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Seagrass Patch Characteristics Alter Direct and Indirect Interactions in a Tritrophic Estuarine Food Web

MATTHEW W. JOHNSON[1,*] and KENNETH L. HECK JR.[2]

[1] *Marine Environmental Science Consortium, Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528*
[2] *University of South Alabama, Department of Marine Sciences, LCSB 25, Mobile, Alabama 36688*

ABSTRACT: We used a mesocosm approach to examine how patch characteristics influenced predation and habitat selection in a tritrophic food web. Our experiments included juvenile red drum (*Sciaenops ocellatus*; RD), juvenile pinfish (*Lagodon rhomboides*; PF), and grass shrimp (*Palaemonetes* sp.; GS), members of a food web common in seagrass meadows of the northern Gulf of Mexico. We added an additional level of complexity to the experiment by including a predator that could feed at two different trophic levels. RD were top predators, PF were both prey items for RD and predators of GS, and GS were prey for RD and PF. We used 4 different artificial seagrass habitats that varied by size (0.049 and 0.203 m^2) and shape (circular and stellate) to control for covariation between patch size and seagrass density. Predation on GS was measured in each habitat when PF, RD, and PF+RD were present, and predation on PF was measured when RD and RD+GS were present. Habitat selection by each of these 3 species was measured individually and in the presence of every other combination of the 3 species. Neither predation nor habitat selection were consistently influenced by patch characteristics (size, shape, or perimeter:area ratios) or the number of trophic levels. For GS, there was a significant negative relationship between patch size and predation rates in the GS+PF+RD treatment. Habitat selection by GS without the threat of predation suggested a preference for smaller habitats, but when in the presences of RD or RD+PF, GS preferred larger habitats. In predation experiments, PF predation by RD showed no significant relationships with patch characteristics or trophic structure. For our habitat selection experiments, PF preference was for larger habitats in the PF only and GS+PF+RD treatments. There were no significant relationships between patch size, shape, or trophic structure and RD habitat selection.

Introduction

Direct effects by predators have been well studied and are often easy to identify (Luttbeg et al. 2003). The introduction of a predator can suppress the number of prey present in a system (McIntosh and Townsend 1996). Indirect effects can often occur in trophic cascades and the effects can be evident to the resource level (i.e., 3 level trophic cascade: predator–prey–resource) and be difficult to discern (Peacor and Werner 2001). Indirect effects at the resource level are possible through two pathways, density-mediated indirect interactions (DMII) and trait-mediated indirect interactions (TMII; Miller and Kerfoot 1987). DMIIs occur when a prey's resources are released due to the loss of prey to predators. TMIIs occur when a predator triggers a change in the behavior or morphology of its prey, resulting in effects that cascade down to the prey's resources (Abrams 1995). The incidence of TMIIs increases relative to the amount of DMIIs as the level of resource increases (Luttbeg et al. 2003). Both types of indirect interactions have been well studied, with examples being found in many marine, freshwater, and terrestrial systems (Dill et al. 2003; Luttbeg et al. 2003; Trussell et al. 2004; Vance Chalcraft et al. 2004).

Of the studies that have examined these relationships, the configuration of habitats can be influential on indirect interactions. According to Ikeda and Nakasuji (2002), the leaf beetle (*Galerucella nipponensis*) had a higher survival rate in the presence of predatory water striders (*Gerris nepalensis*) when rosettes of a host plant (*Trapa japonica*) grow vertically in the water column rather than horizontally on the water's surface, and female leaf beetles preferentially deposited eggs on these vertically growing rosettes. Grabowski (2004) and Grabowski and Kimbro (2005) found that oyster reefs that provided physical relief and complexity altered the predation rate of mud crabs (*Panopeus herbstii*) on juvenile oysters (*Crassostrea virginica*) and hard clams (*Mercenaria mercenaria*) in the presence of a predation threat by toadfish (*Opsanus tau*).

Seagrasses play a critical role in the life histories of many aquatic species (Bell et al. 1987; Boström 2001; Heck et al. 2003). Despite their importance in coastal waters, seagrass meadows continue to decline worldwide, owing to a myriad of natural and anthropogenic factors (Durako 1994; Duarte 1995; Short and Wyllie-Echeverria 1996; Koch and Gust 1999; Eckrich and Holmquist 2000). The result is

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* Corresponding author; current address: Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528; tele: 251/861-7551; fax: 251/861-7540; e-mail: mjohnson@disl.org

the breakup of once continuous seagrass meadows into smaller functional units (Fonseca and Bell 1998; Seddon et al. 2000). This can produce shifts in seagrass patch size, patch shape, and patch perimeter : area (P : A) ratio (i.e., the amount of edge present; see Schumaker [1996] for complete discussion). Restoration efforts for seagrasses often result in a mosaic of seagrass patches that may ultimately coalesce (Fonseca 1993; Fonseca et al. 1998). The presence of smaller patches and increased edge may influence water flow as well as faunal abundance and biological interactions (Fonseca et al. 1982; Keough 1984; Irlandi 1997; Bologna and Heck 2000; Caley et al. 2001), yet, little is known about how the alteration of seagrass landscapes may influence direct and indirect interactions between trophic levels.

Previous experiments examining the roles of seagrass patch size and shape relied heavily on the species-area concept and found that unlike terrestrial environments, larger areas often did not support more species in marine environments (McNeill and Fairweather 1993; Bologna 1998). Studies of bivalves have shown that settlement can occur in greater quantity on patches with increased P : A ratios (Bologna and Heck 2000), but survival of juvenile bay scallops (*Argopecten irradians concentricus*) may not be related to perimeter (Irlandi et al. 1999). For studies where grass shrimp (*Palaemonetes* sp.) and blue crabs (*Callinectes sapidus*) were examined together, grass shrimp were more abundant in smaller patches and blue crabs were more abundant in larger patches (Eggleston et al. 1998). Neither Bell et al. (2001) nor Johnson and Heck (2006) found similar relationships between blue crabs and grass shrimp.

