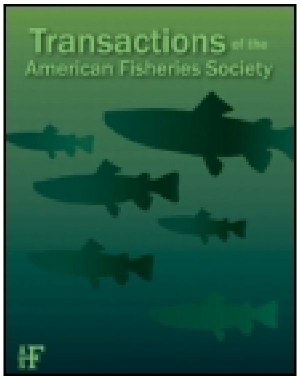
Proximity Effects of Larger Resident Fishes on Recruitment of Age-0 Red Snapper in the Northern Gulf of Mexico

Peter A. Mudrak and Stephen T. Szedlmayer

SEDAR31-RD24

13 August 2012



Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

Proximity Effects of Larger Resident Fishes on Recruitment of Age-0 Red Snapper in the Northern Gulf of Mexico

Peter A. Mudrak [a] & Stephen T. Szedlmayer [a]

[a] Department of Fisheries and Allied Aquacultures, Auburn University, 8300 State Highway 104, Fairhope, Alabama, 36532, USA

Version of record first published: 27 Mar 2012

To cite this article: Peter A. Mudrak & Stephen T. Szedlmayer (2012): Proximity Effects of Larger Resident Fishes on Recruitment of Age-0 Red Snapper in the Northern Gulf of Mexico, Transactions of the American Fisheries Society, 141:2, 487-494

To link to this article: http://dx.doi.org/10.1080/00028487.2012.667045

Transactions of the American Fisheries Society 141:487–494, 2012
© American Fisheries Society 2012
ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2012.667045

ARTICLE

Proximity Effects of Larger Resident Fishes on Recruitment of Age-0 Red Snapper in the Northern Gulf of Mexico

Peter A. Mudrak and Stephen T. Szedlmayer*
Department of Fisheries and Allied Aquacultures, Auburn University, 8300 State Highway 104,
Fairhope, Alabama 36532, USA

Abstract
Small artificial reefs (1.2 × 1.02 × 1.1 m) were placed near to (15 m; *n* = 20) and distant from (500 m; *n* = 20) larger artificial reefs (1.2 × 2.4 × 2.4 m; *n* = 20) in July 2008 and 2009, and each set of reefs (two small and one large) was placed 1.7 km apart at a site 28 km south of Dauphin Island, Alabama, in the northern Gulf of Mexico. Divers used visual surveys to identify and count all fish present on the small reefs and estimated fish lengths in 25-mm categories during August 2008, August 2009, and September 2009. Significantly higher numbers of age-0 red snapper *Lutjanus campechanus* were detected on the small distant reefs (500 m) than on the small nearby (15 m) reefs in all surveys. In addition, significantly higher densities of rock sea bass *Centropristis philadelphica* and pygmy filefish *Stephanolepis setifer* were observed on the small distant reefs compared with the small nearby reefs in both August and September 2009. Mean species richness was significantly higher on the small distant reefs than on the small nearby reefs in August 2009. Differences in reef fish community structure were detected in all three surveys by using nonmetric multidimensional scaling based on Czekanowski's similarity coefficient. This study indicates that if artificial reefs are built to provide habitat for juvenile red snapper, they should not be placed in areas immediately adjacent to existing adult habitat; conversely, habitats intended for adult fish should not be placed near important red snapper nursery areas.

Many biological and physical processes can regulate reef fish abundance, with most fishes showing type III survivorship, in which a large portion of the population dies early in life. These typical high mortalities in early life indicate that the size of many fish populations may be limited during these early stages. For example, high mortality during the larval stage may cause recruitment limitation of adult abundance (Doherty 1982; Victor 1986; Doherty and Fowler 1994), while important limits may also occur at the postsettlement stage (Shulman and Ogden 1987; Hixon and Carr 1997; Hixon and Jones 2005). For example, when recruitment of the Ambon damsel *Pomacentrus amboinensis* was doubled from 1 recruit/m^2 to 2 recruits/m^2, adult abundance did not increase, thus indicating that postrecruitment processes may regulate this population (Jones 1990).

Predation has been identified as a leading cause of reef fish postsettlement mortalities (Carr and Hixon 1995; Steele and Forrester 2002; Almany and Webster 2006). For example, when resident piscivores were removed, there were higher numbers and species richness of juvenile reef fishes (Caley 1993; Beets 1997; Webster 2002; Heinlein et al. 2010). Predator additions have shown similar effects; the introduction of a single invasive lionfish *Pterois volitans* to patch reefs caused a 79% reduction in reef fish recruitment (Albins and Hixon 2008).

Fish living on a reef can affect the environment immediately surrounding the reef. For example, feeding activity by herbivorous fishes can cause a grazing halo in surrounding seagrass beds (Randal 1965). Carnivorous reef fishes are also known to create feeding halos in surrounding habitats, resulting in lower abundances of invertebrates, although these halos are not as apparent as those caused by herbivores (Kurz 1995; Galván et al. 2008). If grazing pressure and predation pressure are higher on plants and invertebrates in the areas surrounding a reef, then predation pressure is probably higher for small fishes as well.

---

*Corresponding author: szedlst@auburn.edu

Received May 6, 2011; accepted September 10, 2011

Previous studies have indicated that the recruit abundance and diversity of reef fishes on patch reefs increase with increasing distance from larger reefs, and this increase has been attributed to reduced predation (Shulman 1985; West et al. 1994; Steele 1997; Belmaker et al. 2005). While these previous studies showed significant predation effects, most did not examine reef fish recruitment at sites more than 50 m from the larger reefs with larger resident predators (Shulman 1985; Connell 1997; Steele 1997; Belmaker et al. 2005). In the present northern Gulf of Mexico reef system, potential predators will forage at least 50 m from the reef (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011). Based on the reported foraging ranges for red snapper *Lutjanus campechanus*, studies that have examined predation effects around 50 m or less from the reef structure are not applicable to systems in the northern Gulf of Mexico, and questions remain concerning the possible isolation refuge effects for northern Gulf of Mexico fishes.

