A comparison of size and age of red snapper (*Lutjanus campechanus*) with the age of artificial reefs in the northern Gulf of Mexico

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Abstract—Despite extensive study, it still is not clear whether artificial reefs produce new fish biomass or whether they only attract various species and make them more vulnerable to fishing mortality. To further evaluate this question, the size and age of red snapper (*Lutjanus campechanus*) were sampled from April to November 2010 at artificial reefs south of Mobile Bay off the coast of Alabama and compared with the age of the artificial reef at the site of capture. Red snapper were collected with hook and line and a fish trap and visually counted during scuba-diver surveys. In the laboratory, all captured red snapper were weighed and measured, and the otoliths were removed for aging. The mean age of red snapper differed significantly across reefs of different ages, with older reefs having older fish. The mean age of red snapper at a particular reef was not related to reef depth or distance to other reefs. The positive correlation between the mean age of red snapper and the age of the reef where they were found supports the contention that artificial reefs in the northern Gulf of Mexico enhance production of red snapper. The presence of fish older than the reef indicates that red snapper are also attracted to artificial reefs.

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Red snapper (*Lutjanus campechanus*, Poey, 1860) has been historically targeted by both sport and commercial fishermen in the Gulf of Mexico (Camber, 1955). Because of intense fishing pressure, the estimated population abundance in this region has decreased and the stock is considered overfished (Schirripa and Legault, 1999; SEDAR[1]). Regulations that decrease the total allowable catch and shorten the recreational season have been enacted over the last several decades to reduce the harvest of this species and increase stock abundance.

The red snapper is a reef-associated fish that uses reef habitat as a resource for both shelter and prey (Ouzts and Szedlmayer, 2003; Szedlmayer and Lee, 2004; Piko and Szedlmayer, 2007; Gallaway et al., 2009). Age-0 red snapper begin to use reefs shortly after they settle out of the plankton and move to available low-relief, structured habitat (Workman and Foster, 1994; Szedlmayer and Howe, 1997; Szedlmayer and Conti, 1999; Szedlmayer and Lee, 2004). These new recruits quickly outgrow their initial benthic habitats and search for larger structured habitats by fall after the spawning season (Szedlmayer and Conti, 1999; Szedlmayer and Lee, 2004; Szedlmayer, 2011). After this initial recruitment, the presence of age-1 and older snapper, through predation and competitive exclusion, may limit the immigration of new recruits to reef structure (Bailey et al., 2001; Piko and Szedlmayer, 2007; Gallaway et al., 2009; Mudrak and Szedlmayer, 2012).

The substrate in the northern Gulf of Mexico is predominately mud and sand and has comparatively few natural reef areas (Parker et al., 1983; Kennicutt et al.,1995; Dufrene, 2005). The lack of naturally occurring reefs has stimulated the deployment of artificial reefs (e.g., decommissioned military tanks and concrete pyramids) by state agencies, private fishermen, and scientists to increase the availability of reef habitat. Several permit areas have been established off the coast of Alabama, where an estimated 15,000 artificial reefs have been deployed (Minton and Heath, 1998). The deployment of new reefs each year continues to add or replace reefs lost to major tropical storms.

The effect of artificial reefs on reef fish populations has been considered for decades. Bohnsack (1989) suggested that artificial reefs may simply aggregate fishes, making resident species easier to harvest and may ultimately decrease their populations. A second possibility is production enhancement, where reefs provide some limiting factor (e.g., habitat) that allows for an increase in the

[1] SEDAR (Southeast Data, Assessment, and Review). 2009. Stock assessment of red snapper in the Gulf of Mexico: SEDAR update assessment. Report of the update assessment workshop;, 24–28 August, 2009, 143 p. Miami, FL. NMFS, SEFSC, NOAA, Miami, Florida. [Available from http://www.sefsc.noaa.gov/sedar.]

available biomass of reef species. The artificial reef system in the northern Gulf of Mexico has been studied extensively— many studies focusing on various life history aspects of red snapper as a means to help resolve the question of whether or not artificial reefs enhance production.

The first group of studies involved diet analyses of the stomach contents of red snapper. If enhanced production is occurring, then red snapper diets should contain reef prey species; but, if only attraction is occurring, red snapper should be feeding on prey species not found on reefs. Evidence supporting both scenarios has been reported. For example, some studies reported that most red snapper prey items were species associated with the water column and sand-mud habitat (McCawley et al., 2006; Wells et al., 2008b). In contrast, other studies showed significant feeding on reef species (Ouzts and Szedlmayer, 2003; Szedlmayer and Lee, 2004; Redman and Szedlmayer, 2009).

Site fidelity of red snapper to artificial reefs also has been used to examine the question of enhanced production on artificial reefs. Again, 2 differing scenarios have been reported. Low residency and lack of site fidelity support the attraction hypothesis (Patterson et al., 2001b, Peabody, 2004), and long-term (>1020 d) residency on artificial reefs and high site fidelity support the production hypothesis (Szedlmayer and Shipp, 1994; Szedlmayer, 1997; Szedlmayer and Schroepfer, 2005; Schroepfer and Szedlmayer, 2006; Topping and Szedlmayer, 2011a; 2011b).

These previous studies indicate that attraction of red snapper to artificial reefs is occurring, but the extent to which artificial reefs also enhance production is an open question. Although it is relatively easy to provide evidence for attraction, it is not as easy to find evidence for production. Therefore, we contend that it still is not clear whether artificial reefs produce new red snapper biomass or whether they only attract fish of this species and make them more vulnerable to fishing mortality.

