Site Fidelity, Movement, and Growth of Red Snapper: Implications for Artificial Reef Management

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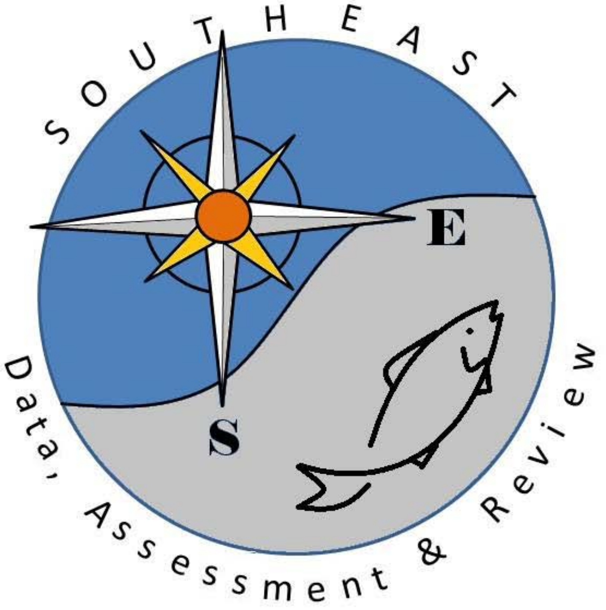

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Site Fidelity, Movement, and Growth of Red Snapper: Implications for Artificial Reef Management

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Abstract.—Red snapper, *Lutjanus campechanus*, (n = 4,317) were captured and tagged at 14 experimental artificial reefs of two designs during quarterly research cruises (n = 17) off coastal Alabama between January 1999 and October 2002. Six-hundred and twenty nine recaptures were reported, representing 578 tagged red snapper. Sixty-five percent of recaptures (n = 412) were made at the site of release on subsequent research cruises, while 217 recaptures were reported by fishers. Eighty-six percent of individuals with known recapture locations moved 2 km or less from the site of release; mean and maximum distances moved were 2.1 km and 201 km, respectively. Nine red snapper moved greater than 80 km. Mean dispersion rate from release sites was 8.6 m d^{-1}. Annual site fidelity of tagged fish was estimated using nonlinear decay models. Estimated annual site fidelity ranged from 48% to 52% $year^{-1}$ and was not significantly affected by artificial reef design, reef fish biomass at the site of release, or artificial reef densities surrounding each tagging site. Growth rates were estimated by regressing the change in red snapper total length versus the days a fish was at liberty. Mean growth rate for all recaptured fish was 0.206 mm d^{-1}. Growth rates were significantly affected by reef size (faster at larger experimental reefs) and reef fish biomass (slower at tagging sites supporting low reef fish biomass), but were not affected by artificial reef density. Moderate site fidelity and low dispersion rates during our study provide support for the hypothesis that artificial reefs off Alabama are suitable habitat for adult red snapper. However, characteristics of artificial reefs, such as reef size and standing stock biomass, may affect red snapper growth. Furthermore, ratios of instantaneous growth in weight to total mortality (G/Z) suggest artificial reefs off Alabama serve as net sinks (i.e., $G/Z < 1$) of red snapper biomass under current fishing mortality rates.

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Introduction

Tagging studies are used both to assess fish migration and movement and to estimate fish growth, mortality, and abundance (Hilborn et al. 1990). In artificial reef research, tagging studies often are used to assess experimental design assumptions (i.e., independence), homing, and movement of reef fishes (Hixon and Beets 1989, 1993; Beets and Hixon 1994; Eggleston et al. 1997; Watterson et al. 1998; Patterson and Cowan 2003). Tag-recapture studies also are used to estimate site fidelity of reef fishes at artificial and natural reefs (Lindberg and Loftin 1998; Szedlmayer 1997; Patterson and Cowan 2003; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006). Site fidelity provides an annual estimate of reef fish immigration or emigration from an artificial reef. Estimates of site fidelity, distance moved, and reef fish growth rates obtained from tagging studies all can be used to make inferences about the resource value of a particular habitat (in this case an artificial reef) or complex of habitats (Lindberg et al. 1990).

It has been hypothesized that site fidelity of reef-associated organisms is dependent on both prey availability and the availability of suitable refuge (resource mosaic hypothesis: Lindberg et al. 1990; Frazer and Lindberg 1994; density-dependent habitat selection: see Lindberg et al. 2006). Reef-associated fish species that rely on benthic prey as a primary component of their diet, such as young-adult red snapper *Lutjanus campechanus*, create a gradient of prey depletion (i.e., feeding halo) around artificial reef structures (Frazer and Lindberg 1994; Lindberg 1996; Bortone et al. 1998) resulting in negative feedbacks to reef fish energetics, residence times, and local abundance, especially if the feeding halos of closely spaced reefs overlap (Lindberg et al. 2006). As a result, the degree of prey depletion and associated negative feedbacks alters the potential for sustained productivity of an artificial reef and artificial reef complexes. It is theorized that bioenergetic demands increase as foraging area increases resulting in increased reef fish emigration from resource-depleted habitats to habitats containing a greater abundance of prey (optimal foraging theory, Charnov 1976).