Red snapper are abundant on reef structures in the northern Gulf of Mexico and support important commercial and sport fisheries (SEDAR 7 2005). The red snapper stock in the northern Gulf of Mexico has been classified as overfished, resulting in severe restrictions on harvest (Goodyear 1994; SEDAR 7 2005; SEDAR 2009). Proper management of red snapper requires an understanding of their life history and the processes that regulate abundance. Thus, identifying population bottlenecks will substantially aid in managing the fishery.

Red snapper recruits first settle to open habitat and reach their highest abundances between July and September and then move to more structured habitats in the fall of their first year (Szedlmayer and Conti 1999; Szedlmayer and Lee 2004); however, they also may settle directly onto reef structures (Szedlmayer 2011). As red snapper grow, they seek out progressively larger structures. By age 2, red snapper have recruited to higher-relief structures, such as gas platforms (Nieland and Wilson 2003; Szedlmayer 2007; Gallaway et al. 2009).

Previous studies have indicated that predators or larger competitors can affect the abundance and distribution of age-0 red snapper. In caging experiments conducted in the field, higher abundances of age-0 red snapper occurred on reefs when predators were excluded; in captivity, age-0 red snapper spent more time associated with complex habitat when a predator (Gulf flounder *Paralichthys albigutta*) was present (Piko and Szedlmayer 2007). Age-0 red snapper were also excluded from complex habitat when older red snapper were added to a tank (Bailey et al. 2001). Based on the life history of red snapper and the potential effects of predators on reef fish recruitment, the proximity of larger artificial reefs and their associated reef fish communities may affect new recruitment of juvenile red snapper to low-relief nursery structures. Through the use of experimental artificial reefs, we examined the potential effects of predator and competitor proximity to reef habitats on the recruitment of age-0 red snapper.

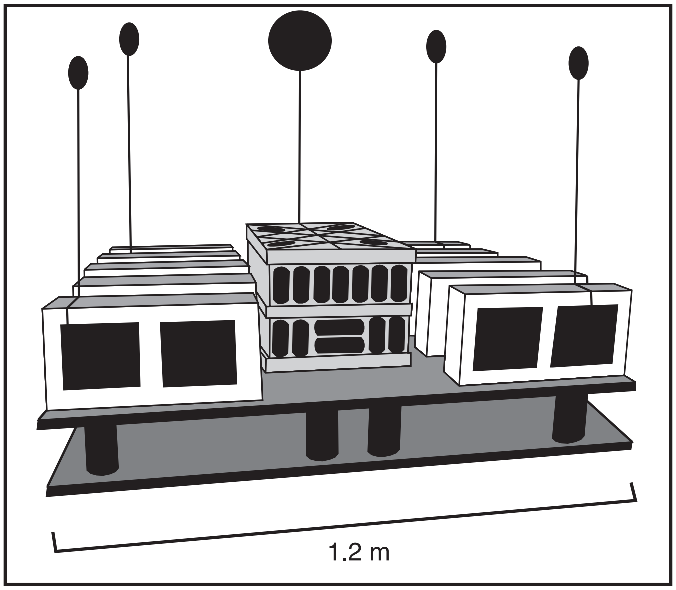


FIGURE 1. Design of the small artificial reefs that were used to study juvenile fish recruitment.

METHODS

The study site was located 28 km south of Dauphin Island, Alabama, in the northern Gulf of Mexico; the site was characterized by sand and mud substrate, and 3% of the sea floor was composed of natural reefs (Parker et al. 1983; Dufrene 2005). Reefs were built within an artificial reef-building zone that also contains many other artificial reefs, including natural gas platforms, liberty ships, concrete pyramids, and army tanks (Minton and Heath 1998). All reefs were placed at depths ranging from 19 to 22 m.

Large steel cage reefs (1.2 × 2.4 × 2.4 m) were deployed on 2 April 2008 ($n = 10$) and 14 April 2009 ($n = 10$). These large reefs provided habitat for larger predatory fishes relative to the smaller fishes typically observed on the smaller "recruitment" reefs. Small reefs (Figure 1) were deployed on 24 and 28 July 2008 ($n = 20$) and 9–10 July 2009 ($n = 20$). Each small reef consisted of a polyethylene plastic pallet (1.22 × 1.02 × 0.14 m), 10 concrete half-blocks (41 × 20 × 10 cm), and a plastic crate (65 × 35 × 28 cm). Small reefs were assembled by using 122-cm cable ties with a tensile strength of 79 kg. A small float (5.1 × 12.7 cm) was tied to each corner of the reef and floated 1 m above the reef. One larger float (15.2-cm diameter) was tied in the center of the reef, also at a height of 1 m. The floats added vertical structure to the reef and facilitated reef relocations with sonar. The small reefs were anchored by attachment to a 1.2-m ground anchor with 1.3-cm-diameter nylon rope. The total volume of the reef was 1.42 m^3. The small reefs provided habitat for age-0 red snapper and other small (mostly <200 mm) reef fishes. One small reef was anchored 15 m (small nearby reef) from the large reef, and a second small reef was anchored 500 m (small distant reef) from the large reef. Each replicate set of reefs included one large reef and two small reefs, and all replicates were equally spaced 1.7 km apart in rows of three, four, and three large reefs. Depth differences among all reefs were less than 3 m.

In 2008, all of the reefs were surveyed on 6 and 15 August 2008 but were subsequently destroyed by Hurricane Gustav in the first week of September. In 2009, reefs were surveyed on 4 and 6 August and again on 9–10 September. A third survey was attempted on 19 November 2009 but was not completed owing to high turbidity and reef damage caused by Tropical Storm Ida.

