Recruitment of Atlantic croaker, *Micropogonias undulatus*: Do postsettlement processes disrupt or reinforce initial patterns of settlement?*

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Abstract.–Understanding the relative importance of pre- and postsettlement processes is critical to understanding the population dynamics of marine fishes. Our goals in this study were 1) to examine habitat preference and habitat use of newly settled Atlantic croaker, *Micropogonias undulatus*, and 2) to determine if postsettlement growth or predation varied with habitat type. Field surveys showed no difference in croaker abundance among three estuarine habitats: marsh edge, seagrass, and sand. Behavioral experiments in laboratory mesocosms suggested that the pattern of similar use of habitats in the field results from a lack of preference among habitats. In a field experiment, croaker recruitment was greater to artificial seagrass than to sand habitats, but there was no difference in fish density in habitats with or without food supplementation. Moreover, growth rates were similar in both sand and artificial seagrass habitats and in habitats with or without food supplementation. In a second experiment, we were unable to detect a difference in the density of newly settled croaker between sand and artificial seagrass habitats, or between habitats with predator access limited by cages and cage controls. Our results demonstrate that newly settled croaker use different estuarine habitats similarly, and there does not appear to be a fitness consequence of using many habitats. We suggest that for habitat generalists, such as the Atlantic croaker, variability in larval supply will be a stronger predictor of population dynamics than will variability of habitat attributes.

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Understanding the causes of fluctuations in population abundance is critical for ecologists and fishery biologists. For marine fishes with life histories in which adults have limited home ranges and larvae are pelagic and advected vast distances from natal sites, an understanding of variability in larval supply to local populations is critical for understanding the mechanisms that produce dynamics in populations (Caley et al., 1996). In addition, habitat selection by settling fish (Carr, 1991; Levin, 1991; Wellington, 1992; Tolimieri, 1995), and habitat-specific growth and mortality (Heck and Orth, 1980; Hixon and Beets, 1993; Levin et al., 1997) may ultimately reinforce or disrupt patterns created by variable larval supply (Jones, 1997). Thus, knowledge of the degree to which processes such as habitat selection, competition, or predation modify initial patterns of larval settlement is important in understanding the population dynamics of marine species.

The importance of variability in postsettlement growth or mortality and the level to which postsettlement processes alter initial patterns of larval settlement can be a function of habitat structure. For example, on coral reefs, holes provide a refuge from predation, and on reefs with large numbers of holes, the importance of predation is reduced (Shulman, 1984; Hixon and Beets, 1993). Similarly, Atlantic cod settle in equivalent densities in a variety of habitats but suffer lower predation rates in structurally complex habitats (Tupper and Boutilier, 1995). Thus, habitat-specific mortality disrupts initial patterns of larval settlement. Differences in habitat structure may also impact growth rates or the ability of fish to procure food (Nelson, 1979; Heck and Thoman, 1981; Stoner, 1982). As examples, 1) pinfish have greater success capturing amphipods in shoal grass (*Halodule wrightii*) than in similar densities of turtle grass (*Thalassia testudinum*) (Stoner,

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1982); 2) Atlantic cod grow faster in seagrass habitats than in sand, rocky reef, or cobble habitats (Tupper and Boutilier, 1995); and 3) pinfish exhibit higher growth rates in seagrass than in sand habitats (Levin et al., 1997).

Atlantic croaker, *Micropogonias undulatus* (hereafter referred to as croaker), range from Cape Cod to Campeche Bank, Mexico (Johnson, 1978), and occur both offshore and in estuaries in a variety of habitats including mud, sand, and seagrass (White and Chittenden, 1977; Johnson, 1978; Rooker et al., 1998). Croaker are an important component of commercial fisheries in the Gulf of Mexico and southeastern United States, often dominating bottom fish landings, and are an important sport fishery in this region (Lassuy, 1983). In the Gulf of Mexico, croaker spawn over the continental shelf or near inlets from September to May with peak levels occurring before January (Johnson, 1978; Cowan, 1988; Cowan and Shaw, 1988). Larval croaker then move toward shore and may be transported hundreds of kilometers before entering estuarine nursery grounds (Cowan and Shaw, 1988; Norcross, 1991). In Texas, recruitment of croaker peaks in November (Rooker et al., 1998). It is not clear whether variability in abundance of juvenile croaker is the result of variability in larval supply or differential postsettlement growth and mortality.

