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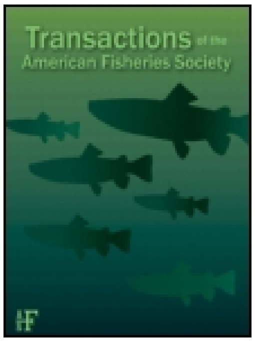

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Abstract.—A tagging study of adult red snapper *Lutjanus campechanus* was conducted in an area of artificial reefs in the northcentral Gulf of Mexico during March 1995 through August 1999. A total of 2,932 red snapper angled at nine artificial reef tagging sites were measured and tagged with internal anchor tags. Tagged fish were either released over their site of capture or transported to another tagging site for release. Of the 561 recaptures made of 519 fish (42 multiple recaptures), 235 recaptures were made at tagging sites on subsequent tagging trips and 326 recoveries were reported by recreational and commercial fishers. Mean distance moved was 29.6 km; the farthest distance moved was 352 km. Mean time at liberty was 404 d; the longest time at liberty was 1,501 d. During the study, two strong hurricanes passed near the study area. The occurrence of hurricanes significantly affected the probability of red snapper movement, as did time at liberty, total length of fish tagged, and transportation of fish to other release sites. The occurrence of hurricanes also significantly affected the distance of red snapper movement, as did time at liberty. Resultant direction of reported movement for all fish was to the east. Observed movement was greater than previously reported for adult red snapper and may be sufficient to facilitate stock mixing in the northern Gulf of Mexico.

Red snapper *Lutjanus campechanus* is a long-lived reef fish that supports economically important commercial and recreational fisheries in the northern Gulf of Mexico (hereafter Gulf). In United States' waters of the Gulf, red snapper are managed as one continuous or unit stock. This management approach is based upon population genetics studies that reported few differences among red snapper from different geographic areas in the northern Gulf. Camper et al. (1993) and Gold et al. (1997) examined mitochondrial DNA (mtDNA) haplotype frequencies of red snapper from different areas in the northern Gulf and concluded that differences were not sufficiently large to reject their null hypothesis of a single panmictic stock. Heist and Gold (2000) concluded that fish from three locations in the northern Gulf and one location off the Yucatan Peninsula in the southern Gulf were not genetically distinct, based on genetic variation in five polymorphic microsatellite loci developed from genomic DNA.

Contrary to the genetic evidence, results of red snapper tagging studies generally have not supported the conclusion that red snapper in the northern Gulf belong to a single stock. Many authors have reported that adult red snapper demonstrate high site fidelity and move little (Beaumariage 1969; Beaumariage and Bullock 1976; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997). The vast majority of tag recoveries in these studies have been of fish that moved short distances (<10 km), if at all. However, some movement on the scale of tens to hundreds of kilometers has been reported (Beaumariage 1969; Beaumariage and Bullock 1976; Szedlmayer and Shipp 1994; Watterson et al. 1998). Nonetheless, it seemed unlikely that large-scale movements by adult red snapper and related stock mixing were extensive enough to produce the observed genetic homogeneity, which was therefore hypothesized to result from other factors. Goodyear (1992, 1995) hypothesized

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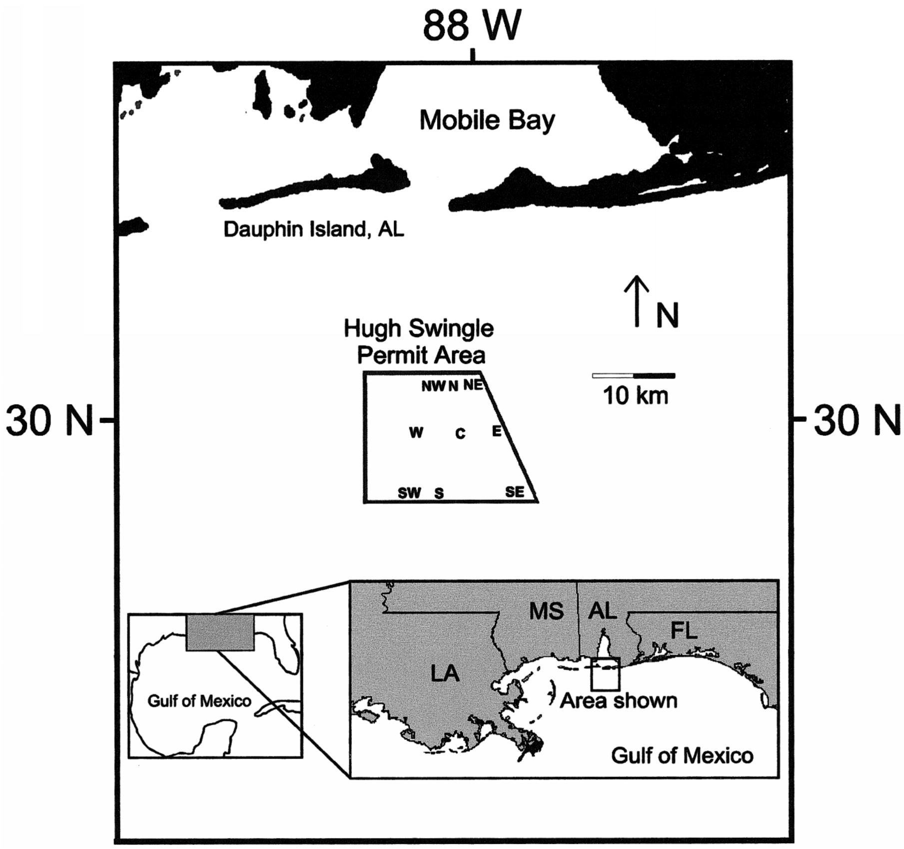

FIGURE 1.—Map of the Hugh Swingle General Permit Area for artificial reef deployment and locations of nine artificial reef tagging sites. Letters indicate geographical location of reefs.

that stock mixing could result from oceanographic transport of planktonic eggs and larvae or from gradual diffusion of adults away from centers of abundance. Gold et al. (1997) hypothesized that observed genetic patterns may indicate historical gene flow, perhaps during the Pleistocene glaciation.

