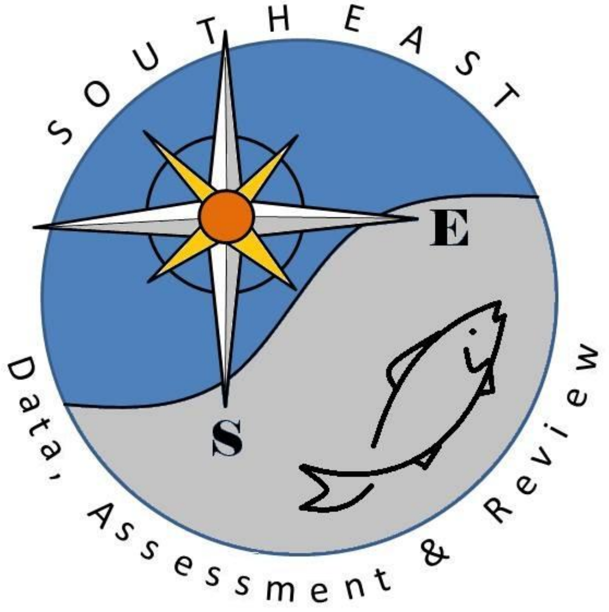
Effects of habitat complexity and predator exclusion on the abundance of juvenile red snapper

A. A. Piko and S. T. Szedlmayer

SEDAR31-RD16

13 August 2012



Journal of Fish Biology (2007) **70,** 758–769
doi:10.1111/j.1095-8649.2007.01336.x, available online at http://www.blackwell-synergy.com

Effects of habitat complexity and predator exclusion on the abundance of juvenile red snapper

A. A. Piko* and S. T. Szedlmayer†

*Marine Fish Laboratory, Department of Fisheries, Auburn University,
8300 State Highway 104, Fairhope, AL 36532, U.S.A.*

(Received 25 January 2006, Accepted 17 October 2006)

Predator exclusion and habitat complexity factors that may affect juvenile red snapper *Lutjanus campechanus* habitat selection were examined in field and laboratory experiments. A significant predator exclusion effect was detected. Uncaged shell habitats showed significantly lower numbers of age 0 year red snapper, and both uncaged shell and block-shell habitats showed significantly lower numbers of age 1 year red snapper compared with caged habitats ($P < 0{\cdot}001$). Habitat complexity also affected age 0 year red snapper, as mean abundance significantly decreased with decreased habitat complexity ($P < 0{\cdot}001$). In the laboratory, age 0 year red snapper association with complex habitats significantly increased with exposure to a predator Gulf flounder *Paralichthys albigutta* ($P < 0{\cdot}001$). This study showed that predator exclusion and habitat complexity were significant factors that affected the abundance of juvenile red snapper in nursery areas of the northern Gulf of Mexico. Predation may affect juvenile red snapper abundance directly through mortality and indirectly by influencing habitat selection. © 2007 The Authors
Journal compilation © 2007 The Fisheries Society of the British Isles

Key words: age 0 year red snapper; habitat preference; predator exclusion.

INTRODUCTION

Past recruitment studies suggested that high mortality during the pelagic stage reduced fish abundance to the point that resources in the benthic stage were not limiting, and post recruitment processes on reef fish abundance were considered negligible (Doherty, 1981). Reef fish populations, however, are not always directly related to past recruitment events and post recruitment mortality was often density-dependent (Jones, 1991; Sogard, 1997). Thus, post recruitment processes may also be important in structuring reef fish populations.

Predation is one factor that has been identified in affecting post recruitment fish populations in marine and freshwater systems (Connell, 1975; Zaret, 1980; Sih *et al.*, 1985; Hixon, 1991; Witting & Able, 1995). For example, Witting & Able (1995) found predation by sevenspine bay shrimp *Crangon septemspinosa*

---

†Author to whom correspondence should be addressed. Tel. and fax: +1 251 990 4858; email: szedlst@auburn.edu

*Present address: Golder Associates, 5100 West Lemon, Suite 114, Tampa, FL 33609, U.S.A.

© 2007 The Authors
Journal compilation © 2007 The Fisheries Society of the British Isles

(Say) affected habitat selection, size and mortality of winter flounder *Pleuronectes americanus* (Walbaum) during settlement.

Habitat complexity is another factor that may affect reef fish populations by reducing predator efficiency and increasing food resources; thus, survival of some species may increase on complex habitats (Jones, 1988; Szedlmayer & Lee, 2004; Topolski & Szedlmayer, 2004). Connell & Jones (1991) monitored recruitment and persistence of striped triplefin blenny *Forsterygion varium* (Forster) on simple and complex habitats. Recruitment did not differ between treatments and emigration did not modify recruitment patterns. After 2 months, complex habitats showed little change in fish abundance, while no fish remained on the simple habitat. Beukers & Jones (1997) used juvenile lemon damselfish *Pomacentrus moluccensis* Bleeker and also showed that survival significantly increased with increased habitat complexity, with predation mortality at 100% on low complexity habitat and 60% on high complexity habitat.

