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J. Carter Watterson
University of South Alabama

William F. Patterson III
University of South Alabama

Robert L. Shipp
University of South Alabama

James H. Cowan Jr.
University of South Alabama

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Movement of Red Snapper, *Lutjanus campechanus*, in the North Central Gulf of Mexico: Potential Effects of Hurricanes

J. CARTER WATTERSON, WILLIAM F. PATTERSON III, ROBERT L. SHIPP, AND JAMES H. COWAN, JR.

Site fidelity and movement of red snapper, *Lutjanus campechanus*, were estimated from a tagging study conducted off the coast of Alabama from March 1995 to January 1997. Red snapper were caught using rod and reel over nine artificial reef sites, with three reefs each located at 21-m, 27-m, and 32-m depths. During the study, 1,604 fish were tagged, and 174 recaptures were made of 167 individuals. On 4 October 1995, the eye of Hurricane Opal passed within 40 km of the artificial reef sites. When recaptures were stratified according to whether or not they were at liberty during Opal, storm effect was the most significant factor in predicting the likelihood of movement and magnitude of movement by tagged red snapper. Eighty percent of recaptured red snapper that were not at liberty during Opal were recaptured at their site of release. Fish that were at liberty during Opal, however, had a significantly higher likelihood of movement away from their site of release ($P < 0.001$). These fish also moved significantly further than those that were not at liberty during Opal ($P < 0.001$). Fish that were at liberty during Opal moved a mean distance (± SE) of 32.6 km (± 6.81), compared to a mean distance (± SE) of 2.5 km (± 1.10) for fish that were tagged and recaptured before Opal, and a mean distance (± SE) of 1.7 km (± 0.43) for fish that were tagged and recaptured after Opal. Heretofore, it has generally been accepted that adult red snapper demonstrate strong site fidelity and genetic homogeneity in the stock was hypothesized to result from larval drift or due to historic mixing on longer time scales. This study documents movement of adult red snapper on spatial scales that would facilitate stock mixing and implicates large-scale climatic events, such as hurricanes, as important factors in stock mixing dynamics.

Red snapper, *Lutjanus campechanus*, is one of the most economically valuable fish species in the Gulf of Mexico (Gulf). Currently, red snapper in the Gulf are managed as a single genetic stock. Camper et al. (1993) concluded that observed genetic homogeneity in red snapper mitochondrial DNA (mtDNA) across the northern Gulf indicated considerable gene flow (Camper et al., 1993). Gold et al. (1997) also reported that spatial and temporal patterns of mtDNA variation among northern Gulf red snapper were consistent with the unit stock hypothesis. In contrast, differences found in red snapper mtDNA in samples from Florida, Alabama, and Texas by Chapman et al. (1995) suggested that fish from different areas in the Gulf were genetically distinct. However, Chapman et al. (1995) noted that their findings may have been biased due to nonrandom sampling of genetically related fish.

In contrast to genetic analyses, tagging studies and ultrasonic tracking experiments have indicated that both juvenile and adult red snapper exhibit strong site fidelity and are essentially nonmigratory (Beaumariage, 1964, 1969; Beaumariage and Bullock, 1976; Fable, 1980; Szedlmayer and Shipp, 1994; Szedlmayer, 1997). However, some movement of red snapper on the scale of kilometers to hundreds of kilometers has been shown to occur or has been conjectured based on anecdotal records (Camber, 1955; Moe, 1963; Topp, 1963, 1964; Beaumariage and Wittich, 1966; Moseley, 1966; Bradley and Bryan, 1975; Beaumariage and Bullock, 1976). Most of the movement observed in these studies, however, was over short distances and was speculated to reflect seasonal patterns (Camber, 1955; Topp, 1963; Bradley and Bryan, 1975; Beaumariage and Bullock, 1976) or be a function of size or age (Camber, 1955; Moseley, 1966; Bradley and Bryan, 1975). Although these factors were believed to be the primary causes of movement, other movement cues were suggested, including depth of habitat (Beaumariage and Wittich, 1966; Moe, 1966; Beaumariage and Bullock, 1976), food availability (Camber, 1955; Topp, 1964; Moseley, 1966; Bradley and Bryan, 1975), and water temperature (Moe, 1963; Topp, 1964). How-

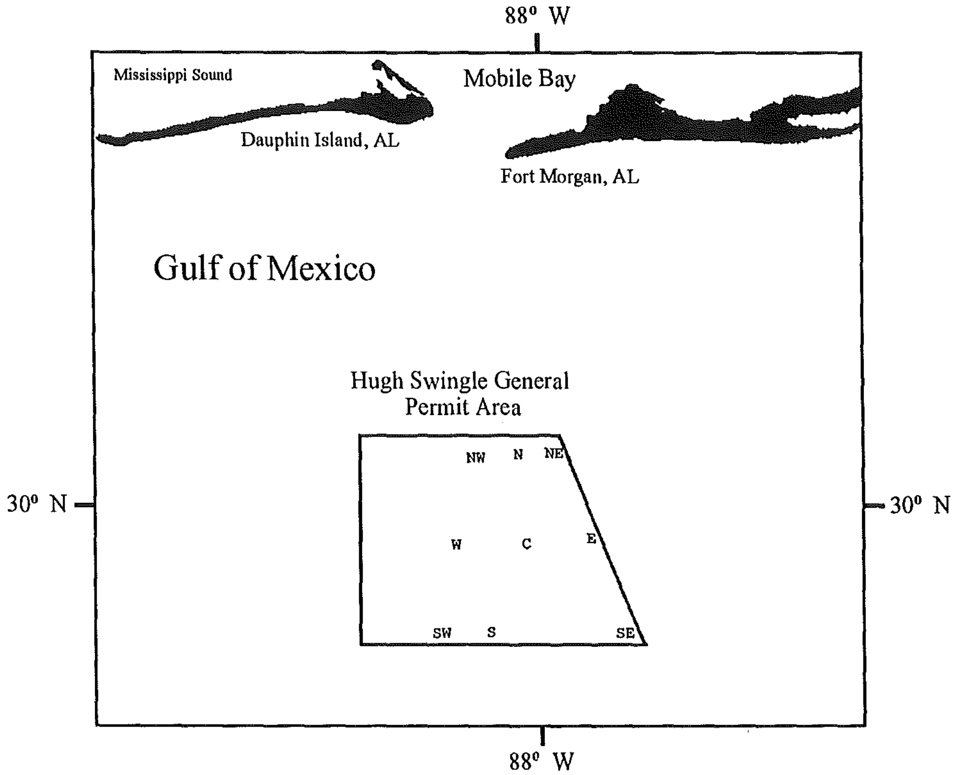

Fig. 1. Map of Gulf of Mexico off the coast of Alabama that shows the locations within the Hugh Swingle general permit area of the nine artificial reef sites in this study.

ever, little, if any, of the movement observed in these studies occurred in a large enough sample of the population, or on large enough spatial scales, to validate the unit stock hypothesis. Conversely, most of these studies found that the majority of tagged individuals remained at or near their site of release.

