THE USE OF ULTRASONIC TELEMETRY TO ESTIMATE RESIDENCY, MOVEMENT PATTERNS, AND MORTALITY OF RED SNAPPER, *LUTJANUS CAMPECHANUS*

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A Dissertation
Submitted to
the Graduate Faculty of
Auburn University
in Partial Fulfillment of the
Requirements for the
Degree of
Doctor of Philosophy

Auburn, Alabama
August 10, 2009

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DISSERTATION ABSTRACT

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Doctor of Philosophy, August 10, 2009
(M.S., California State University Long Beach, 2003)
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171 Typed Pages

Directed by Stephen T. Szedlmayer

Site fidelity, emigration, and mortality were estimated from telemetry for large (500 – 860 mm TL) red snapper *Lutjanus campechanus* ($N = 87$) from four artificial and one natural reef in the northeastern Gulf of Mexico. From December 2005 to December 2008 we used arrays of five ultrasonic receivers at each site. Each array consisted of one receiver at the center with four receivers placed 420 or 1100 m north, south, east, and west of center. As of October 2008, 21% were caught, 34% emigrated, 12% died, 29% are still present, and 4% uncertain. Estimates of total mortality (Z) ranged from 0.54 to

0.58, fishing mortality (*F*) from 0.38 to 0.45, and natural mortality (*M*) from 0.11 to 0.17 using various methods. Median residence time was 572 d, and residence time ranged from 1 to 829 d, with 68% of fish staying at least one year at the site and 80% were present for at least 200 d. Some fish did not show constant residency to one site. Some fish showed directed movements to other sites (~8 km away), and some returned after emigrating. A local regression procedure showed detections at the center receiver were significantly greater during the day than at night, while detections on outside receivers were greater around sunset. Red snapper (*N* = 6) manually tracked for continuous 24-h periods stayed near (< 60 m) the artificial reef (75% of locations within 20 m of the structure), and were significantly further away at night (mean = 19.0 m) than day (mean = 12.2). These patterns suggested that fish tend to move away from the reef at night. Home range size and mean distance from the reef were significantly affected by fish size (range = 550 to 710 mm); larger fish had a greater mean distance and home range size. Estimated mortality rates were similar to past estimates while residence time was longer than any previous estimate. The short-term patterns of fish staying close to structure, and the long-term residency of these fish to the sites indicated that these artificial reef structures provided suitable habitat for red snapper.

ACKNOWLEDGMENTS

I thank S. Beyer, S. Kirkland, D. Miller, D. Nadeau, P. Mudrak, C. Simmons, and T. Syc for long hours in the field. I thank S. Szedlmayer for his great advice, guidance, and sense of humor throughout my research at Auburn University, and Y. Brady, R. Lishak, D. Swann and J. Armbruster for critical review of this dissertation. I also thank NOAA-MARFIN (Grant #NA06NMF4330054), Alabama Marine Resources Division, and Mississippi-Alabama Sea Grant Consortium for funding this project. Finally, I would like to thank my family and friends for making this all possible with their love and support.

Journal format used: Transactions of the American Fisheries Society.

Computer software used: Arcview GIS 3.2A, Corel WordPerfect X4, Microsoft Office Excel 2003, SAS System for Windows V9.1, and Sigma Plot 11.

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CHAPTER 1

THE USE OF ULTRASONIC TELEMETRY TO ESTIMATE MORTALITY RATES OF RED SNAPPER *LUTJANUS CAMPECHANUS*

Abstract.—Mortality rates for red snapper *Lutjanus campechanus* (*N* = 87) were estimated from telemetry from December 2005 to August 2008 in the northeastern Gulf of Mexico. At five separate sites (one natural and four artificial habitats) an array of five receivers was deployed with one receiver at the center (near the reef) and four receivers placed 420 or 1100 m north, south, east, and west of center. These arrays enabled the direct estimation of fishing mortality, natural mortality, and emigration of red snapper acoustically tagged at the sites. Out of the 70 fish that remained at the sites for the 7-d recovery period, 19 were caught, 9 died naturally, and 16 emigrated from the 2-km radius study sites. The Kaplan-Meier (K-M) and staggered entry K-M methods were used to estimate survival from different mortality events, and survival was converted to instantaneous mortality rates. Ricker methods were also used to estimate mortality rates. Estimates of total mortality (*Z*) ranged from 0.54 to 0.58, fishing mortality (*F*) from 0.38 to 0.45, and natural mortality (*M*) from 0.11 to 0.17. These mortality rates were similar to past estimates and provide the first direct estimates of mortality rates for red snapper.

INTRODUCTION

Historically, red snapper *Lutjanus campechanus* have supported an important commercial fishery in the Gulf of Mexico (GOM), and continue to be one of the most sought after recreational fish in the northern GOM (Camber 1955; Stanley and Wilson 1989). Red snapper have been found over natural rock reef habitats in the GOM (Camber 1955; Moseley 1966; Beaumariage 1969; Bradley and Bryan 1975; Fable 1980), but are also closely associated with artificial habitats (Szedlmayer and Shipp 1994; Szedlmayer 1997; Watterson et al. 1998; Patterson et al. 2001; Peabody 2004; Szedlmayer and Schroepfer 2005). Although approximately 14,000 of these artificial habitats have been built in the northern GOM (Minton and Heath 1998), possibly enhancing available habitat (Gallaway et al. 2009), the snapper fishery is still considered overfished (Schirripa and Legault 1999; SEDAR 2005). In order to rebuild red snapper stocks, the National Marine Fisheries Service has recently set an objective of rebuilding stock biomass to a maximum sustainable yield (MSY = 25.4 million pounds) by 2032, which may be accomplished with an instantaneous fishing mortality rate (F) of Fmsy = $F_{\mathrm{SPR}\ 26\%}$ (SPR = spawning potential ratio; DEIS 2006; SEDAR 2005). This objective is based on a conservative assumption of instantaneous natural mortality (M) equal to 0.10/year; however, if M is actually higher, the goal of MSY may be achieved in a shorter period of time (Goodyear 1995; Schirripa and Legault 1999; Slipke and Maceina 2005). Therefore, to allow for an appropriate fishing level for red snapper in the northern GOM, it is important to obtain an accurate estimate of M.

The red snapper fishery has continued for well over a century, and like most exploited fish stocks, the level of M for snapper in the Gulf is not well defined (Camber 1955; Schirripa and Legault 1999). Total mortality (Z) has been obtained for red snapper from fishery independent catch curve analysis (Gitschlag et al. 2003; Szedlmayer 2007); however, the separation of Z into its components of M and F has been difficult. Estimates of M for red snapper have been primarily derived from life history parameter equations based on maximum age, K, and water temperature, with estimates of M for red snapper ranging from 0.02 to 0.40, with 95% confidence intervals from 0.02 to 1.0 (Alverson and Carney 1975; Pauly 1980; Nelson and Manooch 1982; Hoenig 1983; Goodyear 1995; Schirripa and Legault 1999). The presently applied value of M (0.10) is based on maximum ages of red snapper around 40 to 50 years (Hoenig 1983; Szedlmayer and Shipp 1994; Schirripa and Legault 1999; Wilson and Nieland 2001; SEDAR 2005). This value of M (0.10) is conservative when compared to estimates of M based on other life history parameters. Increases in M (e.g., from 0.10 to 0.35) used in the red snapper fishery assessment could show that an $F = 0.19$ would sustain an SPR above 21%, and current levels of F may be at this level (Slipke and Maceina 2005; Szedlmayer 2007). This uncertainty in M has lead to cautious management practices and severe reductions in fishery quotas (Hood et al. 2007). Despite its critical importance in population assessment, no direct measures of natural mortality presently exist for red snapper.

Recent advances in telemetry systems, such as continuous automated monitoring, long-life transmitters, and long distance detection, have allowed researchers to directly estimate natural and fishing mortality in both fresh and saltwater environments (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Pine et al. 2003; Pollock et al. 2004; Young and Isely 2004; Starr et al. 2005). With these advances in technology, estimates of mortality are possible for species like red snapper that inhabit large open water systems. In this study, strategic placement of remote telemetry receivers allowed separation of total declines in tagged fish into its component parts of emigration, natural mortality, and fishing mortality.

METHODS

Study area.—The study sites were located 20 to 30 km south of Mobile Bay, Alabama, USA, an area that includes numerous artificial habitats (> 10,000) and a few natural rock-reef habitats (Schroeder et al. 1988; Minton and Heath 1998). Red snapper were tagged on one natural and four artificial habitats. Artificial habitats included a pipeline covered with a concrete mat (A1), a 15-m sunken barge (A2), a 4.4 x 1.3 x 1.2 m steel metal cage (A3), and a M-60 army tank (A4). The natural habitat (N1) was composed of a 20-m long drowned river bed (~1 m high, ~5 m apart), with undercut banks lined with tree stumps (Figure 1-1). The depths of the sites ranged from 20 to 30 m. These sites were a mix of public (published latitude longitude) and private locations (Figure 1-1).

Fish tagging.—Large red snapper (> 500 mm total length [TL]) were captured at the selected habitats via hook and line. Tagging procedures followed Szedlmayer and Schroepfer (2005). Fish were brought on board the research vessel, placed in a 70-L container of seawater containing MS-222 (150 mg MS-222/L seawater), and quickly anesthetized to level 4 (Summerfelt & Smith 1990). Once sedated, the fish were temporarily removed from the anesthetic to obtain weights and lengths. To implant the ultrasonic transmitter, a small (18 mm) vertical incision was made into the peritoneal cavity with a No. 11 scalpel 2 cm lateral to the ventral midline, the transmitter implanted, and then sutured with plain gut suture (Ethicon, no. 2, 3.5 metric). Also, an internal anchor tag (Floy) was inserted into the incision before it was sutured. Sterile surgical methods and betadine were used throughout the procedure. After surgery, the fish were released after a short, (~1 min) period of recovery at the surface (when fin and gill movements were observed). Fish were released at the capture site by lowering fish to the bottom with weighted line with an inverted barbless hook that was attached to the fish's lower jaw. Upon retrieval of the weighted line the fish was released at depth near the reef site.

Two types of transmitters were used for this study. Individually coded Vemco transmitters (V16-6L-R64K; code intervals: 20 to 69 s, 16 x 94 mm, battery life: 6 years) were used at sites with Vemco VR2 receivers, and Sonotronics transmitters (CT-05-48; continuous, 16 x 79 mm, battery life: 4 years) were used at site A4 where Sonotronics SUR-1 receivers were deployed. Maximum detection ranges were 1600 m for Vemco and 600 m for Sonotronics transmitters.

Continuous remote monitoring.—An underwater acoustic receiver array was deployed at each site that included five separate omni-directional receivers (Vemco VR2 or Sonotronics SUR) moored near the bottom (~5 m). For each array, one receiver was located at the release site (center [C]) and the other four were placed at 1100 m (VR2) or 420 m (SUR) to the north (N), south (S), east (E), and west (W) of the center (Figure 1-2). Receivers placed at 1100 m (or 420) away from the center receiver were predicted to result in complete detection of the fish within a ~2 km (or 1-km) radius of the release site

(Szedlmayer and Schroepfer 2005). All receivers were coated with a copper-based antifouling paint to prevent possible signal occlusion due to biofouling (Heupel et al. 2008).

Detections of fish by these arrays were used to determine if a fish was caught (fishing mortality), died (natural mortality) or emigrated. Fishing mortality was estimated from both tag returns by fishers and from presence (or absence) data recorded by the remote receivers. For example, a fishing mortality was identified by a detection pattern that would show consistent, continuous detections at the center site, followed by a sudden loss of detections at time of capture. Emigration was shown as a decrease in detections of a fish at the center site followed by an increase in detections at a surrounding receiver prior to complete detection loss. A natural mortality was identified when a fish stopped being detected at any outside receiver but was still detected by the center receiver. This natural mortality pattern resulted from a lack of fish movement and decrease in detection range from a transmitter that was lying on the bottom. Each site was periodically checked for dead and alive fish by visual surveys for external tags on swimming fish and with a diver hand-held receiver used to locate tags. A stationary control transmitter was placed 400 m (VR2) or 150 m (SUR) south of the center location at each site to estimate changes in detection range, and enabled contrasts between movements and mortality (Figure 1-2). To increase the probability of tag returns by fishers, a tag return reward of $50 to $150 was advertised via internet fishing forums, posters distributed at local tackle stores and marinas, and newspaper coverage of the project.

Estimates of mortality.—Several methods were used to calculate mortality rates, including equations defined by Ricker (1975), Kaplan and Meier (1958), and Pollock et al. (1989).

Ricker method

Annual exploitation rates (*u*) were derived from tag returns and telemetry-identified fishing mortalities. Exploitation rates were calculated each month as the number of tagged fish captured that month out of the number of tagged fish at risk of being captured at the start of that month. The number of fish at risk at the start of each month was calculated as the fish present at the start of the previous month minus all mortalities (fishing and natural) plus new fish released during the previous month. An adjustment was made to the number of fish at risk that accounted for non-reporting and natural mortalities of fish that emigrated from the sites. The adjustment was based on the rates (proportion) of fisher non-reporting and natural mortality estimated for fish that remained at the sites, and assumes that fish emigrating will incur the same rates as fish remaining at the site. A mean yearly rate was calculated by multiplying the mean monthly *u* by 12. Expectation of natural death (*v*) was calculated monthly from telemetry-detected natural mortalities at each site, and is defined as the number of tagged fish dying naturally that month out of the number of tagged fish at risk of dying at the start of that month. The number of fish at risk of dying at the start of each month was calculated as the fish present at the start of the previous month minus all mortalities (fishing and natural) plus new fish released during the previous month. Also, all fish that emigrated the previous month were removed from the fish at risk so that natural death rate was only calculated for fish remaining at the site because natural mortality could not be detected for fish that emigrated. To estimate annual rates of instantaneous fishing mortality (F) and natural mortality (M), two estimates of instantaneous total mortality (Z) were applied. Total mortality (Z) was estimated from the present telemetry derived estimates of u and v, and from catch-curve analysis in previous studies ($Z = 0.54$; Gitschlag et al. 2003; Szedlmayer 2007). Annual survival (S) was either calculated from the catch-curve or from u and v.

Three separate models were used to estimate M and F. Ricker model (1), where $F = u\,Z\,/\,(1 - S)$ was used to calculate F from the telemetry-based u and the catch curve derived $Z = 0.54$ (with $S = e^{-Z}$), then M was estimated by subtraction ($M = Z - F$). Ricker model (2), where $M = v\,Z\,/\,(1 - S)$ was used to calculate M from the telemetry-based v and the catch curve derived $Z = 0.54$ (with $S = e^{-Z}$), then F was estimated by subtraction ($F = Z - M$). In Ricker model (3), both M and F were calculated separately from telemetry-based estimates of u, v, and Z, using Ricker models (1) and (2), with $S = 1 – (u + v)$ and $Z = \log_e(S)$.

Kaplan-Meier method

Mortality rates were calculated from the survival function, $S(t)$, estimated from the product limit method of Kaplan and Meier (1958), which gives the probabilities (S) of surviving a specified event (i.e. fishing, natural, or total mortality) over a given time (t). This method allows for right censoring of fish that do not undergo an event or were removed by means not related to the events under analysis. The Kaplan-Meier (K-M) event analysis method was applied using the survival function:

$$\hat{S}(t) = \Pi_{tj \leq t} (1 - d_j / r_j);$$

the probability of surviving to t, where t is the time over which survival is estimated from the product of the conditional probabilities of survival at each event point j, and where d_j represents the number of individuals experiencing an event and r_j represents the number of individuals at risk of an event at time t_j (Kaplan and Meier 1958; Allison 1995; Schroepfer and Szedlmayer 2006).

The SAS Lifetest procedure was used and estimates the survival to t assuming fish are released on the same day and examines the entire distribution of event and censor times (Allison 1995). Survival was then estimated at 365 days. By analyzing event times with respect to the same start date, the effects of low sample size (in the beginning of the study) on K-M survival estimates are removed. Survival functions were estimated separately for M, F, and Z. For example, when survival from fishing mortality (event) was estimated, emigration, natural deaths, and fish still present at the end of the study were right censored from the fish at risk. The numbers of fish at risk decreases as fish are removed by both fishing and natural deaths, and due to right censoring of emigration. In this method, individuals censored are assumed to have the same prospect of survival as individuals remaining at the study site. Since survival estimates are independently derived by only considering the specified mortality event, instantaneous annual mortality rates were calculated using the following equations:

$$F = - \log_e[S(365)] ,$$

when survival is based on probability of surviving a fishing mortality over a year;

$$M = -\log_e[S(365)] ,$$

when survival is based on probability of surviving a natural mortality over a year;

$$Z = -\log_e[S(365)] ,$$

when survival is based on probability of surviving any mortality over a year. Variances for K-M survival estimates were defined by Cox and Oakes (1984) as

$$\mathrm{Var}[\hat{S}(t)] = [\hat{S}(t)]^2 \, [1 - \hat{S}(t)] \,/\, r(t),$$

and 95% confidence intervals for K-M were defined by Pollock et al. (1989) as

$$\hat{S}(t) \pm 1.96[\mathrm{var}\ \hat{S}(t)]^{1/2}.$$

Ranges of mortality rates were calculated from the 95% confidence interval ranges of the survival functions at a time of 365 d.

Staggered entry method

The staggered entry method is a modification of the previous K-M survival function method and has been applied to telemetry data (Pollock et al. 1989; Heupel and Simpfendorfer 2002). The staggered entry equation is identical to the K-M, with the exception that this method allows individuals to enter at any time during the study. Individuals that emigrated or did not experience the specified mortality event over the given time period were right censored as discussed above (e.g., a fish emigrating 200 d after release was known to survive a mortality event for at least 200 d). In the staggered entry method, the number of fish at risk could fluctuate from period to period depending on the number of fish present, new releases (additions), and removals from the sites (fishing mortality, natural mortality, emigrations) in the previous period. The survival function was estimated by taking the product of the conditional survival probabilities calculated every 30-d period up to the 960-d study length (i.e. 32 time periods). The mortality rate equations were adjusted to estimate an annual survival $S(365)$ from the survival probabilities at the end of the study $S(960)$ by applying an exponent of 365/960 (e.g. F, M, or $Z = -\log_e[S(960)^{365/960}]$; Starr et al. 2005).

Effects of implantation methods.—The effects of transmitter implantation on behavior or health are usually assumed to be negligible when the transmitter weight is less than 2% of the total body weight of the fish (Winter 1983; Adams et al. 1998; Brown et al. 1999). In this study, transmitter effects were not expected since transmitters (34 g in air) were 1.7% of the body weight of the smallest fish used in the study. To verify that transmitter implantation had little effect on red snapper survival, survival rates between tagged and untagged red snapper were compared in a laboratory holding experiment.

Medium-sized (350-550 mm TL; > 900 g) red snapper were captured hook and line and transported to an 11000-L closed seawater system that consisted of 0.7 x 1.5 m circular tanks ($N = 9$). Water temperature was maintained between 21 to 22 ºC and salinity between 34 to 36 ppt. Only fish that survived a 10-d acclimation period were used in the experiment. Fish were implanted with a 75 x 18-mm, 26-g dummy transmitter following tagging methods used in the field study. Each trial, three implanted and three non-implanted (control) fish were held in each tank for 30 d. After 30 d, the fish surviving the trial were weighed to the nearest g and measured to the nearest mm. The 30-d trials were repeated until survival and growth rates were obtained for 30 implant and 30 control red snapper. Passive integrated transponder (PIT) tags (3 x 1 mm) were implanted into the abdominal cavity of each fish at time of capture for identification of individuals. The PIT tag was assumed not to affect mortality (Park and Park 2009). The lab experiment used smaller fish compared to those tagged in field experiments due to constraints on transporting and holding captive fish. Fish were fed squid and shrimp every 2 d ad libitum. If mortality occurred during a trial the fish was replaced with another fish to keep fish densities constant.

Data analysis.—Differences in mortality were compared between implant and control red snapper in the lab with a 2 x 2 chi-square. A *t*-test was used to compare growth rates ($G = 100*[\log_e \text{end wt} - \log_e \text{start wt}]/\text{experiment days}, \% \text{ d}^{-1}$) between implant and control fish over the 30-d study period.

RESULTS

Red snapper (*N* = 87) were monitored at five different sites (A1-A4, N1; Figure 1-1) for 990 d (December 2005 to September 2008). Total length (TL) of tagged red snapper ranged from 501 to 860 mm, with a mean of 639 mm (SD = 85 mm). These 87 fish remained present at the site, emigrated, died, or were removed by fishers, as determined by detections from the five receivers at each site and by fisher returns (e.g. Figure 1-3; Table 1-1). Event times (or minimum residence time if still present) ranged from 0 to 783 d (Table 1-1). Of the 87 tagged fish, 17 either left the site or died within the first 6 d after release (14 emigrated, 2 died, and 1 unknown), which was assumed to be related to post-release behaviors or mortality. None of the fish that left within 6 d were detected again or returned by fishers. Thus, only the 70 remaining fish were used for mortality rate estimations, and data were analyzed up to 31 August 2008 (just prior to hurricanes Gustav and Ike).

There were 26 fish still present at the various sites at the time of analysis (Table 1-1). Additional emigrations were detected (*N* = 16) after the 6-d post-release period, with two fish in 2006, nine fish in 2007, and five fish in 2008 leaving the site from 28 to 733 d after release. Three fish from the 16 emigrations were last detected at a site when one of the five outer array receivers was not functioning, but were assumed to have emigrated based on the detections from other receivers at that site (unknowns [U]; Table 1-1). There were no natural deaths detected in 2006, but there were five in 2007 and four in 2008 (8 months). Overall, 19 fish were caught at four of the five sites (A1-A4), with 17 fish returned by fishers and 2 estimated from detection data. Site A1 had the highest fishing mortality (13 fish out of 20 released). Nine fish were caught in 2006, five in 2007, and five in 2008. Of the nine fish caught in 2006, all were caught at site A1 in April, May, and June, and six were captured by one fisher. This fisher admittedly targeted this site. Targeting of this study site may have increased exploitation rates beyond actual levels in 2006 ($u = 0.50$, April; 0.75, June), as few fish were at risk during the early part of this study (10 fish in April, 5 in May, and 6 in June). Both the Ricker and staggered entry models are sensitive to low sample sizes in the beginning of the study which resulted in negative or zero M values and F values greater than 1.0. Because of the fishing mortality bias from this particular fisher, these captures were censored in the Ricker and right censored in the staggered entry analysis, and not included in the fishing mortality estimates for these models, but the mortalities from this directed fisher were included K-M mortality estimates.

Ricker Mortality Estimates

The mean yearly exploitation rate (u) was 0.31/year (SE = 0.12). The u decreased each year, from 0.55/year (2006) to 0.19/year (2007) to 0.12/year (only 8 months of 2008). The fisher capture reporting rate was > 90% based on detections and tag returns, with only 2 fish out of 19 not returned by a fisher. If this rate is applied to fish emigrating from the site (assuming those fish incur the same rate of non-reporting), mean overall *u* increases slightly to 0.34/year. Natural death rates (*v*) over all sites was 0.13/year (SE = 0.04). No natural mortality was detected in 2006, *v* was 0.22/year in 2007, and 0.19/year in 2008 (extrapolated from 8 months).

The Ricker model (1) mortality estimates were *F* = 0.40 and *M* = 0.14 (from subtraction), based on a *Z* of 0.54 (Gitschlag et al. 2003; Szedlmayer 2007) and *u* = 0.31/year (Table 1-2). The Ricker model (2) mortality estimates were *M* = 0.16 and *F* = 0.38 (from subtraction), based on the same *Z* = 0.54 and *v* = 0.13/year (Table 1-2). Ricker model (3) mortality estimates were *F* = 0.41 and *M* = 0.17, based on estimates of *u* = 0.31/year, *v* = 0.13/year, and *Z* = 0.58 from the present study (Table 1-2). Ricker model (3) was used to obtain mortality estimates by year from above yearly estimates of *u* and *v*. In 2006, *F* = 0.80 and *M* = 0.0; in 2007, *F* = 0.25 and *M* = 0.28; and, in 2008, *F* = 0.14 and *M* = 0.23.

Kaplan-Meier Mortality Estimates

The estimation of mortality rates using the Kaplan-Meier (K-M) method were based on all data (*n* = 70 fish). All fish were released on the same start date, and as such there was not artificial inflation of mortality rates when few fish were at risk at the beginning of the study. The overall rate of survival (*S*) from all mortality (fishing + natural) was 57% at 365 d (*S*[365]) or *Z* = 0.56 (Table 1-2; Figure 1-4). When survival from fishing mortality was estimated, *S*(365) = 64% and *F* = 0.45 (Table 1-2; Figure 1-5). When survival from natural mortality was estimated, *S*(365) = 90% and *M* = 0.11 (Table 1-2;

Figure 1-5). If the K-M method was applied with the recaptures removed (right censored) from the fisher that targeted site A1, $Z = 0.40$ and $F = 0.33$.

If the K-M method is applied to only 2007 and 2008 data ($n = 44$ fish), F would also decrease from 0.45 to 0.31, but this would exclude most of the fish released at site A1. Site A1 had the most fishing mortalities (13 of 20 fish), and was the first site established. If all sites except A1 were considered ($n = 50$ fish), F would be 0.25; however, if F was based only on site A1, F would be 1.0. Site A4 had the second highest F (0.56), and was a public site. Site N1 was the last site established (December 2007), and showed the lowest $F = 0$, compared to other sites.

Staggered Entry Mortality Estimates

The staggered entry method is the K-M method modified to allow for staggered entry of individuals over the course of the study (Pollock et al. 1989). This method also showed sensitivity to low sample size in the beginning six months of this study. After the first six months (June 2006), the probability of survival (S[180]) dropped to 10% when all fishing mortalities were considered, resulting in an F of 2.3, which is an unrealistic estimate. After removal of the captures from the biased fisher and then analyzing survival from fishing mortality, $S(365) = 68\%$ and $F = 0.39$ (Table 1-2; Figure 1-6). While no natural deaths were detected in 2006 (probably due to low sample size), natural deaths were spread out relatively evenly in the following years. Survival from a natural mortality using the K-M staggered entry was S(365) = 87%, $M = 0.14$; and, survival from all mortality was S(365) = 58%, Z = 0.54 (Table 1-2; Figure 1-7, 1-8).

Transmitter Effects Experiment

The effects of transmitters implanted in red snapper ($n = 32$) were tested against control red snapper ($n = 30$) that were not implanted with transmitters. Overall, fish ranged in length from 417 to 536 mm TL. There was no difference detected between mean starting lengths of implant (466 ± 7 mm TL, mean ± SE) and control (446 ± 7) fish ($P = 0.07$), but there was a significant difference in mean starting weights of implant (1.65 ± 0.08 kg) and control (1.45 ± 0.07 kg) fish ($P = 0.05$). There was a significantly greater proportion of fish dying from the implant treatment ($n = 14$, 44%) than in the control group ($n = 3$, 10%) over the 30-d trial periods ($P = 0.003$). In addition, growth rates (G) for fish surviving the 30-d period were significantly greater for control fish (0.15 ± 0.04 % d^{-1}, mean ± SE) than for implant (-0.02 ± 0.04 % d^{-1}) fish ($P = 0.005$). A preliminary comparison of two implant fish to two control fish (in same tank) showed there was a mean positive growth for implant fish (not statistically different) after a 60-d period of zero growth, and growth rates were similar to control fish up to 180 d (Figure 1-9). Fish in the preliminary trial appeared healthy, but in later trials, both implant and control fish showed signs of infection (necrotic tissue, erythema, and exopthalmia), but clinical tests for the presence of disease were not conducted. The mortality rates for implant fish in the laboratory were not applied to the field study due to the higher survival rates for field fish compared to laboratory fish, based on fisher recaptures, detections of emigration events, and detection of movements around release sites.

