Site Fidelity and Dispersion of Red Snapper Associated with Artificial Reefs in the Northern Gulf of Mexico

WILLIAM F. PATTERSON¹ AND JAMES H. COWAN

University of South Alabama, Department of Marine Sciences LSCB 25, Mobile, Alabama 36688, USA

Abstract.—We examined site fidelity and dispersion of red snapper Lutjanus campechanus associated with artificial reefs via an extensive tagging study conducted off Alabama in the northern Gulf of Mexico (GOM). We tagged 2,932 individuals with internal anchor tags during 28 tagging trips made to nine artificial reef sites from March 1995 to July 1998. Recaptures of tagged fish were made on subsequent tagging trips (n = 235) by the authors and were reported by recreational and commercial fishers (n = 364 through December 2000). Annual site fidelity of tagged fish to individual reefs was estimated with nonlinear decay models of the decline in recaptures made by the authors at tagging sites over time. Site fidelity estimates ranged from 24.8 to 26.5% per year. Mean red snapper dispersion rate estimated with the delta method was 75.4 m per day. Overall, adult red snapper tagged in our study demonstrated lower site fidelity and greater movement than previously reported. Low site fidelity may explain spatial and temporal variability in red snapper biomass observed around reefs and has important implications for red snapper management. In particular, our results do not support the hypothesis that artificial reefs have increased red snapper production, as artificial reefs are more likely merely to attract reef fishes that demonstrate low site fidelity and only partial or opportunistic reef dependency. Managers proposing marine protected areas (MPAs) to increase GOM red snapper biomass should incorporate site fidelity and dispersion rate estimates into source-sink population dynamics models to examine the efficacy of MPAs to achieve this goal.

Introduction

Red snapper *Lutjanus campechanus* are valued as both game and food fish throughout their range and are perhaps the most targeted finfish species in the northern Gulf of Mexico (hereafter, GOM; Minton and Health 1998; Stanley and Wilson 1990, 1991). Based on fisheries landings, there currently appear to be two centers of abundance for GOM red snapper, one in the northwestern GOM off southwest Louisiana (LA) and a second in the north-central GOM off Alabama

Most of the nearshore reef habitat off LA and ALMS is thought to be in the form of manmade structures (Stanley and Wilson 1990; Szedlmayer and Shipp 1994); thus, the red snapper fisheries in these areas are

and Mississippi (ALMS; Goodyear 1995; Schirripa and Legault 1999). These two areas are unusual as centers of reef fish production because they lack significant amounts of natural benthic structure and the seafloor of both is composed mostly of sand and mud sediments. The most pronounced seafloor relief occurs farther from shore associated with shelf edge reef pinnacles and hard ground ledges (LA and ALMS) and salt-dome uplifts (LA only; Fisk and McFarlan 1955; Curray 1960; Ludwick 1964; Parker et al. 1983).

¹Telephone: (251) 861-7563; Fax: (251) 861-7540; Email: wpatterson@disl.org

prosecuted predominantly over artificial reefs (Stanley and Wilson 1990, 1991; Szedlmayer and Shipp 1994; Minton and Health 1998). In the case of LA, more than 3,000 offshore petroleum platforms serve as de facto artificial reefs that have increased the nearshore habitat available to reef fishes (Gallaway 1984; Stanley and Wilson 1990, 1991; Bull and Kendall 1994). Petroleum platforms are less concentrated off ALMS than in the northwestern GOM, but other forms of artificial reefs are present. In fact, the state of Alabama claims the largest artificial reef program in the United States with more than 3,100 km² designated for artificial reef construction and more than 15,000 artificial reefs deployed since the start of the program in 1953 (Minton and Heath 1998; Patterson et al. 2001b).

Proponents of Alabama's artificial reef program cite high catches of red snapper and a profitable sport fishing industry as evidence of a successful and beneficial program (Minton and Heath 1998; Shipp 1999); however, little research has focused on the effect of Alabama's artificial reefs on the population ecology of red snapper. As part of a larger research program aimed at understanding the life history and ecology of red snapper, we conducted a tagging study over artificial reefs off Alabama to estimate red snapper site fidelity to individual reef sites. A second objective of our study was to test what factors affected the rate of fish dispersion away from reef sites. Results are discussed in the context of red snapper fisheries ecology and the potential use of marine protected areas as a management tool to increase red snapper spawning stock biomass.

Methods

From March 1995 to July 1998, we tagged adult red snapper over artificial reef sites (n = nine) located in the Hugh Swingle General Permit Area off the coast of Alabama (Figure 1). Reefs were located between 20 and 38 km south–southeast of Dauphin Island, Alabama and were constructed 18 months prior to the start of the study; details of artificial reef construction are reported in Watterson et al. (1998). Individual reefs were between 4 and 16 km apart in three rows oriented east to west at three different depths (21, 27, and 32 m; Figure 1). Locations of tagging sites were not published prior to or during the study and were assumed to be unknown to commercial and recreational fishers.

Our sampling platform was a charter boat (length = 18.3 m, beam = 5.5 m) that docked at Dauphin Island, Alabama. On each tagging trip, we attempted visits to at least three reef sites. Red snapper were captured on site with rod and reel and placed in holding

tanks on deck. Each fish was measured (total length [TL] mm) and then tagged by inserting an internal anchor tag (yellow Floy FM-89) through a small (@5 mm) incision made with a scalpel in the abdominal cavity. Each tag was marked with a number, the word "reward," and a phone number for fishers to report tag recoveries. We offered a \$5 reward for each tag return, with a chance to win \$500 in a lottery drawing of tag returners. Once tagged, red snapper were either released immediately overboard or translocated in holding tanks to other tagging sites for release. Holding tanks consisted of two 185-l insulated coolers supplied with running seawater.