Artificial reefs or artificial reef complexes that sustain prey resources over time may potentially benefit reef fishes and fishery productivity more by reducing the energetic costs of foraging, increasing growth rates, and increasing site fidelity. While past research has demonstrated reef fish abundance increases both with increasing reef size (see review by Pickering and Whitmarsh 1997) and with spacing (Schroeder 1987; Frazer and Lindberg 1994; Lindberg et al. 2006), the size and spacing of artificial reefs can alter growth rates, site fidelity, and population dynamics of reef fishes (Lindberg 1996; Lindberg and Loftin 1998; Lindberg et al. 2006). Although larger, more widely dispersed reefs may hold greater benefit to fishers (increased catch rates), smaller, more isolated reefs may serve to better benefit marine resources through increased growth rates. In theory, this occurs through reductions in competition and bioenergetic demands at more widely spaced reefs provided that mortality rates do not change as a function of spacing.

In the current study, information obtained from a mark–recapture study was used to estimate site fidelity, movement, growth, and productivity of red snapper at artificial reefs off coastal Alabama. Movement and growth parameters were evaluated in relation to the distribution, abundance, and demographic characteristics of artificial reefs. We first evaluated site fidelity, movement, and growth of all tagged fish captured during our study. We then examined whether habitat characteristics (e.g., density of artificial reefs, reef design/size, and biomass of reef fish residing at tagging sites) affected site fidelity and growth rates of red snapper. Finally, we compared instantaneous rates of growth in weight to total mortality estimates for red snapper from the eastern Gulf of Mexico (SEDAR 2005). We hypothesized red snapper residing at smaller reefs, surrounded by lower densities of artificial reefs, would have higher site fidelity and growth rates than red snapper residing at larger reefs, surrounded by greater densities of artificial reefs.

Methods and Materials

We tagged red snapper at 14 experimental artificial reef sites of two different designs (Tetrahedrons and Reefballs; Table 1) during quarterly research cruises conducted from February 1999 to October 2003. Tagging sites were located 25 to 35 km south-southeast of Dauphin Island, Alabama, in the Hugh Swingle General Permit Area (HSGPA) at depths ranging from 22 to 31 m (Figure 1A). Locations of tagging sites were unpublished and assumed to be unknown to recreational and commercial fishers during the course of our study.

Red snapper were captured from a charter fishing vessel with rod-and-reel and placed in 185-l holding tanks. All red snapper were measured to the nearest mm fork length (FL) and total length (TL) and tagged with a green Floy stainless steel-core internal anchor tag. Tags were inserted through a small incision in the left wall of the abdominal cavity. Each tag included a unique identification number, the word “reward”, and a toll-free telephone number to report the fish upon capture. After tagging, fish were released alive at the site of capture. A $5 reward was offered for each tag return.

Tagged fish were captured during subsequent research cruises and by recreational and commercial fishers. Fish recaptured during research cruises were measured and released; internal anchor tags were replaced if damaged. When available, information on recapture location (e.g., private or public reef; Loran C or GPS coordinates), recapture date, and recapture length were obtained from commercial and recreational fisher recoveries.

Distance Moved and Dispersion Rate

Distance moved and dispersion rate were computed for all recaptures with known recapture locations. Distance moved was determined by measuring the linear distance between the tagging site and the recapture site. Dispersion rate was estimated by dividing the linear distance moved by the number of days at liberty. The delta method (Aitchison 1955; Pennington 1983) was used to obtain unbiased estimates of mean distance moved and rate of dispersion because many fish were recaptured at their site of release, resulting in many zeros for movement and dispersion data.

Negative binomial regressions were computed with PROC GENMOD in SAS (Hilbe 1994) to test the effects of time at liberty, length at tagging, artificial reef density, and season of tagging on red snapper movement and dispersion. Models first were fitted for each independent variable and the single-variable model with the lowest significant P-value ($\alpha = 0.05$) was chosen as the base model. Variables were added to the base model in order of significance to assess whether or not the deviance of the model was significantly reduced (Agresti 1990). Variables continued to be added to the model until the fit of the model was not significantly improved.

Site Fidelity

Site fidelity was estimated by modeling the decay in recaptures made at tagging sites over time (Patterson and Cowan 2003). Nonlinear decay models were initially computed for all recaptures at tagging sites and for all recaptures at tagging sites by reef design (Tetrahedrons and Reefballs). For each model, recaptures were grouped into intervals of days at liberty based on the average time (102 d) between visits to tagging sites. Because fewer red snapper were available for recapture during subsequent time intervals, a correction factor was used to adjust for the reduced number of fish at liberty. The correction factor for each time interval was calculated as the ratio of the number of red snapper at liberty during that particular time interval divided by the total number of fish tagged. The total number of recaptures made was then adjusted by dividing the total number of recaptures made during each sampling interval by that interval’s correction factor.

To estimate site fidelity, a nonlinear decay model was fit to the adjusted number of recaptures with PROC NLIN in SAS (SAS Institute, Inc. 1999):

$$N_t = N_0 e^{-Dt} \quad (1)$$

where N_t is the number of fish recaptured in time interval t, N_0 is the number of fish recaptured in

Table 1. Description and specifications of experimental artificial reefs used as tagging sites.

	Reefball	Tetrahedron
Description	Concrete, dome-shaped reef with a hollow interior cavity and numerous exterior holes	Reinforced, hollow, floorless concrete tetrahedron with four sides containing holes
No. of reef complexes	7	7
No. of reefs per complex	3	3
Height	1.22	1.52
Base diameter	1.52	2.43
Interior cavity diameter (cm)	60	N/A
Exterior hole diameter (cm)	22	30
Number of exterior holes	35-41 per reef	5 per side (20 per reef)
Weight (kg)	1050	1800
Footprint (m^2)	1.82	5.9
Surface area (m^3)	5.25	8.75
Volume (m^3)	1.8	3.5

the first time interval, D is the instantaneous rate in decline of recaptures, and t is time in days.