Habitat requirements for some species may change with growth. Small juvenile fishes may find predator refuge in habitats of varying complexity, but as they grow fishes become less concealed in low complexity habitats and more vulnerable to predation (Shulman, 1984, 1985; Hixon & Beets, 1989; Connell & Jones, 1991). As a result, some fish species shift to more complex habitats as they grow to decrease predation pressure (Szedlmayer & Lee, 2004; Topolski & Szedlmayer, 2004).

As with the above species, juvenile red snapper *Lutjanus campechanus* (Poey) abundance and behaviour may be affected by habitat complexity and predation pressure. For example, Szedlmayer & Conti (1999) and Szedlmayer & Lee (2004) suggested that young red snapper preferred structured habitat compared to open habitat. In laboratory experiments, Szedlmayer & Howe (1997) found age 0 year red snapper spent significantly more time over oyster shell compared to sand substratum, and Bailey *et al.* (2003) found juvenile red snapper spent more time over complex compared to simple substrata, but that larger red snapper forced smaller red snapper away from the complex habitats. From these studies it is clear that juvenile red snapper can shift habitat, whether or not this shift is related to predation pressure is unclear. In addition, no studies have attempted to measure predation effects on habitat selection by juvenile red snapper *in situ*.

The use of artificial habitats has been effective in the study of reef fish recruitment and predation *in situ*. Shulman (1985) placed artificial habitats various distances from a natural reef with resident predators and found a positive relation between increasing distance from the reef and abundance of prey fishes. Hixon & Beets (1989, 1993) used artificial habitats and detected an inverse correlation between maximum number of prey fishes and predator number. They suggested that predation set the upper limit of prey fish abundance on the habitat.

Exclusion cages have been used to study predation effects on juvenile fish recruitment but their utility has been questioned. The most often cited criticisms were increased algal growth due to the elimination of large herbivorous fishes, increased sedimentation due to changed flow rates and increased attraction of fishes to cages (Lassig, 1982; Doherty & Sale, 1985; Bell *et al.*, 1987; Kennelly, 1991). Despite these caging artefacts, with careful planning, such difficulties can be minimized and caging experiments can provide the

© 2007 The Authors

most useful method to study predation effects *in situ* (Connell, 1997). In the present study, caging artifacts were reduced mainly due to the particular habitat, *i.e.* the deeper shelf habitat of the northern Gulf of Mexico. For example, there are few if any large herbivorous fishes and cages were made of thin wire with large mesh that reduced hydrodynamic effects.

This study examined the effects of predator exclusion and habitat complexity on abundance and distribution of juvenile red snapper in the northern Gulf of Mexico. In the field, both artificial habitats and predator exclusion cages were used to test these effects on red snapper abundance. Predator effects were also tested on juvenile red snapper habitat selection under controlled laboratory conditions.

MATERIALS AND METHODS

STUDY AREA

The substratum of the northern Gulf of Mexico consists mainly of sand and mud sediments (Ludwick, 1964). Natural reef areas (rock outcropping) comprise only 3·2% of the bottom in depths of 10–91 m between Pensacola, Florida, and Pass Cavallo, Texas (Parker *et al.*, 1983). These natural reefs, however, support a wide array of invertebrates and reef fishes (Dennis & Bright, 1988; Gittings *et al.*, 1992). Artificial habitat for many fishes and invertebrate species is provided by natural gas drilling platforms in the northern Gulf of Mexico (Stanley & Wilson, 1997; Topolski & Szedlmayer, 2004). In addition, a 3100 km^2 area off the coast of Alabama is an artificial habitat building zone designated for the enhancement of recreational and commercial fisheries. There are >15 000 artificial habitats within this reef building area (Minton & Heath, 1998).

The present study sites were located in this reef building zone south-east of Dauphin Island, Alabama in the northern Gulf of Mexico. Site 1 was 20 km and site 2 was 23 km from the mouth of Mobile Bay (Fig. 1). Both sites were at 20 m depth with a sand and mud substratum.

FIELD EXPERIMENT

Artificial habitats were built from 24 July to 28 August 2001. Shell habitats ($n = 40$), shell-concrete block habitats (block habitats, $n = 40$) and cage habitats ($n = 20$) were built at the two sites (Fig. 1). Habitats were $1 \times 1 \times 0{\cdot}1$ m^3 plots of shell, with four concrete blocks ($20 \times 20 \times 41$ cm, each with two 12×14 cm holes) added for block habitats, while cage habitats were placed over natural sand substratum. Cages were made of 2 mm galvanized steel wire, $1 \times 1 \times 0{\cdot}25$ m, 25×50 mm mesh and were also placed over 20 shell habitats (shell-cage) and 20 block habitats (block-cage). At each site, habitats were placed in four transects with 10 habitats per transect and habitat types alternated at 20 m intervals. Transect direction was dependent on the prevailing winds and currents that affected the vessel drift during habitat building. A PVC stake (1 m × 12 mm diameter) was placed near each habitat to indicate shrimp trawl effects, *i.e.* the stake would be displaced if the habitat was trawled over.