These prior studies suggest that the effects of changing seagrass patch characteristics in marine habitats are more complicated than previously expected. Experiments have been conducted primarily in situ and were influenced by many variables (including trophic structure) that fluctuate spatially and temporally, resulting in data that are unique to a particular time. The number of predators in estuarine habitats is often underestimated (Sheaves 2001), and the threat of an unknown predator could trigger behavioral responses in fishes and decapods that may affect community structure and habitat selection (McCarthy and Dickey 2002; Magoulick 2004; Trussell et al. 2004). The presence of one or more predators in the immediate vicinity or far removed (i.e., up-current) from seagrass meadows may have a substantial effect on their inhabitants. Although strong arguments have been made that inconsistencies in fragmentation research have been due to differential effects of predators (Irlandi et al. 1995; Bologna 1998), no research has separated the consequences of variable trophic structure from the consequences of variable patch characteristics.

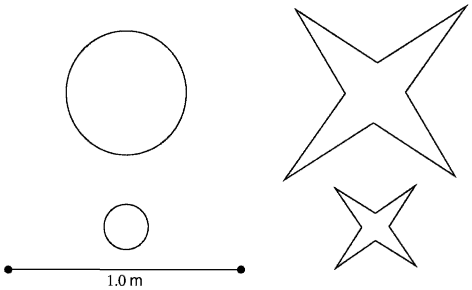
We experimentally tested if changes in seagrass patch size and shape altered the direct and indirect interactions in a tritrophic food chain consisting of red drum (*Sciaenops ocellatus*), pinfish (*Lagodon rhomboides*), and grass shrimp (*Palaemonetes* sp.). We examined predation on pinfish (by red drum) and grass shrimp (by red drum and pinfish) in four different habitats that varied by shape and size. We predicted that the direct interactions between species would result in a greater increase in the overall predation rates in the smaller habitats and the habitats with increased amounts of perimeter. If DMIIs were present, we expected that increased predation on pinfish by red drum would release grass shrimp from predation and enhance their survival. If TMIIs were operating, the presence of a red drum predator could either force pinfish into the seagrass refuges, increasing the number of interactions between pinfish and grass shrimp and resulting in an increased amount of predation of grass shrimp. In this scenario, larger seagrass patches may ultimately be beneficial for grass shrimp survival due to the increased amount of refuge. Forcing of pinfish into the structurally complex seagrass could alternatively decrease the ability of pinfish to forage effectively, ultimately enhancing grass shrimp survival in the presence of red drum. If this is the case, then the effects of patch characteristics would be similar to those that grass shrimp experience when a red drum is the only predator present.

We also examined how the threat of predation influenced habitat selection by testing every possible combination of our tritrophic food chain with each possible pairing of our refuge habitats (artificial seagrass units or ASUs), and recording the seagrass patch with which each of the taxa were associated (in or around ASU) after 24 h. We predicted that the direct interactions (DMIIs) between red drum and pinfish would result in more grass shrimp being collected in the larger habitats due to a decrease in predation pressure. For the indirect interactions (DMIIs and TMIIs), we expected that grass shrimp would prefer larger habitats and habitats with increased amounts of interior, regardless of pinfish behavior while in the presence of red drum.

Methods

PREDATION

To determine if patch size and shape influenced predation through direct and indirect interactions, we used a large flow-through mesocosm system consisting of ten, 1-m^3 tanks (2.4 m in length and



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

Fig. 1. Dimensions, area (A), perimeter (P), and P : A ratios of experimental artificial seagrass units (ASU). Orientation of the stellate ASU is similar to the way it was oriented in the mesocosms.

0.4 m in width) with a water depth of approximately 48 cm. Experiments were conducted outdoors during the daylight periods in a shaded wet lab beneath the Auburn Shellfish Laboratory, at the Dauphin Island Sea Lab (DISL), Dauphin Island, Alabama, USA. Seawater for these experiments was pumped from the Gulf of Mexico, along the south shore of the DISL.

A single ASU, mimicking *Halodule wrightii*, a seagrass common to the Gulf of Mexico, was placed in the center of each tank and oriented to allow unfettered movement around the perimeter of the mesocosm without contacting the ASU. ASUs varied in size (0.2036 and 0.0487 m^2) and shape (stellate or circular; Fig. 1) and leaves were made from green polyethylene ribbon attached to Vexar mesh cut to the appropriate shape at a density of 10,000 blades m^{-2} (Stutes 2000). Use of ASUs allowed the elimination of covariance between habitat complexity and patch characteristics that are often seen in naturally fragmented environments (Fonseca and Bell 1998; Hovel et al. 2002). Although seagrasses do not naturally occur in perfect circular or stellate shapes, we used these shapes to maximize patch perimeter, giving us a range of possible P : A ratios. When seagrasses are planted during restoration efforts, small patches of seagrasses, similar to the size of our ASUs, are common (Fonseca 1993; Fonseca et al. 1998). To ensure that our ASU sizes were large enough to provide adequate protection against predation (Crowder and Cooper 1979; Heck and Orth 1980; Bartholomew et al. 2000; Stunz and Minello 2001; Heck and Orth 2006) and that handling did not influence the feeding ability of the predators, we conducted a pilot study to examine the survival times of pinfish and grass shrimp. During these trials, pinfish survival in the presence of multiple red drum increased from <5 min in a bare mesocosm to in excess of 12 h when a square-shaped ASU, approximately the size of our smallest ASU, was placed within the mesocosm. For grass shrimp, survival in the presence of multiple pinfish was 0% after the first few minutes of each trial in a bare mesocosm. After the addition of a small ASU, grass shrimp predation still occurred, but it took more than 12 h for all the shrimp to be consumed.