Tagged fish were recaptured on subsequent tagging trips and were recovered by recreational and commercial fishers at sites other than tagging sites. Fish recaptured on tagging trips were measured and released, and as much information as possible was obtained from fishers' recoveries. Data from fishers' recoveries included tag number, date of capture, and exact location of capture (i.e., Loran C or GPS coordinates). Additionally, fishers' recoveries were measured (total length [TL] mm) when carcasses could be obtained.

Site Fidelity and Dispersion

To meet the assumption of independence, only data from terminal recaptures of fish recaptured more than once were used in statistical analyses. A priori, factors of interest included size at tagging and translocation prior to release. An unplanned factor added to the study was the exposure of fish to hurricanes. Two hurricanes passed near the tagging sites during the study, one on 4 October 1995 (Hurricane Opal, maximum winds 200 km/h, center within 40 km of tagging sites), and one on 28 September 1998 (Hurricane Georges, maximum winds 150 km/h, center within 50 km of tagging sites). In statistical analyses, models were computed with exposure to hurricanes included as an independent variable to test the effect of hurricanes on red snapper site fidelity and dispersion rate.

Red snapper site fidelity was estimated by modeling the decline in recaptures made by us at tagging sites over time. Three separate models were computed: (1) all recaptures made at tagging sites, (2) recaptures not translocated prior to release, and (3) recaptures of fish tagged and recaptured in the interval between hurricanes. For each model, recaptures from all nine sites were grouped in intervals of days at liberty based on the average time between visits to individual reefs. Because the number of tagged fish available to be

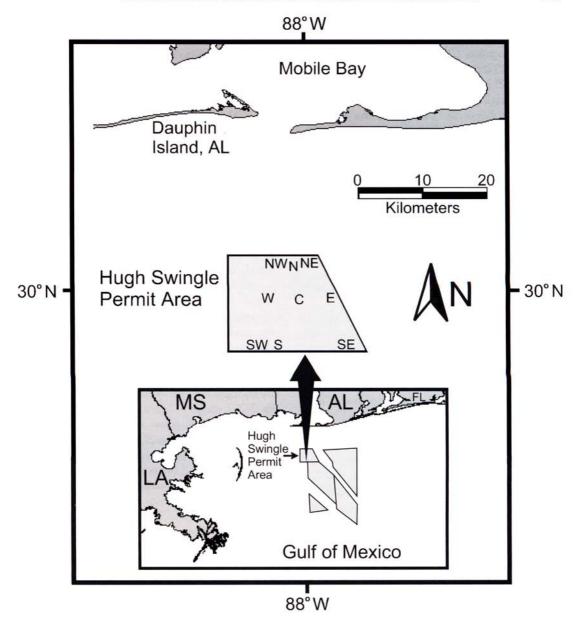


FIGURE 1. Map of tagging sites within the artificial reef permit area off the coast of Alabama in the northern Gulf of Mexico. Gray polygons on inset map denote the total permit area.

recaptured declined in each subsequent time interval, the number of recaptures made during a given interval was adjusted by dividing it by the ratio of the number of tagged fish available over the total number of tagged individuals. The decline in recaptures was estimated by fitting the following nonlinear decay model to the adjusted distribution of recaptures with PROC NLIN in SAS (SAS Institute, Inc. 1996):

$$N_{t} = N_{i}e^{-Dt} \tag{1}$$

where

 N_t = adjusted number of recaptures made in interval t. N_i = estimated number of recaptures in the initial interval.

D = instantaneous rate of decline in recaptures (d^{-1}). t = time (d).

184

Estimates of D were converted from d^{-1} to year by multiplying by 365 d. The instantaneous rate of decline in recaptures (D) is equal to the sum of total mortality (Z) and instantaneous emigration (Q). Total mortality (Z) is the sum of natural mortality (M) and fishing mortality (F); however, we assumed that no fishing mortality occurred at tagging sites (see discussion). Natural mortality (M) was estimated following Royce (1972) and Hoenig (1983), assuming a maximum age for GOM red snapper of 53 years (Wilson and Nieland 2001).

$$M = 4.6/(\text{maximum age})$$
 (Royce 1972) (2)

$$ln(M) = 1.44 - 0.982 * ln(maximum age)$$

(Hoenig 1983) (3)

Once estimates of D and M were computed, we solved for Q by subtraction. Finally, annual site fidelity (SF) was estimated with the following equation:

$$SF = e^{-(Q)} \tag{4}$$

Dispersion rate was estimated by dividing the straight line distance between original site of release and site of recapture by time at liberty. Distance of movement for fishers' recoveries was estimated as the distance between release sites and the Loran C or GPS coordinates where recoveries were made. Fish recaptured by us at their release sites had a dispersion rate of 0 m/d. Since many fish displayed no movement, resulting in many zeroes in the dispersion rate data, the delta method was employed to obtain unbiased estimates of mean dispersion rate (Aitchison 1955; Pennington 1983).