During each survey, two SCUBA divers visually identified, counted, and estimated size-classes (in 25-mm total length [TL] intervals) of all fish present on individual small reefs. In this study, recruits were defined as newly settled age-0 juvenile fish. Divers also observed the large reefs and characterized the size and abundance of the common species that were present. In 2009, divers videotaped (Sony Hi-8) and photographed (Nikon D200) each small reef with its associated fishes. All photographs and video recordings were taken 1.2 m from the reef on a horizontal plane to the reef, facing the open holes of the concrete blocks. In the laboratory, photographs with the highest number of age-0 red snapper for a particular reef were selected for computer-aided enumeration. Each fish in the photograph was identified to species and counted by using Image-Pro image analysis software. Any photographed fish that could not be accurately identified to species was counted and labeled as unknown. Two screens were used to analyze the video recording: a single captured frame of the video was displayed on one screen while the video was played on the second screen. The second screen allowed the counter to simultaneously view the fish in the captured frame and on the moving video for more accurate identification and counting with Image-Pro software.

All fish counts were divided by the volume of the small reef to obtain density (fish/m^3). Red snapper age was estimated based on length. During the August surveys, all red snapper that were 102 mm TL or smaller were classified as age 0. In September, all red snapper that were 127 mm TL or smaller were classified as age 0 (Szedlmayer and Lee 2004). All tomtates *Haemulon aurolineatum* of 76 mm TL or less were considered to be age 0. A few fast-moving and large-schooling species (blue runner *Caranx crysos*, round scad *Decapterus punctatus*, greater amberjack *Seriola dumerili*, and longspine porgy *Stenotomus caprinus*) were excluded from all reef comparisons because of the difficulty in counting them and because of their transient behavior.

Visual estimates of age-0 and age-1 red snapper densities were compared between treatments with a two-way analysis of variance (ANOVA). The mean densities of other common species were compared between treatments with a *t*-test. Differences in mean species richness (species/m^3) were compared between treatments separately for each survey by using a *t*-test. Pearson's product-moment correlation coefficients were calculated for densities of age-0 and age-1 red snapper on the small distant (500 m) reefs. A one-way ANOVA was used to compare densities of age-0 red snapper across years for August surveys. Photograph and video estimates of age-0 red snapper densities were compared between treatments with a *t*-test. The three counting methods (visual, photograph, and video) of age-0 red snapper densities and mean species richness were compared by use of a one-way ANOVA. If significant differences were detected with ANOVA, specific differences were identified by using a Tukey's test.

Fish community patterns between reef types were also compared with nonmetric multidimensional scaling (NMDS; Szedlmayer and Able 1996; Lingo and Szedlmayer 2006; Redman and Szedlmayer 2009). Species abundance data were square-root transformed to reduce the weight of highly abundant species (Field et al. 1982). Czekanowski's similarity coefficients (S_{jk}) were calculated among all individual surveys of each reef and were mapped as NMDS ordination plots:

$$S_{jk} = 100 \times \left(1 - \frac{\sum |y_{ij} - y_{ik}|}{\sum y_{ij} + y_{ik}}\right),$$

where S_{jk} is the similarity between the *j*th and *k*th reefs, y_{ij} is abundance of the *i*th species on the *j*th reef, and y_{ik} is the abundance of the *i*th species on the *k*th reef (Field et al. 1982; Yoshioka 2008). Circles describing the grouping between treatments were drawn by hand on the NMDS ordination plots. One-way analysis of similarity (ANOSIM Global *R*) was used to test for significant differences in the reef fish community between reef treatments for each survey (Clarke and Green 1988; Clarke 1993). All statistical tests were considered significant at *P*-values of 0.05 or less.

RESULTS

In August 2008 and 2009, age-0 red snapper were significantly more abundant on the small distant (500 m) reefs than on the small nearby (15 m) reefs as shown by a significant interaction effect (2008 ANOVA: $F_{1,36} = 19.54$, $P < 0.001$, Figure 2a; 2009 ANOVA: $F_{1,36} = 10.02$, $P = 0.003$, Figure 2b). Similarly, in September 2009, age-0 red snapper were more abundant on the small distant reefs than on the small nearby reefs (ANOVA: $F_{1,36} = 21.60$, $P < 0.001$; Figure 2c). No significant differences were detected for age-1 red snapper abundances between reef treatments (Figure 2). Comparisons of age-0 and age-1 red snapper abundance on the small distant reefs showed a significant negative correlation in August 2008 (Pearson's $r = -0.67$, $P = 0.03$), but significant correlations were not detected for the other two surveys (August 2009: Pearson's $r = -0.59$, $P = 0.07$; September 2009: Pearson's $r = -0.10$, $P = 0.78$). Overall, age-0 red snapper abundance did not significantly differ between August 2008 (mean ± SD = 8.0 ± 11.8 fish/m^3) and August 2009 (11.8 ± 18.8 fish/m^3; ANOVA: $F_{1,38} = 0.6$, $P = 0.44$).

In August 2009, rock sea bass *Centropristis philadelphica* were marginally more abundant on the small distant reefs (mean ± SD = 4.37 ± 6.55 fish/m^3) than on the small nearby reefs (0.14 ± 0.30 fish/m^3; *t*-test: $t_{18} = 2.04$, $P = 0.056$); by

