A comparison of the size and age distribution of red snapper *Lutjanus campechanus* to the age of artificial reefs in the northern Gulf of Mexico

by

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Abstract

Size and age of red snapper, *Lutjanus campechanus,* were sampled from April through November 2010 and compared with the age of the artificial reef at the site of capture. Artificial reefs were deployed in 2006 (*n*=20, 4 year old reefs), 2009 (*n*=10, 1 year old reefs), and 2010 (*n*=10, 0.5 year old reefs). Red snapper were sampled using hook-and-line and a fish trap. After sampling was completed, SCUBA divers estimated the remaining red snapper densities at sample reefs using visual surveys, photographs, and video recordings. Red snapper total densities per reef were estimated from both captured and diver counted fish. In the laboratory, all captured red snapper were weighed (0.1 g), measured (mm), and the otoliths removed for age estimation.

Annual growth increments on each otolith were counted independently four times. After four readings, two readers examined any otoliths with counts that differed and attempted to reach a consensus on age. If an agreement on age could not be reached the otolith was rejected. All otoliths were counted whole if age < 7, while all older otoliths were sectioned for counting. Mean ± SD age of red snapper showed significant differences when compared across reef age, with older reefs yielding older fish: 2006-reefs = 3.6 ± 1.2 years, 2009-reefs = 2.0 ± 1.7 years, 2010-reefs = 1.7 ± 1.0 years (ANOVA: $F_{2, 1025}$ = 194.23, $P < 0.0001$). A significant positive correlation between fish age and reef age was detected with 37% ($r^2 = 0.37$, $P < 0.0001$) of the variance of fish age explained by reef age. Comparisons of a subset (*n* = 8) of 2006 and 2010 reefs, all at the same depth (30 m) also showed a significant reef age effect on fish age, that negated possible depth difference effects (t-test:$_{228}$ = 9.29 $P < 0.0001$). Also, comparisons of

known distances to other "public" reefs failed to detect a significant effect on fish age and density, and negated possible reef proximity effects (fish age: Pearson's $r = 0.160$, $P = 0.345$; density: Pearson's $r = -0.061$, $P = 0.721$). Growth rates were not significantly different among reef ages for all fish < 10 years, indicating that older reefs did not provide "better" habitat (ANCOVA: $F_{3,1018} = 2.98$, $P = 0.085$). These results suggest that new artificial reefs are quickly colonized by young fish, and older reefs are more important for older red snapper. This scenario supports the contention that artificial reefs in the northern Gulf of Mexico are producing red snapper and not just acting as attractants.

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INTRODUCTION

Red snapper, *Lutjanus campechanus* (Poey 1860), has historically been a species targeted by both recreational and commercial fisherman in the Gulf of Mexico (Camber 1955). Due to intense fishing pressure, the estimated population abundance has decreased and the stock is considered overfished (Schirripa and Legault 1999; SEDAR7 2005; SEDAR 2009). Regulations decreasing the total allowable catch and shortening the recreational season have been enacted over the last several decades to reduce the harvest of this species in the hopes that the stock will increase (SEDAR7 2005; SEDAR 2009).

Red snapper are a reef associated fish, using reef habitat for both shelter and prey resources (Outz and Szedlmayer 2003; Szedlmayer and Lee 2004; Piko and Szedlmayer 2007; Gallaway et al. 2009). However, the substrate in the northern Gulf of Mexico is predominately mud and sand, with comparatively few areas of natural reef habitat (Parker et al. 1983; Shultz et al. 1987; Kennicutt et al. 1995; Dufrene 2005). The lack of naturally occurring reefs has prompted the deployment of artificial structures (e.g. decommissioned military tanks and concrete pyramids) by the state of Alabama (Alabama Marine Resources Division), private fishers, 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; Shipp 1999). The deployment of new reefs each year continues to add or replace reefs lost to major tropical storms.

The most common factor examined among studies completed on red snapper is the age of individuals captured (Nelson and Manooch 1982; Szedlmayer and Shipp 1994; Patterson et al. 2001a; Wilson and Nieland 2001; Mitchell et al. 2004; Gazey et al. 2008). The results most often are used for population assessments (SEDAR7 2005; SEDAR 2009), but other studies on ontogenetic shifts in habitat and diet that occur as the fish ages also use otoliths (Szedlmayer and Conti 1999; Rooker et al. 2004). Red snapper are aged by counting the annuli (opaque bands), which have been validated as yearly bands (Szedlmayer and Beyer 2011). Aging can be completed by reading otoliths whole if the individual is generally < 7 years, but older red snapper have thicker otoliths and require sectioning in order to distinguish annuli. Red snapper are a long-lived species and can reach maximum ages of between 31 and 53 years (Szedlmayer and Shipp 1994; Render 1995; Patterson et al. 2001a; Wilson and Nieland 2001).

The availability of suitable habitat is a major factor affecting the survival of red snapper. Red snapper begin to use reefs shortly after settling out of the plankton, with habitat preferences changing in relation to the size of the individual (Szedlmayer and Lee 2004; Szedlmayer 2007; Gallaway et al. 2009). Habitat studies on red snapper indicate that age-0 fish recruit to low relief areas (Workman and Foster 1994; Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Szedlmayer and Lee 2004), with new recruits seeking out and recruiting to available structured habitat (Mudrak and Szedlmayer, unpublished data). Age-0 red snapper typically outgrow low relief habitats and search for larger more structured habitats by the fall following the spawning season (Szedlmayer and Conti 1999; Szedlmayer and Lee 2004). After this initial recruitment, the presence of age-1 and older snapper may limit the immigration of new recruits to reef structure (Bailey et al. 2001; Piko and Szedlmayer 2007).

The effect that artificial reefs have on reef fish populations has been widely debated for decades. Bohnsack (1989) raised the issue that artificial reefs may simply be functioning to aggregate fish, making resident species easier to harvest and ultimately decreasing the population. A second possibility is production enhancement, where reefs provide some limiting factor (e.g. habitat) allowing for an increase in the available biomass of the reef species. While production has been shown on artificial reefs off the coast of Japan to increase the abundance of octopuses (Polovina and Sakai 1989), there are few studies that have convincingly demonstrated that increased production of fishes results from artificial reefs.

In the northern Gulf of Mexico, numerous artificial reefs have been placed in offshore waters to enhance fish production, especially for red snapper, principally due to the relatively low (3.3%) total surface area of natural reef habitat (Parker et al. 1983; Dufrene 2005). However, the debate continues: i.e. artificial reefs only attract fish, are producing fish, or true effects are unknown. Recent reviews have supported all three views (Grossman et al. 1997; Lindberg 1997; Pickering and Whitmarsh 1997; Bortone 1998; Szedlmayer 2007; Gallaway et al. 2009; Cowan et al. 2010). One important aspect of the debate is that attraction and production are not mutually exclusive, and the effect artificial reefs have on reef fish species likely involves both, since reef species must first immigrate to the reefs (Bohnsack 1989; Lindberg 1997).

Several aspects of the life history of red snapper have been examined in an attempt to prove whether artificial reefs produce or only attract the species. Diet analysis of the stomach contents of red snapper is one method to determine if reef resources are being used, but results have differed. If artificial reefs are enhancing red snapper production, their diet would consist of reef species, indicating that red snapper are using the reef as a prey source. However, if only attraction is occurring, red snapper would be feeding on items from surrounding substrate and pelagic habitats. Some studies have indicated attraction because red snapper were mostly feeding on prey from pelagic environments and open sand-mud habitats (McCawley et al. 2006; Wells et al. 2008b), while others have indicated significant feeding on reef species and artificial reefs were enhancing prey resources (Ouzts and Szedlmayer 2003; Szedlmayer and Lee 2004; Redman and Szedlmayer 2009).

The amount of time red snapper spend on a reef (residence time) is another aspect of red snapper ecology that can indicate attraction or production. If reefs are strictly attracting red snapper, studies on residency and site fidelity would show low residency and substantial movement of tagged individuals throughout the Gulf of Mexico. In contrast, long-term residency and high site fidelity would support production, since the reef resources are used for an extended period of time (years). Again, previous studies differ in residency and movement estimates for red snapper. Patterson et al. (2001b) reported mean distance moved was 29.6 km per year based on recaptured marked fish, and Peabody (2004) indicated that red snapper had short residence times on offshore oil platforms based on telemetry, while long-term residency on artificial reefs (up to 1020 d) was reported from both external tags and telemetry methods (Szedlmayer and Shipp 1994; Szedlmayer 1997; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Topping and Szedlmayer, in review).