DISCUSSION

Ultrasonic telemetry allowed continuous, long-term (~3 years) monitoring of tagged red snapper at the 2-km (radius) study sites. The arrangement of receivers also enabled the estimation of emigration, natural mortality, and fishing mortality at various habitat structures. The detection data from the stationary control transmitters in this study were important for a high confidence in the determination of emigration, natural mortality, fishing mortality, and residency. Most studies that employed telemetry techniques to estimate mortality of relatively mobile species (e.g. striped bass, blacktip sharks) have been successful in semi-closed systems and generally have estimated natural death based on lack of movement (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Young and Isely 2004). For example, Heupel and Simpfendorfer (2002) were able to directly detect fishing and natural mortality of juvenile blacktip sharks in Terra Ceia bay by using a large number of VR2 receivers to continuously monitor movement, lack of movement (death), sudden disappearance (capture), and emigration of individuals from the mouth of the bay. More difficulty is encountered when attempting to estimate mortality with telemetry in open ocean systems (vs closed), and has been limited to fish that show moderate residence (Starr et al. 2005). In the present study, high residence of red snapper to reef sites provided a unique opportunity to estimate mortality rates in an open water system (Schroepfer and Szedlmayer 2006).

Values of F for some stock assessments are dependent on M, in which M is determined indirectly from the life history parameter equations, with F only as accurate as M (Manooch et al. 1998). Estimates of M derived indirectly from life history equations from parameters of northern GOM red snapper (Table 1-3; e.g. maximum age, maximum weight, K, water temperature) can range from 0.08 to 0.36 (Chen and Watanabe 1989; Pauly 1980; Hoenig 1983; Peterson and Wroblewski 1984; Jensen 1996; Quinn and Deriso 1999; Slipke and Maceina 2005; Wilson and Nieland 2001; Szedlmayer 2007). The present red snapper fishery assessment models use a conservative M of 0.10, which was lowered from the 0.20 used in an earlier assessment (Goodyear 1995; Schirripa and Legault 1999; SEDAR 2005). The predicted M was lowered due to evidence of older fish (53 years) in the GOM red snapper stock (Schirripa and Legault 1999; Wilson and Nieland 2001). The direct estimates of M from telemetry methods in this study (0.11 - 0.17; 95% CL = 0.04 - 0.27) were consistent with the estimates from the indirect methods and close to levels used in previous assessments. Although this study provides the most recent estimates of M, such estimates will probably change from year to year depending on environmental conditions or from possible increases in density-dependent mortality associated with population increase during the red snapper stock rebuilding phase (Rose et al. 2001; Gazey et al. 2008).

Detection of changes in natural mortality rates over short periods of time (Young and Isely 2004) or during catastrophic environmental conditions (e.g. hurricanes or dead zones) would be more accurately assessed with telemetry methods. There were no natural deaths detected in 2006 probably due to the combination of low sample size and the number of released fish caught by fishers early in the study. In the following years (2007 and 2008), natural deaths were detected at relatively even intervals with no periods of excessively high mortality. Natural mortality may actually be higher, as the staggered entry method does estimate M at 0.25 if only 2007 and 2008 data are considered, but the K-M method stays consistent with an M of 0.12 using the same data set. There was also an increase in M from 2006 to 2007 and 2008 (Ricker model 3). Because sample sizes were greater in 2007 and 2008, and M was relatively consistent (0.28 in 2007, 0.23 in 2008), these estimates are probably better estimates of actual red snapper natural mortality rates.

The direct estimates of F in this study (0.38 - 0.45; 95% CL 0.28 - 0.67) were similar to F for red snapper from the most current stock assessment estimate (0.35; SEDAR 2005) and F (0.29 to 0.47) from the 1999 stock assessment (Schirripa and Legault 1999). Peabody (2004) estimated fishing mortality from tag returns of relatively small red snapper (< 500 mm TL) off Louisiana. Although most fish were smaller than the legal commercial and recreational size limits, their F estimates ($F = 0.36$ to 0.50 at $M = 0.10$ to 0.20) were similar to the present study. In contrast to the reporting rate in present study (~90%), Peabody (2004) believed that reporting was probably < 60% based on lack of returns from commercial fishers, and would result in their $F > 0.7$.

Szedlmayer (2007) estimated an *F* of 0.19 using a *Z* = 0.54 from fishery independent catch curve data and an exploitation rate of 0.15/year from a previous tag and recapture study (Szedlmayer and Shipp 1994). While their *u* was lower than the overall rate in this study (0.31/year), a *u* of 0.15/year is comparable to present estimates 0.19/year in 2007 and 0.12/year in 2008.

The higher exploitation rates in 2006 for the present study may be lower sample sizes inflating exploitation, but also may reflect changes in fishing regulations between years. Total allowable catch (TAC) quotas were decreased from 9.12 million pounds (MP) in 2006 to 6.5 in 2007, and to 5.0 MP in 2008. These reductions in TAC resulted in more restrictive season and bag limits. For example, in 2006 the federal waters were open to recreational red snapper fishing for seven months (April to October 2006) with a four fish bag limit (407 mm TL minimum size), in 2007 a two fish bag limit was instituted, and in 2008 the fishing season was limited to two months (June and July 2008). Though it is difficult to compare the first year of the study due to sample size bias, there was a pattern of fishing mortality that appeared to reflect these changes. Fishing mortality (*F*) was 0.80 in 2006, 0.25 in 2007, and 0.14 in 2008 (Ricker model 3). Given these values, an SPR = 26% may have been achieved in 2008 (Szedlmayer 2007).

It is likely the current fishing rate was actually lower than present overall estimates. The K-M method estimated that *F* would decrease from 0.45 to 0.31 with only 2007 and 2008 data. Also there was an apparent targeting of site A1 with 13 out of 20 recaptures originating from this site. If this directed effort was considered a bias and removed from estimations, *F* decreased to 0.25. At the other extreme fishing mortality rates at site N1 were zero, but this site was established later in the study (December 2007), and inclusion of this site earlier in the study may also have lowered overall *F*.

Detection of a fishing mortality event was typically validated by fisher returns (*n* = 17) making the confidence in our estimate of *F* relatively high. Confidence in the accuracy of detection of natural deaths was somewhat lower since we were not able to retrieve all of the transmitters from dead fish. However, even when independently estimating each type of mortality event, there was a convergence of mortality rates estimated among the various methods (low variability), which increases confidence in the accuracy of *M*. Total mortality (*Z*) estimates showed low variance among the methods used, with estimates of 0.56 (K-M), 0.54 (staggered entry), and 0.58 (Ricker model 3), which are surprisingly similar to a *Z* of 0.54 obtained by both Gitschlag et al. (2003) and Szedlmayer (2007) from catch curves of completely separate fishery independent surveys in the northern GOM. The agreement of mortality rates among the various methods further validates the accuracy of present estimates.

Although the different methods of estimating mortality showed similar results, there were advantages and disadvantages of each method. The staggered entry (modified K-M; Pollock et al. 1989) and K-M methods simplify calculations, with only data needed on the time from release till a mortality event, an emigration, or if a fish is still present. The staggered entry method is suggested as the preferred method if there is a reasonably high initial release of individuals into the study (Heupel and Simpfendorfer 2002). Also, this would be the best method to show seasonal or yearly fluctuations in survival if there are similar sample sizes among periods. The confidence intervals used for the staggered entry method narrowed as the study progressed because sample size increased as more fish were released over the study. The numbers of fish at risk reached 20 by day 450 and fluctuated from 20 to 30 fish up to 960 d as emigration, death, and fishing mortalities removed fish. The K-M method was the least sensitive to fluctuations in sample size and periods of high mortality. The K-M method shows narrower 95% confidence limits in the beginning of the study due to the “release” of all fish ($n = 70$) at day 0. Accuracy of this method is affected by the length of the study, with confidence increasing as more fish progress through the study to experience an event. There were 26 fish still present at the various sites at the time of analysis, which were released at different times in the study, so confidence intervals should continue to narrow as more fish are at liberty for at least 365 d.

The traditional Ricker (1975) methods using u or v rates and some estimate of Z to calculate F or M were very similar to the staggered entry method. The same time periods (30 d) were used to estimate u and v (Ricker), and survival (staggered) with similar numbers of fish at risk at the beginning of each period. The exception was the calculation of exploitation, in which fish at risk was calculated assuming any fish that emigrated had the same probability of natural death or capture as fish experienced within the study sites. The Ricker model (3) estimated the highest (of Ricker models) level of $F = 0.41$ and $M = 0.17$ when $Z = 0.58$ was derived from the present study. These estimates would represent the most independent estimate of mortality rates of the Ricker models, but still agree well with the other two models. Since the estimates of F may have been more accurate (than M) due to validation of detection data with fisher returns, the Ricker model (1; *u* = 0.31/year, Z = 0.54) may give the most accurate estimate of *M* (0.14). Again, the major disadvantage with this method is estimating exploitation rates when few fish are at risk, as in the beginning of this study.

Since *M* represents a measure of the longevity and natural rate of replacement of the population, higher values of *M* may allow for higher catches in the fishery; however, if the fishery is managed assuming a high *M* when its value is much lower, there may be significant problems (Schirripa and Legualt 1999; Slipke and Maceina 2005). The overall natural mortality rates estimated in this study (0.11 - 0.17) were not much higher than the *M* of 0.10 used in the current red snapper fishery assessment; however, as the study progressed into years 2007 and 2008, there was an apparent increase in *M* from 2006 levels, so there is evidence to suggest that natural mortality is actually greater or may be increasing during the red snapper rebuilding period under restrictive management. This higher level of *M* coupled with the lower levels of *F* in 2007 and 2008 may show that the goal of $F_{SPR26\%}$ has already been reached and further reductions of fishing quotas are not warranted.

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TABLES

Table 1-1. Summary of release information (total length, TL; weight, Wt) and number of days (event time) from release until occurrence of the specified event (emigration, E; fishing mortality, F; natural mortality, M; present, P; unknown, U) for ultrasonically-tagged red snapper at various array sites.

Fish	Release	Site	Wt (kg)	TL (mm)	Event time	Event
1	13 Dec 2005	A1	4.3	660	614	E
2	13 Dec 2005	A1	7.3	800	179	F
3	13 Dec 2005	A1	3.0	590	153	F
4	13 Dec 2005	A1	6.0	710	2	E
5	13 Dec 2005	A1	4.0	630	155	F
6	13 Dec 2005	A1	5.5	695	114	F
7	23 Dec 2005	A1	2.9	580	99	F
8	23 Dec 2005	A1	4.0	620	104	F
9	4 Jan 2006	A1	5.0	630	1	E
10	4 Jan 2006	A1	3.5	520	108	F
11	4 Jan 2006	A1	5.0	553	5	E
12	4 Jan 2006	A1	12.5	860	1	E
13	4 Jan 2006	A1	3.5	540	92	F
14	12 Jan 2006	A1	6.0	700	84	F
15	7 Jun 2006	A1	6.5	746	452	M
16	7 Jun 2006	A1	2.8	545	324	F
17	8 Jun 2006	A1	4.7	672	1	E
18	15 Jun 2006	A1	4.5	683	321	M
19	23 Jun 2006	A4	3.3	586	733	E
20	7 Jul 2006	A4	3.2	600	420	E
21	11 Jul 2006	A1	3.7	620	741	F

(continued)

Fish	Release	Site	Wt (kg)	TL (mm)	Event time	Event
22	11 Jul 2006	A1	8.2	815	783	P
23	27 Jul 2006	A2	5.5	691	0	M
24	28 Jul 2006	A2	9.5	823	411	E
25	28 Jul 2006	A2	5.1	680	227	E
26	28 Jul 2006	A2	5.8	730	322	E
27	9 Aug 2006	A3	7.1	760	3	E
28	9 Aug 2006	A3	4.3	660	406	U
29	11 Aug 2006	A3	3.0	605	215	E
30	14 Aug 2006	A3	2.2	538	120	U
31	14 Aug 2006	A3	2.8	537	749	P
32	14 Aug 2006	A3	3.1	569	362	F
33	21 Aug 2006	A3	6.5	740	124	U
34	21 Aug 2006	A3	2.5	543	1	E
35	7 Feb 2007	A2	3.3	555	530	M
36	7 Feb 2007	A2	5.8	690	572	P
37	7 Feb 2007	A3	2.6	549	4	E
38	7 Feb 2007	A3	3.8	610	28	E
39	7 Feb 2007	A3	4.5	640	534	M
40	7 Feb 2007	A3	3.5	580	1	E
41	7 Feb 2007	A3	4.0	613	57	M
42	6 Mar 2007	A1	5.0	665	6	E
43	6 Mar 2007	A1	4.8	660	46	F
44	3 Apr 2007	A2	5.5	690	144	E
45	3 Apr 2007	A2	5.3	680	1	E
46	12 Apr 2007	A3	2.8	565	479	M
47	12 Apr 2007	A3	2.8	555	122	F

(continued)

Fish	Release	Site	Wt (kg)	TL (mm)	Event time	Event
48	12 Apr 2007	A3	4.5	670	508	P
49	21 May 2007	A2	2.5	550	210	M
50	21 May 2007	A2	11.0	800	469	P
51	12 Jun 2007	A3	2.5	590	447	P
52	27 Jun 2007	A1	6.5	645	432	P
53	3 Jul 2007	A2	5.0	705	30	M
54	9 Jul 2007	A2	5.5	710	420	P
55	9 Jul 2007	A2	5.0	710	20	F
56	9 Jul 2007	A3	3.3	620	420	P
57	9 Jul 2007	A3	5.8	730	182	E
58	25 Jul 2007	A3	4.5	685	404	P
59	25 Jul 2007	A3	3.8	660	404	P
60	25 Jul 2007	A3	6.1	760	167	E
61	29 Aug 2007	A4	3.8	645	339	F
62	29 Aug 2007	A4	2.5	550	369	P
63	29 Aug 2007	A4	3.3	601	332	F
64	29 Aug 2007	A4	5.0	710	369	P
65	5 Sep 2007	A4	3.5	635	332	F
66	13 Nov 2007	A1	5.0	705	293	P
67	14 Nov 2007	A4	3.0	579	292	P
68	20 Nov 2007	A3	3.0	605	286	P
69	29 Nov 2007	A3	4.3	658	239	E
70	29 Nov 2007	A3	9.8	810	277	P
71	11 Dec 2007	N1	3.0	573	265	P
72	11 Dec 2007	N1	2.2	501	80	E
73	11 Dec 2007	N1	2.5	550	6	E

(continued)

Fish	Release	Site	Wt (kg)	TL (mm)	Event time	Event
74	11 Dec 2007	N1	1.9	517	265	P
75	18 Dec 2007	N1	2.6	557	1	U
76	18 Dec 2007	N1	2.2	524	4	E
77	8 Feb 2008	A1	3.6	640	47	M
78	8 Feb 2008	A1	3.3	615	121	F
79	10 Jun 2008	A2	3.8	640	83	P
80	10 Jun 2008	A2	7.8	790	83	P
81	10 Jun 2008	A2	6.0	745	83	P
82	16 Jun 2008	N1	2.3	537	77	P
83	16 Jun 2008	N1	2.8	575	77	P
84	2 Jul 2008	N1	3.6	632	1	M
85	2 Jul 2008	N1	2.0	525	3	E
86	10 Jul 2008	N1	2.2	524	53	P
87	10 Jul 2008	N1	2.0	526	53	P

Table 1-2. Instantaneous mortality rates (*Z* = total mortality, *F* = fishing mortality, *M* = natural mortality) of red snapper estimated from telemetry by the Kaplan-Meier, Staggered entry, and Ricker methods. The values in parentheses are 95% confidence limits (CLs). Exploitation = *u*, expectation of natural death = *v*.

Method	Parameters	*Z*	*F*	*M*
Kaplan-Meier	*n* = 70 fish released on day 0	0.56 (0.36 - 0.86)	0.45 (0.28 - 0.67)	0.11 (0.04 - 0.27)
Staggered entry	*n* = 70 fish staggered release	0.54 (0.43 - 0.68)	0.39 (0.30 - 0.52)	0.14 (0.07 - 0.22)
Ricker (1975) model (1)	mean *u* = 0.31/year (this study) *Z* = 0.54 (Szedlmayer 2007)	0.54	0.40	0.14
Ricker (1975) model (2)	mean *v* = 0.13/year (this study) *Z* = 0.54 (Szedlmayer 2007)	0.54	0.38	0.16
Ricker (1975) model (3)	mean *u* = 0.31/year (this study) mean *v* = 0.13/year (this study)	0.58	0.41	0.17

Table 1-3. Methods used to estimate natural mortality (M) from life history parameters for red snapper in the northern Gulf of Mexico. The following parameters were used: $K = 0.17$, $t_0 = -0.79$, $L_\infty = 92.3$ cm (Szedlmayer 2007); $t_{\max} = 52$, $W_{\max} = 22790$ g, inAge = 1, finAge = 52 (Wilson and Nieland 2001); $T = 21.5$ ºC (mean temperature at 30 m from 1Aug2006 - 1Aug2008, continuous loggers deployed during this study). The estimates of M in parentheses use $t_{\max} = 42$ (Szedlmayer and Shipp 1994). The proportion of fish surviving to maximum age is 1% (Ps = 0.01).

Method	Equation	M
Jensen (1996)	$M = 1.5(K)$	0.26
Hoenig (1983)	$\log_e(M) = 1.46 - 1.01 \log_e(t_{\max})$	(0.10) 0.08
Quinn and Deriso (1999)	$M = -\log_e(\text{Ps}) / t_{\max}$	(0.11) 0.09
Peterson and Wroblewski (1984)	$M = 1.92(W_{\max}^{-0.25})$	0.16
Pauly (1980)	$\log(M) = -0.0066 - 0.279 \log(L_\infty) + 0.6543 \log(K) + 0.4634 \log(T)$	0.36
Chen and Watanabe (1989)	$M = 1 / (\text{inAge} - \text{finAge}) \cdot \log_e\{[e^{(K\,\text{finAge})} - e^{(K\,t0)}] / [e^{(K\text{inAge})} - e^{(K\,t0)}]\}$	0.20

FIGURES

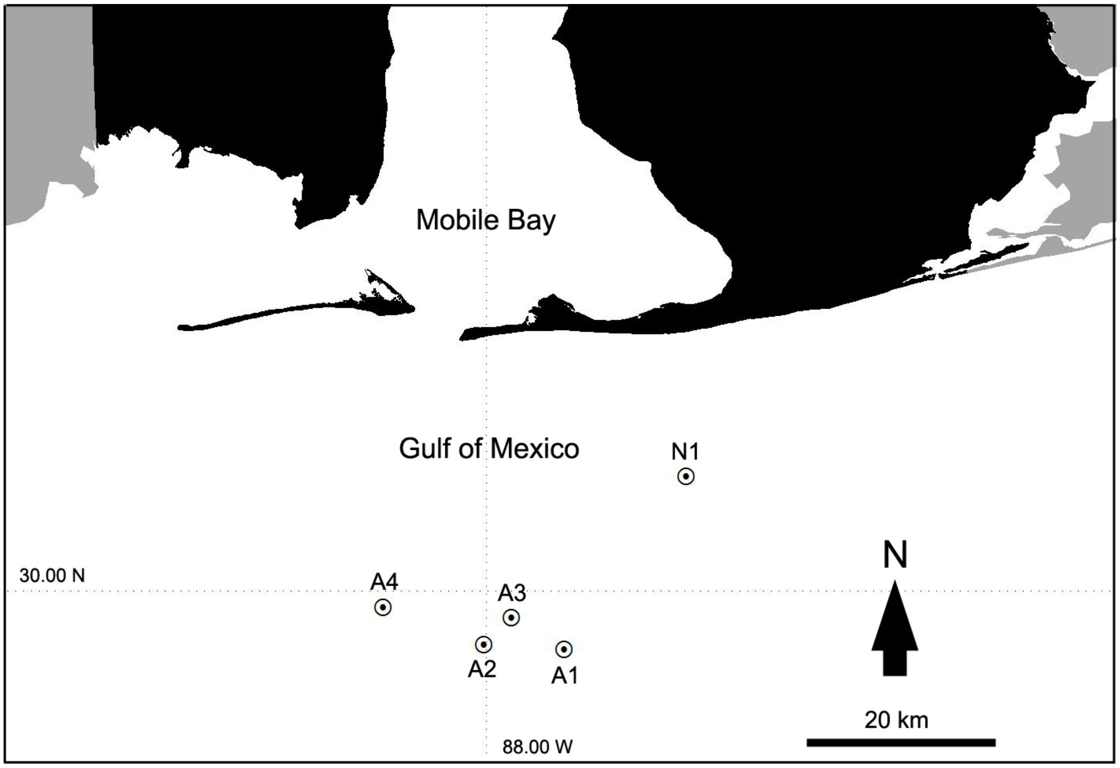

Figure 1-1. Location of study sites in the northeast Gulf of Mexico.

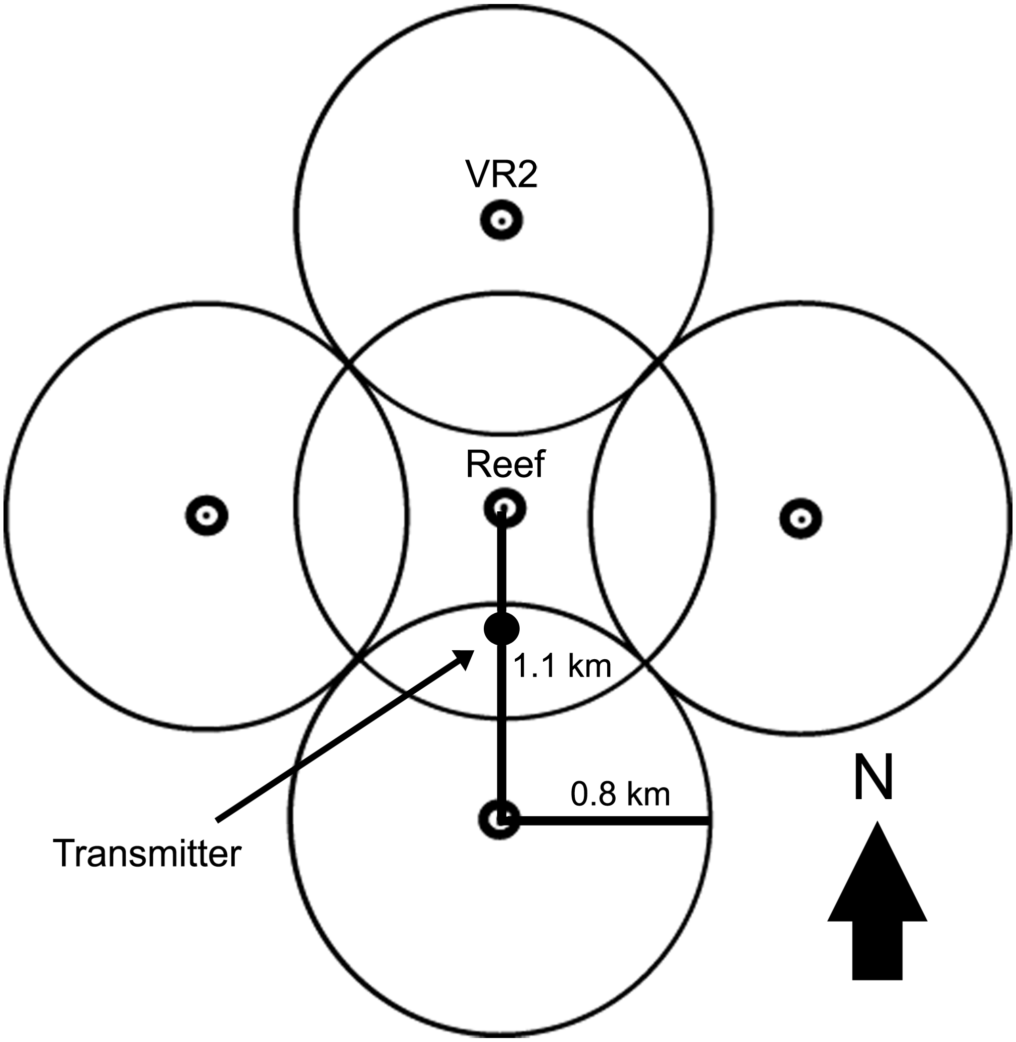

Figure 1-2. Diagram of receiver array setup for each site, with one receiver at the reef and four others surrounding the reef 1.1 km away to the N, S, E, and W. Circles represent detection range of 0.8 km. A stationary control transmitter was placed 400 m S of reef.

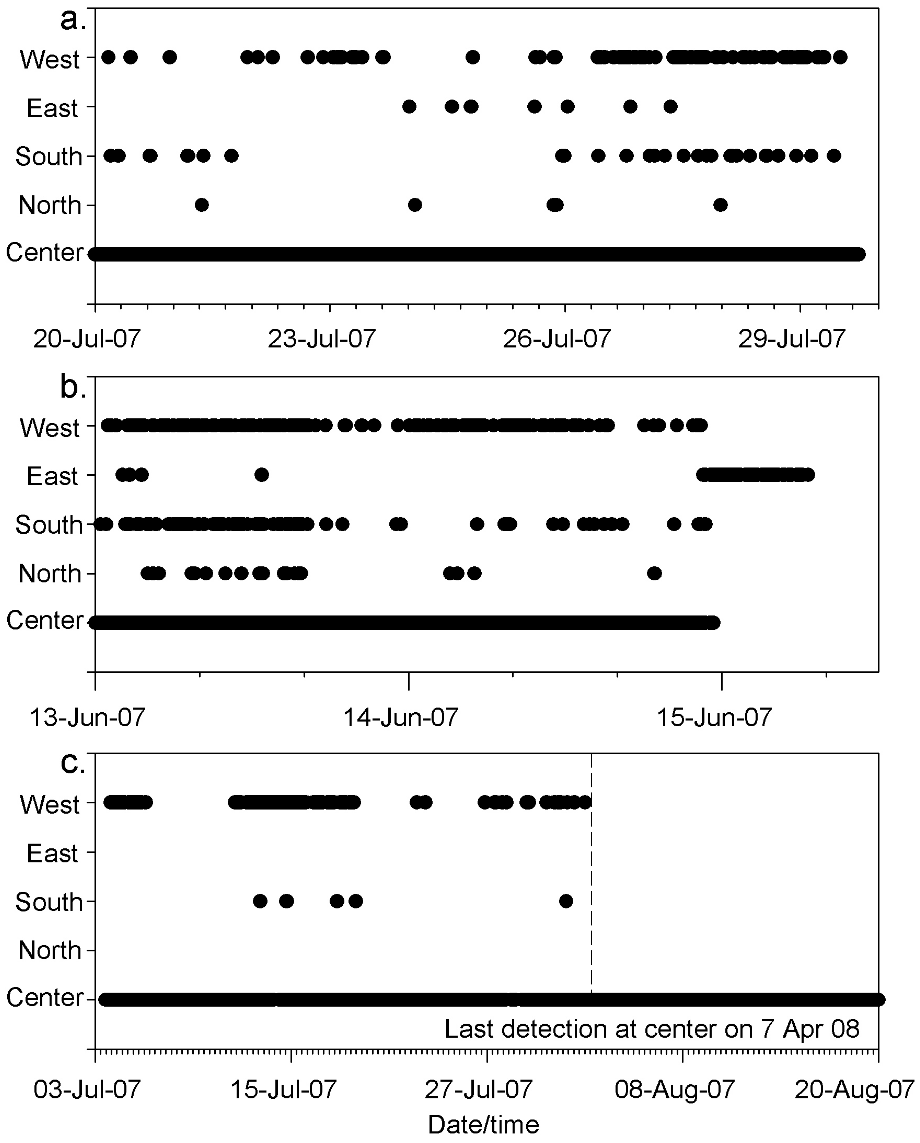

Figure 1-3. Detection plots showing examples of the detection patterns expected from fish experiencing either a) fishing mortality, b) emigration, or c) natural mortality events. Each plot shows a segment of the overall detections of a single fish by the Center, North (N), South (S), East (E), and West (W) receivers at its site of release. The vertical dashed line in plot c is the point at which no further detections were recorded at N, S, E, and W.