The instantaneous rate of decline (D) equals the instantaneous rate of mortality (Z) plus the instantaneous rate of emigration (E), while instantaneous total mortality equals the sum of natural (M) and instantaneous fishing (F) mortalities. Since no recaptures by fishers were reported from tagging sites, fishing mortality was assumed to be zero. Estimates of D were not affected by tag loss because damaged stainless steel-core tags were readily observed during research cruises. Therefore, D equaled $M + E$. An M of 0.1 was assumed for all analyses (SEDAR 2005), allowing E to be computed by subtraction. Site fidelity (SF), as an annual percentage then was estimated with the following equation:

$$SF = e^{-E} \quad (2)$$

Two additional nonlinear decay models were computed to examine both site fidelity at tagging sites surrounded by different densities of artificial reefs (within 0.1 km^2) and site fidelity at tagging sites supporting different biomasses/abundances of reef fish. Because there were few tag returns ($n < 15$) at some artificial reef sites, data were pooled to increase sample sizes. Tagging sites supporting various biomasses of reef fish were pooled as follows: low reef fish biomass = <14 kg reef^{-1}, intermediate reef fish biomass = 15–26 kg reef^{-1}, and high reef fish biomass = >26 kg reef^{-1}. Tagging sites surrounded by varying densities of artificial reefs were pooled as follows: low artificial reef density = <5 reefs/10,000 m^2, intermediate artificial reef density = 6–10 reefs/10,000 m^2, and high artificial reef density = >10 reefs per 10,000 m^2. Reef fish biomasses and artificial reef densities were determined from diver visual surveys and side-scan sonar imagery as reported in Strelcheck et al. (2005).

The effect of tagging site characteristics (reef design, artificial reef density, or reef fish biomass) on site fidelity was tested by transforming (ln + 1) the adjusted number of recaptures for each model and then computing an analysis of covariance (ANCOVA) to test for significant differences in model slopes (rates of decay). A significance level of 0.05 was used for all statistical tests.

Growth Rate

Growth rates for red snapper recaptures were estimated with simple linear regression because most red snapper tagged were small and growth is relatively linear for the first few years of life (Patterson et al. 2001a). Change in TL (length at tagging – length at recapture) was regressed against days at liberty to estimate