To address site fidelity in Gulf red snapper and to learn about the causes of movement, a mark/recapture study of red snapper was conducted over artificial reefs in the north-central Gulf off Alabama. The objective of this study was to tag a large number of red snapper from several artificial reef sites for 2 yr to obtain sufficient sample size over time to test hypotheses about red snapper movement. Movement of tagged red snapper was observed on spatial scales of kilometers to hundreds of kilometers and temporal scales from weeks to years.

The data presented here were collected from March 1995 to January 1998. On 4 October 1995, the eye of Hurricane Opal, which had sustained winds of 240 km hr^{-1}, passed within 40 km of the nine tagging sites. This serendipitous event allowed insight into the potential effect of hurricanes on red snapper movement in the northern Gulf. In this study, hypotheses were tested whether Hurricane Opal, depth of release site, days at liberty, total length at recapture, or transport to a different reef site prior to release significantly affected the likelihood and magnitude of red snapper movement.

Materials and Methods

Red snapper were captured by rod and reel over nine artificial reef sites off the coast of Alabama. The reefs were located 20–32 km south–southeast of Mobile Bay in an area of the continental shelf designated by the state of Alabama as the Hugh Swingle General Permit Area for artificial reef deployment (Fig. 1). (The Hugh Swingle General Permit Area was created in 1986; however, Alabama's artificial reef program in this area has existed for about 50 yr.) The reefs were constructed by Charterboat Captain Mike Thierry and consisted of a variety of materials including tractor trailer beds, newspaper bins, and 55-gallon drums bolted together (Table 1). The composition of each reef was known, therefore, the volume of

TABLE 1. Materials used to construct the nine artificial reefs in this study.

Type of material	Dimensions	Volume (m^3)
55-gallon plastic drum	55.9 cm diameter; 88.9 cm height; 930.25-cm^2 hole on each end; 1,006.4-cm^2 hole on side	0.218
Newspaper vending machine	91.4 cm height; 50.8 cm length; 40.6 cm width; 1,085.1-cm^2 hole in front	0.189
Washing machine	86.4 cm height; 68.6 cm length; 60.9 cm width	0.361
Tractor trailer flatbed welded into a triangle	457.2 cm length of each side; 259.1 cm width	23.5
Fiberglass pipe	81.3 cm diameter; 45.7 cm height; 5,188.7-cm^2 hole on each end	0.252

each reef could be estimated to determine the extent of homogeneity among reefs (Table 2). All of the reefs utilized in the study were deployed at least 18 mo prior to the start of the study, allowing sufficient time to attract fish. The reefs were deployed in a 3 × 3 grid, with reefs spaced approximately 4–16 km apart. Each reef was an individual tagging station, and each of these stations was designated by a compass heading based upon relative orientation within the grid (Fig. 1). Each row of three sites occupied a different depth stratum. The shallow stratum stations were in approximately 21 m of water; the mid-depth stratum stations were in 27 m of water; and, the deep stratum stations were in 32 m of water.

From 22 March 1995 to 1 November 1996, 17 tagging trips were made to capture and tag red snapper; tagging trips were made at approximately monthly intervals from Dauphin Island, Alabama. The following tagging protocol was employed to the extent practicable on each of these trips. During each trip at least three sites were visited. While over each site, the first 25 captured red snapper were tagged with internal anchor tags and released immediately over the capture site. The remaining fish captured over the site, up to an additional 25 fish, were tagged and placed in holding tanks for transport to another one of the nine tagging sites for release. Translocation was done to determine if transported red snapper were more likely to move from their release site and also to determine if transported fish displayed homing instincts that enabled them to return to their site of capture.

During the tagging process, 8–10 anglers caught fish; while one researcher tagged and released captured fish, a second recorded data. Red snapper were caught on rod and reel using bottom rigs, which consisted of two 3/0 hooks baited with either cut fish or squid. Upon capture, both total length (TL) and fork length (FL) of each fish were measured to the nearest mm. Fish were tagged using yellow Floy internal anchor tags marked with the tag number, the word "reward," and a phone number of reporting the recapture. Rewards consisted of $5 per tag return and a chance to win $500 in a drawing of all tag returners. To tag each fish, a small (~5 mm) incision was made with a scalpel in the lower abdomen of the fish, into which the anchor portion of the tag was inserted. Once inserted, the portion of each tag that was external to the fish was approximately 6.5 cm.

During the tagging process, air bladders of embolized fish were deflated and any abnormalities noted. Tagged red snapper were either returned to the water or placed into one of two holding tanks for transport to another site for release; holding tanks were 178-gallon aerated coolers that were supplied with fresh

TABLE 2. Composition and total volume of the nine artificial reef sites over which red snapper were tagged and released in this study.

Site	Composition of artificial reef	Volume (m^3)
NW	5 modules of 3, 55-gallon plastic drums	3.270
N	5 modules of 3, 55-gallon plastic drums	3.270
NE	20 newspaper vending machines	3.776
W	25 newspaper vending machines	4.719
C	25 newspaper vending machines	4.719
E	24 newspaper vending machines	4.531
SW	20 newspaper vending machines	3.776
S	Tractor trailer bed welded into a triangle	23.450
SE	15 washing machines	5.416

seawater during transport. Upon release, both the behavior and condition of all fish (both those transported and those released at site of capture) were observed and documented to estimate potential tagging mortality. The condition of released fish was judged based on the following scale:

Condition: (1) fish oriented to the bottom and swam down vigorously; (2) fish appeared somewhat disoriented upon entering the water, oriented to the bottom, and swam down slowly; (3) fish appeared very disoriented upon entering the water and remained at the surface; and (4) fish was either dead or unresponsive upon being returned to the water. By assuming that only fish that swam straight to depth, without obvious signs of stress, disorientation, or struggle, had the potential to survive the tagging process (fish in condition 1), we believe the potential mortality rate of tagged red snapper to be estimated conservatively.