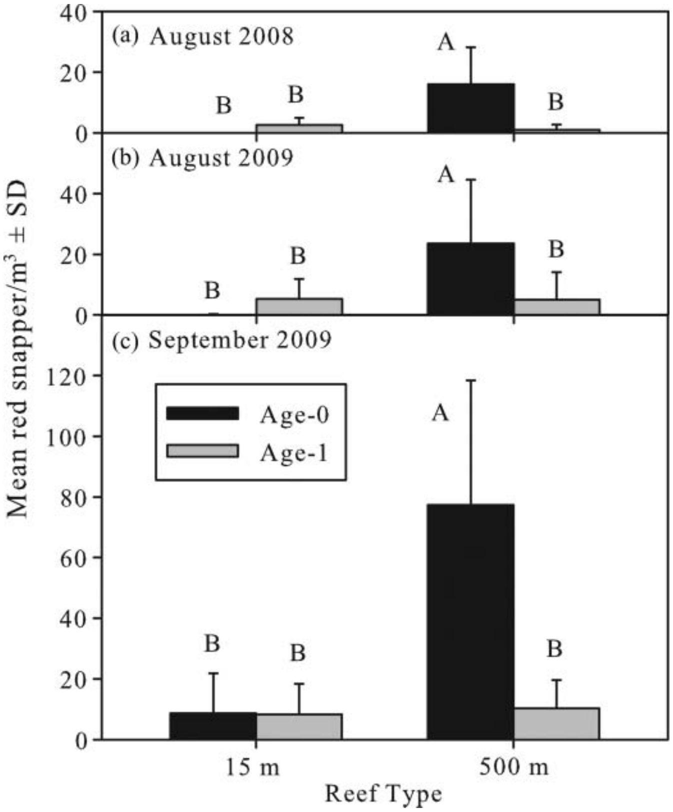


FIGURE 2. Mean (+SD) density (fish/m^3) of age-0 and age-1 red snapper based on visual SCUBA surveys of small artificial reefs placed 15 or 500 m from a larger artificial reef in the northern Gulf of Mexico during **(a)** August 2008, **(b)** August 2009, and **(c)** September 2009. Within a given panel, means with different uppercase letters are significantly different ($P < 0.05$).

September 2009, they were significantly more abundant on the small distant reefs (8.24 ± 9.26 fish/m^3) than on the small nearby reefs (0.00 fish/m^3; t-test: $t_{18} = 2.81$, $P = 0.012$). In August 2009, pygmy filefish *Stephanolepis setifer* were significantly more abundant on the small distant reefs (0.35 ± 0.50 fish/m^3) than on the small nearby reefs (0.00 fish/m^3; t-test: $t_{18} = 2.24$, $P < 0.05$); pygmy filefish were also more abundant in September 2009 on the small distant reefs (0.56 ± 0.80 fish/m^3) than on the small nearby reefs (0.00 fish/m^3; t-test: $t_{18} = 2.23$, $P < 0.05$). In contrast to most other species, age-0 tomtates were significantly more abundant on the small nearby reefs (172.1 ± 225.5 fish/m^3) than on the small distant reefs (2.8 ± 4.4 fish/m^3; t-test: $t_{18} = -2.37$, $P < 0.05$) in September 2009. Age-0 recruits (generally smaller than 76 mm) of several other species (including vermilion snapper *Rhomboplites aurorubens*, lane snapper *Lutjanus synagris*, cubbyu *Pareques umbrosus*, cocoa damselfish *Stegastes variabilis*, snowy grouper *Epinephelus niveatus*, sand perch *Diplectrum formosum*, and wrasses *Halichoeres* spp.) were observed on small reefs in 2009. However, no significant differences in mean abundance were detected between the small nearby reefs and small distant reefs ($P > 0.05$). In August 2009, species richness was significantly higher on the small distant reefs (4.2 ± 1.1 species/m^3) than on the small nearby reefs (2.7 ± 1.6 species/m^3; t-test: $t_{18} = 2.37$, $P < 0.05$).

Predators capable of consuming newly settled reef fishes (i.e., predator TL > 200 mm) were observed on all large reefs. In addition to large fishes, age-0 tomtates, vermilion snapper, and round scad were observed recruiting onto 6 of 10 large reefs in 2009. Although divers were able to detect age-0 tomtates, vermilion snapper, and round scad on the large reefs, no age-0 red snapper were observed on those reefs in August 2008 or August 2009, and fewer than 20 age-0 red snapper were observed on 2 of the 10 large reefs in September 2009.

Significant differences in reef fish communities were detected between reef treatments for all three surveys: August 2008 (ANOSIM Global R: $R = 0.342$, $P < 0.001$; Figure 3a), August 2009 ($R = 0.327$, $P < 0.001$; Figure 3b), and September 2009 ($R = 0.497$, $P < 0.001$; Figure 3c). In all surveys, similar species were observed between the reef treatments, but density differences for particular species probably accounted for the significant differences detected in the total reef fish communities (Table 1).

Similar to the visual surveys performed by SCUBA divers, computer-aided counts of age-0 red snapper from photographs showed significantly higher relative abundances in August 2009 on the small distant reefs (mean ± SD = 12.04 ± 15.69 fish/m^3) than on the small nearby reefs (0.00 fish/m^3; t-test: $t_{18} = 2.43$, $P < 0.05$); the difference was again observed in September 2009 (small distant reefs: 52.68 ± 25.24 fish/m^3; small nearby reefs: 6.76 ± 9.80 fish/m^3; t-test: $t_{18} = 5.36$, $P < 0.001$). Video counts also showed significantly higher age-0 red snapper relative abundances on the small distant reefs than on the small nearby reefs in August 2009 (small distant reefs: 7.51 ± 6.77 fish/m^3; small nearby reefs: 0.00 fish/m^3; t-test: $t_{16} = 3.33$, $P < 0.01$) and in September 2009 (small distant reefs: 21.06 ± 11.15 fish/m^3; small nearby reefs: 1.88 ± 3.05 fish/m^3; t-test: $t_{17} = 4.98$, $P < 0.001$). Comparisons among the three methods for September 2009 showed significantly more age-0 red snapper from diver visual surveys (42.96 ± 46.14 fish/m^3) than from counts derived from photographs (29.72 ± 30.04 fish/m^3) and video recordings (11.97 ± 12.77 fish/m^3; ANOVA: $F_{2,56} = 4.35$, $P < 0.05$). Similarly, in August 2009, visual surveys indicated significantly higher species richness (3.49 ± 1.56 species/m^3) than did photographs (1.80 ± 0.90 species/m^3) and video surveys (1.17 ± 0.68 species/m^3; ANOVA: $F_{2,55} = 21.91$, $P < 0.001$). This was also the case for species richness in September 2009 (visual surveys: 4.68 ± 1.50 species/m^3; photographs: 2.89 ± 0.94 species/m^3; videos: 2.04 ± 0.88 species/m^3; ANOVA: $F_{2,56} = 27.27$, $P < 0.001$).

