fall was greater over a 24-hour period in smaller patches, but over longer time periods, there were no differences among patch sizes. Blue crab survival in a fragmented habitat has shown no relationship (Hovel and Lipcius, 2001; Hovel et al., 2002), had a positive relationship (Hovel, 2003), and a negative relationship (Hovel and Lipcius, 2001) to patch size. Although our organisms were much more mobile (i.e. not tethered) than in previous studies, they do demonstrate the species specific effects that habitat fragmentation can have within an ecosystem. A decline in predation rates of grass shrimp with increasing patch size (when the full suite of organisms are present) suggests that patch size is important; but for pinfish under the same conditions, area does not seem to be critical. We do concede that our "ecosystem" is far from complete and certain limitations that are inherent (i.e. artifacts) with mesocosm studies; however, it does provide valuable information in a manner that has not been utilized in other habitat fragmentation studies.

To our knowledge this is the first attempt to assess the role of fragmentation in habitat preference by organisms. Previous work by other authors (McNeill and Fairweather, 1993; Bologna, 1998; Eggleston et al., 1998; Eggleston et al., 1999; Bologna and Heck, 2000; Bell et al., 2001) have each documented the role of habitat fragmentation on colonization or community structure; however, to this point no attempt has been made to tease apart ecological subtleties associated with community structure. Perimeter and area each have some influence over habitat preference of grass shrimp and pinfish under these conditions. At the most complex trophic design (closest to natural food webs), both pinfish and grass shrimp each show an affinity towards larger patch sizes. For grass shrimp, the decline in predation pressure (Table 2) may explain these

results. Our agreement with Eggleston *et al.* (1998) and Eggleston *et al.*'s (1999) colonization data for grass shrimp suggests that these shrimp may prefer larger habitats rather than densities being controlled by other processes (i.e. predation). For pinfish, the lack of differential predation pressure suggests that habitat preference is ultimately influenced by patch size and shape rather than predation pressure.

The consequences of these results add one more layer to an already complex issue. The possibility that responses to habitat fragmentation (at this scale and without habitat loss) may co-vary with trophic complexity has been ignored and may help explain the large number of inconsistencies within the literature. It is well documented that prey items can influence predator behavior and visa versa (i.e. behavioral cascades) (McCarthy and Dickey, 2002; Pennuto, 2003; Romare and Hansson, 2003; Temming *et al.*, 2004); pinfish and grass shrimp each responded to increasing trophic complexity, while red drum did not. In fifteen publications directly addressing habitat fragmentation or changes in patch configuration within seagrass environments (Irlandi, 1994; Irlandi, 1997; Bologna, 1998; Eggleston *et al.*, 1998; Bologna and Heck, 1999; Eggleston *et al.*, 1999; Irlandi *et al.*, 1999; Bologna and Heck, 2000; Fischer, 2000; Bell *et al.*, 2001; Hovel and Lipcius, 2001; Hovel *et al.*, 2002; Hovel and Lipcius, 2002; Hovel, 2003; Healey and Hovel, In Press), the possibility that trophic structure could explain some degree of variance was never examined. With no empirical testing on the subject, many of these authors bring forth the possibility that differential effects by predators may be influencing their results. Hovel and Lipcius (2001) undertook an extensive survey of the higher order blue crab (*Callinectes sapidus*) predators within the Chesapeake bay, but they only used the numerically dominant predator (large blue crabs) in their analysis. In

addition, their techniques, trawling and suction sampling, are biased against highly mobile predators (i.e. fishes) whose mere presence (although undetected) may exert some influence over lower trophic levels and may help explain some of their temporal variance.

Finally, data from these experiments have demonstrated that habitat fragmentation can influence predation and habitat selection. This response, however, is not consistent across all trophic combinations and because of our mesocosm approach, must be interpreted cautiously. Co-variation of trophic structure and habitat fragmentation in structuring seagrass ecosystems may go a long way to help explain variation in many studies; but on the other hand, this diminishes the possibility that generalities can be drawn about the responses of habitat fragmentation. With only marginal success, most research to date had concentrated on relating macrofaunal organisms in seagrass meadows to biologic descriptors of the grass; however, we suggest that to gain a clearer picture of the mechanics of habitat fragmentation, ecological processes beyond plant features will be required in future research.

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**Table 4.** Results from stepwise linear regressions for grass shrimp and pinfish and Kruskal-Wallis tests for red drum habitat selection experiments. Perimeter, area, P/A ratio, and perimeter + area were independent variables. Results were considered significant at  $p < 0.05$ . Treatment descriptors are as follows: GS=grass shrimp, PF=pinfish, RD=red drum.

