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# Experimental Evaluation of Potential Effects of Habitat Size and Presence of Conspecifics on Habitat Association by Young-of-the-Year Red Snapper

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**The potential effects of habitat size and the presence of larger conspecifics on habitat association by young-of-the-year (YOY) red snapper *Lutjanus campechanus* was evaluated in 2.2 m$^3$ laboratory tanks. Our results indicate that YOY red snapper have a strong affinity for structure, which ranged in these experiments from open-sand bottom to concrete-block, artificial reef–like habitats. Mean distance of YOY red snapper from the blocks decreased significantly and the time spent near the structures increased significantly as the size of the habitat increased. However, when larger subadult snapper were present, both distances to the reefs and time that YOY spent near them was significantly reduced, as the larger conspecifics actively defended the structure from occupation by YOY. If similar interactions occur in situ, small snapper that attempt to move onto reefs from the shrimping grounds that serve as nursery areas for juveniles may be subject to predation pressures by piscivorous fishes inhabiting the reefs. Finally, in experiments that used both larger conspecifics and alternate prey similar in size to the YOY red snapper, results indicated that larger snapper preferentially consumed the alternate prey and did not cannibalize the YOY red snapper. Nevertheless, YOY still were not permitted to occupy the artificial reef habitats in any experiments when larger conspecifics were present in the tanks. If results of these experiments are exportable to the field, they may partially explain the observation that YOY red snapper in natural populations are more often found in shallower water on shrimping grounds, whereas larger juveniles begin to recruit to the offshore reefs once they have obtained a size refuge. If additional studies conclude that YOY red snapper are attracted to larger or more complex habitats but avoid these structures because of pressure from larger juveniles and/or adults, the strategy of continued placement of artificial reefs large enough to attract adult snapper and other piscivores in and near the inshore shrimping grounds should be reassessed.**

The red snapper *Lutjanus camphechanus* is an exploited reef fish in the Gulf of Mexico's (Gulf) snapper-grouper complex that has been commercially important since the late 1800s (Goodyear, 1995). Today, the species is fished both commercially and recreationally (Schirripa and Legault, 1999) and is affected as shrimp fishery bycatch (Goodyear, 1995). Historically, high rates of exploitation caused red snapper stocks to decline throughout the Gulf until the early 1990s (Szedlmayer and Shipp, 1994). In recent years, the stock has begun to recover as a result of management actions (Schirripa, 1998); many have attributed this recovery in part to an increase in habitat in the form of artificial reefs (and oil and gas platforms). This is especially true off coastal Alabama, where >20,000 reefs have been constructed since the 1950s, within 3,100 km$^2$ of permitted artificial reef zones (R. Havard, Alabama Department of Conservation-Marine Resources Division, pers. comm.).

However, factors that affect red snapper population dynamics are poorly known, and there is a persistent and fundamental argument about whether deployment of artificial reefs makes reef fishes more susceptible to exploitation by aggregating individuals or, if the species are habitat limited, whether artificial reefs enhance fish recruitment and biomass production (Bohnsack, 1989; Lindberg, 1997; see papers published in *Fisheries*, April 1997, for review). Toward this end, it has been hypothesized that the two most important factors generating the recruitment bottleneck faced by young-of-the-year (YOY) reef fishes are habitat limitation and density-dependent relationships such as predation and competition. In studies of both artificial (DeAngelis et al., 1979; Shulman et al., 1983; Behrents, 1987; Schroeder, 1987; Anderson et al., 1989; Hixon and Beets, 1989; Parazo et al., 1991; Bry et al., 1992) and natural habitats (Chandler et al., 1985; Shulman, 1985; Doherty, 1987; Richards and Lindeman, 1987; Shulman and Ogden, 1987; Jones, 1988; Hunte and Cote, 1989; Carr, 1989, 1991; Forrester, 1990; Stimson, 1990; Connell and Jones, 1991; Levin, 1991; Stein et al., 1992; Planes et al., 1993), recruitment of juvenile/YOY reef fishes can increase with an increase in reef habitat size and complexity. If substrate or habitat is reduced, a decline in the number of successful recruits occurs. Thus, many agree that recruitment is in part dependent upon the availability of suitable habitat (Shulman, 1985; Schroeder, 1987; Shulman and Ogden, 1987; Hixon and Beets, 1989; Bohnsack, 1990; Connell and Jones, 1991; Planes et al., 1993).

However, density-dependent effects of conspecific adults and other resident fishes on juvenile and YOY reef fishes also are important (Shulman et al., 1983; Shulman, 1985; Behrents, 1987; Jones, 1987, 1988; Richards and Lindeman, 1987; Magnhagen, 1988; Hunte and Cote, 1989; Stimson, 1990; Buchheim and Hixon, 1992; Fowler et al., 1992; Hixon and Beets, 1993; Caley, 1993) and can negatively affect early survivorship of newly settled individuals (Behrents, 1987; Magnhagen, 1988; Stimson, 1990; Fowler et al., 1992; Forrester, 1995; Hixon and Carr, 1997; Steele, 1997; Hixon, 1998).

Little is known about the interaction between adult, juvenile and YOY red snapper in and near artificial reefs. Adults aggregate on or near coral reefs, gravel bottoms, or rock outcroppings, as well as on artificial reefs, petroleum platforms, and wrecks. Young red snapper generally spend their first year of life on the inshore shrimping grounds but have been reported from a variety of habitats, including open sand, relict shell rubble, and artificial structures with some vertical relief (Moe, 1963; Mosley, 1966; Bradley and Bryan, 1975; Holt and Arnold, 1982; Nichols, 1990; Workman and Foster, 1994; Szedlmayer and Howe, 1997; Lee, 1998; Szedlmayer and Conti, 1999).