Collection of tag returns and associated data.—Only tag returns collected from 22 March 1995 until 3 January 1997 were used in analyses in this study. Tag returns occurred in two ways. The first occurred when a previously tagged fish was recaptured at one of the nine tagging stations during research tagging trips, in which case TL and FL were measured, and the condition of both the fish and the tag were recorded. Then, the fish was either released at the site at which it was captured, or it was transported to another site for release. The second way in which a tag return occurred was when a fisher caught a tagged fish and called the phone number printed on the tag. When a tag number was reported by a fisher we attempted to obtain the tag number, the date and location of recapture, and whether the caller was a commercial or recreational fisher. Both TL and FL of the recaptured fish were obtained if the fisher kept the carcass.

Fishers frequently provided Loran C or GPS coordinates where they caught a tagged fish. Eighteen (23.4%) of the recaptures made by fishers, however, could not be used in movement analysis because of insufficient location data. Although location of recapture could not be determined from these 18 recaptures, enough information about each recapture was provided to allow estimation that all were recaptured between 1 and 20 km from their release site. When the location where a fish was recaptured was known, the location was plotted on a chart, and the distance and direction of movement from the site of release was estimated.

Statistical analyses.—Recaptures of fish released on reef S ($n = 13$) were excluded from all statistical analyses, because the volume of reef S was an order of magnitude larger than any other reef and may have biased the movement data. All other reefs were of similar size (Table 2). Also, for magnitude and direction of movement analyses, recaptures for which location of recapture could not be determined ($n = 18$) were excluded.

The categorical modeling procedure (CATMOD) in SAS was employed to determine which factors significantly affected the likelihood of movement (i.e., whether or not a tagged red snapper was recaptured at a site other than its release site) (SAS Institute, Inc., 1985). This procedure fits linear models on categorical data by using a weighted-least-squares method to minimize the residual error for the model. For this analysis, data were partitioned a priori into the following categories: movement: 1, fish recaptured at a site other than its release site; 2, fish recaptured at its release site; opal: 1, Opal stratum one—fish tagged and recaptured prior to 10/4/95; 2, Opal stratum two—fish tagged before and recaptured after 10/4/95 (= at liberty during Opal); 3, Opal stratum three—fish tagged and recaptured after 10/4/95; depth of reef (at release): 1, 21 m (sites NE, N, and NW); 2, 27 m (sites E, C, and W); 3, 32 m (sites SE, S, and SW); transport: 1, fish released at site of capture; 2, fish transported prior to release; days at liberty: 1, $\leq$ 120 days; 2, 121–240 days; 3, 241–360 days; 4, $\geq$ 360 days; TL at recapture: 1, $<$ 350 mm; 2, 351–450 mm; 3, $\geq$ 451 mm.

In this analysis the following hypotheses were tested: $H_{0,1}$, Opal had a significant effect on likelihood of movement; $H_{0,2}$, depth of reef had a significant effect on likelihood of movement; $H_{0,3}$, transport had a significant effect on likelihood of movement; $H_{0,4}$, days at liberty had a significant effect on likelihood movement; and $H_{0,5}$, TL at recapture had a significant effect on likelihood movement. In the likelihood of movement model, movement was the dependent variable, and Opal, depth of reef, transport, days at liberty, and TL at recapture were the independent variables.

To determine which factors had a significant effect on distance moved by recaptured fish, a forward stepwise procedure was used to build a linear regression model with ln(distance + 1) as the dependent variable (SAS Institute, Inc., 1985). In this analysis the following hy-

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TABLE 3. Number of red snapper tagged on 17 sampling trips.

Depth	Tagged before Opal		Tagged after Opal		Total
	Not transported	Transported	Not transported	Transported	
21 m	103	61	162	59	385
27 m	214	145	119	130	608
32 m	173	118	246	74	611
Total	490	324	527	263	1,604

potheses were tested: $H_{0,6}$, Opal had a significant effect on magnitude of movement; $H_{0,7}$, depth of reef had a significant effect on magnitude of movement; $H_{0,8}$, transport had a significant effect on magnitude of movement; $H_{0,9}$, days at liberty had a significant effect on magnitude of movement; and $H_{0,10}$, TL at recapture had a significant effect on magnitude of movement. The independent variables used to build the regression model were Opal, depth of reef, transport, days at liberty, and TL at recapture. The dependent variable distance was transformed by ln(distance + 1) because the raw data did not meet the assumptions of normality and heteroscedasticity.

Raleigh's test was employed to determine if the direction of red snapper movement was significantly different from random (Batschelet, 1981). For this test, uniform fishing effort in time and space around the site of release, and straight-line movement from release site to recapture site was assumed. To examine potential effects of Hurricane Opal on directional movement, data were stratified into the three Opal strata listed above. The following hypotheses were tested: $H_{0,11}$, direction of movement in Opal stratum one was not significantly different from random; $H_{0,12}$, direction of movement in Opal stratum two was not significantly different from random; and $H_{0,13}$, direction of movement in Opal stratum three was not significantly different from random.

RESULTS

During this study, 1,604 red snapper were tagged, with 1,017 released at the site of capture and 587 transported to another site and released (Table 3). Tagged red snapper had a mean TL (± SE) of 336 mm (± 1.84). Eighty-three percent of tagged fish were less than 400 mm TL (Fig. 2). Therefore, the majority of tagged snapper were estimated to be 3 yr old or less (Goodyear, 1995).