A log negative binomial regression model was computed with PROC GENMOD in SAS to test the effects of fish size (TL at tagging), hurricanes, and translocation on red snapper dispersion rate (Hilbe 1994; SAS Institute, Inc. 1996). The model was built using a forward stepwise approach in which regressions first were computed for each independent variable separately. The single-variable model with the lowest significant P-value ($\alpha = 0.05$) was chosen as the base model. Other significant variables were added to the model one at a time in order of significance. Improvement of fit was assessed after each addition by determining if adding a variable significantly decreased the deviance of the model (Agresti 1990). The model-building process was complete when either no significant variables were available to be added or the addition of a variable did not significantly improve the model's fit.

Results

From March 1995 to July 1998, we made 28 tagging trips and tagged 2,932 red snapper (Table 1). Of the tagged fish, 2,053 were released at their tagging sites and 879 were translocated to other tagging sites for release. Mean TL (\pm SE) of tagged fish was 335 mm (\pm 1.34; Figure 2a). From the start of the project until June 1998, the minimum legal size for possession of GOM red snapper for both the commercial and recreational fisheries was 381-mm (15-in) TL, but the size limit for the recreational fishery was increased to 457-mm TL (18-in) TL from June through August 1998 and was 406-mm (16-in) TL thereafter. Therefore, 80% of tagged fish (n = 2,366) were shorter than the recreational size limit, and 77% (n = 2280) were shorter than the commercial size limit at the time of tagging.

Five hundred ninety-nine recaptures of 555 red snapper were made through December 2000. Fortytwo individuals were recaptured twice (23-s recaptures were made by fishers, and 19 were made on tagging trips) and one individual was recaptured three times (all three recaptures were made on tagging trips). Of the 555 terminal recaptures, 264 fish were not at liberty during at least one hurricane; mean time at liberty was 247 d (range = 2-849; SE = 12.1) for fish not exposed to hurricanes and 562 d (range = 12-1,501; SE = 19.2) for fish exposed to hurricanes. Four hundred forty-one recaptures were of fish released at their tagging sites, and 114 recaptures had been translocated prior to release. Two hundred fourteen fish were recaptured on tagging trips, of which 191 recaptures were terminal recaptures. Fishers reported 364 tag recoveries (fishers' return rate = 12.2%), but TL at recapture was measured for only 97 of these fish (Figure 2b).

Site Fidelity and Dispersion

All nonlinear decay models of the decline in recaptures over time were highly significant (p < 0.001; $R^2 > 0.94$; Figure 3). Estimated natural mortality from the methods of Royce (1972) and Hoenig (1983) was 0.087. Estimates of annual site fidelity ranged from 24.8 to 26.5% per year (Figure 3).

Location of recapture was reported for 252 (70%) recoveries reported by fishers, and the farthest movement was 558 km for a fish that was at liberty for 1,136 d (Figure 4). Dispersion rate for fishers' recoveries ranged from 0.46 to 1,356 m/d (Figure 5). Overall, mean dispersion rate (±SD) was 75.4 m/d (±13.6) but was 134.1 m/d (±28.8) for fish exposed to hurricanes and 19.5 m/d (±5.0) for fish not at liberty during hur-

TABLE 1.	Dates of	tagging	trips,	tagging s	ites san	pled.	and	number	of rec	l snapper tagged.	
----------	----------	---------	--------	-----------	----------	-------	-----	--------	--------	-------------------	--

Date	Tagging sites	Number tagged	Date	Tagging sites	Number tagged 86	
22 Mar. 1995	C, SE	94	7 Aug. 1996	SE, NE, N		
3 May 1995	N, NE, NW, C	107	31 Oct. 1996	C, W, NW, SW	189	
20 June 1995	W, S, SW	153	1 Nov. 1996	NE, E, SE	152	
21 June 1995	E, SE, C	118	12 Dec. 1996	N, C, S	150	
29 Aug. 1995	SE, E, NE	129	9 Dec. 1996	NE, E SE	122	
13 Sept. 1995	NW, W, SW	100	26 Mar. 1997	NW, N, NE	114	
14 Sept. 1995	N, C, S	112	27 Mar. 1997	SW, S, C	117	
30 Nov. 1995	S, SE, NW, C	107	29 Apr. 1997	NW, N, NE	42	
12 Dec. 1995	N, SW	73	18 Sept. 1997	NW, N, NE, E	147	
27 Feb. 1996	SW, W, NW	42	23 Sept. 1997	C, SE, S	65	
22 Mar. 1996	N, C, S	41	3 Nov. 1997	NW, N, NE	136	
29 Mar. 1996	NE, SE, E	38	5 Nov. 1997	W, SW, S, C	186	
1 May 1996	S, SE, C	37	25 Feb. 1998	NW, N, NE	147	
12 June 1996	SW, S, W, N, C	50	20 July 1998	NW, N, NE	104	

ricanes and was 90.3 m/d (±29.3) for fish translocated prior to release and 61.6 m/d (±12.0) for fish not translocated prior to release. Dispersion rate single-variable log negative binomial regressions were significant for hurricane and size effects ($\chi^2_{\rm df=1}$ = 2,536.9; p < 0.001 and $\chi^2_{\rm df=1}$ = 4.0; p = 0.047, respectively), but not significant for translocation ($\chi^2_{\rm df=1}$ = 2.7; p = 0.102). Adding the size effect to the hurricane model significantly decreased the model's deviance ($\chi^2_{\rm df=1}$ = 4.1; p = 0.043). Therefore, the final model included hurricane and fish size effects, both of which positively effected red snapper dispersion rate:

Dispersion rate = $e^{\{-20.74+20.96*(Canc)+0.0031*(TL)+\mu\}}$. (5)