DISCUSSION

Age-0 red snapper were always more abundant on the small distant (500 m) reefs than on the small nearby (15 m) reefs. In fact, no age-0 red snapper were observed on the small nearby reefs during August 2008, and only one age-0 red snapper was

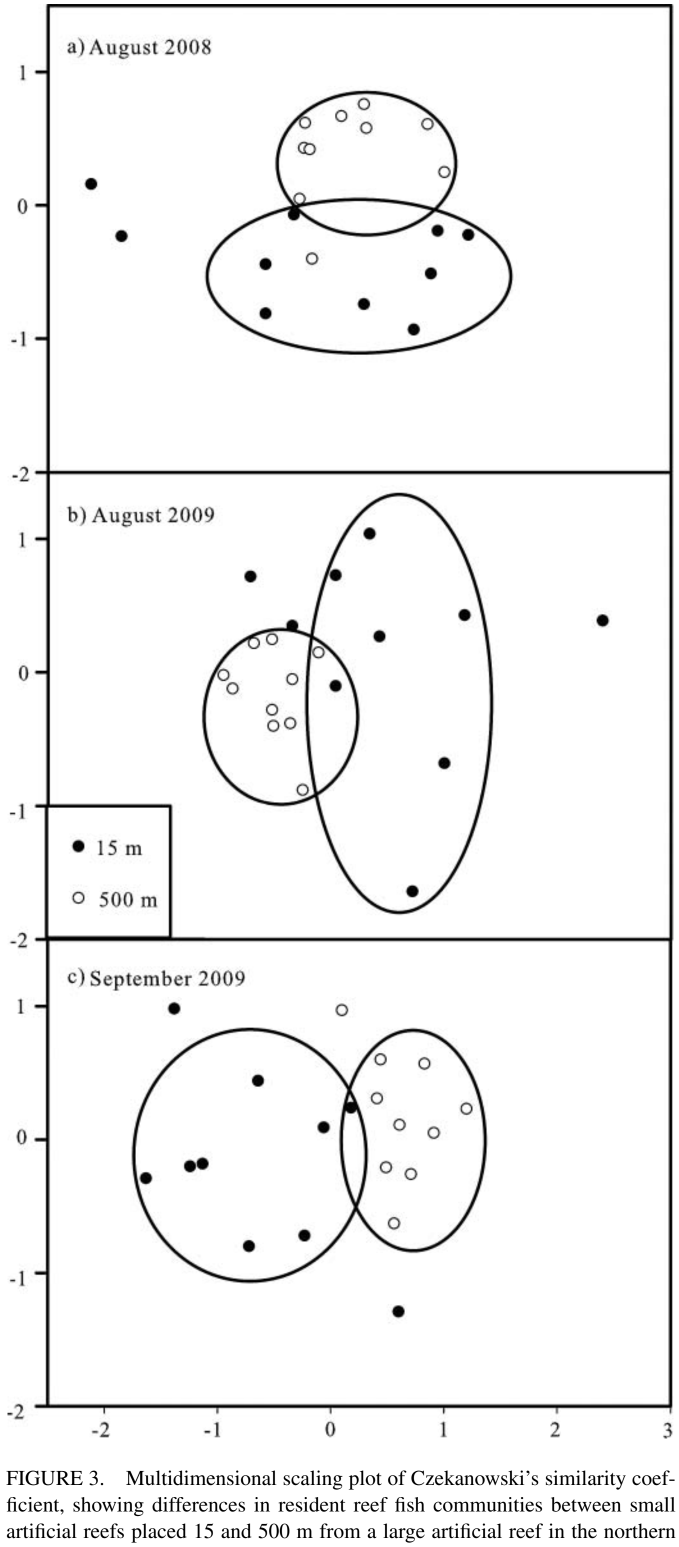


FIGURE 3. Multidimensional scaling plot of Czekanowski's similarity coefficient, showing differences in resident reef fish communities between small artificial reefs placed 15 and 500 m from a large artificial reef in the northern Gulf of Mexico during **(a)** August 2008, **(b)** August 2009, and **(c)** September 2009. Axes are unitless. Hand drawn ovals indicate similar groupings.

observed on the small nearby reefs during August 2009. This clearly shows the strong effect that the proximity of predators and competitors can have on new recruits. Similarly, several previous studies have shown that predators reduced recruitment near larger reefs (Shulman 1985; West et al. 1994; Steele 1997; Belmaker et al. 2005). It was only in September 2009 that age-0 red snapper began to appear in low numbers on the small nearby reefs, indicating that by this time the age-0 red snapper had grown beyond the gape size of smaller potential predators that occupied the large reefs (e.g., tomtate, pigfish, and age-1 red snapper). In addition, by September, the age-0 recruits were probably more competent swimmers, which made them better able to evade larger predators and aggression from other fish.

Several mechanisms may be responsible for the pattern of reduced age-0 red snapper on the small nearby reefs compared with the small distant reefs. Shortly after settlement, age-0 red snapper may suffer predation mortality from the predators inhabiting the larger reefs. In fact, recent observations showed direct predation by adult red snapper (2.5-kg fish) on age-0 red snapper (22 mm standard length; our unpublished data). Though direct observation of predation on recruits attempting to settle onto reefs nearby is difficult to obtain, Belmaker et al. (2005) moved patch reefs closer to a continuous reef with a resident fish community and observed aggregation of predators along with numerous predatory strikes; those authors suggested that the predators were consuming many of the new recruits on the patch reef. Another possibility is that older conspecifics were driving off any new recruits that attempted to settle onto the small nearby reefs, as was shown in a laboratory study of red snapper (Bailey et al. 2001). New recruits may also be able to detect predators or conspecifics on the larger reefs and simply choose to settle elsewhere. Sweatman (1988) found evidence that reef fish recruits used chemical cues to preferentially choose settlement sites based on the presence or absence of conspecifics or competitors. Ultimately, all three mechanisms are probably operating, but it is difficult to partition these factors in the present study.