A new approach to this long-standing question would be to compare the age of resident fish with the age of the artificial reef where they occur. If enhanced production is occurring, new reefs should attract new recruits, and these recruits likely would stay and grow as their reef ages, becoming the dominate age class and would possibly exclude new recruits from the reef habitat. In this case, the age of fish resident at a reef should be positively correlated with the age of the reef. In contrast, if artificial reefs simply attract red snapper, reef age should not be correlated with fish age but, rather, should be related to the proximity of red snapper on other reefs and red snapper movement patterns. For our study, artificial reefs were deployed in 2006, 2009, and 2010, and the size and age of red snapper were compared among these 3 reef ages to help clarify whether artificial reefs may be enhancing red snapper production. The positions of these reefs were not released to the public to reduce the potential effects of variation in fishing mortality on age distributions of red snapper.

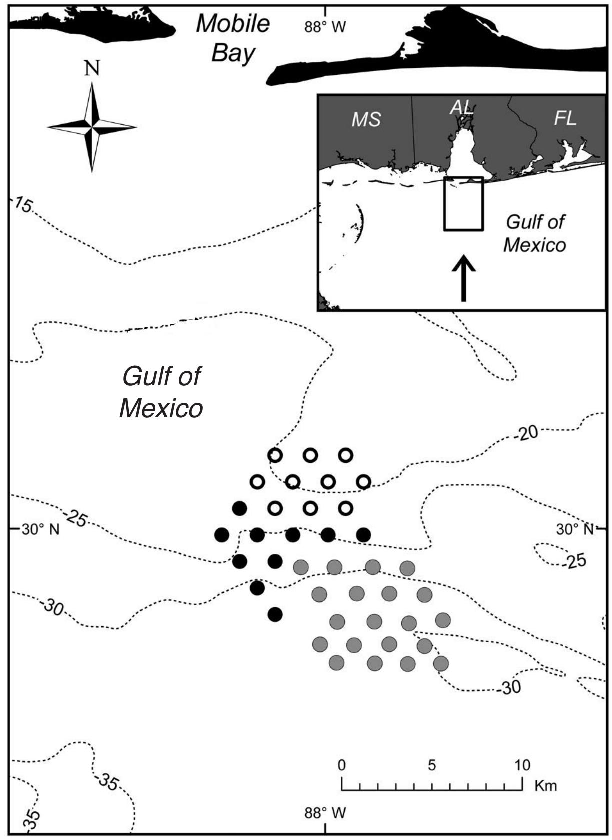

Figure 1

Map of sampling locations in our study of red snapper (*Lutjanus campechanus*) on artificial reefs in the northern Gulf of Mexico in 2010. Gray circles=reefs deployed in 2006; open circles=reefs deployed in 2009; and black circles=reefs deployed in 2010. Dotted lines indicate depth contours at 5-m intervals.

Materials and methods

Sample sites

The area of our study was located 20–30 km south of Mobile Bay, Alabama (Fig. 1). This area has more than 15,000 artificial reefs and a few natural, rocky reefs (Minton and Heath, 1998). For our study, artificial reefs (4.4×1.3×1.2 m, metal cages) were deployed in April 2006 (n=20, which became 4-year-old reefs in our study), April 2009 (n=10, which became 1-year-old reefs in our study), and January 2010 (n=10, which became 0.5-year-old reefs in our study). Reef locations were not published to limit potential fishing mortality. All the reefs we studied were located 1.3–1.7 km from other reefs deployed in this study. These reefs were deployed at the following depths: 27–32 m in 2006, 18–24 m in 2009, and 23–31 m in 2010.

All reefs were sampled from April to November 2010. The reefs deployed in 2010 were not sampled until at least 5 months after their deployment to allow adequate time for the immigration of red snapper (Mudrak and

Szedlmayer, 2012). Red snapper were collected with hook and line and fish trap from each reef. Hook-and-line sampling was standardized to 30 min and 2 individuals who fished. Fishing time was suspended when problems occurred (e.g., internally hooked fish) and continued once both individuals could resume fishing. For hook-and-line fishing, double 6/0 J hooks, 27.2-kg test monofilament line, 45.3-kg test monofilament leader were used, and whole Gulf menhaden (*Brevoortia patronus*) as bait. After completion of hook-and-line sampling, additional fish were collected with a baited fish trap (1.2×1.5×0.6 m; Collins, 1990). In the fish trap, both Gulf menhaden and whole squid (*Loligo* spp.) were used as bait. All fish traps were set for 15 min. After collections of red snapper reached ~50 individuals per reef, a diver released the number of fish caught above 50 fish by opening the trap door and allowing random individuals to escape at the surface—with one exception (73 red snapper were kept on 5 May 2010 because of the possibility of area closures that might have resulted from the Deepwater Horizon oil spill). When the minimum target of 30 individuals per reef was not reached after the first fish trap set, the trap was fished at least one additional time. All red snapper collected from a reef were immediately packed on ice and returned to the laboratory for further processing.

After fish collections were completed, 2 scuba divers completed visual counts and photographic (Nikon D200[2], Nikon Corp., Tokyo) and video (Sony CCD-TR101, Hi8, Sony Corp., Tokyo) recordings to use in estimation of the remaining red snapper at each sample site. A clear plastic jar containing cut Gulf menhaden was used to attract surrounding red snapper into aggregations during visual surveys for increased accuracy of total counts. Divers completed at least 3 full-circle point-and-count surveys, where the divers counted all fish within visual circular range, and the highest count was used for estimates of total abundance. Poor visibility at some sites limited these estimates. In addition, when sharks were present, diver operations were suspended, and visual estimates were completed later within 30 days of the original fish collections.