Use of mesocosms in ecological research should not be without reservations. It is known that mesocosms can alter behavior (Skelly 2002), are often much smaller than natural environments, and restrict organism's movements (Skelly 2002; Ribas et al. 2005). Despite these caveats, mesocosms have been used successfully to measure relative responses among treatments on many occasions (Moksnes et al. 1997; Kneib and Scheele 2000). Although patches smaller than 0.5 m^2 are not normally found in healthy seagrass beds, meadows that have experienced extensive anthropogenic effects (e.g., scarring; Johnson personal observation) or have been recently transplanted commonly consist of patches smaller than 0.5 m^2 (Fonseca 1993). Transplanted seagrasses are often planted as a 10 cm^2 clumps separated from 0.5 to 2 m apart and allowed to coalesce (Fonseca 1993). Under these circumstances, seagrass patch size can be similar to those used in mesocosm studies, allowing for a clearer understanding of the ecological processes at work in seagrass meadows that are in a state of rehabilitation.

We used juvenile red drum, juvenile pinfish, and grass shrimp, because they are common in seagrass habitats throughout the Gulf of Mexico and the southern Atlantic coast of the U.S. (Hoese and Moore 1977; Williams 1984; Swingle 1990; Stunz et al. 1999). Both red drum and pinfish use seagrass beds for settlement, protection, and foraging prior to migration offshore, and grass shrimp spend the warm months foraging on epiphytic algae growing on seagrass blades (Stoner 1980; Bauer 1989; Stunz et al. 1999; Adams et al. 2004). One hundred and fifty juvenile red drum, ranging in size between 30 and 50 cm standard length, with a mean length ± standard deviation (SD) of 39.9 ± 4.7 cm were purchased from a commercial supplier (The Fish Farm, Bacliff, Texas) for this experiment. Pinfish were collected by otter trawl from Big Lagoon, Florida, and ranged in size between 5.9 and 10.4 cm standard length, with a mean of 8.0 ± 0.9 cm. Adult grass shrimp with a carapace length in excess of 1 cm were collected using a beam plankton trawl from Heron Bay Marsh, Alabama Port, Alabama. These three species are hardy and acclimate well to tanks and enclosures (see Coen et al. 1981; Jordan et al. 1997; Rooker et al. 1997; Stunz et al. 1999;

Heck et al. 2000). Although little is known about how these species orient themselves with respect to seagrass patches and edges, smaller juvenile red drum are known to reside preferentially along the edge of seagrass meadows (Holt et al. 1983), while fishes similar to the size we used show little within patch preference (Geraldi unpublished data). Pinfish and grass shrimp have each been observed to forage and reside throughout entire seagrass meadows (Johnson and Heck 2006; Johnson personal observation).

Organisms were allowed to acclimate to a tank environment for a minimum of 24 hours after capture and prior to use. In our trials, red drum (RD), pinfish (PF), and grass shrimp (GS) were each stocked at 1, 6, and 500 animals m^{-2}, respectively, well within reported densities in seagrass meadows (Stunz et al. 1999; Spitzer et al. 2000; Johnson and Heck 2003). We note that 1 red drum m^{-2} (Stunz et al. 1999) is the reported density of smaller fish than the ones used in this experiment, but because the total area of ASUs in any trial never exceeded 1 m^2, we used a single red drum for each trial. Each trial lasted for 24 h and included one of four combinations of animals, RD+PF, RD+GS, PF+GS, RD+PF+GS, and one of four ASUs. Ten replicates were conducted for each possible combination of animals and ASUs. Both ASU and animal configurations were randomly assigned to tanks and days to decrease the likelihood of artifacts. Pinfish and grass shrimp were only used once; red drum were used twice with at least a week between subsequent trials. We ensured that all predators started each trial at a similar satiation level by starving red drum and pinfish for 24 h prior to each trial. Prey items were stocked first and allowed to acclimate for several minutes before the introduction of a predator. At the conclusion of each trial, tanks were drained, animals were enumerated, and a new trial was initiated.

Because predation occurred during our pilot experiments, we concluded that 24 h was an adequate amount of time for each trial. Due to the robustness of these organisms, we did not feel that trials testing nonpredatory losses were necessary. There was no evidence of pinfish expiring for reasons other than predatory consumption by red drum during any of the trials. In our habitat selection experiments, where controls were warranted, we collected 97% of the grass shrimp alive after 24-h trials.

We used a two-way analysis of covariance (ANCOVA) to examine relationships between patch size, shape, and trophic structure on mortality of grass shrimp and pinfish. Because of unanticipated temperature changes during the course of the experiment, we used temperature as a covariate to compensate for temperature effects on rates of predation. Due to the failure of the mortality data to fit the assumptions of ANCOVA, data were successfully transformed using a $\log(x + 1)$ transformation. To examine relationships between mortality (dependent variable) and the independent variables we used stepwise linear regression, where perimeter and area were possible variables for the regression model. We also conducted a linear regression of mortality and P : A ratios (SPSS, version 11.0). Separate analyses were carried out for grass shrimp and pinfish under each possible trophic scenario (i.e., RD+GS, RD+PF+GS, etc.) and for the entire data set (all trophic scenarios combined) for grass shrimp and pinfish. All relationships were considered significant at $p \leq 0.05$.

