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Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish

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Abstract Seagrass meadows are often important habitats for newly recruited juvenile fishes. Although substantial effort has gone into documenting patterns of association of fishes with attributes of seagrass beds, experimental investigations of why fish use seagrass habitats are rare. We performed two short-term manipulative field experiments to test (1) the effects of food supply on growth and densities of fish, and (2) effects of predation on the density and size distribution of fish recruits, and how this varies among habitat types. Experiments were conducted in Galveston Bay, Texas, and we focused on the common estuarine fish, pinfish *Lagodon rhomboides*. In the first experiment, replicate artifical seagrass and sand plots were either supplemented with food or left as controls. Recruitment of pinfish was significantly greater to seagrass than sand habitats; however, we detected no effect of food supplementation on the abundance of recruits in either habitat. Pinfish recruits in artifical seagrass grew at a significantly faster rate than those in sand habitats, and fish supplemented with food exhibited a greater growth rate than controls in both sand and artifical grass habitats. In our second experiment, we provided artificial seagrass and sand habitats with and without predator access. Predator access was manipulated with cages, and two-sided cages served as controls. Recruitment was significantly greater to the cage versus cage-control treatment, and this effect did not vary between habitats. In addition, the standard length of pinfish recruits was significantly larger in the predator access than in the predator exclusion treatment, suggesting size-selective predation on smaller settlers or density-dependent growth. Our results indicate that the impact of predation on pinfish recruits is equivalent in both sand and vegetated habitats, and thus differential predation does not explain the higher recruitment of pinfish to vegetated than to nonvegetated habitats. Since predators may disproportionately affect smaller fish, and a limited food resource appears to be more effectively utilized by fish in vegetated than in unvegetated habitats, we hypothesize that pinfish recruits may select vegetated habitats because high growth rates allow them to achieve a size that is relatively safe from predation more quickly.

Key words Seagrass · Recruitment · Predation · Food limitation · *Lagodon rhomboides*

Introduction

Life histories that include distinct stages of varying dispersal abilities are ubiquitous among diverse animal taxa. Many marine invertebrates and fishes produce highly dispersive planktonic larvae while adults usually exhibit only localized or no movement (Sale 1980; Roughgarden et al. 1988). Because currents can advect the larvae of marine species great distances from their natal site, the supply of new recruits to local populations may be decoupled from reproductive output at that site. In such "open" populations (*sensu* Caswell 1978) variable recruitment may, therefore, have profound consequences for the size or dynamics of populations (e.g., Gaines et al. 1985; Victor 1986; Doherty and Fowler 1994). In order to understand what determines the size or dynamics of marine populations, ecologists must ascertain the mechanisms producing variation in recruitment (the addition of individuals from the larval to the adult habitat), and the degree to which initial patterns of recruitment are altered by post-recruitment mortality.

Understanding the causes and consequences of variable recruitment has been a major focus of workers on marine fishes for the last two decades. Some populations of fishes appear to be strongly influenced by variable recruitment such that population size and dynamics reflects spatial and temporal variability of recruitment (Doherty and Williams 1988). This phenomenon, called "recruitment limitation", has been demonstrated repeatedly in some coral reef fishes (Williams 1980; Doherty

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1983; Victor 1983, 1986; Doherty and Fowler 1994). Recruitment limitation was originally proposed, and continues to be interpreted, as a hypothesis that predicts patterns of abundance within and not among habitat types (Doherty 1996). Thus, workers testing recruitment limitation control for microhabitat variability. However, variability in habitat structure can affect the efficiency, effectiveness or selectivity of predators (Heck and Thoman 1981; Crowder and Cooper 1982; Werner and Gilliam 1984; Sih et al. 1985). In addition, habitat differences may affect competitive interactions (Jones 1988), the abundance of food resources (Levin 1994), or the ability to procure food (Nelson 1979; Heck and Thoman 1981; Stoner 1982). Fully understanding what limits or generates change in fish populations requires that we examine the role of recruitment variability within the mosaic of habitats occupied by fish (Levin 1983).

Seagrass meadows constitute one of the major biogenic habitats in marine and estuarine systems worldwide and are inhabited by a diverse and abundant assemblage of fishes. Both attributes of the seagrass habitat (e.g., Robbins and Bell 1994; Irlandi et al. 1995; Irlandi 1996) and recruitment of fishes (e.g., Adams 1976; Orth and Heck 1980; Stoner 1980a, 1983; Bell and Westoby 1986; Sogard et al. 1987; Worthington et al. 1992) are highly variable in space and time. Fish may recruit to seagrass beds because the complex habitat offers them a refuge from predation (reviewed by Heck and Orth 1980; Orth et al. 1984). Alternatively, habitat selection (Leber 1985; Bell and Westoby 1986) or migration (Sogard 1989) may be the proximate cause of fish (or decapod) relationships with seagrass. In addition, many fishes consume seagrass-associated invertebrates, epiphytes on seagrass, or the seagrass itself (Stoner 1982; Luczkovich et al. 1995); consequently, fish may also respond to variability in macrophyte-associated food resources (Levin 1994).