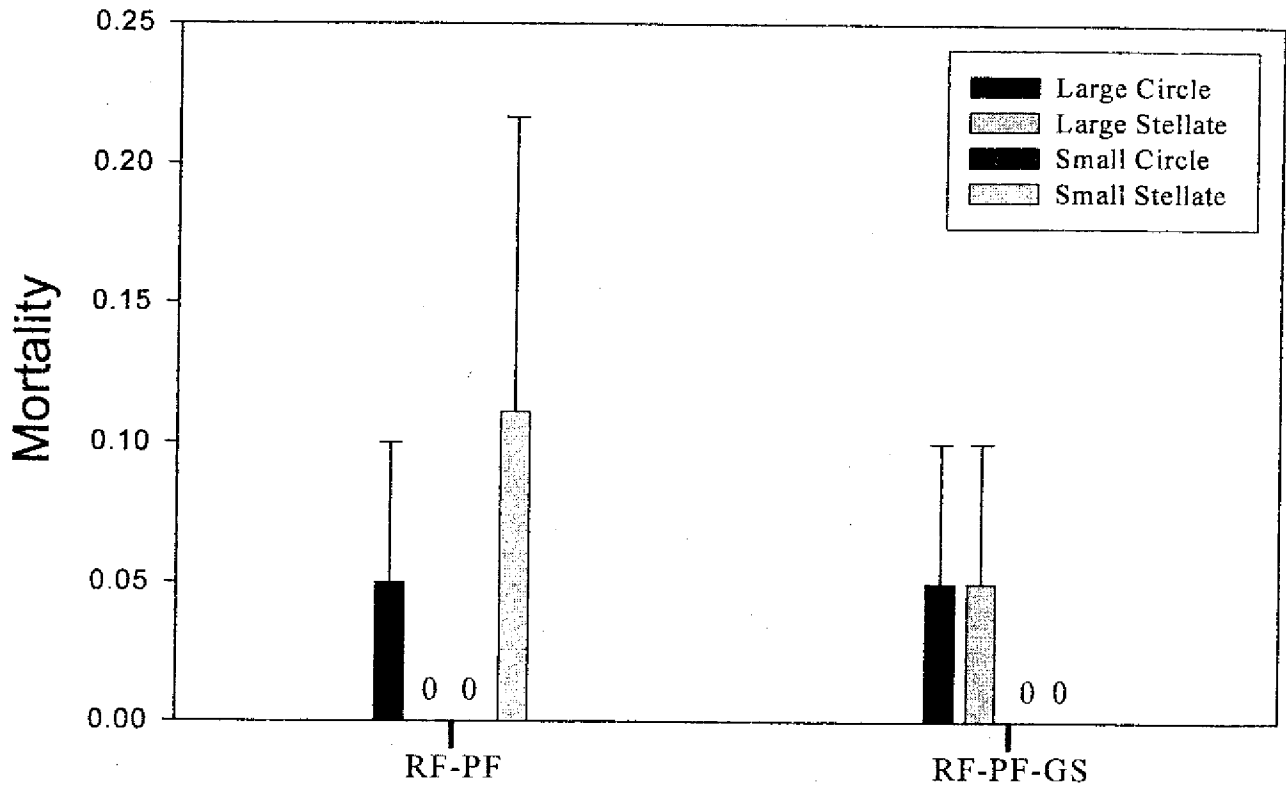
Grass Shrimp	Perimeter			Area			Perimeter/Area Ratio			Perimeter ( $\beta_1$ ) and Area ( $\beta_2$ )			
	p-value	$r^2$	$\beta_1$	p-value	$r^2$	$\beta_1$	p-value	$r^2$	$\beta_1$	p-value	$r^2$	$\beta_1$	$\beta_2$
GS	<0.001	0.17	-0.1	<0.001	0.51	-1.04	<0.001	0.35	0.014	<0.001	0.51	Excluded	-1.04
PF-GS		NS			NS			NS				NS	
RD-PF	0.01	0.06	0.04	0.034	0.04	0.441		NS		0.034	0.04	Excluded	0.441
RD-PF-GS	0.02	0.05	0.005	<0.001	0.14	1.09	<0.001	0.13	-0.007	<0.001	0.14	Excluded	1.092
All Data Combined		NS			NS			NS				NS	