Laboratory analyses

Red snapper size (standard length [SL], fork length [FL], and total length [TL] in millimeters) and total body weight (0.1 g) were measured in the laboratory within 24 h of capture. For red snapper ≥250 mm TL, otoliths were removed with a Bosch fine-cut electric saw. For red snapper <250 mm TL, otoliths were removed with a small knife. Both left and right otoliths were removed from each fish, cleaned, and stored in dry plastic vials for later analysis. Opaque bands were counted on all otoliths for age estimates. For fish <7 years old, bands were counted on whole otoliths that were immersed in water and viewed under a dissecting scope with transmitted light. If ages were ≥7 years, thin otolith sections were prepared and bands were counted at 40× magnification with a compound microscope (Szedlmayer and Beyer, 2011). Opaque bands of sectioned otoliths were counted along the dorsal edge of the sulcus acousticus. Bands on each otolith were counted independently 4 times. After 4 readings, 2 readers examined the remaining otoliths for which counts still differed and attempted to reach a consensus on age. If an agreement on age could not be reached for an otolith, it was rejected. A reference collection of hatchery red snapper that had been released in the wild as age-0 and recaptured as age-1fish (n=22) along with a group that had been reared in captivity to age-1 (n=13) were used to validate counting methods of wild caught age-1 fish. Some of the otoliths of these known age-1 fish showed a “false” annulus (i.e., had 2 opaque bands) but showed age-1 otolith shape patterns (Beyer and Szedlmayer, 2010). Therefore, some of the wild fish <200 mm SL caught in this study that had 2 opaque bands were defined as age-1, on the basis of their age-1 shape patterns appearing similar to the shape patterns of hatchery-reared fish as well as hatchery-born but wild-reared fish.

Video recordings and digital photographs of the studied reefs were examined in the laboratory for comparisons and validation of the divers’ visual counts. In the laboratory, photographs that showed the highest number of red snapper for a particular reef were selected for computer-based counting. All red snapper in these photographs were identified and counted through image analysis with Image-Pro Plus software (vers. 4.5, Media Cybernetics, Rockville, MD). Two screens were used to count fish in video recordings. A single frame captured from the video was displayed on one screen while the video played on the second screen. Because image quality decreases when a single frame of video is captured, we used the full video on the second screen to identify all the fish in the captured frame on the first screen. The captured video image then was marked and the fish in it were counted with Image-Pro software.

Data analyses

Catch per unit of effort (CPUE) for each reef was calculated for both hook and line (CPUE=number caught by 2 individuals/30 min) and trap (CPUE=number caught/15 min). The precision of age estimates between readers was compared with linear regression and average percent error (Beamish and Fournier, 1981). Densities of red snapper were estimated by adding the total number of red snapper caught (from both hook and line and fish trap) to the number of fish counted in the visual survey. Pearson’s correlation coefficient was used to compare densities (number of fish per cubic meter of reef surveyed) among reefs of different ages, with reef age determined by the number of months that a reef had been deployed before the month of sampling. Analysis of variance (ANOVA) was used to compare the SL, weights,

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

and ages of red snapper among the different ages of reefs. If significant differences were detected, a Tukey test was used to show specific differences.

Growth rates were examined with an analysis of covariance (ANCOVA) that compared the mean length at age of red snapper <10 years old between old (2006) and new (2009 and 2010) reefs. This analysis was used to determine if old reefs were providing additional resources, a difference that would be reflected in faster growth rates of red snapper on old reefs than on new reefs. For additional comparisons, Pearson's correlation coefficients were calculated for reef age with red snapper SL, weight, and age. Also examined with Pearson's correlation coefficient was the potential influence of nearby known reefs on the age and abundance of red snapper on the reefs that we surveyed in 2010. Nearby reefs were 0.17–1.7 km away (mean=0.72 km, n=37), or less than the distance between the reef sites sampled in our study. In an effort to remove possible depth effects, the ages of red snapper collected at the same depth (30 m) were compared between the 2006 and 2010 reefs with a t-test. Differences were considered significant at $P\leq0.05$, and all data were analyzed with Statistical Analysis System software (SAS, vers. 9.1, SAS Institute, Inc., Cary, NC).

Results

Red snapper were sampled from April to November 2010 from 37 artificial reefs (2006 reefs=18; 2009 reefs=10; 2010 reefs=9). Visual surveys were completed by divers at later dates at 2 sites because of the presence of sharks on the original sampling date and were not completed on 7 reefs (3 of the 2006 reefs and 4 of the 2010 reefs) because of poor visibility (<1 m).

A total of 1028 red snapper were collected, 439 by hook and line and 589 by trap. Mean ±standard deviation (SD) CPUE for hook and line was significantly greater on the 2006 reefs (20.4 ±8.5 30 min^{-1}) than on the 2009 (6.3 ±8.1 30 min^{-1}) and 2010 reefs (2.6 ±4.6 30 min^{-1}; ANOVA: $F_{2, 34}$=20.38, P<0.0001). No significant differences in CPUE were detected among reef years for trap collections (2006=10.6 ±10.9, 2009=16.6 ±19.9, and 2010=14.3 ±12.7; ANOVA: $F_{2, 34}$=0.6, P=0.55). The SL and weight of red snapper caught by hook and line (429.4 ±79.8 mm, 2531 ±1409 g) were significantly greater than those measures of fish caught by trap (232.6 ±77.6 mm, 538 ±726 g; SL t-test, t_{1018}=39.56, weight t_{1018}=29.41, P<0.0001). Red snapper ages also were significantly different between these 2 sampling methods (hook and line=4.1 ±1.3 years, trap=1.9 ±1.1 years; t-test, t_{1024}=29.68, P<0.0001).

The visual survey methods significantly affected counts of red snapper. Visual counts by divers (mean ±SD=78.3 ±54.8) were significantly higher than counts from image-analysis methods (photograph counts=30.7 ±20.2, video counts=16.5 ±10.3; ANOVA, $F_{2, 42}$=13.37, P<0.0001). Because of these differences, total densities of red snapper were estimated by adding the number of captured fish (hook-and-line and trap samples) to divers' visual counts.