Differences in larval supply or selection of habitats at the time larvae leave the plankton for their demersal juvenile habitat can also produce an association of fishes with seagrass meadows (Bell and Westoby 1986). This idea emphasizes the role of recruitment variability and is in sharp contrast to ideas that fish-seagrass relationships are the result of post-recruitment processes such as predation. Recruitment patterns can be modified or reinforced by post-recruitment processes, and thus, experiments examining both recruitment and post-recruitment processes may be required to fully understand the mechanisms producing patterns of fish abundance (Hixon 1991; Jones 1991). Few field experiments in this vein have been conducted on seagrass fishes (but see Bell and Westoby 1986; Bell et al. 1987; Sogard 1989), and thus many of our conclusions about the dynamics of fish populations in seagrass beds are based on correlative studies. In this study our goal was to experimentally manipulate habitat type, food supply, and levels of predation, and examine their effects on recruitment, post-recruitment mortality, and growth. Specifically, we asked these questions:

1. Does food supply limit the number or growth rates of fish recruits in different habitats?
2. Does predation determine the number or size structure of fish recruits and does the effect vary in different habitats?

Methods

Study site and species

Field experiments were conducted in East Lagoon at the easternmost end of Galveston Island, Texas, United States (29°20′N, 94°44′W). This lagoon is 1.6 km long, *c.* 0.48 km wide and has a maximum depth of 4.6 m. Seven 0.92-m cement culverts connect East Lagoon to the Galveston Ship Channel which runs from the Gulf of Mexico into Galveston Bay. Although seagrasses were once widespread in Galveston Bay, including East Lagoon, areal coverage of seagrasses has decreased 90% from peak levels (Pulich and White 1991), and no natural seagrass habitats presently occur in East Lagoon. This allowed us to establish artifical seagrass beds with desired characteristics without the confounding effects of nearby natural beds. The intertidal edge of the lagoon is marsh habitat dominated by *Spartina alterniflora*. Experiments were situated >8 m from the marsh edge in an average depth of 42 cm at low tide.

Our experiments focused on pinfish *Lagodon rhomboides*. Pinfish are abundant in estuaries from Cape Cod to Florida and throughout the Gulf of Mexico to the Yucatan Peninsula (Darcy 1985). Pinfish generally spawn in offshore waters in late fall through early spring (Hildebrand and Cable 1938), with a peak in January and February (Hoss 1974). Settlement occurs after a pelagic larval life of *c.* 4–6 weeks when fish reach about 12 mm standard length (SL) (Darcy 1985). Pinfish juveniles are common in vegetated areas such as seagrass beds (e.g., Adams 1976; Nelson 1979; Stoner 1980a; Sogard et al. 1987), algal beds (Hyle 1976) and marshes (Minello et al. 1994). At the end of their first summer, juveniles move to deeper waters, often offshore (Weinstein et al. 1977). Prior to this offshore movement juveniles appear to be quite site-attached and do not undergo large-scale movements (Darcy 1985). As adults, pinfish occur in a variety of habitats, but show a preference for vegetated habitats (Darcy 1985).

Pinfish diet changes with age. Newly recruited fish are carnivorous feeding mostly on zooplankton as well as amphipods (Stoner 1980b; Luczkovich et al. 1995). Older juveniles (40–120 mm SL) are omnivorous and consume a variety of invertebrates, algae and seagrass (Livingston 1980; Stoner 1980b; Luczkovich et al. 1995). Adults are omnivorous with broad food habits (Adams 1976), but as they increase in size, the importance of plants in their diet increases (Darcy 1985).

The effects of food supply on pinfish recruitment and growth in varying habitats

To test the null hypothesis that food supply does not affect the abundance or growth of newly settled pinfish, we conducted an experiment in which we manipulated food supply in sand and seagrass habitats. A complete randomized block design with two fixed factors, habitat type and food supplementation, was used for this experiment. Experimental plots within blocks were 8 m apart and blocks were >10 m apart.