Although small red snapper have been collected from a variety of habitat types, their habitat preferences are not well understood. Some have proposed that juvenile red snapper prefer habitat with small-scale (cm) vertical relief (Lee, 1998; Szedlmayer and Conti, 1999), whereas other studies have failed to show an association between habitat type and the presence of juvenile red snapper (Workman and Foster, 1994; Gallaway et al., 1999). Lee (1998) collected age-0 red snapper off Alabama for diet analysis and reported that fish <100 mm SL tended to be found over open substrates, whereas larger juveniles (100–200 mm SL) were most frequently collected on low profile (<1 m) artificial reefs. In a laboratory study, Szedlmayer and Howe (1997) reported that age-0 red snapper more frequently associated with oyster shell habitat than open sand bottom. When all studies are taken together, however, it does seem apparent that small red snapper (<200 mm SL) do not frequently occur with larger red snapper on the same habitats. Anecdotal information gleaned from underwater video observation of artificial reefs by recreational fisherman (mostly spear fisherman) and our own ongoing studies of red snapper populations demographics on Alabama artificial reefs indicate that young snapper (<200 mm SL) rarely are found on reefs with larger juveniles and adults or are subsequently displaced (or consumed) from these habitats by larger snapper if the smaller fish arrive first. It is possible that behavioral interactions among different age classes of red snapper result in segregation, such that young red snapper are forced to occupy different habitats than adults, or that cannibalism or its threat can explain the absence of small snapper on artificial reefs.

In this study, we examined whether YOY red snapper preferentially associate with artificial reef habitat in large laboratory tanks both when larger subadult snapper are absent or when larger subadults are present. We use the term "subadult" to mean 2–3-yr old red snapper that have not yet reached sexual maturity. Specifically, we considered hypotheses concerning YOY habitat association and whether larger red snapper would consume YOY red snapper or alternate prey or both, if offered a choice. These hypotheses are as follows: (1) in the absence of subadult red snapper, there will be demonstrable differences in YOY habitat association, measured as distance from and time spent near artificial reef–like structures, compared with similar measures when subadults are present; and (2) given alternative prey of similar size to that of YOY red snapper, subadult red snapper will preferentially consume conspecifics.

## Methods

*Laboratory experiments.*—Experiment 1: Laboratory studies of YOY habitat association were performed in 2.2 $m^3$ circular tanks (243.84 cm in diameter) at the Dauphin Island Sea Lab, Alabama. While in holding, fish were fed pel-

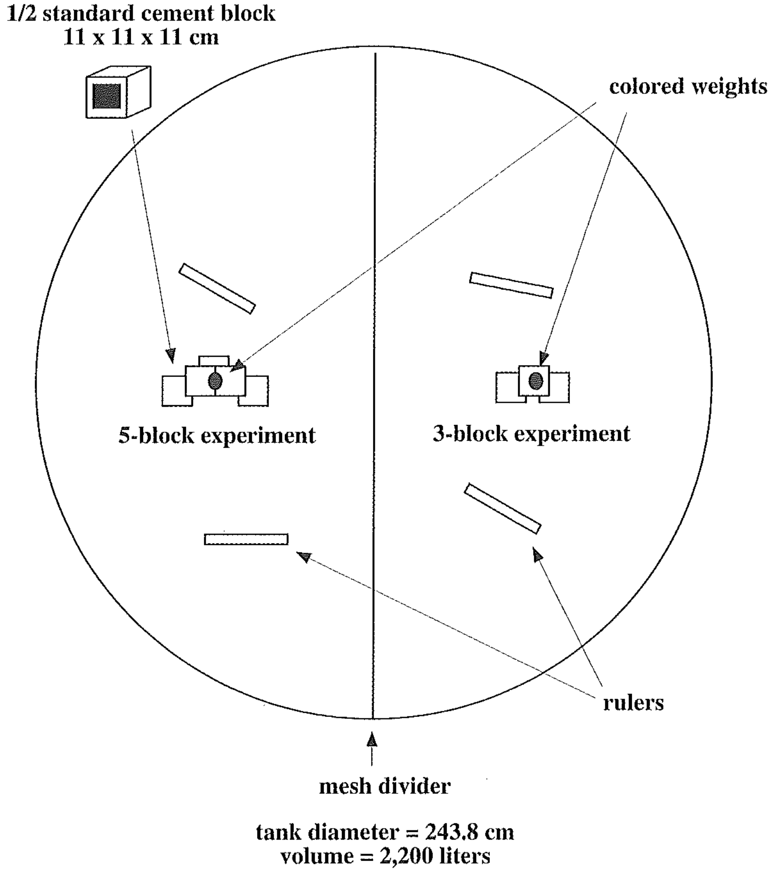


Fig. 1. Artificial reeflike structures placed in a divided 2,200-liter experimental tank. Shown are examples of the 3- and 5-block treatment arrangements, with rulers and colored weights. Figure is shown to scale.

lets, cut baits, and blended food, to insure good condition prior to initiation of experiments (Baird et al., 1991). Both experimental and holding tanks used filtered recirculating seawater maintained at 35 psu and 25 C and were isolated from outside interference by black plastic sheets surrounding the tanks.