Table 1

Average percent error for both sets of independent readings of otoliths from red snapper (*Lutjanus campechanus*) caught in 2010 during our study on artificial reefs in the northern Gulf of Mexico. Included are the percentages of agreement for each difference between readings (first and second reading, coefficient of regression [r^2]=0.83, P<0.0001; third and fourth reading, r^2=0.96, P<0.0001).

	First and second readings	Third and fourth Readings
Average percent error	7.85	1.41
Standard deviation	0.12	0.05
0	62.16%	92.32%
±1	35.89%	7.39%
±2	1.95%	0.29%
≥3	0%	0%

Age-1 red snapper composed the dominate age class on the 2010 reefs and recruited to these reefs in the early summer. Mean ±SD numbers of red snapper per cubic meter of reef structure increased as reef age increased (Pearson's correlation coefficient [r]=0.48, P=0.008) and were significantly greater on 2006 reefs (22 ±13) than on 2009 reefs (12 ±6) and 2010 reefs (8 ±7; ANOVA, $F_{2, 27}$=4.25, P<0.025).

All caught red snapper (n=1028: 2006 reefs=587, 2009 reefs=280, 2010 reefs=161) were used in the final age comparisons. Initial agreement between the first and second independent readings was 62.2% (639/1028). A third and fourth reading increased the accepted otoliths to 92.3% (949/1028). Average percent error was calculated for both sets of independent readings (Table 1). An age consensus was reached on all remaining otoliths (n=79) through simultaneous examination by the 2 readers. The reference collection of age-1 hatchery (n=35, laboratory and wild reared) red snapper showed 25.7% with 2 opaque bands, indicating that counting opaque bands for age-1 fish may not be reliable. Among fish that were <200 mm SL and showed 2 opaque bands (n=72), all were identified as age-1 based on shape, thickness, and location of the opaque bands (Beyer and Szedlmayer, 2010; Szedlmayer and Beyer, 2011).

Mean ±SD red snapper SL, weight, and age were significantly different among 2006 reefs (373.3 ±107.8 mm SL, 1883 ±1388 g, 3.5 ±1.2 years), 2009 reefs (250.2 ±114.7 mm SL, 852 ±1464 g, 2.0 ±1.7 years) and 2010 reefs (222.3 ±78.0 mm SL, 480 ±711 g, 1.7 ±1.0 years; ANOVA, $F_{2, 1025}$=194.2, P<0.0001; Table 2; Figs. 2 and 3). Reef age was positively correlated with red snapper age (Pearson's r=0.61, P<0.0001), standard length (r=0.71, P<0.0001), and weight (r=0.47, P=0.0035). Comparisons of linear growth rates for fish <10 years old showed no significant differences between old (2006)

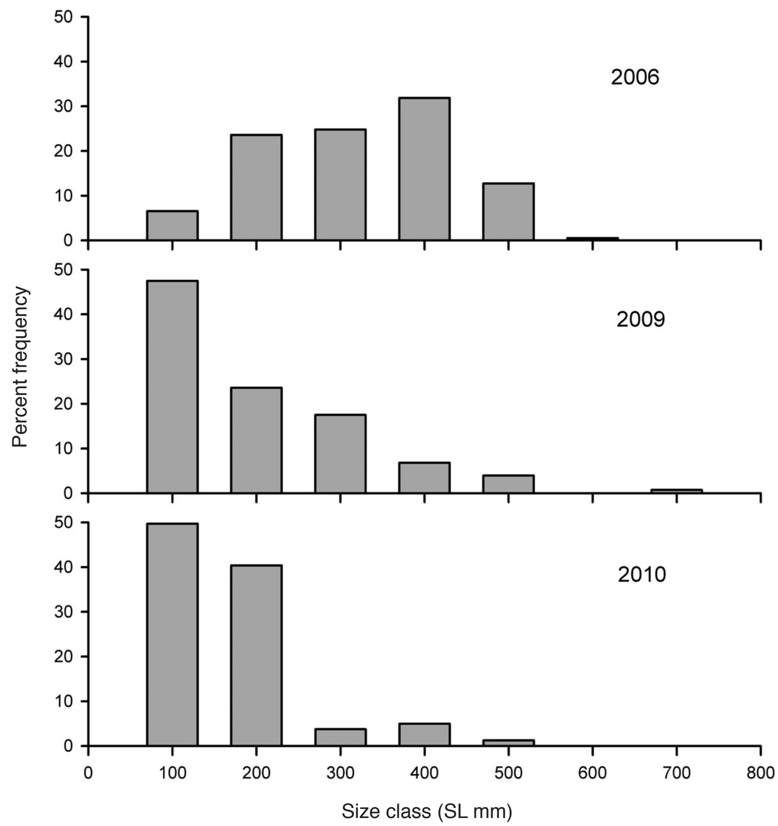

Figure 2

Length frequency of red snapper (*Lutjanus campechanus*) caught in our study on artificial reefs in the northern Gulf of Mexico in 2010, shown by year that reef was deployed, separated into 100-mm standard-length (SL) size classes (e.g., 100=100–199 mm).

Table 2

Mean (±SD) standard length (SL), weight, and age of red snapper (*Lutjanus campechanus*) caught during our study on artificial reefs deployed in 2006, 2009, and 2010 in the northern Gulf of Mexico. Superscript letters are used to indicate significant differences ($P \leq 0.05$). Included for each reef year are the total number of red snapper caught by hook-and-line and trap, mean diver count, and mean density estimate. Estimates of mean density per reef combine diver counts and catch of hook-and-line and trap.