The objective of our study was to examine movement of adult red snapper tagged at artificial reefs off Alabama and to evaluate whether movement of adults was sufficient to facilitate stock mixing. Our approach was to test if time at liberty, fish size, and releasing fish at sites other than the capture site affected the probability and distance of red snapper movement. Effort also was made to test several assumptions of the tagging study, including that tagging did not increase mortality of fish or affect growth of fish, that tags were recognized by fishers, and that recovered tags were reported. When assumptions were not met, we examined potential biases introduced into the statistical analyses of fish movement.

Methods

Tagging and recovery.—Adult red snapper were caught and tagged over nine artificial reef sites located in the Hugh Swingle General Permit Area between 20 and 38 km south−southeast of Dauphin Island, Alabama, from March 22, 1995, to July 20, 1998. Reefs were constructed by a charter boat operator 18 months before the start of the tagging study to allow sufficient time for each reef to attract fish. The nine reefs were deployed over a grid pattern such that reefs were 4–16 km apart (Figure 1; see Watterson et al. 1998 for details). Each reef served as an individual tagging site and was designated by a compass heading which denoted its orientation within the grid. Reefs in each row within the grid occupied similar depths. Approximate depths were 21 m for the northern, 27 m for the central, and 32 m for the southern sites.

TABLE 1.—Scale used to visually assess the condition at release of tagged red snapper.

Condition	Characteristics displayed by fish
1	Fish oriented toward the bottom and swam down vigorously.
2	Fish appeared disoriented upon entering the water, oriented toward the bottom and swam down slowly.
3	Fish appeared very disoriented upon entering the water and remained at the surface.
4	Fish was either dead or unresponsive upon entering the water.

We attempted to sample at least three tagging sites on each tagging trip. Red snapper were angled at tagging sites, measured for total length (TL), and tagged with a yellow Floy FM-89 internal anchor tag, which was inserted through a small (<5 mm) incision made with a scalpel in the fish's abdominal cavity. Each tag was marked with a tag number, the word ''reward,'' and a phone number for fishers to report tag recoveries. A $5 reward was paid for each tag return, and those fishers were entered into a drawing with a chance to win $500. Once tagged, red snapper were either released immediately overboard or transported in holding tanks to other sites for release. The purpose of releasing fish at other sites was to determine whether they homed back to their original site of capture.

Condition categories of tagged red snapper at release were determined (Table 1). Fish released in conditions other than condition 1 were assumed to suffer acute mortality due to the tagging process (see discussion). Therefore, tagging mortality was estimated as the total percentage of fish released in conditions 2, 3, and 4.

Tagged fish were recaptured at tagging sites on subsequent tagging trips and were recovered by recreational and commercial fishers. When a fish was recaptured on a tagging trip, its tag number and total length were recorded and the fish was released. When a fisher reported a tag recovery, as much information as possible was collected. Data from recoveries by fishers were collected through August 31, 1999, which included the tag number, the date of capture, and when possible, the exact location of capture (i.e., Loran C or GPS coordinates). When possible, total length following recapture was obtained from carcasses.

Statistical analyses.—To meet the assumption of independence, only data from terminal recaptures of fish recaptured more than once were used in statistical analyses. The effect of depth of capture, season of capture (winter, spring, summer, or fall), and noncapture-site release on red snapper condition was tested with analysis of variance (ANOVA; SAS 1996). Normality and homogeneity of variances of release condition data were tested with Shapiro–Wilke W and Bartlett's tests, respectively (Sokal and Rohlf 1981; SAS 1996).

Growth rate (mm/d) of recaptured fish (where recapture length was available) was estimated as the slope of the linear regression of their change in total length versus days at liberty (SAS 1996). For fisher recoveries lacking recapture length, the distribution of total length at recapture was simulated with a bootstrap approach. A normal probability density function was constructed based on the estimated growth rate and its variance. To estimate length at recapture for an individual fish, a probability value from 0.0001 to 0.9999 was randomly drawn (with replacement) and the corresponding growth rate was assigned to the fish. The assigned growth rate was multiplied by days at liberty and the product was added to length at tagging to obtain estimated length at recapture. One simulation run was complete when total length at recapture was estimated for all unmeasured fish, and simulated distributions of lengths at recapture were calculated 500 times to account for variability in fish growth. Results from each simulation run were combined with data from measured recaptures, yielding an estimated distribution of lengths at recapture for all fisher recoveries.

The probability of external tag retention as a function of time at liberty was modeled with logistic regression (SAS 1996). Only data from fish recaptured on tagging trips were used in the model. We assumed that all tagged fish recaptured on tagging trips were recognized, even if the external portions of their tags were missing. This assumption was based on the fact that tagged fish that lost the external portions of their tags were easily recognized by their tagging scars. (New tags were inserted into fish that had lost the external portion of their original tags). In the logistic regression analysis, fish that retained their external tags were coded as a success (1) and fish that lost their external tags were coded as a failure (0).

An unplanned factor was added to the study when two strong hurricanes passed near the tagging sites. The center of Hurricane Opal, with maximum winds of 200 km/h, passed within 40 km of the tagging sites on October 4, 1995, and the center of Hurricane Georges, with maximum sustained winds of 150 km/h, passed within 50 km

TABLE 2.—Dates of tagging trips, tagging sites sampled, and number of red snapper tagged.