Artificial reef structures were placed in the tank before equal numbers (12) of YOY red snapper were released into half of a divided tank; structures ranged in size from open sandy bottom (0 blocks) to 1, 3, and 5 blocks (Bohnsack, 1990) (Figure 1). The artificial reef–like habitats consisted of half cinder blocks ~11 cm across each side and were stacked uniformly one on two or two on three when necessary to maximize hole and surface area but to minimize differences in habitat complexity. The number of blocks to be placed in each tank half were randomly assigned prior to an experiment. YOY red snapper were introduced into the tanks at night and allowed to acclimate 12 hr before observations on habitat affinity were made the following morning (Magnhagen, 1988).

To quantify habitat association of YOY red snapper, observations were made directly from photographs, via video and still (slide) photography, recorded over a 4-hr period (Baird and Olla, 1991), with observations consisting of two still photographs and 5 min of videotape made once every half hour (Magnhagen, 1988). Observations were made from a deck high enough above the tank so as to isolate the fish from visual and mechanical disturbance. Two 350-mm graduated rulers were placed into each tank half to serve as references, and measurements of the number of visible snapper and their distance from the structure were taken from slide photographs. In the control experiments without blocks, the center of the tank was marked with a colored weight, and distance was measured from each snapper to the colored weight. Videotape provided further evidence of YOY habitat association on the basis of the estimated fraction of time spent near the reefs, with distance from the structure categorized as 0–20 cm (near the structure) and >20 cm (Carr, 1991; Connell and Jones, 1991). All experiments were replicated three times, with the recorded distances of all visible fish on 16 still photographs or the estimated time that each visible fish spent near or far the structure or the colored weight on eight, 5-min segments of videotape as the sampling units. Sampling units then were averaged over each trial (36 total trials) to produce the experimental units used in statistical analyses. YOY red snapper were chosen to insure that similar-sized individuals (~50–56 mm total length [TL]) were used for all replicates. Naive YOY red snapper were used for each trial, to minimize experimental bias (Buchheim and Hixon, 1992).

Experiment 2: A second group of experiments consisted of YOY red snapper as described above, but with the addition of two previously acclimated (for ~24 hr) subadult red snapper ranging in length from 360 to 367 mm TL to the tanks with the artificial reef–like habitats. In these trials, YOY were introduced into the experimental tanks with the larger snapper at night and acclimated in dark, circular flow-through containers open at the top that did not allow the larger snapper to see or reach the YOY. Approximately 1 hr after sunrise the following morning, YOY were slowly released from the container, at which time the 4-hr experiments were begun.

As with the previously described experiments, photographic observations were made to determine changes in YOY habitat association, due not only to changes in reeflike habitat size but also the presence of subadult red snapper on the reefs. Habitat association of subadult snapper also was recorded and quantified as described for YOY. Again, in all replicate experiments, no one individual red snapper (subadult or YOY) was used more than once.

Experiment 3: Experiments also were performed to test the effect of alternate prey on the habitat associations among the red snapper size groups. Alternative prey, similar in size to the YOY red snapper (i.e., longspine porgies *Stenotomus caprinus* or pinfish *Lagodon rhomboides*) were introduced as described for YOY red snapper. After the larger snappers were placed in the tank and their acclimation completed, six YOY red snapper plus six alternate prey were simultaneously released, and the measurements of habitat association were obtained as above. At the conclusion of the 4-hr trials, numbers of alternative prey or YOY red snapper consumed by older snapper were determined.

*Statistical analysis.*—All statistical analysis was performed by use of StatView 5.0, (SAS Institute, Inc., 1998). Prior to the analysis of variance (ANOVA) across all experiments, we first tested for equality of variance ($F$ test, $\alpha = 0.05$) and normality of distribution (K-S normality test, $\alpha = 0.05$) among dependent variables and for significant differences (ANOVA, $\alpha = 0.05$) among replicates for all experiments. Changes in the dependent variables, i.e., YOY mean distance from the blocks or from the center of the tank, and YOY mean arcsine percent time spent within 20 cm of the blocks or from the center of the tank were then analyzed by use of a 2 × 2 incomplete factorial ANOVA ($\alpha = 0.05$) with replication (36 total trials), with the number of blocks (reef size) and the presence or absence of larger (subadult) conspecifics as main-effect variables. Similarly, changes in the dependent variables subadult mean distance from the blocks or from the center of the tank, and subadult mean arcsine percent time spent within 20 cm of the blocks or from the center of the tank were analyzed by use of 2 × 2 incomplete factorial ANOVA ($\alpha = 0.05$) with replication (24 total trials), with the number of blocks and the presence or absence of alternative prey as main effect variables. Finally, the effects of alternative prey on the previously described YOY dependent variables were analyzed by use of a 2 × 2 incomplete factorial ANOVA ($\alpha = 0.05$) with replication (24 total trials), with the number of blocks and the presence or absence of alternative prey as main effect variables. Any significant main effects were further tested by use of Fisher's PLSD ($\alpha = 0.05$) to distinguish differences among individual treatment group means.

The reader should be aware, however, that because of limited wet-laboratory space, the aforementioned experiments were not performed contemporaneously, nor were all possible treatment combinations investigated (e.g., runs with YOY and alternate prey together in tanks without subadults, subadults only in tanks with alternate prey), which precludes a true factorial arrangement of experimental units. Thus, results from all experiments could not be collapsed into a single analysis because of singularities in the swept-out SSCP matrix.