On 20 February 1996, experimental plots (1 m^2, n=20) were assigned to either a sand (n=10) or seagrass (n=10) habitat. To reduce possible variability in demographic processes due to differences in seagrass structure, we employed standardized artificial seagrass habitats. These structures provide replicates of habitat which are close to the natural habitats of seagrass fishes. Artificial seagrass habitats have previously been used with great success by many workers (e.g., Bell et al. 1987; Sogard 1989). Artificial seagrass habitats (hereafter referred to as “grass”) consisted of a 1-m^2

PVC frame (1.3 cm diameter) which was strung with monofilament forming a grid with 576 points. At each intersection, green ribbon (16 cm tall×5 mm wide), was woven into the monofilament base creating a "seagrass" patch with 576 shoots and 2 leaves per shoot. The ribbon did not become excessively fouled and remained buoyant for the duration of our experiments. Sand habitats were simply bare substratum. To ensure that the PVC frame with only the monofilament grid did not attract fish in greater numbers than bare sand, we performed a preliminary experiment in which we compared pinfish recruitment to bare substrate, PVC frames with only a monofilament grid, and PVC frames with ribbon attached. We detected no difference between bare sand substratum and the PVC frame (Tukey's HSD, P=0.22, n=10); consequently, in the experiments reported here, we used only bare sand rather than a bare PVC frame for control plots.

In the center of each experimental plot, a feeding tube (7.5 cm diameter PVC pipe) was suspended *c.* 15 cm above the substratum by attaching it to a 1.3-cm-diameter PVC pipe driven into the sediment. Supplemental food was added to half of the sand and "grass" replicates (i.e., five sand and five grass habitats received food). The supplemental food was 200 g of fish flesh that was put in a blender with 300 ml of water and blended to produce plankton-sized particles (Forrester 1990). The processed fish was placed in ice cube trays and frozen. Each cube of food provided 11.8 g of plankton-sized fish particles. One cube was added to appropriate replicates daily from 23 February to 3 March 1996 by dropping them into the top of the feeding tubes. As the cubes thawed, a stream of particles bathed the habitat for 5–15 min. Observations both in the field and laboratory indicated that pinfish readily consumed this food. Control plots received an ice cube without food added to it.

The experiment was terminated on 4 March 1996 by sampling pinfish recruits on each of the replicates. Densities of recruits were quantified using drop samplers modified from the designs of Zimmerman et al. (1984) and Fonseca et al. (1990). The drop sampler consisted of a 1-m³ (1×1×1 m) enclosure constructed of 9.5 mm diameter rebar covered with taut 2-mm nylon mesh on four sides. The net was dropped over the experimental plot and a large dip net (90×100 cm) was used to remove fish from the drop sampler. Drop samplers were considered adequately sampled when five passes of the dip net no longer yielded fish (Fonseca et al. 1990). After subjecting the data to an F-max test to ensure homogeneity of variances, a blocked two-factor analysis of variance was used to test the hypothesis that abundances of recruits did not vary among habitat or food supplementation treatments.

Five fish from each treatment within each of four blocks were haphazardly selected for subsequent analysis in the laboratory. These 80 fish were measured to the nearest 0.1 mm (SL) using an image analysis system (Optimas 4.0). Otoliths were removed from fish following the procedures of Secor et al. (1991) and stored in immersion oil for at least 1 week. We then aged fish to the day by enumerating daily growth rings on lapillar otoliths using Optimas 4.0. We did not experimentally verify the existence of daily increments; however, daily increments occur in this family (e.g., Francis et al. 1993), and the size-at-age data we generated are well within what would be expected if rings were deposited daily (Darcy 1985). Each otolith was examined independently three times. If two of the three counts were not identical then that fish was removed from the analysis. When two of the counts agreed, then we used that count as a datum. We then compared growth rates integrated over the life of fish from each of the treatments by comparing the slopes of the length-age regression lines using analysis of covariance.

We examined differences in growth rates in more detail using otolith microstructure. Because the diameter of pinfish otoliths was correlated with pinfish length (r=0.78, n=80), we used otolith measures as a proxy for fish size. We measured the distance from the edge of the otolith to seventh ring from the edge. Consequently, we measured fish growth during 7 days (26 February–3 March 1996) while some experimental plots were receiving supplemental food and others were not. Growth rates of fish vary with age; however, a regression analysis of the width of the last seven growth increments and age indicated that for the restricted age group we examined here, growth rate was not related to age (r^2<0.001, P=0.88, n=80). Otolith distances were converted to daily growth rates (mm SL day^{-1}) using the following equation generated from a regression of otolith diameter on fish length:

Growth=[(otolith distance+0.0434)/0.0208]/7

We used a blocked two-factor analysis of variance to test the hypothesis that growth rates did not vary among habitat or food supplementation treatments.