Discussion

Authors of previous tagging studies of GOM red snapper generally concluded that adult red snapper displayed strong site fidelity to and limited movement from both natural and artificial reefs (Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997). Beaumariage (1969) and his colleagues tagged 1,126 red snapper on natural reefs off northwest Florida (FL) in the 1960s and reported tag returns from 315 fish. Mean time at liberty of reported recoveries was 113 d, and most (90%) were made less than 5 km from release sites; however, several fish moved more than 100 km. Fable (1980) tagged 299 red snapper at petroleum platforms off south Texas (TX) and reported 17 tag returns. He reported little movement away

from platforms, but maximum time at liberty was only 253 d. Szedlmayer and Shipp (1994) tagged 1,155 red snapper over artificial reefs off Alabama in the early 1990s. They recovered 146 tagged fish but confirmed location of recapture for only 37 individuals. The greatest distance moved was 32 km, and the maximum time at liberty was 430 d; mean time at liberty for all recaptures was 113 d. Szedlmayer (1997) released 26 red snapper tagged with ultrasonic transmitters over artificial reefs off Alabama. He was able to detect transmitters up to 1.8 km, and tracked movements of 19 fish for an average of 118 d before individuals were either caught by fishers (n = 14), lost from the study area (n = 5), or the study ended. Maximum observed movement was 0.74 km for a fish that was tracked for 71 d before it was lost from the study area.

While many authors have suggested that red snapper display high site fidelity, others have reported temporal variability in red snapper abundance at natural or artificial reefs. Moseley (1966) observed fluctuations in red snapper abundance on reefs off Texas and hypothesized that passing cold fronts caused offshore migrations. Beaumariage and Bullock (1976) reported seasonal variability of fish abundance at natural reefs off northwest Florida and suggested that fish migrated annually to summer forage grounds. Stanley and Wilson (1997) estimated fish abundance monthly for one year with hydroacoustics and video from a remotely operated vehicle at a petroleum platform off Louisiana and reported significant variability in red snapper biomass among months.

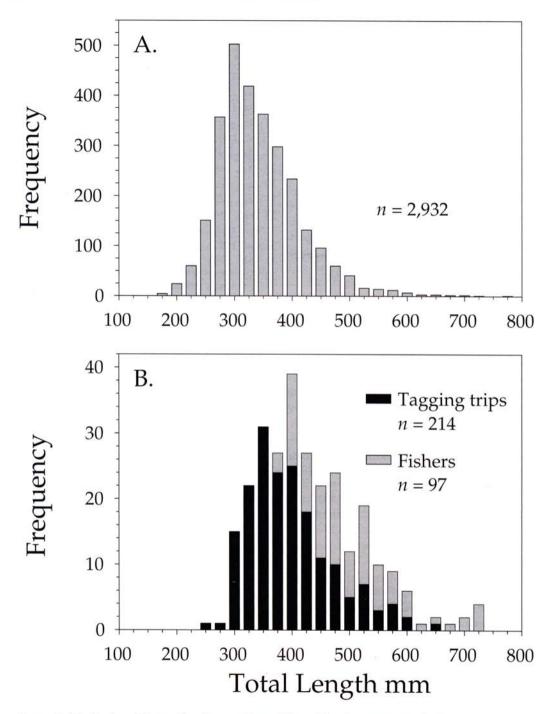


FIGURE 2. Distribution of A. total length at tagging and B. total length at recapture of red snapper tagged in this study.

Red snapper tagged in our study demonstrated relatively low site fidelity to individual artificial reef sites off Alabama. This finding is consistent with studies that reported temporal variability in red snapper

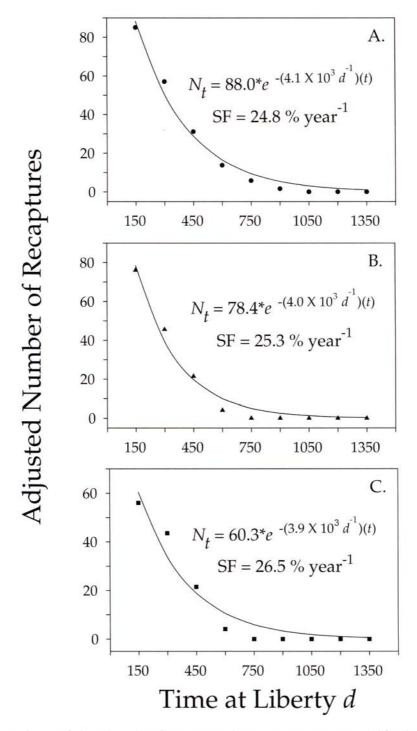


FIGURE 3. Distribution of adjusted number of recaptures made on tagging trips over time and fitted nonlinear decay models for A. all terminal recaptures (n = 191), B. terminal recaptures not translocated prior to release at liberty (172), and C. terminal recaptures of fish tagged and recaptured in the interval between hurricanes (n = 121). Predicted lines follow the model $N_t = N_t e^{-Dt}$, where D is the instantaneous rate of decline d^{-1} and t is time in d. Annual site fidelity (% year⁻¹) estimates are provided for each model.