Date	Tagging sites[a]	Number tagged
Mar 22, 1995	C, WE	94
May 3, 1995	N, NE, NW, C	107
Jun 20, 1995	W, S, SW	153
Jun 21, 1995	E, SE, C	118
Aug 19, 1995	SE, E, NE	129
Jul 13, 1995	NW, W, SW	100
Jul 14, 1995	N, C, S	112
Nov 30, 1995	S, SE, NW, C	107
Dec 12, 1995	N, SW	73
Feb 27, 1996	SW, W, NW	42
Mar 22, 1996	N, C, S	41
Mar 29, 1996	NE, SE, E	38
May 1, 1996	S, SE, C	37
Jun 12, 1996	SW, S, W, N, C	50
Aug 7, 1996	SE, NE, N	86
Oct 31, 1996	C, W, NW, SW	163
Nov 1, 1996	NE, E, SE	152
Dec 2, 1996	N, C, S	150
Dec 9, 1996	NE, E SE	122
Mar 26, 1997	NW, N, NE	114
Mar 27, 1997	SW, S, C	117
Apr 29, 1997	NW, N, NE	42
Sep 18, 1997	NW, N, NE, E	147
Sep 23, 1997	C, SE, S	65
Nov 3, 1997	NW, N, NE	136
Nov 5, 1997	W, SW, S, C	186
Feb 25, 1998	NW, N, NE	147
Jul 20, 1998	NW, N, NE	104

[a] See Figure 1 for locations of these sites.

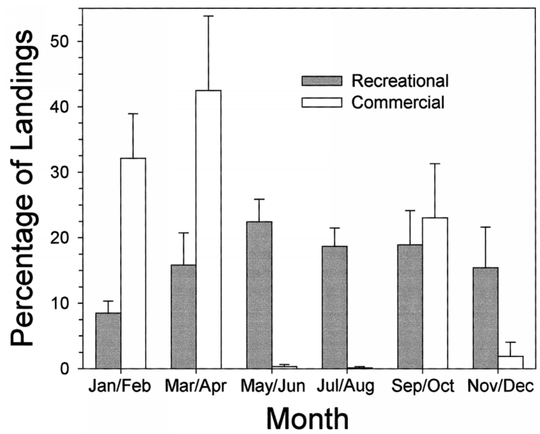

FIGURE 2.—Mean bimonthly commercial and recreational landings (+SE) of northern Gulf of Mexico red snapper from 1995 to 1998 (Schirripa and Legault 1999).

of the tagging sites on September 28, 1998. It became apparent that movement of fish that were at liberty during the hurricanes was on a larger scale than fish not exposed to the storms. In statistical analyses of movement, exposure to hurricanes was therefore included as an independent variable to test the effect of Hurricanes Opal and Georges on the probability and distance of red snapper movement.

Logistic regression was used to test whether time at liberty, length at tagging, exposure to hurricanes, and noncapture-site release significantly affected the probability that tagged fish moved away from their release sites (SAS 1996). In the model, fish recaptured at sites other than their release sites were coded as a success (1), and fish that were recaptured at their release sites were coded as a failure (0).

There were many failures in the distance of movement data; therefore, the delta method was employed to obtain unbiased estimates of mean distance moved and the variance of the mean (Aitchison 1955; Pennington 1983). To test the effects of time at liberty, length at tagging, exposure to hurricanes, and noncapture-site release on distance of red snapper movement, a negative binomial regression model was computed using PROC GENMOD in SAS (Hilbe 1994). In the model, units of distance were hectometers and were rounded to the nearest integer. The model was built using a forward stepwise approach in which regressions first were computed for each of the four independent variables. The single variable model with the lowest significant *P*-value (α = 0.05) was chosen as the base model. Individual variables were added in order of significance, and improvement of fit was assessed by testing whether adding a variable significantly decreased the deviance of the model to which it was added (Agresti 1990). The model building process was complete when no more significant variables were available to be added or the addition of a variable did not significantly improve the fit of the model to which it was added.

Results

Tag Recovery Data

We made 28 trips to tag red snapper from March 1995 to July 1998 (Table 2). The temporal distribution of tagging trips was similar to the temporal distribution of recreational fishing effort in the northern Gulf during that period (Figure 2). Of the total of 2,932 red snapper tagged, we released 2,053 fish at their capture and tagging site and 879 at sites other than their capture sites. Mean TL ($\pm$SE) of tagged red snapper was 335.1 mm ($\pm$1.34) (Figure 3). Throughout most of the project the minimum legal size for possession of red snapper in U.S. waters of the Gulf was 381 mm TL for

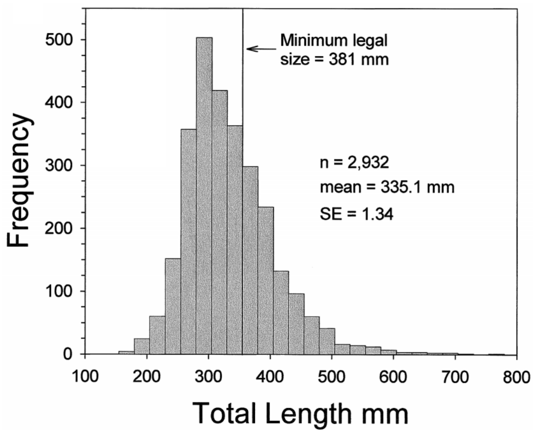

FIGURE 3.—Distribution of red snapper total lengths at tagging. The vertical line indicates the minimum legal size for possession of red snapper in the northern Gulf of Mexico at the time of tagging.