Abundance comparisons of red snapper to artificial reefs have also produced conflicting reports. The increased deployment of artificial reefs off the coast of Alabama in the 1980's appeared to increase red snapper abundance (Szedlmayer and Shipp 1994). Red snapper were also abundant at oil and gas platforms, representing 20% of the yearly species composition (Stanley and Wilson 1997). However, longline sampling of red snapper in the eastern Gulf of Mexico with extensive artificial reef habitat recorded lower catch rates (0.12 red snapper / 100 hook hr), compared to catch rates (1.73 red snapper / 100 hook hr) from open habitats in the western Gulf (Mitchell et al. 2004).

Thus, it is still not clear if artificial reefs produce new red snapper biomass or simply attract fish and make them more vulnerable to fishing mortality. A new approach to this long standing question would be a comparison of resident fish age to artificial reef age. If enhancement is occurring, the reefs will initially attract new recruits, and these recruits will stay and grow as the reef ages and effectively exclude new recruits from immigrating to “their” habitat. In contrast, if the artificial reefs simply attract red snapper, reef age will not be correlated with fish age, with little evidence of competitive exclusion or habitat limitation. In the present study reefs were deployed in 2006, 2009, and 2010 and positions were not released to the public to reduce potential fishing mortality effects on red snapper age distribution. The size and age of red snapper were compared among the three reef ages.

METHODS

Study sites.–The study area was located 20 to 30 km south of Mobile Bay, Alabama (Figure 1). This area has over 15,000 artificial and a few natural rocky reefs. Artificial reefs (4.4 x 1.3 x 1.2 m metal cages, Figure 2) were deployed in April 2006 (n = 20), April 2009 (n = 10), and January 2010 (n = 10). Reef locations were not published which limited potential fishing mortality. The reefs were located at differing depths depending on reef year, with the 2006-reefs ranging from 27 – 32 m, 2009-reefs from 18 – 24 m, and the 2010-reefs from 23 – 31 m.

Field sampling of red snapper.–All reefs were sampled from April through November 2010. The 2010-reefs were sampled no earlier than five months after deployment to allow adequate time for red snapper immigration. Two fish collection methods, hook-and-line, targeting larger red snapper, and a fish trap, targeting smaller red snapper, were used to ensure that representative size distributions of red snapper were sampled from each reef. After fish collections were completed, SCUBA divers estimated the remaining red snapper densities at sample reefs using visual surveys, photographs, and video recordings. Hook-and-line sampling was standardized to 30 min, with two anglers. Fishing time was suspended when problems occurred (e.g. internally hooked fish) and continued once both anglers could resume fishing. Hook-and-line fishing used double 6/0 J hooks, 27.2 kg test monofilament line, 45.3 kg test monofilament leader, and whole Gulf menhaden (*Brevoortia patronus*) as bait. After completion of hook-and-line fishing, additional fish were collected with a baited fish trap (1.2 x 1.5 x 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 reached approximately 50 red snapper, additional fish were released on all but one site (73 red snapper were kept on 5 May 2010 due to the possibility of area closures as a result of the Deepwater Horizon oil spill). When the minimum target of 30 red snapper per reef was not yet collected the trap was fished at least one additional time. All red snapper collected from the reef were immediately packed on ice.

After fishing, two SCUBA divers completed visual, photographic (Nikon D200) and video (Sony Hi-8) surveys to estimate the remaining red snapper at the sample site. A clear plastic jar containing cut menhaden was used to attract surrounding red snapper into aggregations during the visual survey for increased accuracy of total counts. Divers completed at least three visual counts, with the highest count used for total abundance estimates. Poor visibility at some sites limited total abundance estimates. In addition, diver operations were suspended when sharks were present and visual estimates were completed at a later date.

Laboratory analysis.–Red snapper were measured for standard length (SL), fork length (FL), and total length (TL, mm) and weighed (0.01 g) on an Ohaus balance. For red snapper ≥ 250 mm TL, cuts through the cranium, to expose the otoliths, were done using a Bosch fine cut electric saw. For red snapper < 250 mm TL, cuts were made using 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, bands were counted on whole otoliths that were immersed in water under a dissecting scope with transmitted light. If ages were > 7 years, thin otoliths sections were prepared and bands were counted at 40x with a compound microscope (Szedlmayer and Beyer 2011). Opaque bands of sectioned otoliths were counted along the dorsal edge of the sulcus acoustic. Otoliths were counted independently four times. After four readings, two readers examined remaining otoliths where counts still differed and attempted to reach a consensus on age. If an agreement on age could not be reached the otolith was rejected. A reference collection of hatchery red snapper that were released in the wild as age-0 and recaptured as age-1 (n = 22) along with a group that was reared in captivity (n = 13) were used to validate counting methods of the remaining otoliths. Some of these known age-1 fish otoliths showed a "false" annulus (i.e. had 2 opaque bands), but showed age-1 otolith shape patterns (Beyer and Szedlmayer 2010). Thus, some wild fish < 200 mm caught in this study with two opaque bands were defined as age-1, based on age-1 shape patterns similar to hatchery reared fish.

Video recordings and digital photographs of the reefs were examined in the laboratory for comparisons and validation of diver visual counts. In the laboratory, photographs that showed the highest number of red snapper for a particular reef were selected for computer counting. All red snapper in photographs were identified and counted using Image-pro software. Two screens were used to analyze video recordings. A single frame of the video was displayed on one screen while the video played on the second screen. When a single frame of the video is captured, the quality of the image decreases, but the live video screen allowed identification of all fish in the captured screen. The captured screen could then be marked and counted using Image-pro software.

Data Analysis.–Catch per unit effort was calculated for both hook-and-line (CPUE = number caught by 2 fishers per 30 min) and trap (CPUE = number caught per 15 min set) for each reef. A Kolmogorov-Smirnov test was used to test for normality of length and age data. The precision of age estimates between readers was compared using a linear regression and average percent error (Beamish and Fournier 1981). Red snapper densities (number per m^3)

were compared with the number of months the reefs were deployed prior to sampling using Pearson's correlation coefficient. An analysis of variance (ANOVA) was used to compare the SL, weights, and ages of red snapper among the different reef ages. If significant differences were detected a Duncan's multiple comparison test was used to show specific differences. Von Bertalanffy growth models of red snapper total length at age were fitted with nonlinear regression by least squares:

$$TL_t = L_\infty (1 - e^{(-k(t - t_0))}),$$

Where TL_t = total length at age t;

L_∞ = the total length asymptote;

k = growth coefficient;

t = age in yrs; and

t_0 = a hypothetical age when TL is zero.

Growth rates were also examined by linear regressions for red snapper <10 years and compared among reef years using an analysis of covariance (ANCOVA). For additional comparisons, Pearson's correlation coefficients were calculated between reef age and red snapper SL, weight, and age; and between proximity to public artificial reefs and red snapper abundance and age. To eliminate possible depth effects, the ages of red snapper collected from the same depth (30 m) were compared among 2006 reefs and 2010 reefs with a t-test.

RESULTS

Reefs Sampled and Catch Per Unit Effort

Out of the 40 artificial reefs built, 37 reefs were sampled (*n*=18 2006-reefs, *n*=10 2009-reefs, *n*=9 2010-reefs). All reefs were sampled from April through November 2010. Diver surveys were completed at later time periods on two sites due to shark presence on the original sample date, and not completed on seven reefs due to poor visibility.

A total of 1028 red snapper were collected, 437 by hook-and-line, 589 by trap, and 2 by spear fishing. Hook-and-line CPUE was significantly different for the three reef years (ANOVA: $F_{2,34} = 20.38$, $P < 0.0001$). A Duncan's multiple comparison test revealed that the CPUE on the 2006-reefs (mean ± SD = 20.4 ± 8.5 / 30 min) was significantly greater than the 2009 (6.3 ± 8.1 / 30 min) and 2010-reefs (2.6 ± 4.6 / 30 min). No significant CPUE differences were detected among reef years for trap collections (2006 mean ± SD = 10.6 ± 10.9 / 15 min, 2009 = 16.6 ± 19.9 / 15 min, and 2010 = 14.3 ± 12.7 / 15 min; ANOVA: $F_{2,34} = 0.61$, $P = 0.55$). Mean ± SD of SL and weight of red snapper caught by hook-and-line (mean ± SD, 429.44 ± 79.75 mm, 2531 ± 1409 g) were significantly greater than those caught by trap (232.6 ± 77.56 mm, 538 ± 726 g; SL *t*-test: $t_{1018} = 39.56$, weight $t_{1018} = 29.41$, $P < 0.0001$). Mean ± SD age caught by the two sampling methods was also significantly different (hook-and-line = 4.1 ± 1.3 years, trap = 1.9 ± 1.1 years; *t*-test: $t_{1024} = 29.68$, $P < 0.0001$). Using both hook-and-line and the trap allowed for a representative sample to be obtained from the reefs sampled (Table 1).