Reef year	SL (mm)	Weight (kg)	Age (yr)	Hook and line	Trap	Diver count	Density
2006	373.3 ±107.8 [a]	1.88 ±1.39 [a]	3.54 ±1.24 [a]	20.2 ±8.8	12.4 ±11.3	115.5 ±87.8	148.7 ±92.5
2009	250.2 ±114.7 [b]	0.85 ±1.46 [b]	1.98 ±1.70 [b]	5.3 ±6.1	22.5 ±18.4	54.0 ±35.8	81.8 ±41.2
2010	222.3 ±78.0 [c]	0.48 ±0.71 [c]	1.72 ±1.00 [c]	2.3 ±4.6	15.6 ±11.6	36.0 ±31.7	55.6 ±45.6

and new (2009 and 2010) reefs (ANCOVA, $F_{3,\ 1018}$=2.98, P=0.085, power>0.99).

The mean depth (30 m) of the 2006 reefs were significantly greater than the mean depth (20 m) of the 2009 reefs (t-test, t_{26}=16.32, P<0.0001). Because of this depth difference, red snapper also were compared among the 2006 and 2010 reefs (n=8) with the same depth (30 m). These comparisons also showed significantly larger and older red snapper on the 2006 reefs (mean ±SD=368.7 ±5.0 mm SL, 1821 ±1326 g, 3.60 ±1.20 years) compared to 2010 reefs (236.2 ±85.2 mm SL, 578 ±814 g, 1.91 ±1.10 years; t-test, P<0.0001).

Comparisons of our estimates of red snapper abundance and age on artificial reefs by proximity (<1.7 km) to other known reefs not sampled in our study failed to detect a significant effect. These other nearby reefs have published locations because they are part of Alabama's artificial reef program and were deployed

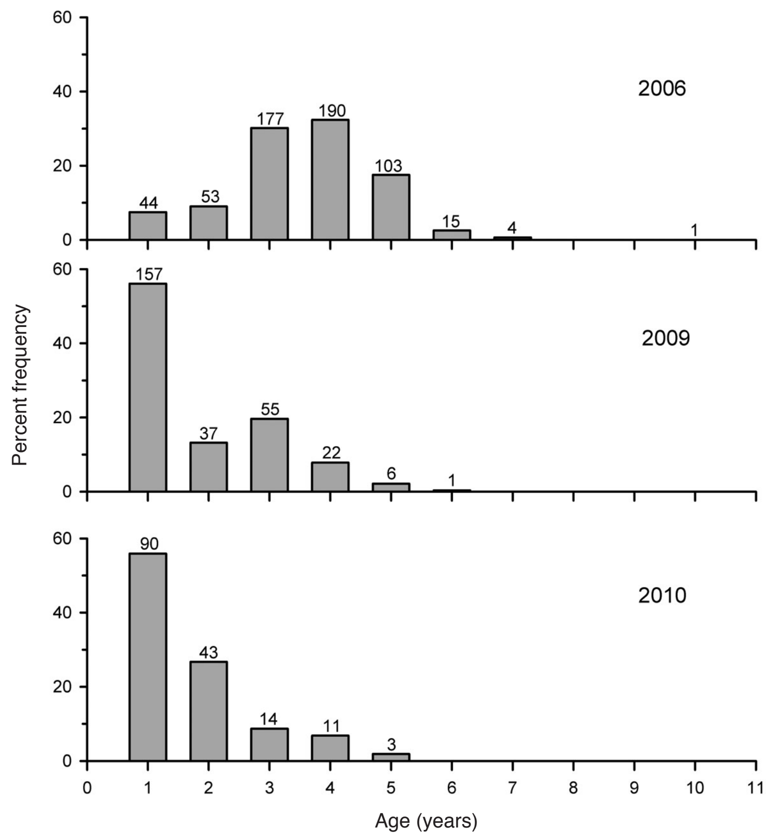

Figure 3

Age frequency, by year that reef was deployed, of red snapper (*Lutjanus campechanus*) caught in our study on artificial reefs in the northern Gulf of Mexico in 2010. Numbers above bars indicate total number of fish caught for each age class.

from 1992 to 2007. The oldest reef (1992) was closest to a 2010 reef that we sampled, and many of the artificial reefs deployed in 2004 and 2007 were within 1.7 km of reefs in all 3 reef ages that we sampled in our study (Fig. 4). No significant correlations were detected between distance to other reefs and abundance (Pearson's r=–0.045, P=0.781), or mean age of red snapper (Pearson's r=0.026, P=0.88; Fig. 5).

Discussion

Evidence for production and attraction

Our study showed that older red snapper were associated with older artificial reefs. Previous studies have compared artificial reef age with estimates of density and size of resident reef fishes but have not examined reef fish age. For example, densities of reef fishes and larger sparids (*Diplodus sargus*, *Diplodus bellottii*, and *Diplodus vulgaris*) have been reported to be significantly higher at older habitats (Lindberg et al., 2006; Santos et al., 2011). Because length varies directly with age with these species up to the age of 3 years (Gordoa and Molí, 1997), it is likely that their age also increased with reef age as was observed with red snapper in our study.

The relation between reef age and fish age shown in our own and these other studies, along with the long-term residence of red snapper on artificial reefs shown in previous studies (Schroepfer and Szedlmayer 2006; Topping and Szedlmayer, 2011a), supports the hypothesis that artificial reefs enhance the production of red snapper (Szedlmayer and Shipp, 1994; Szedlmayer, 2007; Gallaway et al., 2009). If artificial reefs enhance a population and experience no fishing pressure, Powers et al. (2003) estimated that such reefs could increase production by 6.45 kg wet weight/10 m^2 in the first year after their deployment. Because the locations of the reefs in our study were not published, fishing mortality was limited and therefore had the potential to increase production.