Effects of predation on recruitment of pinfish to varying habitats

To test the null hypothesis that predators do not affect the abundance of pinfish recruits in sand or "grass" habitats, we used cages to manipulate predator access to experimental plots. As in the first experiment , we created ten sand and ten artificial seagrass experimental 1-m² plots. On 18 March 1996 an unusually low tide exposed all our habitats to air and thus no pinfish or their predators (mostly blue crabs *Callinectes sapidus*) were present in our plots. On this date, we erected 4-m³ (2×2×1 m) cages (25 mm mesh) around half of the replicates of each habitat treatment. The other half of the replicates were surrounded with cages missing two sides. Preliminary experiments demonstrated that recruitment of pinfish to plots without cages did not differ from plots with cages missing two sides ($F_{1,11}$=1.97, P=0.19). Therefore, given the logistical difficulties in producing additional artificial seagrass plots we opted to run this experiment with cages and cage controls, but without a no-cage treatment. Experimental plots were positioned in a completely randomized block design with 8 m between replicates within blocks and 10 m between blocks. The large mesh of the cage permitted newly recruited pinfish to move freely in and out of the cage walls, but fish and decapod predators >25 mm in smallest dimension were excluded. Because very young pinfish do not appear to undergo extensive movements (Darcy 1985), differences between cage and cage control treatments are likely due to differences in mortality rather than migration.

The experiment was terminated on 25 March 1996 (after 7 days) by sampling pinfish recruits on each replicate using drop samplers as described above. Because data were not normally distributed and variances were not homogeneous even after transformation, these data were analyzed using a nonparametric two-factor analysis of variance (Zar 1984).

Results

The effects of food supply on pinfish recruitment and growth in varying habitats

Recruitment of pinfish was a significant >300% greater to "grass" than to sand habitats ($F_{1,12}$=45.71, P<0.001). We captured an average of 183.5 (SE=23.3) pinfish recruits per 1 m² plot in "grass" habitats versus 56.9 (SE=8.6) in sand habitats (Fig. 1). However, we detected no effect of food supplementation on the number of pinfish recruits in either habitat ($F_{1,12}$=0.46, P=0.51). We also detected no significant effects of the interaction between habitat and food supplementation ($F_{1,12}$=0.099, P=0.76) or the block ($F_{4,12}$=0.58, P=0.69). Overall, pinfish densities averaged 126.6 (SE=17.8) fish per 1 m² plot in the food addition plots and 113.9 (SE=14.1) fish per control plot (Fig. 1).

Pinfish recruits in both food supplementation treatments were a significant 9% larger in "grass" versus sand habitats ($F_{1,79}$=6.57, P=0.01; Fig. 2). However, we detected no difference in the age of fish between the two habitats ($F_{1,72}$=1.70, P=0.20; Fig. 2) because growth

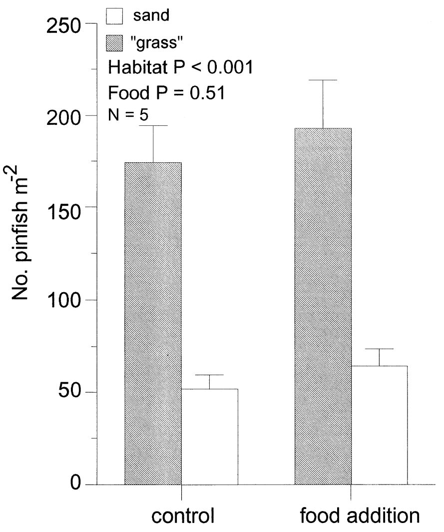

Fig. 1 Pinfish densities (mean+1 SE) in 1-m^2 bare sand and artifical seagrass (*"grass"*) habitats with and without food supplementation. *P* values are from a blocked two-factor analysis of variance and *n* is the number of replicates of each treatment combination

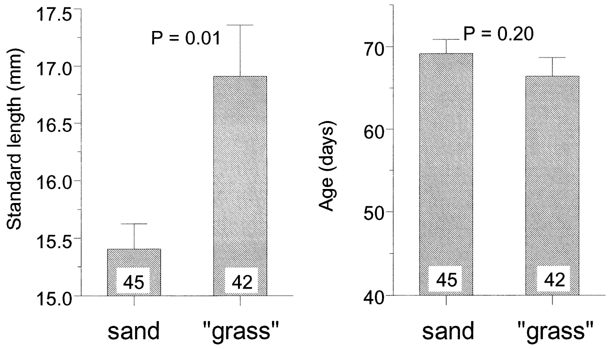

Fig. 2 The standard length (SL) and age (mean+1 SE) of pinfish in 1-m^2 bare sand and grass plots. *P* values are from a blocked two-factor analysis of variance, and data from control and food addition treatments are combined together since this factor was not significant in the analysis; *n* is given at the base of each *bar*

rates differed between habitats. Analysis of covariance revealed that the slope of the length-age regression line was greater in the "grass" than in sand habitats (Fig. 3). Analysis of covariance found no difference in growth rates of fish on plots that were supplemented with food and those of controls (Fig. 3). Thus, for fish that were *c.* 6–14 weeks old, 10 days of food supplementation was not manifested as differences in growth over the life of the fish.