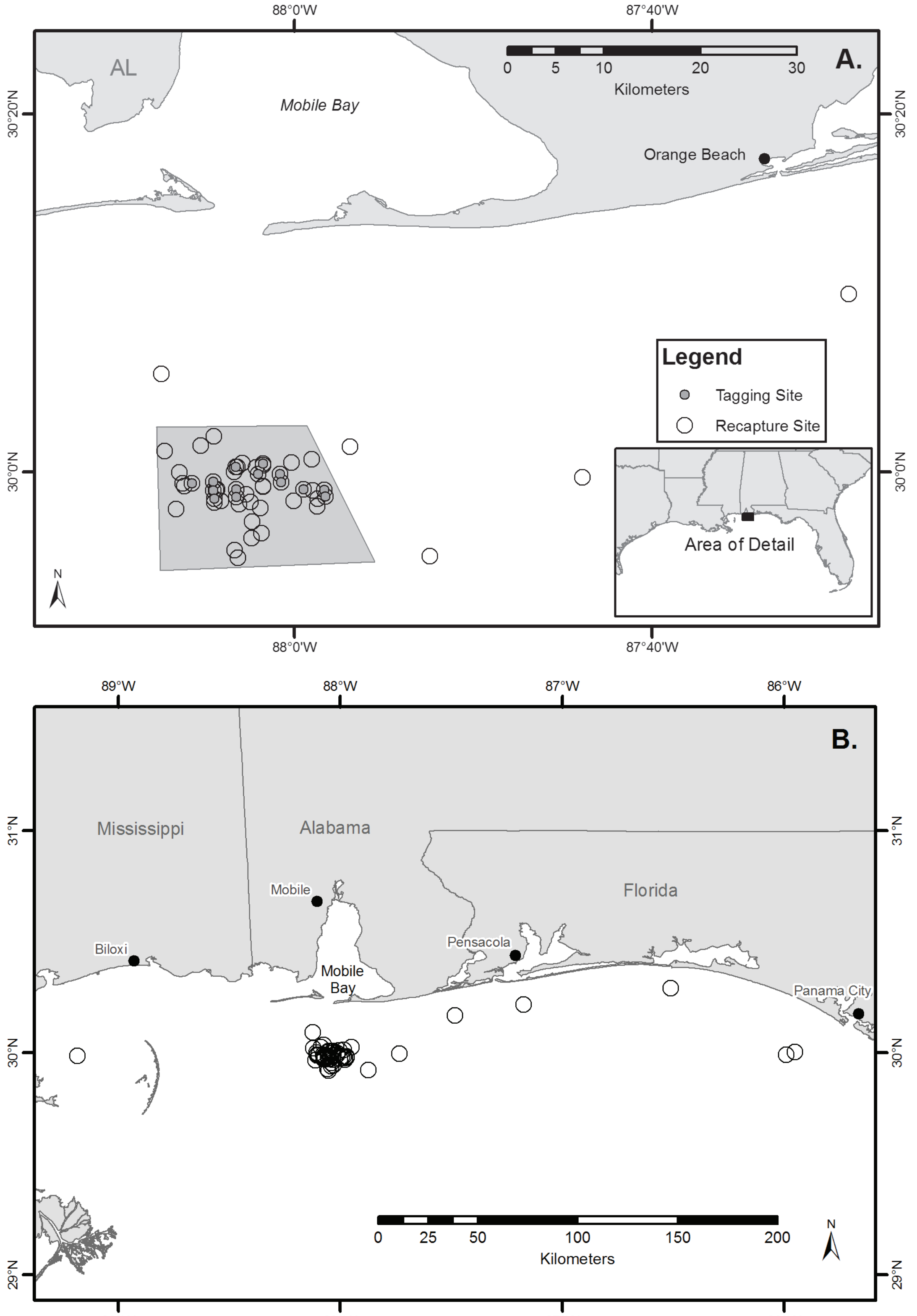

Figure 1. Geographical distribution of red snapper *Lutjanus campechanus* recaptures off coastal Alabama (A) and all red snapper recaptures Gulfwide (B). Open circles may represent multiple recaptures at the same location. Tagging sites are indicated by closed circles. The Hugh-Swingle General Artificial Reef Permit Area is shaded as a gray polygon.

average growth per day. Growth rates were calculated for all recaptures with known recapture lengths, for recaptures at various tagging sites (Tetrahedrons, Reefballs), for recaptures at tagging sites surrounded by differing densities of artificial reefs, for recaptures at tagging sites supporting various biomasses of reef fish, and for recaptures that did or did not move. Analyses of covariance were applied to test for differences in slopes (growth rates) among reef designs, artificial reef densities (low, intermediate, and high), reef fish biomasses (low, intermediate, and high), and movement (recaptured at site of release versus away from the site of release). If the assumption of homogeneity of slopes was rejected when comparing slopes among artificial reef densities or reef fish biomasses, additional analyses of covariance ($\alpha = 0.016$) were applied to test for differences in slopes between treatments (i.e., low versus intermediate, low versus high, and intermediate versus high).

G/Z ratio

The ratio of instantaneous growth in weight (G) to total mortality (Z) over the same time interval can be used as an index for assessing fish production (Houde 1996). G/Z ratios greater than one indicate net production, or increasing fish biomass. To estimate G, mean growth rate for tagged red snapper with known recapture locations was converted to annual instantaneous growth in weight with the length-weight equation in Patterson et al. (2001a). A 406 mm TL red snapper was assumed for the starting length, because this was the legal minimum size limit for recreational harvest during the course of our study. Because growth is basically linear to about 500–600 mm TL, the starting fish length was increased by the mean daily growth rate for recaptured red snapper for one year (481.2 mm TL). The starting and final length were then converted to weight in gm and the following formula was used to calculate G:

$$G = lnW_0 - lnW_t \quad (3)$$

where W_0 is the predicted weight at 406 mm TL and W_t is the predicted weight of that fish at the end of one year (1.49 kg). Average F for 2001–2003 were obtained from SEDAR (2005) for the most vulnerable age-class to the entire eastern Gulf of Mexico red snapper fishery ($F = 0.80$) and for the most vulnerable age-class to the recreational fishery in the eastern Gulf ($F = 0.63$). Alabama and Northwest Florida account for nearly all eastern Gulf recreational landings and therefore are likely representative of F occurring off Alabama, although spatial differences in F may exist in the eastern Gulf. Total mortality was calculated by summing fishing mortality rates with the estimate of natural mortality for red snapper ($M = 0.1$ for age 2+; SEDAR 2005).

Results

Four thousand three hundred and seventeen red snapper were tagged; 2,650 red snapper were tagged at Tetrahedron reefs and 1,667 red snapper were tagged at Reefballs (Table 2). A total of 629 red snapper recaptures were recorded, representing 578 individuals. A majority of these fish were recaptured once ($n = 530$), 45 fish were recaptured twice, and 3 fish were recaptured three times. Recaptures of 363 red snapper were made at release sites, 199 were reported as recoveries by fishers, and 16 were initially recaptured at release sites and subsequently reported by fishers as being captured away from the site of release.

Mean TL at tagging for recaptures was 335 mm (±63.3 mm SD) and mean TL at recapture for fish with known recapture length was 400 mm (±69.8 mm SD). Fish were at liberty on average 401 d (±69.8 mm SD); minimum and maximum days at liberty were 1 and 1,587 d, respectively. A majority of recaptures were at liberty 1 year or less (51.8%); however, 34.5% of red snapper recaptured were at liberty for 1–2 years, and 13.7% of red snapper recaptured were at liberty for greater than 2 years.

Distance moved and rate of dispersion

Specific recapture location was reported by fishers for 116 recaptures and was known for all recaptures made by us at tagging sites (total $n = 479$). Mean (±SD) distance moved for all recaptures was 2.08 km (±0.46). Mean (±SD) distance moved for recaptures reported by fishers was 2.86 km (±0.13). Maximum distance moved was 201 km due east of the release site. Nine fish moved greater than 80 km away from the release site; eight were recaptured between Pensacola and Panama City, Florida, and one was recaptured west of the Chandelier Islands, Louisiana (Figure 1B). Two red snapper tagged at Tetrahedron-7 were recaptured at the same location off Destin, Florida (113 km from release site) and two other red snapper tagged at Reefball-4 were recaptured at the same location off Panama City, Florida (195 km from release site). Eighty-six percent ($n = 412$) of recaptures with known recapture locations were recaptured within 2 km of their release site, 94.6% within 5 km of the release site, and 96.9% within 10 km of the release site. Nearly 97% of recaptures with known recapture locations were from the HSGPA (Figure 1A).