It was also clear that attraction of fish plays an important role in the function of these artificial reefs. For example, fish older than the age of the reef were present on the reefs that we sampled, including 2 of the oldest fish (19 and 14 years old) that were caught on the 2009 reefs. It is possible that larger, older red snapper become less dependent on particular reefs because of relief from predation pressure and may show greater movement among reef sites as they search for new prey resources (including young red snapper) on newly established reefs (Mudrak and Szedlmayer, 2012). However, although attraction is clear and accounts for both the initial recruitment of young fish and the presence of older red snapper, if attraction was the only function of artificial reefs, we would not expect a positive correlation between mean fish age and reef age. Instead, the age distribution of red snapper should be random or related to the proximity of nearby reefs. Hence, this study provides evidence that both attraction and production are important ecological functions of artificial reefs for red snapper populations in the northern Gulf of Mexico.

According to our study and several other studies, young fish (age-0 and age-1) will recruit to new habitat, usually small (1–7 m^3) artificial reefs (Gallaway et al., 2009; Szedlmayer, 2011; Mudrak and Szedlmayer, 2012). Many of these red snapper remain at such habitats for extended periods (up to several years; Szedlmayer,1997; Szedlmayer and Schroepfer, 2005; Schroepfer and Szedlmayer, 2006; Topping and Szedlmayer, 2011a, 2011b) and then begin to show greater movement as they become older and larger and are less vulnerable to predation (Gallaway et al., 2009). For example, on the basis of a 72% residency rate per year from telemetry studies (Topping and Szedlmayer, 2011a), and a mean of 45 age-1 recruits to new (1-year-old) reefs in our study, there would be ~18 age-5 red snapper per reef after 4 years. These estimates are similar to counts recorded for the 2006 reefs in our study, with a mean of 26 age-5 fish per reef (on the basis of proportions of age-5 red snapper among all fish captured from 2006 reefs, extrapolated to mean total densities on 2006 reefs). Also, these residency estimates based on telemetry are underestimates because the time that red snapper reside on a particular reef before being tagged is not included (Topping and Szedlmayer, 2011a). Laboratory and field studies indicate that these older age-5 red snapper may then competitively exclude and even cannibalize new recruits (Bailey et al., 2001; Piko and Szedlmayer, 2007; Mudrak and Szedlmayer, 2012), and perhaps contribute to the association between fish age and reef age. However, attraction may continue to play an important role as older fish that are better able to fend off aggression and cannibalism move to favorable habitats that still harbor abundant prey resources (Ouzts and Szedlmayer, 2003; Szedlmayer and Lee, 2004).

Several studies suggest that red snapper populations have been overfished and that habitat limitation was not the most important controlling factor that contributed to declines in abundance (Schirripa and Legault, 1999; Patterson et al., 2001b; Cowan et al., 2011). Clearly, there was significant fishing mortality of red snapper in the northern Gulf of Mexico (Gil-

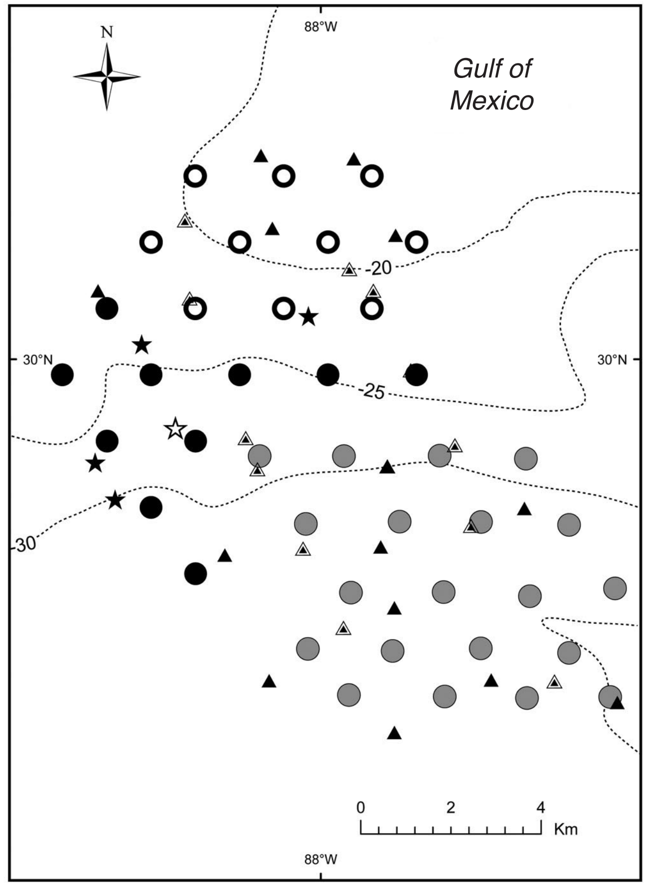

Figure 4

Map showing proximity of publicly known reefs to reefs sampled in 2010 in our study of red snapper (*Lutjanus campechanus*) on artificial reefs in the northern Gulf of Mexico. Note that the positions of the reefs sampled in our study were not released to the public. Study reefs: gray circles=reefs deployed in 2006; open circles=reefs deployed in 2009; and black circles=reefs deployed in 2010. Publicly known reefs: black stars=reefs of army tanks deployed in 1994–1995; black triangles=reefs made of concrete pyramids deployed in 2007; black and white triangles=pyramid reefs deployed in 2004; open star=barge deployed as a reef in 1994. Dotted lines indicate depth contours at 5-m intervals.

lig et al., 2000). However, if fishing mortality was the only limiting factor for red snapper and habitat was not important, we would not expect reef age to have significant effects on fish age (i.e., all reefs, whether fished or not, would show similar age distributions). Red snapper enter the fishery at around age 2 (minimum size: recreational=406 mm TL, commercial=330 mm TL), and the catch consists predominately of 2- to 4-year-old fish. These ages represented 59% (n=602) of the total catch in our study and indicate that fishing mortality was not limiting red snapper abundance on the reefs investigated in our study.