Visual diver surveys were used to count and estimate 25 mm total length (L_T) categories of red snapper, *e.g.* <25 mm, 25–50 mm, 51–75 cm, . . . >150 mm. Red snapper age classes were estimated from known age and L_T relationships (Szedlmayer & Shipp, 1994; Szedlmayer & Conti, 1999). Each habitat was also video recorded for 2 min to verify species identifications. Temperature (° C), salinity and dissolved oxygen (mg l^{-1}) were measured with a remote recording YSI-6920 meter. Habitats were surveyed over five time periods: August (16–17 August 2001), late August (21–30 August 2001), September (5–21 September 2001), October (23–24 October 2001) and November (7–19 November 2001).

© 2007 The Authors
Journal compilation © 2007 The Fisheries Society of the British Isles,

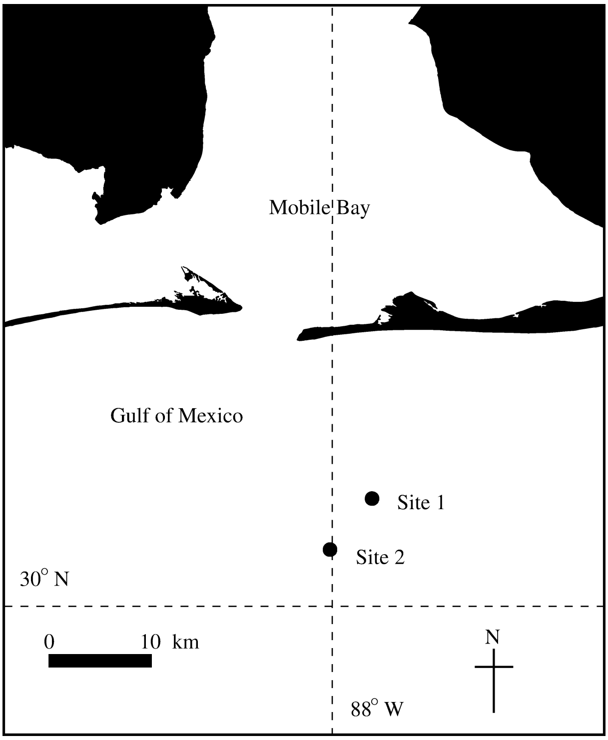


FIG. 1. Study site locations in the north-east Gulf of Mexico.

LABORATORY EXPERIMENT

The effects of predator presence on habitat selection by juvenile red snapper were also tested in the laboratory. Gulf flounder *Paralichthys albigutta* Jordan & Gilbert was chosen as the predator based on visual observations of this predator near the artificial habitats.

Age 0 year red snapper ($n = 30$) were collected with a trap (Collins, 1990) from nursery areas in the northern Gulf of Mexico and transported to the laboratory. Prior to experimental trials, red snapper were held in a circular 1230 l tank (1·5 m diameter and 0·7 m deep). An experimental tank (same dimensions as the holding tank) had a sand substratum with shell on each side, 0·6 m sand strip in the centre and two concrete blocks placed over the shell on one side. The experimental tank and holding tanks were on the same closed circulation seawater system (14 800 l) and exposed to the same water temperature, salinity and lighting. The experimental tank design mimicked the artificial habitats built in the field, having both a simple shell habitat and a complex block-shell habitat.

Preliminary habitat selection trials in the laboratory showed that with less than three fish, the red snapper appeared stressed and did not move for >2 h. In trials with three or four fish, the red snapper showed 'normal' behaviour, *e.g.* slowly exploring all aspects of the tank, with little indication of stress. Therefore, three fish were used in all laboratory habitat selection trials.

Red snapper habitat selection was tested with and without the presence of *P. albigutta*. Three red snapper were released into the experimental tank and allowed to acclimate for 5 min. After acclimation the red snapper were video recorded for 30 min without a predator present with a Sony TR101 Hi-8 video camcorder mounted above the tank. A *P. albigutta* was then added to the experimental tank. Fish were again allowed to

© 2007 The Authors

acclimate for 5 min, then video recorded for 30 min with the predator. Ten trials of habitat selection were completed. The video-tapes were viewed on a Sony EV-2000 Hi-8 VCR and a Sony GVM-1311Q colour video monitor. The position of individual fish in relation to substratum was timed.

STATISTICAL ANALYSIS

To examine overall temporal patterns ANOVA was used to compare mean abundance pooled over habitats. Partial correlations were calculated to compare red snapper abundance to salinity, temperature and dissolved oxygen.