TABLE 1. The mean sizes (mm TL) of all fish in Experiments 1 (YOY only), 2 (YOY and subadults), and 3 (YOY, subadults, and alternate prey). Like letters signify no significance between size groups. a and b are significant in ANOVA at the $P < 0.05$ level. (E) symbolizes those alternate prey that were consumed by adult red snapper.

| Treatment | YOY length ± SD | $P > F$ | Subadult length ± SD | $P > F$ | Alternate prey length ± SD | $P > F$ |
|---|---|---|---|---|---|---|
| 1 | 51.61 ± 10.19 | a | — | | — | |
| 2 | 53.84 ± 9.57 | ab | 362.00 ± 24.20 | a | — | |
| 3 | 56.02 ± 8.64 | b | 366.20 ± 23.35 | a | 64.00 ± 8.84 | a |
| | | | | | 64.89 ± 9.47 (E) | a |

## RESULTS

*Statistical comparisons of fish lengths between experimental groups.*—All dependent variables met the assumptions of ANOVA ($P > 0.05$) after arcsine transformation of the data recorded as percentage, and there was no difference in treatment means that was attributable to replicate for any of the dependent variables ($P >$ 0.05). With the exception of YOY lengths in Experimental groups 1 and 3 (Table 1), there were no significant within-group differences among experiments in the size (TL) of YOY snapper, subadult snapper, or alternative prey used. In addition, the length of alternative prey consumed by larger snapper was not significantly different from those that survived. However, the alternative prey used in Experiment 3 were slightly larger than YOY snapper used in the experiment (Table 1).

*Experiment 1 (YOY snapper only).*—Results with only YOY red snapper in the tanks showed that the mean distance of fish from artificial reefs varied with the number of blocks present in the tank (Fig. 2). The mean distance from the center of the tanks (control = 0 blocks) and the blocks, averaged over all replicates, decreased from open sand bottom control (69.72 ± 26.18 cm) to 1-block trials (34.81 ± 3.64 cm). Mean fish distance from the structure for 3- and 5-block trials was 9.60 ± 13.03 and 16.84 ± 6.57 cm, respectively (Fig. 2).

Block number explained a significant ($F$ = 7.105, $P$ = 0.0011) portion of the variance in the two-way ANOVA that used block number and presence/absence of subadults as main effects across all experiments (df = 36), with PLSD indicating significant ($P < 0.05$) differences in mean YOY distance in trials with YOY only in all combinations of 0–5 blocks, except the 3–5 block trials ($P$ = 0.9721).

From the video tape recordings, the time that YOY red snapper spent near blocks also was dependent on the number of blocks pre-

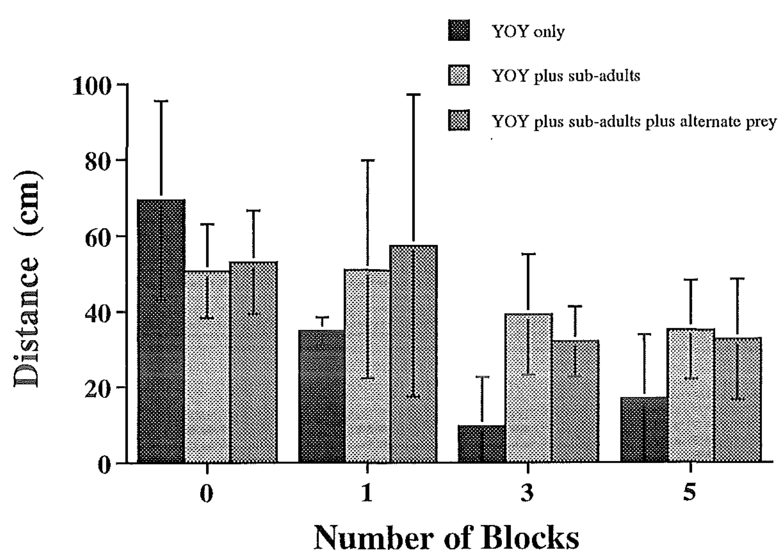


Fig. 2. Mean distance in cm of YOY red snapper from the colored weight in the center of the divided tank in the 0-block control runs, or from the blocks in experiments containing artificial reef habitat.