One hundred seventy-four recaptures were made of 167 tagged red snapper [i.e., seven recaptures were of fish recaptured for a second time (Table 4)]. Seventy-seven recaptures were returned by fishers, and 97 recaptures occurred during tagging trips. Of the 174 recaptures, 80% (n = 139) were of fish released at their capture site, and 20% (n = 35) were of fish that were transported prior to release. Thirty-nine percent (n = 54) of the recaptures of fish released at their capture site were recaptured at a site other than their release site, while 77% (n = 27) of the transported fish were recaptured at a site other than where they were released. Of the 97 recaptures made dur-

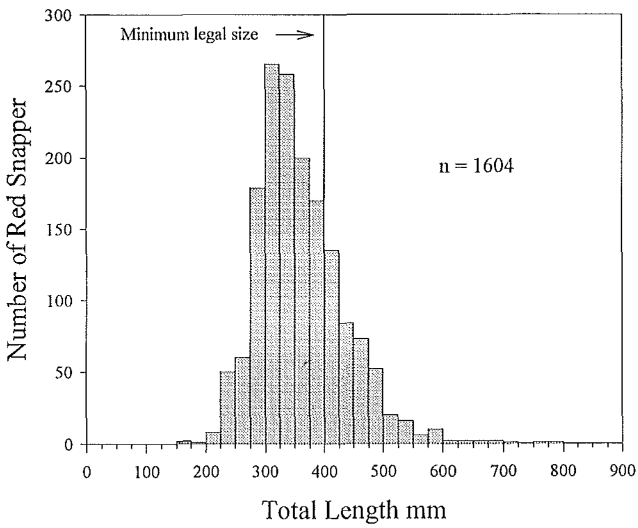

Fig. 2. Distribution of total length of red snapper tagged in this study.

TABLE 4. Individual red snapper that were recaptured twice. Note: none of these fish were transported from their site of tagging prior to release.

Tag number	Capture event	Date	Days at liberty	TL	Site of release
95-0008	Tagging	3/22/95	—	325	C
	First recapture	5/3/95	42	332	C
	Second recapture	7/1/96	424; 466 total	Unknown	9.5 km at 315° from C
95-0021	Tagging	3/22/95	—	335	C
	First recapture	5/3/95	123	340	C
	Second recapture	6/24/95	52; 175 total	Unknown	9.3 km at 225° from C
95-0075	Tagging	3/22/95	—	304	SE
	First recapture	9/14/95	176	367	C; 9.3 km at 135° from SE
	Second recapture	6/22/96	281; 457 total	Unknown	Unknown
95-0739	Tagging	9/13/95	—	271	SW
	First recapture	12/12/95	89	312	SW
	Second recapture	10/31/96	323; 412 total	377	SW
95-0862	Tagging	9/14/95	—	292	C
	First recapture	1/21/96	129	Unknown	Unknown
	Second recapture	6/20/96	150; 279 total	Unknown	Unknown
95-0879	Tagging	11/30/95	—	446	SE
	First recapture	3/26/96	119	464	SE
	Second recapture	5/1/96	64; 183 total	475	SE
95-0995	Tagging	12/12/95	—	384	N
	First recapture	8/7/96	238	433	N
	Second recapture	12/2/96	117; 355 total	465	N

ing tagging trips, 91 were recaptured at their site of release, while 6 recaptures were made at other reef sites.

Before Hurricane Opal occurred, recaptured fish moved little, with 77% of recaptures moving less than 1 km (Table 5). Soon after the passing of Opal, however, movement on much larger spatial scales was observed (Fig. 3). The majority (65%) of fish that moved between 1 and 20 km from their site of release were at liberty during Opal, and virtually all fish (95%) that moved greater than 20 km were potentially affected by Opal (Table 5). Moreover, most recaptures of Opal stratum one fish (77%) and Opal stratum three fish (80%) were recaptured at the site where they were released.

The maximum distance moved and days at liberty by recaptures in this study were high relative to previous studies. The longest distance moved by a tagged red snapper was approximately 265 km to the east by a fish that was at liberty for 374 d (Fig. 3). The longest time a recapture was at liberty was 622 d, while mean days at liberty (± SE) for all recaptures was 207.4 d (± 10.5). The fish which was at liberty for 622 d was recaptured approximately 11 km from its release site.

TABLE 5. Distance moved from release site by tagged red snapper.

Distance from release site (km)	Tagged and recaptured before Opal	Tagged before and recaptured after Opal	Tagged and recaptured after Opal	Total recaptures
<1	24	17	55	96
1–20	6	37	14	57
>20	1	20	0	21
Total	31	74	69	174

Estimation of tagging mortality.—Trends in condition at release followed two patterns. Transported fish were in worse condition at release than fish not transported, and fish caught on deeper stations were in worse condition at release than those caught on shallower stations (Table 6). Of the 167 fish that were recaptured in this study (seven of which were recaptured twice), all but six were released in condition 1 at the time of tagging.

The percentage of fish released in conditions 2, 3, and 4 probably represents a conservative estimate of potential release mortality of tagged fish, because it is likely that some tagged fish that were released in condition 1 died as a result of the tagging process. However, at least some fish in conditions 2, 3, and 4 survived to be recaptured. Based on this rationale, tagging mortality was estimated to be 21% for transported fish and 10% for fish not

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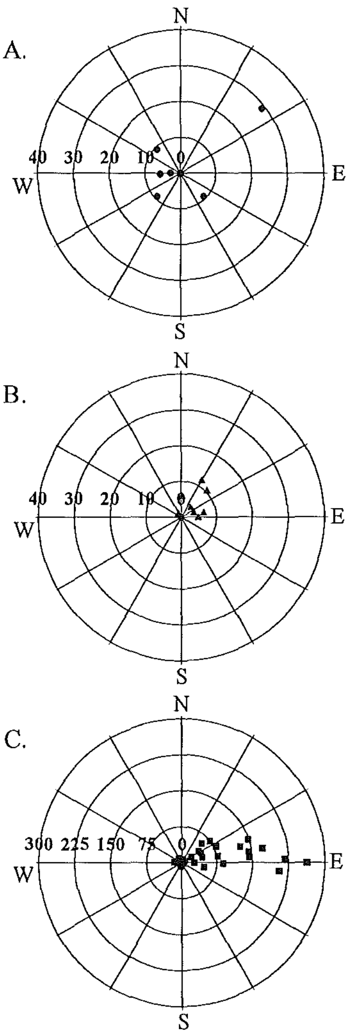

Fig. 3. Polar diagrams of red snapper movement. A. Opal stratum one; radius = 40 km, 24 recaptures at the origin. B. Opal stratum three; radius = 40 km, 44 recaptures at the origin. C. Opal stratum two; radius = 300 km, 14 recaptures at the origin.

transported (Table 6) (Patterson et al., unpubl.).