Distance from large reefs clearly affected the abundance of age-0 red snapper on the small reefs. We assumed that the small nearby reefs were well within the range of the predatory fishes living on the large reefs, whereas the small distant reefs were beyond the usual range of resident predators on the large reefs. This assumption was supported by previous tracking studies in which adult red snapper were continuously located at distances between 5 and 66 m from a reef over 24-h periods (Szedlmayer and Schroepfer 2005; Topping and Szedlmayer 2011). Our assumption was also supported by diver observations indicating that larger resident fish (>300 mm TL) on the large reefs would swim over to the small nearby reefs during visual surveys. The larger fishes included the red snapper, gag *Mycteroperca microlepis*, gray triggerfish, and greater amberjack. No fish over 280 mm TL were observed on the small distant reefs, suggesting

TABLE 1. Comparison of reef fish densities (fish/m^3; for species that contributed >0.02% of the total) between small artificial reefs placed 15 m (nearby) and 500 m (distant) from a larger artificial reef over all surveys conducted during 2008 and 2009 in the northern Gulf of Mexico.

	Distant reefs		Nearby reefs	
Species	Density (fish/m^3)	Percent of total	Density (fish/m^3)	Percent of total
Red snapper	66.58	47.39	12.39	2.38
Vermilion snapper	53.27	37.92	404.15	77.52
Rock sea bass	6.69	4.76	0.07	0.01
Sand perch	3.49	2.48	0.67	0.13
Tomtate	2.46	1.75	96.58	18.53
Pigfish *Orthopristis chrysoptera*	1.94	1.38	1.34	0.26
Bank sea bass *Centropristis ocyurus*	1.83	1.30	0.04	0.01
Cubbyu	1.62	1.15	2.78	0.53
Gray triggerfish *Balistes capriscus*	0.95	0.68	0.53	0.10
Pygmy filefish	0.46	0.33		
Lane snapper	0.39	0.28	0.28	0.05
Wrasses *Halichoeres* spp.	0.32	0.23	0.35	0.07
Snowy grouper	0.21	0.15	0.04	0.01
Short bigeye *Pristigenys alta*	0.07	0.05		
Dwarf goatfish *Upeneus parvus*	0.07	0.05		
Blennies (Blenniidae)	0.04	0.03	0.60	0.11
Cocoa damselfish	0.04	0.03	0.42	0.08
Atlantic spadefish *Chaetodipterus faber*	0.04	0.03	0.21	0.04
Glasseye snapper *Heteropriacanthus cruentatus*	0.04	0.03		
Twospot cardinalfish *Apogon pseudomaculatus*			0.74	0.14

that observed fish typically did not cross the 500 m of open habitat between reefs. In addition (although not quantified), when age-0 red snapper were observed on the small nearby reefs, they tended to hide within the holes and refuges of the reef structure, while age-0 red snapper on the small distant reefs moved freely above and around the reef structure.

A negative correlation was observed between the abundances of age-1 and age-0 red snapper on the small distant reefs. Although this pattern was only significant in August 2008, it was also apparent in August 2009. The lack of any negative correlation in September 2009 again suggests that by this time, age-0 red snapper had grown to sizes that were large enough to afford them some protection from predation or aggression from age-1 red snapper. Similarly, enhanced recruitment of Ward's damsel *Pomacentrus wardi* was observed on reefs from which adult conspecifics had been removed (Sale 1976). If conspecifics are responsible for the exclusion of age-0 red snapper, this may be an example of density dependence. Other studies have found evidence of density dependence in reef fishes. For example, adult bridled goby *Coryphopterus glaucofraenum* caused a density-dependent reduction in the recruitment of juveniles (Forrester 1995), and there was an inverse relation between adult density and subsequent recruitment in millet butterflyfish *Chaetodon miliaris* (Stimson 1990). Tupper and Boutilier (1995) showed that older conspecifics reduced the survival of cunners *Tautogolabrus adspersus*, and no new recruits survived on reefs with the highest densities of conspecifics. Based on the present study results, it is difficult to conclude that older conspecifics were causing density-dependent recruitment in red snapper, as a large number of other predators were also present on the larger reefs. Even so, it appears that predator-free nursery structures may be a limiting resource for age-0 red snapper.

Rock sea bass and pygmy filefish were significantly more abundant on the small distant reefs than on the small nearby reefs. However, most of the individuals observed were adults rather than new recruits, and the adults of these species are generally small; in this study, the largest rock sea bass was 15 cm and the largest pygmy filefish was 12 cm. Thus, in addition to juvenile fish, the adults of smaller reef fishes may also benefit from the reduced predation or competition in habitats located outside of the influence of larger reefs.

Age-0 tomtates showed a pattern opposite to that of red snapper and had higher abundances on the small nearby reefs than on the small distant reefs. Divers observed tomtate recruits on the large reefs—sometimes in numbers exceeding 1,000—despite the presence of numerous predators. It appears that higher counts of tomtates on the small nearby reefs result from their high abundance on the larger reefs. In September 2009, when this pattern was detected, tomtates settled onto reefs at much higher densities than did red snapper. Tomtate densities may be high enough to satiate predators and to allow survival despite heavy predation. These patterns indicate a different survival strategy for tomtates compared with red snapper. Red snapper may actively select predator-free habitat, while tomtates seek out larger reef habitat independent of predator presence. Such differences in life history are known for other reef fishes. Some species (e.g., Ambon damsel) settle directly onto adult habitats (McCormick and Makey 1997), whereas others (e.g., Nassau grouper *Epinephelus striatus* and gag) exploit nursery habitats before moving to larger reefs later in life (Eggleston 1995; Ross and Moser 1995).