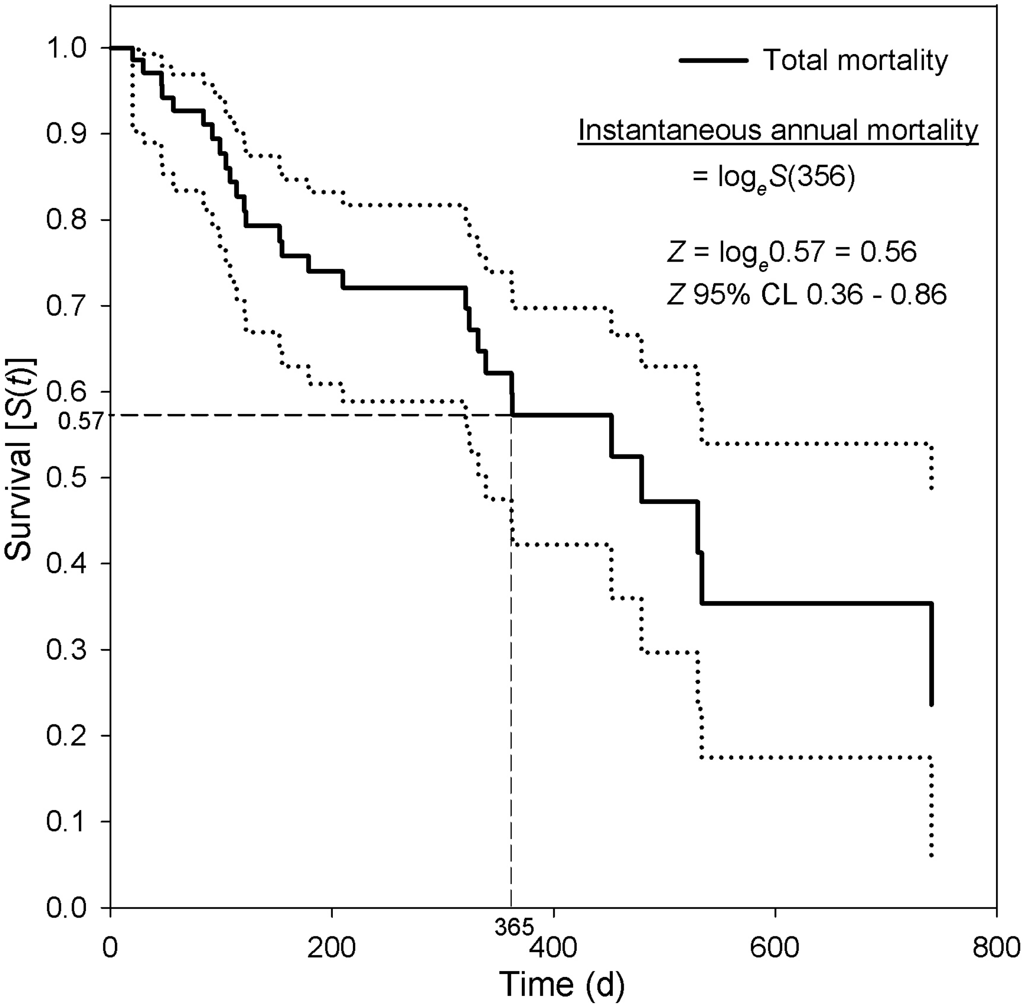

Figure 1-4. Kaplan-Meier (K-M) estimation of survival (*S*) of red snapper from total mortality (fishing and natural mortality). Dashed lines show proportion of fish (57%) surviving total mortality at 365 d (*t*). Dotted lines are 95% confidence limits (CL). Instantaneous total mortality (*Z*) is calculated from proportion surviving at 365 d and *Z* 95% CL is calculated from survival at 365 d at 95% CL.

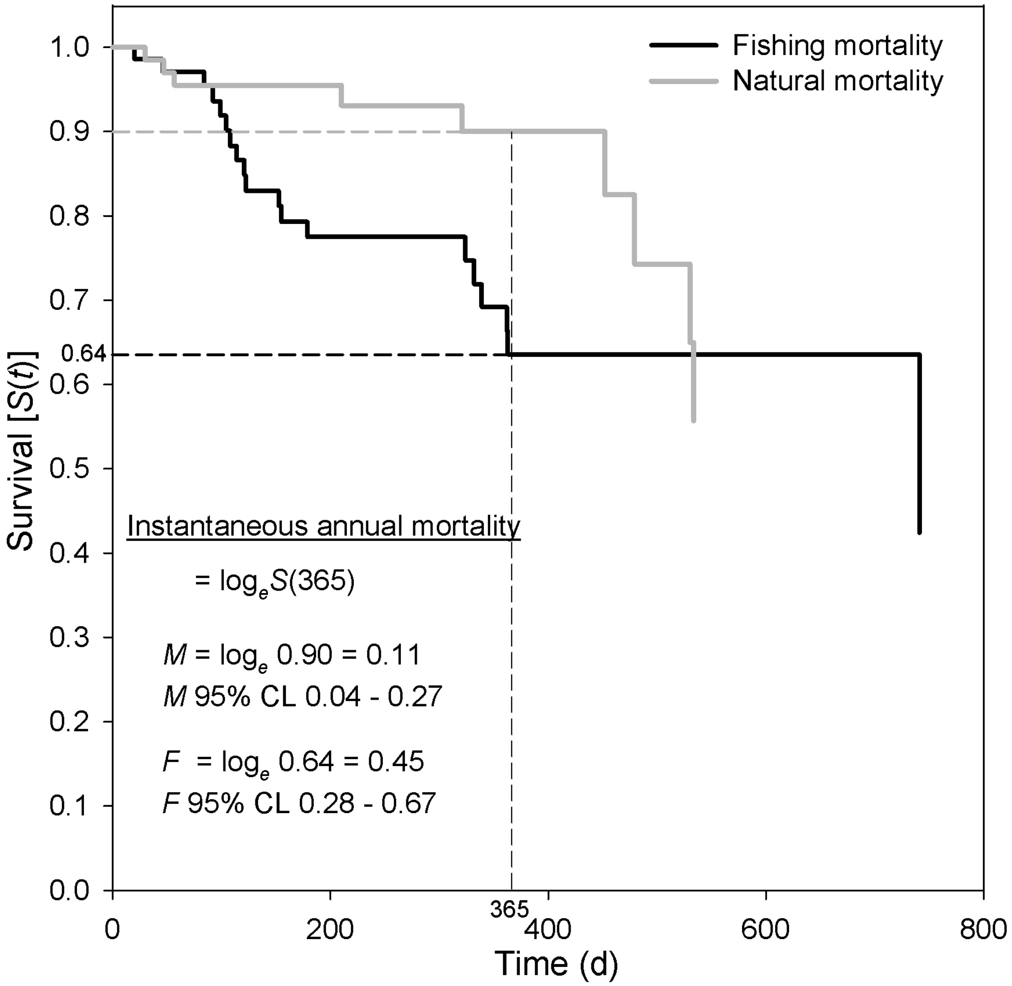

Figure 1-5. Kaplan-Meier (K-M) estimation of survival (*S*) of red snapper from fishing (black) and natural mortality (gray). Dashed lines show proportion of fish surviving fishing and natural mortality at 365 d (*t*). Instantaneous fishing (*F*) and natural (*M*) mortality rates calculated from proportion surviving each mortality at 365 d and 95% CL is calculated from 95% confidence limits of *S*(365) for each survival probability (not shown).

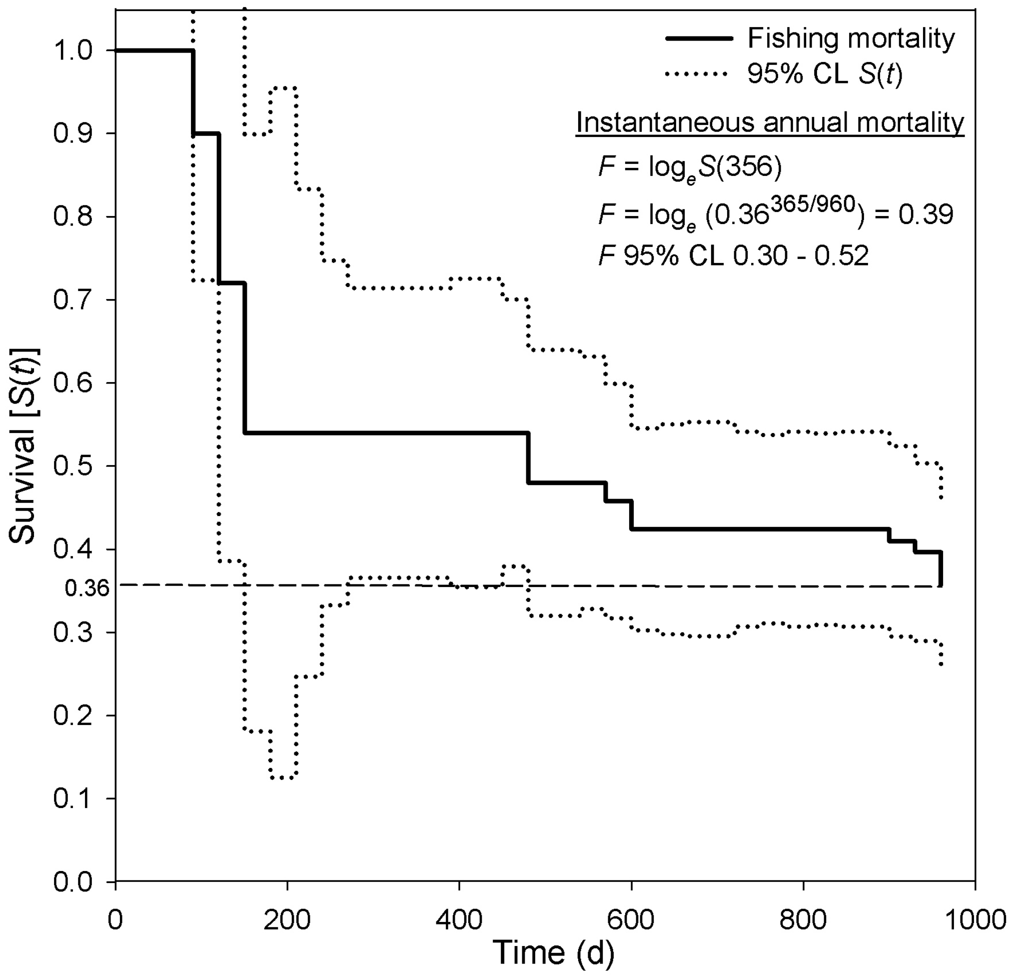

Figure 1-6. Staggered entry estimation of survival (*S*) of red snapper from fishing mortality. Dashed line shows proportion (36%) of fish surviving fishing at 960 d (*t*). Dotted lines are 95% confidence limits (CL). Instantaneous fishing (*F*) mortality rates calculated from proportion surviving at 960 d, adjusted to *S*(365) and *F* 95% CL is calculated from survival at 95% CLs adjusted to *S*(365). Day 0 is 13 December 2005.

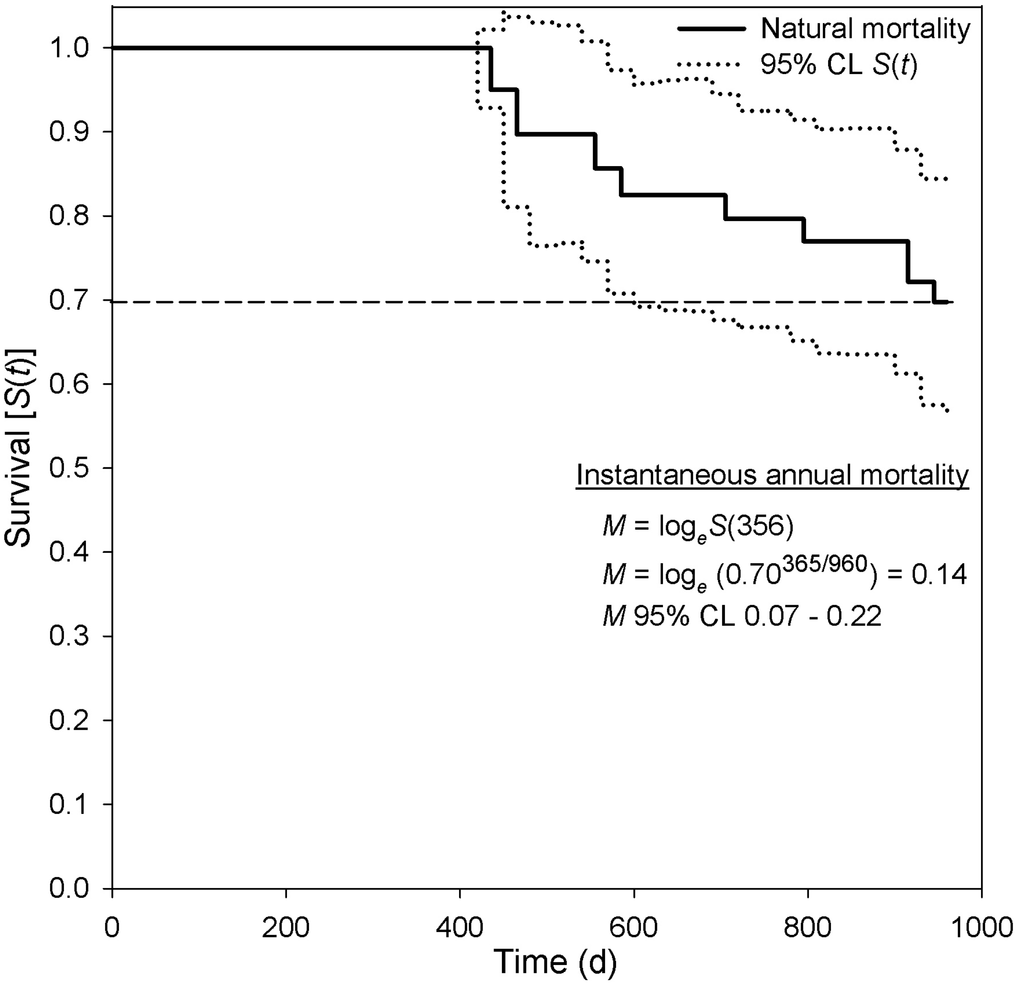

Figure 1-7. Staggered entry estimation of survival (*S*) of red snapper from natural mortality. Dashed line shows proportion (70%) of fish surviving natural mortality at 960 d (*t*). Dotted lines are 95% confidence limits (CL). Instantaneous natural (*M*) mortality rates calculated from proportion surviving at 960 d, adjusted to *S*(365) and *M* 95% CL is calculated from survival at 95% CLs adjusted to *S*(365). Day 0 is 13 December 2005.

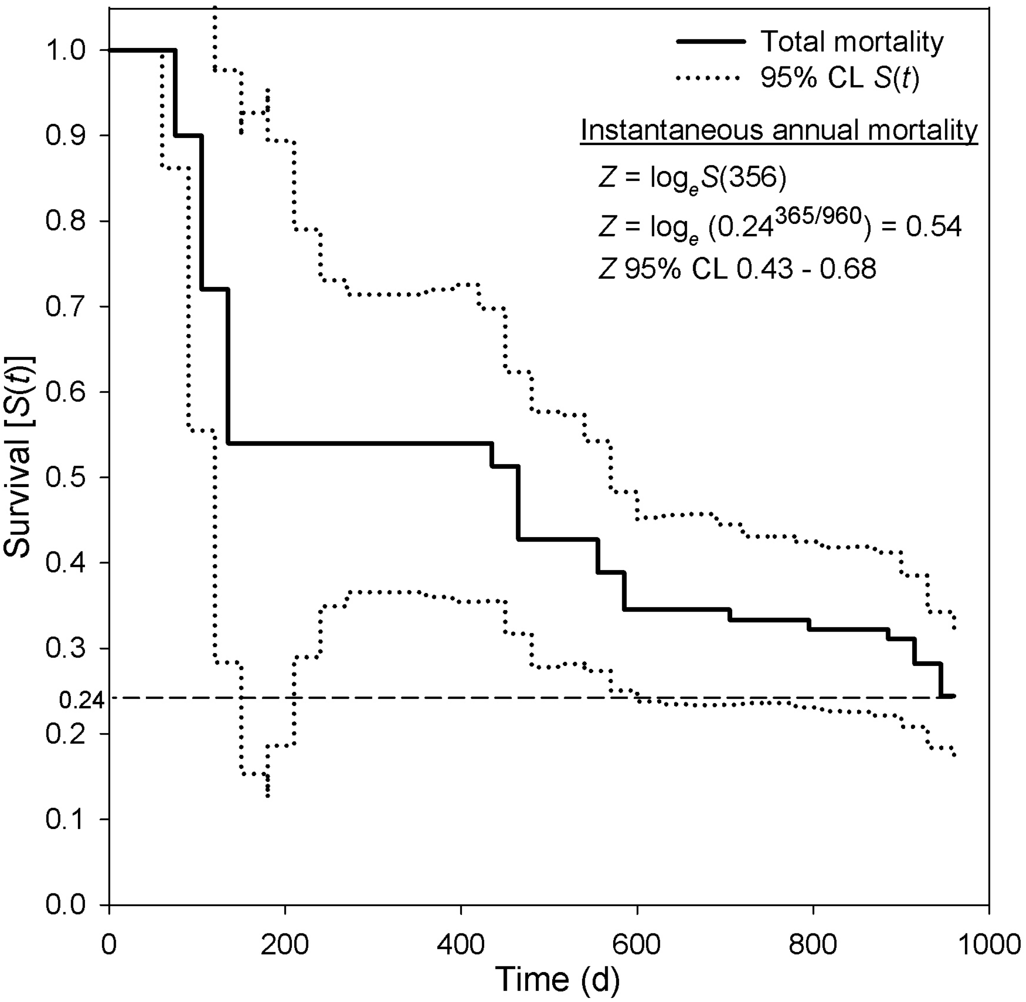

Figure 1-8. Staggered entry estimation of survival (*S*) of red snapper from total mortality (fishing and natural). Dashed line shows proportion (24%) of fish surviving total mortality at 960 d (*t*). Dotted lines are 95% confidence limits (CL). Instantaneous total (*Z*) mortality rates calculated from proportion surviving at 960 d, adjusted to *S*(365) and *Z* 95% CL is calculated from survival at 95% CLs adjusted to *S*(365). Day 0 is 13 December 2005.

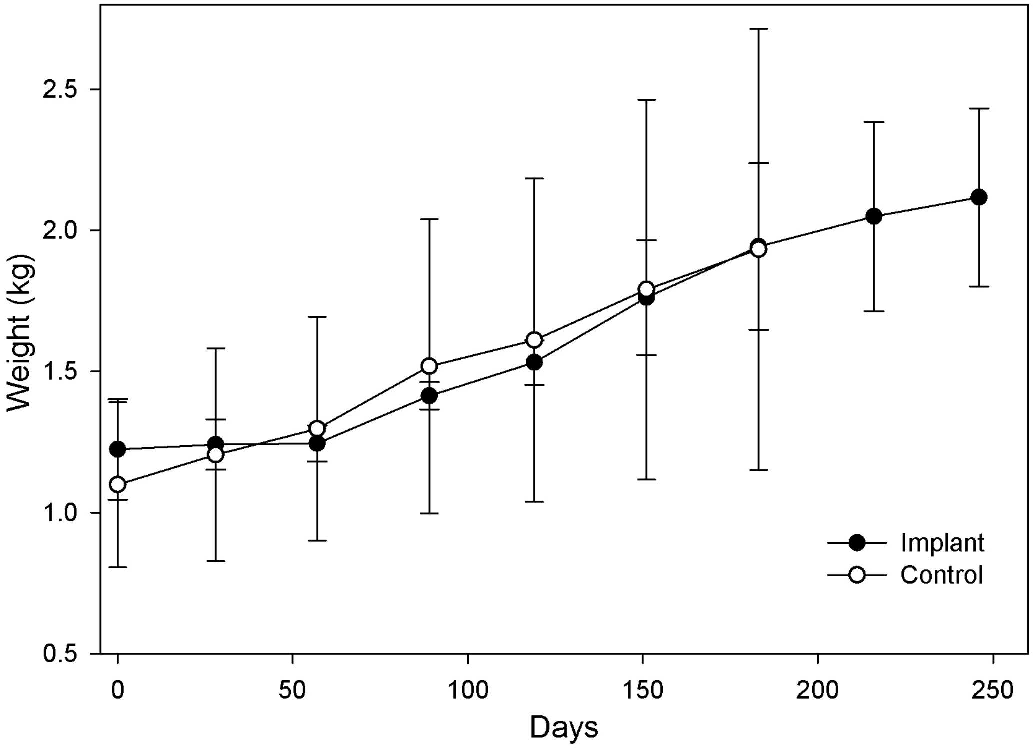

Figure 1-9. Mean weight (± SD) of implant (*n* = 2) and control (*n* = 2) red snapper at each 30-d period.

CHAPTER 2

THE USE OF ULTRASONIC TELEMETRY TO ESTIMATE SITE FIDELITY, RESIDENCE TIME, AND MOVEMENTS OF RED SNAPPER *LUTJANUS CAMPECHANUS*

Abstract.—Residence time, site fidelity, and movements for red snapper *Lutjanus campechanus* (*N* = 87) were estimated from long-term telemetry monitoring (December 2005 to December 2008) at five sites (one natural and four artificial habitats) in the northeastern Gulf of Mexico. Each site consisted of an array of five receivers (one at the center with four receivers placed 420 or 1100 m north, south, east, and west of center). These arrays enabled the estimation of fishing mortality, natural mortality, and emigration. Event analysis was used to estimate site fidelity and residence, based on right censoring fishing and natural mortality. Median residence time was 572 d, with individual times from 1 to 829 d, with 68% of fish staying at least one year at the site and 80% were present for at least 200 d. Several fish (*N* = 6) that emigrated showed directed movements to other sites (up to 8 km away), then returned to original sites. Diel movements away from the structure tended to occur at night. Site fidelity and residence times of red snapper in the present study were greater than any previous study and show the importance of artificial reefs for this species.

INTRODUCTION

Red snapper *Lutjanus campechanus* occur over natural reef structure in the Gulf of Mexico (GOM ; Camber 1955; Moseley 1966; Beaumariage 1969; Fable 1980), and also have a close association with artificial habitat (Szedlmayer and Shipp 1994; Szedlmayer 1997; Watterson et al. 1998; Peabody 2004; Szedlmayer and Schroepfer 2005). Although approximately 10,000 - 20,000 artificial habitats have been deployed in the northern GOM, which may provide benefits of increased food and shelter to red snapper, stocks are still considered overfished (Minton and Heath 1998; Schirripa and Legault 1999; SEDAR 2005; Shipp and Bortone 2009). In contrast, smaller red snapper (< 400 mm total length [TL]) were the most numerically abundant fish species on both natural and artificial habitats off Alabama, and occur in high numbers at oil rigs (Gitschlag et al. 2003, Lingo and Szedlmayer 2006; Wells and Cowan 2007; Gallaway et al. 2009). Despite the fact that only a small proportion of natural reef structure exists in the northern GOM (compared to sand and mud habitat), these artificial structures may significantly increase “red snapper” habitat and probably helped establish a significant red snapper fishery (Parker et al. 1983; Schroeder et al. 1988; Dufrene 2005; Szedlmayer 2007; Shipp and Bortone 2009; Gallaway et al. 2009). Although these artificial structures may provide suitable habitat for red snapper, fishing mortality at these structures may offset any benefits provided by these habitats (Bohnsack 1989; Strelcheck et al. 2007). Benefits of reef structure to red snapper can be addressed with long-term information on site fidelity, residence times, and movement patterns around natural and artificial structures.

The residency of red snapper *Lutjanus campechanus* on natural and artificial structures has been examined by several methods, with varying results (Camber 1955; Moseley 1966; Beaumariage 1969; Bradley and Bryan 1975; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997; Watterson et al. 1998; Patterson et al. 2001; Peabody 2004; Szedlmayer and Schroepfer 2005). Early studies examined the distribution of red snapper catches relative to habitat type, depth, and season (Camber 1955; Moseley 1966; Bradley and Bryan 1975), and more recent studies have used mark-recapture and ultrasonic telemetry to estimate site fidelity and movements (Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997; Watterson et al. 1998; Patterson et al. 2001; Patterson and Cowan 2003; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Diamond et al. 2007; Strelcheck et al. 2007). For the most part, these studies indicate red snapper show some affinity to both natural and artificial structures, but estimates of site fidelity and residence times seem to vary by methods (mark-recapture vs telemetry), habitat type (small artificial reefs vs oil rigs vs natural), hurricanes, transmitter detection range, fish size, and possibly by study length (Diamond et al. 2007; Gallaway et al. 2009).

Recent mark-recapture studies of relatively small red snapper (mean: < 400 mm TL) off Alabama obtained different results even with similar methods (Patterson and Cowan 2003; Strelcheck et al. 2007). Patterson and Cowan (2003) estimated a site fidelity of approximately 25% year^{-1} from declines in captures at tagging sites (minus an assumed natural mortality rate around 0.1 and no fishing mortality). Strelcheck et al. (2007) used the same method, tagged fish at similar habitats, and obtained site fidelity rates around 50% year^{-1}. Differences in the two estimates may be due to shorter time periods between sampling intervals at tagging sites (mean: 150 vs 102 d), which resulted in the higher estimate (Strelcheck et al. 2007).

Mark-recapture studies that attempt to estimate residency and movements must rely on the recapture of tagged fish (fishery dependent), the accuracy of the reported information (location and date), and the willingness of fishers to report a tag (Green et al. 1983). All of these factors may decrease the reliability of residency estimates. In addition, mark-recapture studies lack information on timing of movements and additional movements between mark and recapture. Especially difficult is the detection of movement away from and back to the original release site.

Recently, ultrasonic telemetry methods have greatly improved the spatial and temporal resolution in red snapper movement studies and removed almost all dependence on fishery returns (Szedlmayer 1997, Peabody 2004, Szedlmayer and Schroepfer 2005). Residence times of red snapper ranged from 17 to 597 d at artificial habitats off Alabama, using telemetry to relocate or continuously monitor individual fish, with a median residence time of 373 d and site fidelity of 50% year^{-1} from event analysis (Szedlmayer

1997; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006). Peabody (2004) also used ultrasonic telemetry to monitor the residency and movements of small red snapper (< 450 mm TL; mean: ~300 mm TL; $N = 125$) around oil rigs off Louisiana, with 78% detected from 1 to 202 d after release, and only 13 of the detected fish moved away from the original release location after six months. After 70 d, however, there was only a 50% probability of detection of these fish at the release site possibly due transmitter failure and low detection range (< 75 m due to thermocline). Based on these results, Westmeyer et al. (2007) concluded that red snapper had high short-term fidelity and low long-term fidelity.

Both ultrasonic-telemetry and tag-recapture studies have estimated residence times over a year with site fidelity estimates over 50% year^{-1}. Despite similar estimates, interpretation (i.e. high vs low) of these fidelity rates differ (Schroepfer and Szedlmayer 2006; Strelcheck et al. 2007). Also, previous tagging and telemetry studies have only addressed movements and residency of smaller fish (< 500 TL), with the exception of Szedlmayer and Schroepfer (2005) and Schroepfer and Szedlmayer (2006). Red snapper can attain sizes up to meter or more, so questions still remain on the residency time of larger red snapper (Szedlmayer and Shipp 1994; Wilson and Nieland 2001). This lack of information on larger red snapper leaves large gaps in the understanding of red snapper movements and residency. In addition, information is still needed on long-term seasonal and diel movements around natural and artificial habitats.

Red snapper appear to move away from artificial structures at night (Peabody 2004; Szedlmayer and Schroepfer 2005). This may be in response to more feeding over open habitat prey types with the darkness providing predation protection or that certain prey types were more active at night (Ouzts and Szedlmayer 2003; McCawley and Cowan 2007). No other studies have examined diel patterns of movement, and further studies are needed to help clarify the importance of different habitats for this species.