When we used the technique to examine differences in growth rates only during the those days when we were supplementing food, there was a clear and significant effect of food addition on growth rates (Fig. 4). Growth rates averaged 0.42 mm SL day^{-1} in plots receiving supplemental food, but averaged significantly less (0.40 mm SL day^{-1}) in control plots ($F_{1,72}$=5.67, P=0.02). Using this technique, we also observed that growth rates tended to be greater on "grass" versus control plots (Fig. 4), but this difference was not significant ($F_{1,72}$=2.94, P=0.09). Additionally, the interaction of the food addition treatment with habitat type was not significant ($F_{1,72}$=0.79, P=0.38) suggesting that habitat type did not directly affect the ability of fish to procure the added food. The effect of the block was highly significant ($F_{4,72}$=4.86, P=0.002), indicating that the growth rates are spatially variable.

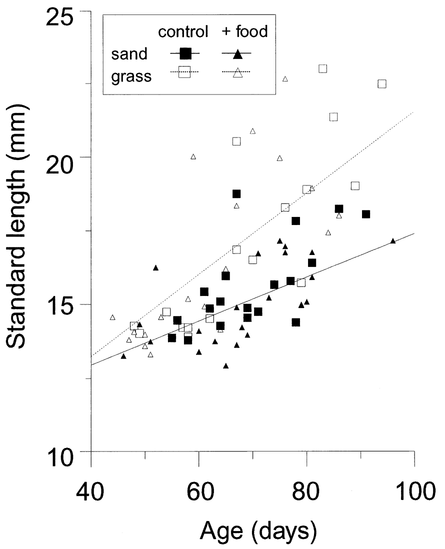

Fig. 3 The relationship between the age of pinfish and their SL in sand and artifical seagrass plots with (*+food*) and without supplemental food. Analysis of covariance showed that the slope of the age-length regression line did not differ between food supplementation and control plots ($F_{1,70}$=0.125, P=0.725), but the slope of the age-length regression line was greater for fish in grass than in sand habitats ($F_{1,70}$=8.321, P=0.005). Regression lines are shown for the pooled food supplementation and control treatments in both grass (*dashed line*) and sand (*solid line*) habitats

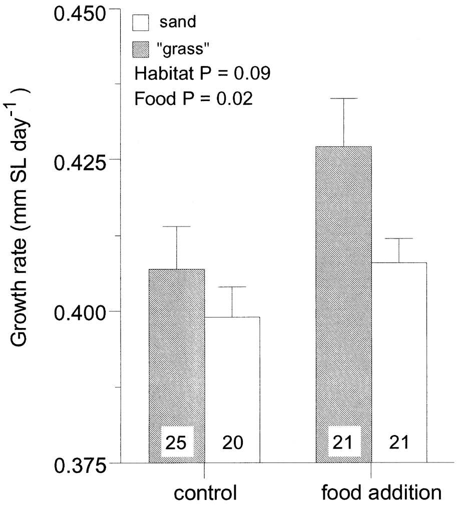

Fig. 4 The growth rate (mean+1 SE) of pinfish as determined by an analysis of otolith microstructure in 1-m^2 bare sand and artifical seagrass (*"grass"*) habitats with and without food supplementation. *P* values are from a blocked two-factor analysis of variance, and *n* is given at the base of each *bar*

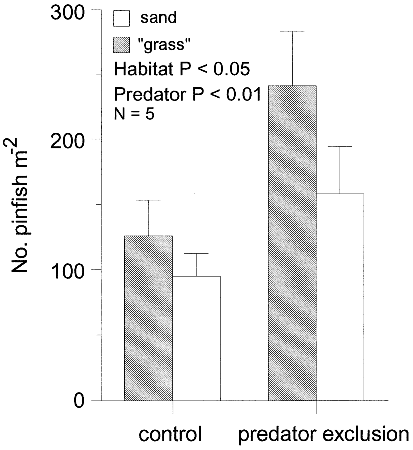

Fig. 5 Pinfish density (mean+1 SE) in 1-m^2 bare sand and artifical seagrass (*"grass"*) habitats that were either fully caged with 25-mm mesh (predator exclusion) or surrounded by a two-sided cage control (control). P values are from a nonparametric analysis of variance, and *n* is the number of replicates of each treatment combination