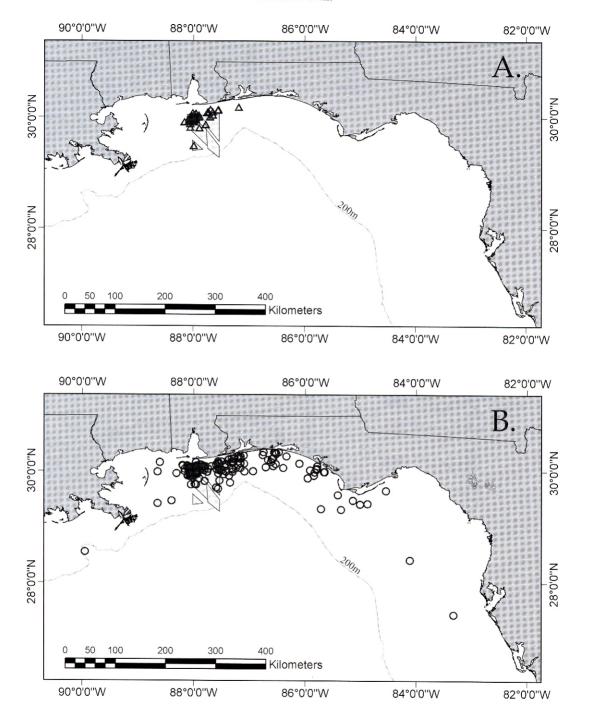


FIGURE 4. Spatial distribution of tag recoveries reported by fishers that were A. not exposed to hurricanes (n = 147) and B. exposed to hurricanes (n = 105).

abundance on natural and artificial reefs (Moseley 1966; Beaumariage and Bullock 1976; Stanley and

Wilson 1997) and is incongruous with the widely reported conclusion that red snapper display strong site

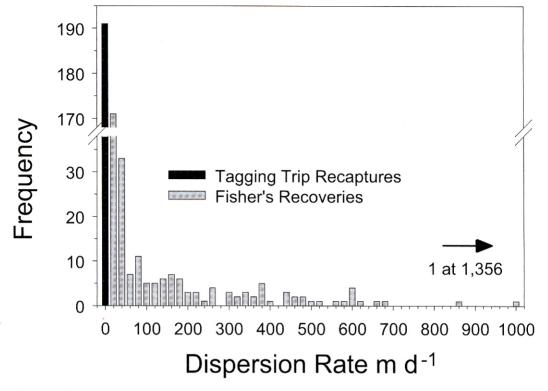


FIGURE 5. Distribution of estimated dispersion rate for individual tagged red snapper recaptured on tagging trips (black bar) and recovered by fishers (gray bars).

fidelity (Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997). It should be noted, however, that movement reported from red snapper tagging studies appears correlated to study scale and sample size (Patterson et al. 2001b). Furthermore, authors of previous studies drew conclusions about red snapper site fidelity from qualitative assessments of recapture data, not from quantitative estimates of site fidelity.

In estimating site fidelity, we assumed that no fishing mortality (*F*) took place at tagging sites. This assumption was based on the fact that no fishers' recoveries were reported from our tagging sites. If fishing mortality did occur at tagging sites but was not reported, we would have underestimated site fidelity. Estimated *F* of GOM red snapper ages 3–6—the approximate age distribution of recaptured fish (see Patterson et al. 2001a)—during 1995–1998 was 0.36 (Schirripa and Legault 1999). If fishing mortality occurred at a similar rate at tagging sites, estimated annual site fidelity would only increase from 24.8 to 35.0% per year for the model that included all recaptures made at tagging sites.

Too few tagged red snapper translocated prior to release or exposed to hurricanes were recaptured at tagging sites to model declines separately for these two factors. We attempted to account for the effect of these factors on site fidelity by modeling the decline in recaptures without individuals translocated prior to release or exposed to hurricanes. Estimated site fidelity increased slightly when transported individuals or individuals exposed to hurricanes were excluded, which supports the findings of Patterson et al. (2001b) that translocation and exposure to hurricanes increased the likelihood of recapture by fishers away from release sites.

Fish movement away from artificial reef sites was observed on two scales. Fish exposed to hurricanes moved farther than individuals not exposed to hurricanes, but fish exposed to hurricanes also were at liberty longer than those not exposed to hurricanes. We attempted to account for differences in time at liberty between the two groups by computing dispersion rate, which incorporated both distance moved and time free. In doing so, we made implicit assumptions that fish moved at a constant

rate and in a straight line. While it is unlikely these assumptions were met, our estimates of dispersion rate are nonetheless informative as measures of red snapper emigration away from release sites. Furthermore, observed movement and dispersion rate estimates reported here likely are conservative. Size limits and management regulations may have caused underreporting by fishers of fish that moved away from their release sites (Fable 1990; Patterson et al. 2001b). Additionally, Patterson et al. (2001b) estimated that red snapper tagged in our study had less than a 25% probability of retaining their tags after being at liberty for two years. Thus, fish movement may have been underestimated because the longer tagged fish were at liberty the lower the likelihood they would be recognized as tagged fish.