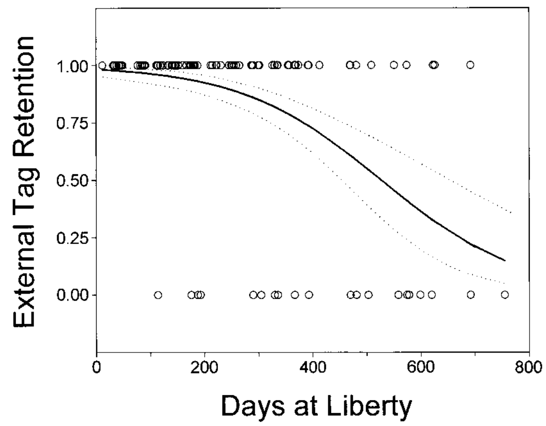

FIGURE 4.—Logistic regression of tag retention versus time at liberty for red snapper recaptured at tagging sites ($N = 214$). Probability of tag retention = $1/[1 + \exp(-4.042 + 0.00767 \cdot D)]$, where D = days at liberty. Plotted are the fitted line (solid) and 95% confidence intervals (dotted).

both the commercial and recreational fisheries; the size limit was increased to 457 mm TL from June through August 1999 for the recreational fishery. When tagged, 80% of the fish ($N = 2{,}366$) were shorter than the legal size limit.

Overall, 86% of tagged fish ($N = 2{,}535$) were condition 1 when released (Table 3). Percentage data were not significantly different from normal (Shapiro–Wilke test, $P > 0.05$), and variances were not significantly different among factor levels (Bartlett's test, $P > 0.05$). Depth of capture site (ANOVA, $F_{2,100} = 6.19$, $P = 0.003$) and release of fish at noncapture sites (ANOVA, $F_{1,101} = 17.26$, $P < 0.001$) significantly affected the percentage of fish released in condition 1; season of capture did not significantly affect fish release condition (ANOVA, $F_{3,99} = 1.27$, $P = 0.41$).

During the study, 561 recaptures were tallied, involving 519 red snapper; that is 42 were recaptured more than once, 40 being recaptured twice (21 by fishers and 19 on tagging trips) and 1 three times (all during tagging trips). Of the 519 recaptured fish, 98.5% were condition 1 when released; 255 were at liberty during the hurricanes (154 during Opal, 94 during Georges, and 7 during both hurricanes); 408 had been released where captured and 111 had been released at noncapture sites; and 214 were recaptured on tagging trips (of which 193 recaptures were terminal recaptures). Of the 326 recoveries reported by fishers (fisher return rate = 11.1%), recreational fishers reported 321 (recreational return rate = 10.9%) and commercial fishers reported 5 (commercial return rate = 0.2%).

The probability of external tag retention declined significantly with time at liberty (logistic regression, $\chi^2 = 40.08$, df = 1, $P < 0.001$; Figure 4). Lack-of-fit analysis was not significant for the model ($\chi^2 = 132.88$, df = 212, $P = 0.9999$), but the fitted line was estimated better for fewer days at liberty because there were more samples over this portion of the curve. For example, the esti-

TABLE 3.—Number and percentage of tagged red snapper released in condition 1 in the northern Gulf of Mexico, Hugh Swingle Permit Area, March 1995 to July 1998.

Transportation and condition	Number and percent in condition by depth of release site: 21 m	27 m	32 m	All depths
Fish transported	91% (113 of 124)	80% (280 of 351)	74% (299 of 404)	79% (692 of 879)
Fish not transported	91% (855 of 940)	91% (459 of 505)	87% (529 of 608)	90% (1,843 of 2,053)
Mean in condition 1	91% (968 of 1,064)	86% (740 of 856)	82% (828 of 1,012)	86% (2,535 of 2,932)

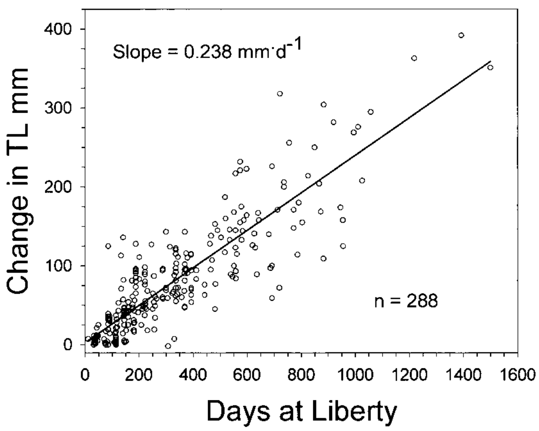

FIGURE 5.—Linear regression of change in total length (ΔTL) versus time at liberty for tagged red snapper [ΔTL = 2.34 mm + (0.238 mm/days at liberty)].

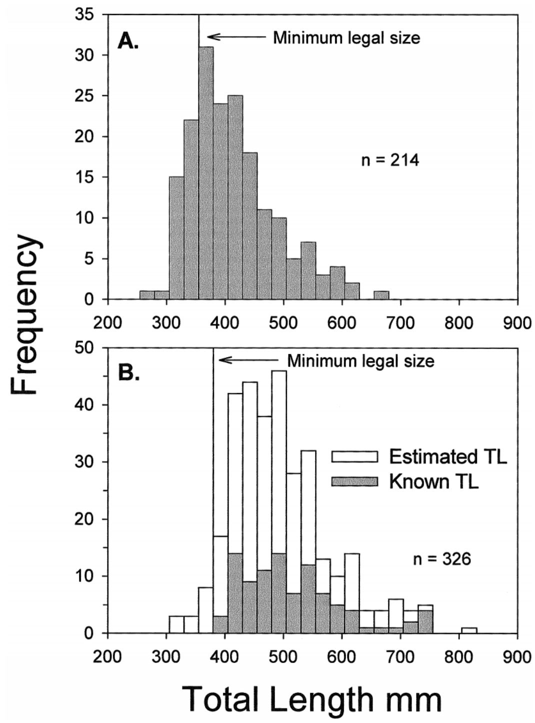

FIGURE 6.—Distribution of total length (TL) at recapture for terminal recaptures of red snapper that were **(A)** recaptured on tagging trips or **(B)** recovered by fishers. Distribution of estimated total length for fisher recoveries is the average of 500 simulations. Vertical lines in each plot represent the minimum legal size for possession of red snapper in the northern Gulf of Mexico during most of the study.

mated 95% confidence interval for probability of tag retention for fish at liberty for 200 d was 0.87–0.96 but was 0.05–0.37 for fish at liberty for 755 d, the longest time at liberty for fish recaptured at tagging sites (Figure 4).