HABITAT SELECTION

To examine the effects of patch shape and size on direct and indirect interactions as they pertain to habitat selection, we used a large, 10 tank mesocosm setup similar to the predation experiment, and the same ASUs; during this experiment two of the four possible ASUs were placed on either end of each tank. Tanks were 2.3 m long and 0.45 m in width, had drains with stoppers at each end of the tank, were filled to a depth of 45 cm with fresh seawater (approximately 1 m^3), and had a single air stone hanging in the middle along its western edge. Due to the volume of water and the duration of the trials, experiments were conducted without flowing water for the entire 24-h period. We installed a small track located in the center of each tank that allowed a 3 mm PVC divider to be inserted, dividing the tank in two equal sections. Upon termination of each trial, this divider was placed in the tank, the stoppers removed on each end, and each half of the tank was drained independently. This enabled organisms inhabiting the ASUs to be collected separately in mesh bags placed at the drain pipes. We conducted 10 trials of each combination of ASUs (Fig. 1) and organisms (PF+GS, RD+GS, RD+PF, RD+PF+GS) along with 5 controls with only a single species present (RD, PF, GS) for a total of 330 trials. Each trial lasted 24 h and animals and ASU layout was completely randomized for day, treatment, and in tank configuration. Upon the termination of each trial, we determined the proportion of organisms present in each habitat.

As in the previous experiment, we used red drum, pinfish, and grass shrimp. Thirty-five red drum (mean ±SD standard length of 43.3 ± 2.7 cm) used during the previous predation experiment were retained and used in this experiment. Pinfish standard length was 4.3 ± 0.6 cm and all grass shrimp were adults in excess of 1 cm carapace length. All pinfish and grass shrimp were collected in the previously described manner. Red drum, pinfish, and grass shrimp were stocked at densities of 1, 6, and 500 organisms m^{-2}, respectively. To reduce the possibility of intratank predation, all animals were fed to satiation prior to the initiation of each trial.

Statistical analysis of the effect of trophic level on habitat preference was carried out using a method adopted from Peterson and Renaud (1989). One limitation of having two habitats in the same tank is that they are not independent of each other and have correlated error rates. As abundance rises on one ASU, it must decline on the other. Comparing these habitats per se does not meet the independence assumption of analysis of variance (ANOVA), but the Peterson and Renaud (1989) method produces a single value that does satisfy this assumption. This value measures change in preference by comparing the difference in organism density between habitats from one situation to differences between habitats under a different situation. For each ASU combination, we compared the difference in the number of grass shrimp between habitats in our control treatments to the number of grass shrimp between habitats when pinfish were present. To facilitate comparison between habitats, organism densities were reported on a per m^2 basis. Habitat preference data were transformed to meet the normality and variance assumptions of ANOVA using an $x = 2 \arcsin \sqrt{p}$ transformation. Using the values derived from the Peterson and Renaud method, we used ANOVAs to make all pairwise comparisons of habitat preference for each species under each habitat configuration and every trophic level configuration. We also used a stepwise linear regression analysis to examine relationships between perimeter and area (possible dependent variables) and habitat preferences of grass shrimp and pinfish when exposed to different trophic levels. We calculated linear regressions between P : A ratios and habitat preference of grass shrimp and pinfish. For red drum, we made all pairwise comparisons of trophic levels (RD, RD+GS, and RD+PF) for each ASU size and shape combination using a Mann-Whitney U nonparametric test. Because our use of a singe red drum resulted in binary data, we used a Kruskal-Wallis nonparametric test to examine the relationship between perimeter, area, P : A ratios, and red drum habitat selection. All relationships were considered significant at $p \leq 0.05$.

Results

PREDATION

In the predation experiments, mean mortality for pinfish ranged between 0% and 11% (Fig. 2), and grass shrimp mortality ranged between 3% and 25% (Fig. 3). Patch size and patch shape played a minor role in explaining the amount of mortality experienced by pinfish when in the presence of a red drum predator, or when both red drum (predator) and grass shrimp (prey) were present. Only with the large circular ASU did predation occur under both trophic combinations (Fig. 2). Whether the data were analyzed as a whole (all trophic levels combined), or individually (separate trophic levels), none of the ANCOVA results comparing mortality of pinfish with varying temperature as a function of patch size and shape were significant.

Grass shrimp mortality occurred in every ASU, regardless of treatment (Fig. 3). When only a red drum was present, more grass shrimp were consumed on the large circle and small ASUs; when only pinfish were present, the greatest amount of predation occurred on the large circle, large stellate, and small stellate ASUs. There was signifi-

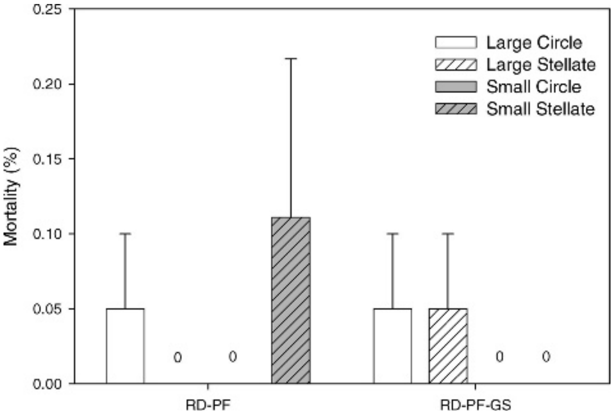


Fig. 2. Mean ±SE of pinfish mortality during 24-h mesocosm trials.