Comparisons of SCUBA Visual, Photographic, Video counts, and Density estimates

There was a significant difference in red snapper counts depending on the sampling method used (ANOVA: $F_{2, 42}$= 13.37, P <0.0001). A Duncan test revealed that the counts from the visual SCUBA surveys were significantly higher than the other methods (mean ± SD, visual counts = 78.3 ± 54.8; photograph counts = 30.7 ± 20.2, and video counts = 16.5 ± 10.3). Visual diver counts of red snapper were significantly different between the 2006 and 2010 reefs (ANOVA: $F_{2, 27}$= 3.85, P <0.034).

Total red snapper densities were estimated by adding captured fish (hook-and-line and trap samples) to visual counts (Table 2). Age-1 red snapper began recruiting to the 2010 reefs in the early summer, and the densities increased through the fall (Figure 3). Densities of red snapper were significantly different between the 2006 and the 2010-reefs (ANOVA: $F_{2, 27}$= 4.25, P <0.025). Mean density (number of red snapper / m^3 of reef structure) was 22 ± 13 on the 2006-reefs, 12 ± 6 on the 2009-reefs, and 8 ± 7 on the 2010-reefs.

Comparisons of Size and Age of Red Snapper among Reef Ages

All red snapper caught (n= 1028) were used in the final age comparisons. Initial agreement between the 1st and 2nd independent readings was 62.2% (639/1028). A 3rd and 4th reading increased the accepted otoliths to 92.3% (949/1028). Average percent error was calculated for all independent readings (Table 4). An age consensus was reached on all remaining otoliths (n = 79) by simultaneous examination by two readers. The reference collection of age-1 hatchery red snapper showed 25.7 % (9/35) with two opaque bands, suggesting that counting opaque bands for age-1 fish may not be reliable. Among fish that were < 200 mm SL and showed two opaque bands (n = 72), all were identified as age-1 based on shape, thickness, and location of the opaque bands (Szedlmayer and Beyer 2010, Szedlmayer unpublished data; Figure 4).

Mean ± SD red snapper standard length, weight, and age were significantly different among 2006-reefs (373.29 ± 107.83 mm SL, 1883.1 ± 1388.1 g, 3.6 ± 1.2 years), 2009-reefs (250.20 ± 114.71 mm SL, 852.0 ± 1464.4 g, 2.0 ± 1.7 years) and 2010-reefs (222.25 ± 78.04 mm SL, 480.1 ± 710.6 g, 1.7 ± 1.0 years; ANOVA: $F_{2,\,1025} = 194.23$, $P < 0.0001$; Table 3; Figure 5).

Mean length frequency distributions of red snapper by reef were normally distributed (Kolmogorov-Smirnoff ; SL: $D_{37} = 0.143$, $P = 0.055$). The mean age distribution by reef age was not normal, with the 2009 and 2010-reefs skewing the data due to the high frequencies of age-1 and age-2 red snapper at these reefs (Kolmogorov-Smirnoff ; 2006-reefs: $D_{18} = 0.175$, $P > 0.15$, 2009 and 2010-reef: $D_{19} = 0.307$, $P < 0.01$; Figure 6). Reef age was positively correlated with red snapper age (Pearson's $r = 0.61$, $P < 0.0001$), standard length (Pearson's $r = 0.71$, $P < 0.0001$), and weight (Pearson's $r = 0.47$, $P = 0.0035$).

The von Bertalanffy growth model which best described red snapper TL at age (n = 1028) was

$$TL\ (\text{mm}) = 936.37[1 - e^{-0.205(t + 0.142)}], \qquad (r^2 = 0.99).$$

The growth equation from the present study is similar to other growth equations (Figure 7). Comparisons of linear growth rates for fish <10 years showed no significant differences between old (2006) and new (2009 and 2010) reefs (ANCOVA: $F_{3,\,1018} = 2.98$, $P = 0.085$, power > 0.99).

Depth and Fishing Pressure Effects

The depths of the 2006-reefs were significantly greater than the depths of the 2009-reefs (t-test: $t_{26} = 16.32$, $P < 0.0001$). Due to this depth difference, red snapper were also compared among 2010 and 2006-reefs (n = 8) from the same depth (30 m). These comparisons still detected significantly larger and older red snapper on 2006-reefs (mean ± SD = 368.73 ± 105.02 mm SL, 1820.8 ± 1326.3 g, 3.60 ± 1.20 years) compared to 2010-reefs (236.19 ± 85.24 mm SL, 578.0 ± 814.1 g, age: 1.91 ± 1.10 years, *t*-test: $P < 0.0001$).

Comparisons of red snapper density and age on artificial reefs in this study to the proximity of known public reefs failed to detect a significant effect. No significant correlations were detected between reef distance to known public reefs and mean density (Pearson's $r = -0.061$, $P = 0.721$) or mean age of red snapper (Pearson's $r = 0.160$, $P = 0.345$).

DISCUSSION

Evaluation of technique

This study supports previous findings showing the importance of using various sampling methods to effectively sample all size classes of red snapper on artificial reefs (Szedlmayer et al. 2004, Szedlmayer 2007; Gallaway et al. 2009). Comparisons of the sampling methods and the catch per unit effort in this study showed that hook-and-line and traps were size selective. The size of red snapper caught by hook-and-line was significantly larger than red snapper caught in the trap. The trap consistently collected smaller red snapper, with the smaller sizes possibly related to the trap only fishing on the bottom or the addition of squid as bait. Similar gear selectivities were shown in an earlier fishery independent study in the northern Gulf of Mexico (Szedlmayer et al. 2004). Gear selectivity has long been recognized (Myers and Hoenig 1997; McClanahan and Mangi 2004; Wells et al. 2008a) and as shown in this study, several different gears were needed to collect the full size range of red snapper on artificial reefs in the northern Gulf of Mexico.

Visual diver counts were used to estimate the remaining red snapper still present on the reef after hook-and-line and trap sampling. The video and photograph methods had significantly lower counts than diver visual surveys. These differences were mostly due to fish swimming throughout the water column that could be counted by divers, but were not captured with photographs or video recordings. The use of a bait jar was intended to attract fish closer to reduce these differences, but only had limited success. Comparisons of remote underwater baited cameras have reported similar results, with visual SCUBA (or diver operated video) surveys showing the greatest abundance and diversity (Bortone et al. 1991; Francour et al. 1999; Tessier et al. 2005; Watson et al. 2005; Langlois et al. 2006). Due to lower counts from photographs and video recordings, the diver visual counts were used in the red snapper density estimates for each reef. The photographs and video recordings were still used to verify species, ensuring that reef fish counts were actually of red snapper and not some other similar species (e.g. lane snapper, *Lutjanus synagris,* gray snapper, *Lutjanus griseus,* or vermillion snapper, *Rhomboplites aurorubens*).

Growth bands in red snapper otoliths were deposited annually, consisting of one opaque and one translucent zone (Szedlmayer and Beyer 2011). However, there is some uncertainty as to when opaque bands were formed. Based on marginal increment analysis, red snapper formed opaque bands from winter to summer (Patterson et al. 2001a; Wilson and Nieland 2001; Allman et al. 2005). However, Szedlmayer and Beyer (2011) showed that opaque band formation occurred predominately from August to early December from a mark and recapture study, and suggested formation was related to post spawning. In the present study red snapper showed variation in band formation with 25% of age-1 fish showing two opaque bands. The formation of two opaque bands in the first year was based on comparisons of otolith size and shape from wild fish captured in this study to otoliths from known age hatchery red snapper that were released into the wild and recaptured as age-1. These recaptured age-1 fish also showed two opaque bands in 24 % of the fish examined (Szedlmayer unpublished data). Thus, similar to Beyer and Szedlmayer (2010), aging of age-1 red snapper may be more accurate by examination of shape variables along with opaque band counts.