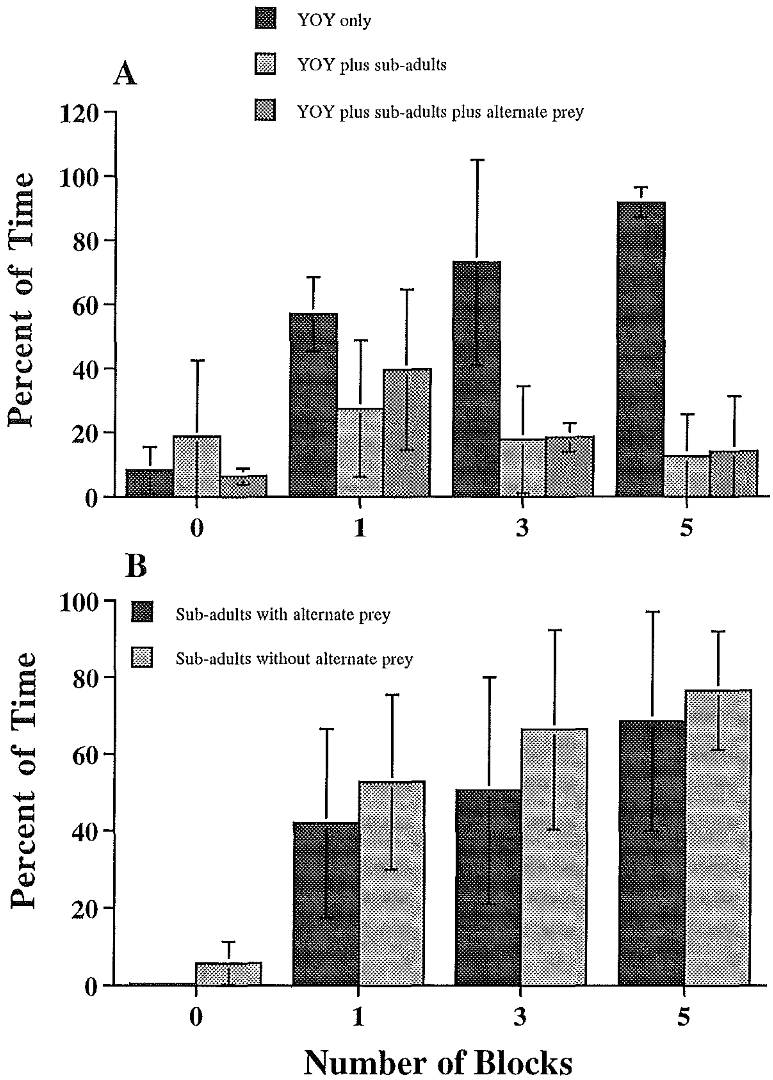


Fig. 3. Mean percentage of time spent within 20 cm of the colored weight in the center of the divided tank in the 0-block control runs, or from the blocks in experiments containing artificial reef habitat. (A) YOY red snapper. (B) Subadult red snapper.

sent (Fig. 3). In Experiment 1, YOY red snapper spent 8.2 ± 7.2% of the recorded time near (0–20 cm) the center of the tank in the control runs (0 blocks). The mean percentages of time spent near the reeflike structures (0–20 cm) increased to >57.0 ± 11.5% in 1-, 73.0 ± 32.0% in 3- and 91.7 ± 4.7% in 5-block trials.

Similarly, block number explained a significant ($F$ = 6.615, $P$ = 0.0016) portion of the variance in YOY time spent within 20 cm of the blocks in the two-way ANOVA that used block number and presence/absence of subadults as main effects across all experiments (df = 36), with PLSD indicating significant differences in mean time spent near the blocks in trials with YOY only between all combinations of 0–5 blocks ($P < 0.05$).

*Experiments 1, 2, and 3 (YOY plus subadults plus alternate prey).*—Red snapper YOY mean distance in Experiment 2 and 3 controls (0 blocks), ignoring the effects of presence or absence of alternate prey, was 50.65 ± 12.35 cm from the center of the tank but increased to 50.93 ± 28.69 cm in 1 block runs (Fig. 2). YOY mean distance then decreased slightly in 3- (39.12 ± 15.94 cm) and 5-block (35.06 ± 13.03 cm) runs when larger red snapper were present in the tanks. When alternative prey were present in the tanks with YOY and subadult red


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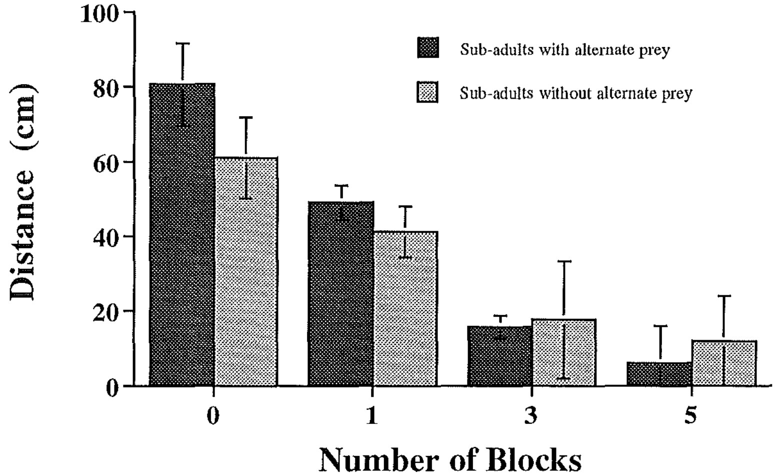


Fig. 4. Mean distance in cm of subadult red snapper from the colored weight in the center of the divided tank in the 0-block control runs or from the blocks in experiments containing artificial reef habitat.

snapper, results indicate that YOY habitat association was not affected, with mean distances from the reefs being similar to trials with subadults alone (Fig. 2).

The presence of subadult red snapper failed to explain a significant ($F = 3.25$, $P = 0.0828$) portion of the variance in the two-way ANOVA that used block number and presence/absence of subadults as main effects across all experiments (df = 36), nor was the interaction between block number and presence/absence of subadults significant ($F = 2.760$, $P = 0.0607$). However, it is apparent in Figure 2 that, when subadults were present in the tanks, YOY stayed farther from the blocks than when the larger fish were absent. We infer that lack of significance at $\alpha = 0.05$ is attributable to high variability in the observed distance measurements and thus are willing to accept $\alpha < 0.10$ as meaningful in this case.

In the two-way ANOVA that used block number and presence/absence of alternative prey as main effects in Experiments 2 and 3 (df = 24), neither block number ($F = 0.985$, $P = 0.4247$) nor presence/absence of alternate prey ($F = 0.002$, $P = 0.9619$) were significant main effects, which again implies that presence of subadult red snapper was the dominant factor affecting the distance of YOY snapper from the blocks.