Emigration from reef structures have been attributed to hurricanes (Watterson et al. 1998; Patterson et al. 2001) and cold fronts (Moe 1963; Moseley 1966; Bradley and Bryan 1975). These studies that attributed increased movements to hurricanes were based on a greater dispersal of recaptures after storm events, but could not examine the exact point when fish emigrated. Early studies also suggested an inshore-offshore movement for red snapper presumed to be related to changes in temperature or cold fronts, but were only based on seasonal distribution of fishery catches. Resolving some of the factors that may trigger red snapper movements (emigration and immigration) at both artificial and natural habitats would help determine why these fish are associated with these structures.

In the present study, long-term (> 3 years) telemetry monitoring methods were used to assess site fidelity, residency, and movements of red snapper at artificial habitat sites and a natural habitat site. Strategically placed remote telemetry receivers and long-term transmitters (~5 years) were used to assess these aspects of red snapper ecology. In addition, diel and seasonal movement patterns were examined along with factors that may have influenced these behaviors.

METHODS

Red snapper were tagged with Vemco or Sonotronics transmitters and monitored at five sites (Figure 1-1) with VR2 or SUR remote receiver arrays over a 3-year period. For details of site descriptions, tagging procedures, and receiver array design see Chapter 1. These arrays were designed to detect mortality (fishing and natural) and emigration of red snapper released at each site, based on specific detection patterns (Figure 1-3). The estimates of natural and fishing mortality were necessary to accurately assess site fidelity and residence time with event analysis (Schroepfer and Szedlmayer 2006).

Detection range and frequency validation.— A stationary control transmitter was placed 400 m south of the center receiver at each site (except for A4) to account for possible environmental effects on detection range and frequency, and interference due to "signal collisions" of Vemco transmitters when multiple tagged fish were present at a study site. The mean detection range (averaged across sites and days) was based on the percentage of the maximum expected detections of the control transmitter by receivers as distance from the control transmitter increased (center, C = 400 m; south, S = 700 m; east, E = 1170 m; west, W = 1170 m; north, N = 1500 m; Figure 1-2). The maximum expected detections for an individual transmitter was determined from the relation between the number of transmitters present and the detection frequency of individual transmitters. Transmitters were placed next (< 15 cm) to a VR2 receiver (in air) and the total detections of each transmitter were recorded for 1 h before transmitter number was increased (+ 1). The detections of control transmitters at each study site were then compared to the expected detection frequency based on the number of tagged fish present (+ control; i.e. number of transmitters present) at each site and converted to a percent of expected detections. The detection rate of the control transmitter was also used as a calibration measure for environmental effects on detection rates. The effects of abiotic factors (wave height, wind speed, water temperature, thermocline) on detection frequency were examined with a stepwise multiple regression (Cody and Smith 2006). Wind speed and wave height were obtained from NOAA buoy station 42040 (102 km S of Mobile Bay). Continuous water temperatures (1-h resolution) were recorded throughout the study by waterproof temperature loggers (Onset HOBO® U22 Water Temp Pro v2) moored at the bottom (~20 – 30 m) and midwater (~15 m) at each site. Receivers were coated in antifouling paint to prevent signal occlusion from biofouling (Heupel et al. 2008)

Residency and site fidelity estimation.—Residence time was estimated with event analysis, which calculates the survival function *S*(*t*), the probability (*S*) or proportion of fish residing at the site over time (*t*). Emigration (event) times were analyzed by the product limit method of Kaplan and Meier (1958). This method allows for right censoring of fish that have not experienced an event by the time of analysis (fish still present) or were removed by means not related to the events under analysis (fishing and natural mortalities). The Lifetest procedure in the statistical analysis system program (SAS) was used to estimate the Kaplan-Meier (K-M) survival function (Chambers and Leggett 1989; Allison 1995; Schroepfer and Szedlmayer 2006). This analysis estimated residence to the site at t assuming fish were released on the same day and examined the entire distribution of emigration and right censor times. Median residence time is the number of days when only 50% of the fish still reside at the sites. Site fidelity was then defined as the proportion of fish remaining at the sites at 365 d. The K-M survival (residence) function $S(t)$ is defined as the proportion of individuals residing to t:

$$\hat{S}(t) = \Pi_{tj \leq t}(1 - d_j / r_j),$$

where t is the time over which residence is estimated from the product of the conditional probabilities of residence at each emigration j, and where d_j represents the number of individuals that emigrated and r_j represents the number of individuals at risk of an emigration at time t_j (Kaplan and Meier 1958). Variances and 95% confidence intervals for K-M residence estimates were defined by Cox and Oakes (1984) and Pollock et al. (1989) as:

$$\mathrm{Var}[\hat{S}(t)] = [\hat{S}(t)]^2 \, [1 - \hat{S}(t)] \, / \, r(t),$$

$$[\hat{S}(t)] \pm 1.96[\mathrm{var}\ \hat{S}(t)]^{½}.$$

Wide area surveys.— It was expected that some fish would migrate away from the study site (Szedlmayer and Schroepfer 2005). Attempts were made twice per year to relocate these fish outside each of the 12 km^2 study sites by setting up a grid of listening stations surrounding the site. A Vemco VR2 receiver was deployed from the surface to a depth of 10 m for 10 min every 1.5 km around each study site (Figure 2-1). There were 18 stations per site (2 complete rings around release habitat) that covered a total of 40 km^2 of search area around each study site.

Data analysis.— Residency and site fidelity were estimated based on an event analysis method, which considers emigrating completely out of the study site an event, and fish that did not emigrate were right censored at the time of their last known presence at the study sites (Chambers and Leggett 1989; Ohta and Kakuma 2005; Schroepfer and Szedlmayer 2006). The effect of fish size (TL) on residence time was tested with a log-rank test of association within the SAS Lifetest procedure (Kalbfleisch and Prentice 1980). Log-rank tests for homogeneity (Lifetest procedure) were used to compare between various residence curves (Klein and Moeschberger 1997). The number of fish emigrating in each season was compared to the null hypothesis of equal proportions of fish emigrating each season (summer, 21 June; fall, 23 September; winter, 21 December; spring, 21 March) with a likelihood ratio chi-square test to examine seasonal emigration. A likelihood ratio chi-square test was also used to test whether equal proportions of fish emigrated from the release site in a N, S, E, and W direction. These proportions also include directions for fish that relocated to other habitats within the detection range of N, S, E, or W receivers at a study site and movement to other study sites.

Patterns of movement and emigration were compared to environmental factors (water temperature, wave height, wind speeds, cold fronts, hurricanes). Estimates of residency and emigration were derived from both Sonotronics and Vemco telemetry data, but due to differences in technology, only Vemco VR2 receiver data (with V16 transmitters) were used for movement pattern analysis (sites A1, A2, A3, and N1). To examine periodicity of detections, a Fast Fourier Transformation (FFT) was applied to a continuous time series of the total number of detections per hour at the center receiver (Peabody 2004, Meyer et al. 2007). A local regression (LOESS procedure, SAS; Cleveland 1979; Cleveland and Devlin 1988; Cohen 1999) was also used to examine diel periodicity of movements from detection rate at 1-h intervals. The LOESS procedure can determine the pattern of diel movements away from the center receiver (assuming lower detections when fish are further away) or toward the surrounding receivers (increase in detections as fish move toward N, S, E, and W) by using a local regression to estimate regression surfaces fitted to data points (total detections/h) within a chosen neighborhood (smoothing factor) of each value of the independent variable (Cleveland 1979; Cleveland and Devlin 1988; Cohen 1999; Peabody 2004). The smoothing parameter was determined from the SmoothSelect macro in SAS, which selects the smoothing parameter that yields the smallest AIC_{C1} statistic (Cohen 1999). The same time series used for the FFT analysis was analyzed with LOESS. Total detections/h on the center receiver and the combined total detections/h on outside receivers (N, S, E, W) for fish at a site were obtained each hour over 24-h diel cycles (0000 - 2300 hours), with each day of the time series yielding one data point for each 1-h period. The detections on the outside receivers were combined due to fish moving in different directions from the reef. Statistical differences were all considered significant at $P \leq 0.05$.

RESULTS

Detection Range and Frequency Validation

Mean detections transmitter^{-1} h^{-1} significantly decreased as the number of transmitters present next to a VR2 receiver was increased, and was described by a negative logarithmic relation ($R^2 = 0.99$, $P < 0.0001$; Figure 2-2). Detections transmitter^{-1} h^{-1} decreased from 92 for 1 transmitter present to 15 detections transmitter^{-1} h^{-1} when 15 transmitters were present. Total detections/h increased to a maximum of 280 when 9 transmitters were present, but total detections decreased when more than 10 transmitters were present due to excessive signal collisions ($R^2 = 0.95$; Figure 2-2). Based on these results, a maximum of 10 transmitters (fish + control) was not exceeded at each release site.

The relation between number of tagged fish present and detection rate was used to estimate the maximum detections expected at each site for each day. A fish was considered present at a particular site only after it was detected a minimum of five times at that site for a particular day. The percentage of maximum expected detection rate was estimated over the dates the controls were present (June 2006 - August 2008) and over the distances these controls were placed away from the C, S, E, W, and N VR2s (Figure

2-3). There were seasonal periods when control transmitter detection rates were reduced below expected rates due to reduced detection ranges (Figure 2-3). Mean percent of expected detections at 400 m was reasonably high (mean 79 ± 14% , SD; Figure 2-4) ranging from 60% (N1) to 90% (A3) over the study period. Estimates were about 25% lower at site N1 at 400 m than at all other sites, which may be due shallower depths (20 m [N1] vs 30 m [A1, A2, A3]). Based on the predicted relation of the mean percent of maximum expected detections of the control transmitter to receiver distance ($R^2 = 0.98$, $P = 0.03$), the mean percentage of expected detections was about 46% at 800 m and 65% at 700 m, with individual sites ranging from 60% (N1) to 80% (A3; Figure 2-4).

Variability in detection rate of the control transmitter by the C, S, E, and W receivers was not significantly affected by wave height or wind speed, but water temperature and the absolute difference between water temperatures at a depth of 30 m and 15 m (i.e. strength of thermocline) both significantly affected detections of the control transmitter. The detections of the control transmitter by the center VR2 receiver significantly decreased as water temperature increased at the bottom at each site (Partial $R^2 = 0.34$; Figure 2-5, Table 2-2). The mean detections of the control transmitter by the E, W, and S VR2s were significantly affected by the absolute difference in water temperatures between the bottom and mid-water (Partial $R^2 = 0.45$; Figure 2-6, Table 2-2). Water temperature was also positively correlated with absolute temperature difference (Pearson's $r = 0.36$, $P < 0.0001$), so it was difficult to separate these effects. Wind speed and wave height were removed from the model because partial $R^2 < 0.05$. The stepwise regression indicated absolute temperature difference was more important in the model than wind speed and wave height, but absolute temperature difference was negatively correlated to wind speed ($r = -0.45$, $P < 0.0001$), and wind speed was positively correlated to wave height ($r = 0.80$, $P < 0.0001$). This result suggests that wind speed and wave height help to mix the water column, reducing temperature differences between the bottom and mid-water.

Residence Time and Site Fidelity

Red snapper ($n = 87$) were monitored at five different sites (A1-A4, N1; Figure 1-1) for up to 1100 d (December 2005 to December 2008). Red snapper size range was 501 to 860 mm TL, with a mean of 639 mm (SD = 85 mm). Fish either remained present at the site, emigrated, died, or were removed by fishers, as determined by detections from the five receivers at each site and by fisher returns (Table 2-1; Figure 2-7). Individual fish were detected at sites from 1 to 829 d (Table 2-1). Within 6 d of release, 14 fish emigrated, 2 died, and 1 was undetermined. After this initial post-release effect (< 6 d), it appeared that fish recovered and assumed normal movement behavior. Past this 6-d recovery period the minimum residence time was 28 d (max, 829). The movements or deaths of these 17 fish (within 6 d of release) were assumed to be related to post-release behaviors or mortality. Fish 31 showed this post-release emigration behavior (Figure 2-8). One day after being released at site A3, this fish was detected at three separate sites. Overall it moved 20 km, from A3 to A2, then to A1, then back to A2 in a 24-h period, and then remained resident to that area for 758 d (until hurricane Gustav). None of the other fish that left within 6 d of release were detected again or returned by fishers at the time of analysis (17 December 2008; Table 2-1). The fate of five fish was unknown following their last detection due to failure of an outside receiver or during a hurricane when detection range was affected. These fish were assumed to have emigrated based on the data from other receivers at that site.

Residence time estimates derived from the K-M event analysis method varied slightly depending on the data set used in the analysis. The most accurate estimate was calculated after the removal of the 17 fish leaving or dying immediately after tagging (< 6 d), since this behavior appeared to be related to capture or tagging. Red snapper (n = 70 fish) median residence time (when 50% of fish still present) was 572 d (333 to 810 d, 95% confidence limits [CL]). The annual site fidelity estimate was 68% year^{-1} (Figure 2-9). A log-rank test of association did not detect a significant effect of fish size (TL) on residence time (P = 0.55). When fish with residence times < 6 d were included in the analysis (N = 87 fish) , median residence time was reduced to 411 d (270 to 553 d, 95% CL); however, a log-rank test of homogeneity did not detect a significant difference between these two K-M residence (survival) plots (P = 0.08; Figure 2-9). The K-M plot derived from all 87 fish showed a steep initial slope, after which this slope showed the same pattern (slower rate of emigration) as the plot of fish with > 6 d residence. The site fidelity estimate with all fish considered was 56% year^{-1} (Figure 2-9). The estimate of residence time was also affected by hurricanes Gustav and Ike. The estimate of median residence time (N = 70) just before these storms was 733 d (377 to 1088 d, 95% CL), with 13 fish classified as emigrations and 3 unknown (Figure 2-10). Just after the storms, median residence time was reduced to 572 d (340 to 803 d, 95% CL), with 18 fish classified as emigrations and 5 unknown (Figure 2-10). These additional emigrations due to the hurricanes caused little change in the site fidelity estimates (77% year^{-1} to 73% year^{-1}; Figure 2-10). There was an apparent increase in emigration associated with strong cold fronts in November 2008 that reduced the site fidelity estimate to 68% year^{-1}.

Storm Effects on Movement Patterns

Some fish (N = 13) showed movement patterns related to storms. Seven emigrations appeared to occur during or just after hurricanes Gustav (31 August 2008) and Ike (11 September 2008). During these storms, wave heights in the study area were as high as 11 m and wind gusts as high as 100 km/h, which reduced detection range and made it difficult to determine the fate of these fish. At least one fish died during these storms based on detections before and after storm (e.g. Figure 1-3). Before the storm 26 fish were present, and immediately after the storm 18 fish were left. One fish (#87) at site N1 that was lost after these hurricanes, returned two months later (24 October 2008) from the east, remained a month, then this fish and three others emigrated to the east at the end of November 2008. These latter movements in November were during or right after several cold fronts passed over the area (Fish#s 74, 82, 86, 87 ; Figure 2-7). Fish 22 also showed movements associated with cold fronts and hurricanes. These movements were to another site ~2 km ESE of site A1 that was located during a wide area survey. This large fish (815 mm TL) moved regularly to this alternate site, with winter spent at the release site and spring and summer spent at the alternative site over two years (Figure 2-11). Another large red snapper (Fish 70) released at site A3 on 29 November 2007 moved to site A1 (~ 6 km apart) on two separate occasions, staying at the alternate site for up to 21 d before returning to the release site and was still detected as of fall 2008. These directed movements all occurred as strong storm fronts passed over the study sites around 19 January, 25 January, 13 February, and 6 March 2008. The movement time between study sites (6 km) was relatively short (1.3 to 4.8 h) compared to the residence time of this fish at those sites (Figure 2-12). Ten fish moved to other locations, but returned to their release sites after long-term absences up to 7 months, with some fish staying for the remainder of the study or again emigrating from the site.

The number of fish ($N = 25$) emigrating from the 12-km^2 study sites in each season was compared to the null hypothesis of equal proportions of fish emigrating each season. There was a significant difference in the proportions (vs equal) of fish emigrating in summer (48%), winter (28%), fall (20%), and spring (4%; $P = 0.01$). There were also significant differences in the direction that fish emigrated from the release site with 51% to the E, 26% to the S, 11% to the N, and 11% to the W ($P = 0.003$).

Diel Movement Patterns

Diel patterns were detected that showed red snapper would move away from the reef sites at night. A time series of total detections/h for 10 fish (released at site A1) from 12 January 2006 to 31 March 2006 (just prior to capture of these fish) was obtained for FFT spectral analysis. The periodogram created from the spectral analysis had a strong peak at a period of 24.0 h/cycle that indicated a daily sinusoidal cycle in detection frequencies (Figure 2-13). These data were also analyzed with the LOESS procedure (local regression), with a datum point of total detections/h from each 1-h period of each day ($n = 78$ d). Detections at the center receiver (near the structure) were greater during daylight hours (0700 - 1500 hours), with a peak in detections at 0700 hours (around sunrise for this time of year). Pooled detections at the outside receivers (1.1 km away) were lowest at sunrise (0700 hours) and tended to increase throughout the day, with a maximum at 1500 hours and remaining relatively high throughout the night (Figure 2-14). Based on data that showed detections decreased as the transmitters were further from receivers, fish showing these patterns ($n = 42$) were in close proximity to the reef at sunrise and gradually moved further from reefs toward the end of the day and at night, again remaining close to the reef around sunrise (e.g., Figure 2-14).

Not all fish at all sites showed movement away from the structure at night, and fish that did move away from the structure at night did not do so every night. For example, Fish 1493, showed movement away from the structure during both night and day, but only in July 2008 (Figure 2-15, 2-16). Movements away from the structure from 1 July to 18 Jul 2008 were significantly directed toward the west, as shown by a negative correlation between detections/h at the center and the west receivers (Pearson's correlation: $r = -0.72$, $P < 0.0001$), with the other receivers only having weak correlations with detections at the center. Fish 1493 also had higher detections at the west receiver than the center receiver over several days (extended periods away from the release site) and suggested that this fish was moving between the release site and another structure ~1 km to the west. Movement patterns of Fish 1493 were also significantly correlated with tidal stage, but it was difficult to isolate tidal effects from diel effects, because tidal cycles were significantly correlated to diel cycles ($r = 0.41$, $P < 0.0001$). The influence of both tide and diel periods on Fish 1493 detections/h by the west receiver were analyzed for each day (1 July - 18 July 2008) with a stepwise regression. Over this 18-d period, detections on 12 d were significantly affected by diel period (R^2 range: 0.09 - 0.65, $P < 0.02$) and detections on 7 d were significantly affected by tidal cycles (R^2 range: 0.19 - 0.72, $P < 0.006$). All r values (correlation coefficient) were negative, indicating Fish 1493 tended to move toward the west during low tides and at lower light levels (e.g., Figure 2-15).

DISCUSSION

The residence, site fidelity, and movement patterns of red snapper around various structured habitats off Alabama were successfully estimated with long-term continuous telemetry. The design of the receiver arrays in this study proved successful in monitoring red snapper movements around artificial and natural habitats in an open water system. To date, this study is the longest telemetry study for red snapper, which probably contributed to the highest residence time and site fidelity estimates obtained for this species at artificial habitats, with many fish resident for over a year (*n* = 25) and some as long as two years (*n* = 4). The higher estimates of median residence time (572 d) and site fidelity (up to 77%) were also due to concurrently estimating natural mortality, fishing mortality, and post-release behaviors. The size of the fish used (> 500 mm TL) provided the opportunity for the use of long-life transmitters (4 to 6 years) that had large detection ranges (up to 1600 m). The use of these transmitters may account for the longer residence time and higher fidelity estimates compared to studies with smaller red snapper (< 500 mm) and shorter-lived transmitters (Peabody 2004; McDonough 2009). Also, unique to this study was the use of stationary control transmitters that allowed for far more accurate estimation of mortality, movement patterns, and residence.

Detection Range and Frequency Validation

Residence studies typically release multiple fish at one location, but do not account for changes in detection frequency that are related to different numbers of tagged fish present. Multiple Vemco Rcode transmitters within the detection range of a receiver significantly affected detection frequency of individual transmitters due to signal collisions of transmitters with the same frequency (kHz) that have pseudo-random ID code intervals (e.g. pulse train every 20 - 69 s in this study). Although the effects of multiple transmitters (present at one location) on the individual detection rate of those transmitters were described and have been previously considered in study designs (Vemco), these effects are typically ignored (assumed constant) during the study.

In the present study, significant changes in detections of the stationary control transmitter occurred as fish left or were added to a site. If ignored, these detection changes would be interpreted as seasonal movement patterns. The rate of signal collisions that cause individual transmitters to have fewer detections when other transmitters are present is most affected by the time interval between coded pulse trains (Vemco, personal communication). The 20 - 69 s "pseudo-random" pulse interval used in this study was an appropriate balance between fewer signal collisions (at greater intervals) and shorter intervals needed to detect fish emigrating from the site. It may have been possible to use an even higher interval and still detect emigration based on the typical time difference (~30 min) between a fish's last detection on the center and outside receivers during an emigration. Rarely did fish emigrate at the same time, so signal collisions did not significantly affect our ability to detect fish passing by outside receivers as they left the site. Since detection range was frequently > 1 km, fish were consistently detected by outside receivers when still present at the release site, but at a reduced rate compared to the detections at the center.

Seasonal detection rate of individual fish were affected by the release and removal of fish at each site over the study. There was additional variability in seasonal detection rate attributed to environmental variables (water temperature and thermocline), which were only detected due to the deployment of the control transmitter. Peabody (2004) experienced a significant reduction in detection rate when a “strong” thermocline developed between the fish (below the thermocline) and VR2 receivers (above the thermocline). Since VR2s in the present study were moored at similar depths where red snapper were present (near the bottom), when a thermocline developed, the detection rate of the control transmitter actually increased. This was probably due to sound propagation within a zone in the water column of similar density (Brumbaugh, Sonotronics, inc.).

Telemetry studies should consider detection range changes when determining seasonal movements from detection frequencies (e.g. Arendt et al. 2001; Starr et al. 2002; Szedlmayer and Schroepfer 2005; Topping et al. 2006; Meyer et al. 2007). A number of studies have tested the detection range of the transmitters used in their fish, but these tests are typically short term, before permanent array deployment (Arendt et al. 2001; Simpfendorfer et al. 2002; Finstad et al. 2005; Giacalone et al. 2005; Szedlmayer and Schroepfer 2005; Heupel et al. 2006). Topping et al. (2006) manually tracked a fish implanted with both a constant pinger and a coded transmitter to compare actual movements of the fish from surface tracking of the constant pinger to detections of this fish on VR2s. Hedger et al. 2008 conducted simulated tracks (pulling transmitters with a boat) to determine accuracy of position estimation. While these short-term tests are important for understanding detection rates related to movements of fish, they cannot account for seasonal variability. The mean detection rate (percentage of expected detections) determined at increasing distances from the control transmitter in the present study was similar to detection range estimates from Szedlmayer and Schroepfer (2005). Both this study and Szedlmayer and Schroepfer (2005) had a detection rate as high as 100% at 600 m, a steep drop to 50% at 800 m, and a maximum detection distance of 1600 m. In the present study, the mean detection range significantly changed over the study, but was adequate (~80% at 400 m) to sufficiently detect fish leaving the site.

Residence Time and Site Fidelity

Telemetry studies of red snapper and other species have detected an initial post-release emigration behavior of some tagged fish that is likely related to capture and handling stress associated with tagging procedures (Gurshin and Szedlmayer 2004; Peabody 2004; Schroepfer and Szedlmayer 2006; McDonough 2009). Initial high declines (emigration plus mortality in this study) are typically referred to as the "bathtub effect" in post-surgery survival studies, and survival (i.e. emigration) rates quickly 'level off' after this initial loss (Gavrilov and Gavrilova 1991). In this study, 15 of the 87 (17%) released fish emigrated (and 2 died) within the first 6 d. These fish were never detected again and were not reported as captured by fishers. In Schroepfer and Szedlmayer (2006), 12 of 77 red snapper were "lost" within 3 d and they considered this initial loss of fish a tagging artifact. Peabody (2004) released 125 red snapper, but never detected 28 (22%) of these fish at the study sites, and they were never reported caught by fishers. McDonough (2009) released fish at the same oil rigs ("the Circle") as Peabody (2004) and had at least 53% (of 36 fish) leave the site (or were not detected) within the 14-d study period. The early emigrations are most likely due to capture and tagging stress and after some initial recovery period the remaining fish show a significantly lower emigration rate (Figure 2-4). This information should be valuable for obtaining estimates of dispersal rates due to catch and release management strategies.

Since traditional mark-recapture studies cannot constantly monitor the presence or absence of tagged fish at study sites, it is uncertain if red snapper in these studies show the same initial post-release behavior (and mortality). If all tagging methods cause this behavior then previous estimates of site fidelity and residence time based on mark-recapture may be lower than actual "normal" red snapper behavior because conventional tagging can not account for this effect (Szedlmayer and Shipp 1994; Patterson et al. 2001; Patterson and Cowan 2003; Diamond et al. 2007; Strelcheck et al. 2007). Patterson and Cowan (2003) calculated a site fidelity (SF = e^{-Q}; Q = instantaneous emigration rate) of approximately 25% year^{-1}, with an instantaneous rate of decline of recaptures D = 1.47/year for fish at their site and assuming no fishing mortality, where Q = D – instantaneous total mortality (Z = 0.09). Strelcheck et al. (2007) estimated an overall SF of 51.5% year^{-1} from a D = 0.72/year, assuming a Z or M of 0.10 (no fishing mortality). Estimation of *"D"* from the total losses of fish at sites in the present study was 1.15/year with a SF estimate of 68% year^{-1}. The difference in these two estimates was probably due to the ability in the present study to account for fishing mortality, natural mortality, emigration, and initial stress response (emigration and mortality).

Another factor that may have attributed to differences in site fidelity estimates between previous and the present study was differences in tagged fish size. Two main hypotheses of size effects have been suggested to explain relations in movement patterns: 1) larger fish may move more since their size may make them less susceptible to predation or 2) smaller fish may move more or show less fidelity due to competitive exclusion from preferred habitat by larger conspecifics (Szedlmayer and Schroepfer 2005; Strelcheck et al. 2007). This study had the largest mean fish sizes for any red snapper tagging study (mean: 639 mm), and fish size did not affect residence time for the size range monitored (501 to 860 mm TL). Szedlmayer and Schroepfer (2005) also were unable to correlate residence time to fish size, but did find that larger red snapper spent less time within receiver range. Patterson et al. (2001) found that movements away from tagging sites increased with fish size, and Diamond et al. (2007) also showed a fish size effect where larger fish had a greater probability of movement. Patterson et al. (2001) and Diamond et al. (2007) tagged much smaller fish on average (Patterson et al. 2001, 335 mm; Diamond et al. 2007, 363 mm TL [TTU tagging]) compared to the present study. Peabody (2004) used telemetry methods for smaller red snapper on oil rigs, and estimated shorter residence times than found in the present study; however, this difference in residence may have also been affected by habitat, transmitter life (~200 vs 2000 d nominal battery life), and thermocline rather than fish size.

The spatial scale that site fidelity has been estimated is inconsistent and may affect what constitutes high site fidelity of red snapper (Schroepfer and Szedlmayer 2006; Strelcheck et al. 2007). McDonough (2009) suggested that a better approach for estimating site fidelity should be in the context of a fish's home range (rather than the detection range of the transmitters used). The spatial scale of site fidelity should be defined; however, definitions of home range can vary from daily activity spaces to seasonal area use, and measurements of home range tend to increase with temporal scale (Zeller 1997; Heupel et al. 2004; Topping et al. 2005; Topping et al. 2006). Strelcheck et al. (2007) suggested that since red snapper can live up to 50 years (Wilson and Nieland 2001, they show relatively low site fidelity to small artificial reefs (0.1% of fish remaining after 10 years). As shown in the present study, red snapper will stay at one artificial site for extended periods then quickly move over open sand-mud habitat to another artificial site for extended periods. If only the first site was considered it might be concluded that red snapper showed low site fidelity to artificial reefs, but high habitat fidelity is apparent when accounting for movement and residency to a second artificial reef. Thus, the demonstration of residence to a single structure may not be as important as the overall high use of these types of habitats. The general residence to areas that are subjected to more intense fishing pressure, such as the Hugh Swingle General Permit Area, has been suggested by Strelcheck et al. (2007) to be detrimental to red snapper. However, there are a high number of artificial structures in this area with a range of fishing mortalities (see Chapter 1), and many of these structures were privately deployed with unpublished locations or have been relocated to unknown locations by hurricanes

(Minton and Heath 1998; Turpin and Bortone 2002; Larsen 2005). These “private” unpublished structures may provide benefits to red snapper that offset any higher fishing mortality at “public” (published) reefs (Turpin and Bortone 2002; Larsen 2005).