Artificial reef succession and red snapper densities

Many studies have shown that artificial habitats are rapidly settled by reef fishes (Lukens 1981; Solonsky 1985; Walsh 1985; Leitão et al. 2008; Redman and Szedlmayer 2009). In a four year study of an artificial reef system in the U. S. Virgin Islands, most reef fishes that immigrated to the reefs were juveniles and these immigrants then stayed on these reefs through adulthood (Ogden and Ebersole 1981). Also, fish abundances can be reduced by catastrophic events, but fish will re-colonize the reefs back to pre-event densities (Bohnsack 1983). Two years after a red tide event off the coast of Florida, the invertebrate and demersal fish communities were similar to those before the red tide (Dupont et al. 2010). The artificial reefs used in this study are probably functioning as in the above studies. Based on density patterns over several years, it appears that young reefs fill up quickly over the first year and reach a carrying capacity with little increase over the next few years.

The reefs in the present study supported higher densities of red snapper compared to previous studies. In a study of the demolition of eight offshore oil platforms, mean density was 0.24 red snapper m^{-3} (Gitschlag et al. 2003). In another study of platforms that used stationary hydroacoustics and visual diver counts, the mean density of red snapper was 0.16 m^{-3} (Stanley and Wilson 1997). The total red snapper density estimates in the present study were substantially higher than these platform estimates and ranged from 1.6 – 47.9, with a mean of 15.7 red snapper m^{-3} of reef. One difference between the present study and these previous studies on platforms were substantial differences in the size of the structures, since the platforms encompass the entire water column. The volume of the platforms ranged from 1037 – 29,860 m^3 (Gitschlag et al. 2003) and 19,800 m^3 (Stanley and Wilson 1997), whereas all reefs in the current study had a volume of 6.9 m^3. However, even if the volume estimates of the platforms were reduced by two-thirds (water column habitat not typically used red snapper), mean platform red snapper densities (0.57 / m^3) would still be considerably less than present metal cage estimates.

These differences in the density of red snapper among artificial habitats may be due to increased habitat complexity of cage reefs, providing better habitat protection for younger red snapper, additional prey resources, and fewer resident larger predators compared to platforms. The densities of damselfish (*Pomacentrus moluccensis*) found on highly complex coral reefs with predators were similar to reefs where predators were excluded, indicating that these corals provided protection for prey (Beukers and Jones 1997). Similarly, higher densities of young (age-0 and age-1) red snapper were shown with increasing complexity of reef structure (Lingo and Szedlmayer 2006; Piko and Szeldmayer 2007). With large structures, such as platforms, complexity probably decreases and potential predators probably increases, and therefore do not support as many red snapper per unit volume as the more complex smaller structures. For example, an inverse relation was shown between red snapper abundance and the density of offshore platforms, possibly due to an increased exposure of young red snapper to predator aggregations around the platform (Gallaway et al. 1999). The higher densities of red snapper on the reefs used in the present study indicate that these reefs are providing red snapper additional protection from predation, and increasing the overall carrying capacity.

Artificial Reefs Effects on Red Snapper

Several alternate factors, aside from reef age, could have affected the size and age of red snapper caught. First, differential growth rates may have caused larger fish on the older reefs. To examine this factor, linear growth rates on the 2006-reefs were compared to the 2009 and 2010-reefs and no differences in growth rates were detected between reef ages, thus reefs in this study were providing similar resources. Second, the mean depth of the 2006-reefs was 30 m while the mean depth of the 2009-reefs was 20 m, and previous studies have indicated that larger, older red snapper were more common in deeper offshore waters compared to shallower nearshore waters (Render 1995; Mitchell et al. 2004). However, in this study an analysis of reefs from the same depth (30 m) still showed significantly larger and older red snapper on the 2006-reefs compared to the 2010-reefs. Third, distance from natural or artificial reefs has been shown to be an important factor affecting the density of reef fishes (Jessee et al. 1985; Sogard 1989; Strelcheck et al. 2005; Shipley and Cowan 2010). In this study, the closest known public reefs to sample reef sites were used to test for reef proximity effects on age and density of red snapper, but these comparisons failed to detect any reef proximity effects.

The von-Bertalanffy growth curve of red snapper was similar to other length at age studies (Nelson and Manooch 1982; Szedlmayer and Shipp 1994; Patterson et al. 2001a; Wilson and Nieland 2001). All models predict rapid growth for the first 10 years, after which growth slows. It appears that growth of red snapper in the current study was slightly faster than all growth models except Patterson et al. (2001a). This may be due to the large number of red snapper caught that were < 250 mm SL (n = 395, 38.6 % of the total catch) in comparison to other studies where smaller fish were under-represented due to sampling methods. Despite few older fish caught in the present study (3 red snapper > 10 yrs, maximum = 19 yrs), the calculated L_{∞} of 937 mm closely matches several other studies, 975 mm (Nelson and Manooch 1982) and 935 mm (Wilson et al. 2001).

Evidence that artificial reefs are producing red snapper

Several studies that analyzed the diet and site fidelity of red snapper in the northern Gulf of Mexico concluded that artificial reefs only attract the species. Several lines of evidence would be necessary to conclude that reefs are sites of attraction. Diet analysis of red snapper would show an opportunistic feeding pattern, with reef species occasionally being consumed, and pelagic and open habitat prey items being the majority of the prey consumed. McCawley et al. (2006) concluded that red snapper foraged on species found in the water column and sand-mud associated species. However, problems with prey identification (accounting for 40.23 % of prey by weight in July) may have limited identification of prey habitat type and the location of red snapper feeding. Another diet study using stable isotopes similarly concluded that prey was predominately from sand and mud habitats (Wells et al. 2008b), but conclusions were based on prey identified only to family, making it difficult to distinguish between reef associated or open water prey types.

In contrast, production would be supported if the reefs are providing additional food resources and increasing the species feeding efficiency (Bohnsack 1989). Several studies have concluded that artificial reefs in the northern Gulf of Mexico enhanced prey resources for red snapper (Ouzts and Szedlmayer 2003; Szedlmayer and Lee 2004; Redman and Szedlmayer 2009). For example, tunicates were the second most important prey species in the stomachs of medium red snapper (300 – 399 mm) during the day (Ouzts and Szedlmayer 2003). Also, on artificial reefs where epibenthic growth was limited using anti-fouling paint, red snapper were significantly smaller and less abundant compared to reefs with epibenthic communities (Redman and Szedlmayer 2009). When the stomach contents of red snapper caught over open habitat were compared to those of red snapper caught over artificial reefs distinct differences were found, with reef fishes including *Halichoeres* spp., *Serranus* spp., and *Centropristis* spp. only in the diet of red snapper caught over artificial reefs (Szedlmayer and Lee 2004). These studies indicated that artificial reefs were being used for supplemental prey resources. The present study provides support for this conclusion i.e., fish are staying and growing on artificial reefs in part due to additional prey resources provided by the structures.

Studies on residence time have previously used tagging studies with internal anchor tags, but have transitioned to ultrasonic telemetry studies. This change is not only due to the constant tracking that telemetry allows, but also due to problems with tag shedding and lack of position accuracy from fisher reported recaptures. Patterson et al. (2001b) relied on accurate reporting of locations by fishers and reported short residency and average movement of 30 km per year, providing evidence that artificial reefs are only attracting red snapper. However, inaccuracies of fisher reported recapture locations has been documented using ultrasonic telemetry (Szedlmayer and Schroepfer 2005). More recently, telemetry methods showed long-term residency of 1020 d for red snapper (Topping and Szedlmayer, in review). The present finding of older fish on older reefs results supports these previous telemetry studies that showed long-term residency of red snapper on artificial reefs.

This study compared the age of red snapper to known age artificial reefs and showed significantly older fish on older reefs. Several other studies have compared the artificial reef age with density and size estimates of resident reef fishes (Lindberg et al. 2006; Santos et al. 2011). Both of these previous studies found significantly higher densities of reef fishes at older reef ages compared to younger reefs. In addition, Santos et al. (2011) found that there was a greater density of larger Sparids (*Diplodus sargus*, *Diplodus bellottii*, and *Diplodus vulgaris*) at older habitats. Since length varies directly with age until approximately age 3 with these species (Gordoa and Molí 1997), it is likely that the age also increased with reef age consistent with the present study.