Total length at recapture was measured for all terminal recaptures made on tagging trips and for 95 (29%) recaptures reported by fishers. The linear regression of change in length versus time at liberty was statistically significant ($F_{1;286} = 631.0$, $P < 0.001$, $R^2 = 0.76$). The slope of the regression was 0.238 mm/d with a variance of 0.0231 (Figure 5). Mean length at recapture ($\pm$SE) was 390 mm ($\pm$5.50) for recaptures made on tagging trips and 490 mm ($\pm$8.83) for measured recoveries reported by fishers (Figure 6). Mean length at recapture of combined distributions of fisher recoveries with known and estimated lengths at recapture ranged from 470 mm ($\pm$6.42) to 483 mm ($\pm$6.92) for 500 bootstrapped simulation runs (Figure 6b).

Red Snapper Movement

Five red snapper recaptured on tagging trips were recaptured at tagging sites other than those where they were released. Of these five fish, two moved from site SE to site C (8.5 km), one moved from site SE to site N (13.1 km), one moved from site C to site N (6.0 km), and one moved from site S to site SW (0.5 km). The fish that moved from site S to site SW had been transported from site SW to site S before release; this was the only transported fish (out of 111) that was recaptured at its original capture site.

Location of recapture was reported for 232 recoveries reported by fishers (71% of fisher recoveries). The farthest distance a red snapper moved was 352 km; it had been at liberty for 598 d (Figure 7). This individual, recaptured off Dog Island, Florida, following Hurricane Georges, moved farther than any red snapper reported from previous tagging studies (Table 4). Another red snapper at liberty during Hurricane Georges was caught by a recreational fisher west of the Mississippi River delta and southeast of Grand Isle, Louisiana, or approximately 259 km southwest of its release site; it was at liberty for 1,367 d (Figure 7b). The maximum time at liberty was 1,501 d; this fish had moved 3.5 km to the east−southeast of its release site. Mean time at liberty was 404 d, which was 2 to 3.5 times longer than the mean time at liberty for recaptures from previous studies (Table 4).

Although some westward movement was reported, the predominant direction of red snapper movement was east, which corresponded to the areas of highest recreational landings in the north-

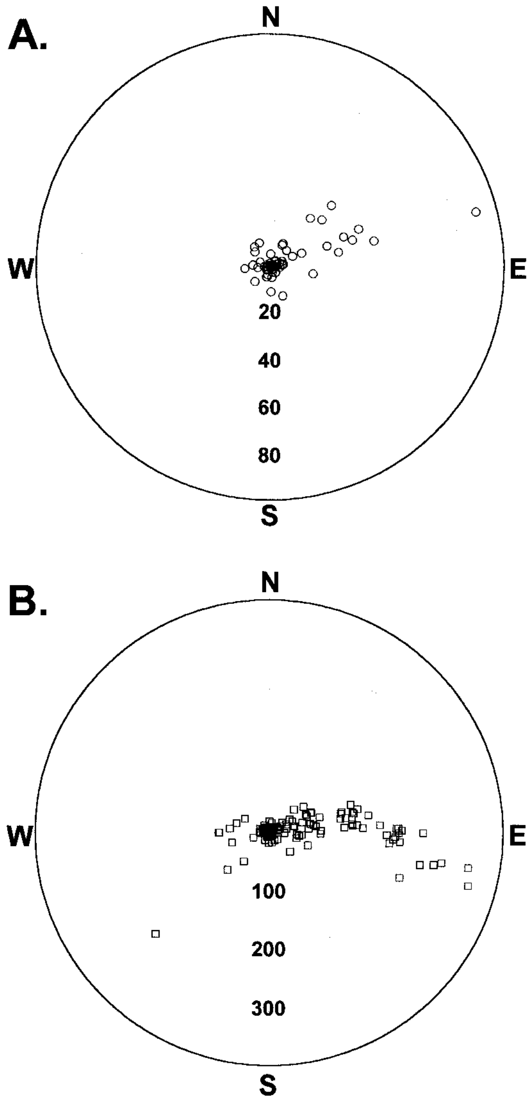

FIGURE 7.—Polar diagrams of red snapper movement for **(A)** fish not at liberty during Hurricanes Opal or Georges and **(B)** fish at liberty during those hurricanes, where the center is the tagging site and the circles or squares are the recovery locations (as defined by distance and compass direction). Units of distance for each plot are kilometers.

ern Gulf (Figures 7, 8). The mean vector of reported movement was 42.4 km to the east (compass heading = 271°) for individuals at liberty during hurricanes and 7.4 km to the east−northeast (compass heading = 293°) for individuals not at liberty during the two hurricanes.

The logistic regression that modeled the probability of fish movement was significant (χ^2 = 204.76, df = 4, $P < 0.001$), and lack-of-fit analysis for the model was not significant (χ^2 = 455.727, df = 5, P = 0.9693). All four independent variables were significant in the model ($P < 0.01$), and each had a positive effect on the probability of red snapper movement. Therefore, as time at liberty and length at tagging increased, the probability of fish movement increased. Hurricane exposure and noncapture-site release also increased the probability of fish movement.