Predator exclusion effects in the field experiment were tested after correcting for attraction effects of the cages. The abundances of age 0 and age 1 year red snapper on the cage alone habitats were averaged and then subtracted from the abundance of red snapper on the shell-cage and block-cage habitats. To examine habitat preference the mean number of age 0 year red snapper attracted to cages alone was not removed, and all habitat types were treated as different levels of complexity. Complexity levels were based on the surface area that each different component added to each m^2 plot. Block surface area was calculated from simple linear measurements (each block = 5129 cm^2) while shell surface areas were measured using Image-Pro Plus 4.5 image analyses programme (total shell surface area for each habitat = 128 940 cm^2). Also, the wire cage added to the habitat structure, but only added 162 cm^2 surface area. Listed in order of increasing complexity were cage alone, shell, shell-cage, block and block-cage habitats. For both predator exclusion and habitat complexity analyses, repeated measures analyses of variance (rmANOVA) and least squares means were used to compare age 0 and age 1 year red snapper abundance among habitat types (Zar, 1984).

Differences in size frequency distribution were compared with contingency tables and χ^2 (Cody & Smith, 1997). Each distribution by habitat type was compared to other distributions by habitat type.

ANOVA was used to compare mean time spent for all three fish on each habitat with and without a predator in laboratory experiments. One trial was excluded because during that trial one red snapper aggressively defended the complex habitat and chased the other two red snappers. The two chased red snappers stayed at the surface of the water, avoiding both the predator and the aggressive red snapper.

All statistical tests were considered significant at $P < 0{\cdot}05$, and when significant effects were detected Student-Newman-Keuls (SNK) multiple comparisons tests were used to show specific differences.

RESULTS

Age 0 year red snapper abundance was significantly higher (mean = 21·9 m^{-2}) in late August, then declined to similar levels in October and November [means = 13·8 and 11·8 m^{-2}, Fig. 2(a)]. Age 1 year fish showed a similar pattern, with fish significantly more abundant in late August, then declined overall habitats with few age 1 year fish observed in October and November [ANOVA, d.f. = 4 and 359, $P < 0{\cdot}001$, Fig. 2(b)].

Red snapper abundance showed no significant partial correlation with temperature, dissolved oxygen or salinity (temperature: $r = 0{\cdot}17$, d.f. = 8, $P > 0{\cdot}05$; dissolved oxygen: $r = 0{\cdot}07$, d.f. = 8, $P > 0{\cdot}05$; salinity: $r = -0{\cdot}10$, d.f. = 8, $P > 0{\cdot}05$). In addition, PVC stakes showed no indication of shrimp trawl activity at either site. Temperature ranged from 20·8 to 30·1° C, with a mean ± S.D. = 25·9 ± 3·3° C, dissolved oxygen ranged from 3·3 to 7·5 mg l^{-1}, with a mean ± S.D. = 6·0 ± 1·3 mg l^{-1} and salinity ranged from 32 to 40, with a mean ± S.D. = 35·2 ± 2·4.

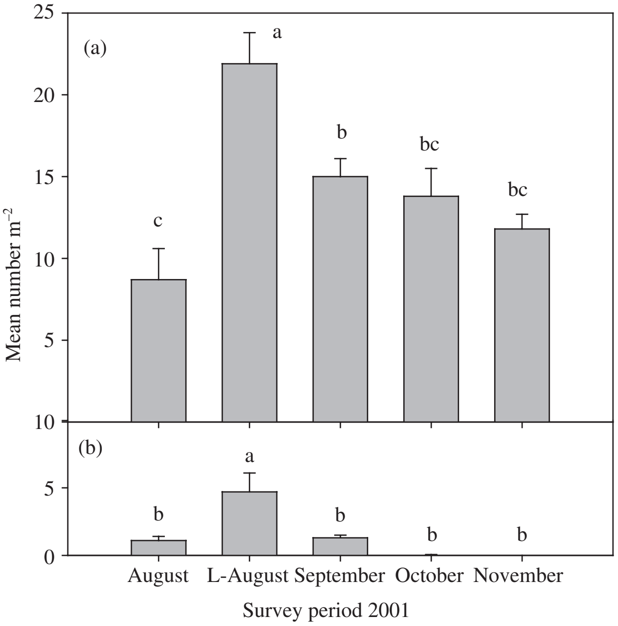


FIG. 2. Mean + S.E. number m^{-2} of (a) age 0 and (b) age 1 year red snapper by survey period. Bars with different lower case letters show significant differences ($P < 0{\cdot}05$) within age classes.