The delivery of larval croaker recruits to estuarine nursery habitats is dependent on large-scale oceanographic processes (Cowan and Shaw, 1988). Once fish arrive at estuaries, delivery into suitable habitats is dependent on currents and tidal processes (Norcross, 1991). As fish that are competent to settle approach nursery grounds they have the opportunity to choose specific microhabitats. In this paper we examined patterns of microhabitat preference and use by newly settled croaker, as well as the consequences of microhabitat associations. Specifically we asked 1) Do croaker have specific microhabitat preferences and are these preferences reflected in patterns of abundance in the field? 2) Does food supply limit the number or growth rates of croaker recruits in different habitats? 3) Does predation determine the number of recruits in different habitats?

Methods

Habitat use by newly recruited croaker

To determine what habitats newly recruited Atlantic croaker use, we conducted a field survey during November 1996 at Christmas Bay (29°03'N, 95°10'W), near Galveston, TX. Christmas Bay is a shallow estuary and contains the most easterly well-developed seagrass bed in Texas. A detailed description of this site can be found in Thomas et al. (1990). The seagrass bed is dominated by *Halodule wrightii* with an average density of 10,469 shoots/m^2 (SE=461). An epibenthic sled was used to quantify fish abundance in three habitats: bare sand, seagrass meadow, and marsh edge. We defined marsh edge habitat as the subtidal substrata directly adjacent to a *Spartina alterniflora* marsh. The sled consisted of a 0.66 m × 0.5 m opening fitted with a 3-m long net (1-mm mesh) with a removable codend. Habitats were sampled by placing the sled on the substratum, extending a 15-m rope in a semicircular fashion (to avoid disturbing sampling area) and pulling the sled through a 10-m^2 area. Each habitat was sampled four times at two different sites, resulting in eight samples per habitat type. Differences in croaker density were examined with a two-way analysis of variance with both site and habitat type as fixed effects. In this and subsequent analyses, if we failed to reject the null hypothesis of no difference in croaker abundance between habitats, then power analysis was performed. If statistical power was low, we calculated the number of replicates required to achieve sufficient power to accept the null hypothesis.

To examine habitat preference we performed choice experiments in laboratory mesocosms. Six 117-L mesocosms were constructed from round circular plastic tanks (41.3 cm diameter × 60 cm). The mesocosms were filled with 5 cm of sand, a plastic mesh screen was placed on top of the sand, and an additional 5 cm of sand was placed over the mesh. Each tank was filled with filtered seawater and maintained at ambient light and temperatures. We divided mesocosms in half, with each half randomly receiving a sand or grass habitat. Sand habitat was the sand bottom described above. To construct seagrass habitats, cores of seagrass were randomly collected from the field and brought to the laboratory where they were washed and dipped in fresh water. After leaves were wiped to remove any epiphytic growth, the cores were planted in each mesocosm.

One croaker (15–20 mm SL) was introduced to the center of each mesocosm and monitored for any abnormal behavior for 24 h. After the initial acclimation period, the location of each croaker was visually determined hourly for ten consecutive hours. Visual observations were performed by a single observer peering into the mesocosm, without disturbing the fish. This was repeated for six mesocosms over two days for a total of 12 mesocosm observations. New fish were used for each trial. Percent occurrence in each habitat was determined for all twelve trials. A one-way t-test determined if percent occurrence in seagrass was different from 50%.

Effects of food supply on recruitment and growth of croaker in varying habitats

Field experiments were conducted in East Lagoon, located at the eastern most end of Galveston Island, TX (29°20'N, 94°44'W). East Lagoon is 1.6 km long, 0.48 km wide, and has a maximum depth of 4.6 m. Water is exchanged tidally by means of seven 0.92 m-diameter cement culverts with the Galveston Ship Channel, which runs from the Gulf of Mexico into Galveston Bay. A detailed description of this site can be found in Levin et al. (1997). Seagrass, once widespread in Galveston Bay, including East Lagoon, has decreased by 90% from peak levels (Pulich and White, 1991); no natural seagrass habitats presently are found in East Lagoon. The absence of natural seagrass beds allowed us to establish artificial seagrass beds with desired characteristics, without the confounding effects of a natural seagrass bed. Experiments were located >8 m from the *Spartina alterniflora* dominated marsh edge and placed at an average low tide depth of 42 cm.