This relation between reef age and fish age supports previous studies that indicated red snapper production from artificial reefs (Szedlmayer and Shipp 1994; Szedlmayer 2007; Gallaway et al. 2009). The increased production is likely due to an increase in available reef habitat, which has previously been found to be a controlling factor affecting the density and growth of red snapper (Szedlmayer and Shipp 1994; Szedlmayer and Conti 1999; Gazey et al. 2008). Red snapper are recruiting to the newly deployed reefs rapidly as juveniles (approximately age-1) and then residing on these reefs for several years. If these reefs were only attracting red snapper, there would be no correlation between fish age and reef age, since red snapper would simply be migrating to and from reefs. In this case, the age distribution would have been random, with no clear dominate age classes. However, dominate age classes for each reef year were found and correlated with reef age, providing evidence that artificial reefs are producing rather than simply attracting red snapper. If artificial reefs are enhancing the population and experiencing no fishing pressure, Powers et al. (2003) estimated that these reefs could increase production by 6.45 kg wet wt 10 m^{-2} in the first year. Since the reefs used in the current study were unpublished, fishing mortality was limited and following Powers et al. (2003), had the potential to increase production.

Several studies suggest that red snapper populations are overfished and that habitat limitation is not a controlling factor (Schrippa and Legault 1999; Patterson et al. 2001b; Cowan et al. 2010). Clearly there is significant fishing mortality of red snapper in the northern Gulf of Mexico (Gillig et al. 2000). However, if fishing mortality was the limiting factor for red snapper and habitat was not important, we would not expect differences in fish age resulting from reef age (i.e. all reefs whether fished or not would show similar age distributions). Red snapper enter the fishery around age 2, (recreational size minimum = 406 mm, commercial = 330 mm), with the catch predominately consisting of 2 to 4 year fish. If fishing mortality was effectively limiting red snapper, these ages would be harvested and drastically decreased when analyzing the age distribution. However, these ages represented 59 % (n =602) of the total catch, indicating that fishing mortality was not controlling the red snapper population.

One substantial difference between the present study that suggests habitat limitations and previous studies that suggested fishing mortality limitations was fishery independent data compared to fishery dependent data. While other studies mainly used fishery dependent data of red snapper caught by recreational and commercial fishers (Szedlmayer and Shipp 1994; Baker and Wilson 2001; Patterson et al. 2001a; Wilson et al. 2001), this study used fishery independent methods from unpublished artificial reefs, and this key difference may account for differing results. In the present study, fishing mortality probably had little influence on age distributions from artificial reefs sampled. In addition, we were able to sample smaller red snapper that fishery dependent sampling programs cannot access due to size limitations on the fishery.

The significant differences between red snapper on the three reef years provide support for increased red snapper production from artificial reefs. Eventually, the number of artificial habitats placed off the coast of Alabama will eliminate the habitat limitation and the addition of more artificial structures will no longer increase the population. Future research examining the carrying capacities of artificial habitats is needed and would provide information on when overall environmental carrying capacity for red snapper has been reached and limit additional artificial reef construction. Additional fishery independent studies, using similar methodologies done throughout the northern Gulf of Mexico would be useful in making better management decisions regarding total allowable catch limits, based on comparisons of regional catch per unit effort and length at age data.

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TABLES

Table 1.–Mean ± SD standard lengths and weights of red snapper (n = 1020) caught by hook-and-line and trap for each reef age. Eight fish were not included; six due to an inability to get accurate length and weight estimates after sharks attacked the fish, and two that were obtained by spear gun.

Year	Method	*n*	SL (mm)	Weight (g)
2006	Hook-and-line	357	434.20 ± 71.04	2,544 ± 1,199
2006	Trap	224	276.23 ± 82.37	829 ± 949
2009	Hook-and-line	53	423.19 ± 105.68	2,742 ± 2,365
2009	Trap	225	208.89 ± 70.15	407 ± 569
2010	Hook-and-line	21	364.38 ± 113.70	1,772 ± 1,338
2010	Trap	140	200.94 ± 40.50	286 ± 183

Table 2.–Summary of catch and visual surveys for all reefs sampled. Reefs where a visual survey was not completed or recordings were not taken are indicated by a double dash (--).

Reef	Date	Depth	Year	HL catch	HL time	HL CPUE	Trap catch	Trap time	Trap CPUE	Visual	Density	Pictures	Video
1	18-May-10	32	2006	29	31	28	5	17	4	75	109	--	--
2	20-May-10	31	2006	32	30	32	2	15	2	124	158	57	46
3	2-Jun-10	30	2006	34	30	34	0	15	0	--	34	--	--
4	9-Nov-10	29	2006	0	15	0	28	15	28	23	51	--	6
5	26-May-10	29	2006	13	21	19	4	30	2	111	128	47	21
7	11-Oct-10	32	2006	11	30	11	35	15	35	50	96	--	12
8	10-Jun-10	31	2006	26	30	26	0	15	0	99	125	23	10
9	21-Jun-10	31	2006	29	30	29	30	15	30	250	303	--	--
10	28-May-10	30	2006	23	30	23	0	33	0	54	77	25	14
11	18-Jun-10	27	2006	25	30	25	14	15	14	225	264	78	11
12	20-Apr-10	29	2006	19	30	19	23	30	12	200	242	--	10
13	8-Jul-10	30	2006	13	30	13	0	30	0	--	13	--	--
14	5-May-10	29	2006	22	30	22	11	16	10	42	75	--	12
15	19-Oct-10	29	2006	11	30	11	21	15	21	52	84	41	19
17	24-May-10	32	2006	15	30	15	2	30	1	23	40	8	13
18	23-Jul-10	32	2006	16	30	16	13	30	7	300	329	38	--
19	4-Aug-10	31	2006	20	30	20	22	30	11	--	42	--	--
20	14-May-10	31	2006	25	30	25	20	15	20	104	149	11	--
31	26-May-10	18	2009	1	30	1	14	30	7	23	38	8	5

Table 2.–(continued)

Reef	Date	Depth	Year	HL catch	HL time	HL CPUE	Trap catch	Trap time	Trap CPUE	Visual	Density	Pictures	Video
32	20-May-10	20	2009	10	30	10	28	31	14	130	168	45	28
33	20-Apr-10	21	2009	0	30	0	11	30	6	75	86	--	15
34	18-May-10	18	2009	14	18	23	18	15	18	45	77	8	--
35	24-May-10	20	2009	0	30	0	26	62	6	53	79	26	--
36	5-May-10	22	2009	3	30	3	70	15	70	17	90	--	--
37	14-May-10	24	2009	1	30	1	1	15	1	13	15	--	6
38	28-May-10	21	2009	3	30	3	23	15	23	35	61	17	9
39	10-Jun-10	19	2009	4	30	4	19	45	6	71	94	25	20
40	2-Jun-10	18	2009	17	29	18	15	15	15	78	110	27	17
41	4-Aug-10	23	2010	0	10	0	11	60	3	--	11	--	--
43	8-Jul-10	26	2010	1	9	3	0	30	0	--	1	--	--
44	18-Jun-10	27	2010	0	15	0	2	30	1	9	11	7	7
45	23-Jul-10	25	2010	0	10	0	4	30	2	9	13	--	--
46	13-Oct-10	23	2010	0	15	0	28	15	28	65	93	15	8
47	11-Oct-10	29	2010	13	30	13	23	15	23	75	111	37	20
48	19-Oct-10	29	2010	0	15	0	28	15	28	22	50	18	--
49	9-Nov-10	31	2010	7	30	7	17	15	17	--	24	--	--
50	1-Nov-10	30	2010	0	15	0	27	15	27	--	27	--	--

Table 3.–Comparison of red snapper mean ± SD standard length, weight, and age for each reef year using ANOVA and a Duncan's new multiple range test. Different letters are used to indicate significant differences ($P \leq 0.05$).

Reef Year	SL (mm)	Weight (kg)	Mean Age
2006	373.29 ± 107.83 (a)	1.883 ± 1.388 (a)	3.54 ± 1.24 (a)
	(*n* = 581)	(*n* = 581)	(*n* = 587)
2009	250.20 ± 114.71 (b)	0.852 ± 1.464 (b)	1.98 ± 1.70 (b)
	(*n* = 280)	(*n* = 280)	(*n* = 280)
2010	222.25 ± 78.04 (c)	0.480 ±0.711 (c)	1.72 ± 1.00 (c)
	(*n* = 161)	(*n* = 161)	(*n* = 161)

Table 4.–Average percent error for all independent readings. Included are the percentages of agreement for each difference (1st and 2nd reading $r^2 = 0.83$, $P < 0.0001$; 3rd and 4th reading $r^2 = 0.96$, $P < 0.0001$).