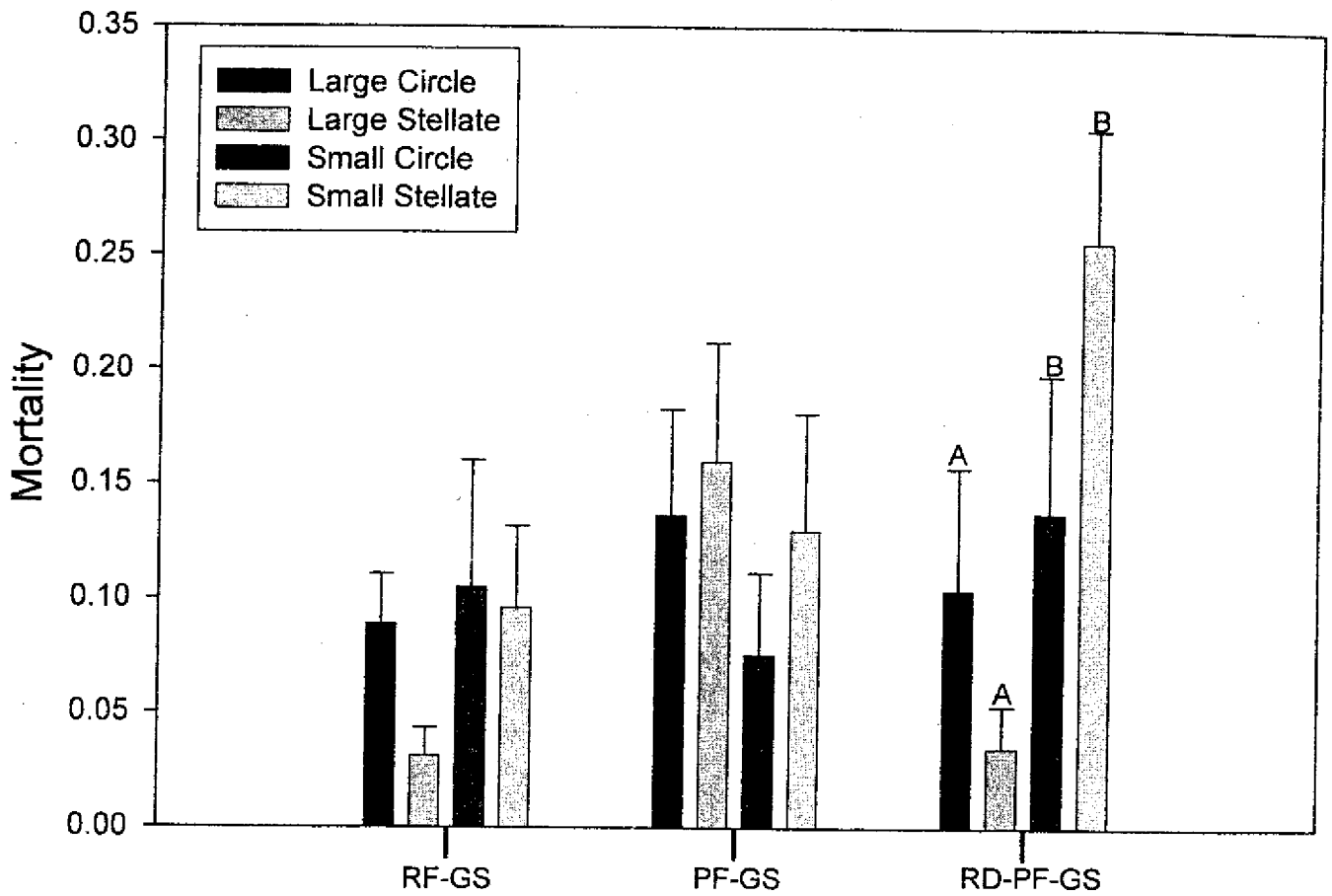
Pinfish	Perimeter			Area			Perimeter/Area Ratio			Perimeter ( $\beta_1$ ) and Area ( $\beta_2$ )			
	p-value	$r^2$	$\beta_1$	p-value	$r^2$	$\beta_1$	p-value	$r^2$	$\beta_1$	p-value	$r^2$	$\beta_1$	$\beta_2$
PF	0.11	0.107	0.165	0.001	0.179	2.484		NS		0.001	0.179	Excluded	2.484
PF-GS		NS			NS			NS				NS	
RD-PF		NS			NS			NS				NS	
RD-PF-GS	0.001	0.097	0.13	0.018	0.048	0.005	<0.001	0.14	1.09	<0.001	0.16	0.14	0.006
All Data Combined		NS			NS		0.025	0.013	-0.004			NS	