Estimation of growth.—Total length of 99 of the 167 recaptured red snapper was measured at the time of recapture. (Note: to meet the assumption of independence, only the second recapture of fish recaptured twice was used in all statistical analyses.) Growth rate of these fish was estimated by the slope of the regression of their change in TL versus days at liberty (Fig. 4). The regression was statistically significant ($P < 0.001$), with a slope of 0.254 mm d^{-1}. Therefore, the estimated growth rate of tagged red snapper was 0.254 mm d^{-1}, or 93 mm yr^{-1}, which was then used to calculate the expected TL of recaptures for which TL at time of recapture was not known. In the statistical analyses that follow, TL at time of recapture was known for 99 recaptures and estimated for the other 68 fish (Fig. 5).

Estimation of tag loss.—Tag loss was estimated as the percentage of tagged fish recaptured on the tagging sites that did not have the external portion of their tags present. To estimate tag loss, it was assumed that all tagged fish that were recaptured on the tagging site were recognized as tagged fish, regardless of whether the external portion of a tag was present. Recaptures that did not have the external portion of their tag present were easily detected via a tagging scar, and often times a small portion of monofilament extended from the scar. If the external portion of a fish's tag was missing, the tag was replaced.

Fish at liberty less than 120 d lost only 4% of their external tags. Ten percent of fish at liberty between 120 and 240 d were missing the external portion of their tags. For fish at liberty between 240 and 360 d 20% were missing the external portion of their tags. And, for fish at liberty longer than 360 d, 33% lost the external portion of their tags.

TABLE 6. Percentage (n of total number tagged) of red snapper released in condition 1.

Transportation	Depth of release site			Overall in condition 1
	21 m	27 m	32 m	
Fish transported	91% (110 of 120)	75% (206 of 275)	75% (145 of 192)	79% (461 of 587)
Fish not transported	91% (244 of 265)	91% (303 of 333)	89% (373 of 419)	90% (920 of 1,017)
Mean in condition 1 at each depth	92% (354 of 385)	84% (509 of 608)	85% (518 of 611)	86% (1,381 of 1,604)

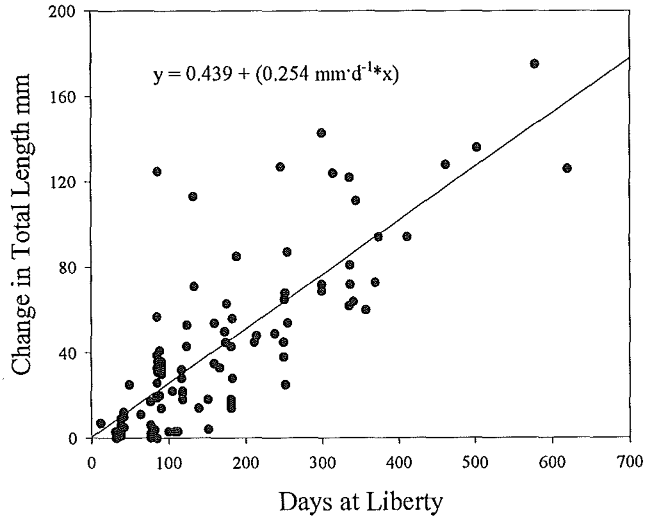

Fig. 4. Regression of change in total length versus days at liberty for recaptured red snapper with known total length at time of recapture (n = 99; R^2 = 0.65).

Likelihood of movement.—The CATMOD procedure in SAS was used to compute a linear model that fit the likelihood of movement by tagged red snapper as a function of the independent variables Opal, depth of release, transport, days at liberty, and TL at recapture. The goodness-of-fit test for the model, which compared the model in this analysis to an unrestricted model, was significant (P = 0.008). However, only two independent variables were significant in the model. These were Opal (P < 0.001) and depth of reef (P = 0.014). Multiple comparison contrasts between different levels of storm and depth of reef were made to test which levels of each factor were significantly different. For the storm effect, fish in Opal stratum two had a significantly higher likelihood of movement than fish in Opal stratum one (P < 0.001), and fish in Opal stratum three (P < 0.001). For the depth of reef effect, the only significant contrast was between fish released at shallow stratum stations and fish released at deep stratum stations (P < 0.001). Fish that were released at shallow stratum stations were less likely to move than fish released at deep stratum stations.

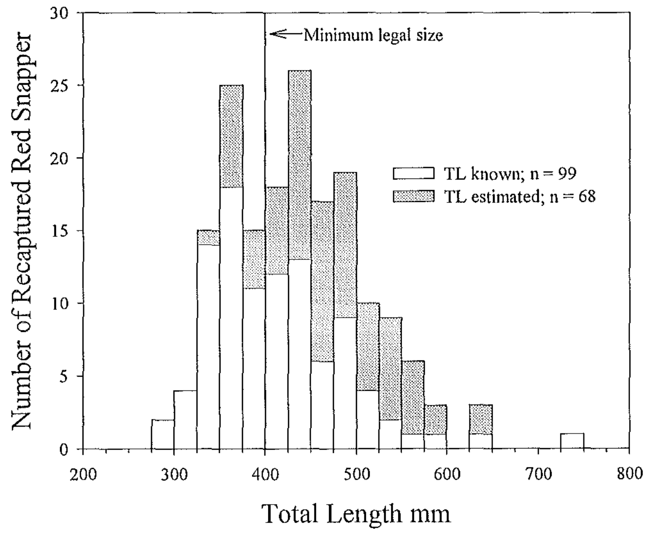

Fig. 5. Distribution of total length at time of recapture for 167 recaptured red snapper.

To determine what factors contributed to likelihood of movement when the effect of Opal was removed from the model, the CATMOD procedure was run without Opal stratum two fish; the truncated data set contained 96 recaptures. The variable storm was left in the model to test if fish in Opal stratum three were more likely to move than fish in Opal stratum one (i.e., to test whether Opal may have altered the ability of the reefs to hold fish). The only variable that was significant when modeling the truncated data was transport (P = 0.002). Fish that were transported to another reef site for release had a higher likelihood of movement than fish not transported.