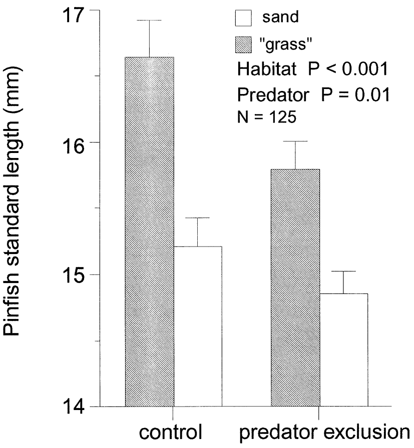

Fig. 6 The standard length (mean+1 SE) of pinfish collected from 1-m^2 plots of bare sand or artifical seagrass that were either fully caged with 25 mm mesh (*predator exclusion*) or surrounded by a two-sided cage control (*control*). *P* values are from a blocked two-factor analysis of variance, and *n* refers to the number of fish measured within each treatment combination

Effects of predation on recruitment of pinfish to varying habitats

When we presented "grass" and sand habitats with and without predator access, there were clear effects of both habitat and predators on pinfish densities and size structure (Fig. 5). As in the first experiment recruitment was significantly greater to "grass" versus sand habitats (H=5.09, P<0.05, n=5), with pinfish abundances about 1.5 times greater in the "grass" than sand treatment. Excluding predators by provision of cages also had a dramatic effect on recruit density (Fig. 5). Recruitment was a significant *c.* 1.8 times greater inside the cage versus cage control treatment (H=6.77, P<0.01, n=5). The exclusion of predators resulted in an increase of fish in both the sand and "grass" habitats, as is evidenced by the lack of a significant habitat-predator exclusion interaction in the analysis (H=2.52, P>0.05).

We also examined differences in pinfish length among sand and "grass" plots with and without predator access. As in the food supplementation experiment, fish were larger in the "grass" compared to sand habitat (Fig. 6, $F_{1,517}$=27.44, P<0.001). In addition, the SL of fish averaged a significant 1.2 mm greater in the control than in predator exclusion treatments (Fig. 6, $F_{1,517}$=6.55, P=0.01). The interaction between the habitat and predator access was not significant ($F_{1,517}$=1.277, P=0.26); however, there was a significant block effect ($F_{4,12}$=3.75, P=0.03).

Discussion

Effects of predation on the distribution, abundance and size frequency of recruits

Although predation is often hypothesized to be an important process determining the distribution of seagrass fishes (reviews by Heck and Orth 1980; Orth et al. 1984), experimental evidence supporting this hypothesis is sparse. Manipulative field experiments by Bell and colleagues (Bell and Westoby 1986; Bell et al. 1987) suggest that at small spatial scales (meters) habitat selection rather than predation is the leading determinant of fish distributions. Our results are consistent with this hypothesis. We invariably found more pinfish recruits in "grass" than in sand habitats. Moreover, the effects of predation did not vary between sand and "grass" habitats. If predation produced the pattern of greater fish density in "grass" than sand habitats, then one would predict a greater effect of predators in sand than "grass" habitats, as shown by Summerson and Peterson (1984). This prediction was not fulfilled. If fish were restricted to "grass" habitats in an effort to avoid predation, then one would also predict that the effects of predators would be greater in sand than "grass" habitats. Thus, the much higher recruitment of pinfish to "grass" than sand patches and the equivalent effect of predation in both sand and "grass" suggest that habitat selection rather than the direct or indirect effects of predators is responsible for this pattern.

The small size of the experimental "grass" habitats may have reduced the value of these plots as refuges and thus unnaturally increased rates of predation. However, seagrass habitats are often very patchy at small spatial scales (Fonseca and Kenworthy 1987; Robbins and Bell 1994; Irlandi et al. 1995), and individual patches of seagrass <1 m^2 that are isolated from other seagrass patches are common (Irlandi 1996). Thus, although the experimental plots used in these experiments were small, they were representative of some types of natural seagrass habitats.