Our finding of higher abundances of tomtates on the small nearby reefs differs from several studies that showed higher recruitment with increasing distance from a reef (Shulman 1985; Steele 1997; Belmaker et al. 2005). This difference may result from a difference in scale among studies. Previous studies looked at fine-scale differences, with the farthest reefs being less than 50 m from the large reef, while in the present study small reefs were placed 500 m from the large reefs. Alternatively, tomtates in the northern Gulf of Mexico may simply be an exception to an otherwise common pattern.

In August 2009, mean species richness was higher on the small distant reefs than on the small nearby reefs. Similar patterns were reported by Shulman (1985) and Belmaker et al. (2005), who found higher diversity on small reefs that were placed farther away from a large reef than on those placed closer to a large reef. Caley (1993) observed higher species richness of nonpiscivorous reef fish recruits on reefs where resident predators had been removed. Again, this pattern could be caused by (1) prey fish avoidance of habitats that have resident predators or (2) predator reduction of species richness by occasionally preying on members of rare species.

All three survey techniques used in this study were able to detect significantly higher densities of age-0 red snapper on the small distant reefs. On average, the visual surveys gave the highest counts, photographs gave intermediate counts, and video recordings always gave the lowest abundances. Tessier et al. (2005) also obtained higher counts with visual surveys than with video techniques. Willis et al. (2000) obtained higher abundance estimates and higher precision with video surveys than with visual surveys, but those authors used an unmanned, baited video technique rather than a diver-operated video camera. However, baited video methods may have attracted fish from the surrounding area and biased their fish counts. In any photographic or video survey, there will always be fish on the reef that are out of range and undetectable. However, as fish abundance increases, diver counts become more difficult. Thus, as a trade off, photographs can provide more-precise counts for comparative purposes without the difficulty of counting swimming fish but will be less accurate than diver visual counts of total reef fish abundance. Visual surveys also showed higher mean species richness than photographs or video recordings, similar to the results of Tessier et al. (2005). The visual survey was able to detect rare and cryptic species, such as twospot cardinalfish and belted sandfish *Serranus subligarius*, which were not detected in photographs or video counts. The visual survey was also the only method that detected the single age-0 red snapper on the small nearby reefs in August 2009. In conclusion, visual surveys are needed to detect rare or cryptic species and to measure species richness, while photographs are more appropriate for comparative measures of relative abundance.

The results of this study can be used to improve the construction and placement of artificial reefs. West et al. (1994) concluded that low-relief artificial reefs would most benefit juvenile rockfishes *Sebastes* spp. if they were built in areas without adjoining adult habitat. Likewise, this study indicates that if artificial reefs are built to provide habitat for juvenile red snapper, they should not be built in areas immediately adjacent to existing adult habitat. Furthermore, artificial reefs that are meant to provide habitat for adult fish should not be built near important red snapper nursery habitats.

ACKNOWLEDGMENTS

We thank M. Piraino, T. Syc, and D. Topping for building reefs and conducting field surveys. This project was funded by the Marine Resources Division of the Alabama Department of Conservation and Natural Resources. This is a contribution of the Alabama Agricultural Experiment Station and the Department of Fisheries and Allied Aquacultures, Auburn University.

REFERENCES

Albins, M. A., and M. A. Hixon. 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. Marine Ecology Progress Series 367:233–238.

Almany, G. R., and M. S. Webster. 2006. The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reefs 25:19–22.

Bailey, H. K., IV, J. H. Cowan Jr., and R. L. Shipp. 2001. Experimental evaluation of potential effects of size and presence of conspecifics on habitat association by young-of-the-year red snapper. Gulf of Mexico Science 19:109–131.

Beets, J. 1997. Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. Marine Ecology Progress Series 148:11–21.

Belmaker, J., N. Shashar, and Y. Ziv. 2005. Effects of small-scale isolation and predation on fish diversity on experimental reefs. Marine Ecology Progress Series 289:273–283.

Caley, M. J. 1993. Predation, recruitment and the dynamics of communities of coral-reef fishes. Marine Biology 117:33–43.

Carr, M. H., and M. A. Hixon. 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. Marine Ecology Progress Series 124:31–42.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Clarke, K. R., and R. H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Marine Ecology Progress Series 46:213–226.

Connell, S. D. 1997. The relationship between large predatory fish and recruitment and mortality of juvenile coral reef-fish on artificial reefs. Journal of Experimental Marine Biology and Ecology 209:261–278.

Doherty, P. 1982. Some effects of density on the juveniles of two species of tropical, territorial damselfish. Journal of Experimental Biology and Ecology 65:249–261.

Doherty, P., and T. Fowler. 1994. An empirical test of recruitment limitation in a coral reef fish. Science 263:935–939.

Dufrene, T. A. 2005. Geological variability and Holocene sedimentary record on the northern Gulf of Mexico inner to mid-continental shelf. Master's thesis. Louisiana State University, Baton Rouge.

Eggleston, D. B. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. Marine Ecology Progress Series 124:9–22.

Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for analyzing multispecies distribution patterns. Marine Ecology Progress Series 8:37–52.

Forrester, G. E. 1995. Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. Oecologia 103:275–282.

Gallaway, B. J., S. T. Szedlmayer, and W. J. Gazey. 2009. A life history review for red snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. Reviews in Fisheries Science 17:48–67.

Galván, D. E., A. M. Parma, and O. O. Iribarne. 2008. Influence of predatory reef fishes on the spatial distribution of *Munida gregaria* (= *M. subrugosa*) (Crustacea; Galatheidae) in shallow Patagonian soft bottoms. Journal of Experimental Marine Biology and Ecology 354:93–100.

Goodyear, C. P. 1994. Red snapper in U.S. waters of the Gulf of Mexico. Miami Laboratory, Southeast Fisheries Science Center, Contribution MIA-93/94–63, Miami.

Heinlein, J. M., A. C. Stier, and M. A. Steele. 2010. Predators reduce abundance and species richness of coral reef fish recruits via non-selective predation. Coral Reefs 29:527–532.

Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science 277:946–949.

Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. Ecology 86:2847–2859.