One substantial difference between our study, which suggests habitat limitation, and previous studies, which

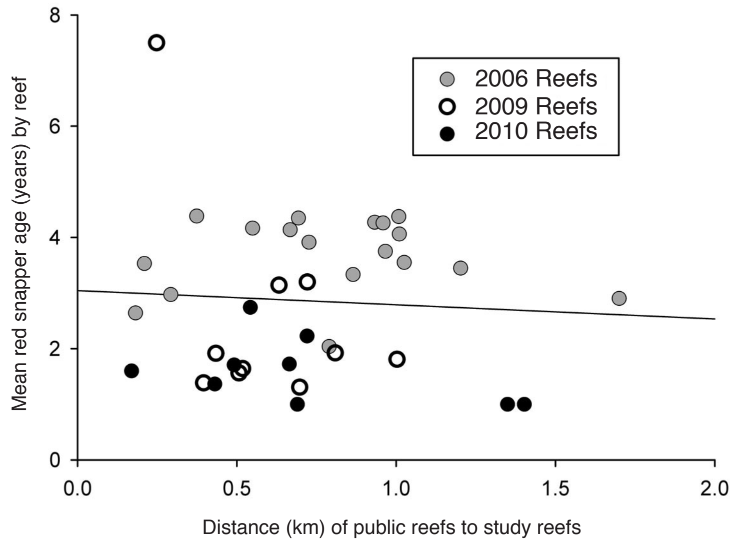

Figure 5

Comparison of mean age of red snapper (*Lutjanus campechanus*) caught in 2010 in our study of artificial reefs in the northern Gulf of Mexico with proximity to publicly known reefs <1.7 km from our sampled reefs, which were deployed in 2006, 2009, and 2010. Line is linear regression that showed no significant relation between red snapper age and distance to known reefs (Pearson's correlation coefficients [r]=0.026, P=0.88).

suggested fishing mortality limitation, was the use of fishery-independent data rather than fishery-dependent data. Although other studies used mainly fishery-dependent data on red snapper caught by sport and commercial fishermen (Szedlmayer and Shipp, 1994; Baker and Wilson, 2001; Patterson et al., 2001a; Wilson and Nieland, 2001), we used fishery-independent methods at unpublished artificial reef sites. These fishery-independent methods also allowed us to sample red snapper that were too small to be counted with fishery-dependent methods. In addition, fishing mortality at reef sites surveyed in our study was probably far more reduced than at known reefs because the locations of the artificial reefs that we sampled were unpublished and likely had limited access for fishing.

Several alternative factors, aside from reef age, could have affected the size and age of red snapper caught on the artificial reefs examined in our study. Additional prey may be one important factor that created differences in habitat value among reefs of different ages, and these differences may have resulted in larger, older fish at older reefs. If older reefs were providing more prey resources, we would expect that red snapper on these reefs would have higher growth rates, especially the relatively young (<10-year-old) individuals that have a nearly linear growth rate. Yet no significant differences in mean growth rates of red snapper were detected among the reefs sampled, despite their age differences. Even so, older reefs often have more well-developed epifaunal benthic communities that can influence habitat value (Redman and Szedlmayer, 2009), and this development might be expected for older artificial reefs like those in our study. If older reefs actually provide more prey resources or greater habitat complexity and shelter than younger reefs, attraction to these "better" reefs may account for some of the older ages and higher abundances of red snapper on older reefs. However, we still are left with the same conclusion: artificial reefs enhance red snapper production. One implication of our study is that habitat value may vary not only spatially (e.g., open versus structured habitats) but also temporally (e.g., new versus older, more "developed" reefs). Therefore, we need to include a temporal component to habitat value, whereby new artificial reefs may need time to develop before they start to enhance production.

Another factor that may have caused differences in the ages of fish among reefs was reef depth. The mean depth of the 2006 reefs was 30 m, but the mean depth of the 2009 reefs was 20 m, and there is some evidence that larger, older red snapper were more common in deeper offshore waters than in shallower nearshore waters (Render, 1995; Mitchell et al., 2004). However, comparisons of reefs with the same mean depth (30 m) and distance from shore (27 km) still showed significantly larger and older red snapper at the 2006 reefs than at the 2010 reefs. In addition, the distances among the reefs that were farthest apart were relatively smaller (14 km) than the distance across the continental shelf (110 km) where depth-related differences in size and age may be more apparent (Mitchell et al., 2004).

We also considered the possible emigration of larger, older red snapper from other reef sites or an effect of nearby reefs not sampled in our study. Proximity to other natural or artificial reefs has been shown in other studies to be an important factor that can affect density of reef fishes (Jessee et al., 1985; Sogard, 1989; Strelcheck et al., 2005; Shipley and Cowan, 2010). In our study, no significant relations were detected between proximity of our study reefs to other reefs and red snapper ages or abundance. In general, other artificial reefs were, for the most part, evenly distributed across our overall study area (Fig. 1) and would not be expected to bias red snapper age distribution to either younger or older reef sites in our study (Fig. 4).