Magnitude of movement.—The linear regression model with ln(distance + 1) as the dependent variable, which resulted from the forward stepwise modeling procedure only included the variables storm and depth of reef. The model was significant ($P < 0.001$) but explained less than half of the variance in ln(distance + 1) ($R^2 = 0.38$). Storm effect explained 32% of the variance in ln(distance + 1), while depth of reef explained only 6% of the variance in ln(distance + 1). The Student–Newman–Keuls multiple comparison procedure was run on both Opal effect and depth of reef effect to test which levels of each factor were significantly different ($P < 0.05$) with respect to magnitude of movement. For the storm effect, distanced moved by Opal stratum two fish [mean (± SE) = 32.6 km (± 6.81)] was significantly different than distance moved by Opal stratum one fish [mean (± SE) = 2.5 km (± 1.10)] and Opal stratum three fish [mean (± SE) = 1.7 km (± 0.43)]. For the depth of reef effect, movement of fish that were released at the mid-depth stratum sites [mean (± SE) = 31.1 km (± 8.83)] was significantly different than movement of fish released at shallow stratum sites [mean (± SE) = 11.8 km (± 5.45)], and fish released at deep-stratum sites [mean (± SE) = 5.4 km (± 2.41)].

When fish that were at liberty during Opal were excluded from the magnitude of movement analysis, the only factor that was significant was transport ($P < 0.001$). This result was expected, because transport was also the only significant factor in the likelihood of movement analysis on the truncated data set. In the truncated data set, fish that were transported before release moved further [mean (± SE) = 5.1 km (± 2.44)] than fish that were not transported [mean (± SE) = 0.9 km (± 0.29)].

Directional movement.—Eighty-three recaptures were made at sites other than where they were released. Of these, five were recaptured within 1 km of their release site, two on tagging trips and three by fishers. Once fish released on site S and fish whose location of recapture was unknown were excluded from the data set, sample sizes used in directional movement analysis for each Opal stratum were 30 for stratum one, 54 for stratum two, and 52 for stratum three. Mean vectors of movement for each Opal stratum were 0.53 km at an angle of 54.0° for stratum one, 2.3 km at an angle of 47.4° for stratum three, and 27.2 km at an angle of 11.6° for stratum two (an angle of 0° is due east) (Fig. 5). For fish in Opal stratum one, direction of movement was not significantly different from random ($P \gg 0.10$). For fish in Opal strata two and three, however, direction of movement was significantly different from random ($P < 0.01$ for both).

Discussion

Tagging mortality.—Estimated tagging mortality was 10% for fish released over the site where they were caught and 21% for fish that were transported to another site for release; these estimates were within the range of estimates from a previous study (Render and Wilson, 1994). Render and Wilson (1994) examined tagging mortality of red snapper caught adjacent to a Louisiana oil rig located in 21 m of water. Some fish were released into large-volume hoop nets that were moored on the oil rig, while others were transported to an aquarium in New Orleans for longer term observation. The authors reported that there was no statistical difference in the mortality rates of tagged versus untagged, gas bladder deflation versus no deflation, and tagging with deflation versus tagging without deflation treatment groups. For fish released into hoop nets, mortality estimates ranged from approximately 34% in winter to 15% in summer. Tagged fish that were transported to the aquarium were held between 30 and 40 d and had mortality rates of 18% for tagged fish and 20% for tagged and deflated fish. Render and Wilson (1994) also reported that most of the mortality suffered by tagged fish occurred early in the time period during which fish were held.

Growth of tagged fish.—The estimated growth rate of tagged fish was 0.254 mm d^{-1}, which was within the range of Gulf red snapper growth rate estimates reported in the literature (Szedlmayer and Shipp, 1994; reviewed in

Goodyear, 1995). Szedlmayer and Shipp (1994) estimated that tagged red snapper grew at a rate of 0.22 mm d^{-1}, while their estimate of growth rate derived from otolith-aged fish was 0.27 mm d^{-1}. Goodyear (1995) pooled data from several sources to estimate growth of Gulf red snapper, with the mean growth rate for fish under 10 yr old estimated to be 0.30 mm d^{-1}.

Effects of transportation.—Of the recaptures made of fish that were released over their site of capture, the majority (61%) apparently remained at their site of release. The converse was true of fish that were transported prior to release, as 77% were recaptured at a site other than where they were released. In fact, when fish that were at liberty during Opal were removed from the data set, the only significant factor in the likelihood of movement analysis was transport. This suggests that transporting fish increased the probability of movement away from site of release. It is not known if transported fish initially swam down to the reef over which they were released, then immediately swam away, or if they slowly moved away over time. One can speculate that every artificial reef has a finite carrying capacity, whereby the release of up to 25 new individuals may have exceeded capacity, and the need to reduce biomass may have resulted in a higher likelihood of movement by transported fish. Alternatively, red snapper are gregarious and territorial in the laboratory, suggesting that it may have been difficult for the potentially stressed transported snapper to establish themselves in a new location.

Tag loss effects.—Tagged fish had a higher probability of tag loss as days at liberty increased. While we are confident that all tagged fish that were recaptured at tagging sites were recognized as such, we assume that tags of some fish recaptured by fishers went unrecognized. Both tag loss and this latter assumption have important implications.

Fish that were transported prior to release were almost twice as likely to be recaptured somewhere other than their site of release, which means they had a much higher likelihood of being recaptured by a recreational or commercial fisher. Moreover, transported fish experienced only half of the recapture rate of fish not transported, even after accounting for differences in tagging mortality. This disparity could be explained by higher sampling effort on tagging sites than the fishing effort on reefs to which tagged fish moved. However, Watterson (1997) estimated that the annual fishing mortality rate on tagged fish at reefs other than the tagging sites was nearly four times higher than at the tagging sites (if all recaptures made at tagging sites had been harvested).

A second explanation for the lower recapture rate of transported fish actually may be attributable to differences in reporting rates. Some fish, transported or otherwise, that were recaptured by recreational or commercial fishers simply may not have been reported. There were only a handful of recaptures returned by commercial fishers, which implies that they either did not intercept as many of the tagged fish as recreational fishers or they did not report recaptures they made. If commercial fishers were as likely to recapture a tagged fish as recreational fishers, their lack of reporting could have resulted in significant underestimation of recapture rate for fish that were recaptured at sites other than the tagging sites. This probably was compounded by tag loss, the third potential explanation for the lower recapture rate of transported fish. Several recreational fishers reported recaptures of fish that were missing the external portion of their tags. Many times they found the anchor portion of a tag while cleaning their catch; however, commercial fishers typically sell their catch whole and thus were not likely to find an anchor while cleaning a tagged fish.