Long-Term Movement Patterns

The directed movements (e.g. 8 km in 1.6 h) of some red snapper in this study to other structured habitats indicates possible previous knowledge of these alternate sites. For example, Fish 70 emigrated from its original site (A3) to another site (A1), then returned to A3. The movements to and from different habitat structures may provide benefits that make up for the expenditure of energy associated with excursions (Wakeman et al. 1979). Consistent with this idea of ecological benefit for “movers,” Diamond et al. (2007) showed higher growth rates for movers compared to “stayers.”

Movement to and from particular habitats appears important to other fish species, and has been shown in homing studies (Mathews 1990; Mitamura et al. 2005). Homing of red snapper has not been verified in other tagging studies that have translocated fish to other habitats, but these fish did tend to leave the release site at a higher rate than non-translocated fish (Watterson et al. 1998; Patterson et al. 2001; Peabody 2004). Patterson et al. (2001) had one (out of 111) fish return to the original capture site, but this may have been due to random chance since other fish released were caught at other tagging sites that were not the original capture site. Peabody (2004) also had fish move to other sites, with no returns to the original capture site. The present study is the first to show red snapper returning to their original release site after emigrating distances as far as 8 km, and being absent for as long as seven months.

It is uncertain what causes red snapper to move from one artificial habitat to another. Most likely it is a balance of available prey, shelter, and spawning opportunities, and different artificial reefs probably provide differing levels of these resources (e.g. Matthews 1990). This balance may have been shown by Fish 22, which was generally present at the release site in winter and moved to a nearby alternate site in spring and summer (spawning period) over two consecutive years (Figure 2-11). This fish showed movements to and from sites that appeared related to cold fronts in both fall and spring, and hurricanes in August. It is possible these storms triggered a movement to a structure that provided better protection. Overall, seven fish were lost during hurricanes Gustav and Ike, but most fish (73%) remained at study sites, despite waves to 11 m and winds up to 100 km/h. Mark-recapture studies have detected greater dispersal of red snapper from recaptures after hurricanes (Watterson et al. 1998; Patterson et al. 2001). In contrast, the present study was similar to other telemetry studies that showed most red snapper remained resident to reef structures through major hurricanes (Szedlmayer and Schroepfer 2005; Peabody 2004). Differences in hurricane related dispersal between studies may be due to differences in reef type and size, with fish remaining on larger, stable structures (Watterson et al. 1998; Patterson et al. 2001; Szedlmayer and Schroepfer 2005; Peabody 2004). Seasonal differences in emigration were also detected, with most emigration occurring in the summer (48%) and winter (28%). Also, a greater proportion of these emigrations of red snapper were toward the east (51%). Other studies of red snapper in the northern GOM have also detected this eastward component to recaptures or relocations (Beaumariage 1969; Watterson et al. 1998; Peterson et al. 2001; Peabody 2004). Other studies have attributed these eastward displacements to hurricanes, or to higher fishing pressure to the east, which would produce a similar result even if fish randomly dispersed at various directions from the study site (Patterson et al. 2001). In the present study, 95% of fisher recaptures were at the release sites and most fish remained at sites through the hurricanes. Another possible cause may be the pattern of cold fronts that move from west to east. For example, site N1 was the shallowest site and might be more affected by cold fronts compared to deeper sites. In November 2008, four fish emigrated from this site towards the east right before or after several cold fronts, so it is possible that these fish were avoiding wave action and cold water masses by moving to deeper sites as suggested by Moseley (1966).

Diel movements

Diel movement patterns were detected for red snapper in this study, and patterns were similar to diel movements described from previous telemetry studies of red snapper and other lutjanids (Peabody 2004; Lindholm et al. 2005; Szedlmayer and Schroepfer 2005; Meyer et al. 2007; McDonough 2009). Detection patterns showed diel movements for fish over all seasons; however, some fish only showed diel patterns during specific seasons (e.g. Fish 21; Figure 2-15) and patterns were not always consistent each day. When patterns were detected, fish moved away from the structure late in the day or at sunset and returned sometime before sunrise. Both Peabody (2004) and Szedlmayer and

Schroepfer (2005) indicated red snapper moved away from the reef at night from a decrease in detections of fish by a central receiver. Other telemetry studies have also shown detections decreased at night, but these patterns were attributed to movement into structure rather than movement away from structure (Arendt et al. 2001; Giacalone et al. 2005; Topping et al. 2006). In the present study, detections also increased at surrounding receivers when detections decreased at the center receiver, thus movement away from structure was validated, and supports the results of Peabody (2004) and Szedlmayer and Schroepfer (2005). Szedlmayer and Schroepfer (2005) used transmitters comparable to this study, and found some fish (*N* = 4) showed diel patterns, with varied results between day and night detections, but their detection of short diel movements from the reef may have been limited by the low spatial resolution as a result of the detection ranges of these transmitters (800 m). The diel movements for large red snapper in this study were relatively consistent with patterns for smaller red snapper monitored by Peabody (2004) at oil platforms. In contrast, McDonough (2009) found red snapper were significantly further from the same platforms during the day than at night during a short-term telemetry study (14 d) in late spring and early summer. These spatial and temporal differences in diel movement patterns in these telemetry studies may indicate that habitat use (reef vs sand) may vary with season and location, and may be due to seasonal or daily changes in diets (Outz and Szedlmayer 2003; McCawley and Cowan 2007). Variability of reef and sand organisms in diets of red snapper during both day and night, and over seasons, may result in diel movement variation that simply reflects food availability near the structure over diel and seasonal cycles (Outz and Szedlmayer 2003; McCawley and Cowan 2007).

In summary, this three-year study showed long-term residence of red snapper at both artificial and natural habitats in the northern Gulf of Mexico. The design of the receiver arrays deployed at each site and the type of transmitter (long-term and long-range) used enabled continuous monitoring of fish within a relatively large area (12 km^2). The addition of a control transmitter to the design of this telemetry array showed that detection rates were affected by environmental variables and need to be considered in future telemetry studies. These telemetry methods provided estimates of residence that took into account natural mortality, fishing mortality, and post-release behaviors. The consideration of these factors and length of this study have contributed to higher site fidelity rates (68 - 77% $year^{-1}$) and longer residence times (median: 572 d, range: 20 - 829 d) of red snapper to artificial and natural habitat types than previously reported in other tagging studies. An important fact to point out is that the fish tagged at each site were present for some undetermined amount of time prior to their initial capture at that structure, as is true in other tagging studies. Thus, residence time and fidelity are underestimated in all tagging studies. Though fidelity of most fish to the original release location was high, some fish did move around the release site, and others emigrated to other sites. This is the first study to detect directed movements to and from artificial habitat sites as far as 8 km. Movements away from an artificial structure may occur for various reasons and seemed to occur randomly in this study, with only seasons having any significant effect on timing of emigration in this study, and this seasonal effect appears partially related to hurricanes and cold fronts. Diel movements are probably related to foraging behavior as indicated by some diel diet shifts shown in previous studies (Outz and Szedlmayer 2003), but these movements were not consistent among different fish or seasons. These movement patterns showed red snapper had a strong association with these artificial habitats, and this implies that these artificial reefs provide suitable habitat for these fish.

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TABLES

Table 2-1. Summary of release information (total length, TL; weight, Wt) and number of days (event time) from release until occurrence of the specified event (emigration, E; fishing mortality, F; natural mortality, M; present, P; unknown, U) for ultrasonically-tagged red snapper at various array sites.

Fish	Release	Site	Wt (kg)	TL (mm)	Event time	Event
1	13 Dec 2005	A1	4.3	660	614	E
2	13 Dec 2005	A1	7.3	800	179	F
3	13 Dec 2005	A1	3.0	590	153	F
4	13 Dec 2005	A1	6.0	710	2	E
5	13 Dec 2005	A1	4.0	630	155	F
6	13 Dec 2005	A1	5.5	695	114	F
7	23 Dec 2005	A1	2.9	580	99	F
8	23 Dec 2005	A1	4.0	620	104	F
9	4 Jan 2006	A1	5.0	630	1	E
10	4 Jan 2006	A1	3.5	520	108	F
11	4 Jan 2006	A1	5.0	553	5	E
12	4 Jan 2006	A1	12.5	860	1	E
13	4 Jan 2006	A1	3.5	540	92	F
14	12 Jan 2006	A1	6.0	700	84	F
15	7 Jun 2006	A1	6.5	746	452	M
16	7 Jun 2006	A1	2.8	545	324	F
17	8 Jun 2006	A1	4.7	672	1	E
18	15 Jun 2006	A1	4.5	683	321	M
19	23 Jun 2006	A4	3.3	586	733	E
20	7 Jul 2006	A4	3.2	600	420	E
21	11 Jul 2006	A1	3.7	620	741	F

(continued)

Fish	Release	Site	Wt (kg)	TL (mm)	Event time	Event
22	11 Jul 2006	A1	8.2	815	829	P
23	27 Jul 2006	A2	5.5	691	0	M
24	28 Jul 2006	A2	9.5	823	411	E
25	28 Jul 2006	A2	5.1	680	227	E
26	28 Jul 2006	A2	5.8	730	322	E
27	9 Aug 2006	A3	7.1	760	3	E
28	9 Aug 2006	A3	4.3	660	406	U
29	11 Aug 2006	A3	3.0	605	215	E
30	14 Aug 2006	A3	2.2	538	120	U
31	14 Aug 2006	A3	2.8	537	758	E
32	14 Aug 2006	A3	3.1	569	362	F
33	21 Aug 2006	A3	6.5	740	124	U
34	21 Aug 2006	A3	2.5	543	1	E
35	7 Feb 2007	A2	3.3	555	530	M
36	7 Feb 2007	A2	5.8	690	572	U
37	7 Feb 2007	A3	2.6	549	4	E
38	7 Feb 2007	A3	3.8	610	28	E
39	7 Feb 2007	A3	4.5	640	534	M
40	7 Feb 2007	A3	3.5	580	1	E
41	7 Feb 2007	A3	4.0	613	57	M
42	6 Mar 2007	A1	5.0	665	6	E
43	6 Mar 2007	A1	4.8	660	46	F
44	3 Apr 2007	A2	5.5	690	144	E
45	3 Apr 2007	A2	5.3	680	1	E
46	12 Apr 2007	A3	2.8	565	479	M
47	12 Apr 2007	A3	2.8	555	122	F

(continued)

Fish	Release	Site	Wt (kg)	TL (mm)	Event time	Event
48	12 Apr 2007	A3	4.5	670	574	P
49	21 May 2007	A2	2.5	550	210	M
50	21 May 2007	A2	11.0	800	489	E
51	12 Jun 2007	A3	2.5	590	493	P
52	27 Jun 2007	A1	6.5	645	478	P
53	3 Jul 2007	A2	5.0	705	30	M
54	9 Jul 2007	A2	5.5	710	487	P
55	9 Jul 2007	A2	5.0	710	20	F
56	9 Jul 2007	A3	3.3	620	466	P
57	9 Jul 2007	A3	5.8	730	182	E
58	25 Jul 2007	A3	4.5	685	450	P
59	25 Jul 2007	A3	3.8	660	450	P
60	25 Jul 2007	A3	6.1	760	167	E
61	29 Aug 2007	A4	3.8	645	339	F
62	29 Aug 2007	A4	2.5	550	477	P
63	29 Aug 2007	A4	3.3	601	332	F
64	29 Aug 2007	A4	5.0	710	379	E
65	5 Sep 2007	A4	3.5	635	332	F
66	13 Nov 2007	A1	5.0	705	339	P
67	14 Nov 2007	A4	3.0	579	400	P
68	20 Nov 2007	A3	3.0	605	286	M
69	29 Nov 2007	A3	4.3	658	239	E
70	29 Nov 2007	A3	9.8	810	323	P
71	11 Dec 2007	N1	3.0	573	265	U
72	11 Dec 2007	N1	2.2	501	80	E
73	11 Dec 2007	N1	2.5	550	6	E

(continued)

Fish	Release	Site	Wt (kg)	TL (mm)	Event time	Event
74	11 Dec 2007	N1	1.9	517	338	E
75	18 Dec 2007	N1	2.6	557	1	U
76	18 Dec 2007	N1	2.2	524	4	E
77	8 Feb 2008	A1	3.6	640	47	M
78	8 Feb 2008	A1	3.3	615	121	F
79	10 Jun 2008	A2	3.8	640	150	P
80	10 Jun 2008	A2	7.8	790	150	P
81	10 Jun 2008	A2	6.0	745	83	E
82	16 Jun 2008	N1	2.3	537	161	E
83	16 Jun 2008	N1	2.8	575	184	P
84	2 Jul 2008	N1	3.6	632	1	M
85	2 Jul 2008	N1	2.0	525	3	E
86	10 Jul 2008	N1	2.2	524	137	E
87	10 Jul 2008	N1	2.0	526	137	E

Table 2-2. Stepwise multiple regression for bottom water temperature and absolute temperature difference between 30 and 15 m depths, on detections of the control transmitter by the center (Model $R^2 = 0.51$) and outside receivers (south, east, west; Model $R^2 = 0.59$).

Location	Variable	Parameter	Partial R^2	P
C	Water temperature	- 31.0	0.34	< 0.0001
$n = 417$	Temperature difference	56.0	0.17	< 0.0001
S, E, W	Temperature difference	81.0	0.45	< 0.0001
$n = 443$	Water temperature	-12.4	0.14	< 0.0001

FIGURES

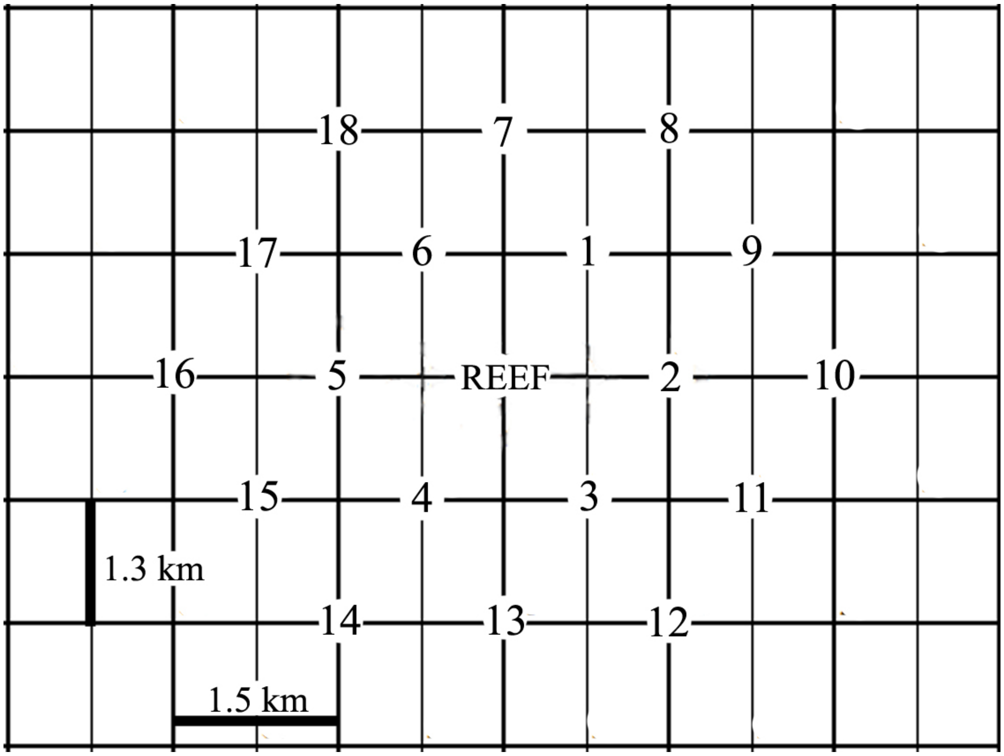

Figure 2-1. Wide area survey grid with numbered listening stations surrounding a single release site. Each location was scanned with a surface (VR60) and submersible (VR2 and SUR) receiver for the presence of fish that may have moved from the release location (reef).

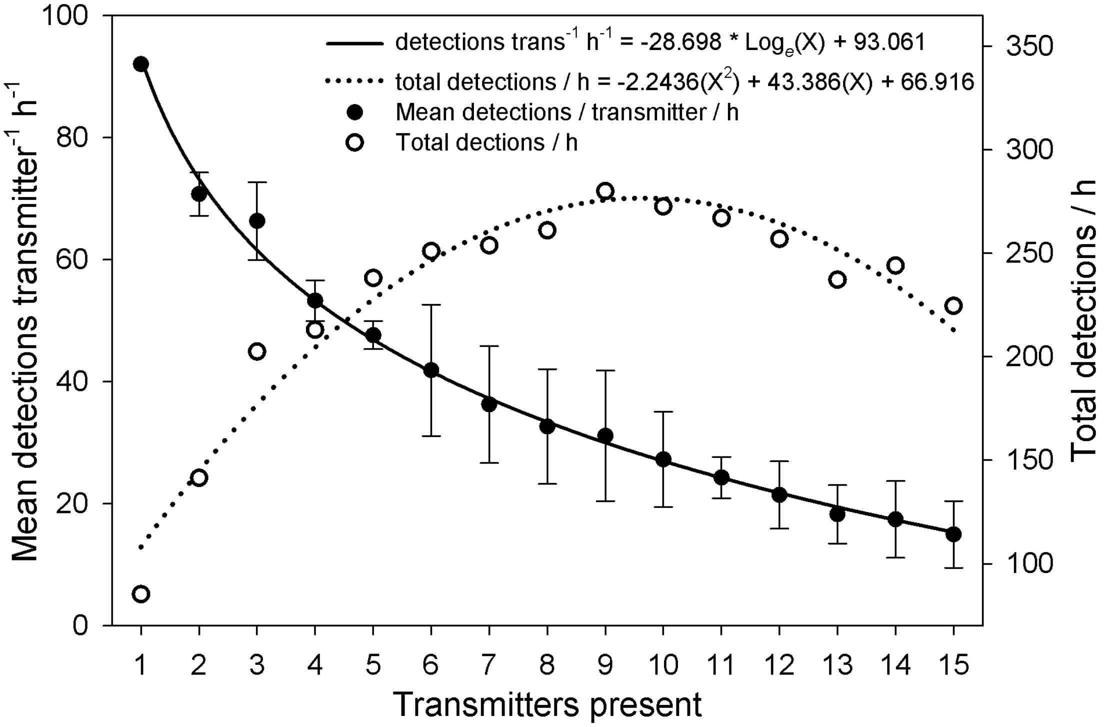

Figure 2-2. Comparison of mean detections transmitter^{-1} h^{-1} (± SD) to number of transmitters present showed a negative logarithmic relation (solid line; $R^2 = 0.99$). Comparison of total detections/h to transmitter number showed a quadratic relation (dotted line; $R^2 = 0.95$).

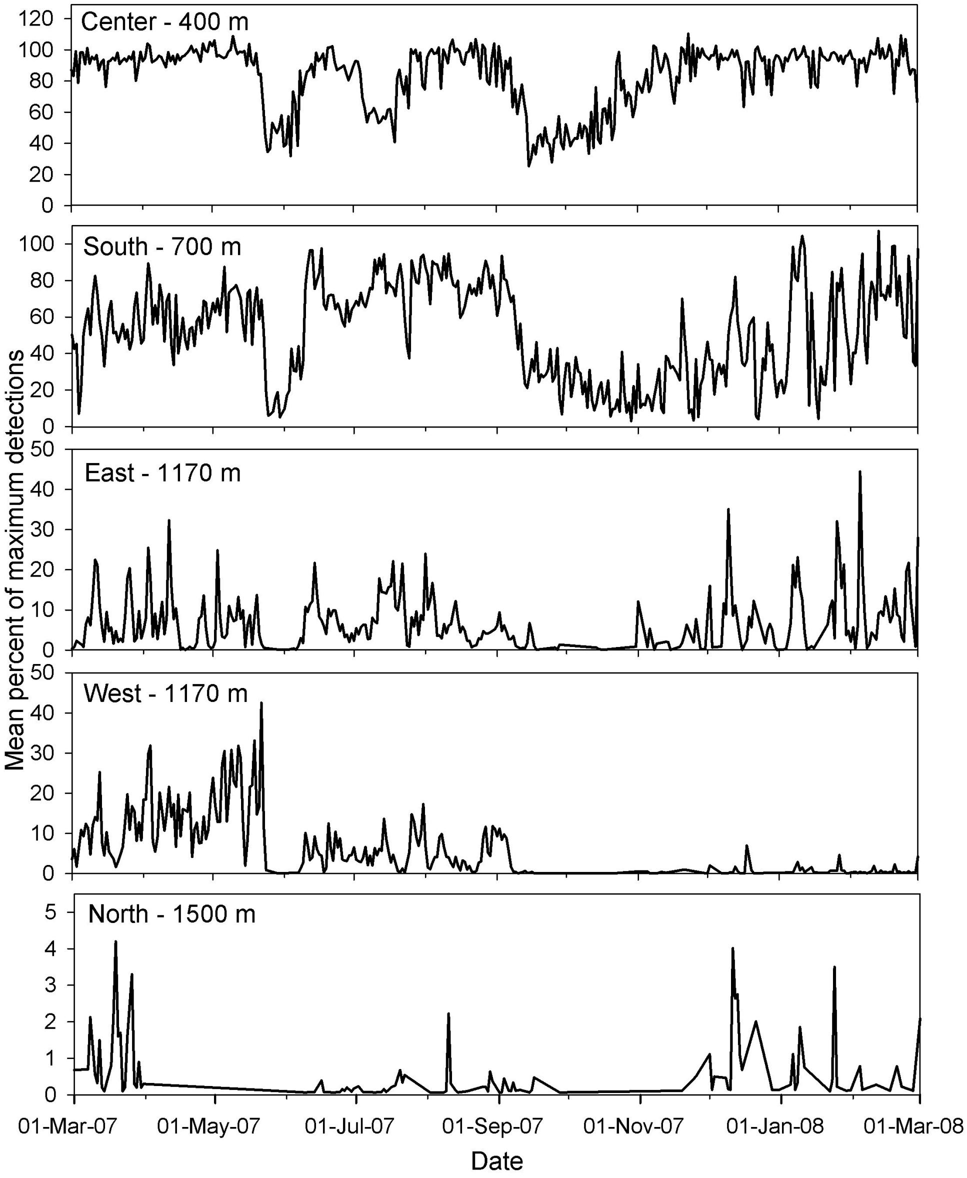

Figure 2-3. Mean control transmitter detections at each distance (averaged across center, south, east, west, and north locations on each date for sites A1, A2, and A3) shown as the mean percent of the maximum expected detections. Expected detections calculated from the relation of detections transmitter^{-1} h^{-1} (Figure 2-2) to number of transmitters (fish) present at a given location. Note: different y-axis scales.

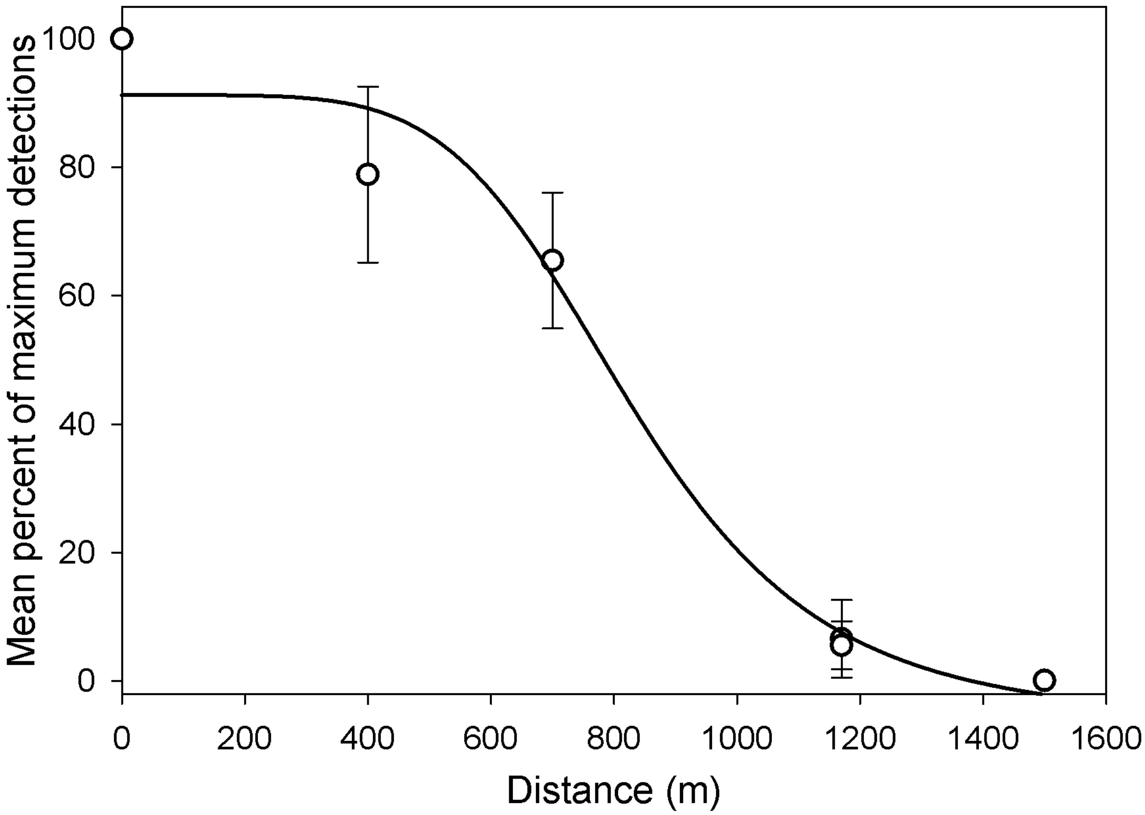

Figure 2-4. A logistic relation of the mean percent of maximum expected detections of the control transmitter to receiver distance (± SD; $R^2 = 0.98$). Sites (A1, A2, A3, and N1) are averaged over all days the control transmitters were present (June 2006 - August 2008).

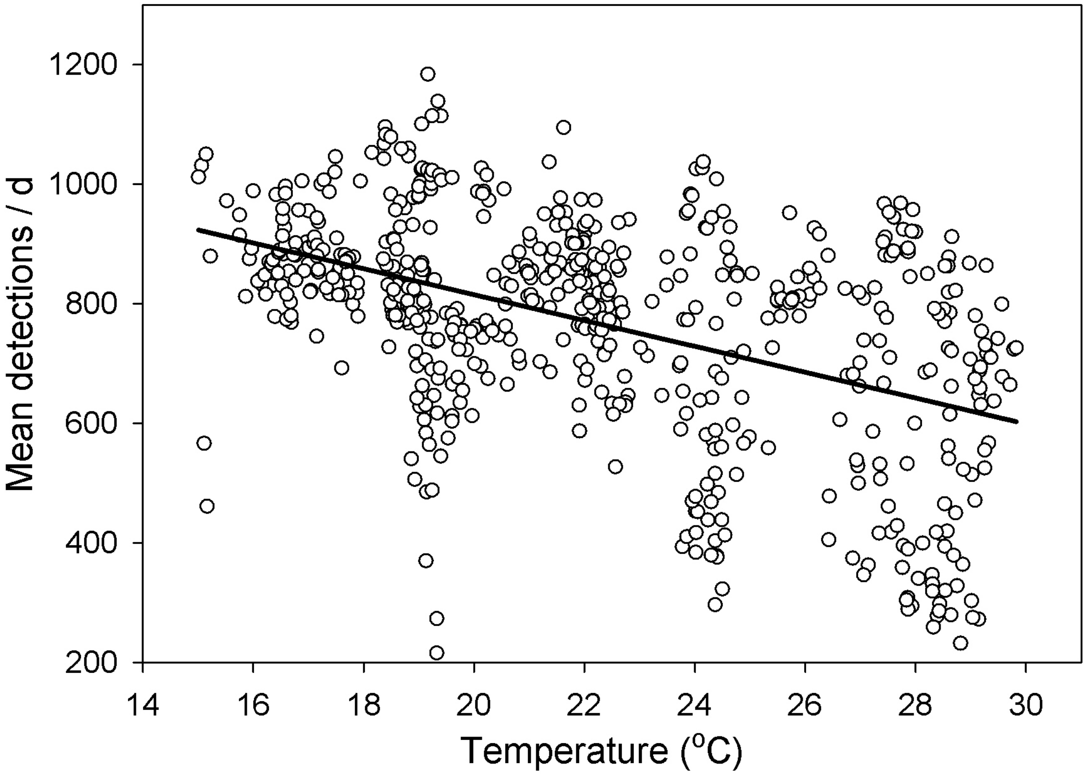

Figure 2-5. Relation of mean detections/d of the control transmitter by the center VR2s (averaged across sites A1, A2, and A3 each day) to bottom (~ 30 m) water temperature. Solid line is a linear regression (Partial R^2 = 0.34; see Table 2-2).