Overall there was a significant predator exclusion effect on the abundance of age 0 year red snapper. After removal of fish attracted to habitats due to cages, age 0 year red snapper still showed significant differences between caged and uncaged shell habitat types [rmANOVA, d.f. = 3 and 76, $P < 0{\cdot}001$; Fig. 3(a)]. In contrast, significant differences were not detected for age 0 year red snapper abundance between block-cage and block habitat types after removal of the cage effect [Fig. 3(a)]. For age 1 year red snapper there was a significant predator exclusion effect on the abundance for both block and shell habitat types. Age 1 year red snapper also showed the highest mean abundance on the most complex habitat types (block-cage), but did not show significant differences between block and shell-cage habitat types [rmANOVA, d.f. = 3 and 76, $P < 0{\cdot}001$; Fig. 3(b)].

Habitat complexity significantly affected age 0 year red snapper mean abundance, as abundance decreased with decreasing complexity (rmANOVA, d.f. = 4 and 94, $P < 0{\cdot}001$, Fig. 4). Only shell and cage (alone) did not show significant differences in abundance. No age 1 year red snapper were observed on the cage alone habitats. Significant differences in size frequency distributions were apparent, with smaller fish more common on less complex shell habitats (shell), and larger fish on the more complex block habitats (χ^2, d.f. = 6, $P < 0{\cdot}001$; Fig. 5).

In the laboratory, age 0 year red snapper showed similar mean time periods on block-shell compared to shell in the absence of the predator. After the predator was added red snapper shifted habitat and spent significantly more time

© 2007 The Authors
Journal compilation © 2007 The Fisheries Society of the British Isles,

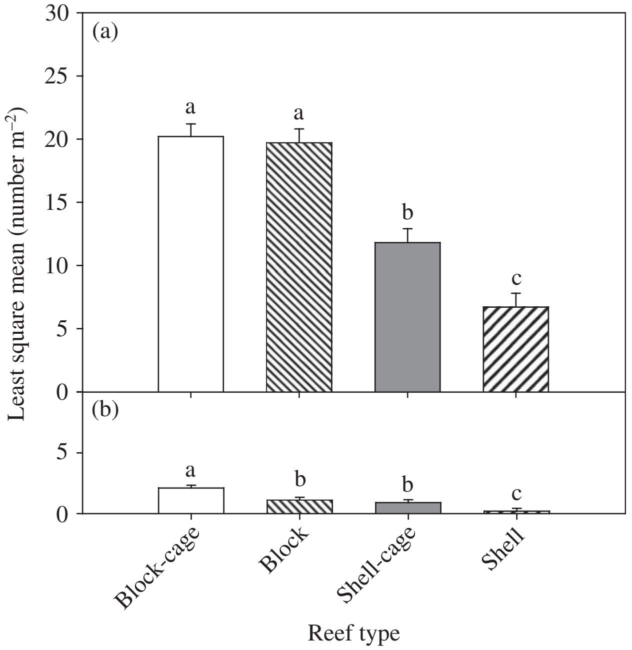


FIG. 3. Predator exclusion effect on the mean + S.E. number m^{-2} of (a) age 0 and (b) age 1 year red snapper by habitat type. Red snapper abundances were corrected for fish attracted to cage alone habitats. Bars with different lower case letters show significant ($P < 0{\cdot}05$) differences.

on the block-shell compared to the shell habitat (ANOVA, d.f. = 3 and 32, $P < 0{\cdot}001$, Fig. 6). Over the 30 min trial periods, red snapper mean time on the block-shell habitat was 14 min without the predator and 28 min with the predator (Fig. 6).

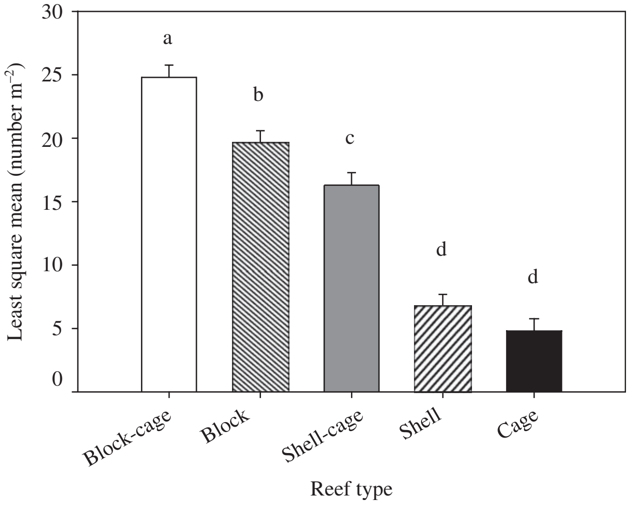


FIG. 4. Habitat effect on the mean + S.E. number m^{-2} of age 0 year red snapper. Different lower case letters denote significant ($P < 0{\cdot}05$) differences.