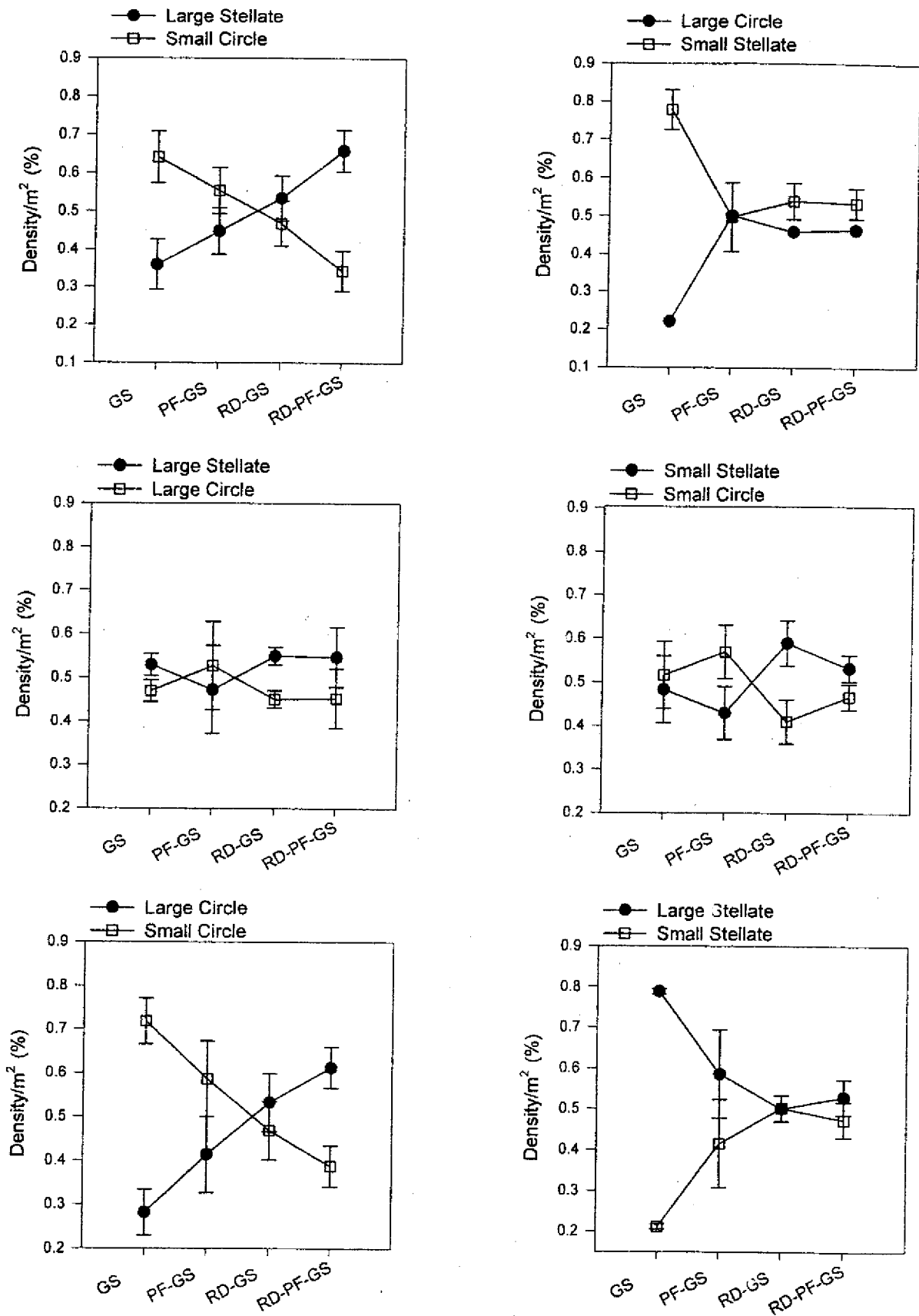
Red Drum	Perimeter		Area		Perimeter/Area Ratio	
	p-value		p-value		p-value	
RD	NS		NS		NS	
RD-GS	NS		NS		NS	
RD-PF	NS		NS		NS	
RD-PF-GS	NS		NS		NS	
All Data Combined	NS		NS		NS	