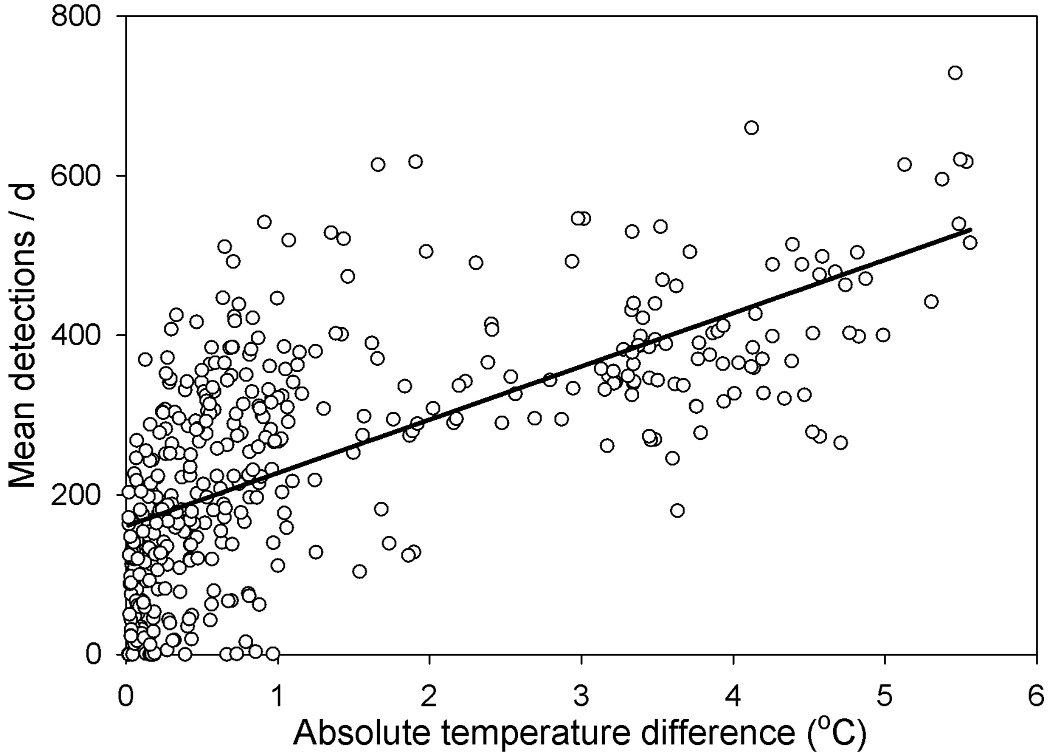

Figure 2-6. Relation of mean detections/d of the control transmitter by the surrounding VR2s (averaged across E, W, and S VR2s at sites A1, A2, and A3 each day) to absolute temperature difference between the bottom (~ 30 m) and at a depth of 15 m. Solid line is a linear regression (Partial $R^2 = 0.45$; see Table 2-2).

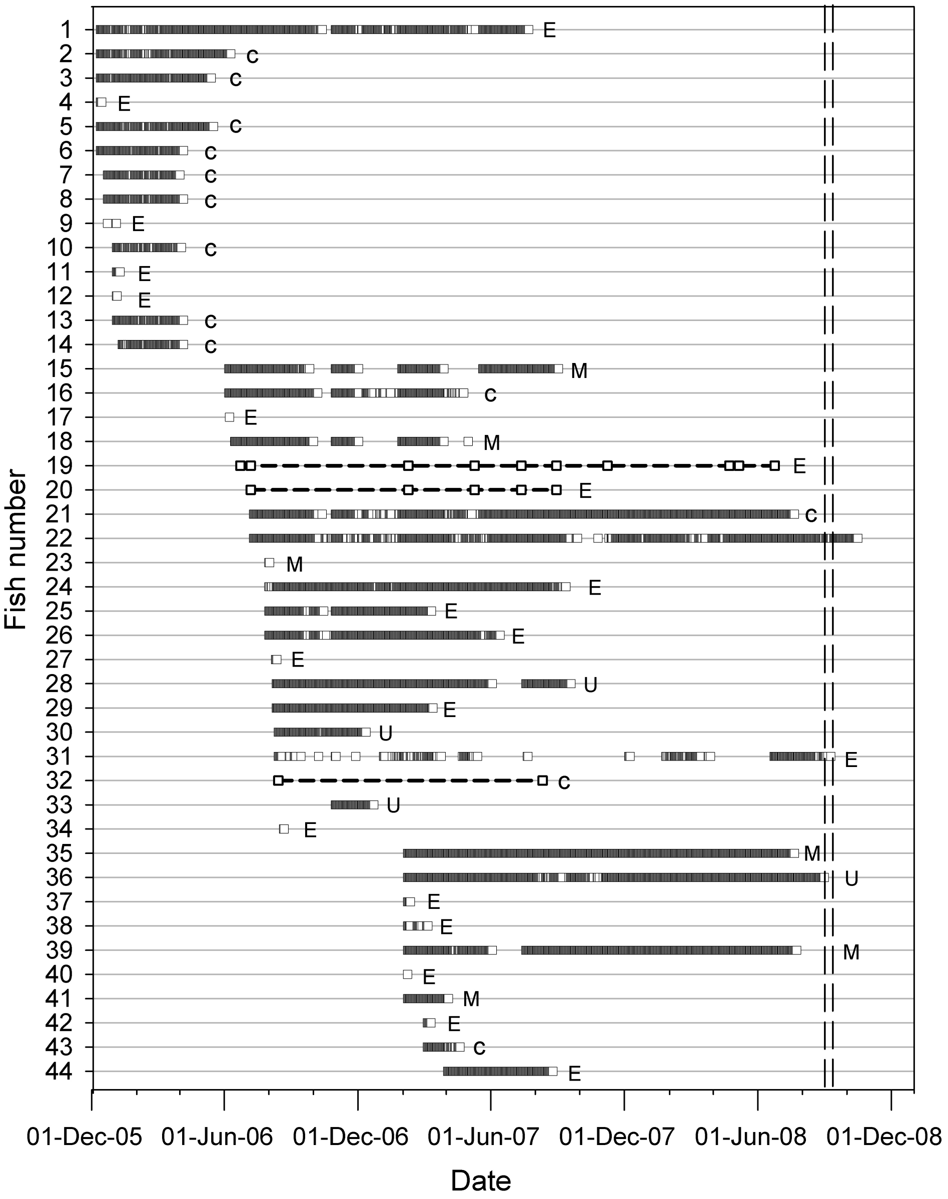

Figure 2-7. Daily presence of red snapper (*N* = 87) released at all sites. Points represent dates a fish was present (i.e. detected at least five times by any receiver). Horizontal dashed lines represent fish that were relocated (points) until the last known date present (endpoint). Letters indicate events (C, caught; M, natural mortality; E, emigration; U, unknown) and fish without letters were still present. Vertical dashed lines show dates of hurricanes Gustav (1 September 2008) and Ike (11 September 2008).

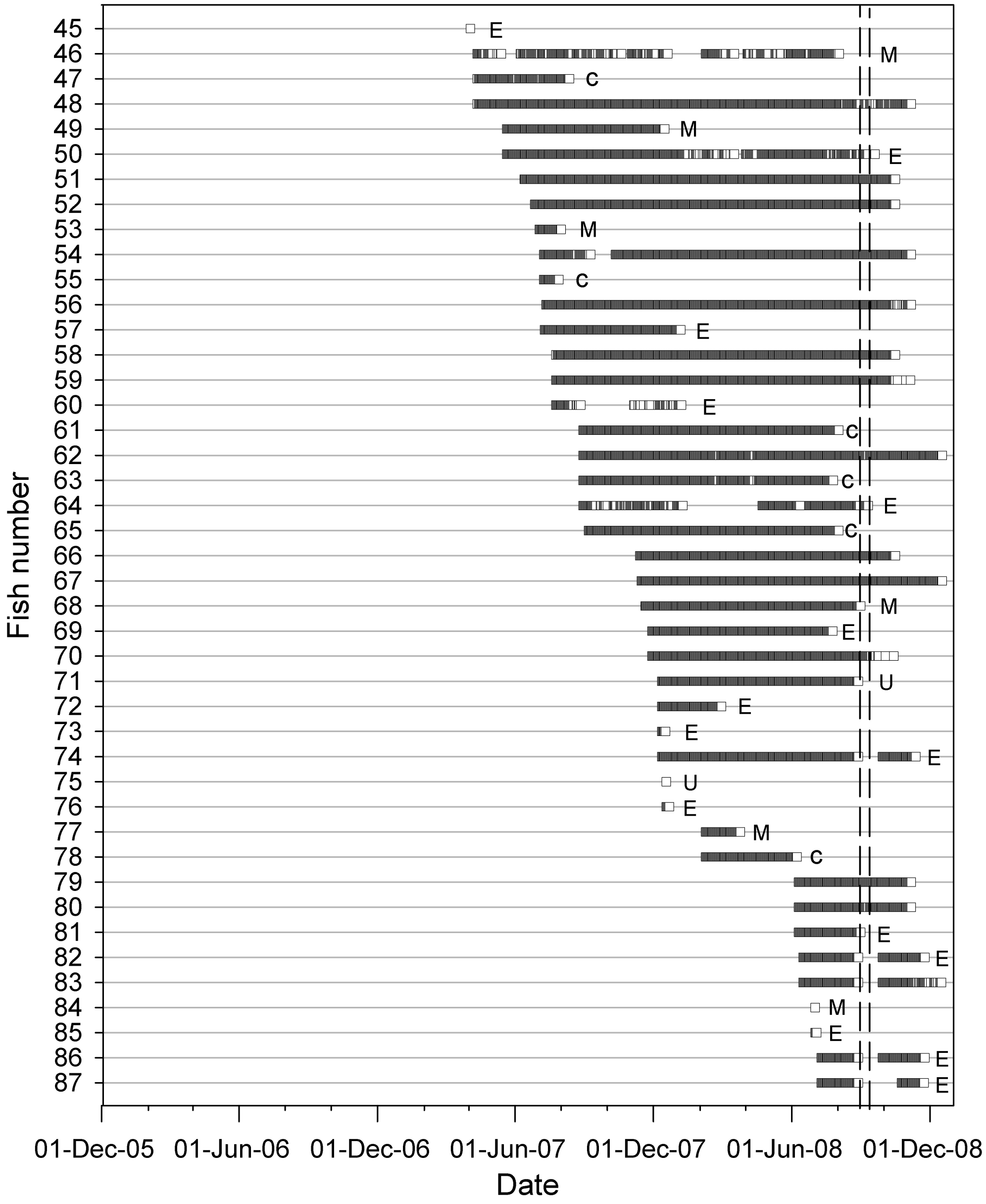

Figure 2-7. (continued)

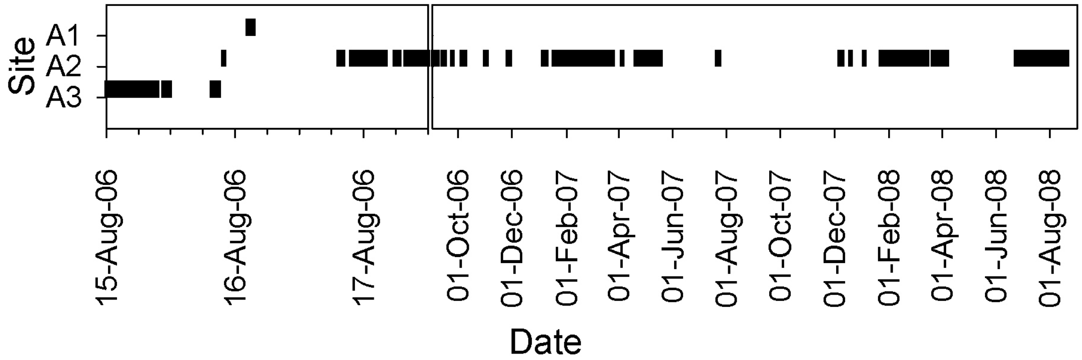

Figure 2-8. Daily presence of Fish 31 (released 14 August 2006 at site A3) at sites A1, A2, and A3. Vertical dashes (presence) represent dates the fish was detected by any receiver at the three sites (5 receivers / site). Note: After release fish left A3 at 2157 hours on 15 August 2006, moved to A2, then moved to A1 (0230 hours), and returned to A2 at 2020 hours on 16 August 2006 (~20 km over 24 h).

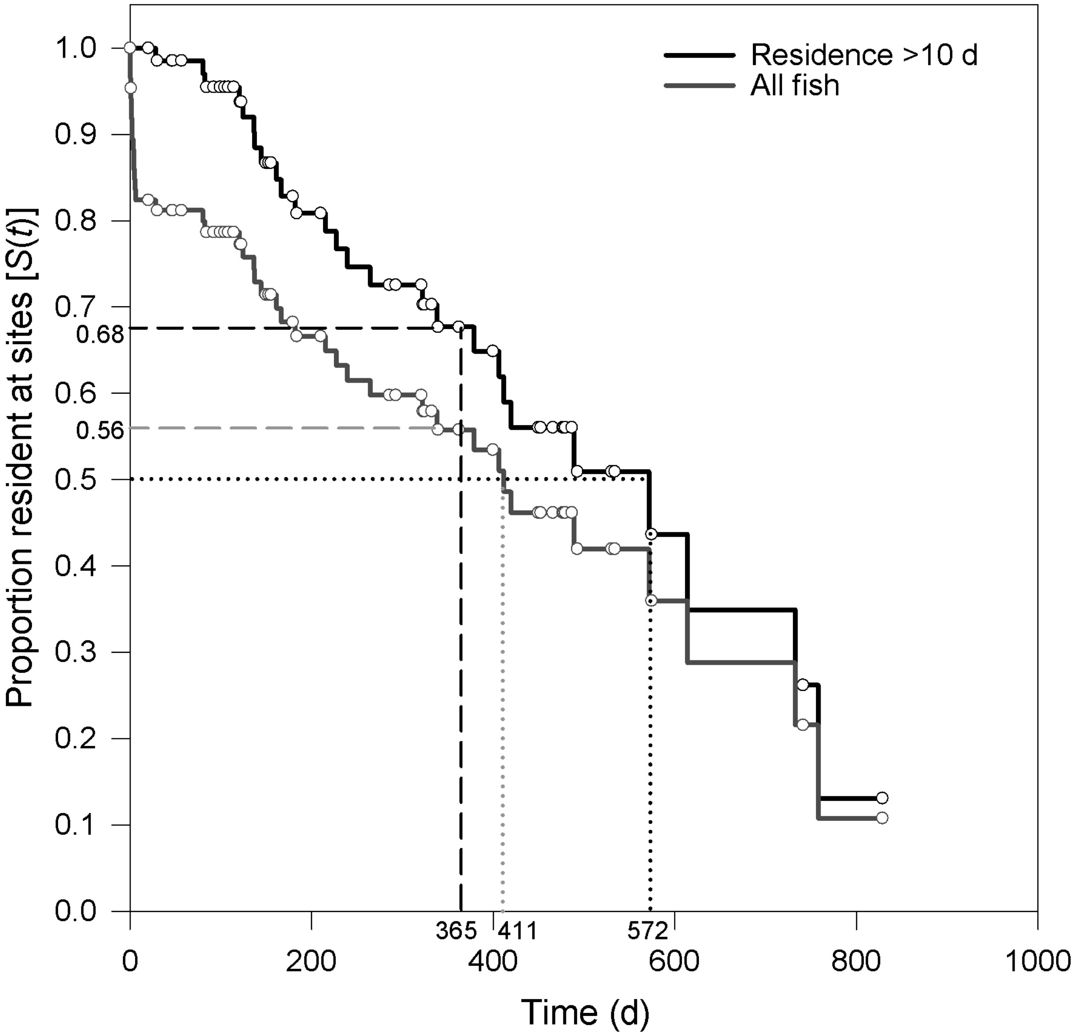

Figure 2-9. Kaplan-Meier survival (i.e. residence) curves showing the proportion of red snapper remaining at study sites over time (d). The black line excluded fish leaving the site within the 6-d post-release period, and the gray line shows all fish released. Dotted lines show median residence times (50% remaining) and dashed lines show proportion of fish remaining at 365 d (site fidelity). Open circles show right-censor times of fish that were caught, died, or were still present at the end of the study.

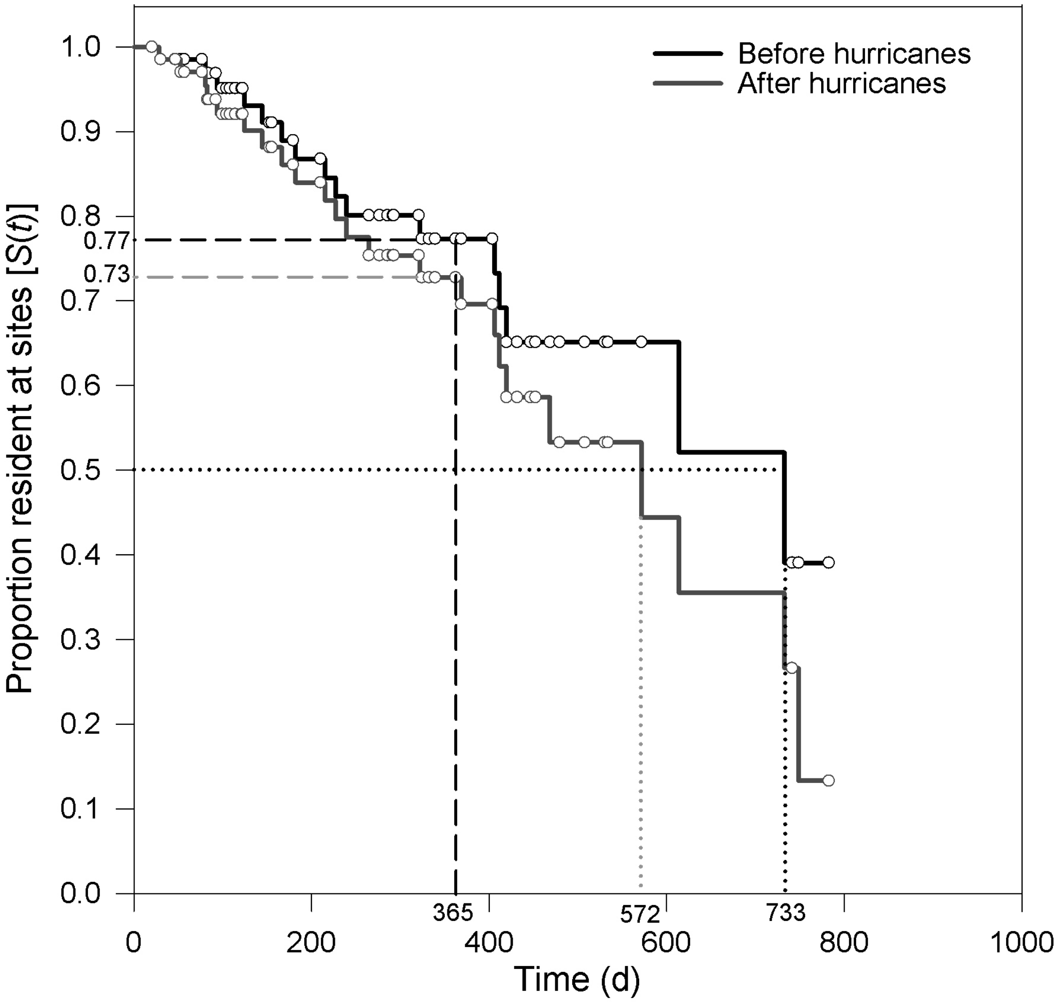

Figure 2-10. Kaplan-Meier survival (i.e. residence) curves showing the proportion of red snapper remaining at study sites over a given time (d). The black line shows residence of fish present before hurricanes Gustav and Ike, and the gray line immediately after these storms. Dotted lines show median residence times (50% remaining) and dashed lines show proportion of fish remaining at 365 d (site fidelity). Open circles show right-censor times of fish that were caught, died, or were still present at the end of the study.

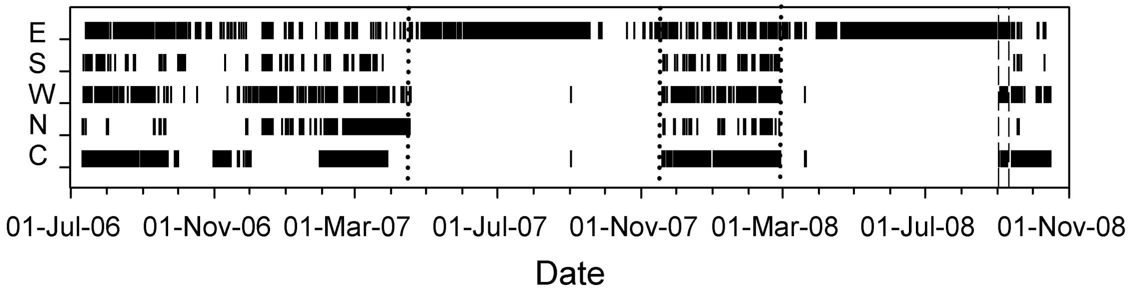

Figure 2-11. Daily detections of Fish 22 by the east (E), south (S), west (W), north (N), and center (C) receivers at site A1. Vertical dashes represent each date the fish was detected by the specified receiver. Vertical dotted lines indicate strong cold fronts and two vertical dashed lines show hurricanes Gustav and Ike. A wide area survey located this fish ~2 km east of the center during periods when fish was only detected by the E receiver.

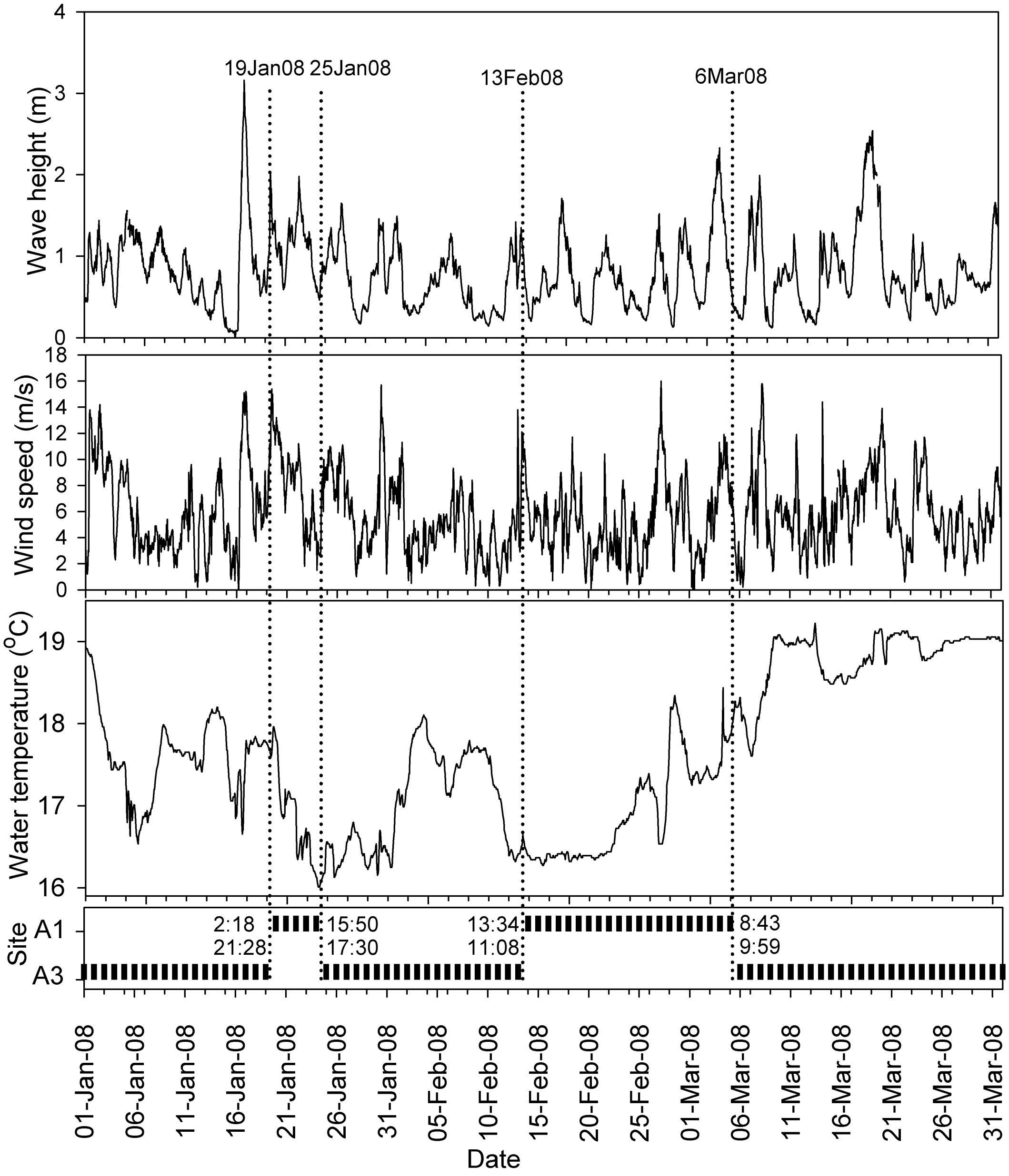

Figure 2-12. Daily presence (bottom panel) of Fish 70 at site A3 and at site A1 (6 km away). The times of emigration and immigration are given (e.g. fish left A3 at 2128 hours and was detected at A1 at 0218 hours). Vertical dotted lines indicate dates fish relocated. Note: the entire range of dates detected at A3 are not plotted (see Figure 2-7).