To test the null hypothesis that food supply does not limit abundance or growth rates of croaker recruits in different habitats, we conducted an experiment in which food supply was manipulated in sand and seagrass habitats. On 20 February 1996 we created five blocks each consisting of four 1-m^2 experimental plots. Within each block, food supply and habitat type were manipulated orthogonally. To control for differences in seagrass structure or seagrass-associated food resources, we used artificial seagrass habitats. Artificial seagrass habitats were constructed from a 1-m^2 polyvinylchoride (PVC) (1.3 cm diameter) frame, strung with monofilament to form a grid consisting of 576 points. At each of these points a 16 cm × .5 cm strand of green ribbon was woven in, such that the frame consisted of 576 shoots of seagrass, each shoot having two leaves. No excessive fouling was observed on the frame or ribbon for the duration of the experiment. We performed a preliminary experiment to determine if the structure of the PVC-frame would attract more fish recruits than bare sand, and no difference was found between the bare sand plot and the PVC-frame ($F_{2,23}$=0.512, α=0.61, 1–β=0.76). Consequently we performed subsequent experiments without a PVC-frame control.

Food supply was experimentally manipulated with feeding tubes in each experimental plot. Feeding tubes were constructed of a 7.5-cm diameter length of PVC pipe attached to a 1.3-cm diameter PVC pipe stake, with the bottom of the tube about 15 cm from the substratum, and the top always above the water line. We provided supplemental food daily for seven days, from 23 February to 3 March 1996, to half of the sand and seagrass replicates (i.e. five sand and five seagrass plots received food). Food consisted of 200 g of fish flesh and 300 mL of water blended to produce plankton-size particles (Forrester, 1990; Levin et al., 1997). The fish purée was placed in ice cube trays and frozen. Each frozen cube yielded 11.8 g of fish flesh. One cube of frozen food was placed in the feeding tubes of appropriate replicates, whereas control plots received one ice cube and no food was added. As the ice cube containing food melted, it delivered a continuous stream of particles to the habitat for 5–15 min. We observed fish readily consuming the supplemented food in both the field and laboratory.

On 4 March 1996, the experiment was terminated by sampling each plot. Recruit density was quantified by using 1 m^3 (1 × 1 × 1 m) drop samplers (Zimmerman et al., 1984; Fonseca et al., 1990). Drop samplers were constructed of 9.5-mm diameter rebar covered on four sides with taut 2-mm nylon mesh. A dip net (90 × 100 cm, 2-mm nylon mesh) was used to retrieve fish from the samplers, and replicates were considered adequately sampled when five consecutive passes of the dip net yielded no fish (Fonseca et al., 1990). A blocked two-factor analysis of variance was used to test the hypotheses that the abundance of newly recruited croaker did not vary among habitat or food supplemented treatments.

Five fish from each replicate were haphazardly selected for further analysis. We measured the 80 selected fish to the nearest 0.1 mm (SL), removed their otoliths, and stored them in immersion oil for one week. Fish age was then determined by enumerating the daily growth rings on the lapillar otolith by using an image analysis system. The existence of daily rings on croaker otoliths has been validated previously (Nixon and Jones, 1997). Each otolith was examined independently three times. If two of the three counts did not agree, the fish was discarded and another selected. When two of the three counts were the same, that count was used as a datum in the analysis.

Differences in growth rates were examined by using otolith microstructure. Because otolith diameter was correlated to fish length (r=0.73, n=75), we used otolith measures as a proxy for growth rate. Measurements were taken inward from the edge of the otolith to the seventh ring. This distance corresponded to growth during our seven days of food supplementation. Otolith distances (μ) were then converted into daily growth rates (mm SL/day), by using the following equation generated from a regression of otolith diameter on fish length:

$$Growth = \left[(otolith\ distance + 0.002)\ /\ 0.014\right]/7.$$

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 croaker to varying habitats

The null hypothesis that predation has no effect on recruitment of croaker in sand or seagrass habitats was tested by using cages to limit predator access to experimental plots. On 18 March 1996, a fortuitous seasonal low tide completely exposed the study site to air, allowing us to erect cages and to ensure that no recruits or predators occupied the cages at the start of the experiment. Cages ($2 \times 2 \times 1$ m) were constructed with 25-mm mesh on four sides, whereas cage controls had mesh on two sides. Mesh was large enough to be transparent to croaker recruits, but fine enough to prevent predators from entering the cages. A randomized block design was employed, with habitat (sand or grass) and predator access (cage or cage control) as fixed effects. Replicates were placed 8 m apart, and blocks were separated by 10 m. The experiment was terminated after 7 d. Drop samplers were used to quantify recruits as described previously.