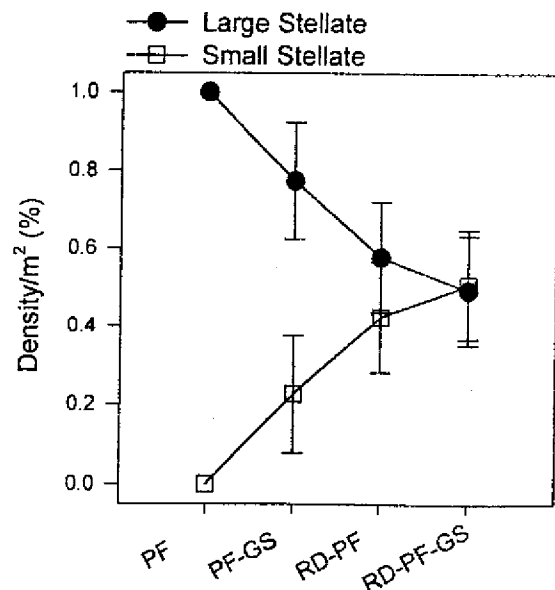
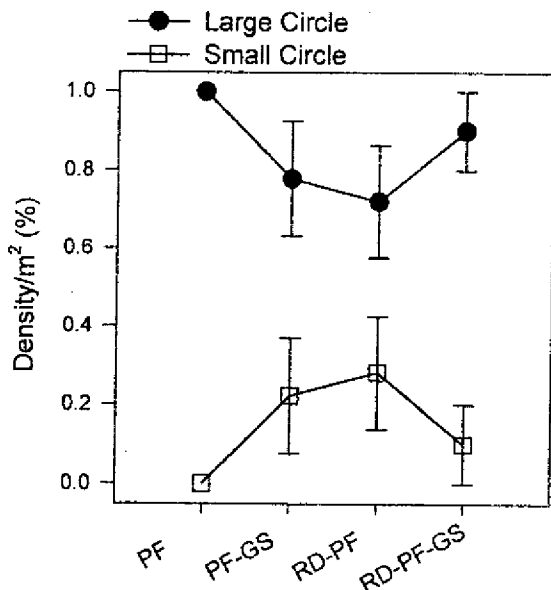
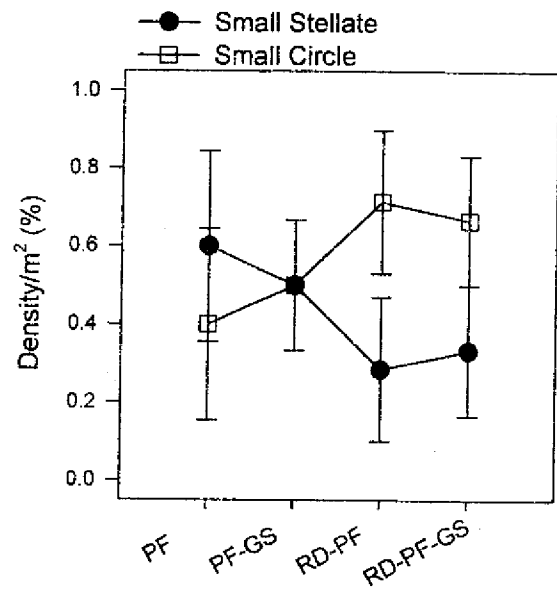
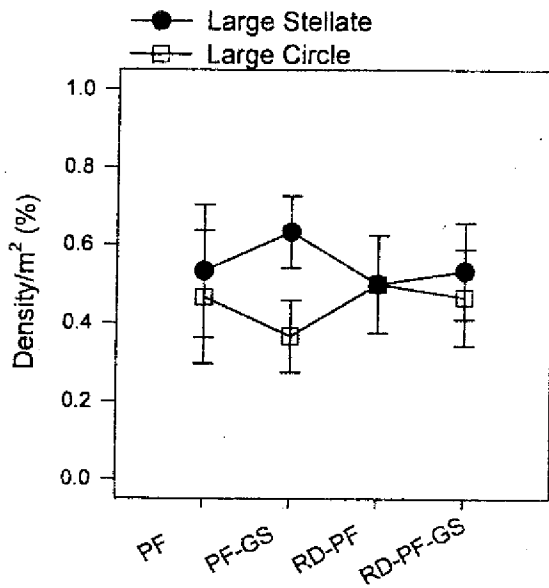
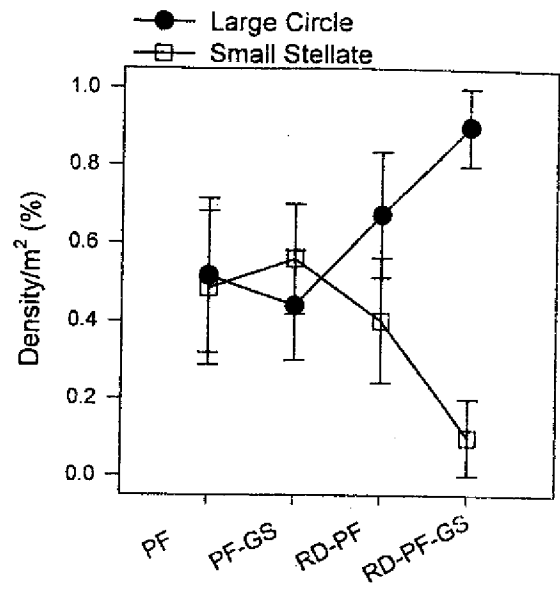
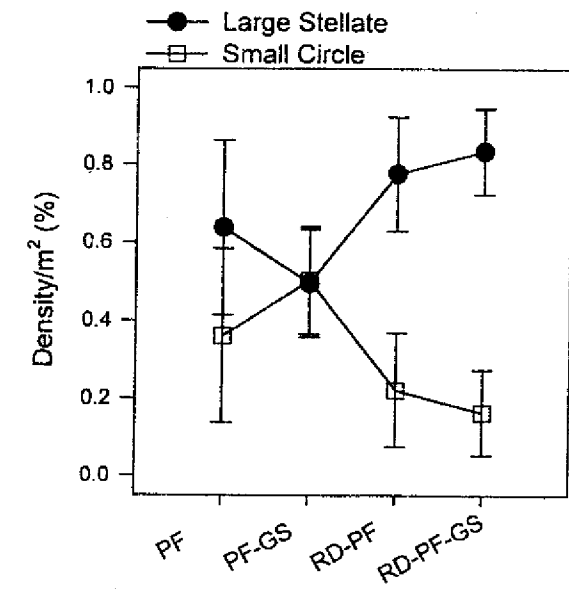
**Figure 1.** Mean  $\pm$  S.E. pinfish mortality during 24-hour mesocosm trials. Results were considered significant at  $p < 0.05$ . Treatment descriptors are as follows: GS=grass shrimp, PF= pinfish, RD=red drum.