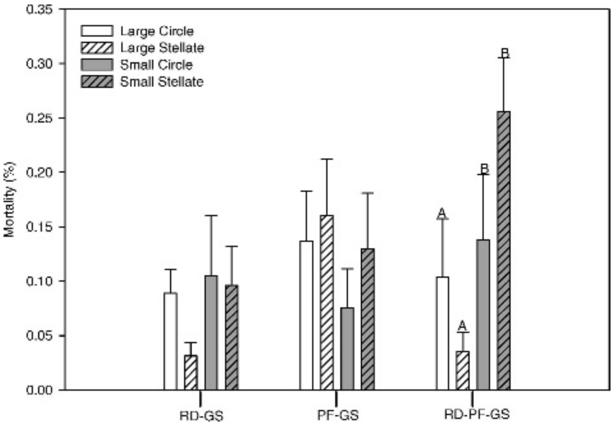


Fig. 3. Mean ±SE of grass shrimp mortality during 24-h mesocosm trials. Significant pairwise comparisons are grouped by letters.

cantly more grass shrimp predation ($F_{1,36} = 6.08$, $p = 0.019$) in the smaller habitats when both predators were present. Predation ranged between 3% and 10% in the small ASUs, and between 13% and 26% in the larger ASUs. When we examined the entire data set (all trophic treatments combined) for the influence of patch size and shape, there was a significant interaction between size and shape ($F_{1,115} = 4.607$, $p = 0.034$), indicating that grass shrimp mortality was not consistently influenced by either patch size or shape.

Linear regressions of perimeter and area, as well as P:A ratios, yielded few significant relationships, regardless of prey item or predator. For pinfish, when the data were examined by trophic level and with all levels combined, the results were nonsignificant. Area and P : A ratios did appear to influence grass shrimp mortality when predation was due to both red drum and pinfish (area—$F_{1,38} = 5.35$, $p = 0.026$; P : A—$F_{1,38} = 4.89$, $p = 0.033$). These relationships each explained ~12% of the variance in the models (area—$r^2 = 0.0124$; P : A—$r^2 = 0.0114$); the relationship between area and mortality was slightly negative (slope = 0.002) and the relationship with P : A ratios was slightly positive (slope = −0.249). When all treatment combinations were included, there were no significant relationships between any of the independent variables and mortality of grass shrimp.

HABITAT PREFERENCE

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 trials that contained both large and small habitats. When presented with the large and small stellate ASUs, grass shrimp were found at a higher density in the larger habitat (Fig. 4). When a single predator was present, grass shrimp density in any given habitat ranged between 40% and 60%. In trials where grass shrimp were present with two predators and ASUs that varied by shape and size, they were found in higher densities on the large stellate than the small circle. More grass shrimp were collected on the small stellate than the large circle. In trials with only grass shrimp and either two large or two small habitats, mean grass shrimp densities were higher in the stellate ASUs. When confronted with predation, grass shrimp altered their habitat preference in 8 of 18 pairwise comparisons (Table 1). In habitats where both ASUs were the same shape, there was a significant difference between grass shrimp alone and grass shrimp with predators. For the large circle-small circle treatment, the large ASUs initially contained 28% of the grass shrimp without predators and 62% after predator additions. The large stellate-small stellate treatments showed grass shrimp densities in the larger habitats of approximately 20% and 80%; after the addition of predators, each ASU contained approximately 50% of the animals. When confronted with two predators and habitats of varying size, there was also a change in habitat preference by grass shrimp. The large stellate-small circle treatments showed a shift in shrimp density with predators from 35% to 65% on the large ASUs while grass shrimp density in the large circle-small stellate treatment shifted from 20% on the large habitats without predators to approximately 50% with predators.

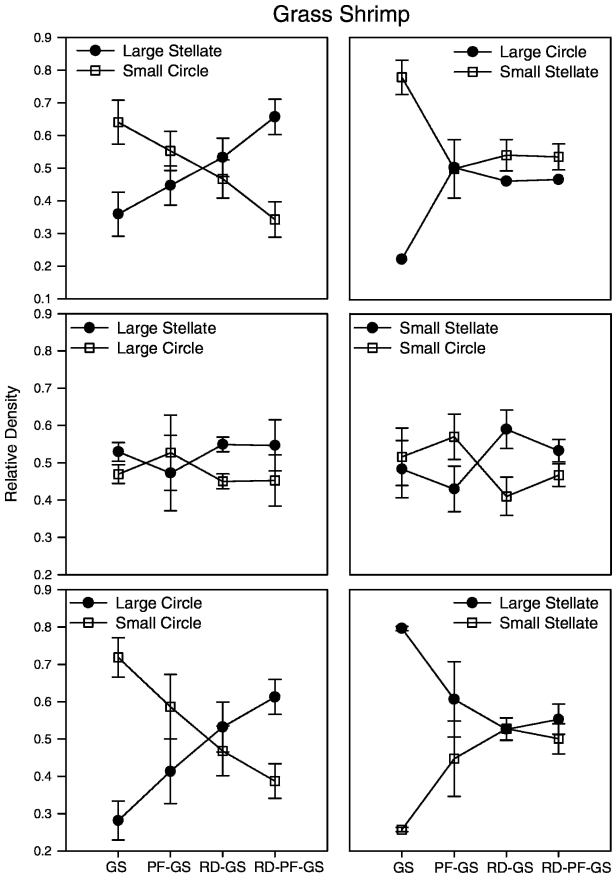


Fig. 4. Mean relative densities ±SE m^{-2} of grass shrimp in each of the two artificial seagrass units.

Habitat selection by pinfish varied greatly depending on habitats and the presence of other trophic levels (Fig. 5). 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 pinfish in the large circle-small circle treatment, but did not hold true in the large stellate-small stellate treatment after red drum were introduced alone or with grass shrimp. For treatments with the

TABLE 1. Pairwise comparisons (p values) for grass shrimp and pinfish habitat selection experiments. Statistical analysis of habitat preference was conducted using methods described in Peterson and Renaud (1989). ASU = artificial seagrass unit, PF = pinfish, GS = grass shrimp, and RD = red drum.