Mean distance moved by recaptured red snapper was 29.4 km (Figure 9). Distance of movement in single-variable, negative binomial regressions was significant for exposure to hurricanes (χ^2 = 131.33, df = 1, $P < 0.001$), time at liberty (χ^2 = 24.35, df = 1, $P < 0.001$) and length at tagging (χ^2 = 4.63, df = 1, P = 0.023) but not for noncapture-site release (χ^2 = 0.05, df = 1, P = 0.830). When time at liberty was added to the hurricane-exposure model, lack of fit was not significant (χ^2 = 412.00, df = 421, P = 0.6136) and the model's deviance was significantly decreased (χ^2 = 39.31, df = 1, $P < 0.001$). Length at tagging then was added to the model, but its addition increased the model's deviance. Therefore, the final model included only exposure to hurricanes and time at liberty effects, both of which had a positive effect on distance of red snapper movement.

Discussion

The current study differed from previous tagging studies of Gulf red snapper in several ways. The temporal and spatial scales of the study and the large number of fish tagged ensured large numbers of recaptures over time, which enabled us to test factors potentially affecting red snapper movement. Previous studies relied on relatively small samples sizes and authors only conjectured as to what factors affected red snapper movement. This study was designed to test which factors affected the probability and distance of red snapper movement; we also tested several assumptions and addressed potential biases introduced into statistical tests when assumptions were not met.

Condition of Tagged Fish

Patterson (1999) proposed that the percentage of tagged red snapper released in condition 1 could be used as a proxy for survival, the assumption being that fish released in conditions 2, 3, and 4 suffered acute mortality as a result of the tagging process. This assumption is supported by results of previous studies of red snapper release mortality, as well as by the fact that nearly all recaptures

TABLE 4.—Results from red snapper tagging studies conducted in the northern Gulf of Mexico.

Study	Maximum distance moved (km)	Maximum time at liberty (d)	Site fidelity	Mean time at liberty (d)
Beaumariage 1969	279	2,049	90% recaptured within 5 km of release site	113
Fable 1980	5	253	94% recaptured at release site	112
Szedlmayer and Shipp 1994	32	430	76% recaptured within 2 km of release site	137
Watterson et al. 1998	265	622	55% recaptured within 2 km of release site	207
This study	352	1,501	36% recaptured within 2 km of release site	404

had been released in condition 1. Gitschlag and Renaud (1994) reported that red snapper release mortality inferred from the condition of released fish at the surface correlated well with mortality estimates from in situ caging experiments. They also reported that most mortality suffered by red snapper held in cages or laboratory tanks occurred soon after capture, as did Render and Wilson (1994). Szedlmayer and Shipp (1994) held 30 tagged red snapper in the laboratory for 6 months with no mortality or signs of infection, implying that fish released in condition 1 in our study probably did not suffer chronic injuries leading to mortality.

If the percentage of tagged red snapper released in conditions 2, 3, and 4 is used as an estimate of tagging mortality, then the estimates of mortality presented here (14% overall) are within the range of red snapper release mortality reported from other studies. Render and Wilson (1994) reported an overall release mortality rate of 20% for red snapper caught off Louisiana. Gitschlag and Renaud (1994) presented data from several studies of red snapper release mortality, and mean mortality rate ($\pm$SE) was 14% ($\pm$4.5) for seven studies that were conducted at depths similar to our study. Therefore, it did not appear that our tagging methods significantly affected release mortality of tagged red snapper.

Growth of Tagged Fish

Tagging did not appear to affect growth of red snapper. We estimated the growth of tagged fish to be 0.238 mm/d (TL), whereas Patterson et al. (in press) estimated that otolith-aged red snapper in the size range of individuals we tagged grew at a rate of 0.240 mm/d (TL). The growth rate of our tagged fish also was similar to growth rates of Gulf red snapper reported by other investigators (Render 1995; Szedlmayer and Shipp 1994).

Recognition of Tagged Fish

Several factors may have influenced whether tags were recognized by fishers. The ventral placement of internal anchor tags may have made them more difficult to see than dorsally placed tags (Fable 1990; Nielsen 1992). Fouling of tag shafts by algae and barnacles also may have decreased tag visibility. Many recaptures made on tagging trips were of fish with badly fouled tags, and several

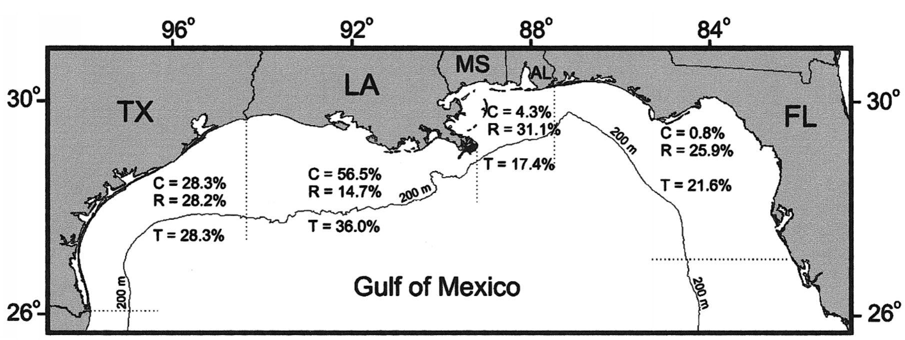

FIGURE 8.—Map depicting the mean percentage (from 1995 to 1998) of northern Gulf of Mexico commercial (C), recreational (R), and total (T) red snapper landings from demarcated areas (Schirripa and Legault 1999).