In the single-variable, negative binomial regression models, distance moved was significant both for days at liberty ($X^2 = 16.47$, $p < 0.0001$) and for artificial reef density ($X^2 = 7.76$, $p < 0.005$). Length at tagging and season did not significantly affect the distance red snapper moved. When artificial reef density was added to the days at liberty model, model deviance increased. The final model included only days at liberty, which had a positive effect on distance moved.

Mean rate of dispersion for all recaptures was 8.6 m (±2.53) per day. Rate of dispersion for recaptures made away from the site of release ranged from 0.22 to 8,080 m per day. The maximum rate of dispersion was by a red snapper that was tagged at Tetrahedron-4 and recaptured the next day at Tetrahedron-8. In the single-variable, negative binomial regression models, rate of dispersion was significant both for days at liberty ($X^2 = 26.06$, $p < 0.0001$) and for artificial reef density surrounding tagging sites ($X^2 = 6.43$, $p < 0.011$). When artificial reef density was added to the days-at-liberty model, model deviance increased. Therefore, the final model included only days at liberty, which had a positive effect on rate of dispersion.

Site Fidelity

The decline in recaptures over time for all nonlinear decay models was highly significant ($p < 0.001$, $r^2 > 0.94$) (Figure 2). Annual site fi-

Table 2. Number of red snapper tagged at each tagging site over time. T = Tetrahedron; RB = Reefball.

Date	Tagging Site													
Tagged	T2	T3	T4	T5	T6	T7	T8	RB1	RB2	RB4	RB5	RB6	RB7	RB8	Total
Feb-99	49	42	24	50	28	40	47	18	14	13	20		32	8	385
May-99	12	23	9	55	11	21	26	25	18	18	7		35	4	264
Sep-99	41	25	20	29	1	19	15	15	11	19	2	4	24	8	233
Dec-99	56	31	43	50	13	13	17	20	17	28	7	21	11	6	333
Feb-00	15	19	21	37	6	21	32	9	22	11		2	11	25	231
May-00	19	21	15	22	1	4	19	19	18	8	2	11	33	14	206
Sep-00	6	52	26	15	50	23	40	13	9	18	7	11	30	24	324
Dec-00	37	37	69	64	43	53	62	49	30	38	22	33	59	36	632
Apr-01	20	12	28	44	7	14	29	21	29	13	21	10	41	11	300
May-01		2	13				10	8	6				26		65
Jul-01	9			6						1		1		4	21
Sep-01	19	24	15	33	12	30	26	37	31	10	22	16	36	23	334
Dec-01	28	33	27	42	32	46	45	24	21	6		10	17	15	346
Mar-02	10				5					1		6			22
Jun-02	16	57	22	5	3	20	7	10	22	2		4	50	10	228
Sep-02		57	26	32		38			23				25	46	247
Oct-02	34				35		38	3		14		22			146
Total	371	435	358	484	247	342	413	271	271	200	110	151	430	234	4317

delity was 51.5% year^{-1} for all recaptures. Site fidelity ranged from 48.3% year^{-1} to 54.6% year^{-1} for the various levels of reef type, reef fish biomass, and reef density factors. There were no significant differences in annual site fidelity among levels within any single factor.

Growth Rate

Mean growth rate for all recaptures was 0.206 mm d^{-1}. Growth rates were significantly greater for red snapper recaptured at Tetrahedrons (0.215 mm d^{-1}) than for red snapper recaptured at Reefballs (0.194 mm d^{-1}; Figure 3A) ($p = 0.029$). Fish movement did not affect growth rate; mean growth rate of red snapper that moved (0.213 mm d^{-1}) was similar to mean growth rate of red snapper recaptured at the site of release (0.206 mm d^{-1}; Figure 3B) ($p = 0.40$). Growth rates were significantly different for red snapper recaptured at tagging sites supporting different reef fish biomasses ($p = 0.026$). Red snapper recaptured at tagging sites supporting low biomasses of reef fish grew significantly slower than red snapper recaptured at tagging sites supporting intermediate and high biomasses of reef fish (low versus intermediate, $p < 0.001$; low versus high, $p = 0.006$). Growth rates did not significantly differ between tagging sites supporting low and intermediate reef fish biomasses ($p = 0.58$) or among tagging sites surrounded by different densities of artificial reefs ($p = 0.13$; Figure 3C).

G/Z ratios

The instantaneous growth coefficient estimated over the range of lengths considered (406–481 mm TL) was 0.54 year^{-1}. Ratios of G/Z were less than 1 for both total mortality rates considered ($Z = 0.73$ or 0.90 year^{-1}), ranging from 0.60 to 0.74.

Discussion

Several tagging studies have been conducted off coastal Alabama since 1990 to evaluate growth, movement, and site fidelity of red snapper (Szedlmayer and Shipp 1994; Patterson and Cowan 2003; Szedlmayer and Schroepfer 2005). Each of these studies tagged fish residing on artificial reefs to assess red snapper population dynamics, and in some instances, artificial reef ecology. In the current study, our objective was to examine differences in red snapper population dynamics in relation to various artificial reef characteristics (reef design, densities, carrying capacities). By examining habitat related differences in site fidelity, movement, and growth, this study sought to make inferences about the habitat quality of particular reef designs and locations.