While predation did not appear to affect the distribution of pinfish, the exclusion of predators did have a strong effect on the abundance of fish. In both sand and "grass" habitats we found about 1.8 times the number of fish in cage than in cage-control treatments. Consequently, predators may affect the local population size of pinfish, even if they do not affect the distribution of recruits among habitats. In a methodologically similar caging experiment, Bell et al. (1987) found that the wrasse *Achoerodus viridis* recruited in similar numbers to caged and cage-control artifical seagrass plots, and therefore concluded predation was not important in their system. However, they noted that these wrasses recruited as readily to the structure of the cage as to their artificial seagrass, so that the addition of a cage resulted in a >171-fold increase in recruit density. Since *A. viridis* appears to cue in on structure and does not occur in sand habitats to any great extent, Bell and co-workers were unable to examine the significance of recruitment versus post-recruitment predation in sand habitats because of cage artifacts present in this experiment. Although pinfish recruits were present in higher densities in our "grass" habitats, large numbers of recruits ($>50\ m^{-2}$) did occur in sand. Because an unstructured sand plain appears to represent a viable alternative habitat for these fish, our experiment did not suffer caging artifacts as strong as those that have plagued other caging studies with fish (e.g., Doherty and Sale 1985; Bell et al. 1987). In preliminary work, we did not find a difference in pinfish densities between no cage and cage control patches (see preliminary data in methods). Furthermore, pinfish densities in uncaged control plots in the food addition experiment were similar to those we measured in our caging experiment (Fig. 1 versus Fig. 5). Although these two experiments were conducted several weeks apart, this observation in combination with our preliminary work supports the notion that caging artifacts were minor in our experiment. Thus, we conclude that the strong effect of predation on the abundance of pinfish in our experiment was real.

There was also a clear difference in the sizes of fish in predator access versus control plots. Fishes in plots that were exposed to predators were significantly larger than those in predator exclusion plots. This pattern suggests that predators differentially preyed upon smaller recruits, or that the reduced density in plots exposed to predation resulted in faster growth rates of survivors. Carr and Hixon (1995) also demonstrated that the experimental removal of predators on coral reefs resulted in a significant decrease in the size of a damselfish. Juvenile blue crabs appeared to be the most abundant predator in our site, and are size-selective predators (West and Williams 1986; Micheli 1995). Kneib (1982) demonstrated that blue crabs actively feed in a size-selective manner on another estuarine fish, *Fundulus heteroclitus*, although the large blue crabs in his study appeared to affect larger, adult *F. heteroclitus* (50 mm SL) more than smaller larvae and juveniles (10–20 mm SL). The small blue crabs in our site may prey selectively on smaller size classes of pinfish if they are easier to capture, and this would produce the pattern we observed.

Flounder were also present in our site and could have impacted pinfish populations. In North Carolina estuaries, southern flounder *Paralichthys lethostigma* appear to prey on the largest size classes of small fishes such *Cyprinodon variegatus* and *Fundulus heteroclitus*, and intermediate size classes of larger fish such as spot *Leiostomus xanthurus* (Wright et al. 1993). Consequently, flounder may have depressed pinfish numbers, but seem an unlikely cause of the size shift we observed. It is also possible that the difference in pinfish size between predator-exclusion and control plots was the result of the cage mesh excluding larger fish. However, since the larger fish in control plots averaged <17 mm SL and the cage mesh was 25 mm, it seems unlikely that the cage mesh had much of an effect. Additionally, Bell et al. (1987) used cages with 13 mm mesh, yet the modal length of *A. viridis* was 34 mm. Thus, it seems unlikely that our larger mesh filtered smaller sizes classes since the largest fish we captured was 25.8 mm; however, in the absence of direct experimental evidence this remains a possibility.

Effects of food supply on the distribution, abundance and growth of recruits

When we experimentally added food to sand and "grass" plots, there was no effect on the density of pinfish recruits and this result was consistent in both habitats. Since newly settled pinfish readily consume zooplankton (Livingston 1980; Stoner 1980b; Luczkovich et al. 1995), it is not surprising that artificial food supply did not affect either the between-habitat distribution of fish or their abundance within habitat types. As pinfish age and their diet shifts towards benthic invertebrates and plant matter (Darcy 1985), it is possible that the distribution of benthic prey will play a larger role in their distribution or abundance. For example, Levin (1994) showed that the distribution of a temperate wrasse that consumes seaweed-associated invertebrates was related to the distribution of its prey. Thus, small-scale patchiness of prey species within seagrass beds, may produce corresponding patchiness of pinfish.

The addition of food had a significant effect on the growth rates of pinfish. The growth rate of fish in food-addition treatments was $0.02\ mm\ day^{-1}$ greater than in control plots. This small daily difference would produce a difference of 0.2 mm in length by the end of our 10-day supplemental feeding, and if this growth rate continued it would produce a 1.4 mm difference after 68 days, the mean age of the fish on our plots. This value is close to the significant 1.5 mm difference we observed between sand and "grass" habitats. If predation is size-dependent, as suggested by our predator exclusion experiments, then differences in growth rates may have important consequences for dynamics of pinfish populations.