Comparison of collection methods

This study supports previous studies on the importance of using several collection methods to adequately estimate size and age distribution of red snapper on artificial reefs (Myers and Hoenig, 1997; McClanahan and Mangi, 2004; Szedlmayer, 2007; Wells et al., 2008a; Gallaway et al., 2009). Hook-and-line and fish-trap methods are known to be size selective, and red snapper caught in our study were consistently larger with hook-and-line than with fish traps. This difference occurred mostly because larger fish are able to swallow whole bait and smaller fish consume smaller portions. In addition, smaller fish are more likely to enter a trap, and larger fish may be limited by the size of a trap opening. The distinct size differences observed in our study also could have been influenced by differences in bait: the fish traps had squid in addition to Gulf menhaden, but the hook-and-line bait was strictly Gulf menhaden.

The divers' visual counts were used to estimate the red snapper remaining present on the reef after hook-and-line and trap sampling. At 2 sample sites, visual surveys were conducted a maximum of 30 days after our initial sampling because sharks were present during our initial sampling. Although it is possible that additional red snapper immigrated to the reef at these 2 sites within that 30-d time period, it is unlikely that enough fish recruited to cause a bias in our abundance estimates. This notion is supported by evidence from telemetry studies of high site fidelity for red snapper (72% residency rate per year; Topping and Szedlmayer 2011a) and by the fact that diver counts typically underestimate abundance. In comparison with results from visual surveys, counts were significantly lower from the video and photographic methods. These differences mostly were due to fish swimming throughout the part of the water column that was not within the field of view of the cameras. A bait jar was used with the intent to attract fish closer to the cameras and reduce these differences, but it had only limited success. Comparisons of counts from remote, underwater, baited cameras with those from scuba-diver surveys have shown similar results, with diver visual surveys showing the greatest abundance and diversity of fishes among the methods compared (Tessier et al., 2005; Langlois et al., 2006). Because counts from photographs and video recordings were lower, we used the divers' counts in our estimates of red snapper density for each reef. However, the photographs and video recordings were still important in verifying species identification.

Artificial reef succession and red snapper densities

The reefs in our study supported higher densities of red snapper than reefs sampled in previous studies. In a demolition study of 9 offshore oil platforms, mean density of red snapper was 0.24 individuals/m^3 (Gitschlag et al.[3]). In another study of platforms where stationary hydroacoustics and visual diver counts were used, mean density was 0.16 individuals/m^3 (Stanley and Wilson, 1997). Substantially higher than these platform estimates, the estimates from our study of total density of red snapper were 1.6–47.9 individuals/m^3, with a mean of 15.7 individuals/m^3. One difference between our study and these previous studies was the larger size of the platforms surveyed which also encompassed the entire water column. The volume of these platforms varied: 1037–29,860 m^3 (Gitschlag et al.[3]) and 19,800 m^3 (Stanley and Wilson, 1997); in contrast, all reefs in our study had a volume of 6.9 m^3. However, even if the volume estimates of these platforms were reduced by two-thirds (to account for the habitat in the upper water column that red snapper typically do not use), mean densities of red snapper on platforms would be 0.73 individuals/m^3 (Gitschlag et al., 2000[3]) and 0.47 individuals/m^3 (Stanley and Wilson, 1997)—levels that would still be considerably less than the estimates from our study of artificial reefs formed from metal cages.

These differences in the density of red snapper among artificial habitats may be due to higher habitat complexity and associated enhanced protection from predation, additional prey resources, and fewer resident larger predators at cage reefs than at platforms. The densities of lemon damselfish (*Pomacentrus moluccensis*) found on highly complex coral reefs with predators were similar to densities found on reefs where predators were excluded, indicating that these complex coral habitats provided protection for this species (Beukers and Jones, 1997). Similarly, higher densities of young (age-0 and age-1) red snapper were shown to inhabit increasing complex reef structure (Lingo and Szedlmayer, 2006; Piko and Szedlmayer, 2007) with an absence of predators (Mudrak and Szedlmayer, 2012). At large structures, such as platforms, complexity probably is lower and the abundance of potential predators likely is higher than at the smaller artificial reefs used in our study. Therefore, these larger reefs may not support as

[3] Gitschlag, G. R., M. J. Schirripa, and J. E. Powers. 2001. Estimation of fisheries impacts due to underwater explosives used to sever and salvage oil and gas platforms in the U. S. Gulf of Mexico. OCS Study MMS 2000–087, 94 p. Final report prepared by the National Marine Fisheries Service for the U.S. Dept. of the Interior, Minerals Mgmt. Service, Gulf of Mexico OCS Region, New Orleans, LA. [Available from http://www.boemre.gov/itd/abstracts/2000-087a.html.]

many red snapper per unit of volume as more complex, smaller structures. For example, an inverse relation was shown between the abundance of red snapper and the density of offshore platforms—possibly a result of greater exposure of young red snapper to predators that aggregate around such platforms (Gallaway et al., 1999). The higher densities of red snapper on the reefs found in our study indicate that these artificial reefs may provide red snapper enhanced protection from predation as well as greater overall carrying capacity.

Conclusions

The significant differences observed in ages of red snapper among artificial reefs of different ages provide support for the hypothesis that artificial reefs enhance red snapper production. Although it is obvious that red snapper are attracted to artificial reefs, especially as young new recruits, and older red snapper may show more transient behavior among reefs, it appears that many red snapper reside on particular reefs for several years and that artificial reefs may allow for higher biomass of red snapper by providing additional reef habitat. However, at some point, the number of artificial reefs placed in the northern Gulf of Mexico may surpass the region's carrying capacity and the addition of more artificial structures will no longer increase the population of red snapper. Future research that examines the carrying capacities of artificial habitats is needed and would provide information on when an overall environmental carrying capacity for red snapper has been reached. Additional fishery-independent studies throughout the northern Gulf of Mexico, with methods similar to those used in our study, would be useful for making better management decisions regarding catch limits for red snapper.

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