Results

Habitat preference and use by newly recruited croaker

The density of newly settled croaker (mean TL=14.48, SE=0.15) did not differ among sand, seagrass, or marsh edge habitats ($F_{2,18}$=0.86, α=0.44, β=0.13) (Fig. 1). The density of croaker recruits also did not vary between sites ($F_{1,18}$=0.09, α=0.77) and the interaction between habitat and site was not significant ($F_{2,12}$=1.07, α=0.37).

Our observation on the behavior of croaker recruits in mesocosms did not reveal a preference between sand and seagrass habitats (one way *t*-test, *t*=1.64, df=11, α=0.13). An average of 36% (SE=16) of the time was spent in seagrass, and 64% (SE=16) in sand.

Effects of food supply on croaker recruitment and growth in varying habitats

The abundance of newly settled croaker differed between experimental habitats ($F_{1,11}$=5.98, α=0.03) with greater recruitment in sand ($\bar{X}$=31.6/m^2, SE=6.5) than in seagrass habitats ($\bar{X}$=13.7/m^2, SE=5.9) (Fig. 2). Conversely, we did not detect a difference ($F_{1,11}$=0.13, α=0.73) in the number of croaker in food-supplemented plots ($\bar{X}$=23.2/ m^2, SE=8.3), compared with control plots ($\bar{X}$=22.1/m^2, SE=4.1) (Fig. 2). The interaction between habitat and food-supplementation was not significant ($F_{1,11}$=0.96, α=0.35). The statistical power of this experiment was low (1–β=0.18);

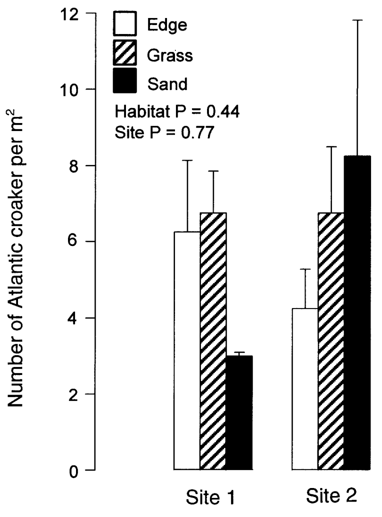

Figure 1

Atlantic croaker densities (mean +1 SE) sampled from three estuarine habitats: marsh edge (edge), seagrass bed (grass), and barren sand (sand). *P* values from two-way analysis of variance.

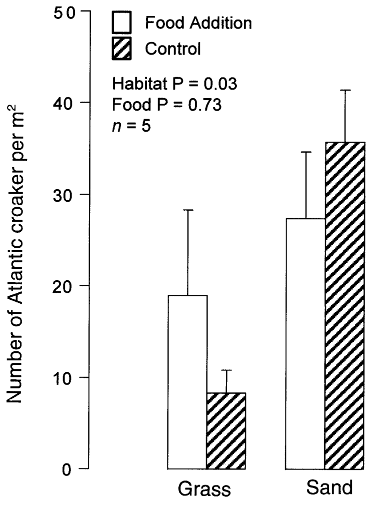

Figure 2

Atlantic croaker density (mean +1 SE) in 1-m^2 artificial seagrass (grass) and sand habitats, with (food addition) and without (control) food supplementation. *P* values from a blocked two-factor analysis of variance.

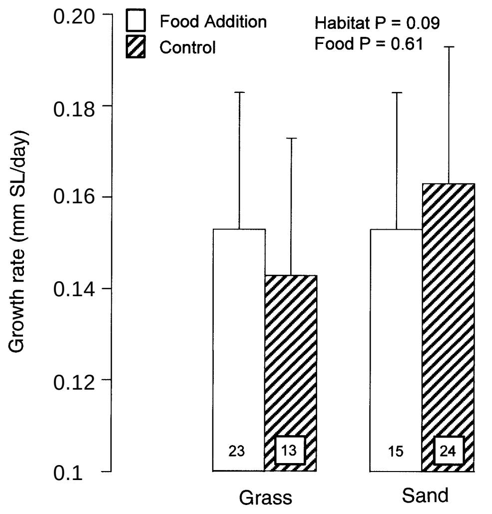

Figure 3

Growth rate (mean +1 SE) determined from analysis of otolith microstructure in croaker from 1-m^2 artificial seagrass (grass) and sand habitats with (food addition) and without (control) food supplementation. *P* values are from a blocked two-factor analysis of variance, and *n*, the number of fish sampled, is given at the base of each bar.

however, given the small difference in average croaker density between food-supplementation and control plots (1.1/m^2) and the high within-treatment variation, we would have needed 55 replicates to achieve sufficient power ($1-\beta=0.95$) to accept the null hypothesis of no difference between treatment means.