The estimated percentage of time spent near the structure, with addition of subadult snapper, indicated that YOY red snapper spent <20% of their time near block(s) or near the center of the tank in controls (Fig. 3). These values changed little when alternative prey also were present in the tanks (Fig. 3).

The presence of subadult red snapper explained a highly significant ($F = 33.423$, $P = 0.0016$) portion of the variance in YOY time spent near blocks in the two-way ANOVA that used block number and presence/absence of subadults as main effects across all experiments (df = 36), and the interaction between block number and presence/absence of subadults also was significant ($F = 8.347$, $P = 0.0004$). It is apparent in Figure 3 that when subadults were present in the tanks, YOY spent less time near the blocks than when the larger fish were absent.

In the two-way ANOVA that used block number and presence/absence of alternative prey as main effects in Experiments 2 and 3 (df = 24), neither block number ($F = 0.666$, $P = 0.5851$) nor presence/absence of alternate prey ($F = 0.018$, $P = 0.8947$) were significant main effects, which further indicates that the presence of subadult red snapper also was the dominant factor affecting the time that YOY spent within 20 cm of the blocks.

Subadult mean distance from reefs, ignoring the effects of presence or absence of alternate prey, also was found to be dependent on the number of blocks present. Mean distance from the center of the tank in controls (0 blocks) was 61.02 ± 10.86 cm. With an increase in number of blocks, red snapper subadult mean distance from blocks decreased to 41.15 ± 8.84, 17.56 ± 15.61, and 11.68 ± 12.20 cm in 1-, 3-, and 5-block runs, respectively. These values changed little when alternative prey also were present in the tanks (Fig. 4).

In the two-way ANOVA that used block number and presence/absence of alternative prey as main effects in Experiments 2 and 3 (df = 24), block number explained a highly significant ($F$ = 11.851, $P$ = 0.0002) portion of the variance in subadult distance from the blocks, whereas the presence/absence of alternate prey had negligible ($F$ = 1.296, $P$ = 0.2718) effects, which indicates that habitat size was the dominant factor affecting habitat association in subadult red snapper.

The mean percentage of time that larger red snapper spent near the center of the tank (controls) or near blocks also increased with an increase in available habitat in the tanks. The larger subadult red snapper spent <6% of their time near the center of the tank in the 0-block controls, but this increased to 52.7 ± 22.8% when 1 block, 66.3 ± 26.0% when 3 blocks, and 76.5 ± 15.5% of the time when 5 blocks were present in the tank (Fig. 3). These values changed little when alternative prey also were present in the tanks (Fig. 3).

Similarly, in the two-way ANOVA that used block number and presence/absence of alternative prey as main effects in Experiments 2 and 3 (df = 24), block number explained a highly significant ($F$= 47.957, $P$< 0.0001) portion of the variance in the time that subadult red snapper spent within 20 cm of blocks, whereas the presence/absence of alternate prey again had negligible ($F$ = 1.480, $P$ = 0.2413) effects. Cannibalism did not occur in either the control trials in Experiments 2 and 3 or in those containing block(s). However, the subadult red snapper did consume some of the alternate prey in Experiment 3 trials (Table 1). Nine were consumed, including both pinfish and longspine porgies.

Although not precisely quantified, the behavior of YOY red snapper in control runs (0 blocks) across all treatments was similar, with fish appearing restless and swimming continuously around the sides of the experimental tank while avoiding the subadults when both were present. In 1-block trials, mean YOY distance from the block was higher when larger fish were present. Although the subadults, on average, did not spend more than a few minutes at a time around the block, they did actively defend YOY from occupying the blocks. In 3- and 5-block trials, larger snapper had a strong negative effect on habitat association of YOY in the tanks. Mean YOY distance from the blocks changed from ~10–15 cm without the subadults to >40 cm when larger snapper were present, whereas subadult distances from the reefs typically were <20 cm. Never did we observe a YOY move toward the structure while a subadult was facing them. Only when the larger snapper had their tails toward the group did some of the YOY swim toward the artificial habitat.

The distance measurements for subadults in the control runs (0 blocks) were similar to the YOY distance measurements in control runs in the absence of larger snapper. The subadults in the controls almost always stayed near the sides of the tank. They did not swim as continuously as the YOY in Experiment 1 but instead stayed close to one another against one side of the tank. Only when they began to chase YOY red snapper or alternate prey did they show any long-term movements. For the larger snapper in the tanks with only 1 block, apparently only one fish was able to occupy a block at any moment. In most instances, one subadult appeared to become dominant and actively denied access of YOY, or the second larger snapper, to the block. Those subadults that stayed near or in a single block appeared restless. Very rarely would they stay in the block for more than a few minutes at a time. They swam from the block to the tank side and back again to chase away the YOY that ventured too near the block. One block apparently was not sufficient habitat for two of the larger snapper. The subadults in the experiments with 3 and 5 blocks more aggressively defended the blocks from occupation by YOY. Nevertheless, YOY constantly tried to maneuver near the blocks. But as soon as the subadults recognized that YOY had moved toward the blocks, they immediately chased them off.

We interpret these combined results to indicate that habitat size strongly influenced habitat association in both size groups of snapper used in these experiments and that the presence of larger snapper was a major factor contributing to changes in YOY habitat association when both YOY and subadults were together in the tanks. The presence of alternative prey apparently had little effect on the interaction between the size groups of snapper.