Distances moved and mean dispersion rate were comparable to two previous studies (Szedlmayer and Shipp 1994; Watterson et al. 1998), but were much lower than movement and dispersion rates reported by Patterson and Cowan (2003). Szedlmayer and Shipp (1994) reported recapturing 76% of tagged red snapper within 2 km of release sites and maximum distance moved was 32 km. Watterson et al. (1998) reported recapturing 80% of red snapper not at liberty during Hurricane Opal at their release site; mean distance moved for fish not at liberty during Hurricane Opal ranged from 1.7 to 2.5 km. In this study, mean distance moved by red snapper was 2.1 km and 86% of red snapper were recaptured within 2 km of their release site. Our results are an order of magnitude less than reported for tagged red snapper at liberty during hurricanes (Watterson et al. 1998; Patterson and Cowan 2003). Fish at liberty during Hurricane Opal moved a mean distance of 32.6 km (Watterson et al. 1998). Mean distance moved by tagged red snapper at liberty during Hurricanes Opal and Georges was 29.6 km (Patterson and Cowan 2003). Despite these differences, our results indicate red snapper do move long distances in the absence of hurricane activity. Maximum distance moved in this study was 201 km, compared to 252 km and 352 km reported by Watterson et al. (1998) and Patterson and Cowan (2003), respectively.

Overall, site fidelity for red snapper in this study was similar to the results of Szedlmayer and Shipp (1994) and Watterson et al. (1998) who qualitatively concluded red snapper exhibit strong site fidelity during nonhurricane periods. In contrast, site fidelity estimates presented in this study were nearly twice as high as those

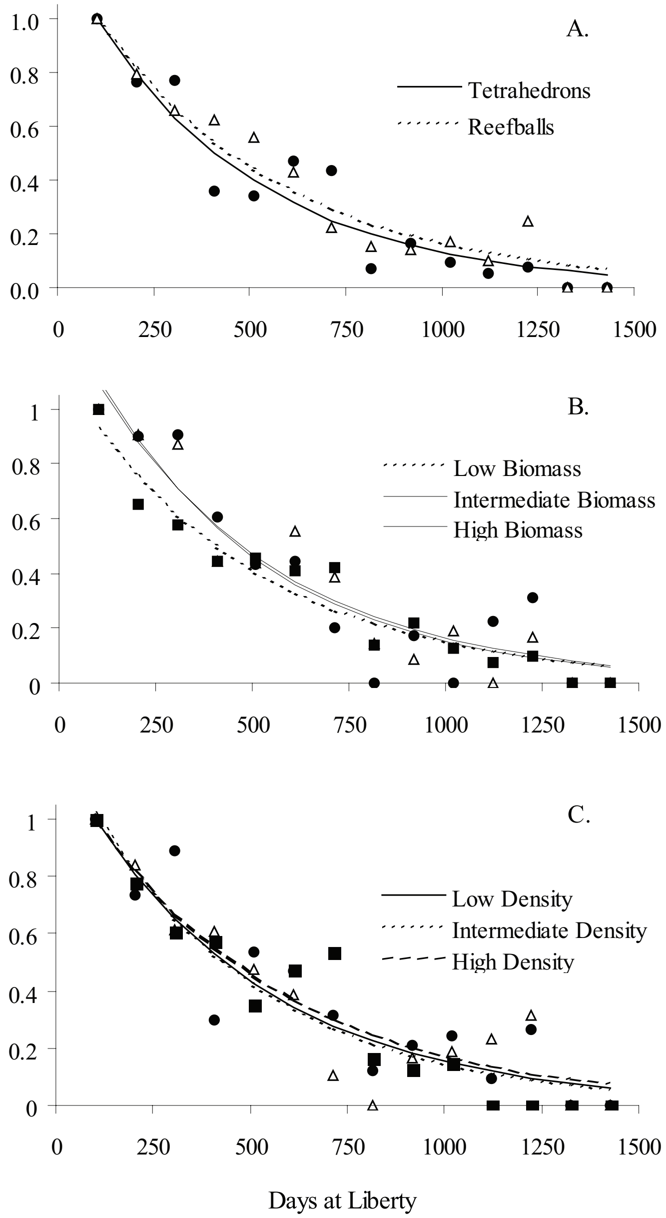

Figure 2. Relative number of red snapper recaptures made on tagging trips over time fitted with non-linear decay models for (A) two artificial reef designs, (B) different levels of reef fish biomass, and (C) different densities of artificial reefs surrounding tagging sties.

presented in Patterson and Cowan (2003), which is the only other study of red snapper that has quantitatively estimated site fidelity. Site fidelity in the Patterson and Cowan (2003) study was approximately 25% year^{-1}, regardless of whether or not fish were at liberty during hurricanes. Although the same methods and similar sized fish were used to quantify site fidelity between this latter study and the current study, several key differences exist between these two studies, including the absence of hurricanes and more frequent sampling during our study. Although Patterson and Cowan (2003) did estimate site fidelity for red snapper not at large during hurricanes, sample size was small (n = 121) relative to this study (n = 340). In addition, mean time between sampling intervals was much less for the current study (102 d versus 150 d). Increased sampling effort potentially allowed a greater number of red snapper to be recaptured, as well as a greater number of red snapper to be tagged per sampling period, thereby increasing estimates of site fidelity.