**Figure 2.** Mean  $\pm$  S.E. grass shrimp mortality during 24-hour mesocosm trials. Results were considered significant at  $p < 0.05$ . Treatment descriptors are as follows: GS=grass shrimp, PF= pinfish, RD=red drum.

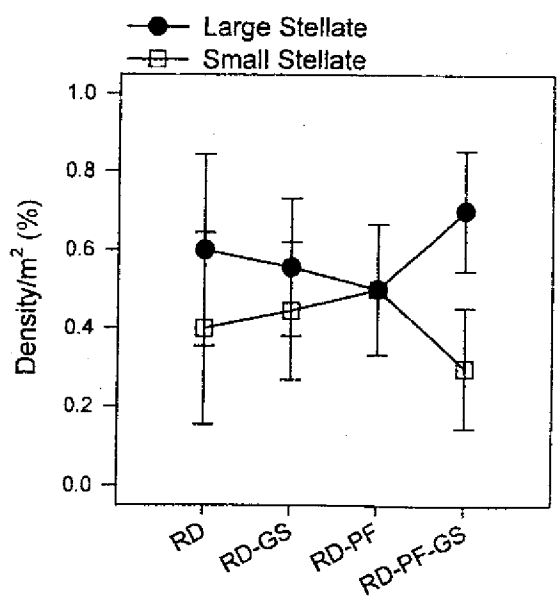
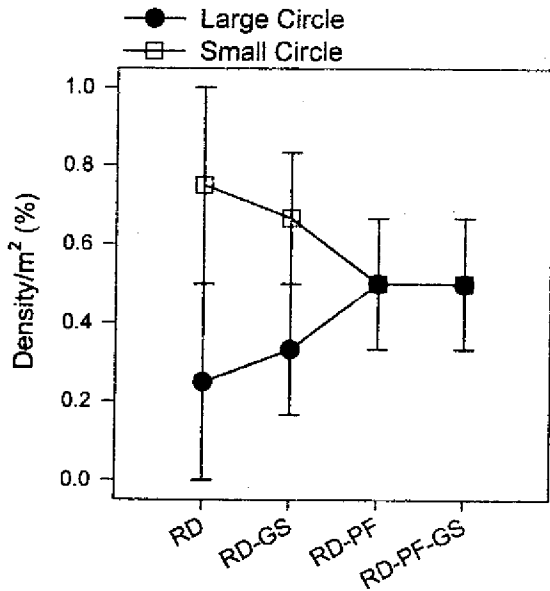
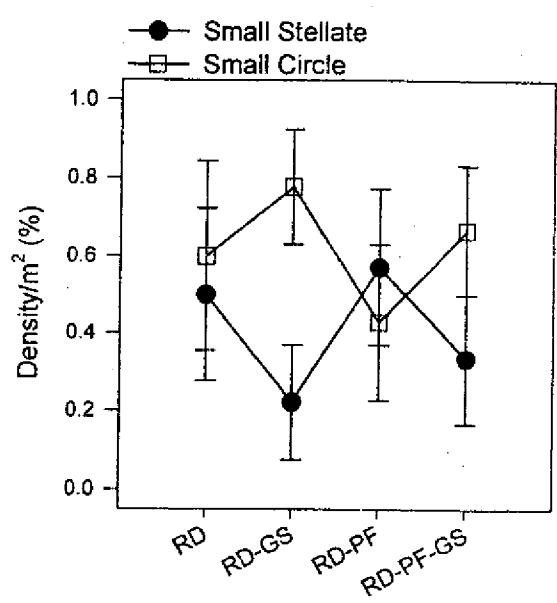