Implications of Red Snapper Movement on Fisheries Management

Site fidelity and dispersion rate estimates computed here have important implications for management of GOM red snapper, particularly in the artificial reef area off Alabama. Among other factors, Bohnsack (1989) proposed that artificial reefs were more likely to increase production of reef fishes that displayed high site fidelity and obligatory reef dependency and were more likely merely to attract reef fishes that displayed migratory behavior and partial or opportunistic reef dependency. Following this reasoning, the perception that adult red snapper display high site fidelity to artificial reef sites has driven the discussion of the effect of artificial reefs on red snapper fisheries ecology off Alabama. Szedlmayer and Shipp (1994) concluded that artificial reef areas off Alabama increased production of red snapper rather than attracting and concentrating fish from surrounding areas, based on their findings that fish displayed high site fidelity to artificial reefs and that red snapper grew faster and had higher juvenile abundances off Alabama than other areas in the GOM. Authors of more recent studies, however, have reported results inconsistent with the conclusions of Szedlmayer and Shipp (1994). Results presented here indicate that site fidelity of red snapper to artificial reefs was relatively low and dispersion rate was considerable. Furthermore, Patterson et al. (2001a) reported that growth of red snapper captured off Alabama was similar to fish caught in the northwestern GOM, and Gallaway et al. (1999) reported that catch per unit effort and habitat suitability index values for juvenile nursery areas off ALMS were similar to other areas in the GOM.

Bohnsack (1989) also proposed that habitat-limited reef fishes would be more likely to experience increased production with the creation of artificial reefs than fishes that are recruitment-limited. While it is possible that creation of artificial reefs off Alabama and the deployment of petroleum platforms as de facto artificial reefs in the northwest GOM have shifted the center of the GOM red snapper fishery from its historic center off the west coast of Florida (Carpenter 1965; Stearns 1884; Collins 1885; Goodyear 1995), to our knowledge, there exist no data to support the contention that natural reef habitat currently limits GOM red snapper stock size (Cowan et al. 1999). The likelihood that artificial reefs have increased production of red snapper in the northern GOM is further diminished when one considers that this stock is currently estimated to be overfished (Schirripa and Legault 1999) and year-class strength appears to be driven by natural and anthropogenic (shrimp trawl bycatch) sources of mortality on juveniles rather than by adult habitat availability (Bohnsack 1989; Goodyear 1995; Cowan et al. 1999). An equally plausible explanation of the role of northern GOM artificial reefs is that they serve as a net sink of red snapper production, as the period of artificial reef creation off Alabama is coincident with the fishing down of the northern GOM red snapper stock to the point where spawning potential ratio is estimated to be less than 5% (Schirripa and Legault 1999).

While the benefits of artificial reefs to fishing, such as aggregating fishes and increasing catch rates, are well documented (Polovina 1991; Stone et al. 1991), few studies have shown conclusively that artificial reefs increased fishery production (but see Polovina and Sakai 1989; Butler and Herrnkind 1997). Pitcher and Seaman (2000), however, proposed that artificial reefs deployed in no-take marine protected areas (MPAs) could help mitigate overfishing and habitat degradation. Marine protected areas, in general, have been proposed as a management tool to increase spawning stock biomass of overfished reef fishes, including red snapper (Plan Development Team 1990; Holland and Brazee 1993; Roberts 1998; Bohnsack 2000). In theory, marine reserves benefit fisheries by allowing sedentary reef fish species to accumulate biomass in no-take sanctuaries and then export recruits or biomass to surrounding areas via larval dispersal or emigration of postsettlement juveniles or adults (Bohnsack 1993; Roberts and Polunin 1993). In practice, increases in reef fish biomass within the boundaries of established MPAs have been observed in many reef ecosystems around the world (e.g., Babcock et al. 1999; Chiappone et al. 2000; Williams and Polunin 2000; Jouvenel and Pollard 2001), but benefits to fisheries operating outside MPA boundaries have not been reported widely (but see Russ and Alcala 1999; Roberts et al. 2001).

Crowder et al. (2000) reviewed the MPA literature and concluded that the lack of evidence for MPA benefits to fisheries may be explained partially by poor design with respect to MPA size and/or placement. Through simulation analysis, the authors demonstrated that source-sink population dynamics of reef fishes need to be understood and accounted for in MPA siting in order to produce maximum benefits, including benefits to fisheries. It follows that stagespecific dispersion rates are important parameters to estimate for complete understanding of reef fish source-sink population dynamics. Recent studies of reef fish larval dispersal suggest that local retention of larvae near spawning sites may be greater than previously hypothesized (Swearer et al. 1999; Cowen et al. 2000; Warner et al. 2000). Thus, juvenile or adult emigration may be the most important mechanism by which MPAs enhance fisheries in surrounding areas (Chiappone and Sullivan Sealey 2000). Therefore, it is paramount that managers account for movement of adults when examining the efficacy of MPAs to rebuild spawning stock biomass of heavily fished stocks because small MPAs, while politically and socially more feasible than large MPAs, may not provide sufficient protection for nonsedentary reef fishes such as red snapper that are only partially reef-dependent. If managers continue to explore the potential of MPAs as management tools to increase spawning stock biomass of GOM red snapper, then site fidelity and dispersion rate estimates should be incorporated into source-sink population dynamics models to examine the efficacy of MPAs to achieve this goal.

Acknowledgments

Funding for this project was provided by the United States' National Oceanographic and Atmospheric Administration through MARFIN grant number NA57FF0054. The authors thank Mike and Ann Thierry for deploying artificial reefs used in this study and for allowing us to tag red snapper onboard their charter fishing vessel Lady Ann. The authors thank Walter Ingram for advice concerning statistical tests

and Yvonne Allen for help with figure preparation. The authors acknowledge a great debt to all volunteer fishers who helped in the tagging process and to all commercial and recreational fishers who reported tag recoveries.