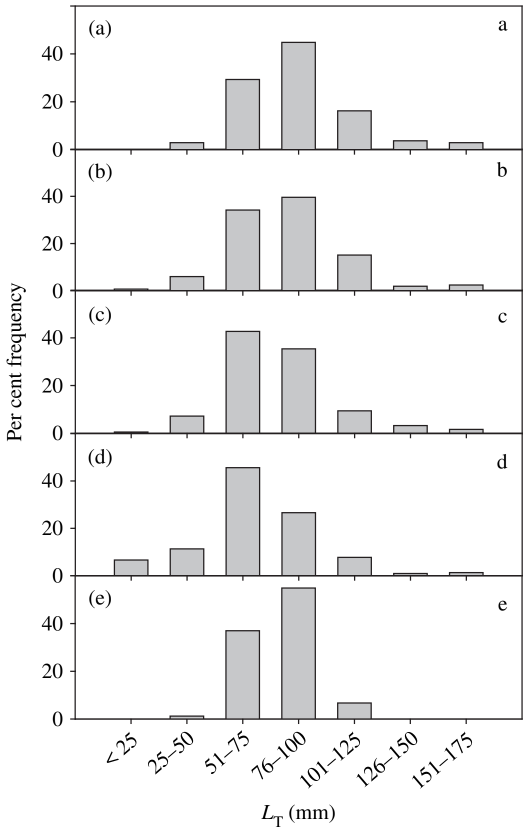


FIG. 5. Red snapper per cent total length (L_T) frequency distribution by habitat type: (a) block-cage, (b) block, (c) shell-cage, (d) shell and (e) cage. Different lower case letters show significant ($P < 0·05$) differences.

DISCUSSION

Overall, a significant predator exclusion effect was detected. Uncaged shell habitats showed significantly lower numbers of age 0 year red snapper, and both uncaged shell and uncaged block-shell habitats showed significantly lower numbers of age 1 year red snapper compared to caged habitats. Previous studies have used predator exclusion cages to study the effects of predation, and to address criticisms of caging artifacts, many have used the approach of partial cages in an attempt to mimic cage artifacts but at the same time have prey exposed to predators (Steele, 1996; Connell, 1997; Hindell *et al.*, 2002). The use of partial cages, however, probably results in a predation level that falls somewhere between no cage and full cage predation levels, *e.g.* 'partial meshed walls provided prey with a refuge that was not available on open areas' (Doherty & Sale, 1985). This difficulty was eliminated in the present study by first correcting for cage alone treatments before making other comparisons. The end result was a direct comparison of habitat exposed to predators to habitat with reduced predator exposure.

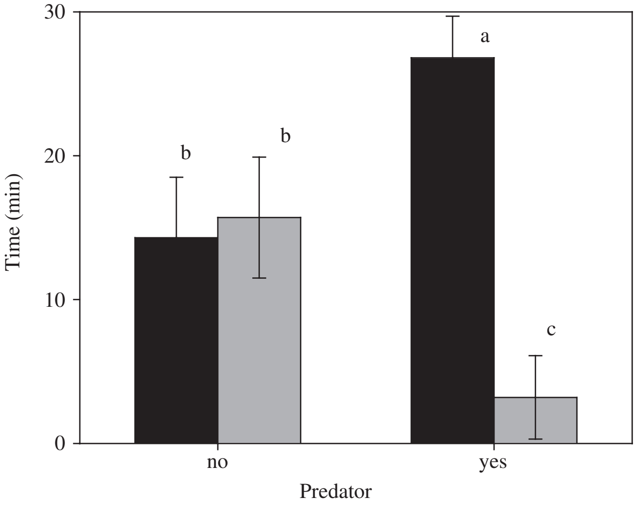


FIG. 6. Red snapper habitat preference in laboratory experiments. Mean + S.E. time over complex (concrete block; ■) or simple (shell; ▩) substratum both with and without a predator present. Different lower case letters show significant ($P < 0{\cdot}05$) differences among treatments.

Fish species contributing to predation on reef fishes are not always known. Large piscivores were not resident on these artificial habitats (Lingo & Szedlmayer, 2006). Schools of larger fishes, *e.g.* red drum *Sciaenops ocellatus* (L.) jack crevalle *Caranx hippos* (L.) and blue runner *Caranx crysos* (Mitchill) were observed passing close by and on one occasion observed feeding on age 0 year red snapper. Thus, transient predators may be a source of predation on juvenile red snapper. In this study, three cages were also pulled off the habitats. On one occasion, two large red drum (*c.* 600 mm L_T) were under the cage. Other studies have also shown transient predators contribute to predation on reef fishes. For example, remote video showed transient predators such as jacks (Carangidae) and barracuda (Sphyraenidae) regularly visited experimental habitats (Carr & Hixon, 1995). In addition, Connell (1997) found mortality of tethered fishes was minimal within cages designed to exclude only large transient predators.