In the analysis of our food-addition experiment, we did not find a significant interaction between habitat type and food supplementation, suggesting that the effect of adding food was equivalent in both habitats. However, this result is misleading. We held the amount of food added to each plot constant, yet fish densities were about 3 times greater in “grass” than in sand plots. Consequently, per capita delivery of food was far less in “grass” compared to sand habitats. The fact that we did not find a significant interaction between food-supplementation and habitat type even though per capita rates of food addition were greater in the sand than “grass” habitat, suggests that (1) fish were able to use smaller amounts of food available per individual in the “grass” to achieve similar growth rates to those in the sand, and/or (2) the reduction in flow velocity by attenuation of wind waves by artifical grass resulted in the deposition of suspended food particles (Peterson et al. 1984). When we examined length-age relationships we found growth rates of fish to be greater in “grass” than in sand habitats, and the analysis of otolith microstructure also suggested that growth was greater in the “grass”, although this was not statistically significant. The evidence from this experiment demonstrates that food supply limits the growth rate of pinfish, and that either available food resources are more readily utilized in vegetated than in unvegetated habitats, or the delivery of food is greater to vegetated habitats. Work in freshwater tidal creeks suggests that foraging profitability of blue spotted sunfish *Enneacanthus gloriosus* and mummichogs *Fundulus heteroclitus* is greater in vegetated rather than unvegetated portions of creeks (Rozas and Odum 1988). However, studies investigating the effects of vegetation on growth rates of suspension-feeding bivalves provide evidence for the hypothesis that the deposition of suspending particles at the edge of seagrass beds is an important process affecting growth. Determining the mechanism producing higher growth rates of pinfish in the “grass” habitat will require further experiments in which per capita rates of food addition are held constant.

Studies on reef fish have demonstrated that supplemental feeding results in increased growth and/or earlier maturation rates (Jones 1986; Forrester 1990). In addition, Thresher (1983) found higher growth rates in fishes when potential competitors for food were experimentally removed from reefs compared to control reefs. In the Caribbean Carpenter (1990) and Robertson (1991) showed large increases in herbivorous fishes after the die-off of the grazing urchin *Diadema antillarum*, which depletes algae below levels maintained by fish grazing. In California kelp beds, Anderson and Sabado (1995) found that a planktivorous fish in environments with a high supply of plankton had greater growth rates than those habitats with a lower supply of plankton. These studies as well as the results presented here, suggest that food limitation may be a common phenomenon in marine and estuarine fishes.

Conclusions: why do pinfish use seagrass habitats?

The density of pinfish recruits in our experimental “grass” habitats was about three times greater than the density of recruits in sand habitats, and this corresponds with the general notion of pinfish as primarily seagrass inhabitants (Adams 1976; Nelson 1979; Livingston 1980; Stoner 1980a; Sogard et al. 1987). Our data suggest that the impact of predation on pinfish recruits is equivalent in both sand and vegetated habitats, and thus differential predation may not explain the higher recruitment of pinfish to vegetated habitats in Texas. Similarly, the facts that pinfish recruited in greater numbers to an artifical habitat composed of green ribbon than to a sand habitat, and that the addition of food did not affect densities of recruits, suggest that food supply is not of direct importance in determining the early distribution of pinfish recruits. The key to the higher recruitment of pinfish in vegetated than in unvegetated habitats may lie in size-selective predation and habitat differences in growth rates. Our data suggest that (1) predators may disproportionately affect small fish; and (2) a limited food resource may be more effectively utilized by fish in vegetated than in unvegetated habitats. Additionally, there may be increased benthic food resources in vegetated habtitats (Summerson and Peterson 1984). Pinfish recruits may select vegetated habitats because high growth rates allow them to more quickly achieve a size that is relatively safe from predation. Consequently, seagrass, per se, may not be a refuge from predation, but it could afford the opportunity for fish to achieve a refuge in size.

Pinfish in this study recruited in extremely high numbers to both sand and “grass” experimental plots. Indeed, the recruitment we observed was far greater than that reported by other studies in other locations (e.g., Adams 1976, Summerson and Peterson 1984; Fonseca et al. 1990, 1996). Thus, some caution is warranted before generalizing these results to other locations. Additionally, these were short-term experiments and it is possible that important patterns may not have had time to emerge during the experiment. However, it is clear that interactions between recruitment variability, competition, and predation are important in determining the distribution and abundance pinfish, and studying the interactive effects of these factors on demersal fish populations will be crucial to our understanding of the mechanisms underlying the population dynamics of marine and estuarine fishes.

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