Several telemetry studies off coastal Alabama have also examined residence time and site fidelity of red snapper (Szedlmayer 1997; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006). Szedlmayer (1997) reported red snapper residence times ranging from 17 to 597 d, while Schroepfer and Szedlmayer (2006) reported red snapper residence times ranging from 1 to 595 d, with a mean residence time of 218 d. Both of these studies concluded red snapper exhibit high site fidelity. Szedlmayer and Schroepfer (2005) used 'event analysis' to reanalyze residency data from both of the previously published telemetry studies, as well as unpublished tagging data. Using event analysis, mean residence time was estimated to be 373 d, which is similar to the results of this study. The authors concluded red snapper exhibit high site fidelity and stated their estimate of mean residence time was likely underestimated. However, their results indicate only a 50% probability of detecting ultrasonically tagged red snapper one year after release. Additionally, because fish lost immediately after tagging were not used for analysis, it appears site fidelity was likely overestimated by Szedlmayer and Schroepfer (2005) and may have been both less than the results of this study and more similar to the results of Patterson and Cowan (2003) if all tagged fish were used for analysis.

Despite variable estimates of site fidelity observed in this study and other studies at small artificial reefs, we conclude site fidelity is relatively low for red snapper captured at small artificial reefs, especially given the fact that red snapper live in excess of 50 years (Wilson and Nieland 2001). There was only a 50% probability of recapturing a tagged red snapper one year after release. Our study largely tagged small, sub-legal red snapper, which have previously been shown to move less than larger, legal-sized red snapper (Patterson et al. 2001b). As red snapper size increases, movement is expected to increase, resulting in even lower estimates of site fidelity. Even if movement away from the site of capture does not increase with increasing size, the cumulative effect of a 50% decrease in site fidelity per year is substantial (e.g., 3% probability after 5 years, 0.1% probability after 10 years). Therefore, regional rather than site-specific site fidelity may be more significant, especially if movement occurs in a limited area where red snapper are subjected to high rates of fishing mortality. As indicated by our study, 97% of tagged fish caught were recaptured within the HSGPA, which is a designated artificial reef area heavily fished primarily by recreational anglers. Limited movement within this area might actually be detrimental to red snapper given high fishing mortality rates.

Artificial reef design, reef fish biomass, and artificial reef densities did not significantly affect site fidelity of red snapper. Based on the resource mosaic hypothesis (Lindberg et al. 1990), we expected smaller, more isolated reefs supporting lower biomasses of reef fish to have the highest site fidelity. This is predicted to occur because reef fishes are potentially less likely to move between reefs during foraging due to increased risks of predation and reduced proximity to shelter. When reef densities are high, distances between reefs are shorter and reef fish may move among reefs more readily, resulting in increased movement and an expanded 'home' range.

Our intent was to evaluate site fidelity of red snapper at individual tagging sites. However, data were pooled among sites because of low sample

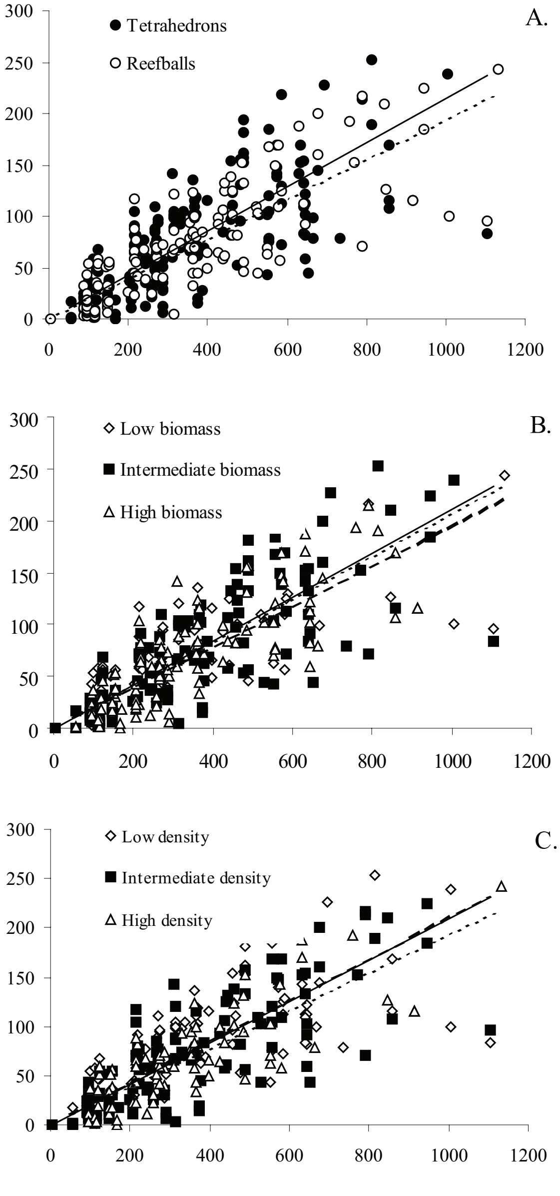

Figure 3. Linear regressions of change in red snapper total length (mm) versus days-at-liberty for: (A) two artificial reef designs, (B) different levels of reef fish biomass, and (C) different densities of artificial reefs surrounding tagging sites.