References

- Agresti, A. 1990. Categorical data analysis. Wiley, New York. Aitchison, J. 1955. On the distribution of a positive random variable having a discrete probability mass at the origin. Journal of the American Statistical Association 50:901–908.
- Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. Changes in community structure in temperate marine reserves. Marine Ecology Progress Series 189:125–134.
- Beaumariage, D. S. 1969. Returns from the 1965 Schlitz tagging program including a cumulative analysis of previous results. Florida Department of Natural Resources Technical Series 59:1–38.
- Beaumariage, D. S., and L. H. Bullock. 1976. Biological research on snappers and groupers as related to fishery management requirements. Pages 86–94 in H. R. Bullis, Jr. and A. C. Jones, editors. Colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean. Florida Sea Grant Colloquium Report 17, Gainesville, Florida.
- Bull, A. S. and J. J. Kendall, Jr. 1994. An indication of the process: offshore platforms as artificial reefs in the Gulf of Mexico. Bulletin of Marine Science 55:1086–1098.
- Bohnsack, J. A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bulletin of Marine Science 44:631–644.
- Bohnsack, J. A. 1993. Marine reserves: they enhance fisheries, reduce conflicts, and protect resources. Oceanus 36:63–71.
- Bohnsack, J. A. 2000. A comparison of the short-term impacts of no-take marine reserves and minimum size limits. Bulletin of Marine Science 66:635–650.
- Butler, M. J. I. V, and W. F. Herrnkind. 1997. A test of recruitment limitation and the potential for artificial enhancement of spiny lobster (*Panulirus argus*) populations in Florida. Canadian Journal of Fisheries and Aquatic Sciences 54:452–463.
- Carpenter, J. S. 1965. A review of the Gulf of Mexico red snapper fishery. U.S. Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries Circular 208, Washington, D.C.
- Chiappone, M., and K. M. Sullivan Sealey. 2000. Marine reserve design criteria and measures of success: lessons learned from the Exuma Cays Land and Sea Park, Bahamas. Bulletin of Marine Science 66:691–705.
- Chiappone, M., R. Sluka, and K. M. Sullivan Sealey. 2000. Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. Marine Ecology Progress Series 198:261–272.
- Collins, J. W. 1885. The red snapper grounds in the Gulf of Mexico. Bulletin of the United States Fish Commission 5:145–146.

- Cowan, J. H., Jr., W. Ingram, J. McCawley, B. Sauls, A. Strelcheck, and M. Woods. 1999. The attraction vs. production debate: does it really matter from the management perspective? A response to the commentary by R. L. Shipp. Gulf of Mexico Science 17:137–138.
- Cowen, R. K., M. M. Kamazima, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: open or closed? Science 287:857–859.
- Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. Bulletin of Marine Science 66:799–820.
- Curray, J. R. 1960. Sediments and history of Holocene transgression, continental shelf, northern Gulf of Mexico. Pages 221–226 in F. P. Shepard, F. B. Phleger, and T. H. van Andel, editors. Recent sediments, northwest Gulf of Mexico. American Association of Petroleum Geologists, Tulsa, Oklahoma.
- Fable, W. A., Jr. 1980. Tagging studies of red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) off the south Texas coast. Contributions in Marine Science 23:115–121.
- Fable, W. A., Jr. 1990. Summary of king mackerel tagging in the southeastern USA: mark–recapture techniques and factors influencing tag returns. Pages 161–167 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Fisk, H. N., and E. McFarlan. 1955. Late Quaternary deltaic deposits of the Mississippi River. Pages 272–302 in A. Poldervaart. Crust of the Earth. Geological Society of America Special Paper 62, Boulder, Colorado.
- Gallaway, B. J. 1984. Assessment of platform effects on snapper populations and fisheries. In Proceedings of the Fifth Annual Gulf of Mexico Information Transfer Meeting. Department of Interior, Minerals Management Service, OCS Study/MMS85–0008, New Orleans, Louisiana.
- Gallaway, B. J., J. G. Cole, R. Meyer, and P. Roscigno. 1999. Delineation of essential habitat for juvenile red snapper in the northwestern Gulf of Mexico. Transactions of the American Fisheries Society 128:713–726.
- Goodyear, C. P. 1995. Red snapper in U.S. waters of the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science Center, MIA-95/96–05, Miami.
- Hilbe, J. M. 1994. Log negative binomial regression using the GENMOD procedure in SAS/STAT software. Pages 1199– 1224 in Proceedings of Nineteenth Annual SAS Users Group International Conference. SAS Institute, Inc., Cary, North Carolina.
- Hoenig, J. M. 1983. Estimating mortality rate from maximum observed age. Internal Council for the Exploration of the Sea 1982 Meeting collected papers. ICES, Copenhagen.
- Holland, D. S., and R. J. Brazee. 1993. Marine reserves for fisheries management. Marine Resource Economics 11:157–171.
- Jouvenel, J. Y., and D. A. Pollard. 2001. Some effects of marine reserve protection on the population structure of two spearfishing target-fish species, *Dicentrarchus labrax*