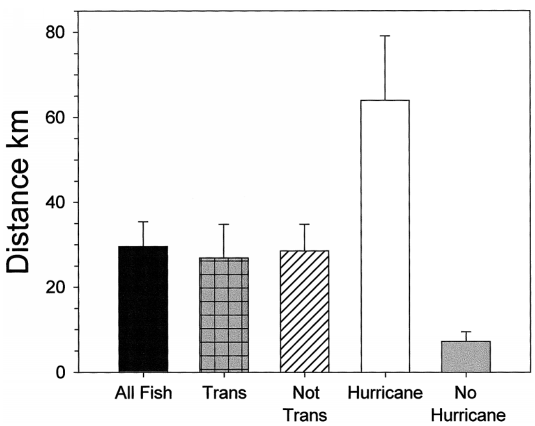

FIGURE 9.—Unbiased estimates of the mean distance (+SE) of red snapper movement computed with the delta method. Fish were either transported from the capture and tagging site to another site for release (trans) or released at the capture and tagging site (not trans).

fishers reported recovering red snapper with fouled tags. Not only can fouling render tags unrecognizable, it also can cause harm to tagged fish and increase tag abrasion leading to tag loss (Dunning et al. 1987; Mattson et al. 1990; Nielsen 1992).

Internal anchor tags were chosen for use in this study due to high retention rates reported for red snapper and other species. Szedlmayer and Shipp (1994) reported 100% tag retention for red snapper held in laboratory tanks for 6 months, and Smith et al. (1990) reported pond-reared shortnose sturgeon *Acipenser brevirostrum* had 100% tag retention after 139 d. Dunning et al. (1987), in a double tagging experiment with Hudson River striped bass *Morone saxatilis,* estimated that retention rate of internal anchor tags was 98% after 2 years but was only 42% for T-bar anchor tags after 1 year. Fable (1990) reported tag return rates for Gulf and south Atlantic king mackerel *Scomberomorus cavalla* that were eight times higher for internal anchor tags than dart tags, and 84% of individuals at liberty less than 2 years retained internal anchor tags.

Contrary to the high retention rates reported for internal anchor tags, tag retention was relatively poor in our study. Although confidence intervals for tag retention were wide for fish at liberty longer than 450 d, even the upper 95% levels were much lower than retention rates reported for other species. Of the 245 recoveries reported by fishers after January 1997, 61 (25%) were of fish missing the external portion of their tags; anchor portions of these tags were found by chance when fish were cleaned. With such a high percentage of tags found only by chance, we speculate that many recaptures went completely unnoticed by fishers.

Tag loss may have caused the fisher reporting rate of recaptured tagged fish to be much lower than the actual recovery rate, and a low reporting rate would have caused movement of tagged fish to be underestimated. That is, time at liberty significantly affected both the probability and distance of red snapper movement, so that fish that were the most likely to move, and probably moved the farthest, were least likely to be recognized as tagged and reported.

Reporting Rate

In addition to tag loss, other factors may have affected the fisher reporting rate. Fishers may have been reluctant to report recoveries of undersized fish, reporting few shorter than the legal size limit (381 or 457 mm, depending on when the recapture occurred). As might be expected, no carcasses of undersized fish were returned by fishers. Five recoveries were reported as undersized and discarded when caught, and the remaining undersized recoveries (9–16, depending on the simulation) may have been sublegal discards or estimated to be shorter than they actually were. If undersized recoveries were not fully reported, movement of small fish would be underestimated. We attempted to avoid this potential bias in statistical analyses by using length at tagging instead of length at recapture as the factor representing fish size.

Management regulations also may have affected the fisher reporting rate in other ways. Although token regulations were in place by the late 1980s, before 1990 both the recreational and commercial fisheries were essentially unregulated (Goodyear 1995). Because of concerns over the status of the Gulf red snapper stock, the commercial fishery has been managed under a quota system since 1991, and the National Marine Fisheries Service (NMFS) has closed the fishery when the quota was met in every year since. During the same period the recreational fishery routinely overran its total allowable catch (TAC) until congressional passage of the Sustainable Fisheries Act of 1996 (U.S. Public Law 104–297), which mandates that NMFS close the recreational fishery when its portion of TAC has been landed. As a result, NMFS closed the recreational fishery in December 1998 and from September through December 1999. These regulatory actions may have caused fishers to be less willing to cooperate in returning tagged fish. Beaumariage (1969) tagged fish off northwest Florida in the 1960s when no fishery regulations existed for Gulf red snapper and reported a tag return rate of 28% for red snapper, which is 2.5 times higher than the fisher reporting rate in our study. Citing a sharp drop in tag return rates for Gulf and south Atlantic king mackerel following the advent of fishery regulations in the early 1980s, Fable (1990) suggested that by not reporting tag recoveries fishers were expressing their resentment of the regulations.

Differences in the spatial and temporal distribution of effort between the commercial and recreational red snapper fisheries also may have affected tag recoveries. During the study, the recreational fishery was much more evenly distributed across all months than was the commercial fishery (Schirripa and Legault 1997, 1999). Total allowable catch was essentially equal for each fishery (approximately 2.1×10^3 metric tons per year), but the commercial fishery was only open each year for brief periods during winter and fall and operated as a derby. In a derby fishery, commercial fishers may not have taken the time, or even had access to a telephone, to report tag returns. The number of tags reported by commercial fishers was disproportionately low, even though the commercial fishery averaged only about 10% of annual landings east of the Mississippi River (the area where all but one of the reported recoveries were made). If nonreporting of tag recoveries by commercial fishers existed, it may have biased reported movement to appear eastward because the bulk of commercial landings came from the northwestern Gulf. Alternatively, there is much more natural hard-bottom habit for red snapper off northwest Florida than to the immediate west of the artificial reef area where we tagged fish (Parker et al. 1983; Schroeder et al. 1995); thus, reported movement to the east may accurately reflect movement in the tagged population.

Red Snapper Movement and Implications for Stock Mixing

Authors of previous studies of red snapper movement generally concluded that adult fish demonstrate high site fidelity (Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997). Even Watterson et al. (1998), working with preliminary data from our study, reported that 80% of fish not at liberty during Hurricane Opal were recaptured at their sites of release and concluded that fish not exposed to hurricanes remained loyal to their release sites. In the expanded study presented here, increases in sample size and the temporal scale allowed us to observe red snapper movement on two different scales, one for fish exposed to hurricanes and one for fish not exposed to hurricanes. This demonstrated that, over time, fish not exposed to hurricanes also had a low probability of remaining at their release sites. We found that only 55% of recaptures not at liberty during hurricanes had remained at their release sites, a scale of movement away from release sites much greater than that reported by Watterson et al. (1998). Moreover, our estimates of red snapper movement away from release sites are probably conservative because of tag loss and probable under-reporting of tag recoveries made by fishers.