sizes. Pooling data may have limited our ability to determine whether artificial reef characteristics, such as size and spatial proximity to other artificial reefs, affected red snapper site fidelity. Additionally, there was only a two-fold difference in artificial reef sizes used in this study (Table 1). Lindberg et al. (2006) found gag, *Mycteroperca microlepis*, residence times were greater on large, more widely spaced artificial patch reefs when compared to smaller, more closely spaced artificial patch reefs that were 4X smaller in size (4 m^3). The small patch reefs used by Lindberg and Loftin (1998) were 2X larger than the largest artificial reefs (Tetrahedrons) used in this study. Because our artificial reefs were small, bioenergetic demands might have not have been significantly different to reduce red snapper residency. Also, McCawley (2003) found a major portion of red snapper diet (41% by weight) may be derived from food/prey residing in the water column. Although a majority of a red snapper's diet is still from benthic prey (55% by weight), the dependence on water column prey for food could reduce the negative energetic feedbacks hypothesized by the resource mosaic hypothesis (Lindberg et al. 1990). If this was the case, then the abundance and distribution of pelagic prey may have played an important role in structuring our artificial-reef fish assemblages. Nevertheless, recent work done by Shipley and Cowan (NOAA Fisheries, unpublished data) both demonstrates the likelihood of foraging halos around reefs of the size studied here and show that prey concentrations diminish when the halos overlap. These results are based upon a synthesis of results from multiple studies in this region and suggest that reefs should be spaced about 600 m apart to reduce competitive interference.

Growth rates of red snapper recaptured in our study were comparable to previous studies (Szedlmayer and Shipp 1994; Watterson et al. 1998; Patterson et al. 2001a), which indicated growth rates of tagged red snapper range from 0.22 to 0.25 mm d^{-1}. Our study estimated the mean growth rate of all recaptures to be 0.21 mm d^{-1}. Growth rates were significantly different between artificial reef designs and among reefs supporting different biomasses of reef fish. The significantly higher growth rate observed at Tetrahedrons, the larger of the two artificial reefs in our study, was an unexpected result; the resource mosaic hypothesis predicts slower growth rates at larger artificial reefs (Lindberg et al. 1990). Similarly, slower growth rates were observed at tagging sites supporting lower biomasses of reef fish; however, ecological theory predicts tagging sites supporting higher biomasses of reef fish would have slower growth rates. As discussed above, differences in our results relative to those predicted by ecological theory include the size of artificial reefs used, data pooling, and the relative importance of pelagic prey. With respect to pelagic prey, Tetrahedrans could simply attract more pelagic prey than Reefballs, resulting in little or no expected negative feedbacks from benthic foraging. Additionally, artificial reef sites with lower reef fish biomasses may have lower available prey bases for reasons unrelated to the size and design of our experimental artificial reefs. Furthermore, growth rates of red snapper residing at reefs surrounded by relatively low artificial reef densities could simply reflect differences in prey availability or quality and not represent negative-density dependent processes.

Our results are contrary to those of Lindberg et al. (2006), who found gag growth to be greater at smaller rather than larger artificial reefs. They concluded gag selected shelter at the expense of maximizing growth. Artificial reef size and spacing, reef fish biomass, and the ability of anglers to easily locate artificial reefs all likely affect the overall level of red snapper productivity achieved at an artificial reef or complex of artificial reefs. Unfortunately, because of the design and scale of our study, such differences were not observed. Further research is needed to elucidate whether artificial reef spacing and reef fish biomass play an important role in structuring artificial reef fish assemblages in the northern Gulf of Mexico.

In summary, site fidelity was higher and both distances moved and rates of dispersion were lower for red snapper when compared to previous studies. The low rate of dispersion of red snapper, at least during nonhurricane years, within the complex of artificial reefs (n = 20,000) off coastal Alabama supports the potential for localized production of *adult* red snapper, assuming mortality does not exceed growth. Although there is no evidence that natural habitat limits the current population size of red snapper, artificial reefs off coastal Alabama have allowed reef fish to inhabit areas that previously attracted few adult fishes of recreational or commercial value. If red snapper are retained along the Alabama shelf and artificial reefs provide suitable habitat for red snapper growth, reproduction, and survival, it is plausible for enhancement of production to occur. However, characteristics of artificial reefs, such as reef size and standing stock biomass, may affect the overall rate of red snapper growth. In addition, if fishing mortality exceeds either productivity or recruitment and if red snapper production is not limited by the availability of habitat (Cowan et al. 1999), then high fishing mortality rates may offset or diminish any net gains in productivity resulting from artificial reef construction. Based on a recent stock assessment of red snapper (SEDAR 2005), fishing mortality rates in the eastern Gulf of Mexico were estimated to be well above levels producing maximum sustainable yield, thus the likelihood artificial reefs off Alabama have a net positive effect on red snapper population productivity appears to be remote at this time. Instead, Alabama's artificial reef program may be serving as a net sink for red snapper production. The lower rates of dispersion and higher site fidelity of red snapper observed in this study may further diminish productivity during nonhurricane periods when red snapper dispersion rates are lower, thus making them even more vulnerable to fishing mortality along the Alabama shelf. However, movement during both hurricane and nonhurricane periods likely diminishes the extent of spatial differences in *F* occurring in the eastern Gulf red snapper population.

As a final thought, our study results imply that increases in fish mortality attributable to artificial reefs could be offset to result in a zero sum game, or that reefs could be used to produce new fish biomass if some fraction of reefs were deployed in areas of limited or no fishing, such as no take reserves. As our understanding continues to improve, we think we will be well positioned in the future to use artificial reefs as conservation management tools designed to do more than simply create new fishing opportunities.

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