- (Moronidae) and *Sparus aurata* (Sparidae), in shallow inshore waters, along a rocky coast in the northwestern Mediterranean Sea. Aquatic Conservation: Marine and Freshwater Ecosystems 11:1–9.
- Ludwick, J. C. 1964. Sediments in the Northeastern Gulf of Mexico. In R. L. Miller, editor. Papers in marine geology: Shepard commemorative volume. MacMillan, New York.
- Minton, V., and S. R. Heath. 1998. Alabama's artificial reef program: building oases in the desert. Gulf of Mexico Science 16:105–106.
- Moseley, F. N. 1966. Biology of the red snapper, Lutjanus aya Bloch, of the northwestern Gulf of Mexico. Publication of the Institute of Marine Science, Texas 11:90–101.
- Parker, R. O., D. R. Colby, and T. D. Williams. 1983. Estimated amount of reef habitat on a portion of the U.S. south Atlantic and Gulf of Mexico Continental Shelf. Bulletin of Marine Science 33:935–940.
- Patterson, W. F., III, J. H. Cowan, Jr., C. A. Wilson, and R. L. Shipp. 2001a. Age and growth of red snapper from an artificial reef area in the northern Gulf of Mexico. U.S. Fishery Bulletin 99:617–627.
- Patterson, W. F., III, J. C. Watterson, R. L. Shipp, and J. H. Cowan, Jr. 2001b. Movement of tagged red snapper in the northern Gulf of Mexico. Transactions of the American Fisheries Society 130:533–545.
- Pennington, M. 1983. Efficient estimators of abundance for fish and plankton surveys. Biometrics 39:281–286.
- Pitcher, T. J., and W. Seaman. 2000. Petrarch's principle: how protected human-made reefs can help the reconstruction of fisheries and marine ecosystems. Fish and Fisheries 1:73– 81.
- Plan Development Team. 1990. The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. NOAA Technical Memorandum NMFS-SEFSC-261, Miami.
- Polovina, J. J. 1991. Fisheries application and biological impacts of artificial habitats. In W. Seaman, Jr. and L. M. Sprague, editors. Artificial habitats for marine and freshwater fisheries. Academic Press, New York
- Polovina, J. J., and I. Sakai. 1989. Impacts of artificial reefs on fishery production in Shimarmaki. Japanese Bulletin of Marine Science 44:997–1,003.
- Roberts, C. M. 1998. Sources, sinks, and the design of marine reserve networks. Fisheries 23:16–19.
- Roberts, C. M., and N. V. C. Polunin. 1993. Marine reserves: simple solutions to managing complex fisheries? Ecological Applications 6:947–961.
- Roberts, C. M., J. A. Bohnsack, F. Gell, J. P Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. Science 294:1920–1923.
- Royce, W. E. 1972. Introduction to fishery sciences. Academic Press, New York.
- Russ, G. R., and A. C. Alcala. 1999. Management histories of Sumilon and Apo Marine Reserves, Philippines, and their influence on national marine resource policy. Coral Reefs 18:307–319.
- SAS Institute, Inc. 1996. Statistics version 6.11. SAS Institute Inc., Cary, North Carolina.
- Schirripa, M. J. and C. M. Legault. 1999. Status of the red snapper stock in U.S. waters of the Gulf of Mexico: up-

- dated through 1998. NOAA/ NMFS Sustainable Fisheries Division, SFD-99/00-75, Miami.
- Shipp, R. L. 1999. The artificial reef debate: are we asking the right questions? Gulf of Mexico Science 17:51–55.
- Stanley, D. R., and C. A. Wilson. 1990. A fishery-dependent based study of fish species composition and associated catch rates around oil and gas structures off Louisiana. U.S. Fishery Bulletin 88:719–730.
- Stanley, D. R., and C. A. Wilson. 1991. Factors affecting the abundance of selected fishes near petroleum platforms off Louisiana. U.S. Fishery Bulletin 89:149–159.
- Stanley, D. R., and C. A. Wilson. 1997. Seasonal and spatial variation in the abundance and size distribution of fishes associated with a petroleum platform in the northern Gulf of Mexico. Canadian Journal of Fisheries and Aquatic Sciences 54:1166–1176.
- Stearns, S. 1884. On the position and character of the fishing grounds of the Gulf of Mexico. Bulletin of the United States Fish Commission 4:289–290.
- Stone, R. B., L. M. Sprague, J. M. McGurrin and W. Seaman, Jr. 1991. Artificial habitats of the world: synopsis and major trends. Pages 31–60 in W. Seaman, Jr. and L. M. Sprague, editors. Artificial habitats for marine and freshwater fisheries. Academic Press, New York.
- Swearer, S. E., J. E. Caselle, D. W. Lea, and R. R. Warner. 1999.

- Larval retention and recruitment in an island population of a coral-reef fish. Nature (London) 402:799–802.
- Szedlmayer, S. T. 1997. Ultrasonic telemetry of red snapper, *Lutjanus campechanus*, at artificial reef sites in the northeast Gulf of Mexico. Copeia 1997:846–850.
- Szedlmayer, S. T., and R. L. Shipp. 1994. Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the northeastern Gulf of Mexico. Bulletin of Marine Science 55:887–896.
- Warner, R. R., S. E. Swearer, and J. E. Caselle. 2000. Larval accumulation and retention: implications for the design of marine reserves and essential fish habitat. Bulletin of Marine Science 66:821–830.
- Watterson, J. C., W. F. Patterson, III, R. L. Shipp, and J. H. Cowan, Jr. 1998. Movement of red snapper, *Lutjanus campechanus*, in the north central Gulf of Mexico: potential influence of hurricanes. Gulf of Mexico Science 16:92–104.
- Williams, I. D., and N. V. C. Polunin. 2000. Differences between protected and unprotected reefs of the western Caribbean in attributes preferred by dive tourists. Environmental Conservation 27:382–391.
- Wilson, C. A., and D. A. Nieland. 2001. Age and growth of red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Louisiana. U.S. Fishery Bulletin 99:653–664.