The last factor that potentially could have affected the reporting rate of fishers is the minimum size at which red snapper may be legally harvested in the Gulf. The minimum size for Gulf red snapper is 15 inches (381 mm); over 80% of the fish tagged in this study were under this size limit. Most recaptured red snapper had grown through the size limit or were estimated as having done so. However, over a third of recaptures were of fish less than the minimum legal size. A few of these fish were recaptures made by recreational fishers (the growth function may have underestimated the size at recapture of these fish), but over 90% of the undersized fish were made at tagging sites. If recreational and commercial fishers caught tagged fish that were shorter than the legal size limit and did not report the tag numbers, this could have biased our results toward the appearance that larger fish were more likely to move. However, because size of fish at recapture was not a significant factor in any statistical analysis, we do not feel that this potential error strongly biased these results.

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Movement of tagged red snapper.—In both the likelihood of movement and magnitude of movement analyses, storm effect and depth of release effect were the only factors that were significant, with storm effect explaining more of the variance in the data. A priori, we expected the same factors to be significant in both analyses. It should follow that if one group of fish is more likely to move than another, its members will move on average further, unless there are a few outliers in the second group that move great distances. Despite the fact that likelihood and magnitude of movement appear to be linked, the regression used to describe magnitude of movement of the full data set does a poor job of fitting the transformed distance data. Therefore, there is a substantial amount of variance in the movement data that remains unexplained.

The mean vector of movement for all three Opal strata was to the east or east-northeast; however, direction of movement was significantly different from random only in Opal strata two and three. There are several possible explanations for the similarities in the mean directions moved by fish in all three Opal strata. It is possible that direction of movement was simply a reflection of fishing effort. There appears to be more fishing effort off Alabama and northwest Florida than off Mississippi and southeast Louisiana (Goodyear, 1995; Schirripa and Legault, 1997), however, this may be because there is more suitable red snapper habitat in these areas (whether natural or artificial). A second possible explanation is that there is a natural tendency for red snapper from offshore Alabama to move eastward, and the magnitude of this movement was magnified by Opal. Beaumariage (1969) summarized the results of a 4-yr tagging study of red snapper off northwest Florida, and the mean vector of movement for fish that moved more than 5 km from their release site was to the east-southeast. This adds support for the argument that there is a natural tendency for red snapper in the north-central Gulf to move eastward.

From the fishery-dependent data (Goodyear, 1995; Schirripa and Legault, 1997), it appears that the center of the Gulf red snapper population is off southwest Louisiana, with a smaller center of abundance off Alabama. For many years the Gulf red snapper stock has been severely overfished [current spawning potential ratio estimates for the stock are less than 10% (Schirripa and Legault, 1997)], but due to management efforts in the 1990s the stock has begun to recover. As the stock rebuilds, young fish are beginning to occur in greater numbers off northwest Florida, an area that had become commercially extinct, but which historically supported a substantial red snapper fishery (Camber, 1955; Carpenter, 1965; Goodyear, 1995; Schirripa and Legault, 1997). It is possible that red snapper from a center of abundance off Alabama are moving eastward and recruiting to waters off northwest Florida. Again, Opal may have simply amplified movement that was already occurring.

Previous tagging studies of Gulf red snapper have generally concluded that these reef fish demonstrate high site fidelity. Fable (1980) tagged 293 red snapper at six different locations off south Texas in the late 1970s. Of his 17 returns, only one fish was recaptured at a site other than where it was released, and only moved 5 km. From 1962 to 1965, Beaumariage (1969) and his colleagues at the Florida Department of Natural Resources tagged 1,126 off northwest Florida. They recaptured 28% of the fish they tagged, over 90% of which were recaptured within 5 km of the site where they were released. Of the fish that moved significant distances from their site of release, most (63%) were recaptured in the summer of 1966, and the mean vector of movement was to the south-southeast. Of these fish, the longest movement observed was 279 km for a fish that was at liberty for 424 d. The longest time a fish was at liberty during their study was 1,163 d.

Szedlmayer and Shipp (1994) reported that red snapper tagged on artificial reefs off Alabama showed strong site fidelity and implied that the strength of site fidelity demonstrated by this species may give rise to localized population demographics. They tagged 1,155 red snapper in the early 1990s and recovered 146 fish. Of their recaptures, however, the authors only used 37 tag returns in movement analysis. They reported that 76% of these fish were recaptured within 2 km of their release site, while five fish were recaptured greater than 10 km from their site of release; maximum time at liberty was 430 d. The recaptures that the authors excluded from movement analysis were ones for which they felt fishers gave insufficient data on location of recapture (Stephen Szedlmayer, pers. comm.). It is possible that by excluding 75% of their recaptures from movement analysis, the authors underestimated the overall magnitude of movement by the tagged population.

In this study, red snapper generally displayed strong site fidelity, as nearly 80% of the recaptures that were not at liberty during Opal were recaptured at their site of release. Fish that were at liberty during Opal had a much higher likelihood of moving away from their release site; however, 20% of recaptured fish not at liberty during Opal were also recaptured at a site other than where they were released. In all likelihood, this is probably an underestimate of the true number of fish that were not at liberty during Opal that moved away from their release site. Goodyear (1995) hypothesized that slow diffusion of adult red snapper away from centers of abundance in the Gulf may provide sufficient gene flow to prevent genetic divergence in the stock. Although the relatively small, young fish we tagged generally exhibited strong site fidelity, movement on a scale that may be sufficient to preclude genetic divergence in Gulf red snapper was observed. Moreover, if larger, older fish typically move greater distances, larval drift may not be the only explanation for genetic homogeneity in this stock.

Fish that were at liberty during Opal did not show strong site fidelity. The average distance moved by fish at liberty during Opal was 32.6 km, with eight fish moving over 100 km and three fish moving over 200 km. This is by far the most movement observed in northern Gulf red snapper, and we suggest that the likelihood and magnitude of movement is the result of Hurricane Opal. Other studies have also suggested that storms may impact reef fish movement. Bell and Hall (1994) indicated that Hurricane Hugo altered the distribution of gag, *Mycteroperca microlepis*, and scamp, *Mycteroperca phenax*, off South Carolina. Moseley (1966) implied that red snapper off Texas demonstrated onshore and offshore movements in response to passing cold fronts. Interestingly, in 1966, when Beaumariage (1969) observed the largest magnitude of movement in tagged red snapper off northwest Florida, Hurricane Alma passed through his tagging area in the northeastern Gulf and came ashore at Cape San Blas, Florida.