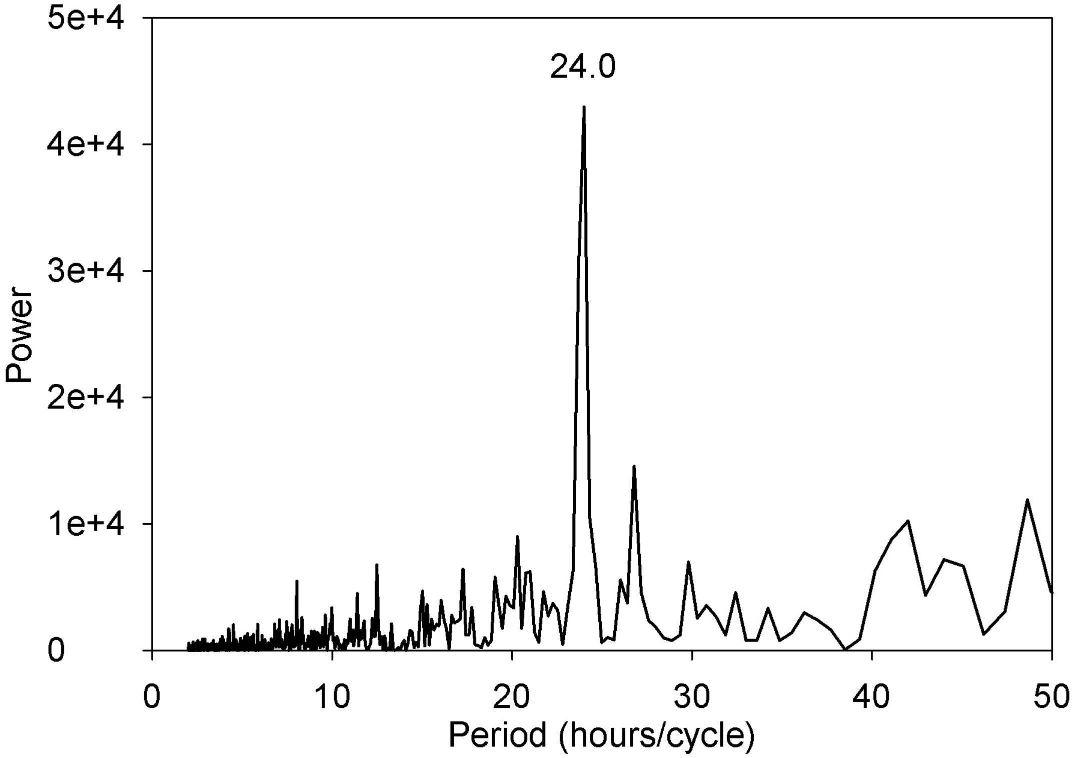

Figure 2-13. Time-series spectral analysis of total detections/h of 10 red snapper by the center receiver at site A1 from 12 January to 31 March 2006. This periodogram shows a strong peak at a period of 24 h indicating a diel cycle in detection frequencies.

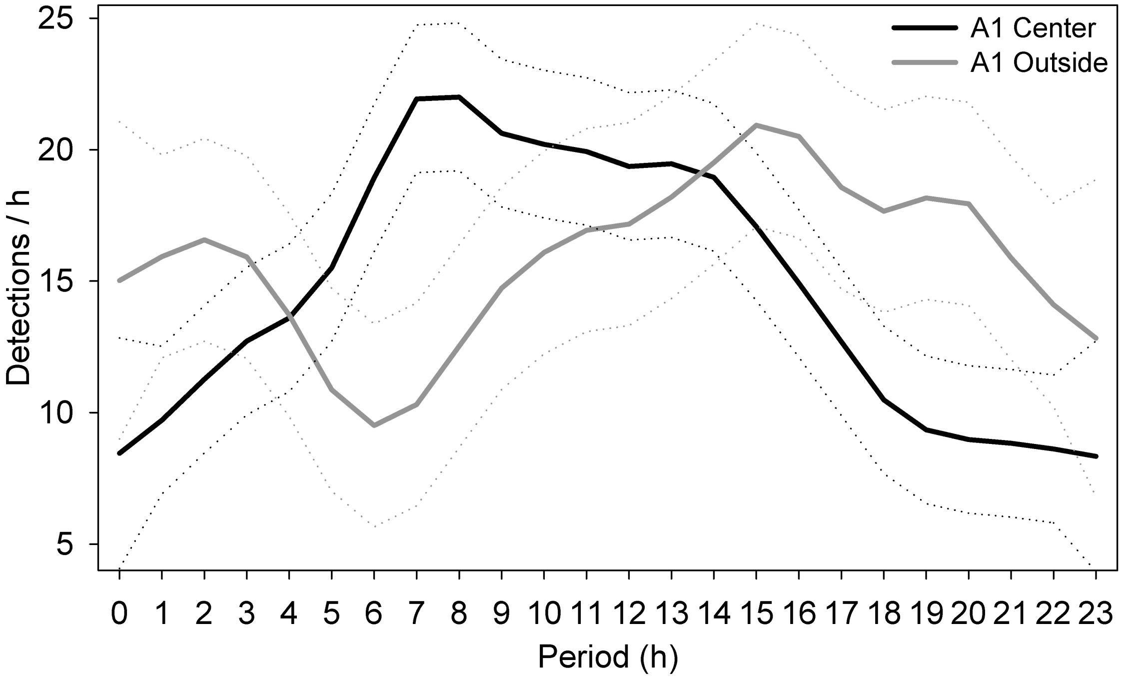

Figure 2-14. Diel detection patterns of 10 red snapper from the center (black line) and outside (gray line) receivers at site A1 from 12 January to 31 March 2006 (*n* = 78 d) as described by local regressions. Dotted lines are 95% confidence limits.

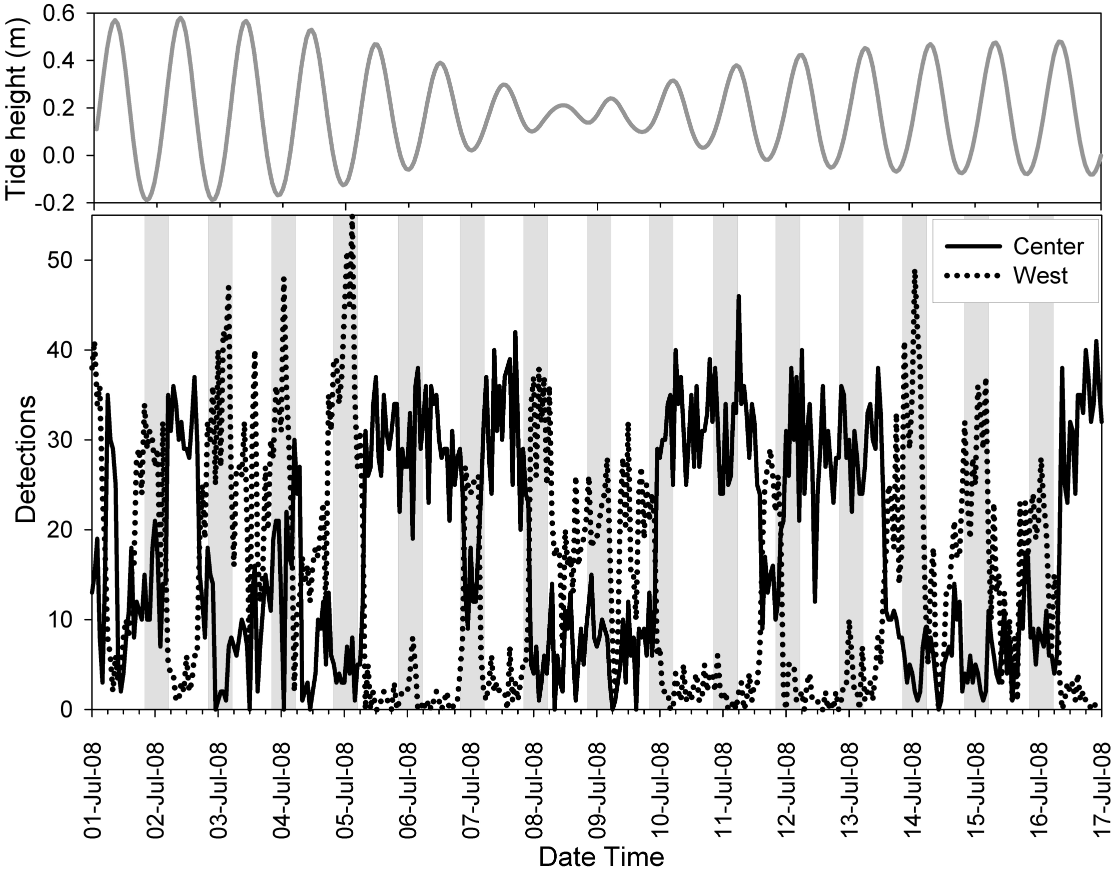

Figure 2-15. Total detections each hour of Fish 21 by the center (solid black line) and the west (dotted black line) receivers at site A1 from 1 July to 17 July 2008. Shaded bars show nighttime periods. Tidal cycle (gray solid line) is plotted in upper panel.

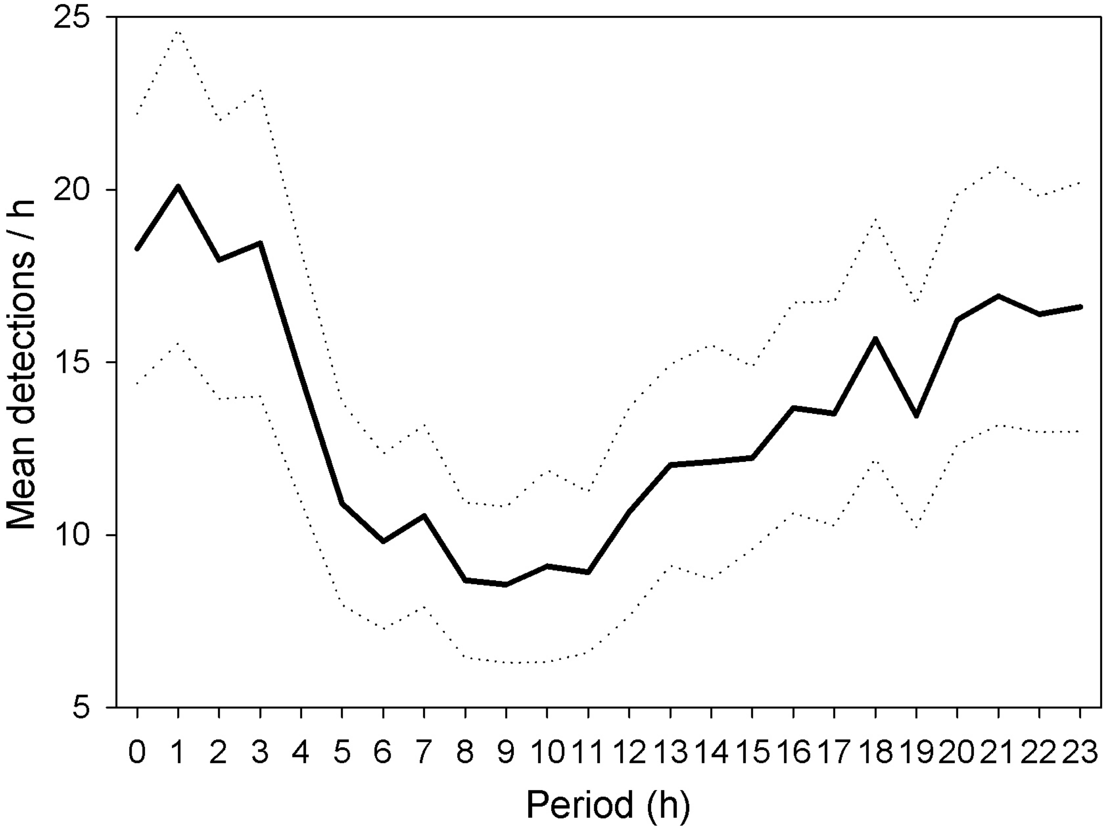

Figure 2-16. Mean detections/h for each period (0 - 2300 hours) by the west receiver at site A1 for Fish 21 from 1 July to 17 July 2008. Dotted lines are 95% confidence limits.

CHAPTER 3

HOME RANGE AND DIEL MOVEMENT PATTERNS OF RED SNAPPER *LUTJANUS CAMPECHANUS*

Abstract.—Information on the fine-scale movements of red snapper around artificial habitats is critical to understanding the importance of these structures. Large (550 - 710 mm total length) red snapper *Lutjanus campechanus* (*N* = 6) were manually tracked at an artificial reef in the northeastern Gulf of Mexico over continuous 24-h periods. These fish were also remotely monitored over a year with an array of five telemetry receivers, with one receiver near the reef (center) and four receivers placed 420 m north, south, east, and west of center. Over these 24-h periods, red snapper stayed near (< 60 m) the artificial reef (75% of locations within 20 m of the structure), but were significantly further from the reef at night (mean = 19.0 m) than day (mean = 12.2 m). Home range size and mean distance from the reef were significantly affected by fish size. The minimum residence time was 332 d for a fish that was caught, and up to 477 d for fish still remaining at the site at the end of the study. The close proximity of these fish to the reef over 24 h, along with the long-term residency provide evidence that these artificial reef structures are important habitat for red snapper.

INTRODUCTION

Red snapper *Lutjanus campechanus* were the most numerically abundant fish species on both natural and artificial habitats off Alabama, USA (Gitschlag et al. 2003, Lingo and Szedlmayer 2006; Wells and Cowan 2007; Gallaway et al. 2009). Although natural habitat is relatively rare in the northern GOM (Parker et al. 1983; Schroeder et al. 1988; Dufrene 2005), approximately 10,000 - 20,000 artificial habitats have been deployed in the northern GOM, which may enhance available natural habitat by providing benefits of increased food and shelter to red snapper (Minton and Heath 1998; Gallaway et al. 2009; Shipp and Bortone 2009). Information on the fine-scale use of these artificial structures by red snapper is lacking, and would help clarify the importance of these structures to red snapper.

Estimates of residency of red snapper to natural and artificial structures with mark-recapture and telemetry methods have varied, but indicate that red snapper have a strong association to these structures (Beaumariage 1969; Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997; Peabody 2004; Szedlmayer and Schroepfer 2005). While these previous movement studies have focused on residency, few red snapper movement studies have examined the fine-scale use of these structures and the adjacent silt-sand habitat

(Szedlmayer 1997; Szedlmayer and Schroepfer 2005; McDonough 2009). Szedlmayer (1997) used telemetry to relocate red snapper monthly at release sites and adjacent structures. Although most fish showed long-term residence, movement was detected to other structures 88 to 700 m from the release site. The temporal resolution in this study allowed residency estimates, but was not adequate for defining fine-scale diel patterns. Szedlmayer and Schroepfer (2005) addressed fine-scale area use of artificial reefs by red snapper by manually tracking fish over 9 to 16-h periods. Over these periods, red snapper ($N = 4$) used a small area (mean = 2,314 m^2), and fish were located relatively close to the reef (mean = 29 m; maximum = 66 m). Also, red snapper tended to be closer to the reef at dawn than at dusk or nighttime periods. While their study addressed night and crepuscular movements, data were lacking for daytime movements. Peabody (2004) used low-resolution (~75 m) remote receivers to continuously monitor small red snapper (< 500 mm TL) at oil platforms and found a crepuscular pattern of movement away from the structure. McDonough (2009) conducted two 14-d telemetry (VRAP) studies of red snapper at the same oil rigs off Louisiana. Diel patterns of movement for red snapper were not consistent among years or months (i.e. May 2006, May 2005, and August 2005). Also, differences in distance between day and night were small, and mean distances from structure were all within 110 m.

Similarly, diet studies have suggested that red snapper may use different habitats over diel and seasonal cycles (Ouzts and Szedlmayer 2003; McCawley and Cowan 2007). Diet studies have indicated red snapper may have some degree of dependence on reef, sand-mud, and water column organisms that may change depending on time of day or season (Ouzts and Szedlmayer 2003; McCawley and Cowan 2007). Collectively, these previous telemetry and diet studies indicated that red snapper stay relatively close to the reef structure and feed on reef or water column organisms, but also move into adjacent sand habitats to take advantage of additional foraging opportunities.

Red snapper feed on a large range of prey types and probably play an important ecological role as the numerically dominant top predator around natural and artificial habitats in the northern GOM (Lingo and Szedlmayer 2006; McCawley and Cowan 2007; Wells and Cowan 2007). As the top predator, red snapper most likely structure the spatial distribution and abundance of prey on and around these habitats. Despite the ecological and economic importance of red snapper, no study has examined the fine-scale habitat use and home ranges of red snapper at small artificial reefs (i.e. army tank, vs oil rig) over continuous 24-h periods.

Determining the home range areas of red snapper at artificial reefs over diel periods can clarify what benefits red snapper obtain from these structures and adjacent open habitats. Short-term (24 - 792 h) tracking methods have been used to directly determine the diel movement patterns of fish (e.g. Szedlmayer and Able 1993; Meyer et al. 2000; Lowe et al. 2003; Topping et al. 2005), and when combined with longer-term (> 1 year) residency information (Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Topping et al. 2006), can provide better understanding of how a fish may use available habitat. In the present study, both long-term telemetry monitoring (> 1 year) and short-term, high-resolution manual tracking (24 h; ±5 m) methods were used to assess residency, home range area, and diel movements of red snapper at an artificial habitat.

METHODS

Study area.—The study site was located in the northeastern Gulf of Mexico, 25 km south of Mobile Bay, Alabama, USA. Red snapper were tagged at a public (published latitude and longitude) artificial habitat (site A4, M-60 army tank, 7 m x 3 m ; Figure 1-1). The depth at this site was 26 m.

Fish tagging.—Large red snapper (> 500 mm total length [TL]) were captured at site A4 with hook and line. Tagging procedures followed Szedlmayer and Schroepfer (2005). Fish were brought on board the research vessel, placed in a 70-L tank of seawater containing MS-222 (150 mg MS-222/ L of seawater), and quickly anesthetized to level 4 (Summerfelt & Smith 1990). Once sedated, the fish were temporarily removed from the anesthetic to obtain weights and lengths. To implant the ultrasonic transmitter, a small (18 mm) vertical incision was made into the peritoneal cavity with a No. 11 scalpel slightly above the ventral midline, the transmitter implanted, and then sutured with plain gut suture (Ethicon, no. 2, 3.5 metric). Also, an internal anchor tag (Floy) was inserted into the incision before it was sutured. Sterile surgical methods and betadine were used throughout the procedure. After surgery, the fish were released after a short, (~1 min) period of recovery at the surface (when fin and gill movements were observed). Fish were released at the capture site by lowering fish to the bottom with weighted line with an inverted barbless hook that was attached to the fish's lower jaw. Upon retrieval of the weighted line the fish was released at depth near the reef.

Continuous remote monitoring.—Sonotronics transmitters (CT-05-48; continuous and coded, 16 x 79 mm, battery life: 4 years) were used at site A4 where Sonotronics SUR receivers were deployed. These transmitters had a unique frequency and pulse interval for each fish that was recorded by Sonotronics underwater receivers (SUR). Maximum detection ranges were 600 m for these transmitters, but for array design a conservative detection range of 300 m was assumed to ensure detection of emigrating fish. An underwater acoustic receiver array was deployed at site A4 that included five separate SUR omni-directional receivers moored near the bottom (5 m). One receiver was located at the center release site (C) and the other four were placed 420 m to the north (N), south (S), east (E), and west (W) of the center (Figure 3-1). This design of receiver positions was able to detect all fish within a 1 km radius of the release site based on preliminary range tests. A stationary control transmitter was moored 5 m above the bottom at a distance of 150 m south of the center receiver. This control transmitter was used to detect any reduction in detection range of transmitters due to environmental factors. All receivers were coated with antifouling paint to prevent decreased detections due to biofouling (Heupel et al. 2008).

Manual continuous surface tracking.—Transmitters used in the present study also transmitted a continuous acoustic 'ping' that enabled manual tracking of fish from a 11-m research vessel. The research vessel was fitted with a Vemco V10 directional acoustic hydrophone and a VR60 surface receiver (Holland et al. 1983; Topping et al. 2005). Red snapper were tracked for multiple, 24-h diel periods around an artificial habitat (site A4). Fish were manually tracked seven months after release. Positions of latitude and longitude were recorded at 30-min intervals with a Global Positioning System (GPS) as the boat was positioned over the fish. This method provided both the fine-scale temporal and spatial (~5 m) resolution needed for estimates of habitat use over diel periods (Worton 1989; Seaman and Powell 1996; Lowe et al. 2003; Topping et al. 2005).

Data analysis.—Position fixes (latitude and longitude) for red snapper and the position of the artificial habitat were plotted in a Geographic Information System (ArcView GIS, version 3.2a). Area use was calculated with ArcView GIS by use of the Animal Movements Analyst Extension (AMAE; Hooge et al. 1999, 2001). To describe each fish's home range a 95% kernel utilization distribution (KUD) was used, which estimates the area that a fish has a 95% probability of being located within over the duration of the tracks (Worton 1989; White and Garrott 1990; Seaman and Powell 1996; Topping et al. 2005). A 50% KUD (50% probability polygon) was used to determine each fish's core range. The ad hoc smoothing value (AMAE home range) was used when calculating the KUDs. Analysis of area use was also estimated with the minimum convex polygon (MCP) method to provide results comparable with previous studies (Zeller 1997; Szedlmayer and Schroepfer 2005). The MCP area was determined separately for all locations for each fish (i.e. 100% MCP), and for all locations for all fish around the reef. Distances away from the center of the habitat to each position fix (locations) were measured with the distance tool from the AMAE in ArcView GIS. The proportion of locations from the center of the reef in 10-m distance bins (up to maximum distance a fish moved) was determined for each red snapper. Proportions were adjusted with a arcsine-square root transformation, and differences between mean transformed proportions (10-m distances) were analyzed with a mixed model repeated measures analysis of variance (fixed, 10-m distance bins; random, fish; rmANOVA). The effect of fish size (TL) on mean distance from the center reef, and on log transformed measures of home range size were analyzed with a linear regression (Jones 2005; Cody and Smith 2006; Nanami and Yamada 2008). Mean distances from the center site were compared between day and night periods for each fish with a paired *t*-test (Zar 1984). Mean distances from the center for each fish were also examined at 1-h intervals over a 24-h diel cycle. A mixed model (fixed, 1-h periods; random, fish) rmANOVA was used to compare mean distances between 1-h time intervals over 24 h diel cycles. A Student-Neuman-Keuls multiple comparison test was used to detect all pair-wise differences in means when a difference was detected by the rmANOVA (Cody and Smith 2006). Bearings from the center reef to each fish location were calculated with ArcView GIS (Bearing and Distance Extension 1.1, ESRI script, Ron Schultz 2003, www.esri.com/arcscripts). Mean bearings were estimated following methods described by Kölliker and Richner (2004). Rayleigh's *z*-test was used to test for directionality (non-random direction) of locations from the center reef (Batschelet 1981; Kölliker and Richner 2004). The proportions of locations within 30° intervals (arcs) over a 360° range around the reef were determined for each fish for visual comparisons. All differences are considered statistically significant when $P \leq 0.05$.

RESULTS

Red snapper (*N* = 6) were both manually tracked for multiple 24-h periods from the surface and monitored with automated receivers (SUR) up to 477 d at site A4 (Figure 1-1; army tank). Fish showed long-term residency to this site, and were manually tracked > seven months after initial release (Table 3-1; Figure 3-2). Fish 1, 2, and 3 were tracked over two complete 24-h periods (24-25 June 2008 and 2-3 July 2008), while fish 4, 5, and 6 were intermittently tracked (located every few hours) on 24-25 June 2008 and tracked continuously (once every 30 min) on 2-3 July 2008 (Table 3-1). Red snapper ranged in size from 550 to 710 mm TL (mean = 620; SD = 56) and had a mean weight of 3.5 kg (SD = 0.9). All red snapper stayed within a relatively small area that encompassed the artificial structure during both tracks. Limited movements over these short-term tracks resulted in small home range estimates. Mean home range area estimates with the 95% KUD were 1,758 m^2 (SD = 376), while mean core area (50% KUD) was 254 m^2 (SD = 103). The mean 100% MCP area was 1,719 m^2 (SD = 787). An area of 5,704 m^2 was obtained when all locations of all fish were encompassed by a MCP. An area of 829 m^2 was obtained where each fish's 100% MCP completely overlapped (15% of total MCP area; Figure 3-3). The reef area was completely within this area of 100% overlap (i.e. this small area encompassing the reef was used by all red snapper tracked). The 95% KUD area significantly increased with fish size (TL; $R^2 = 0.73$, $F = 10.8$, $P = 0.03$); however, the core area and 100% MCP were not significantly affected by fish size. A significant positive linear relation was detected between the log-log transformation of 95% KUD and TL ($R^2 = 0.73$, $P = 0.03$; $\log_{10}$ [95% KUD] = 2.1384 $\log_{10}$ [TL] - 2.732). Over both 24-h tracks, all fish stayed relatively close to the center reef structure (mean distance = 15.1 m; SD = 1.8; Table 3-1). About 75% of all fish locations (on average) were within 20 m of the center of the reef, and 93% were within 30 m (Figure 3-4). Mean proportion of locations within 0-10 m (37%) and 10-20 m (38%) were significantly different from proportions within 20-30 m (18%) and 10-m bins from 30-70 m (< 5%) from the center reef (rmANOVA: $F_{6,30} = 58.91$, $P < 0.0001$; Figure 3-4). A significant positive relation was detected between mean distances red snapper were located from the center and total length ($R^2 = 0.79$, $F_5 = 15.2$, $P = 0.02$; Figure 3-5). Mean distances that red snapper (N = 6) were from the reef during the tracks were significantly different between day (mean = 12.2 m; SD = 2.0) and night (mean = 19.0; SD = 2.8; Paired t-test: $t_5 = -5.41$, $P < 0.003$; Figure 3-3). Diel differences in mean distance from reef for 1-h intervals were detected for some hours of day and night, and were consistent with greater distances at night, though significant differences were not detected between all day and night periods (rmANOVA: $F_{23,113} = 5.99$, $P < 0.0001$; Figure 3-6). Distances from the reef reach a maximum around 0200 to 0300 hours, with mean distances appearing to increase as nighttime progressed (Figure 3-6). Locations of red snapper were skewed northwards of the structure. Mean bearings of individual red snapper were within a north quadrant from 322° and 19°, and overall bearings for each fish were significantly different from random

(Rayleigh's *z*-test: $P < 0.02$). The northward directional movement of all fish were evident during both tracks (e.g., Figure 3-7).

After tracking these fish, they continued to show long-term residency to site A4, with some fish (#'s 2, 5) still present at the end of the study (17 December 2008). After tracking, three of the six fish were caught in late July and early August 2008, and one of the fish (#1) appeared to emigrate from the site at the end of August 2008 as hurricanes Gustav and Ike affected the study area (Figure 3-2). Wave heights up to 11 m and winds up to 100 km/h were recorded near the study area, and caused enough turbulence to break three of the five receivers from their moorings at a depth of 26 m. Two fish were detected by the remaining two receivers at the site over the duration of the storm, with a short loss of detections (< 24 h) at the peaks of these storms.

DISCUSSION

The present study was the first to examine fine-scale movements and home ranges of large red snapper (> 500 mm TL) around an artificial reef. Telemetry methods used were successful in detecting even small diel differences in distances red snapper moved from the structure and were able show residence of these same fish to this site up to 477 d.

The 24-h manual surface tracking showed these large red snapper remained relatively close to the reef structure, with 75% of locations within 20 m of the reef, and the mean distance from the reef was 15.1 m. Similar short-term movement distances for red snapper (mean, 29 m) were shown by Szedlmayer and Schroepfer (2005) for crepuscular and nighttime periods. While Szedlmayer and Schroepfer (2005) did not measure distance over complete day periods, their area use estimates for red snapper with a 100% MCP (1,074 to 3,361 m^2) were also similar to 100% MCP estimates of the present study (1,068 to 3,207 m^2). The 50% KUD core area estimates were small (137 to 446 m^2) and each fish's core areas intersected the reef structure. Also, the area in which each fish's 100% MCP overlapped included the reef structure. The inclusion of the reef structure within these core areas shows the importance of these structures to red snapper over daily scales.

Red snapper were continuously detected during the 24-h tracking periods, which showed that red snapper did not move inside the army tank structure, as such movements into structured habitats would have caused a complete loss of detection (Bradbury et al. 1995; Giacalone et al. 2005; Topping et al. 2005; Topping et al. 2006). Red snapper will on occasion move inside the army tank structures, as directly observed during daytime SCUBA surveys (Author, personal observation).