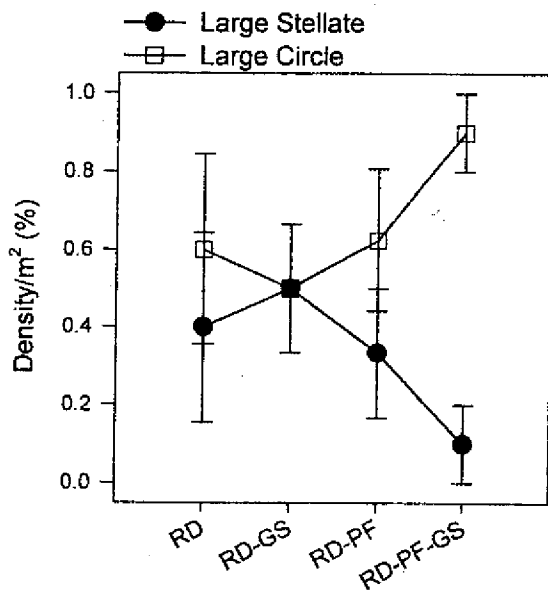
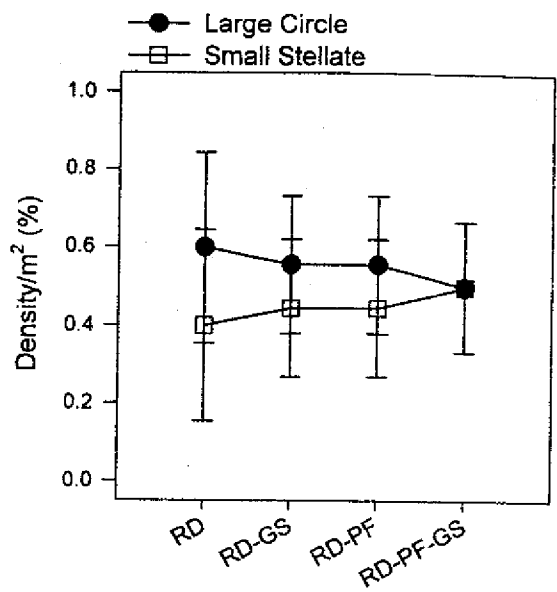
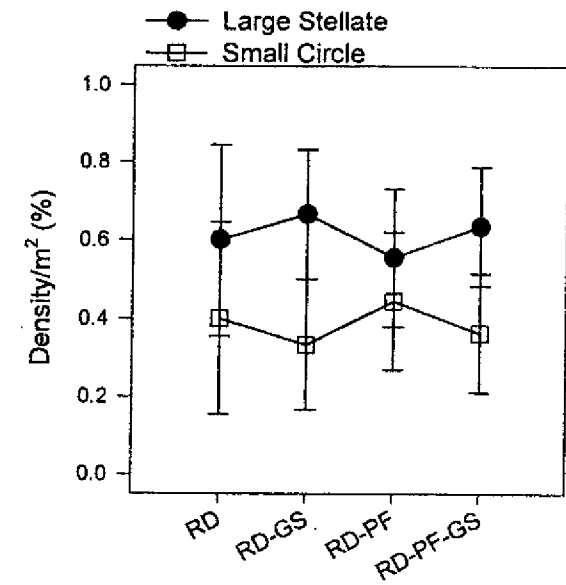


**Figure 3.** Habitat selection, reported as mean density/m<sup>2</sup> ± S.E., for grass shrimp mesocosm experiments. Treatment descriptors are as follows: GS=grass shrimp, PF= pinfish, RD=red drum.