## Discussion

*YOY red snapper habitat association.*—When only YOY red snapper were in the tanks, there was an inverse relationship between the number of blocks present and the distance of YOY from artificial reef habitat and a positive relationship between number of blocks and time spent near them, which indicates that YOY habitat association was influenced by the presence of structure. As the number of blocks increased, the distance from blocks decreased by >4-fold, and time spent near the reefs increased by


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>11-fold from the controls (0 blocks) to the 5-block trials. Thus, YOY red snapper appear to have a strong affinity for habitat with some vertical relief and/or refuge space. Similar results have been reported by other researchers for juvenile red snapper (Szedlmayer and Howe, 1997; Lee, 1998; Szedlmayer and Conti, 1999) and for other YOY reef fishes (Shulman, 1984; Anderson et al., 1989; Buchheim and Hixon, 1992).

Studies of artificial reefs placed off southeastern Florida found that small juvenile fishes recruited more often to artificial reefs than to sand bottoms (Bohnsack, 1990; Bohnsack et al., 1994). Hixon and Beets (1993) found that small juvenile fish, including juvenile grunts (fam. Haemulidae), were more abundant on artificial reefs with many holes than on reefs without holes and that removing small shelters from an artificial reef significantly reduced the number of small fishes (Hixon and Beets, 1989).

The mean distances of YOY snapper from blocks were not significantly different between the 3- and 5-block trials. Having 3 blocks in the tank apparently was sufficient shelter for 12 YOY, and two additional blocks in 5-block trials appeared to have little or no effect on YOY habitat association. Many researchers have found that juvenile fish abundance increases with habitat size but only up to a certain reef size. If artificial or natural reef becomes too large, the density of small fishes declines, because of either increases in the abundance of larger predators or competition (Shulman, 1984; Hixon and Beets, 1989, 1993; Bohnsack et al., 1994; Hixon and Carr, 1997). Moreover, Lindberg and Loftin (1998) found that the growth rate of juvenile gag grouper *Mycteroperca microlepis* decreased with increasing artificial reef size.

*YOY habitat association: modification by subadult snapper.*—Addition of larger subadult red snapper to the experiments changed the habitat associations of YOY red snapper dramatically. The distance measurements for YOY red snapper, in the presence of larger snapper, showed that YOY did not stay near artificial reef habitats in the tanks, nor did they stay near the larger fish. When subadults were present, the mean distances in 3- and 5-block experiments were ~40 cm, compared with 10–15 cm when larger snapper were absent. Although our ANOVA results did indicate a significant difference in the size of YOY red snapper between Experiments 1 and 3, the difference was ~5 mm TL; we do not consider this to be biologically meaningful. It is not expected that this small size difference can account for changes in habitat affinity displayed by YOY red snapper in our experiments. Therefore, because subadults were not used in Experiment 1, we conclude the change in mean distances from the block(s) between Experiment 1 and Experiments 2 and 3 are due primarily to the presence of larger snapper and defense of their habitat against occupation by smaller snapper. Similarly, Shulman (1985) showed that aggression in grunt schools affected the access of smaller conspecifics to shelter sites. Behrents (1987) and Buchheim and Hixon (1992) demonstrated that fierce interactions between adult and small juvenile gobies and blennies, respectively, prevented smaller fishes from staying in their shelter holes for any length of time.

Although we did not demonstrate that interactions between different size classes of red snapper directly increased the mortality rate of YOY in our experiments, Behrents (1987) found that recruitment and survivorship of juvenile bluebanded gobies *Lythrypnus dalli* was dependent on the number of adult conspecifics when shelter was limiting. As in the results with YOY red snapper, Behrents found that larger adults actively displaced smaller fishes from shelters. Stimson's (1990) results on the reef fish *Chaetodon miliaris* showed that by reducing adult densities, densities of new recruits increased. Forrester (1995) and Steele (1997) provided experimental evidence for the density dependence of postsettlement mortality of gobies in tropical and temperate reef environments, respectively. In both experiments, juvenile and/or adult goby densities were manipulated over natural (realistic) ranges observed in situ. For the temperate gobies (*L. dalli* and *Coryphopterus nicholsii*), over the period from the start of the experiment until the time when maturity was reached by each species (1–3 months), mortality was strongly density dependent, thus eliminating any linear relationship between adult density and recruit density. For the tropical species (*Coryphopterus glaucofraenum*), survival of adult gobies showed a strong inverse relationship with their initial density. Individually marked gobies, however, grew at similar rates across all densities, which suggests that density-dependent mortality was not associated with decreased growth rate and thus likely did not result from competition for food. In addition, accumulation of new recruits on reefs was also much lower when adult densities were high, compared with when adult densities were low (Forrester, 1995). Although evidence was weak, both studies implicated predation as the likely cause of the observed density-dependent mortality.

Although we did not include other predators in our experiments, changes in YOY red snapper habitat association consistent with our experimental results in the presence of larger conspecifics could make small snapper more vulnerable to predation in situ, even as cannibalism was not implicated. Hixon and Beets (1989, 1993) found a strong negative relationship between number of large adult piscivores and maximum number of smaller fish allowed on reefs. More recently, Hixon and Carr (1997) found that schooling carangids, as they swam between coral reefs, spent more time on reefs with high prey densities than on those with less prey. This led Hixon (1998) to caution that the mechanisms underlying density-dependent predation have not been thoroughly explored in reef fishes and suggested a mechanism for predator response whereby local distribution of predators may shift in response to local prey density, thus increasing density dependence (an aggregative response).