	First and Second Reading	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 %

FIGURES

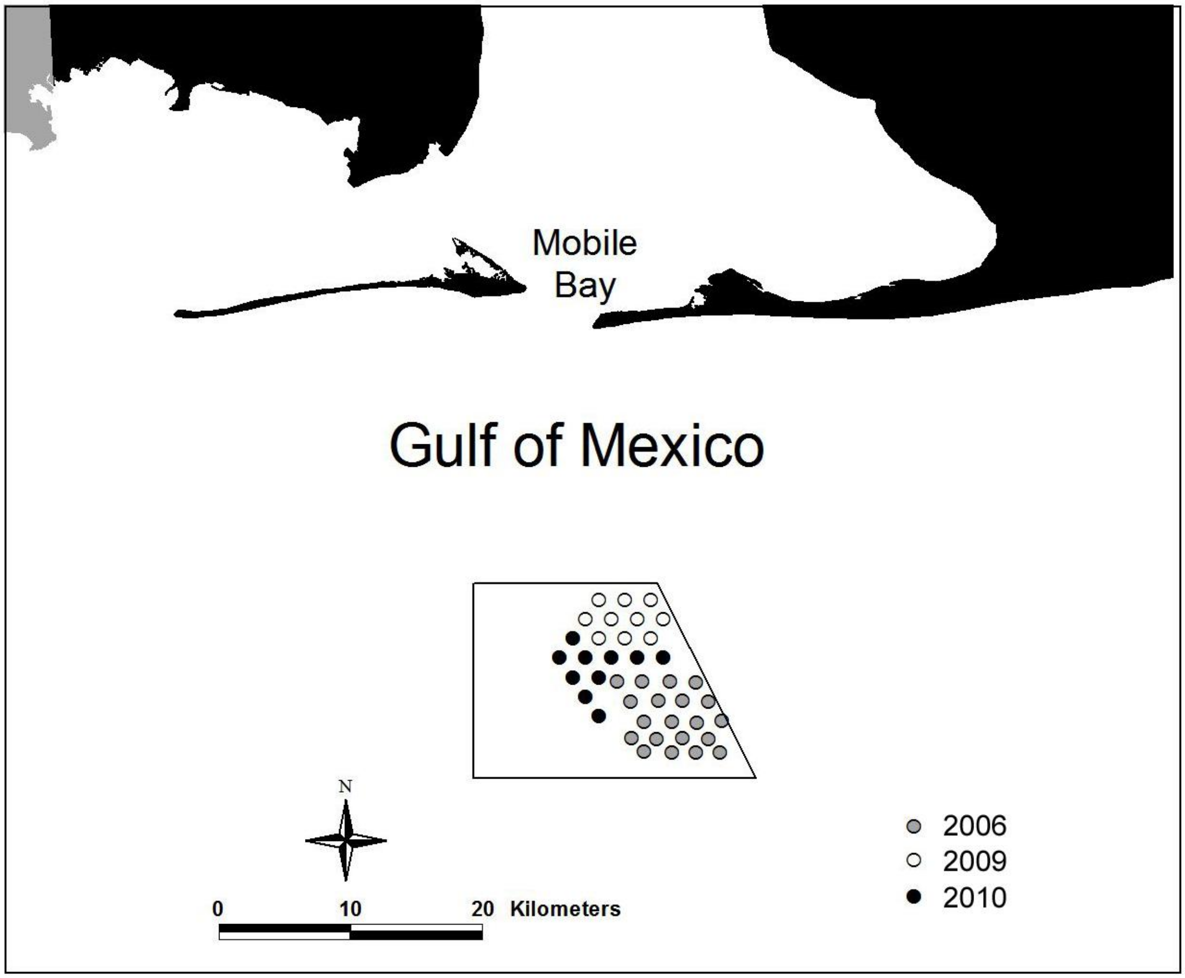

Figure 1.–Locations of artificial reefs. Reef years are indicated by different shading.

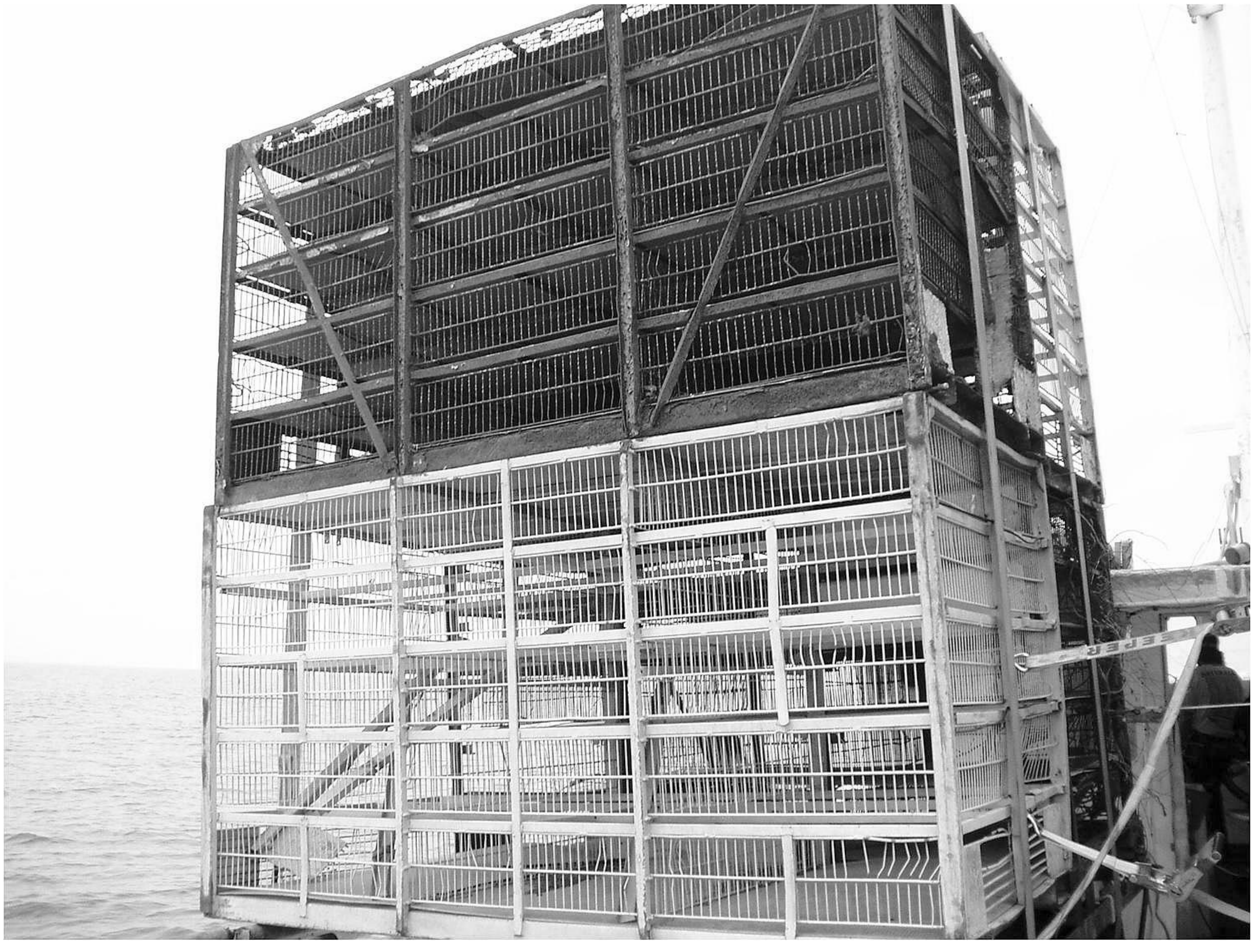

Figure 2.–Photograph of metal cage reefs.