Growth rates of newly recruited croaker were the same in sand and grass habitats ($F_{1,70}=2.79$, $\alpha=0.09$, $\beta<0.001$), as well as with or without food supplementation ($F_{1,70}=0.26$, $\alpha=0.61$, $\beta=0.004$) (Fig. 3). The interaction between habitat and food-supplementation on the growth rate of newly recruited croaker was not significant ($F_{1,70}=0.49$, $\alpha=0.49$). Growth averaged 0.148 mm SL/day (SE=0.03) in grass and 0.158 mm (SE=0.03) in sand. Average growth rates of 0.153 mm/day (SE=0.03) were observed for both control and food addition treatments (Fig. 3). These growth rates are similar to growth rates reported elsewhere (Warlen, 1981; Cowan, 1988; Nixon and Jones, 1997), suggesting that our back calculation of growth rates from otolith measures were not seriously biased.

Effects of predation on recruitment of croaker to varying habitats

When we examined recruitment of croaker to experimental plots with or without predator access, we were unable to detect an effect of predation on croaker recruitment ($F_{1,12}=0.01$, $\alpha=0.92$) (Fig. 4). Croaker density averaged 10.7/m^2 (SE=3.8) in the caged replicates, and 15.8/m^2 (SE=10.1) in cage controls (Fig. 4). In contrast with the food supplementation experiment, we did not detect a difference in recruitment between grass and sand habitats ($F_{1,12}=0.96$, $\alpha=0.34$) (Fig. 4). The interaction between habitat and predator access was also not significant ($F_{1,12}=0.10$, $\alpha=0.76$). This experiment also suffered from low power ($1-\beta=0.06$). Sufficient power to accept the null hypothesis of no difference in croaker density between cage and cage-control treatments ($1-\beta=0.95$), would have required 550 replicates.

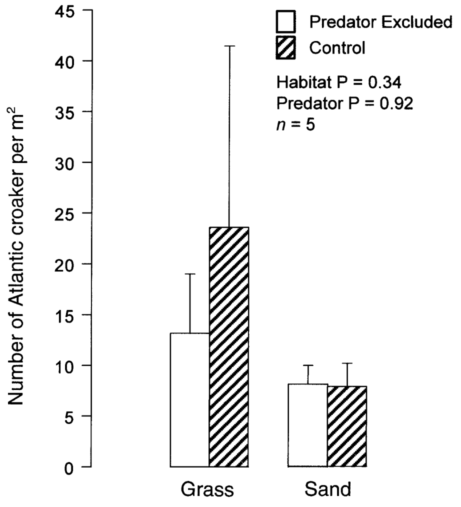

Figure 4

Atlantic croaker density (mean +1 SE) in 1 m^2 artificial seagrass (grass) and sand habitats with predators excluded and allowing predatory fish and decapod access (control). *P* values from a blocked two-factor analysis of variance.

Discussion

Recruitment of fishes with open populations is affected by variability in larval supply (Jenkins et al., 1996; Hamer and Jenkins, 1997), habitat selection by settling larvae (Bell et al., 1987) and postsettlement mortality (Orth et al., 1984), growth (Levin et al., 1997), and migration (Sogard, 1989). Understanding how these processes interact with each other to determine population size has been a major focus of researchers on tropical and temperate reefs (Doherty and Williams, 1988; Caley et al., 1996) and recently in seagrass meadows (Bell et al., 1987; Jenkins et al., 1996; Hamer and Jenkins, 1997). There has also been a growing awareness that understanding how demographic processes vary with habitat structure will be critical for predicting population size in fishes that occur in heterogeneous habitats (Levin, 1994). In this study we examined patterns of abundance of newly settled Atlantic croaker and demonstrated that these fish use different estuarine habitats similarly. The results of our mesocosm experiment suggest that the pattern of similar recruitment in different habitats results from a lack of preference for specific habitats. In addition, when we investigated habitat differences in postsettlement growth or survivorship, we were unable to detect strong consequences of using one habitat over another.