ASU layout		Large Stellate-Small Circle	Large Circle-Small Stellate	Large Circle-Large Stellate	Small Circle-Small Stellate	Large Circle-Small Circle	Large Stellate-Small Stellate
Grass Shrimp							
GS versus	PF+GS	0.364	0.019	0.575	0.575	0.233	0.167
	RD+GS	0.078	0.008	0.557	0.286	0.018	<0.001
	RD+PF+GS	0.006	0.002	0.783	0.196	0.003	<0.001
PF+GS versus	RD+GS	0.308	0.673	0.473	0.06	0.306	0.461
	RD+PF+GS	0.019	0.61	0.519	0.024	0.074	0.607
RD+GS versus	RD+PF+GS	0.133	0.248	0.971	0.756	0.342	0.583
Pinfish							
PF versus	PF+GS	0.664	0.723	0.545	0.745	0.169	0.178
	RD+PF	0.657	0.847	0.918	0.335	0.085	0.017
	RD+PF+GS	0.465	0.15	0.933	0.395	0.343	0.006
PF+GS versus	RD+PF	0.247	0.542	0.366	0.308	0.813	0.392
	RD+PF+GS	0.087	0.026	0.507	0.372	0.503	0.218
RD+PF versus	RD+PF+GS	0.718	0.015	0.82	0.851	0.335	0.608
Red Drum							
RD versus	RD+GS	ns	ns	ns	ns	ns	ns
	RD+PF	ns	ns	ns	ns	ns	ns
	RD+PF+GS	ns	ns	ns	ns	ns	ns
RD+GS versus	RD+PF	ns	ns	ns	ns	ns	ns
	RD+PF+GS	ns	ns	ns	ns	ns	ns
RD+PF versus	RD+PF+GS	ns	ns	ns	ns	ns	ns

same sized ASUs, mean habitat preference ranged between 30% and 70% for all trophic combinations, while for habitats that varied by both shape and size, pinfish densities were higher in the larger ASUs for each treatment, except for the stellate treatment, when all three taxa were present. Pairwise comparisons of changes in habitat preference, as related to trophic structure, indicated statistically significant differences in 3 of 36 comparisons (Table 1). Differences were in treatments where ASU size was the only parameter that varied.

Although not significant, in habitats where ASUs varied by both size and shape (Fig. 6), red drum were found more often in the larger habitats. In habitats where shape was the only variable, red drum were found more often in circular ASUs. When presented with ASUs that varied by size, red drum were not found in any particular habitat, but alone or with grass shrimp, more red drum were collected in the small circular ASUs than the large ASUs. For the stellate ASUs, more red drum were collected in the large ASUs. Pairwise comparisons indicated no significant differences between red drum habitat preference and the number of trophic levels present.

To examine the role that perimeter and area played in influencing habitat preference, we combined each of the data sets for all three animals and examined them strictly on how they related to perimeter, area, and P : A ratios (Figs. 1 and 7). Our regression analysis resulted in multiple significant relationships for grass shrimp (Table 2). Without predators, grass shrimp density showed a negative relationship with area and a positive relationship with P : A ratios. These models explained 35% and 51% of the variance in the data, respectively. When red drum were present, grass shrimp had a generally positive relationship with area and a negative relationship with P : A ratios. 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 abundance data set, regression analysis indicated a significant and positive relationship between area and abundance when pinfish were held by themselves, and between area and P : A ratios when both predator and prey items were present (Table 2). When the entire data set was combined, there was a significant negative relationship between P : A ratios and pinfish abundance.

For red drum, our analyses showed no significant relationships between habitat preference and perimeter, area, or P : A ratios. 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

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, 1999; Bell et al. 2001). At the spatial scale of

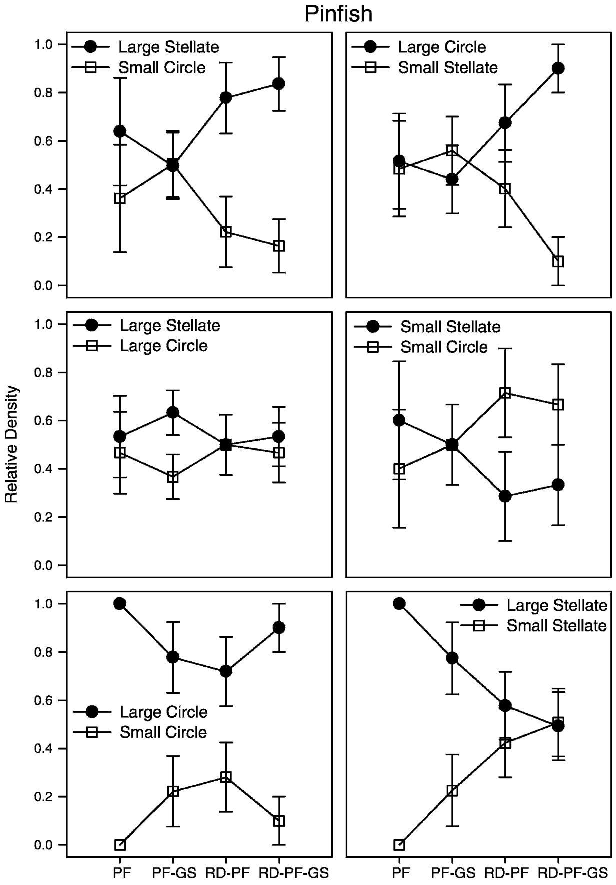


Fig. 5. Mean relative densities ±SE m^{-2} of pinfish in each of the two artificial seagrass units.