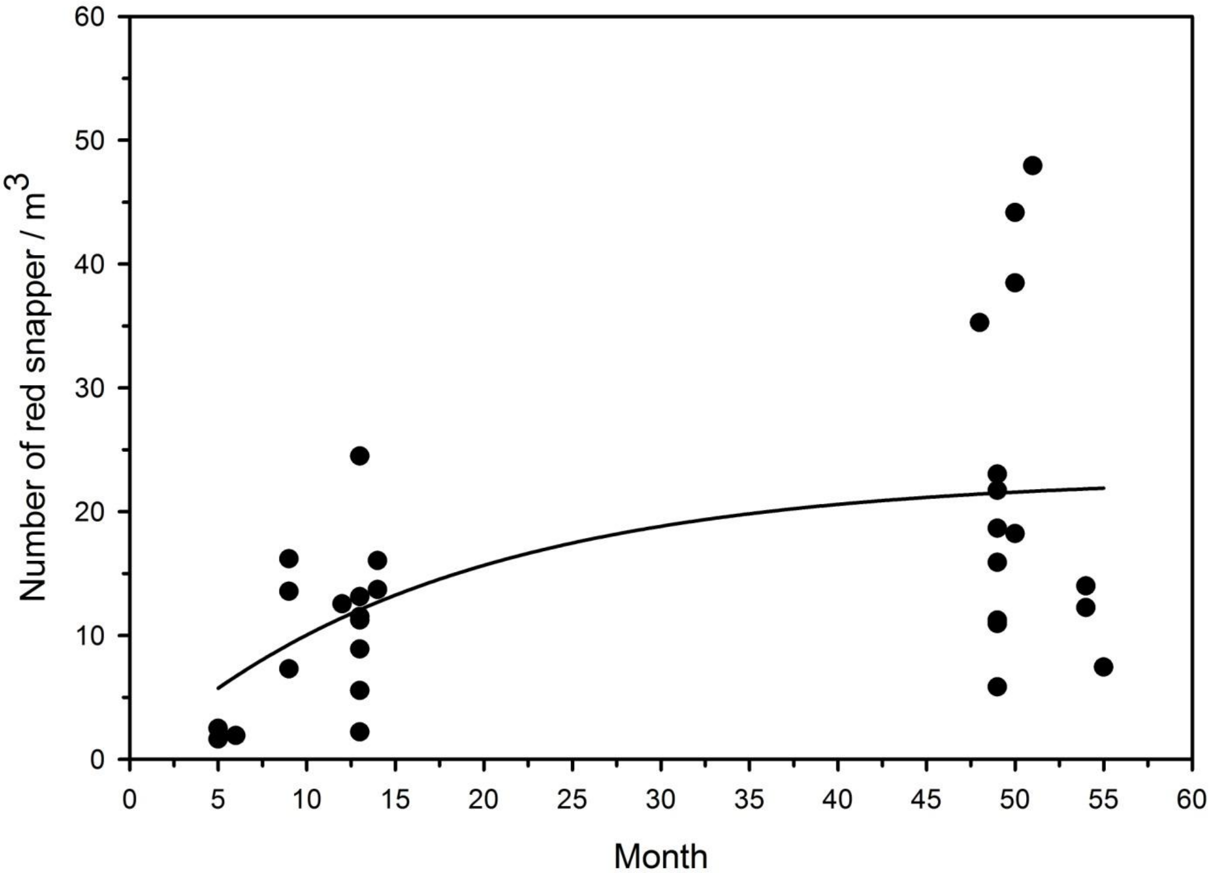

Figure 3.–The density of red snapper on artificial reefs as reef age increased ($r^2 = 0.284$).

Sampling did not occur between 15 and 47 months.

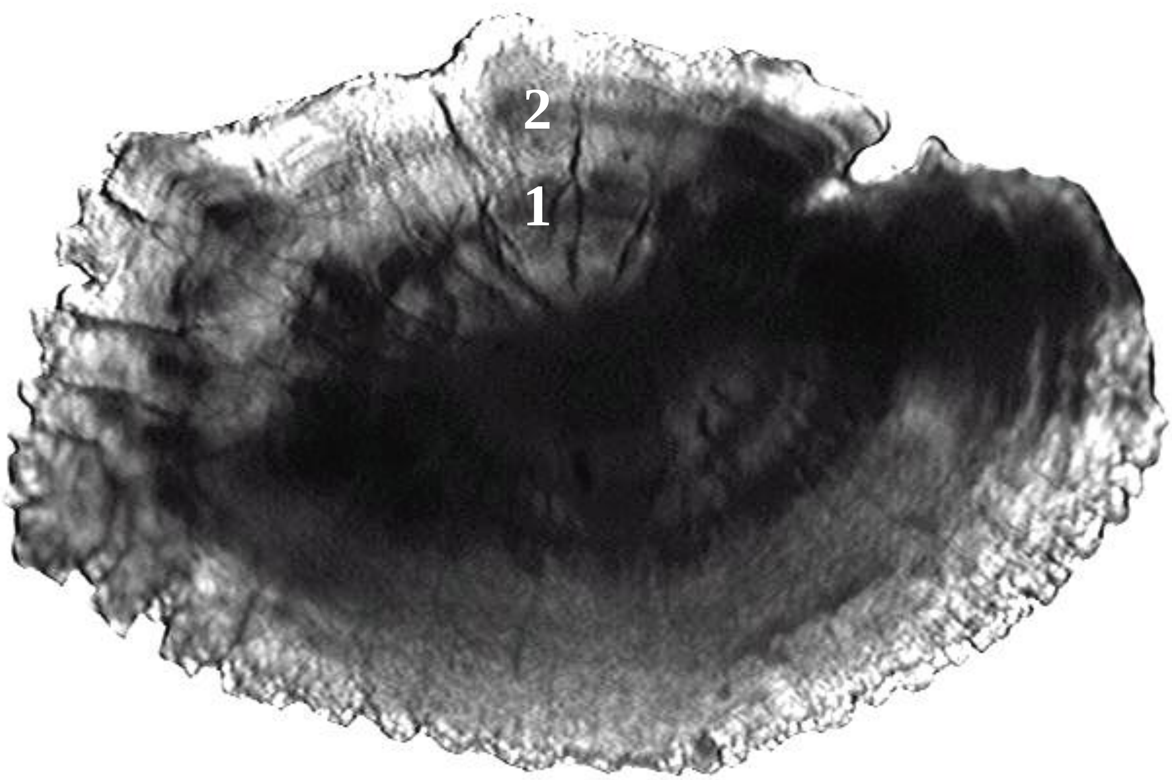

Figure 4.–Image of an age-1 otolith with 2 opaque bands.

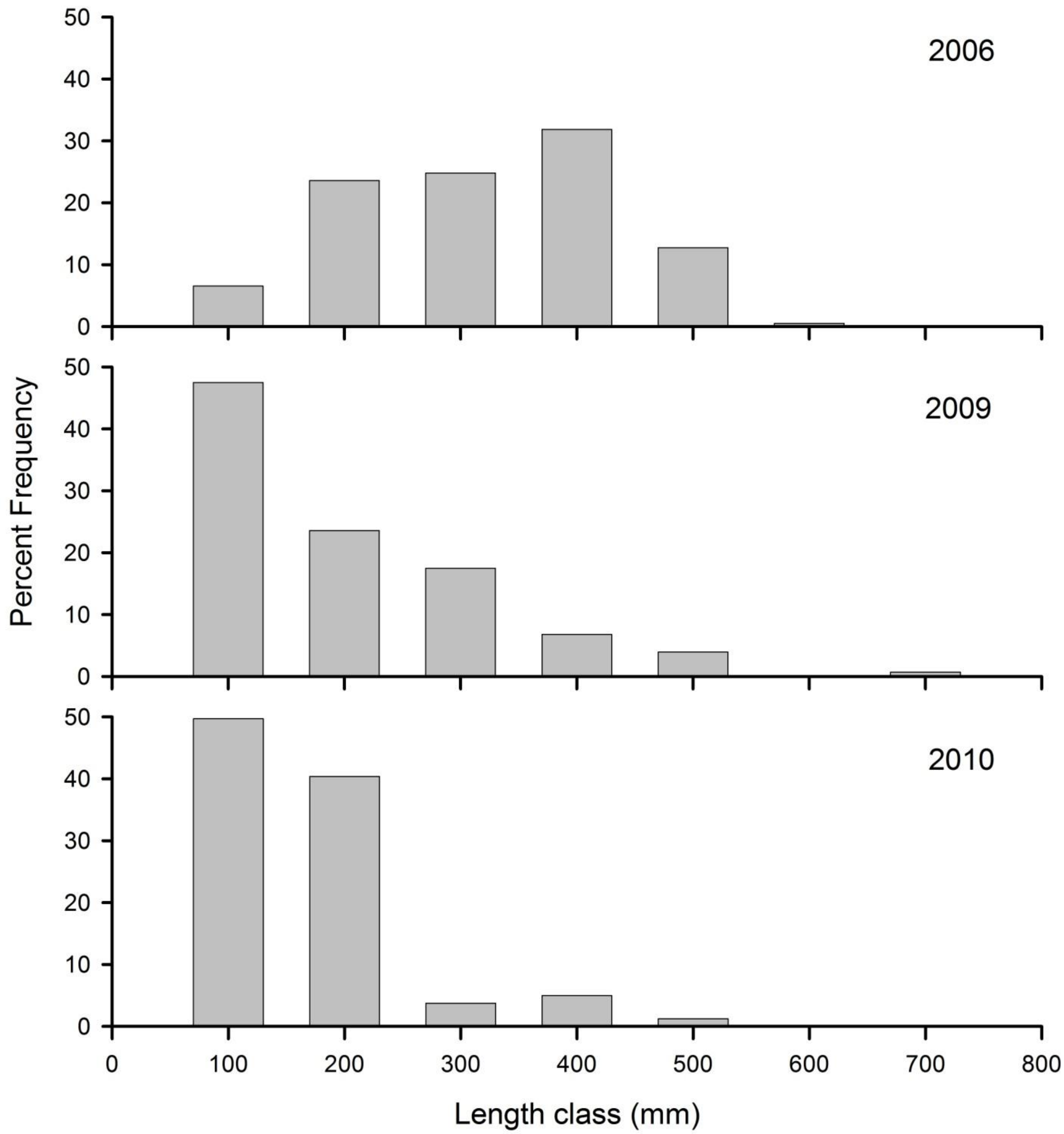

Figure 5.–Red snapper SL (mm) percent frequency by reef year, separated into 100 mm categories (e.g. 100 = 100 – 199 mm).