The only other study to examine fine-scale movements of red snapper over 24-h diel periods was McDonough (2009), who found red snapper were closer to the oil platform depending on year and month of tracking. In May 2006, McDonough (2009) estimated mean distances from the structure ranged between 29 and 32 m that were similar to past (29 m, car and truck bodies; Szedlmayer and Schroepfer 2005) and present estimates (19 m). However, in that same study a mean distance range of 105 to 110 m in May 2005 was greater than estimates by Szedlmayer and Schroepfer (2005) or the present study. McDonough (2009) did not give maximum distances for red snapper, but reported that fish frequently moved outside of the detection range of 150 - 350 m. Szedlmayer and Schroepfer (2005) reported maximum distances up to 66 m, which is almost identical to results of the present study (max, 61 m). Differences in mean overall distances and diel distances red snapper moved from the reef may simply reflect changes in prey availability (Ouzts and Szedlmayer 2003; McCawley and Cowan 2007). The greater distances red snapper moved at an oil platform in the McDonough (2009) study may be due to increased competition for these food resources at a site that can have significantly greater numbers of red snapper (and other species) than found at smaller artificial reef sites (Turpin and Bortone 2002; Gitschlag et al. 2003; Lingo and Szedlmayer 2006)

Intraspecific differences in home range and distances fish move on daily scales have been attributed to body size (Jones 2005; Topping et al. 2005; Nanami and Yamada 2008), reef shape (Zeller 1997; Eristhee and Oxenford 2001; Topping et al. 2005), and habitat availability (Matthews 1990). A positive relation between home range size and fish size may be influenced by the greater resource demand of larger fish, and this relation can vary by trophic feeding level (i.e. carnivore vs herbivore; Brett 1965; Harestad and Bunnell 1979; Wakeman et al. 1979; Jones 2005; Topping et al. 2005; Nanami and Yamada 2008). In the present study, a positive relation was detected even though there was a small size range of tracked red snapper (550 to 710 mm TL). Based on the present relation of fish size and movements, little movement for red snapper ≤ 100 mm TL would be expected; a home range of 35 m^2 would be obtained from the log-log relation (i.e. $\log_{10}$ [home range] = 2.1384 $\log_{10}$ [TL] - 2.732). In contrast, Chapin et al. (2009) showed greater movement for smaller snapper (mean, 110 mm TL), with observed movements up to 206 m from release sites over 243 d, thus further study is needed for comparisons of fish size to daily movement patterns.

Nanami and Yamada (2008) estimated home range sizes of 93 to 3,638 m^2 for another lutjanid (*Lutjanus decussatus*) over various size ranges (100 to 250 mm TL) on a shallow (2 m) fringing reef. A relation of home range size to body size (TL) was also detected for *L. decussatus*, even though fish were smaller than red snapper tracked in the present study. These home range sizes of *L. decussatus* were similar to red snapper in the present study tracked on what would be considered a patch reef in other studies (e.g. Zeller 1997). Meyer et al. (2007) detected much greater movements of a large (520 to 890 mm fork length) lutjanid (*Aprion virescens*) tracked with remote receivers deployed along fringing reefs. These lutjanids showed movements along these fringing reefs up to 24 km over diel periods, with regular diel shifts in area use to 9 km. These studies suggested that red snapper may show greater movements on natural reef types where the structure covers a larger area or has an elongated shape, such as a fringing reef. Differences in reef shape and size may help explain the differences in distances red snapper moved around artificial reefs in the present study versus red snapper around oil platforms (McDonough 2009). Topping et al. (2005) showed significantly greater home range sizes for a labrid (*Semicossyphus pulcher*) tracked along a elongated, rocky coastline (1,930 - 82,070 m^2) relative to the same species tracked in an embayment (938 - 6,690 m^2), and this movement was related to movement to and from foraging and nighttime resting habitats over diel cycles. A serranid (*Paralabrax clathratus*) was also tracked at the same study area, and overall home range sizes were smaller (33 to 11,224 m^2) than those of *S. pulcher*, in which differences were attributed to differences in diet (Lowe et al. 2003; Topping et al. 2005). Red snapper diets change ontogenetically, seasonally, and over diel cycles (Ouzts and Szedlmayer 2003; McCawley and Cowan 2007), and differences in movement patterns may reflect changes in prey availability at different habitats (Matthews 1990). The small home range sizes of red snapper that encompassed the reef structure in the present study would suggest that artificial reefs and adjacent mud-sand habitat can provide the daily resources (food and shelter) that this species requires within a relatively small area.

It was unclear what factor was responsible for the skewed northward movement patterns of red snapper around the artificial habitat. These fish were located on all sides of the reef at some point during the tracks, such that their home range areas encompassed the reef area, but movements were skewed to the north side of the reef. Water currents have been found to affect the position of fish on reefs, and may affect prey distribution (Kingsford and MacDiarmid 1988; Webster and Hixon 2000). Accurate current directions and speeds were not measured in the present study, but should be considered in future studies of red snapper movement patterns.

The long-term data from the present study showed some red snapper remained within the 1.6 km^2 study area up to 477 d (n = 2), some fish were removed prematurely by fishers (n = 3) after 332 d, and one moved during hurricanes after 379 d. Long-term telemetry data for red snapper of other studies have shown similar residence times at artificial habitats (Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Topping dissertation, Chapter 1, 2). These previous studies showed red snapper occasionally moved greater distances (excursions and relocations) compared to movements measured on a daily scale in the present study; however, in those studies, fish would be resident on one habitat for extended periods then quickly move to another habitat and would again take up residence. It is likely that while red snapper were resident on a particular site they would show home ranges and movement patterns similar to red snapper in the present study. Diel movements, especially movements from the structure during nighttime periods, are probably related to foraging behavior as indicated by diel diet shifts shown in previous studies (Ouzts and Szedlmayer 2003). If red snapper were feeding over these tracking periods, the relatively short distances fish moved from the structure indicated that the artificial structure and nearby silt-sand area provided the resources these fish needed on daily scales. Overall, this study showed that this artificial reef area provided suitable habitat for red snapper over a wide range of temporal and spatial scales.

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TABLES

Table 3-1. Summary of telemetry data for red snapper (*N* = 6) manually tracked for 24-h periods at site A4 on 24 to 25 June 2008 and 2 to 3 July 2008. Home range area (m^2) is estimated with the 95% kernel utilization distribution (KUD) and core range by the 50% KUD. Area was estimated for all data points with a minimum convex polygon (MCP). Bearing = mean bearing (degrees); distance = mean distance (m) of all points from center of structure; *N* = number of locations for all tracks; DAL = days at liberty.

Fish	Date released	Dates tracked	TL (mm)	DAL (d)	*N*	95% KUD (m^2)	50% KUD (m^2)	100% MCP (m^2)	Bearing (deg)	Distance (m ± SD)
1	29 Aug 2007	24 Jun 2008	710	379	80	2,125	233	1,880	19	17.3 ± 10.8
2	14 Nov 2007	24 Jun 2008	579	400	80	1,704	218	1,631	347	13.0 ± 7.7
3	05 Sep 2007	24 Jun 2008	635	332	79	1,906	262	3,207	323	15.0 ± 9.7
4	29 Aug 2007	02 Jul 2008	645	339	58	2,158	446	1,325	326	17.3 ± 11.4
5	29 Aug 2007	02 Jul 2008	550	477	58	1,234	230	1,068	350	13.5 ± 8.9
6	29 Aug 2007	02 Jul 2008	601	332	58	1,421	137	1,200	345	14.5 ± 9.6

FIGURES

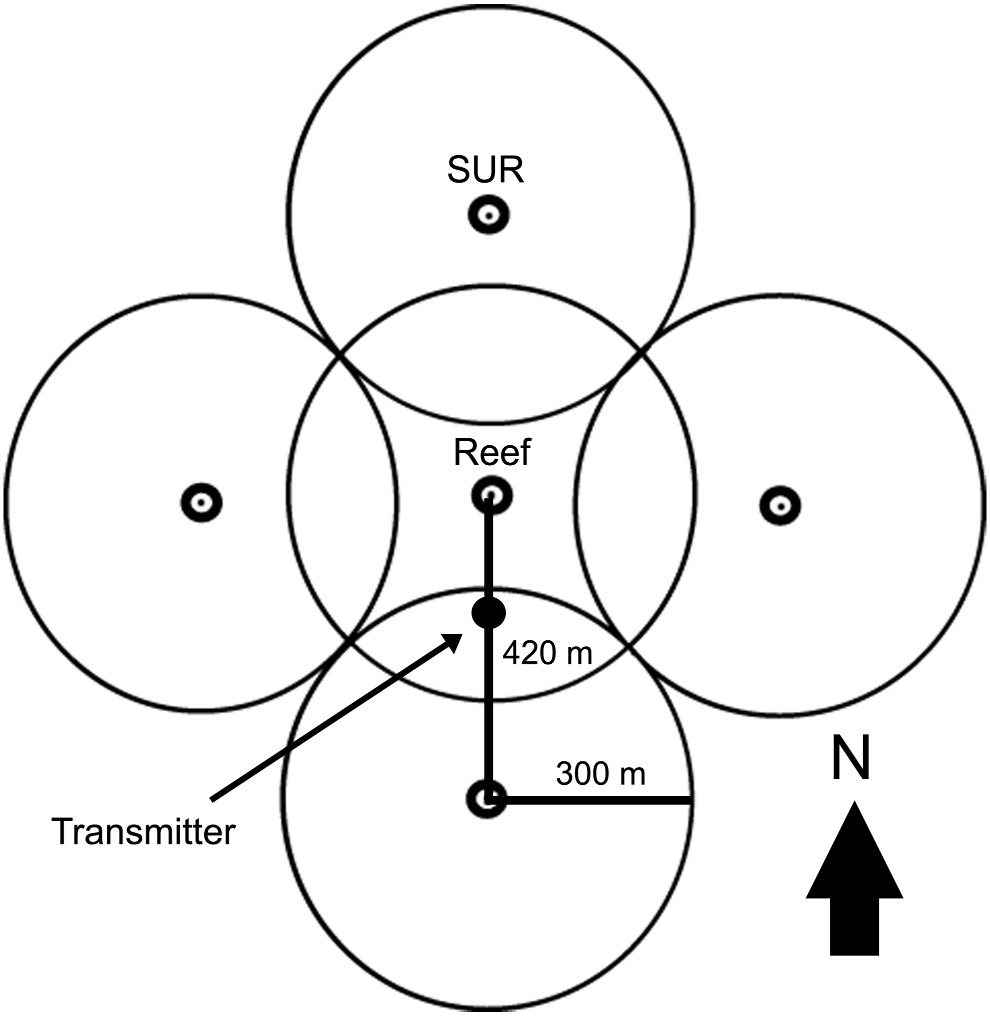

Figure 3-1. Receiver array at site A4, with one receiver at the reef and four others surrounding the reef 420 m away to the N, S, E, and W. Circles represent detection range of 300 m. A control transmitter was placed 150 m S of reef.

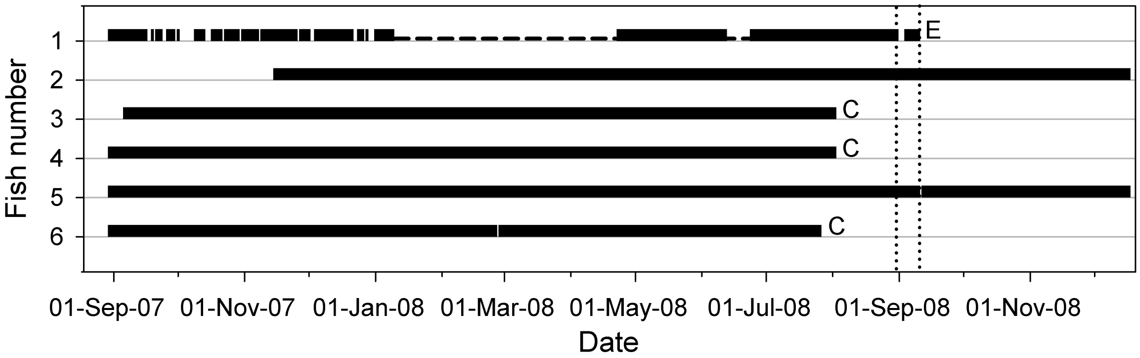

Figure 3-2. Daily presence of red snapper (*N* = 6) at site A4. Vertical dashes represent dates a fish was present (i.e. detected at least five times by any receiver). Horizontal dashed lines represent dates that center SUR was not recording. Letters at end of record indicate events (C, caught; E, emigration; no letter, present). Vertical dotted lines show dates of hurricanes Gustav (1 September 2008) and Ike (11 September 2008) passed near the study area.

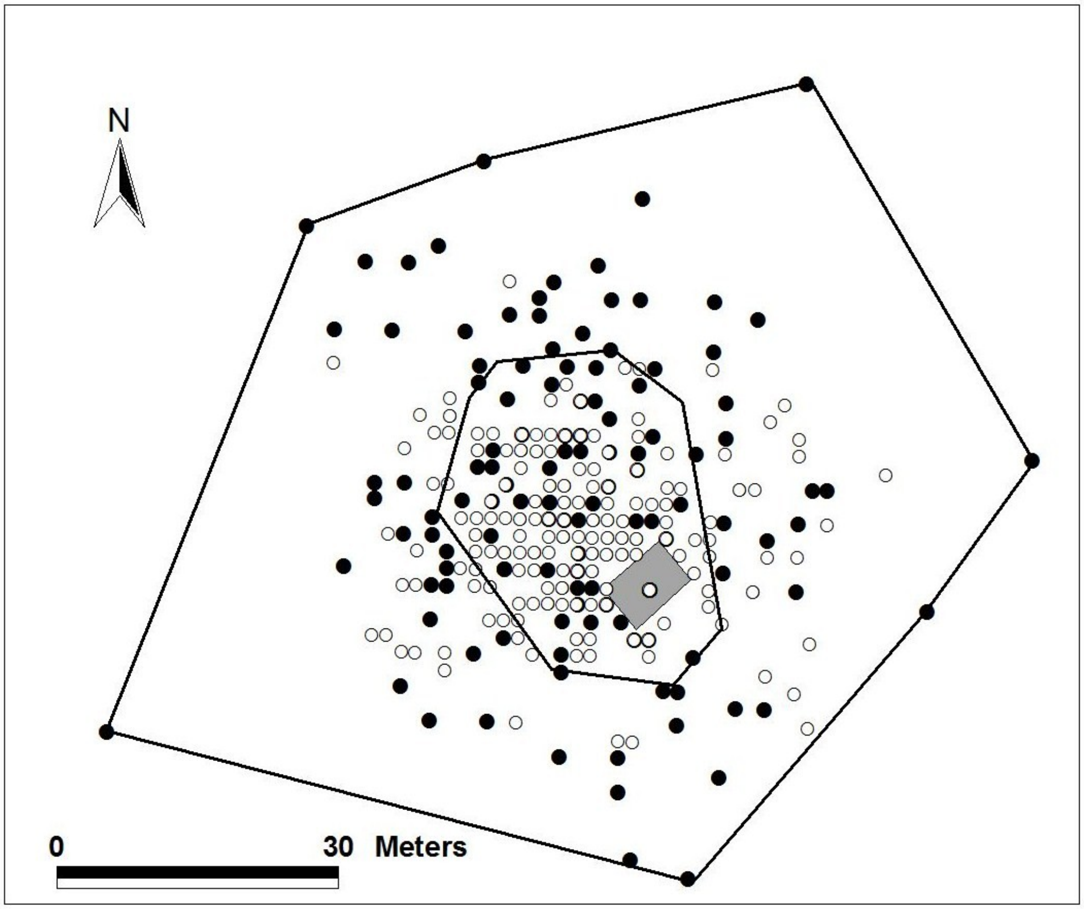

Figure 3-3. Day (open circles) and night (solid circles) locations of red snapper (*N* = 6) at site A4 (gray rectangle = army tank) over all 24-h tracks. Mean distances from the reef over day (12.2 m; SD = 2.0) and night (19.0 m; SD = 2.8) intervals were significantly different (paired *t*-test: $t_5 = -5.41$, $P = 0.003$). Outer polygon = 100% MCP for all fish locations (5,704 m^2). Inner polygon = area of 100% overlap of 100% MCPs for each fish (829 m^2).

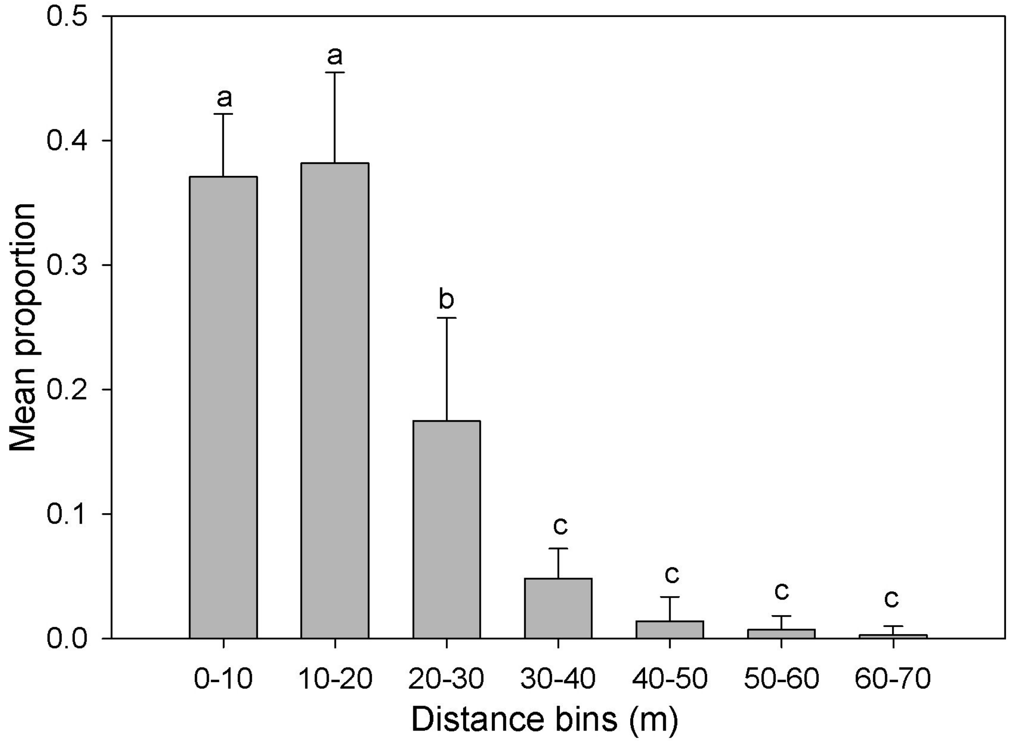

Figure 3-4. Mean proportion (+ SD) of red snapper (*N* = 6) manual tracking locations within 10-m distance intervals from the center of the reef. Different letters indicate significant differences between an arcsine-square root transform of actual proportions shown ($P \leq 0.05$).

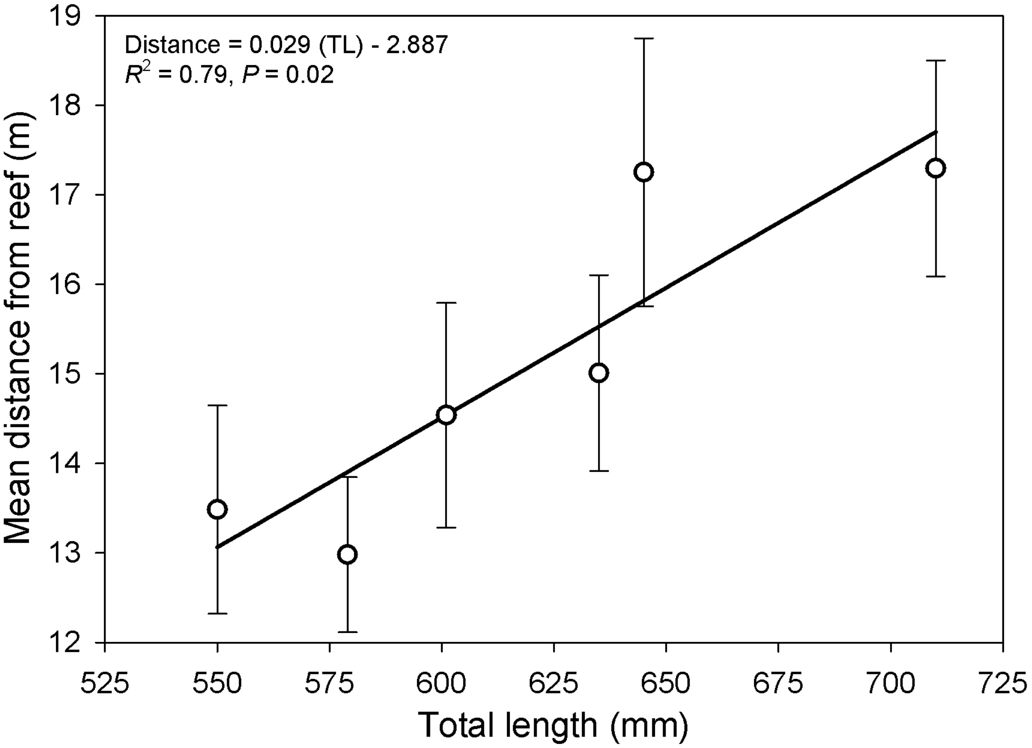

Figure 3-5. Relation between red snapper (N = 6) total length (TL) and the mean distance (± SE) these fish were located from the center of the reef over all 24-h tracks.

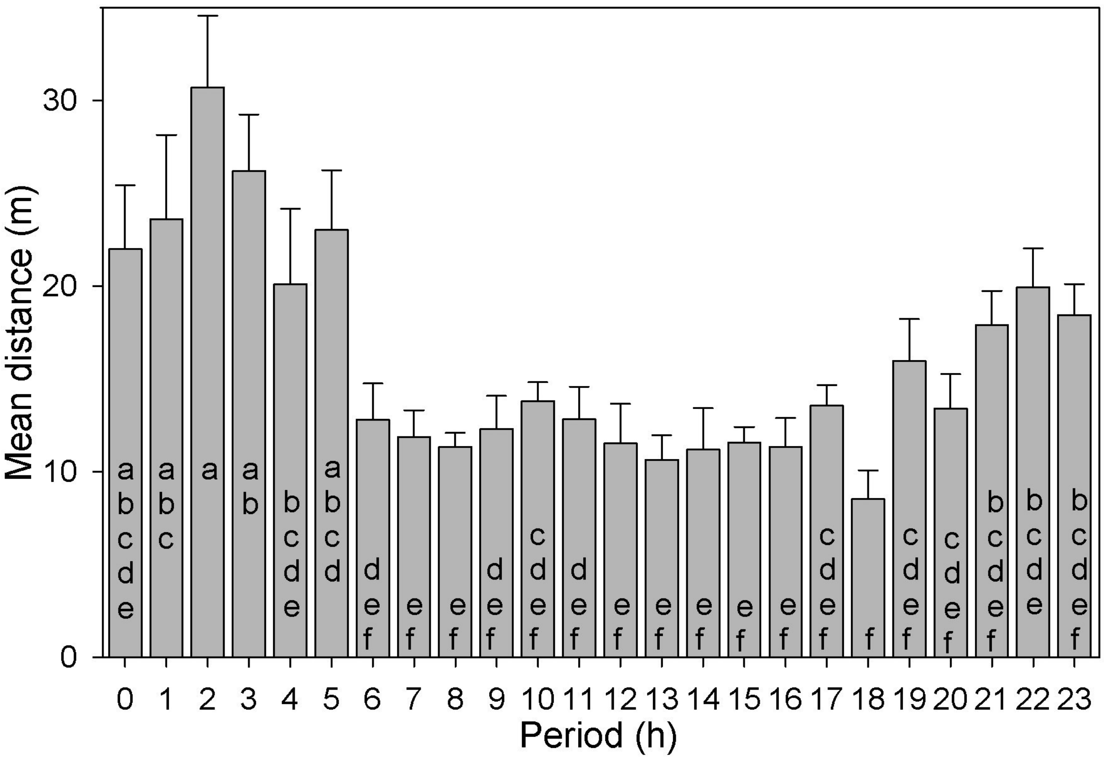

Figure 3-6. Mean distance (+ SD) red snapper (*N* = 6) were located from the center of site A4 during diel time periods (0000 - 2300 hours; i.e. 0 - 23 h) over all 24-h tracks. Time periods with different letters indicate significantly different mean distances ($P \leq 0.05$).

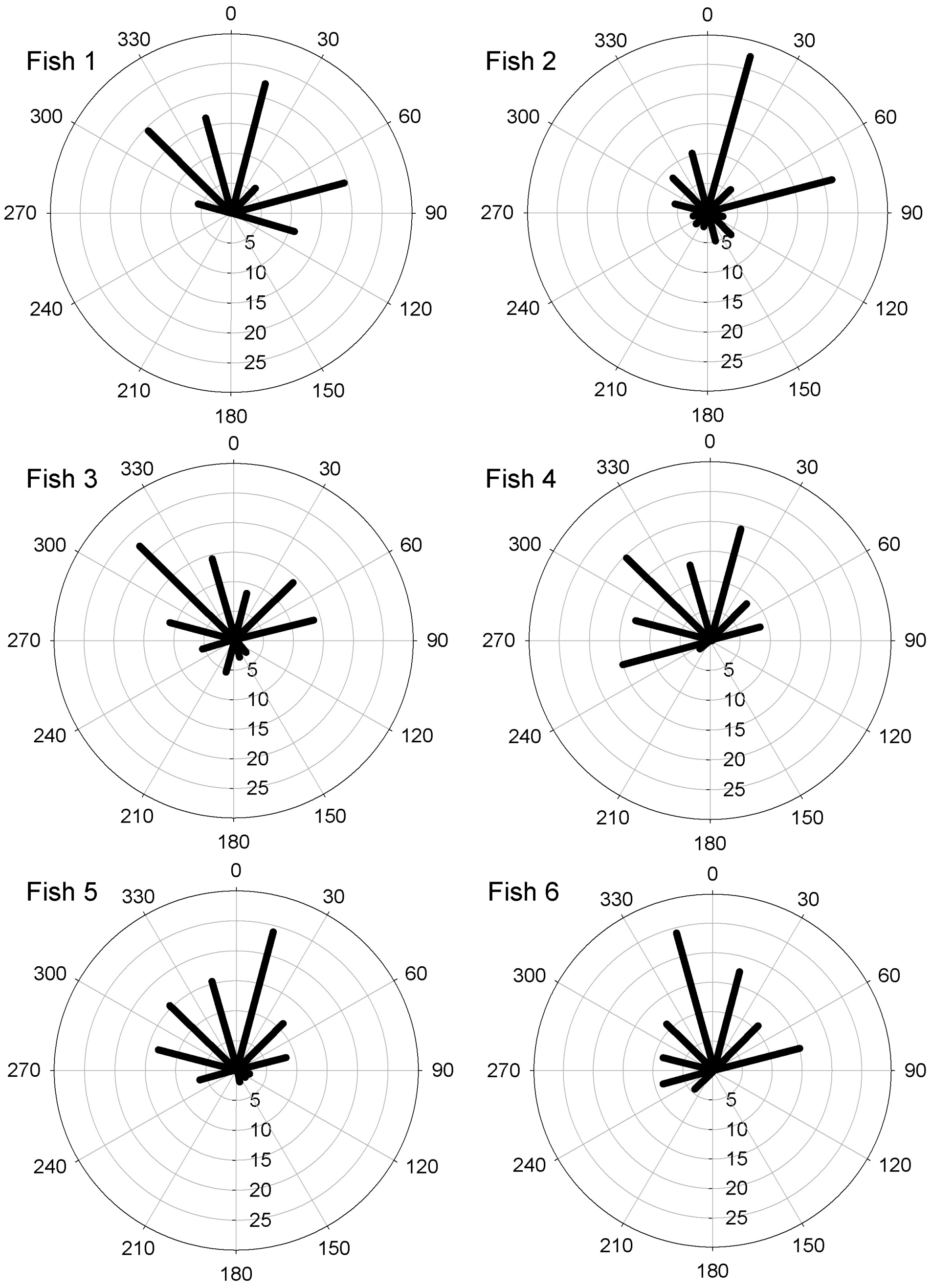

Figure 3-7. Compass plots for each red snapper ($N = 6$) of the percentage of locations within each 30º arc around the center of site A4 from 24-h manual tracks on 2 - 3 July 2008. North is 0º.