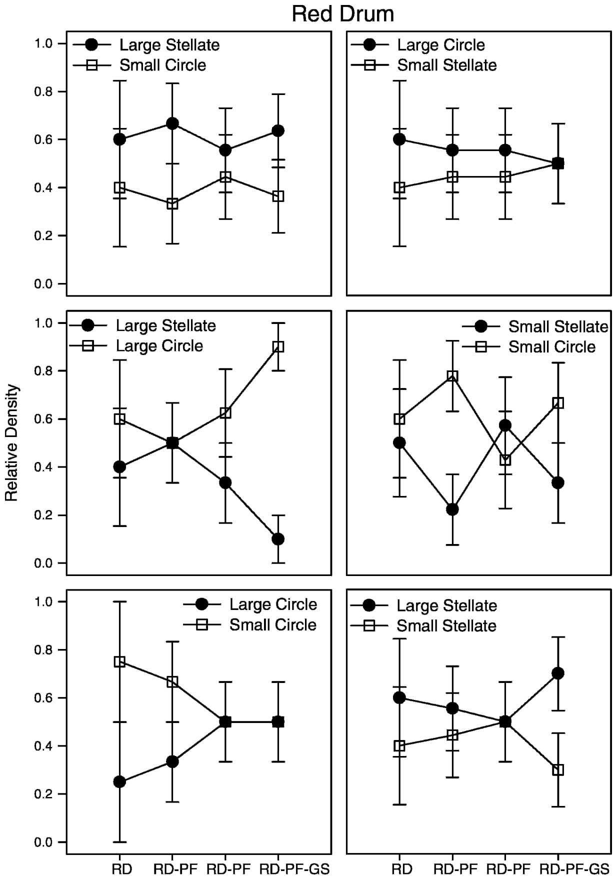


Fig. 6. Mean relative densities ±SE m^{-2} of red drum in each of the two artificial seagrass units.

our experiment (0.04–0.2 m^2), the effects of variation in habitat shape and size on habitat choice and predation rates varied depending on the species composition present.

Results of our single species habitat selection experiments suggest that grass shrimp preferred smaller habitats over larger habitats approximately 75% of the time, while pinfish and red drum each also preferred the larger habitats 3 to 1 over the smaller habitats. Contrary to our initial predictions, addition of either a red drum or pinfish with grass shrimp resulted in a decline in preference between habitats. Regardless of the fact that pinfish consumed more grass shrimp than red drum, the response was stronger with the addition of a red drum (Table 1). These data suggest that habitat selection by grass shrimp is more important in the presence of red drum than pinfish. This shift in habitat usage in the presence of red drum may be responsible for the lower predation rate of grass shrimp by red drum as compared to pinfish. For pinfish, the addition of a red drum predator resulted in an increase of preference of one habitat in three treatments and a decrease in the other three (Fig. 5). The decline in discrimination between habitats was greater when pinfish were presented with grass shrimp as prey when compared to the presence of a predation threat by red drum. The trend towards a lack of preference in our habitat selection experiments may be due to the fact that predation rates were not significantly different among the four ASUs, suggesting that one habitat may be as safe as another when a single predator was present.

Habitat preference of red drum varied, depending on the prey item present and the shape of the ASU (Fig. 6). In the large habitats, there was a decline in preference with the addition of grass shrimp and an increase with the addition of pinfish. On the small ASUs, habitat preference increased with the addition of grass shrimp and declined with the addition of pinfish. When both prey items were present and when red drum preferred one habitat over the other, neither grass shrimp nor pinfish preferred one habitat over the other and vice versa. This reaction, along with the effect of red drum

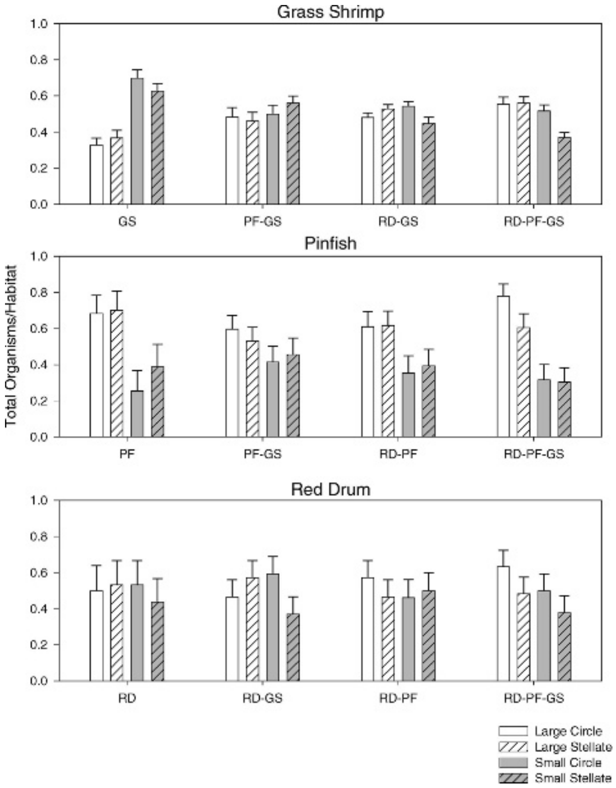


Fig. 7. Mean ±SE of the total number of organisms found per habitat during habitat selection experiments.

predation on grass shrimp and pinfish, may be explained by the microhabitat choices of the predators. Red drum would often assume a position along the edge of the ASU; even without the threat of predation, pinfish would remain within the seagrass patch. Thus, for both prey species to mitigate predation by red drum, it would be advantageous to reside in larger patches where there was more available habitat in which to hide. For predation of grass shrimp by pinfish, the amount of edge or patch size may not be a factor because both species coinhabit the same patches and interactions are unavoidable.