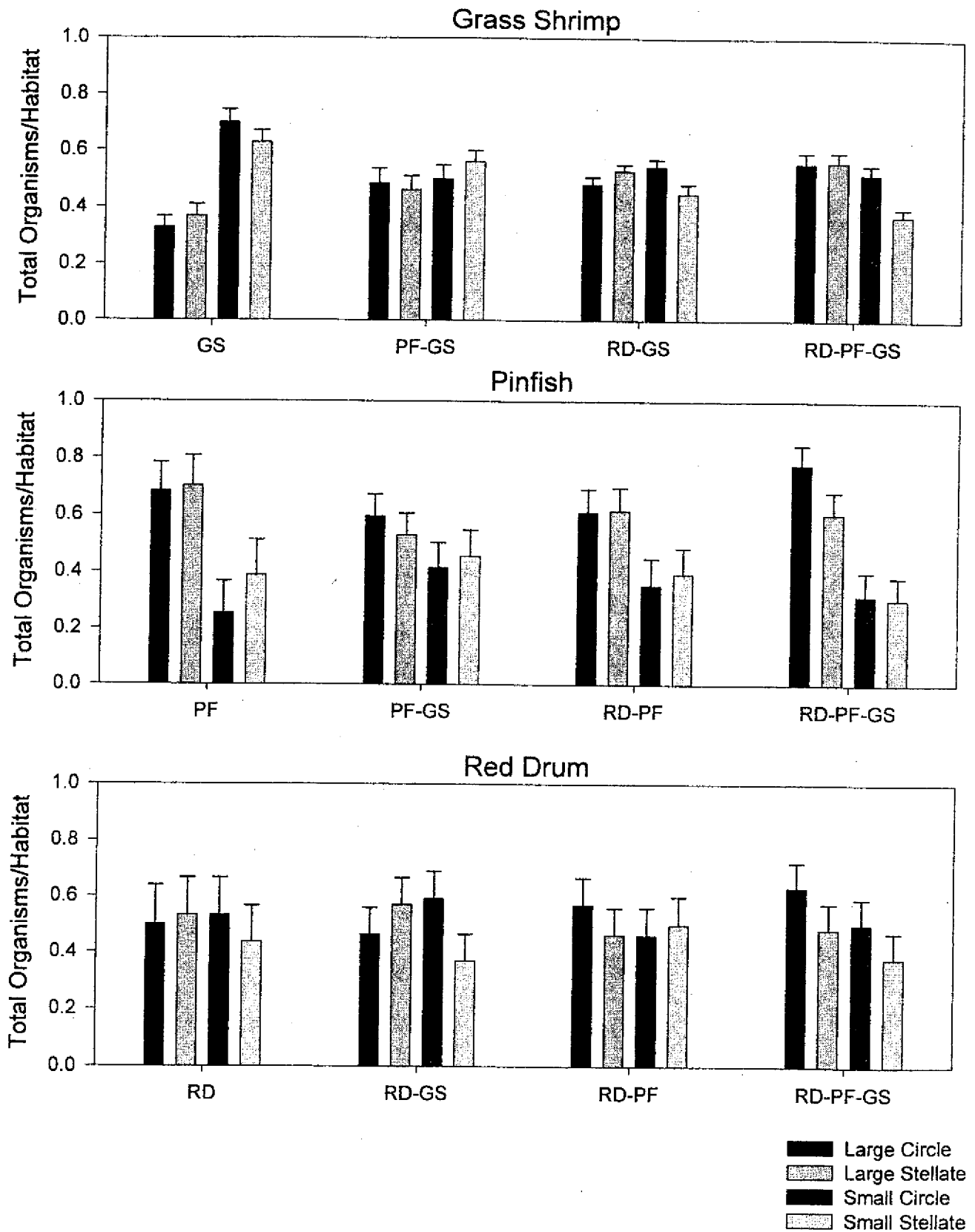


**Figure 4.** Habitat selection, reported as mean density/m<sup>2</sup> ± S.E., for pinfish mesocosm experiments. Treatment descriptors are as follows: GS=grass shrimp, PF= pinfish, RD=red drum.





**Figure 5.** Habitat selection, reported as mean density/m<sup>2</sup> ± S.E., for red drum mesocosm experiments. Treatment descriptors are as follows: GS=grass shrimp, PF=pinfish, RD=red drum.



**Figure 6.** Mean  $\pm$  S.E. total number of organisms found per habitat during habitat selection experiments. Treatment descriptors are as follows: GS=grass shrimp, PF= pinfish, RD=red drum.