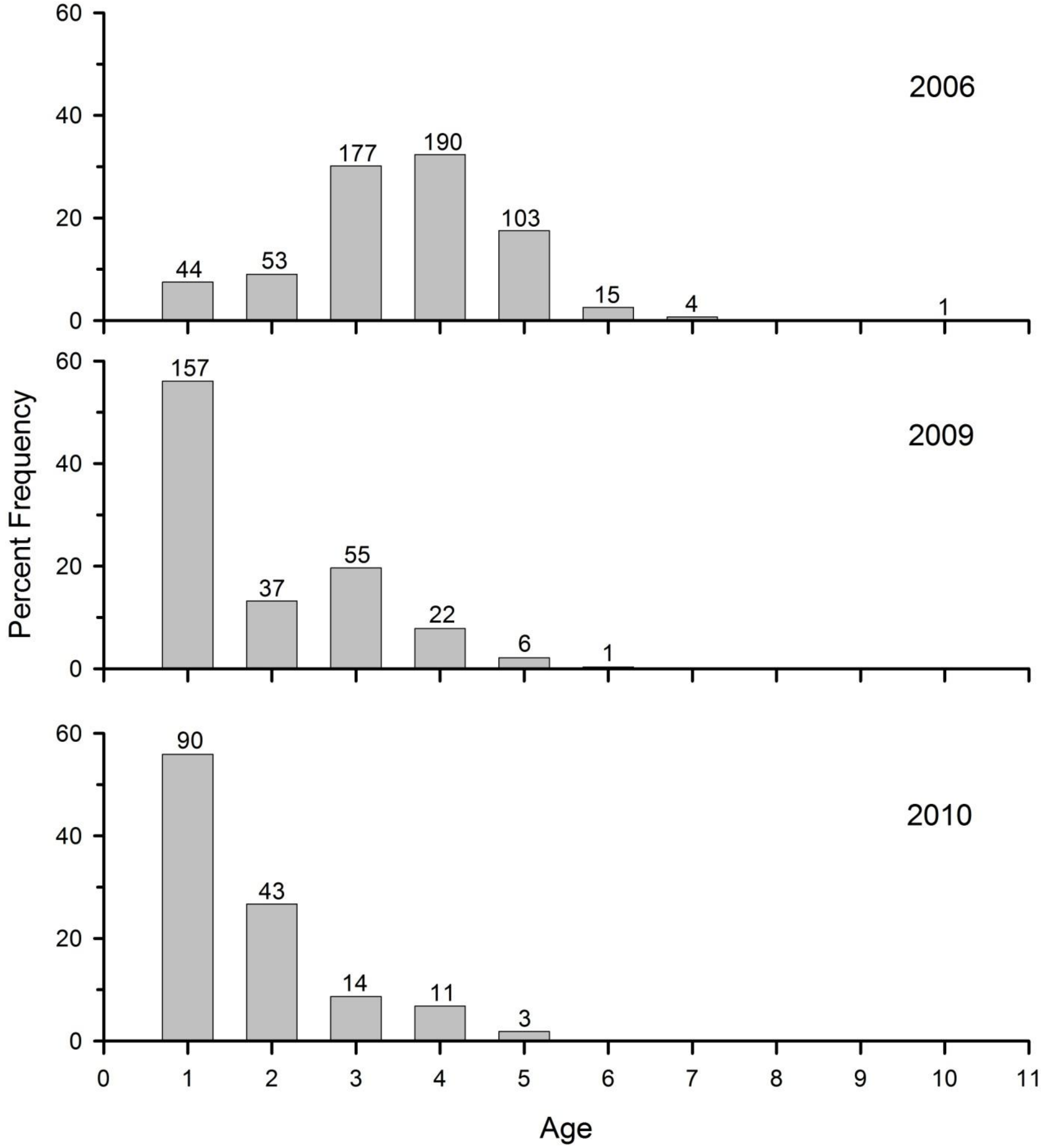

Figure 6.–Percent frequency of red snapper age (years) by reef year. Total number of fish caught for each age class indicated by numbers above bars.

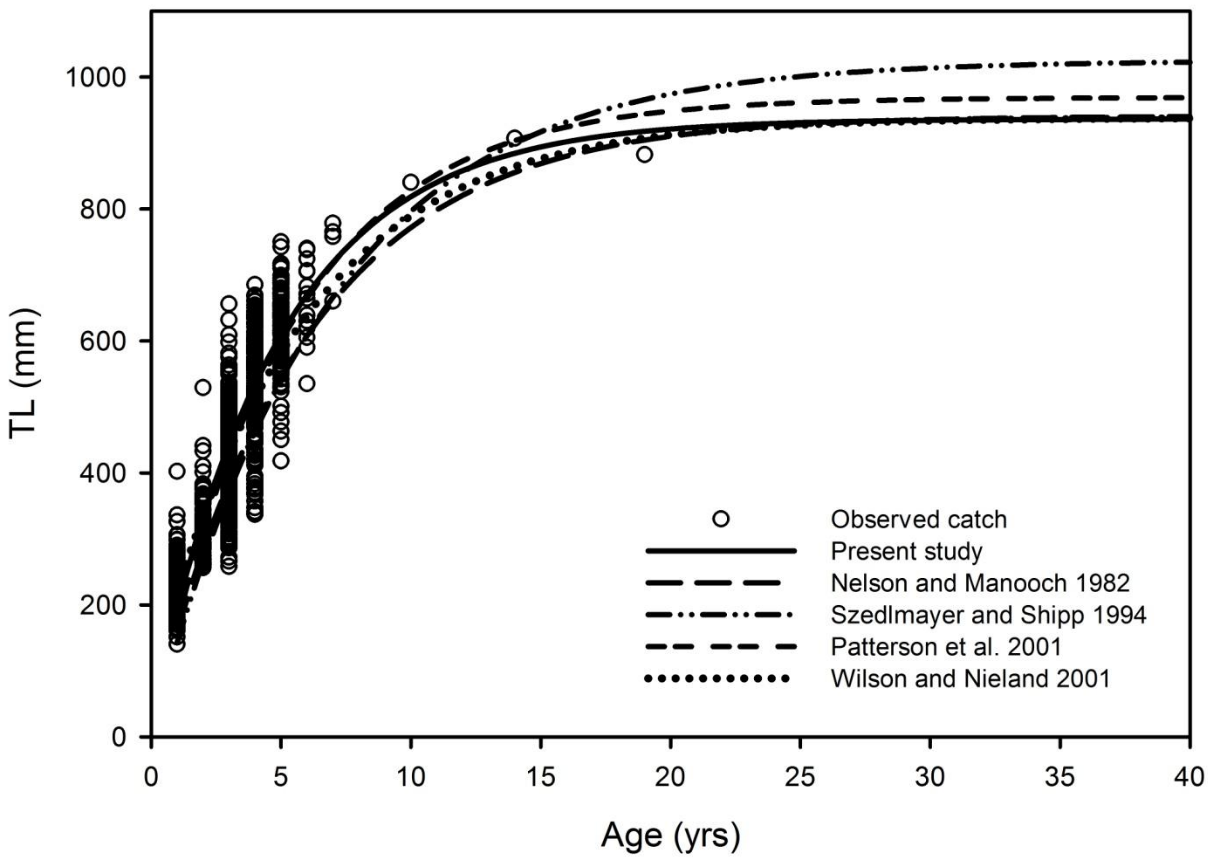

Figure 7.–Comparison of von Bertalanffy growth models for red snapper in the northern Gulf of Mexico. Length at age data for the present study indicated as open circles.