Although not significant, the response of red drum to the addition of pinfish was not constant among habitats, suggesting that one habitat may facilitate predation (direct interaction) over another. Indirectly, the presence of grass shrimp may have also influenced the interaction between red drum and pinfish. When grass shrimp were added, red drum predation of pinfish was reduced in the smaller habitats and increased in the large stellate habitats (Fig. 2); there was also an overall drop in the number of pinfish consumed by red drum. Initially, this suggests that the presence of grass shrimp as prey may be initiating a response from pinfish, in which they move deeper into the refuge habitat to pursue grass shrimp rather than to avoid predation by red drum. Due to the increased predation of grass shrimp when both predators were present, our grass shrimp data does not support this conclusion. Predation on grass shrimp by pinfish and red drum varied greatly depending on habitat, but as we predicted, when TMIIs were present there was a significant negative relationship between area and grass shrimp predation. As a result, we have concluded that a spatial structure-mediated indirect effect (a form of TMII, see Ikeda and Nakasuji [2002]) may exist in this experimental food web. Since behavior modification of pinfish by predators is known to occur (Jordan et al. 1997), increased physical interactions between grass shrimp and pinfish may explain the increase in grass shrimp predation on the smaller habitats by pinfish in the presence of RD.

In addition to using complex habitats, we also used a complex tritrophic food web. Typically, energy transfer examined in similar experiments is linear (Werner and Peacor 2003); that is a predator

TABLE 2. Results from stepwise linear regressions for grass shrimp and pinfish habitat selection experiments. PF = pinfish, GS = grass shrimp, and RD = red drum.

	Perimeter : Area Ratio			Perimeter (β_1) and Area (β_2)			
	p Value	r^2	β_1	p Value	r^2	β_1	β_2
Grass shrimp							
GS	<0.001	0.35	0.014	<0.001	0.51	Excluded	−1.04
PF+GS	ns			ns			
RD+GS	ns			0.034	0.04	Excluded	0.441
RD+PF+GS	<0.001	0.13	−0.007	<0.001	0.14	Excluded	1.092
All data combined	ns			ns			
Pinfish							
PF	ns			0.001	0.179	Excluded	2.484
PF+GS	ns			ns			
RD+PF	ns			ns			
RD+PF+GS	<0.001	0.14	1.09	<0.001	0.16	0.14	0.006
All data combined	0.025	0.013	−0.004	ns			

only feeds upon a single prey taxon. Our study used a predator (red drum) that had the ability to feed at either of the lower trophic levels (grass shrimp or pinfish). If grass shrimp were preferred by red drum over pinfish, this would release pinfish from predation by red drum and further suppress grass shrimp densities due to consumption by both predators. If red drum consumption of pinfish remained unchanged when grass shrimp were present then consumption of grass shrimp and pinfish would still occur, but to a lesser extent. Red drum consumption on pinfish could release grass shrimp from predation by both red drum and pinfish or just pinfish. This large number of possible scenarios is more likely to be similar to natural food webs than the typical three species food chains used in most mesocosm experiments, and the inconsistencies in our results may be a more accurate representation of what is actually occurring in coastal ecosystems. As such, it may be difficult to decipher the effect of patch dynamics on small prey taxa in situ because of the unfettered and highly variable movement of higher order predators (Sheaves 2001).

The inconsistency in our results has implications for studies of patch characteristics and habitat fragmentation per se (see Andrén (1994) for review). To our knowledge, this is the first attempt to assess the role of simultaneous changes in patch size and shape on habitat preference by marine organisms. Previous work (McNeill and Fairweather 1993; Eggleston et al. 1998, 1999; Bologna and Heck 2000; Bell et al. 2001) made no attempt to tease apart ecological subtleties of how community structure is influenced by changing patch size and shape. The possibility that responses to these changes covary with trophic complexity has been ignored and may help explain the large number of inconsistencies within the literature. In fifteen publications directly addressing habitat fragmentation per se or changes in patch configuration within seagrass environments (Irlandi 1994, 1997; Bologna 1998; Eggleston et al. 1998, 1999; Bologna and Heck 1999, 2000; Irlandi et al. 1999, Fischer 2000; Bell et al. 2001; Hovel and Lipcius 2001, 2002; Hovel et al. 2002; Hovel 2003, Healey and Hovel in press), the possibility that variations in trophic structure could explain their results was never examined, although many authors suggested that differential effects by predators might be influencing their results. Hovel and Lipcius (2001) undertook an extensive survey of the higher predators within the Chesapeake Bay, but used only the numerically dominant predator (large blue crabs) in their analyses and ignored overall trophic structure. Their sampling techniques (trawling and suction sampling) are biased against highly mobile predators (i.e., fishes) whose mere presence may exert influence over lower trophic levels, helping to explain temporal variance.

Our trials demonstrate how variable TMIIs can be under different conditions. The magnitude of response of indirect interactions can depend on the habitat and the community composition at the time of the response. Typically, parameters that can determine the strength of these interactions are considered separately from the surrounding community in which species are imbedded (Werner and Peacor 2003). As such, the variability of these responses reinforces the concept that naturally occurring ecosystems are more complicated than they are often assumed, and that there is a need to explore increasingly complex ecosystems to determine if the consequences of indirect interactions can be extended beyond simple systems (Werner and Peacor 2003). If covariation of trophic structure and patch dynamics can alter organism's responses at small spatial scales, it is highly likely that this also occurs at larger spatial scales and may help explain inconsistencies in previous research. Most research to date has concentrated on relating macrofaunal organisms in seagrass meadows to the physical characteristics of seagrasses. We conclude that additional ecological processes (e.g., diel patterns, current movements, and predators) must be considered to fully understand the effects of changes in patch size and shape on the inhabitants of seagrass meadows.

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