Clearly, the scale of movement by fish that were at liberty during Opal is sufficient to promote genetic mixing of Gulf red snapper, especially when one considers the frequency of hurricanes in the Gulf. For a species that can live over 50 yr, individuals are likely to be affected by several hurricanes over the course of their lives. Gold et al. (1997) speculated that the observed genetic homogeneity in mtDNA haplotype frequencies in northern Gulf red snapper may reflect historic stock distributions, such as during Pleistocene glaciation, and may not reflect present-day stock mixing dynamics. They offered this reasoning because observed movement in adult Gulf red snapper did not seem sufficient to promote stock mixing, and the hypothesis that stock mixing occurs in the plankton remains untested. We believe that this caveat to the conclusion that Gulf red snapper constitute a single genetic stock may be unnecessary (Gold et al., 1997), as we have demonstrated for the first time that adult red snapper at times do move distances sufficient to facilitate stock mixing.

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Literature Cited

BATSCHELET, E. 1981. Circular statistics in biology. Academic Press. New York.

BEAUMARIAGE, D. S. 1964. Returns from the 1963 Schlitz tagging program. Florida Board of Conservation Technical Series No. 43:1–34.

———. 1969. Returns from the 1965 Schlitz tagging program including a cumulative analysis of previous results. Florida Department of Natural Resources Technical Series No. 59:1–38.

———, AND L. H. BULLOCK. 1976. Biological research on snappers and groupers as related to fishery management requirements. *In* Proceedings: colloquium on snapper–grouper fishery resources of the western central Atlantic Ocean. H. R. Bullis, Jr. and A. C. Jones (eds.) Florida Sea Grant Colloquium Report 17. 86–94.

———, AND A. C. WITTICH. 1966. Returns from the 1964 Schlitz tagging program. Florida Board of Conservation Technical Series No. 47:1–51.

BELL, M. AND J. W. HALL. 1994. Effects of Hurricane Hugo on South Carolina's marine artificial reefs. Bull. Mar. Sci. 55(2–3):836–847.

BRADLEY, E., AND C. E. BRYAN. 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970–1974. Proc. Gulf Carib. Fish. Inst. 27:77–106.

CAMBER, C. I. 1955. A survey of the red snapper fishery of the Gulf of Mexico, with special reference to the Campeche Banks. Florida Board of Conservation Technical Series No. 12:1–64.

CAMPER, J. D., R. C. BARBER, L. R. RICHARDSON, AND J. R. GOLD. 1993. Mitochondrial DNA variation among red snapper (*Lutjanus campechanus*) from

DOI: 10.18785/goms.1601.13

the Gulf of Mexico. Mol. Mar. Biol. Biotechnol. 2(3):154–161.

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.

CHAPMAN, R. W., S. A. BORTONE, AND C. M. WOODLEY. 1995. A molecular approach to stock identification and recruitment patterns in red snapper, *Lutjanus campechanus*. Final report for Cooperative Agreement NA17FF0379-03 Marine Fisheries Initiative (MARFIN) Program. Institute for Coastal and Estuarine Research, University of West Florida, Pensacola, Florida 32514, and Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412.

FABLE, W. A., JR. 1980. Tagging studies of red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) off the south Texas coast. Contrb. Mar. Sci. 23:115–121.

GOLD, J. R., F. SUN, AND L. R. RICHARDSON. 1997. Population structure of red snapper from the Gulf of Mexico as inferred from analysis of mitochondrial DNA. Trans. Am. Fish. Soc. 126:386–396.

GOODYEAR, C. P. 1995. Red snapper in U.S. waters of the Gulf of Mexico. NMFS, SEFSC, Miami Laboratory, Miami MIA-95/96-05.

MOE, M. A., JR. 1963. A survey of offshore fishing in Florida. Florida Board of Conservation Technical Series No. 4:1–117.

———. 1996. Tagging fishes in Florida offshore waters. Florida Board of Conservation Technical Series No. 49:1–40.

MOSELEY, F. N. 1966. Biology of the red snapper, *Lutjanus* aya Bloch, of the northwestern Gulf of Mexico. Pub. Inst. Mar. Sci Tex. 11:90–101.

RENDER, J. H., AND C. A. WILSON. 1994. Hook-and-line mortality of caught and released red snapper around oil gas platform structural habitat. Bull. Mar. Sci. 55:1106–1111.

SAS. 1985. Software Package: Statistics Version 6.03. SAS Institute Inc., Box 8000, Cary, NC 27511-8000.

SCHIRRIPA, M. J., AND C. M. LEGAULT. 1997. Status of the red snapper stock in U.S. waters of the Gulf of Mexico. NMFS, SEFSC, Miami Laboratory, Miami. MIA-97/98-05.

SZEDLMAYER, S. T. 1997. Ultrasonic telemetry of red snapper, *Lutjanus campechanus*, at artificial reef sites in the northeast Gulf of Mexico. Copiea 4: 846–850.

———, AND R. L. SHIPP. 1994. Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the northeastern Gulf of Mexico. Bull. Mar. Sci. 55(2–3):887–896.

TOPP, R. W. 1963. The tagging of fishes in Florida 1962 program. Florida Board of Conservation Professional Papers Series No. 5:1–76.

———. 1964. Residence habits of the red snapper. Underwater Nat. 2(3):15–17.

WATTERSON, J. C. 1997. Estimates of site fidelity and short term movements of red snapper (*Lutjanus campechanus*) based upon mark/recapture on north central Gulf of Mexico artificial reefs. Master's Thesis, University of South Alabama, Mobile, AL.

DEPARTMENT OF MARINE SCIENCES, LSCB 25, UNIVERSITY OF SOUTH ALABAMA, MOBILE, ALABAMA 36688-0002. (WFP) PRESENT ADDRESS: DIVISION OF MARINE FISHERIES, NORTH CAROLINA DEPARTMENT OF ENVIRONMENT AND NATURAL RESOURCES, MOREHEAD CITY, NORTH CAROLINA 28557. Send reprint requests to WFP. Data accepted: August 31, 1998.