We suggest that shifts in predator distribution in response to changes in habitat via artificial reef construction potentially may provide another mechanism for an aggregative response. For example, Shipp (1999) concluded that placement of artificial reefs on the Alabama shelf led to a fundamental change in habitat that resulted in the displacement of small benthic fishes. Examination of table 1 in Shipp (1999) reveals that 66–87% of the specimens caught in trawls prior to deployment of the artificial reefs were juveniles. Some of these were juveniles of reef species that later, after artificial reef deployment, were harvested from the area as adults of exploitable size. This led Cowan et al. (1999) to suggest that the fundamental transformation of habitat occurred at the expense of a region on the shelf that previously provided a nursery function to many species of fishes. They further suggested that nursery habitat was traded for adult habitat, complete with a rich set of predators, without consideration of the ecosystem consequences of the tradeoff.

Although not directly quantified, we observed that over all treatments and block types, YOY red snapper attempted to maintain distance between themselves and their larger conspecifics. However, the difference in separation between YOY and subadults appeared to be somewhat lower in 5-block runs. This was most likely due to the increased refuge that larger structure provided. Larger numbers of blocks provided more hiding places that were out of sight of larger snapper than did 1- or 3-block trials. Behrents (1987) found that, when habitat was not limiting, juvenile gobies were able to persist by taking refuge from adults in numerous unoccupied shelter holes. A juvenile temperate reef blennioid fish *Forsterygion varium* had higher survival rates in areas of higher habitat complexity, even in the presence of larger resident adults due to high availability of shelter sites (Connell and Jones, 1991). In our experiments with YOY red snapper, two subadults could not occupy the entire artificial reef structure when it consisted of 5 blocks. This allowed for greater movement onto the blocks by YOY red snapper.

Similar to results with the YOY snapper, larger subadult red snapper showed a strong preference for artificial habitats over sand bottom. The larger the artificial structure, the more time subadults spent near block(s). Similar results have been found for large juveniles and adults of other reef species (Shulman, 1984; Behrents, 1987; Hixon and Beets, 1989, 1993; Bohnsack, 1990; Connell and Jones, 1991; Bohnsack et al., 1994). For red snapper, these results suggest that the larger the artificial reef, the greater the larger snapper's affinity will become for the structure, perhaps up to some critical reef size and depending on fish size and numbers. As with YOY in Experiment 1, subadult distances from blocks in 3- and 5-block trials were not appreciably different, presumably because adequate protection was afforded by having only 3 blocks in the tank.

*YOY and subadult snapper interactions: modification by alternate prey.*—Subadult red snapper mean distances from the blocks did not differ in trials between Experiment 2 and those with alternate prey in Experiment 3. This was result was anticipated because subadult association with the artificial reef habitat was not expected to vary with the addition of alternate prey. However, we did not perform runs with only alternate prey and YOY red snapper in tanks together, so we are unable to speculate about whether the presence of alternate prey on reefs would affect YOY habitat association.

The alternate prey apparently was more attractive as food for the larger snapper, perhaps because they were larger than the YOY red snapper used in the experiments (Table 1). Thus, ingestion occurred more frequently between subadults and alternate prey (9 times) than between subadults and YOY red snapper (0 times). Both of the alternate prey species were consumed.


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*Implications: recruitment and artificial reef construction.*—There is increasing evidence that large declines in YOY red snapper populations may be due in part to shrimp fishery bycatch (Nichols, 1989, 1990; Goodyear and Phares, 1990; Goodyear, 1992, 1995). This is a significant problem that may have negative affects on YOY red snapper recruitment to reef habitats. Because of high bycatch mortality, the recruitment bottleneck for red snapper may not be habitat limitation for older individuals. However, if hard-bottom reef-like habitats are made available to YOY near the shrimping grounds, it may be possible to greatly reduce YOY bycatch mortality both by providing new reef habitat and by providing refuge from shrimp trawls and predation. Shulman and Ogden (1987) found that factors controlling benthic mortality were far more important in determining adult population dynamics in French grunts *Haemulon flavolineatum* than was juvenile recruitment to reefs. They further hypothesized that, for two out of every three coral reef species that have been found to be recruitment limited, a decrease in benthic mortality may lead to a greater increase in adult populations than an increase in recruitment rates to reefs. If this is true for red snapper, and if it is possible to place artificial habitats in a way to attract YOY red snapper off the shrimping grounds without making them more vulnerable to larger predators, resource managers may be able to significantly reduce bycatch mortality and increase adult populations. Toward this end, future laboratory experiments should include the addition of alternate predators with YOY and larger red snapper. If larger red snapper are able to prevent YOY from recruiting to artificial reefs to which they are attracted, YOY may be more likely to be consumed by other predatory fish that inhabit reefs. A number of previous studies have suggested that if adequate refuge is not available, and if adult piscivorous fishes are abundant, predation may be the most important factor structuring reef fish communities (Behrents, 1987; Hixon and Beets, 1989, 1993; Bohnsack, 1990; Buchheim and Hixon, 1992; Caley, 1993; Bohnsack et al., 1994; Hixon and Carr, 1997; Hixon, 1998).

If the results of these experiments are exportable to the field, they may partially explain the observations that YOY red snapper in natural populations are more often found in shallower water on shrimping grounds, whereas larger juveniles begin to recruit to the offshore reefs once they have obtained a size refuge. If additional studies conclude that YOY red snapper are attracted to larger or complex habitats but avoid these structures because of pressure from larger juveniles and/or adults, the strategy of continued placement of artificial reefs large enough to attract adult snapper and other piscivores in and near the inshore shrimping grounds should be reassessed.

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