Mean time at liberty of fish recaptured in this study was much longer than mean time at liberty reported from previous red snapper tagging studies (Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Watterson et al. 1998). It is possible that fish from other studies were as likely to move as a function of time at liberty as were fish from this study; however, the temporal scale of previous studies may have been too short to observe fish movement. In a 4-year study of 1,126 tagged red snapper off northwest Florida, Beaumariage (1969) reported a high tag recovery rate of 28%. However, recaptured red snapper were at liberty on average for only 113 d; hence, most recaptures were made near their sites of release. We report here that time at liberty significantly affected the probability and distance of red snapper movement away from release sites; similarly, other studies have shown that the longer the mean time at liberty, the greater movement of tagged red snapper (Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997; Watterson et al. 1998).

Distances moved by individual red snapper in this study also were greater than distances previously reported; the greatest distance had been 279 km (Beaumariage 1969). Beaumariage (1969) reported that six red snapper recaptured off northwest Florida in the 1960s moved over 100 km, which until now was the largest scale of movement reported for Gulf red snapper. In our study, 34 fish moved over 100 km from their release sites, 15 of which moved over 200 km and 2 of those over 300 km. We also recorded, for the first time, a fish movement from the northeastern Gulf to the northwestern Gulf.

Before this study, the conclusion that Gulf red snapper constitute a single stock was not supported by tagging data, which had suggested adult red snapper move little. Although some studies showed movement of red snapper on spatial scales of tens to hundreds of kilometers (Beaumariage 1969; Szedlmayer and Shipp 1994), most recaptured fish did not move at all. Because existing data indicated that movement of adult red snapper was limited, Goodyear (1992, 1995) proposed that stock mixing may result from oceanographic transport of eggs and larvae, or from gradual diffusion of adult fish away from centers of abundance. Gold et al. (1997) added that the contemporary genetic homogeneity of northern Gulf red snapper possibly resulted from historical mixing and that if modern subpopulations exist, they have had insufficient time for genetic divergence.

Although stock mixing may occur planktonically and although current genetic variability in Gulf red snapper surely reflects historical mixing, we have documented movement of adult red snapper that may be sufficient to promote stock mixing, especially considering the relatively small number of migrants necessary to maintain genetic homogeneity between geographic areas (Allendorf 1983; Shaw et al. 1999; Heist and Gold 2000). In fact, as few as 1 migrant per 1,000 breeding individuals in a generation may be sufficient to preclude genetic differentiation among areas (Nolan et al. 1991). In light of this, and because all recoveries reported by fishers were larger than estimated size at maturity for Gulf red snapper (approximately 290 mm TL; Goodyear 1995; Render 1995; Collins et al. 1996), fish at liberty during Hurricanes Opal or Georges demonstrated movement that potentially could affect genetic mixing in the northern Gulf. Clearly, movement of fish exposed to hurricanes was on a scale and in a direction that would facilitate genetic mixing in the northeastern Gulf. Our first-time documented movement of a red snapper from east to west of the Mississippi River delta is also pertinent to stock mixing. If other recoveries of tagged individuals that moved from the northeastern to the northwestern Gulf went unreported (for reasons discussed above), the potential for stock mixing was even greater than reported movement would indicate.

Although the scale of movement was much greater for fish at liberty during Hurricanes Opal or Georges, movements of fish at liberty at times other than during the storms may be sufficient to support Goodyear's (1992) hypothesis that stock mixing of Gulf red snapper could result from gradual diffusion of adults away from centers of abundance. Our observed movement to the east may also support that hypothesis. From fisheries-dependent data, it appears there is a center of red snapper abundance off southwest Louisiana and a second center off Alabama (Goodyear 1995). Waters off northwest Florida historically supported a large red snapper fishery; however, during the late 1980s and early 1990s the abundance of red snapper in this area plummeted (Camber 1955; Carpenter 1965; Goodyear 1995). Estimates from virtual population analysis indicate that young cohorts of red snapper (fish <5 years old) now are much more abundant Gulf-wide than they have been in the recent past (Schirripa and Leg ault 1999). Management regulations have successfully decreased fishing mortality on young Gulf red snapper, and as the abundance of young fish has increased, anecdotal information and fisheries-dependent data suggest that numbers of red snapper off northwest Florida are increasing (Schirripa and Legault 1999). It is possible that, as the stock recovers, fish from a center of abundance off Alabama are recruiting to Florida waters.

Summary

This study supports the conclusion that northern Gulf red snapper constitute a single stock. Hurricanes had the greatest effect on red snapper movement, but movement of fish not at liberty during hurricanes may be sufficient to support stock mixing via gradual diffusion of adults. Before this study, limited evidence indicated that larger, older fish may move greater distances than small, young fish (Beaumariage and Wittich 1966; Moe 1966). We report here that size significantly affected probability of movement, and the longer fish were at liberty the farther they moved. Therefore, because mostly small, young fish were tagged in this study, the rates of movement we reported here may be less than rates for larger fish. Movement of fish that were at liberty during Hurricanes Opal or Georges demonstrated the greatest potential to promote stock mixing. The frequency of hurricanes in the Gulf implies that they potentially play an important role in stock mixing dynamics of red snapper, especially considering that Gulf red snapper can reach age 50 or more and are likely to be exposed to several hurricanes over the course of their lives (Patterson et al. in press; Render 1995; Watterson et al. 1998).

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