Jones, G. P. 1990. The importance of recruitment to the dynamics of a coral reef fish population. Ecology 71:1691–1698.

Kurz, R. C. 1995. Predator-prey interactions between gray triggerfish (*Balistes capriscus* Gmelin) and a guild of sand dollars around artificial reefs in the northeastern Gulf of Mexico. Bulletin of Marine Science 56:150–160.

Lingo, M. E., and S. T. Szedlmayer. 2006. The influence of habitat complexity on reef fish communities in the northeastern Gulf of Mexico. Environmental Biology of Fishes 76:71–80.

McCormick, M. I., and L. J. Makey. 1997. Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. Marine Ecology Progress Series 153:247–257.

Minton, R. V., and S. R. Heath. 1998. Alabama's artificial reef program: building oases in the desert. Gulf of Mexico Science 16:105–106.

Nieland, D. L., and C. A. Wilson. 2003. Red snapper recruitment to and disappearance from oil and gas platforms in the northern Gulf of Mexico. Pages 73–81 *in* D. R. Stanley and A. Scarborough-Bull, editors. Fisheries, reefs, and offshore development. American Fisheries Society, Symposium 36, Bethesda, Maryland.

Parker, R. O., D. R. Colby, and T. D. Willis. 1983. Estimated amount of reef habitat on a portion of the U.S. South Atlantic and Gulf of Mexico continental shelf. Bulletin of Marine Science 33:935–940.

Piko, A. A., and S. T. Szedlmayer. 2007. Effects of habitat complexity and predator exclusion on the abundance of juvenile red snapper. Journal of Fish Biology 70:758–769.

Randal, J. E. 1965. Grazing effects on sea grasses by herbivorous reef fishes in the West Indies. Ecology 46:255–260.

Redman, R. A., and S. T. Szedlmayer. 2009. The effects of epibenthic communities on reef fishes in the northern Gulf of Mexico. Fisheries Management and Ecology 16:360–367.

Ross, S. W., and M. L. Moser. 1995. Life history of juvenile gag, *Mycteroperca microlepis*, in North Carolina estuaries. Bulletin of Marine Science 56:222–237.

Sale, P. F. 1976. The effect of territorial adult pomacentrid fishes on the recruitment and survival of juveniles on patches of coral rubble. Journal of Experimental Marine Biology and Ecology 24:297–306.

SEDAR (SouthEast Data, Assessment, and Review). 2009. Stock assessment of red snapper in the Gulf of Mexico: SEDAR update assessment. Southeast Fisheries Science Center, Miami. Available: http://www.sefsc.noaa.gov. (January 2009).

SEDAR 7 (SouthEast Data, Assessment, and Review). 2005. Stock assessment report of SEDAR 7, Gulf of Mexico red snapper. Southeast Fisheries Science Center, Charleston, South Carolina. Available: http://www.sefsc.noaa.gov. (January 2009).

Shulman, M. J. 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66:1056–1066.

Shulman, M. J., and J. C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Marine Ecology Progress Series 39:233–242.

Steele, M. A. 1997. The relative importance of processes affecting recruitment of two temperate reef fishes. Ecology 78:129–145.

Steele, M. A., and G. E. Forrester. 2002. Early postsettlement predation on three reef fishes: effects on spatial patterns of recruitment. Ecology 83:1076–1091.

Stimson, J. S. 1990. Density dependent recruitment in the reef fish *Chaetodon miliaris*. Environmental Biology of Fishes 29:1–13.

Sweatman, H. 1988. Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. Journal of Experimental Marine Biology and Ecology 124:163–174.

Szedlmayer, S. T. 2007. An evaluation of the benefits of artificial habitats for red snapper, *Lutjanus campechanus,* in the northeast Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute 59:223–230.

Szedlmayer, S. T. 2011. The artificial habitat as an accessory for improving estimates of juvenile reef fish abundance in fishery management. Pages 31–44 *in* S. A. Bortone, F. P. Brandini, G. Fabi, and S. Otake, editors. The use of artificial reefs in fishery management. CRC Press, Boca Raton, Florida.

Szedlmayer, S. T., and K. W. Able. 1996. Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey estuary. Estuaries 19:697–709.

Szedlmayer, S. T., and J. Conti. 1999. Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. U.S. National Marine Fisheries Service Fishery Bulletin 97:626–635.

Szedlmayer, S. T., and J. D. Lee. 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. U.S. National Marine Fisheries Service Fishery Bulletin 102:366–375.

Szedlmayer, S. T., and R. L. Schroepfer. 2005. Long-term residence of red snapper on artificial reefs in the northeastern Gulf of Mexico. Transactions of the American Fisheries Society 134:315–325.

Tessier, E., P. Chabanet, K. Pothin, M. Soria, and G. Lasserre. 2005. Visual censuses of tropical fish aggregations on artificial reefs: slate versus video recording techniques. Journal of Experimental Marine Biology and Ecology 315:17–30.

Topping, D. T., and S. T. Szedlmayer. 2011. Home range and movement patterns of red snapper (*Lutjanus campechanus*) on artificial reefs. Fisheries Research 112:77–84.

Tupper, M., and R. G. Boutilier. 1995. Effects of conspecific density on settlement, growth and post-settlement survival of a temperate reef fish. Journal of Experimental Marine Biology and Ecology 191:209–222.

Victor, B. C. 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecological Monographs 56:145–160.

Webster, M. S. 2002. Role of predators in the early post-settlement demography of coral-reef fishes. Oecologia 131:52–60.

West, J. E., R. M. Buckley, and D. C. Doty. 1994. Ecology and habitat use of juvenile rockfishes (*Sebastes* spp.) associated with artificial reefs in Puget Sound, Washington. Bulletin of Marine Science 55:344–350.

Willis, T. J., R. B. Millar, and R. C. Babcock. 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. Marine Ecology Progress Series 198:249–260.

Yoshioka, P. M. 2008. Misidentification of the Bray-Curtis similarity index. Marine Ecology Progress Series 368:309–310.