We found no evidence suggesting that habitat selection by settling larvae and habitat-specific postsettlement mortality are important in determining population size in croaker; however, this conclusion is based on nonsignificant statistical tests rather than explicit acceptance of the null hypothesis of no difference between treatments. Recent reviews have stressed the importance of power analysis in detecting a type-II errors (Peterman, 1990; Reed and Blaustein, 1995; Thomas and Juanes, 1996), and because we wished to draw conclusions from “negative” results, power analysis was particularly important. In this study, when a difference between treatment means was not detected, we examined power in an attempt to determine our ability to accept the null hypothesis. If the power of the test was too low to accept the null hypothesis ($\beta \leq 0.05$), the number of replicates required to achieve this power level was calculated. For example, no difference was detected in mean croaker number between plots from which predators were excluded and control plots, but the power of this experiment was low ($1-\beta=0.06$). Sufficient power to be able to accept the null hypothesis, would have required 550 replicates. Our level of replication was inadequate because of the extreme variability in croaker densities among experimental plots—variation likely produced by a combination of stochastic settlement and habitat-specific mortality. The effect of this variability was to weaken the power of our experiments to detect small, but real differences among treatments. Although our experimental design precluded the detection of small treatment effects, the high number of replicates required to detect these small effects suggests that other processes are likely to be more important in determining variability in abundance.

Although many estuarine species select vegetated over unvegetated habitat at settlement (Orth et al., 1984), in some cases, initial patterns of settlement have little to do with habitat selection by individual organisms. Settlement may occur at the first suitable habitat encountered regardless of specific attributes of that habitat (Bell and Westoby, 1986). Additionally, current patterns may exclude delivery of competent larvae to some habitats (Morgan et al., 1996); therefore, even ideal habitats may seldom receive recruits. In such cases, larvae do not select against a habitat, instead that habitat is never an available choice. By experimentally providing habitats, and by using a blocked sampling design such that all habitats were available in a particular location, we eliminated the possibility that settling croaker would not have the opportunity to choose a habitat. In our field sampling and experiments, croaker had the opportunity to choose between vegetated and unvegetated habitats, but they did not consistently choose one habitat over another. By contrast, in an identical experiment performed at the same time and in the same study site, pinfish (*Lagodon rhomboides*) showed strong responses to habitat, food supply, and predators (Levin et al., 1997). Pinfish occurred in much higher densities in vegetated than in unvegetated habitats and also grew faster in grass habitats supplemented with food than in unsupplemented or unvegetated habitats. In addition, the presence of predators reduced pinfish numbers by 50%. The pinfish and croaker occupying experimental plots were similar in size (15–25 mm SL), and at this size the diets of the two species are similar (Darcy, 1985; Soto et al., 1998). Thus, it is likely that the lack of response by croaker to the habitat attributes we investigated is the result of characteristics of the species rather than an artifact of sampling or experimental design.

Selection for specific habitats at settlement may overwhelm variation in larval supply, thus producing variability in recruitment that is associated with the preferred habitat. This appears to be the case for pinfish (Levin et al., 1997). Although croaker often form part of fish assemblages within seagrass (Rooker et al., 1998), they appear to have broad microhabitat preferences, and our results suggest that there is no strong fitness consequences for croaker using vegetated versus unvegetated habitats. As a result, resources associated with the benthic habitat seem unlikely to determine population size of newly recruiting croaker. Rather, where and when larvae that are competent to settle are delivered should determine population size in croaker. The contrasting results for croaker and pinfish may reflect a more general difference in the processes determining population sizes of fish. For fishes, such as pinfish, where settling larvae select specific habitats and postsettlement processes reinforce initial settlement patterns, spatial and temporal variability in habitat should be a strong predictor of future population size. Habitat generalists, such as croaker, can occupy a range of habitats in any particular location, and thus variability in a specific resource may not determine population size. Consequently, processes affecting larval supply will be more important predictors of population size than resource-related characteristics.

Generalizations about the relative importance of processes affecting recruitment in fishes have been elusive (Caley et al., 1996). Although it is widely recognized that understanding the roles of both pre- and postsettlement is critical, there is still little consensus on the relative importance of different processes in determining population size. We suggest that neglecting the behavioral and ecological characteristics of individual species may be a major obstacle in reaching widely accepted generalizations about processes affecting recruitment. By performing similar experiments on different species we may uncover generalizations about processes affecting fish populations that have thus far been difficult to attain.

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