Habitat complexity also affected juvenile red snapper abundance in this study. The higher complexity block habitats supported more red snapper, both age 0 and age 1 years, compared to the shell habitats. The lower abundance of juvenile red snapper in the lower complexity habitats may be related to predator refuge size, as these habitats may not have provided large enough hole sizes for these young red snapper, especially as they increased in size as the season progressed (Szedlmayer & Conti, 1999). Also, later in October and November, no age 1 year red snapper were observed on the experimental habitats in this study. This pattern may result from a further habitat shift to larger, more complex structures not examined in this study, but suggested by Szedlmayer & Lee (2004). Although correlations between habitat complexity of natural reefs and fish abundance have not produced consistent results (Risk, 1972; Luckhurst & Luckhurst, 1978; Carpenter *et al.*, 1981), other studies with artificial habitats have shown that fish abundance increased with complexity (Shulman, 1984;

© 2007 The Authors

Hixon & Beets, 1989, 1993; Eggleston *et al.*, 1997; Topolski & Szedlmayer, 2004; Lingo & Szedlmayer, 2006).

Shifts by red snapper to more complex habitat due to predation pressure observed in the field were supported by laboratory experiments. Preference for the block habitat was significantly increased when a predator was introduced into the experimental tank. This suggested that predators can affect fish abundance indirectly through habitat selection.

Juvenile red snapper were most abundant in late August, subsequently numbers decreased. Decreased abundance was in part due to predation effects, but also may reflect a change in foraging needs or food availability. For example, Szedlmayer & Lee (2004) found a habitat shift by juvenile red snapper (70–160 mm standard length, L_S) to more complex structures coincided with a diet shift.

Competition also appears to affect habitat selection. Intraspecific competition for complex habitat was apparent in one laboratory trial from this study. In that trial, one red snapper aggressively chased the other red snapper away from the blocks, forcing them to stay at the surface of the water. Bailey *et al.* (2003) also found that larger red snapper aggressively defended complex habitats in the laboratory, significantly decreasing the time age 0 year red snapper spent over complex habitat compared to trials without larger red snapper present.

For management concerns mortality of juvenile red snapper due to shrimp trawl by-catch has been estimated to be very high in the Gulf of Mexico (Gallaway & Cole, 1999). In contrast, there were no indications of shrimp trawling on the experimental habitats (*i.e.* all stakes were intact over the survey period). This may simply be the result of reduced trawling effort in the particular study area east of the Mobile Bay Delta (Gallaway & Cole, 1999). The decline in abundance on the artificial habitats in this study was probably due to other factors, such as predation mortality and emigration to larger more complex habitats.

In this study, processes that affect reef fish abundance in the northern Gulf of Mexico were similar to past studies on tropical coral reefs (Sale, 1991). Predation and habitat complexity appear to be important factors for juvenile red snapper abundance. High habitat complexity and predator exclusion both resulted in greater abundance of juvenile red snapper on experimental habitats in nursery areas of the Gulf of Mexico. Predation may affect red snapper abundance and distribution through mortality and indirectly by influencing habitat selection. Further studies are needed to partition other possible causes for increased abundance on complex habitats, *e.g.* food effects, survey period, competition or differential habitat selection.

We thank M. Boles, A. Ouzts, C. Furman, M. Lingo and R. Schroepfer for assistance with data collection. We thank M. Maceina and A. Guarino for statistical assistance. This is a contribution of the Department of Fisheries and Allied Aquacultures, Auburn University, and the Alabama Agricultural Experiment Station. All work was carried out under Auburn University Animal Care and Use Committee approval, under Protocol 001Z-R-0992.

References

Bailey, K. H., Cowan, J. H. Jr & Shipp, R. (2003). Experimental evaluation of potential effects of habitat complexity and presence of conspecifics on behavior of young-of-the-year red snapper on artificial reefs. *Gulf of Mexico Science* **19,** 119–131.

Bell, J. D., Westoby, M. & Steffe, A. S. (1987). Fish larvae settling in seagrass: do they discriminate between beds of different leaf density? *Journal of Experimental Marine Biology and Ecology* **111,** 133–144.

Beukers, J. S. & Jones, G. P. (1997). Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* **114,** 50–59.

Carpenter, K. E., Miclat, R. I., Alvaladejo, V. D. & Corpuz, V. T. (1981). The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proceedings of the 4th International Coral Reef Symposium* **2,** 497–502.

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

Cody, R. P. & Smith, J. K. (1997). *Applied Statistics and the SAS Programming Language*. Upper Saddle River, NJ: Prentice Hall, Inc.

Collins, M. R. (1990). A comparison of three fish trap designs. *Fishery Bulletin, U.S.* **9,** 325–332.

Connell, J. H. (1975). Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In *Ecology and Evolution of Communities* (Cody, M. L. & Diamond, J. A., eds), pp. 460–490. Cambridge: Belknap-Harvard University Press.

Connell, S. D. (1997). Exclusion of predatory fish on a coral reef: the anticipation, preemption and evaluation of some caging artefacts. *Journal of Experimental Marine Biology and Ecology* **213,** 181–198.

Connell, S. D. & Jones, G. P. (1991). The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *Journal of Experimental Marine Biology and Ecology* **151,** 271–294.

Dennis, G. D. & Bright, T. J. (1988). Reef fish assemblages on hard banks in the Northwestern Gulf of Mexico. *Bulletin of Marine Science* **43,** 280–307.

Doherty, P. J. (1981). Coral reef fishes: recruitment-limited assemblages? *Proceedings of the 4th International Coral Reef Symposium* **2,** 465–470.

Doherty, P. J. & Sale, P. F. (1985). Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs* **4,** 225–234.

Eggleston, D. B., Lipcius, R. N. & Grover, J. J. (1997). Predator and shelter-size effects on coral reef fish and spiny lobster prey. *Marine Ecology Progress Series* **149,** 43–59.

Gallaway, B. J. & Cole, J. G. (1999). Reduction of juvenile red snapper bycatch in the U.S. Gulf of Mexico shrimp trawl fishery. *North American Journal of Fisheries Management* **19,** 342–355.

Gittings, S. R., Bright, T. J., Schroeder, W. W., Sager, W. W., Laswell, J. S. & Rezak, R. (1992). Invertebrate assemblages and ecological controls on topographic features in the northeast Gulf of Mexico. *Bulletin of Marine Science* **50,** 435–455.

Hindell, J. S., Jenkins, G. P. & Keough, M. J. (2002). Variability in the numbers of post-settlement King George whiting (Sillaginidae: *Sillaginodes punctata*, Cuvier) in relation to predation, habitat complexity and artificial cage structure. *Journal of Experimental Marine Biology and Ecology* **268,** 13–31.

Hixon, M. A. (1991). Predation as a process structuring coral reef fish communities. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 475–508. San Diego, CA: Academic Press.

Hixon, M. A. & Beets, J. P. (1989). Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science* **44,** 666–680.

Hixon, M. A. & Beets, J. P. (1993). Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* **63,** 77–101.

Jones, G. P. (1988). Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **123,** 115–126.

Jones, G. P. (1991). Post-recruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 294–328. San Diego, CA: Academic Press.

© 2007 The Authors

Kennelly, S. J. (1991). Caging experiments to examine the effects of fishes on understorey species in a sublittoral kelp community. *Journal of Experimental Marine Biology and Ecology* **147,** 207–230.

Lassig, B. R. (1982). Determinants of the structure of small-scale coral patch reef fish assemblages. PhD dissertation, Macquarie University, Sydney.

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

Luckhurst, B. E. & Luckhurst, K. (1978). Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* **49,** 317–323.

Ludwick, J. C. (1964). Sediments in northeastern Gulf of Mexico. In *Papers in Marine Geology* (Miller, R. L., ed.), pp. 204–238. New York: MacMillan Co.

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

Parker, R. O. Jr, Colby, D. R. & Willis, T. D. (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.

Risk, M. J. (1972). Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin* **153,** 1–6.

Sale, P. F. (1991). Reef fish communities: open nonequilibrial systems. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 564–598. San Diego, CA: Academic Press.

Shulman, M. J. (1984). Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology* **74,** 85–109.

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

Sih, A., Crowley, P., McPeek, M., Petranka, J. & Strohmeier, K. (1985). Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* **16,** 269–311.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60,** 1129–1157.

Stanley, D. R. & Wilson, C. A. (1997). Seasonal and spatial variation in the abundance and size distribution of fishes associated with a petroleum platform in the northern Gulf of Mexico. *Canadian Journal of Fisheries and Aquatic Sciences* **54,** 1166–1176.

Steele, M. A. (1996). Effects of predators on reef fishes: separating cage artifacts from effects of predation. *Journal of Experimental Marine Biology and Ecology* **198,** 249–267.

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

Szedlmayer, S. T. & Howe, J. C. (1997). Substrate preference in age-0 red snapper, *Lutjanus campechanus*. *Environmental Biology of Fishes* **50,** 203–207.

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

Szedlmayer, S. T. & Shipp, R. L. (1994). Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the northeastern Gulf of Mexico. *Bulletin of Marine Science* **55,** 887–896.

Topolski, M. F. & Szedlmayer, S. T. (2004). Vertical distribution, size structure, and habitat associations of four Blenniidae species on gas platforms in the northcentral Gulf of Mexico. *Environmental Biology of Fishes* **70,** 193–201.

Witting, D. A. & Able, K. W. (1995). Predation by sevenspine bay shrimp *Crangon septemspinosa* on winter flounder *Pleuronectes americanus* during settlement—laboratory observations. *Marine Ecology Progress Series* **123,** 23–31.

Zar, J. H. (1984). *Biostatistical Analysis*, 2nd edn. Englewood Cliffs, NJ: Prentice Hall, Inc.

Zaret, T. M. (1980). *Predation and Freshwater Communities*. New Haven, CT: Yale University Press.